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Vertebrate fauna from the Deccan volcanic province: Response to volcanic activity

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ABSTRACT

During the last two decades, extensive paleontological research in the main Deccan volcanic province has led to a better understanding of biodiversity close to the Cretaceous-Paleogene boundary. Several infratrappean localities exposed in Jabalpur, Kheda, Balasinor, Rahioli, Dohad, and Bagh in the Narmada Valley (India) preserve one of the most geographically widespread dinosaur nesting sites known in the world. The well-studied intertrappean beds, such as those of Naskal on the southern margin, Asifabad and Nagpur on the eastern margin, Kisalpuri and Mohgaon Kalan on the northeastern margin, and Anjar on the northwestern margin of the main Deccan volcanic province, have yielded Maastrichtian fish (*Igdabatis*) and dinosaur remains and palynofossils (*Aquilapollenites-Gabonisporites-Ariadnaesporites*), either separately or in association, that suggest a Maastrichtian age for these beds. Only two intertrappean sections, Papro on the northern margin and Jhilmili on the northeastern margin of the main Deccan volcanic province, have produced Paleocene fossils. The fossil record from the infratrappean and intertrappean beds demonstrates that the dinosaurs survived the early phase of volcanism, though there was an apparent decline in their diversity, and that freshwater vertebrate fauna was least affected by the initial volcanic activity. The episodic nature of Deccan volcanism may possibly explain the survival of many freshwater and terrestrial communities during the periods of quiescence. In addition, as in the case of the late Maastrichtian sections in eastern Montana, North America, detritus-feeding freshwater vertebrate communities possibly had greater potential for survival than the terrestrial communities dependent on primary productivity. A close examination of the vertebrate faunal distribution across the two stratigraphic intervals (infratrappean and intertrappean) suggests that sampling bias in the infratrappean beds may have also masked the actual diversity of these beds.

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INTRODUCTION

The Deccan Traps, representing one of the largest continental flood basalts on Earth's surface, cover about two thirds of peninsular India. At many places on the eastern, southern, northern, and southwestern margins of the main Deccan volcanic province, the Deccan volcanic flows are found in association with sedimentary beds that have been designated as infratrappean beds (or Lameta Formation), intertrappean, and supratrappean beds, depending on their physical position with respect to the volcanic flows (Fig. 1). The infratrappean beds (= Lameta Formation) occur below the local basal flows, whereas the intertrappean beds, deposited during the dormant stages of the volcanic activity, occur intercalated within the lava flows. The sediments immediately overlying the youngest volcanic flow are referred as supratrappean beds and are generally not encountered in outcrops.

Recent radiometric and paleomagnetic studies of basalt flows in the Western Ghats indicate that Deccan volcanism took place in three short phases interspersed with quiescent periods of considerable time (Chenet et al., 2007, 2008, 2009). Phase I, with an estimated volume of ~6%, occurred close to base of C30n at ca. 67.4 Ma in the late Maastrichtian (Chenet et al., 2007, 2009). Phase II, consisting of several eruptive events of considerable volume (~80% volume of total Deccan Traps), took place within C29r below the Cretaceous-Paleogene transition over a short period of time ranging from thousands to tens of thousands of years (Chenet et al., 2008; Jay and Widdowson, 2008; Jay et al., 2009). Phase III eruptions, representing ~14% of Deccan Traps volume, occurred at or near the base of C29n within the early Danian (Jay and Widdowson, 2008; Jay et al., 2009; Keller et al., 2012).

Currently, there are two competing and widely debated hypotheses to explain the cause of mass extinction at the Cretaceous-Paleogene (also known as KTB after Cretaceous-Tertiary) boundary: (1) the asteroid impact hypothesis of Alvarez et al. (1980) and (2) the volcanic hypothesis of McLean (1985), Courtillot et al. (1986), and Officer et al. (1987). Ever since the Deccan volcanic activity of India was suggested as a causal link for this extinction event (McLean, 1985; Officer et al., 1987; Courtillot et al., 1986, 1988), the sedimentary beds occurring in association with the Deccan Traps (infratrappean, intertrappean, and supratrappean beds) and yielding plant and animal fossils have received wide attention from the geoscientific community worldwide. In the last three decades, application of bulk screen-washing techniques on the infratrappean and intertrappean beds to recover fossils from different stratigraphic levels of the main Deccan volcanic province has yielded very promising results. A variety of vertebrate microfossils, ostracods, molluscs, foraminifers, and charophytes previously unknown from the main Deccan volcanic province have been documented. In the following sections, we present a brief history of paleontological research in the main Deccan volcanic province, the distribution, depositional environment, and age of infratrappean and intertrappean beds, and finally an analysis of the response of vertebrate fauna to volcanic activity.

HISTORY OF PALEONTOLOGICAL RESEARCH IN THE MAIN DECCAN VOLCANIC PROVINCE

There are three phases during which paleontological research was carried out on the Deccan infratrappean and intertrappean beds. During the first phase, which spans India's pre-independence era, most of the early studies were carried out by British geologists, army men, and medical officers. W.H. Sleeman made the first discovery of fossils from the main Deccan volcanic province in 1828 (Sleeman, 1844). These fossils, represented by caudal vertebrae, were later referred to a sauropod dinosaur *Titanosaurus indicus* by Lydekker (1877), which is now regarded as an invalid species (Wilson and Upchurch, 2003). Following this, Hislop (1860) published a detailed account on the molluscan fauna of the Deccan infratrappean and intertrappean beds. Later on, Woodward (1908) documented the presence of fishes (*Lepisosteus indicus*, *Eoserranus hislopi*, *Pycnodus lametae*) from the infratrappean beds of Dongargaon in Chandrapur District, Maharashtra State (Fig. 2). Additional fish remains represented mainly by scales were described by Hora (1938) from the intertrappean beds of Deothan and Kheri in Madhya Pradesh (Fig. 3). Many skull bones, dentitions, and postcranial bones of dinosaurs were also reported from the infratrappean beds of

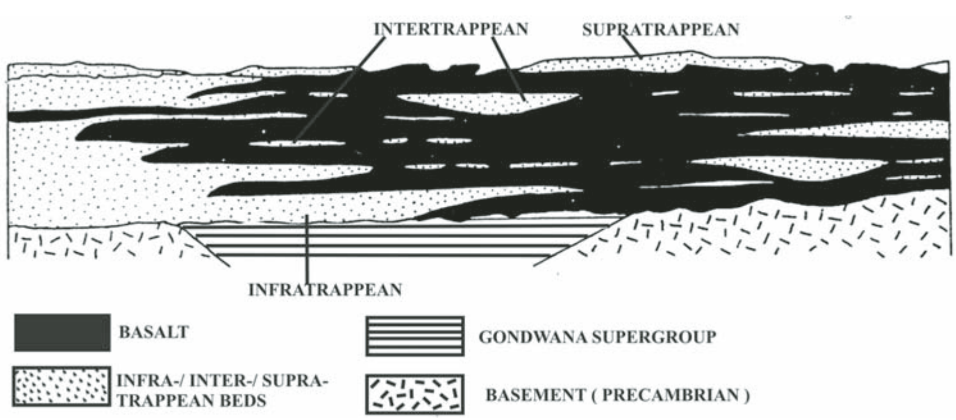

Figure 1. Schematic diagram showing the physical position of infratrappean, intertrappean, and supratrappean beds with respect to Deccan volcanic flows (modified after Sahni et al., 1994).

