Two long geological records of continental ecosystems

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Abstract

The early Paleogene continental sequence of northwestern Wyoming and south central Montana (USA) and the Neogene Siwalik sequence of northern Pakistan are exceptionally long, fossiliferous, and well studied in terms of geology, paleontology, mammalian evolution, paleoecology, and paleoclimatology. Each record spans about 15 myr of alluvial deposition in a foreland basin. The fluvial systems differed in size, drainage of floodplains, and change in alluvial architecture through time. Both sequences preserved abundant paleosols, which are a source of paleoclimatic signals in stable isotopes from soil carbonates. Fossil collections from both records are dominated by vertebrate remains and especially by mammals; the Paleogene sequence also preserved abundant floral remains. Patterns of vertebrate preservation differed markedly between the two sequences, placing inherent limitations on paleoecological reconstruction and on the scope of evolutionary studies of mammalian lineages.

In this introductory paper, we summarize the major similarities and differences in geologic setting, chronology and time resolution, and mammalian faunal composition of these two long sequences. Finally, we present a brief overview of the organization of papers in this special issue.

1. Introduction

In this thematic issue, the geology, paleontology, paleoecology and evolutionary history of two exceptionally long, continental sedimentary sequences are compared. One sequence spans the Paleocene to early Eocene of northwestern Wyoming and south central Montana. The other encompasses the middle Miocene to Pleistocene “Siwalik” record of northern Pakistan. (For the sake of brevity, we refer to these records as the “Paleogene” and “Neogene” records below). Each sequence is well studied, with geological and paleontological work beginning in the nineteenth century, and each contains a rich fossil record, especially of fossil vertebrates. Both records span over 15 million years of relatively continuous, predominantly alluvial deposition. Intensive field programs have been conducted since the mid-1970’s up to the present time in each area. These are currently the two longest and best-studied continental sequences in terms of geological and biological history.

In July, 1992, at the Fifth North American Paleontological Convention in Chicago, we convened a symposium to compare the two sequences. The goals of the symposium were: (1) to demonstrate how similarities and differences in the two fossil records reflect depositional and other taphonomic controls on preservation, (2) to evaluate how preservational differences affect paleoecological and evolutionary interpretations based on these sequences, (3) to compare geological and biological indicators of paleoclimate in these
broadly similar depositional settings, and (4) to contrast the evolution of mammalian lineages and of terrestrial ecosystems in the early and late Cenozoic.

Comparison of these two areas has stimulated collaboration between members of two research groups, synthesis of long-term trends for each sequence, and evaluation of research questions and approaches that bear upon such long, rich records. The symposium was a first step toward building a general understanding of basin-scale controls on different kinds of ecosystems and organic records.

Broad similarities between the two records invite comparison of general patterns of environmental, taphonomic, and evolutionary change. Both sequences are set in foreland basins—the Paleogene rocks resulting from Laramide orogeny and the Siwalik molasse from collision of the Indian subcontinent with Asia. Each sequence is thousands of meters thick and divided into multiple formations. Formation boundaries are time-transgressive by up to 1 myr over lateral distances of around 40 km. Facies changes between formations reflect the proportion of channel versus floodplain deposits and the degree of drainage of floodplains. Both sequences contain well developed paleosols. The Paleogene fossil record includes diverse aquatic and terrestrial vertebrates, invertebrates, and macroflora and pollen. The Neogene fossils are similar except for a near absence of floral remains; proxy evidence of floral changes is recorded in carbon isotopes from paleosol carbonates. In each area, the abundance of vertebrate remains and species richness vary substantially over time, reflecting changes in preservational bias and episodes of immigration and extinction.

Important differences between the two records pertain to scale and history. The Paleogene sequences of Wyoming and Montana (Fig. 1) encompass much of the original floodbasin area. The documented Siwalik record of the Potwar Plateau, Pakistan (Fig. 2), while approximately the same area as the distribution of Paleogene outcrop, represents a smaller window into a much larger original floodbasin—extending along the southern margin of the rising Himalayas. In terms of climatic and biotic history, the early Paleogene world differed markedly from that of the Neogene.