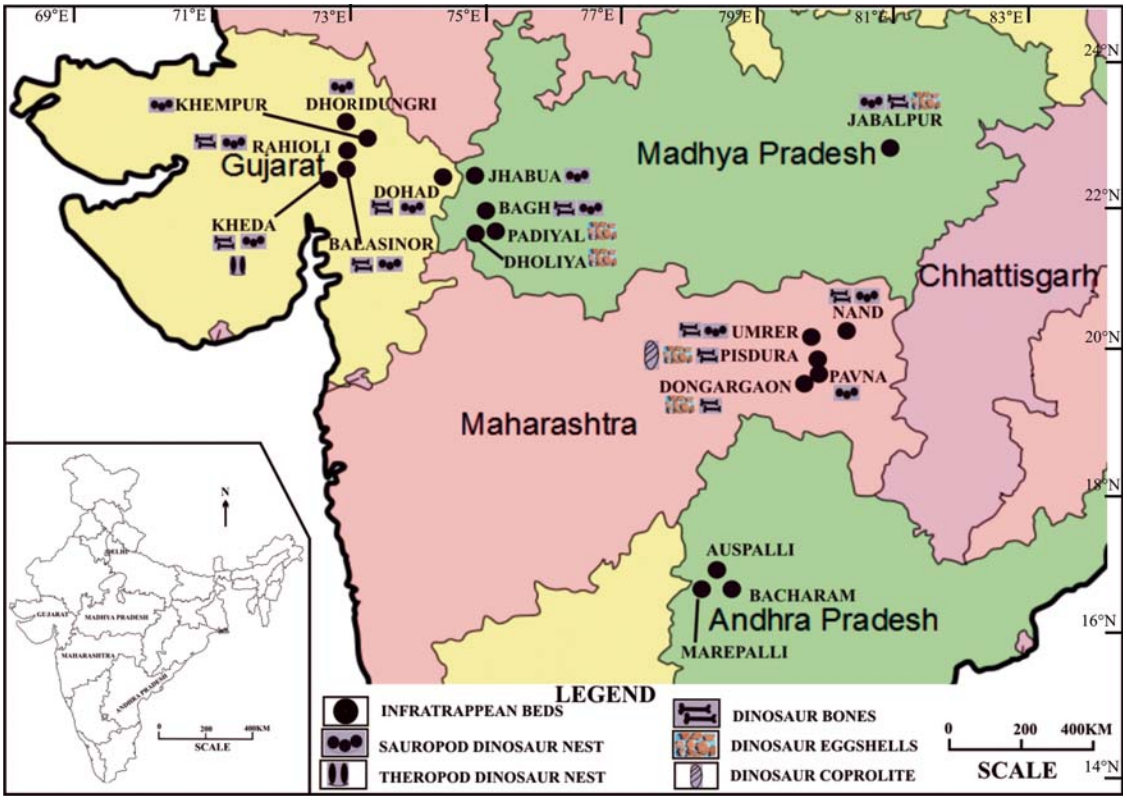

Figure 2. Map showing the infratrappean vertebrate fossil sites along the Narmada Valley and in Central and South India. Inset shows outline map of India highlighting the states in which the fossil sites are located.

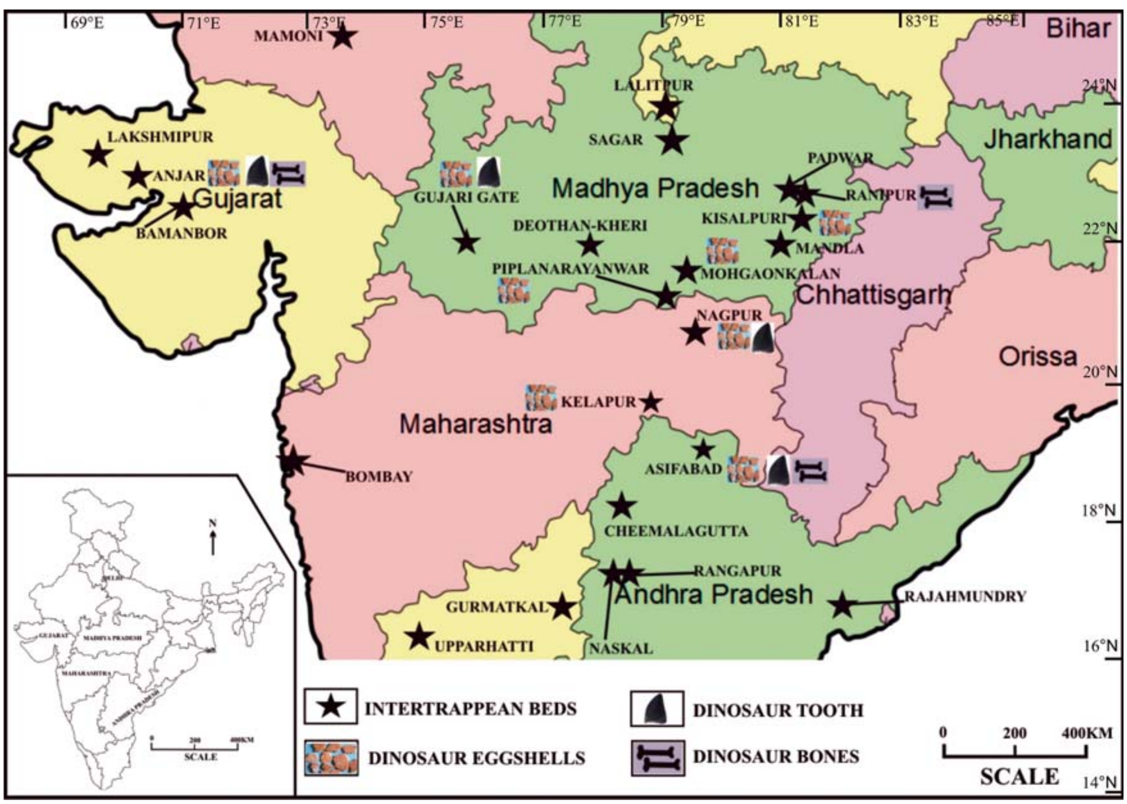

Figure 3. Map showing vertebrate fossil–yielding intertrappean sites of the Deccan volcanic province. The inset map of India highlights the states in which these fossil sites are located.

Pisdura and Dongargaon in Maharashtra, and Jabalpur (Fig. 2) in Madhya Pradesh (Matley, 1921, 1923, 1929; von Huene and Matley, 1933). During this phase, frog remains (*Indobatrachus pusillus* [Owen, 1847] Noble, 1930) and a turtle plastron (*Carteremys leithii* [Carter, 1852]) were reported from the intertrappean beds of Bombay (Fig. 3).

In the second phase, representing the period immediately after the independence of India in 1947 to ca. 1980, the majority of the studies on fossil biota from the main Deccan volcanic province were confined to foraminifers from the intertrappean beds of Rajahmundry (Bhalla, 1967) or to plant fossils from the intertrappean beds of Central and Southern India (Prakash, 1960; Shivarudrappa, 1976–1977; Bhatia and Mannikeri, 1976; Bande et al., 1986). Some vertebrate fossils, such as frogs, turtle, and dinosaur remains, were also recorded from the infratrappean beds of Pisdura, Dongargaon, and Jabalpur (Jain, 1977; Chatterjee, 1978) and the intertrappean beds of Bombay (Chiplonkar, 1940; Verma, 1965). Prior to 1980, the Deccan Traps were considered to span a duration of 30–50 m.y., based on K-Ar dating of the basaltic flows (Alexander, 1981) and molluscs, charophytes, and other plant fossils from the intertrappean beds (Hislop, 1860; Sahni, 1934; Hora, 1938; Prakash, 1960; Bhatia and Mannikeri, 1976; Shivarudrappa, 1976–1977).

The third phase of research on the Deccan infratrappean and intertrappean biota started in the beginning of 1980. Following the publications by McLean (1985) linking Deccan Traps to the Cretaceous-Paleogene boundary mass extinction and Courtillot et al.'s (1986) interpretation of Deccan volcanism as a short-duration event (<1.0 m.y.) close to the Cretaceous-Paleogene boundary, renewed interest was generated in the study of Deccan infratrappean and intertrappean biota. Moreover, the introduction of bulk screen-washing methods in the early 1980s for the collection of vertebrate microfossils substantially increased the diversity of various vertebrate groups. Prior to this phase of research activity, very few vertebrate taxa were known from the Lameta Formation and intertrappean beds of eruptive phase II. Following the application of bulk screen-washing techniques, almost all vertebrate groups (fishes, amphibians, turtle, snakes, lizards, turtles, crocodiles, dinosaurs, and mammals), with the exception of birds, have been reported from the infratrappean and intertrappean beds (Table 1). In addition to vertebrate microfossils, ~100 species of ostracods have also been documented from the infratrappean and intertrappean beds during phases II and III (see Khosla et al. [2011] for references), and planktic foraminifera were discovered in the intertrappean beds between phase II and phase III basalt flows at Jhilmili and Rajahmundry (Fig. 3; Keller et al., 2008, 2009a, 2009b).

DISTRIBUTION, DEPOSITIONAL ENVIRONMENT, AND AGE OF THE INFRATRAPPEAN AND INTERTRAPPEAN BEDS

The infratrappean beds and phase II and phase III intertrappean beds are widely known throughout the main Deccan volcanic province in outcrops and subsurface sections, whereas the supratrappean beds are known only from subsurface sections. Though marine infratrappean and intertrappean strata spanning the Cretaceous-Paleogene boundary have been delineated in more than 50 Oil and Natural Gas Corporation (ONGC) deep wells in Krishna-Godavari Basin (Raju et al., 1991; Jaiprakash et al., 1993; Keller et al., 2011, 2012), the present paper is restricted to predominantly continental outcrops from the main Deccan volcanic province.

Infratrappean Beds or Lameta Formation

Distribution

The infratrappean beds are exposed in discontinuous patches from Balasinor (Gujarat) in the west to Ambikapur (Madhya Pradesh) in the east, and from Sagar (Madhya Pradesh) in the north to Dongargaon, Pisdura (Maharashtra), and Marepalli (Andhra Pradesh) in the south (Fig. 2), and they reach a maximum thickness of 75 m, with a thick section known from the type area at Jhiraghat near Jabalpur in Central India. In the type section near Jabalpur, this formation consists of a Green Sandstone, Lower Limestone, Mottled Nodular Bed, Upper Limestone, and Upper Sandstone (Matley, 1921). The latter two units were redesignated as Upper (calcified) Sandstone by Tandon et al. (1995). Not all these units are preserved in the western part and in the Nand-Dongargaon Basin, where the Upper (calcified) Sandstone occurs as the most common lithologic unit.

Depositional Environment

The infratrappean beds (Lameta Formation) consist of sandstones, clays, limestones, and marls that are underlain by Precambrian basement or rocks of the Gondwana Supergroup. From time to time, the infratrappean beds have been interpreted as continental (Matley, 1921; Sahni and Mehrotra, 1974), fluvial and shallow-marine (Kumar and Tandon, 1979), shallow-marine (Chanda, 1967), tidal and estuarine (Singh and Srivastava, 1981; Singh, 1981; Saha et al., 2010), and pedogenically modified palustrine mudflat deposits (Brookfield and Sahni, 1987). Sedimentological and isotopic analyses of pedogenic carbonates and calcretes favored an alluvial-plain setting, with braided streams, palustrine flats, and sheetfloods under semiarid climatic conditions for the Lameta outcrops of Jabalpur (Ghosh et al., 1995; Tandon et al., 1995). The Lameta Formation of the Kheda and Dongargaon areas was interpreted as pedogenically altered overbank, channel, paludal, and lacustrine deposits of an alluvial-plain setting (Mohabey, 1996). Oxygen and carbon isotope studies of sauropod dinosaur eggshells from the infratrappean beds of Balasinor led Sarkar et al. (1991) to conclude that the Lameta dinosaurs consumed water from freshwater pools in a semiarid climate and ate C3 plants. On the whole, the burden of evidence, both paleontological and sedimentological, favors a pedogenically altered, paludal/lacustrine depositional environment in an alluvial-plain setting under semiarid climate conditions during deposition of the Lameta Formation.

TABLE 1. LIST OF VERTEBRATE FOSSILS DESCRIBED FROM THE DECCAN INFRA- AND INTERTRAPPEAN BEDS

Stratigraphic position	Taxon	Locality	State
Intertrappean beds phase II volcanism	***Fishes:***		
	Igdabatis indicus Prasad and Cappetta, 1993	Asifabad, Naskal	Andhra Pradesh
		Gurmatkal	Karnataka
		Nagpur	Maharashtra
		Kisalpuri	Madhya Pradesh
		Piplanarayanwar	Madhya Pradesh
	Rhombodus sp.	Asifabad	Andhra Pradesh
		Piplanarayanwar	Madhya Pradesh
	Raja sudhakari Prasad and Cappetta, 1993	Asifabad	Andhra Pradesh
	Rajiforme indet. (Prasad and Cappetta, 1993)	Asifabad	Andhra Pradesh
	Siluriformes indet. (Cione and Prasad, 2002)	Naskal	Andhra Pradesh
	Clupeidae (Hora, 1938; Prasad and Srinivasan, 1990)	Gurmatkal	Karnataka
		Deothan-Kheri	Madhya Pradesh
	Cyprinidae (Hora, 1938)	Deothan-Kheri	Madhya Pradesh
	Polycanthidae (Hora, 1938)	Deothan-Kheri	Madhya Pradesh
	Serranidae (Hora, 1938	Deothan-Kheri	Madhya Pradesh
	Nandidae (Hora, 1938)	Deothan-Kheri	Madhya Pradesh
		Gurmatkal	Karnataka
	Pristolepidae (Hora, 1938)	Deothan-Kheri	Madhya Pradesh
		Gurmatkal	Karnataka
	Horaclupea intertrappea Borkar, 1973	Bamanbor	Gujarat
	Palaeopristolepis feddeni Borkar, 1973	Bamanbor	Gujarat
	Palaeopristolepis chiplonkari Borkar, 1984	Bamanbor	Gujarat
	Indiaichthys bamanborensis Arratia et al., 2004	Bamanbor	Gujarat
	Percomorpha indet. (Arratia et al., 2004)	Bamanbor	Gujarat
	Pycnodontidae indet.	Naskal, Asifabad	Andhra Pradesh
		Rajahmundry	Andhra Pradesh
		Nagpur	Maharashtra
		Piplanarayanwar	Madhya Pradesh
		Gurmatkal	Karnataka
	Lepidotes sp. (Mohabey, 1996)	Nagpur	Maharashtra
	Lepisosteus indicus Woodward, 1908	Nagpur	Maharashtra
		Piplanarayanwar	Madhya Pradesh
		Kisalpuri	Madhya Pradesh
		Gujri Gate	Madhya Pradesh
		Naskal, Asifabad	Andhra Pradesh
	?Belonostomus sp. (Gayet et al., 1984)	Nagpur	Maharashtra
	Phareodus sp., Osteoglossidae indet.	Naskal, Asifabad	Andhra Pradesh
		Nagpur, Kelapur	Maharashtra
		Kisalpuri	Madhya Pradesh
		Piplanarayanwar	Madhya Pradesh
		Deothan-Kheri	Madhya Pradesh
	Enchodus ferox Leidy, 1855	Nagpur	Maharashtra
	Enchodus sp. (Gayet et al., 1984)	Nagpur	Maharashtra
	Palaeolabrus cf. *dormaalensis* (Prasad and Sahni, 1987)	Asifabad	Andhra Pradesh
	Palaeolabrus sp. (Gayet et al., 1984)	Nagpur	Maharashtra
	?*Sphyraena* (Gayet et al., 1984)	Nagpur	Maharashtra
	Percoidei indet. (Gayet et al., 1984)	Nagpur	Maharashtra
	Ostracion sp. (Gayet et al., 1984)	Nagpur	Maharashtra
	Otoliths:		
	Heterotidinarum heterotoides Nolf et al., 2008	Naskal	Andhra Pradesh
	Osteoglossidarum deccanensis Rana, 1988	Naskal, Rangapur	Andhra Pradesh
	Osteoglossidarum intertrappus Rana, 1988	Naskal, Rangapur	Andhra Pradesh
	Notopteridarum nolfi Rana, 1988	Naskal, Rangapur	Andhra Pradesh
		Cheemalagutta	Andhra Pradesh
	Clupeidarum valdiyai Rana and Sahni, 1989	Nagpur	Maharashtra
	Clupeidarum sahnii (Rana, 1996)	Rangapur	Andhra Pradesh
	Gonorynchidarum rectangulus (Rana, 1988)	Naskal, Rangapur	Andhra Pradesh
		Nagpur	Maharashtra
	Gonorynchidarum sp. (Nolf et al., 2008)	Rangapur	Andhra Pradesh
		Nagpur	Maharashtra
	?Ariidae (Nolf et al., 2008)	Naskal, Rangapur	Andhra Pradesh
	Ariidae indet. (Bajpai and Srinivasan, 1996)	Anjar	Gujarat
	Anthracoperca bhatiai (Rana, 1996)	Naskal, Rangapur	Andhra Pradesh
	Percoideorum citreum Nolf et al., 2008	Naskal	Andhra Pradesh
	Percoideorum nagpurensis (Rana and Sahni, 1989)	Nagpur	Maharashtra
	Percoideorum rangapurensis Rana, 1988	Naskal, Rangapur	Andhra Pradesh

(*Continued*)

TABLE 1. LIST OF VERTEBRATE FOSSILS DESCRIBED FROM THE DECCAN INFRA- AND INTERTRAPPEAN BEDS (*Continued*)