The greenhouse climate of the later Mesozoic continued into the early Paleogene, with relatively equable climatic conditions on land and low climatic gradients from low to high latitudes (Frakes, 1979; Frakes et al., 1992). For the Cenozoic, the early Eocene exhibited maximal greenhouse conditions. But the Neogene was well into the icehouse state, with strong seasonality of temperature developing in the annual cycle and climatic gradients steepening between low and high latitudes. Predominantly mesic, forested terrestrial biomes were more widespread in the Paleogene, while the Neogene was characterized by expansion of more xeric and open biomes (Singh, 1988). The paleolatitudes of the two field areas differed by almost 20 (with the Bighorn Basin at 46-50 N and the Potwar Plateau at 25-30 N). But the mean climatic temperatures of the two areas would have differed much less than two such Recent locales because of changes in the latitudinal distribution of heat from the Paleogene to the Neogene (Axelrod, 1984; Crowley and North, 1991).

2. Geographic and geologic settings

The Paleogene record of northwestern Wyoming and south central Montana encompasses the deposits of three contiguous structural basins (Fig. 1). The northernmost basin, the Crazy Mountains Basin, in Montana, features predominantly Paleocene sediments (Hartman et al., 1989). The Clarks Fork Basin (the northern extension of the Bighorn Basin), straddling the Montana-Wyoming border, contains deposits spanning the late Cretaceous to earliest Eocene (Gingerich, 1983). The Bighorn Basin, farther south and east in Wyoming, has a predominantly Eocene section northwest of Worland, extending to the latest early Eocene (Bown and Rose, 1987). Exposures are nearly continuous between the Clarks Fork and Bighorn basins and discontinuous between the Clarks Fork and Crazy Mountains basins. Correlation has been accomplished mainly by lithostratigraphy and biostratigraphy, with support from paleomagnetic stratigraphy and radiometric dating (see below). Biostratigraphic zonation is
based upon the local stratigraphic ranges of mammals.

Two formations are widely recognized in the Paleogene basins: the older Fort Union Formation and the younger Willwood Formation. In the Crazy Mountains Basin, the local formation names are the Bear, Lebo, and Melville formations (Hartman et al., 1989); these formations have alternatively been considered members of the Fort Union Formation. According to biochronology and paleomagnetic stratigraphy, the Fort Union Formation is predominantly Paleocene in age and the Willwood Formation is predominantly Eocene in age (Archibald et al., 1987; Krishtalka et al., 1987). Over most of the Bighorn and Clarks Fork basins the boundary is gradational and time transgressive, with the transition in the latest Paleocene in the Clarks Fork Basin (Van Houten, 1944; Rose, 1981) and in the early Eocene in parts of the central Bighorn Basin (Wing and Bown, 1985).

In North American land mammal ages, the record of these three basins spans the Puercan (earliest Paleocene) through the late Wasatchian (early Eocene) ages. Fig. 3 diagrams the relationship between lithostratigraphy, biostratigraphy, and chronostratigraphy for this Paleogene record.

The Siwalik Group of the Indian subcontinent refers to molassic deposits shed from the southern margin of the Himalayas during much of Neogene time (Fatmi, 1973). Siwalik sediments extend from Afghanistan to Burma. The sequence discussed here outcrops in the Potwar Plateau of northern
Pakistan in a broad synclinorium (Fig. 2). The Potwar Plateau is blanketed by Pleistocene loess and alluvium, and Siwalik rocks are exposed where the modern drainage system, especially the Soan and Gabhir Rivers and their tributaries, has eroded into the plateau. Siwalik rocks extend in near continuous exposure along the northern and southern margins of the Potwar Plateau. Fieldwork has been concentrated in two major areas: a northern region well exposed around the towns of Dhok Pathan and Khaur (Fig. 2) and beyond (the "Khaur area" in earlier literature) and a southern region well exposed around the towns of Nagri, Chinji, and Kanatti and beyond (the "Chinji area"). Geologic and paleontologic work has also extended into the eastern Potwar Plateau in the vicinity of Jhelum (e.g., N.M. Johnson et al., 1982; Khan, 1993): this succession preserves substantial Upper Siwalik deposits. Much of the plateau between these regions is covered, and correlation is accomplished by means of lithostratigraphy and paleomagnetic stratigraphy.