Stratigraphic position	Taxon	Locality	State
Intertrappean beds phase II volcanism	Percoidei sp. 1 (Nolf et al., 2008)	Naskal, Rangapur	Andhra Pradesh
	Percoidei sp. 2 (Nolf et al., 2008)	Rangapur	Andhra Pradesh
	Percoidei indet. (Bajpai and Srinivasan, 1996)	Anjar	Gujarat
	?*Centropomidarum takliensis* (Rana and Sahni, 1989)	Nagpur	Maharashtra
	Dapalis erici Nolf et al., 2008	Rangapur	Andhra Pradesh
	Ambassidarum cappettai (Rana and Sahni, 1989)	Nagpur	Maharashtra
	Apogonidarum curvatus (Rana, 1996)	Naskal, Rangapur	Andhra Pradesh
	?*Pristolepidinarum jaegeri* (Rana and Sahni, 1989)	Nagpur	Maharashtra
	Blenniidarum sp. (Nolf et al., 2008)	Rangapur	Andhra Pradesh
	Serranidarum sp. 1 (Bajpai and Srinivasan, 1996)	Anjar	Gujarat
	Serranidarum sp. 2 (Bajpai and Srinivasan, 1996)	Anjar	Gujarat
	Amphibians:		
	Indobatracus pusillus (Owen, 1847) Noble, 1930	Bombay	Maharashtra
	Gobiatinae (Discoglossidae, ?Hylidae)	Naskal	Andhra Pradesh
	Ranoidea (Ranidae or Rhacophoridae) (Prasad and Rage, 2004).	Naskal	Andhra Pradesh
	Leptodactylidae or Hemisotidae (Prasad and Rage, 2004)	Naskal	Andhra Pradesh
		Kisalpuri	Madhya Pradesh
	Pelobatidae indet. (Sahni et al., 1982)	Nagpur	Maharashtra
	Lizards:		
	Anguidae indet. (Prasad and Rage, 1995)	Naskal	Andhra Pradesh
	Litakis sp. (Rana, 2005)	Nagpur	Maharashtra
	Pristiguana sp. (Rana, 2005)	Nagpur	Maharashtra
	Iguanidae indet. (Rana, 2005)	Nagpur	Maharashtra
	Agama sp. (Rana, 2005)	Rangapur	Andhra Pradesh
	?*Contogenys* sp. (Rana, 2005)	Nagpur	Maharashtra
	Eumeces sp. (Rana, 2005)	Rangapur	Andhra Pradesh
	Exostinus estesai Rana, 2005	Nagpur	Maharashtra
	Gekkonid eggshells (Sahni et al., 1984)	Nagpur	Maharashtra
		Anjar	Gujarat
	Turtles:		
	Carteremys leithii (Carter, 1852) Williams, 1953	Bombay	Maharashtra
	cf. *Carteremys leithii* (de Lapperent de Broin et al., 2009)	Lakshmipur	Gujarat
	Carteremys sp.(de Lapperent de Broin et al., 2009)	Kisalpuri	Madhya Pradesh
	Sankuchemys sethnai Gaffney et al., 2003	Bombay	Maharashtra
	Cf. Bothremydidae (de Lapperent de Broin et al., 2009)	Upparhatti	Karnataka
	Crocodiles:		
	Crocodylia indet. (Rana, 1990; Prasad and de Lapparent de Broin, 2002)	Naskal, Asifabad	Andhra Pradesh
		Nagpur, Kelapur	Maharashtra
		Kisalpuri,	Madhya Pradesh
		Piplanarayanwar	Madhya Pradesh
		Gujri Gate	Madhya Pradesh
		Anjar	Gujarat
		Bombay	Maharashtra
	Crocodylidae indet. (Singh et al., 1998)	Bombay	Maharashtra
	Dyrosauridae indet. (Khosla et al., 2009a)	Kisalpuri	Madhya Pradesh
	Eggshells (Singh et al., 1998).	Bombay	Maharashtra
	Snakes:		
	Indophis sahnii Rage and Prasad, 1992	Naskal	Andhra Pradesh
		Kelapur	Maharashtra
		Anjar	Gujarat
		Gujri Gate	Madhya Pradesh
		Piplanarayanwar	Madhya Pradesh
	Madtsoiidae indet. (Rage et al., 2004)	Kelapur	Maharashtra
	Serpentes *incertae sedis* (Rage and Prasad, 1992)	Naskal	Andhra Pradesh
	Coniophis sp. (Rage et al., 2004)	Naskal	Andhra Pradesh
	Dinosaurs:		
	Indeterminate sauropod bones (Rao and Yadagiri, 1981; Ghevariya, 1988; Mathur and Sharma, 1990)	Asifabad	Andhra Pradesh
		Ranipur	Madhya Pradesh
		Anjar	Gujarat
	Theropod teeth (*Massospondylus rawesi*, Lydekker, 1890)	Nagpur	Maharashtra
		Anjar	Gujarat

(*Continued*)

TABLE 1. LIST OF VERTEBRATE FOSSILS DESCRIBED FROM THE DECCAN INFRA- AND INTERTRAPPEAN BEDS (*Continued*)

Stratigraphic position	Taxon	Locality	State
Intertrappean beds phase II volcanism		Gujri Gate	Madhya Pradesh
		Asifabad	Andhra Pradesh
	Sauropod eggshells (Sahni et al., 1984)	Asifabad	Andhra Pradesh
		Nagpur, Kelapur	Maharashtra
		Piplanarayanwar	Madhya Pradesh
	?*Hypselosaurus* sp. (Srinivasan, 1996)	Mohgaon Kalan	Madhya Pradesh
	Subtiliolithus kachchhensis (Khosla and Sahni, 1995)	Anjar	Gujarat
	Ornithoid eggshells (Bajpai et al., 1993)	Anjar	Gujarat
		Gujri Gate	Madhya Pradesh
		Kisalpuri	Madhya Pradesh
	Mammals:		
	Deccanolestes hislopi Prasad and Sahni, 1988	Naskal, Rangapur	Andhra Pradesh
	Deccanolestes robustus Prasad et al., 1994	Naskal, Rangapur	Andhra Pradesh
	Deccanolestes narmadensis Prasad et al., 2010	Kisalpuri	Madhya Pradesh
	Sahnitherium rangapurensis Rana and Wilson, 2003	Rangapur	Andhra Pradesh
	Kharmerungulatum vanvaleni Prasad et al., 2007a	Kisalpuri	Madhya Pradesh
	Bharattherium bonapartei Prasad et al., 2007b (=*Dakshina jederi* Wilson et al., 2007)	Kisalpuri	Madhya Pradesh
		Naskal	Andhra Pradesh
Infratrappean beds below phase I and/or phase II volcanism	***Fishes:***		
	Igdabatis indicus Prasad and Cappetta, 1993	Pisdura	Maharashtra
		Jabalpur	Madhya Pradesh
		Marepalli	Andhra Pradesh
		Nand-Dongargaon	Maharashtra
	Rhombodus sp.	Marepalli	Andhra Pradesh
	Lepisosteus indicus Woodward, 1908	Dongargaon	Maharashtra
		Marepalli	Andhra Pradesh
		Jabalpur	Madhya Pradesh
	Pycnodus lametae Woodward, 1908	Dongargaon	Maharashtra
	Pycnodontidae indet.	Jabalpur	Madhya Pradesh
	Eoserranus hislopi Woodward, 1908	Dongargaon	Maharashtra
	Lepidotes deccanensis Sykes, 1851	Nand-Dongargaon	Maharashtra
	Clupea sp. (Mohabey, 1996)	Nand-Dongargaon	Maharashtra
	Nandidae indet. (Mohabey, 1996)	Marepalli	Andhra Pradesh
	Osteoglossidae indet. (Mohabey, 1996)	Marepalli	Andhra Pradesh
		Dongargaon	Maharashtra
		Jabalpur	Madhya Pradesh
	Enchodus sp. (Jain and Sahni, 1983; Mohabey, 1996)	Nand-Dongargaon	Maharashtra
		Pisdura	Maharashtra
		Marepalli	Andhra Pradesh
	Arius sp. (Jain and Sahni, 1983)	Pisdura	Maharashtra
	Crocodiles:		
	Crocodylia indet.	Marepalli	Andhra Pradesh
	Dyrosauridae indet (Rana, 1987)	Auspalli,	Andhra Pradesh
		Marepalli	Andhra Pradesh
	Turtles:		
	Shweboemys pisdurensis (Jain, 1986)	Pisdura	Maharashtra
	Eggshells (Bajpai et al., 1997)	Rajahmundry	Andhra Pradesh
	Snakes:		
	Sanajeh indicus (Madtsoiidae) Wilson et al., 2010	Kheda	Gujarat
	Madtsoia pisdurensis (Madtsoiidae) Mohabey et al., 2011	Pisdura	Maharashtra
	Dinosaurs:		
	Jainosaurus (=*Antarctosaurus*) *septentrionalis* (von Huene and Matley, 1933) Hunt et al., 1994	Pisdura	Maharashtra
		Jabalpur	Madhya Pradesh
	Jainosaurus cf. *septentrionalis* (Wilson et al., 2011)	Jabalpur	Madhya Pradesh
	Isisaurus colberti (Jain and Bandyopadhyay, 1997) Wilson and Upchurch, 2003	Dongargaon	Maharashtra
	Titanosauriformes indet. (Wilson and Mohabey, 2006)	Nand	Maharashtra
	Indosuchus raptorius von Huene and Matley, 1933	Jabalpur	Madhya Pradesh
	Indosaurus matleyi von Huene and Matley, 1933	Jabalpur	Madhya Pradesh
	Laevisuchus indicus von Huene and Matley, 1933	Jabalpur	Madhya Pradesh
	Lametasaurus indicus von Huene and Matley, 1933	Jabalpur	Madhya Pradesh

(*Continued*)

TABLE 1. LIST OF VERTEBRATE FOSSILS DESCRIBED FROM THE DECCAN INFRA- AND INTERTRAPPEAN BEDS (*Continued*)

Stratigraphic position	Taxon	Locality	State
Infratrappean beds below phase I and/or phase II volcanism	*Rajasaurus narmadensis* Wilson et al., 2003	Rahioli	Gujarat
	Rahiolisaurus gujaratensis Novas et al., 2010	Rahioli	Gujarat
	Oospecies:		
	Megaloolithus cylindricus Khosla and Sahni, 1995	Jabalpur	Madhya Pradesh
	M. mohabeyi Khosla and Sahni, 1995	Dholiya	Madhya Pradesh
	M. padiyalensis Khosla and Sahni, 1995	Padiyal	Madhya Pradesh
	M. jabalpurensis Khosla and Sahni, 1995	Jabalpur	Madhya Pradesh
	M. dholiyaensis Khosla and Sahni, 1995	Dholiya	Madhya Pradesh
	M. dhoridungriensis Mohabey, 1998	Dhoridungri	Gujarat
	M. khempurensis Mohabey, 1998	Khempur	Gujarat
	M. megadermus Mohabey, 1998	Dohad	Gujarat
	M. baghensis Khosla and Sahni, 1995	Bagh	Madhya Pradesh
	Sauropod eggshells (Jain and Sahni, 1985)	Pisdura	Maharashtra
	Ellipsoolithus khedaensis (Family Elongatoolithidae) (Mohabey, 1998; Loyal et al., 1998).	Kheda	Gujarat
	Mammals:		
	Avashishta bacharamensis Anantharaman et al., 2006	Bacharam	Andhra Pradesh

Age

For a long time, the Lameta Formation was regarded as Turonian in age, based on the similarity of dinosaur fauna between the Lameta Formation and the Maevarano Formation of Madagascar, which was initially assigned a Turonian age (von Huene and Matley, 1933; Chiplonkar, 1986). While reviewing the Lameta dinosaur fauna, Buffetaut (1987) rejected the Turonian age for the Lameta Formation and favored a Maastrichtian age. The latter age was confirmed by the subsequent discoveries of a Maastrichtian fish (*Igdabatis*, *Rhombodus*; Jain and Sahni, 1983; Courtillot et al., 1986) and a palynological assemblage consisting of *Ariadnaesporites* and *Aquilapollenites* (Dogra et al., 1988). The Maastrichtian age for the Lameta Formation was further supported by a $^{40}Ar/^{39}Ar$ age of 66.4 ± 1.9 Ma (Courtillot et al., 1988) for the basal flow overlying the Maastrichtian sediments at Dongargaon (Fig. 2). However, paleomagnetic studies of the volcanic flows overlying the Lameta Formation at Jabalpur had placed these flows in magnetochron C30n (Courtillot et al., 1986) and thus in phase I of Deccan volcanism. Hence, the fossils and radiometric data from the Lameta Formation underlying the basal volcanic flows indicate a late Maastrichtian lower age limit for the Deccan volcanic eruptions.

Intertrappean Beds

Distribution

The intertrappean sedimentary beds are found mainly along the southern, eastern, northeastern, and northwestern margins of the main Deccan volcanic province. The well-known intertrappean sections are from Gurmatkal and Upparhatti (Karnataka State), Naskal, Rangapur, and Asifabad (Andhra Pradesh State), Nagpur and Bombay (Maharashtra State), Mohgaon Kalan, Jhilmili, Kisalpuri, Mandla, Padwar, Ranipur, Piplanarayanwar, and Gujri Gate (Madhya Pradesh State), Anjar and Bamanbor (Gujarat State), Mamoni (Rajasthan State), and Papro (Uttar Pradesh state) (Fig. 3). At present, there are no paleomagnetic or geochronological controls on the position of the intertrappean beds between the lava flows. However, based on geochemical characteristics, Jay and Widdowson (2008) correlated the basaltic flows on the southeastern, eastern, northeastern, and northern margins of the main Deccan volcanic province with the Poladpur and Ambenali Formations of the Wai Group in the Western Ghats. In view of this and the presence of Maastrichtian fossils and dinosaur remains in the intertrappean beds of Gurmatkal, Naskal, Rangapur, Asifabad, Nagpur, Mohgaon Kalan, Kisalpuri, Mandla, Padwar, Ranipur, Piplanarayanwar, Gujri Gate, Anjar, and Mamoni (Fig. 3), we prefer to place these beds in phase II volcanism.

The intertrappean beds of Jhilmili (Fig. 3), with early Paleocene fossils and lower and upper traps placed within chrons C29r and C29r/C29n, respectively, were considered to lie between phases II and III (Keller et al., 2009b). The intertrappean beds of Papro (Fig. 3), with Paleocene palynofossils, may also be placed between volcanic phases II and III. The intertrappean beds of Bombay were placed within phase III (Cripps et al., 2005). Currently, there are limited fossil data to pinpoint the position of Upparhatti and Bamanbor (Fig. 3) intertrappean beds within the lava flow stratigraphy of the main Deccan volcanic province. Compared with the Lameta Formation, the intertrappean beds of phases II and III are relatively thin, generally reaching a few centimeters to 30 cm in thickness, and rarely measuring up to 5 m, except at Jhilmili, where these intertrappean beds measure 13.5 m (Keller et al., 2009a, 2009b).

Depositional Environment

Since the pioneering work of Hislop (1860), many intertrappean outcrops have been investigated from the paleontological point of view. Of these, the intertrappean beds of phase II, such as Rangapur, Naskal, Asifabad, Nagpur, Kisalpuri, Piplanarayanwar, and Anjar (Fig. 3), have been intensively studied for vertebrate microfossils. Generally, they are composed of siltstones, mudstones, sandstones, clays, marls, and shales, frequently associated with a prominent fossiliferous chert and occasionally with a limestone bed. The Deccan intertrappean beds are traditionally considered freshwater lacustrine deposits that filled low-lying areas on the surface of the lava flows during the dormant stages of volcanism.

The phase II intertrappean beds of Naskal and Anjar (Fig. 3) were studied in some detail in the context of their depositional environment. Based on sedimentological, paleontological, and taphonomic studies, the Naskal intertrappean beds were interpreted as alkaline lake deposits in a floodplain setting intermittently subjected to subaerial exposure, leading to the development of two phases of paleosols (Khajuria and Prasad, 1998). Sedimentological studies of the iridium-bearing Anjar intertrappean section indicated a freshwater lacustrine environment in a semiarid climate setting (Khadkikar et al., 1999). However, the mixed presence of marine and nonmarine biota in the intertrappean beds of phase II at Asifabad and Nagpur (Fig. 3) indicates some marine influence in these areas (Sahni, 1983; Prasad and Sahni, 1987). This has been proven by the recent discovery of planktonic foraminifers from the intertrappean beds occurring between phase II and phase III basalt flows at Jhilmili in Central India (Keller et al., 2009b).

Age

Early paleontological studies overestimated the age of Deccan intertrappean beds as Early Tertiary (with the majority favoring an Eocene age) based on fish, molluscs, and plant fossils, including charophytes and plant megafossils (Hislop, 1860; Sahni, 1934; Hora, 1938; Bhatia and Mannikeri, 1976; Shivarudrappa, 1976–1977; Bande et al., 1986), and the absence of dinosaurs as compared to their frequent occurrence in the Lameta Formation (Matley, 1921, 1929; von Huene and Matley, 1933, Chatterjee, 1978). Khajuria et al. (1994) discussed in detail the inadequacy of these fossils for assigning an Eocene age for the intertrappean beds. Further, dinosaur remains (a few bones and teeth, and several eggshell fragments) have been found in many intertrappean beds (Rao and Yadagiri, 1981; Vianey-Liaud et al., 1987; Prasad, 1989; Sahni and Bajpai, 1988; Ghevariya, 1988; Mathur and Sharma, 1990).