Both the northern and southern exposures of the Potwar Plateau span deposits of four super-
posed formations representing "Lower" and "Middle" Siwalik rocks. "Upper" Siwalik deposits are less well known at this time, although stratigraphic and paleontologic work in the eastern Potwar Plateau forms the basis for current biostratigraphic zonation of the younger Siwalik record. Four of the classic Siwalik formations of Pilgrim (1926 and earlier papers) have their type sections in the Potwar Plateau (Fatmi, 1973; Shah 1977). The Kamlial Formation rests unconformably on an erosion surface of Eocene marine rocks in the succession of the Potwar Plateau. Overlying the Kamlial Formation is the Chinji Formation; together these formations constitute the Lower Siwalik sequence. The Nagri Formation overlies the Chinji Formation and is overlain by the Dhok Pathan Formation; together the Nagri and Dhok Pathan formations comprise the Middle Siwalik record. These four formations are distinguished by differences in the ratio of fine-grained to coarse-grained sediments, by thicknesses of sandy units, and by color. The composite Siwalik sequence is about 2000 m thick in the southern Potwar Plateau and about 4000 m thick along the northern Potwar Plateau, reflecting in part the proximity of the northern area to the depositional axis of the foreland basin (Tauxe and Opdyke, 1982; Johnson et al., 1985).

Biostratigraphic zonation of the Siwalik record is based on local ranges of mammals (Barry et al., 1982). Differences in the times of appearance of widely distributed higher taxa (such as genera of equids and murids) as well as the endemic components of Siwalik faunas have made application of European land mammal ages limited. Siwalik and Neogene European mammalian faunas share no species in common; in comparing Siwalik, West Asian, and European faunas, Flynn and Jacobs (1990) found about 25% faunal similarity at the generic level. Correlations with African and other South Asian faunas have been more informative (Jacobs et al., 1989). Barry et al. (1982) erected a local biostratigraphic zonation for the Potwar Plateau comprised of four interval-zones. Siwalik deposits also contain a detailed record of paleomagnetic reversals (e.g., N.M. Johnson et al., 1982, 1985; Tauxe and Opdyke, 1982). The interrelations of lithostratigraphy, biostratigraphy, and chronostatigraphy (Fig. 4) have been well documented (e.g., Flynn et al., 1990) over the last twenty years.
3. Chronology and time resolution

Similar approaches to chronology have been undertaken in both the Paleogene and Neogene sequences. In both areas, the estimation and resolution of absolute ages is based on a combination of biostratigraphy, magnetostratigraphy, and radiometric methods. The Paleogene of Wyoming and Montana is dated and correlated internally (from basin to basin) by means of a detailed biostratigraphy (e.g., Gingerich et al., 1980; Krause and Gingerich, 1983; Archibald et al., 1987). Estimates of absolute age are supported by several magnetic reversal boundaries documented in the Crazy Mountains Basin and the Clarks Fork Basin (Butler et al., 1981, 1987) and Ar/Ar dates on rare ash deposits from the Bighorn Basin (Wing et al., 1991). Also, global changes in carbon and oxygen isotopes and in mammalian faunas at the Paleocene–Eocene boundary permit correlation of the Wyoming Paleogene record to the Palaeocene–Eocene boundary (Rea et al., 1990; Koch et al., 1990). Dating and correlation of Siwalik rocks are partly on a detailed, Neogene magnetic record (Fig. 4). The presence of cosmopolitan mammalian genera in Siwalik permits correlation with Eurasian and mammalian faunas (e.g., Barry et al., 1982, despite fairly high Siwalik endemism. Also, volcanic sediments are the source of fission age estimates from the Potwar Plateau (Johnson et al., 1982).