Subsequent findings of Maastrichtian fishes (Prasad and Cappetta, 1993) and the *Ariadnaesporites-Aquilapollenites-Gabonisporites* palynological assemblage (Mathur and Sharma, 1990; Sahni et al., 1996; Kumaran et al., 1997; Dogra et al., 2004; Singh et al., 2006) from the majority of the intertrappean beds favor a Maastrichtian age. A couple of intertrappean outcrops from the main Deccan volcanic province have been assigned a younger early Paleocene age. The northernmost intertrappean section near Papro in Lalitpur District (Uttar Pradesh State) has been assigned an early Paleocene age based on a palynological assemblage consisting of *Dandotiaspora dilata*, *Dandotiaspora pseudoauriculata*, *Dandotiaspora plicata*, *Spinizonocolpites echinatus*, *Matanomadhiasulcites* sp., and *Lakiapollis ovatus* (Singh and Kar, 2002).

The Anjar intertrappean section in Kachchh, western India, was initially designated as Cretaceous-Paleogene age based on anomalous concentrations of iridium in the sediments sandwiched between volcanic flows III and IV (Bhandari et al., 1996). However, later paleontological studies demonstrated that the intertrappean beds overlying the iridium-bearing levels yield Maastrichtian fossils, including dinosaur remains (Bajpai and Prasad, 2000), and the high iridium concentration was attributed to leaching from the Deccan volcanic flows (Khadkikar et al., 1999). As a result, the iridium-enriched levels of the Anjar intertrappean beds are no longer regarded as representing the Cretaceous-Paleogene boundary. Therefore, no fossiliferous intertrappean outcrop spanning the Cretaceous-Paleogene transition has been recorded from the main Deccan volcanic province to date.

More recently, Keller et al. (2009a, 2009b) reported the presence of early Danian planktic foraminifers in the intertrappean beds between volcanic phases II and III at Jhilmili in Chhindwara District (Madhya Pradesh State). However, the Maastrichtian to Danian transition has yet to be discovered in this area.

On the whole, the fossil record from the infratrappean and intertrappean outcrops is in agreement with the fossil record from the subsurface intertrappean sections of ONGC wells in the Krishna-Godavari Basin, where the shallow-marine foraminiferal assemblages from the infratrappean beds and phase II intertrappean beds indicate a late Maastrichtian age, and phase III intertrappean and supratrappean beds indicate an early Paleocene (Danian) age for the Deccan volcanism (Raju et al., 1991; Jaiprakash et al., 1993; Keller et al., 2011, 2012). The paleontological data from infratrappean and intertrappean beds from the main Deccan volcanic province outcrops and from shallow-marine subsurface sections are in agreement with radiometric dates from a thick Deccan volcanic pile from the Western Ghats, which indicate that Deccan volcanism began ca. 67.4 Ma and terminated around 62 Ma (Venkatesan et al., 1993; Chenet et al., 2007, 2008).

RESPONSE OF VERTEBRATE FAUNA TO DECCAN VOLCANISM

One frequently asked question is whether Deccan volcanism was capable of affecting the ecosystems at the global level, and, if so, what were its effects at the site of eruption? To seek answers to these questions, one should examine the fossil evidence from the sediments deposited prior to the initiation of volcanism (infratrappean) and those deposited during (intertrappean) or immediately after Deccan volcanic activity.

Fishes, Crocodiles, Turtles, and Snakes

A comparison of the infratrappean and intertrappean vertebrate fauna demonstrates that at least 10 infratrappean fish taxa (five each at species and family level) survived into the intertrappean beds of phase II (Table 1; Fig. 4). Although some indeterminate anurans and lizards were reported by Jain and Sahni (1983) and Mohabey (1996), no recognizable amphibian and lizard remains have been recorded to date from the infratrappean beds. On the other hand, the intertrappean amphibians and lizards are represented by at least four and six families, respectively. Two crocodilian groups (Crocodylia indet. and Dyrosauridae) of the infratrappean beds survived into the intertrappean beds (Fig. 4). The lone turtle species (*Shweboemys pisdurensis* Jain, 1986) known from the infratrappean beds belongs to the family Podocnemididae. In comparison, the intertrappean turtles are identified as *Carteremys leithii* (Carter, 1852), *Sankuchemys sethnai* Gaffney et al., 2003 of the family Bothremydidae, and an indeterminate form distinct from all these taxa (de Lapparent de Broin et al., 2009). The infratrappean snake fauna is represented

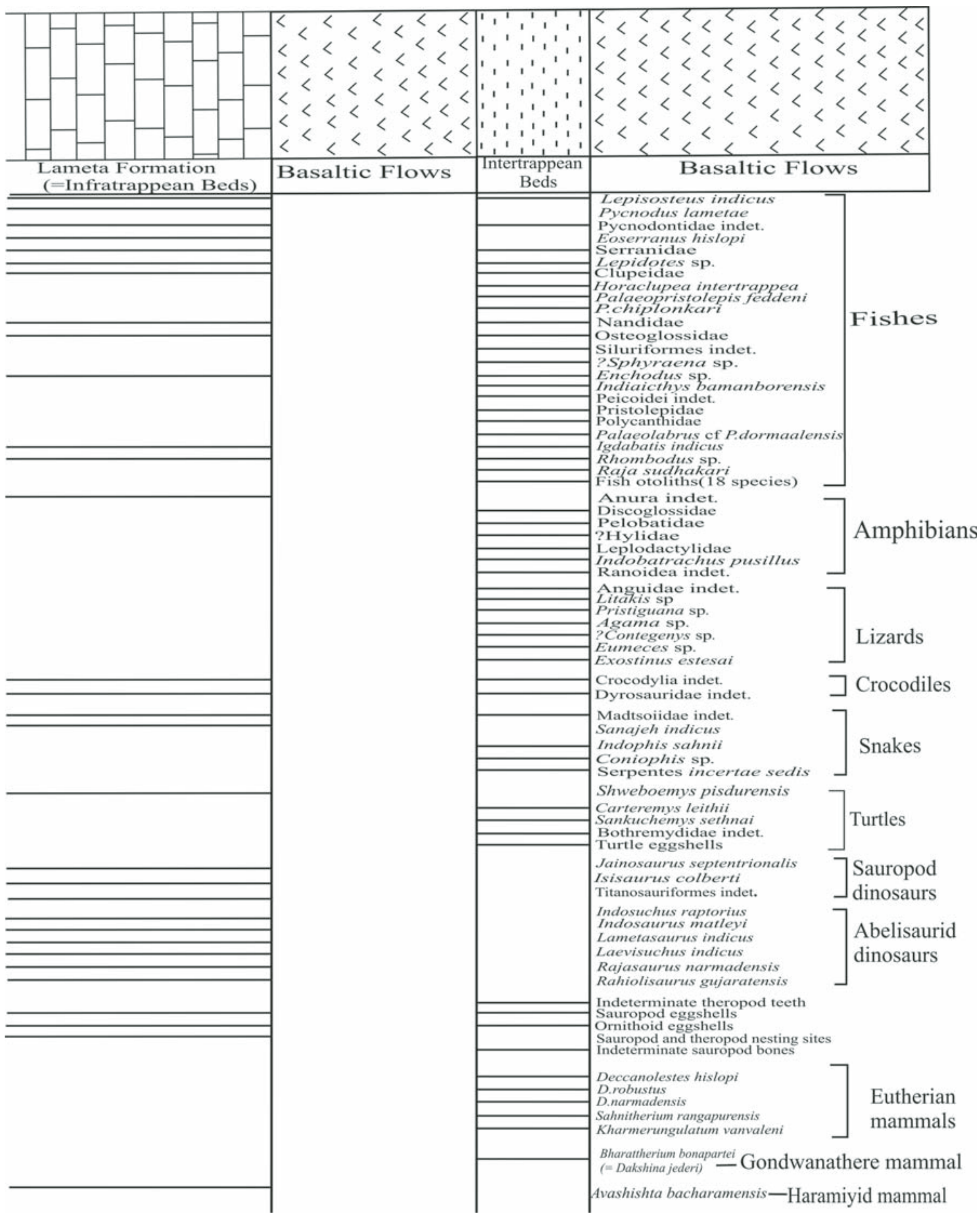

Figure 4. Range chart of various vertebrate groups across the Deccan volcano-sedimentary sequences.

by two taxa: *Sanajeh indicus* Wilson et al., 2010 and *Madtsoia pisdurensis* Mohabey et al., 2011 of the family Madtsoiidae. Not only did the madtsoiid snakes survive into the intertrappean beds at the family level, but so did three new taxa: *Indophis sahnii* (?Nigerophiidae) Rage and Prasad, 1992, Serpentes *incertae sedis* (Rage and Prasad, 1992), and *Coniophis* (Aniliidae) (Rage et al., 2004) appear at this stratigraphic level.

Dinosaur Bones, Nesting Sites, Eggshells, and Teeth

Lameta Formation

One of the most important fossil findings from the main Deccan volcanic province in the last three decades is the discovery of geographically extensive nesting sites and eggshells in the Lameta Formation (below phase II volcanism) over a stretch of 1000 km from Jabalpur in the east to Balasinor in the west and in the Nand-Dongargaon Basin in Central India (Fig. 2). These nesting sites are located near Jabalpur in the upper Narmada Valley, Bagh, Jobat, Dohad, Kheda, Balasinor, and Rahioli in the lower Narmada Valley, and Pavna and Dongargaon in the Nand-Dongargaon Basin (Fig. 2). In all these sites, nests and eggshells belonging to nine oospecies of *Megaoolithus* (Table 1) were documented from a fine- to medium-grained calcretized sandstone (Srivastava et al., 1986; Mohabey, 1998; Vianey-Liaud et al., 2003). Only one oospecies of *Ellipsoolithus* (Table 1) has so far been described from the Lameta Formation near Kheda (Mohabey, 1998). The occurrence of nests in a similar lithofacies has been attributed to strong nesting site selectivity, and extensiveness of nesting sites with morphologically similar eggs was shown as evidence for colonial nesting (Sahni et al., 1994; Mohabey, 2001).

Besides nesting sites and eggshells, the Lameta Formation at Jabalpur, Balasinor, Pisdura, Dongargaon, and Nand has been the source for all known Cretaceous dinosaur taxa from India named on the basis of skull and postcranial bones (Sleeman, 1844; Lydekker, 1877; Matley, 1921, 1923, 1929; von Huene and Matley, 1933; Chatterjee, 1978; Berman and Jain, 1982; Srivastava et al., 1986; Mathur and Srivastava, 1987; Jain and Bandyopadhyay, 1997; Wilson et al., 2003; Novas et al., 2010; Wilson and Mohabey, 2006; Wilson et al., 2011). To date, three titanosaurid sauropods and six abelisaurid theropods have been described from the Lameta Formation.[1]

Intertrappean Beds

Another significant finding from the main Deccan volcanic province is the occurrence of dinosaur remains in the intertrappean beds. All the early reports of skeletal remains of dinosaurs, coprolites, and dinosaur nesting sites were from the Lameta Formation (Matley, 1921; Matley, 1929; von Huene and Matley, 1933; Chatterjee, 1978; Berman and Jain, 1982; Srivastava et al., 1986; Mathur and Srivastava, 1987). Prior to 1980s, dinosaurs were considered to have been restricted to the Lameta Formation, and the intertrappean beds were generally regarded as lacking dinosaur fossils. This was one of the reasons for assigning an Early Tertiary (Eocene) age for the intertrappean beds. However, since 1980, several dinosaur fossils, including a few bones and teeth, and many eggshell fragments, have been documented from phase II intertrappean beds. Moreover, they have been reported from widely separated intertrappean sections such as those of Asifabad (Rao and Yadagiri, 1981; Sahni et al., 1984; Prasad, 1989), Nagpur (Vianey-Liaud et al., 1987), Anjar (Ghevariya, 1988; Sahni and Bajpai, 1988; Bajpai et al., 1993; Bajpai and Prasad, 2000), Ranipur (Mathur and Sharma, 1990), Mohgaon Kalan (Srinivasan, 1996), and Kisalpuri (Khosla et al., 2004) (Fig. 3). More recently, dinosaur eggshell fragments have also been found in the intertrappean beds of Kelapur (Maharashtra) and Piplanarayanwar and Gujri Gate (Madhya Pradesh) (Fig. 3) (work in progress at Delhi University).

These intertrappean eggshells are generally thin as compared to those of the Lameta Formation. Although they have not been studied as extensively and in as much detail as those of the Lameta Formation, limited ultrastructural studies indicate that eggshells from Asifabad, Nagpur (Sahni et al., 1984; Vianey-Liaud et al., 1987), Mohgaon Kalan (Srinivasan, 1996), Kelapur, and Piplanarayanwar belong to sauropod dinosaurs, and those from Anjar (Bajpai et al., 1993), Kisalpuri, and Gujri Gate are assignable to the ornithoid type. Until now, no parataxonomic classification has been attempted for the intertrappean dinosaur eggshells.

Depositional Environment of Dinosaur Fossils: Lameta versus Intertrappean

The Lameta Formation is generally thick, reaching a maximum thickness of 75 m, and the dinosaur nests and eggs are preferentially preserved in a sandy calcretized unit of the carbonate facies at Jabalpur, Rahioli, and Dongargaon (Mohabey, 2001). At Jabalpur, the dinosaur skeletal remains were recovered from the base and within the lower limestone. At Rahioli, dinosaur bones occur within a conglomerate horizon underlying the dinosaur egg-bearing sandy calcrete (Mohabey, 2001). In the Nand-Dongargaon Basin, dinosaur bones are reworked and transported elements within the overbank red and green clays, whereas the eggs are exclusively found in sandy calcrete and channel sandstone (Mohabey, 2001). In the area near the Bagh Caves in the lower Narmada Valley, dinosaur-egg yielding levels of the Lameta Formation are confined to the sandy and nodular calcretes of massive cherty limestone (Mohabey, 2001).

In contrast, the intertrappean beds are relatively thin (generally a few centimeters to 30 cm thickness, rarely reaching 5 m) with widely varying lithologies consisting of soft siltstone,

[1]Titanosaurid sauropods: *Jainosaurus* (= *Antarctosaurus*) *septentrionalis* (von Huene and Matley, 1933) Hunt et al., 1994; *Jainosaurus* cf. *septentrionalis* (Wilson et al., 2011); *Isisaurus colberti* (Jain and Bandyopadhyay, 1997) Wilson and Upchurch, 2003; Titanosauriformes indet. (Wilson and Mohabey, 2006). Abelisaurid theropods: *Indosuchus raptorius* von Huene and Matley, 1933; *Indosaurus matleyi* von Huene and Matley, 1933; *Laevisuchus indicus* von Huene and Matley, 1933; *Lametasaurus indicus* von Huene and Matley, 1933; *Rajasaurus narmadensis* Wilson et al., 2003; and *Rahiolisaurus gujaratensis* (Novas et al., 2010) (see Table 1).

shale, mudstone, marl, and clay. Sporadic dinosaur bones have been reported from the phase II intertrappean beds at Asifabad, near Hyderabad (Rao and Yadagiri, 1981), and Ranipur (Mathur and Sharma, 1990). However, the comparatively thick (~3.5 m) intertrappean beds of Anjar have yielded several large, yet to be described dinosaur bones (Ghevariya, 1988).

A major difference between the dinosaur fauna of the Lameta Formation and phase II intertrappean beds is the abundance of bones and nesting sites and fully preserved eggs in the former as compared to relatively limited presence of bones and no complete eggs or nesting sites in the latter. In view of the fact that the Lameta and phase II intertrappean dinosaur fossils were preserved in two distinctly different lithofacies, it is difficult to say whether there was a true decline of dinosaurs from the Lameta Formation to phase II intertrappean beds or whether this is an artifact of preservation. Depositional environments seem to have played an important role in the preservation of dinosaur fossils. The hard, sandy carbonate facies of the Lameta Formation deposited in a coastal-plain environment and proximal to the dinosaur habitat might have ensured better preservation of bones and complete eggs. In comparison, the intertrappean depositional environments represented by thin lacustrine facies distal to the dinosaur habitat may have received transported eggshell fragments and occasional large bones.

Mammals

At least two major groups of mammals have been documented from three widely separated phase II intertrappean sites. The intertrappean beds of Naskal near Hyderabad (Fig. 3) yielded the most diversified microvertebrate assemblage, including the first Cretaceous mammals of India. *Deccanolestes hislopi* was the first eutherian mammal recorded from the intertrappean beds of Naskal (Prasad and Sahni, 1988). Following this report, a few more taxa, such as *Deccanolestes robustus* (Prasad et al., 1994) and *Sahnitherium rangapurensis* (Rana and Wilson, 2003), were also documented from this area. Later on, one more species of *Deccanolestes* (*Deccanolestes narmadensis* Prasad et al., 2010) and a possible ungulate (*Kharmerungulatum vanvaleni* Prasad et al., 2007a) were described from the intertrappean beds of Kisalpuri in Central India (Fig. 3). Phylogenetic analysis of *Deccanolestes* has shown that it belongs to an insectivorous group of mammals (Adapisoriculidae), and this group possibly originated in India and dispersed to Africa and Europe some time close to the Cretaceous-Paleogene boundary (Goswami et al., 2011; de Bast et al., 2012).