The temporal resolution of individual strata localities differs for Paleogene versus Neogene localities, mainly because of the differing freedom of available chronostratigraphic markers. A individual localities in the Paleogene basins are based on linear interpolation between datums, with refinement from the number of pa and their relative maturities (e.g., Bown and...
In the Paleogene record, while the best age resolution is on the order of \(10^5\) yr, most localities do not lie near dated horizons. Dens.: sampling from multiple lateral sections in the Potwar Plateau, the high frequency of Neogene paleomagnetic reversals, and the calibration of the geomagnetic reversal time scale provide an age resolution on the order of \(10^5\) yr for most individual strata and localities (Tauxe and Opdyke, 1982; Johnson et al., 1985) and in some cases, \(10^4\) yr (Tauxe and Badgley, 1988). Hence, age estimates for most fossiliferous units are more finely resolved by about an order of magnitude for Siwalik localities.

4. Mammalian evolution and faunas

While both Paleogene and Neogene sequences contain fossilized remains of fishes, aquatic and terrestrial reptiles, birds, and mammals, the mammalian fossils are the most comprehensively studied in terms of systematic paleontology, functional anatomy, evolutionary rates, and faunal turnover. Over much of each sequence, mammalian remains are more abundant than those of other vertebrate groups. In addition, each area has been the focus of research about mammalian evolution (e.g., patterns of diversification among early Cenozoic mammals for the Paleogene, and hominoid systematics and paleoecology for the Neogene).

The two sequences contain substantially different kinds of mammals (Table 1). If we consider the major higher taxa of mammals (approximately orders), the Paleocene and Eocene portions of the Paleogene basins contain, respectively, 16 and 18 higher taxa. One Paleocene group did not continue into the Eocene (the rare arctostylopid Arctostylops with closest relatives outside of North America), and three groups appeared in the early Eocene for the first time (true primates, artiodactyls, and perissodactyls). Otherwise, the Paleocene and Eocene localities have many higher taxa in common, although there is considerable taxonomic turnover at the level of genera and species. About half of the Paleogene groups in Table 1 left no living descendants, according to current knowledge of mammalian phylogeny. Only one of these now-extinct groups is present in the Siwalik record (Creodonta); these Miocene creodonts are the last known worldwide (Barry, 1980). Eight of the 13 Siwalik higher taxa were present in the Eocene or earlier, and several families (e.g., Adapidae, Equidae, Hyaenodontidae) occurred in both the Paleogene and Neogene records.

From the standpoint of ecological diversity, Paleogene and Neogene mammalian faunas in general differed substantially. In the Paleocene, both therian and non-therian mammals experienced a radiation in size, trophic habits, and locomotor capabilities; and for the first time, mammals became the dominant vertebrates in terrestrial ecosystems (e.g., Janis and Damuth, 1990). Ecological diversity increased through the later
Cenozoic, with expansion in the size range of mammals in many clades, further trophic and locomotor specialization, and occupation of a wider range of habitats. Typical mammalian species richness from rich, relatively unbiased fossil localities differs little between the Paleogene and the Neogene in general (Gingerich, 1987), but differences in the range of body size, locomotor specialization, and trophic habits are great.

5. Organization and subjects of this issue

Here we note the major themes of the papers that follow. The first two papers establish the physical setting of these stratigraphic records. Willis and Behrensmeyer summarize similarities and differences in the physical substrates of the two sequences, as created by large fluvial systems draining rising mountain belts. Behrensmeyer, Willis, and Quade compare the extensive paleosol record of the Paleogene and Neogene sequences. In the Paleogene Willwood Formation, paleosols are the primary source of vertebrate fossil remains, whereas Siwalik paleosols have low fossil productivity.

Next, climatic and floral records are presented. Climatic conditions, including mean and seasonal range of temperature and precipitation, are potentially recorded via geological and biological indicators. In these fluvial sequences, the principal geological indicators are isotopes of oxygen and carbon from paleosol carbonates and fossils. The principal biological indicators are ecological attributes of floral and faunal composition that are correlated with climatic conditions in modern biotas. In both sequences, paleosol and other floodplain carbonates provide a stable isotope stratigraphy indicative of vegetation and climate. Koch, Zachos, and Dettman evaluate the oxygen and carbon isotopic records in paleosol carbonates, bivalve molluscs, and mammalian enamel from the Paleogene of the Bighorn and Clarks Fork basins. For the Siwalik sequence, Quade and Cerling document a major shift in carbon-isotopic composition of paleosol carbonates around 7 Ma that signifies the spread of C4 grasslands.

One of the major differences between these Paleogene and Neogene sequences is that the Paleogene record from Wyoming and Montana contains a rich floral record, while the Potwar Siwaliks contain scant floral remains. Wing, Hickey, and Alroy document the Paleogene floral record from the Bighorn Basin, where taxonomic diversity, composition, and abundance of floral remains are correlated with depositional environments.

Vertebrate taphonomy in relation to depositional environments follows. Badgley et al. summarize patterns in the distribution of vertebrate remains among different environments of deposition. In both sequences, the abundance of certain aquatic and terrestrial vertebrates is correlated with particular depositional environments. Different taphonomic processes have prevailed in each record, resulting in generally better taxonomic resolution (greater frequency of specimens identifiable as to species) of fossil mammals in the Paleogene record.

Faunal turnover among mammals for each record is documented next, followed by evolutionary patterns (species longevities, rates of change, and modes of speciation) at the species level. Maas et al. review changes in generic richness and patterns of generic turnover in 17 faunal zones from the middle Paleocene through the early Eocene (about 8 myr). Barry et al. summarize patterns of turnover among Siwalik mammals, compiled for intervals of 0.5 myr from 18 to 7 Ma. Gingerich and Gunnell evaluate species longevities, rates of morphological change, and speciation patterns for mammalian lineages from the latest Paleocene and early Eocene of the Clarks Fork Basin. Flynn et al. review species longevities and evolutionary patterns for Siwalik mammals over a span of 11 myr. Overall, Neogene lineages are substantially longer-lived than Paleogene lineages.

Next, paleoecological aspects of the Paleogene and Neogene mammalian assemblages are evaluated. Gunnell et al. compare the trophic structure and diversity of the Paleogene and Neogene mammalian faunas. Trophic structure was determined as the frequency of generic diversity among five categories of feeding specialization—herbivore, frugivore, omnivore, insectivore, and carnivore—as assessed from morphology of teeth and jaws.
Among modern mammalian faunas, size distributions reflect conditions of vegetation and climate (e.g., Legendre, 1986) as well as biotic interactions within and between mammalian trophic levels (e.g., Brown, 1987). Morgan et al. contrast the size distributions of Paleogene and Neogene mammalian faunas and note the timing of size change within lineages in relation to climatic and biotic changes in each record.

In the final paper, Badgley and Behrensmeyer summarize and compare the preservational, paleoecological, and evolutionary patterns in both records. Changes in the size and spacing of channels as well as in sediment accumulation rates led to changes in the kinds and distribution of habitats and in the prevailing taphonomic processes in both sequences. Intervals of climatic change witnessed episodes of first and last appearances as well as ecomorphic changes in mammalian faunas. Episodes of faunal change also occurred when local climatic changes were not evident. For mammals in each record, immigration made a greater contribution than did local speciation to increases in species richness. Ecological and evolutionary changes were out of step as often as they were synchronous.

Comparison of the geological and paleontological records from the early Paleogene of Wyoming and Montana with the Siwalik Neogene of Pakistan offers a unique opportunity to evaluate faunal and floral change in relation to each other and to changes in tectonic, climatic, and taphonomic processes. Broad trends that emerge from the Paleogene and Neogene examples invite further evaluation of these records and comparison with other Cenozoic sequences.

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