These discoveries of eutherian mammals from the main Deccan volcanic province assume great significance in light of recent molecular phylogenies suggesting the former Gondwanaland as a center of origin for certain placental mammal orders (Springer, 1997; Waddell et al., 1999). As compared to a moderately diverse mammalian assemblage known from the intertrappean beds, only one possible haramiyidan mammal tooth (*Avashishta bacharamensis* Anantharaman et al., 2006) has been described from the infratrappean beds. The latter was recovered from the infratrappean beds of Bacharam, Rangareddi District, Andhra Pradesh (Anantharaman et al., 2006). The poor mammalian record from the infratrappean beds can be attributed to sampling bias. So far, samples from 10 phase II intertrappean sections have been bulk screen-washed, out of which only three turned out to be mammal-bearing. Out of four infratrappean sections (i.e., Pisdura, Jabalpur, Bacharam, and Marepalli; Fig. 2) subjected to bulk screen-washing, only one has produced a mammalian fossil. Thus, future works focused on washing of large numbers of samples may improve the diversity of infratrappean mammalian fauna.

SURVIVAL PATTERNS: LAMETA VERSUS INTERTRAPPEAN

The Lameta (infratrappean) fauna is represented by 12 fish, two crocodile, one turtle, two snake, and nine dinosaur taxa (three sauropod and six theropod) and 10 dinosaur oospecies (Table 1). In comparison, the phase II intertrappean vertebrate fauna is represented by 47 fish species (including 21 otolith species), five amphibian, eight lizard, four snake, three crocodile, four turtle, and six mammalian taxa. Besides these, sauropod and ornithoid eggshells, theropod teeth, and a few large sauropod bones are also known from the intertrappean beds. The diversity of intertrappean vertebrate fauna more than doubled, at least in the case of fish, snakes, and turtles at species and higher taxonomic levels.

This diversity increase may be due to sampling bias or the availability of more nutrients in the ecosystem following the initial phase of volcanism. Although the infratrappean beds have been extensively prospected for dinosaurs, very few sections have been explored for vertebrate microfossils by means of bulk screen-washing methods. In contrast, large numbers of intertrappean sections have been investigated based on this method. In addition, following erosion and transportation of materials from the newly deposited mafic volcanic rocks, many new nutrients might have been added to the lacustrine bodies, which may have played an important role in increasing their biodiversity. To discriminate between these two plausible explanations for the increased biodiversity in the intertrappean beds, more infratrappean sections need to be sampled on a larger scale.

Overall, the infratrappean vertebrate fauna survived Deccan volcanism phase I and, with the exception of dinosaurs, proliferated in the intertrappean ecosystems. This pattern of vertebrate survival from the infratrappean to intertrappean beds has a close parallel with the continental late Maastrichtian record of the western interior of North America (eastern Montana). There, the uppermost Cretaceous (late Maastrichtian) Hell Creek Formation yielded 107 vertebrates species, of which 52 species (49%) survived into the lower part of the overlying Lower Paleocene Tullock Formation (Archibald, 2011). Compared to 28% survival in land-dwelling animals, freshwater animals such as bony fishes, amphibians, turtles, crocodiles, and champsosaurs had a high survival rate of 76%. Sheehan and Fastovsky (1992) inferred a higher rate of survival for freshwater faunas (90%) as compared to land-dwellers (12%). This differential pattern of extinction of freshwater and terrestrial vertebrates has been explained in terms of dependence of land-based communities on primary productivity in contrast to buffering of freshwater communities from extinction by detritus feeding when there was a temporary drop in primary productivity (Sheehan and Fastovsky, 1992).

A similar explanation can be offered for the preferential survival of the predominantly freshwater aquatic community compared with the terrestrial community from the time of deposition of infratrappeans to intertrappean beds. There is a notable increase in the diversity of the intertrappean freshwater vertebrates such as fishes, turtles, and snakes as compared to that of the infratrappean vertebrates (Fig. 5). The freshwater vertebrates constitute 52%, while the terrestrial vertebrates form 49% of the infratrappean vertebrate fauna (Fig. 5). In contrast, the intertrappean vertebrate fauna is dominated by freshwater vertebrates (70%), compared to terrestrial vertebrates (30%). Additionally, it is quite possible that depositional environments also played a significant role in the preservation of fossils. The humid, tropical, lacustrine environments of the intertrappean beds had possibly greater potential for the preservation of vertebrate fossils as compared to overbank, paludal environments of the semiarid climate during deposition of the infratrappean beds. Prasad and Khajuria (1995) suggested that the survival of Deccan phase I volcanism by freshwater communities might be related to the episodic nature of the volcanic eruptions, and the fauna could have recovered from the environmental stress during the repose periods.

Invertebrates also seem to have responded to the initial Deccan volcanic activity in this manner. Khosla et al. (2011) described 41 species of freshwater ostracods from the Lameta Formation of Jabalpur, Pisdura, and Dongargaon. According to these authors, of the 41 species, five are indeterminate, six are new, and 30 are common to the intertrappean beds. Besides their common occurrence in Maastrichtian infratrappean and intertrappean beds, many of these Maastrichtian species are found in association with Danian planktic foraminifers and brackish-water ostracod species in Jhilmili intertrappean beds (Keller et al., 2009b). This demonstrates that the ostracods of the Maastrichtian intertrappean beds survived into the early Paleocene, apparently without major extinctions due to volcanism (Sharma and Khosla, 2009; Khosla et al., 2011).

According to Cripps et al. (2005), the third and last phase of Deccan volcanism did not affect life significantly. Cripps et al. (2005) considered the intertrappean beds of Bombay as part of the Mumbai Island Formation (Salsette Subgroup) overlying the Wai Subgroup of main Deccan volcanic province and hence representative of the final phase III of Deccan volcanism that followed the Cretaceous-Paleogene boundary mass extinction. Singh and Sahni (1996) assigned a Maastrichtian age for the intertrappean beds of Bombay on the basis of an ostracod assemblage similar to that of other intertrappean outcrops of the main Deccan volcanic province. However, the recent report of similar ostracod assemblage in association with early Paleocene (Danian) planktic foraminifers from the intertrappean beds of Jhilmili argues against the use of ostracods as age markers for the intertrappean beds. Palynofacies analysis of Bombay intertrappean beds led Cripps et al. (2005) to conclude that these beds were deposited in a lagoonal environment proximal to land, sheltered from a strong marine influence and more organic rich in comparison to those of the main Deccan volcanic province. Because of the absence of evidence for wildfires that would cause mass mortality and increase the availability of plant material to the lagoonal ecosystem throughout the numerous pyroclastic eruptions in this region, Cripps et al. (2005) argued that the late-stage explosive Deccan volcanism might not have caused a major ecosystem collapse.

However, based on palynofloral analysis of the Lameta Formation and succeeding intertrappean beds in Nand-Dongargaon Basin in Maharashtra, Samant and Mohabey (2005) concluded that the initial Deccan volcanic activity affected the plant community. The floral transition from the Lameta Formation to the overlying intertrappean stratigraphic levels is marked by a decline in diatom diversity and abundance, an increase in angiosperm and pteridophyte diversity at the expense of gymnosperms, and the first appearance of dinoflagellates (Samant and Mohabey, this volume). They attributed these floral changes to initial physiographic and chemical changes caused by Deccan volcanism. Though Samant and Mohabey (2005) observed total absence of diatoms and dinoflagellates in spore-pollen–rich intertrappean beds at higher stratigraphic levels, the spore-pollen assemblages from the intertrappean beds of different stratigraphic levels are generally more or less similar. Even the pollen-spore assemblage represented by *Ariadnaesporites*, *Aquilapollenites*, *Gabonisporites*, *Azolla*, etc. is broadly similar to Lameta and intertrappean beds. A marked difference in the palynofloral assemblage has only been noticed between the Maastrichtian outcrops and the Paleocene intertrappean beds of Papro, Lalitpur (Singh and Kar, 2002).

SUMMARY

Intensified vertebrate faunal studies in recent years have revealed the presence of widespread nesting sites over an area of 1000 km in an east-west direction along the Narmada Valley and in Central India. Following the application of bulk screen-washing methods, there has been a remarkable improvement in the record of diversity of vertebrate fauna of the Deccan infratrappean and intertrappean beds. As a consequence, all vertebrate groups, with the exception of birds, have been recovered from the intertrappean beds. In comparison to the common occurrence of dinosaur skeletal remains and nesting sites and eggs in the Lameta Formation, the phase II intertrappean beds yielded only isolated teeth and bones in a few sites and eggshell fragments at many localities. This apparent decline of the dinosaur fauna subsequent to the eruption of the first phase of Deccan volcanism might be attributed to taphonomic bias, as the infratrappean and intertrappean dinosaur-bearing sedimentary facies are distinct from each other. A comparison of vertebrate fauna from the

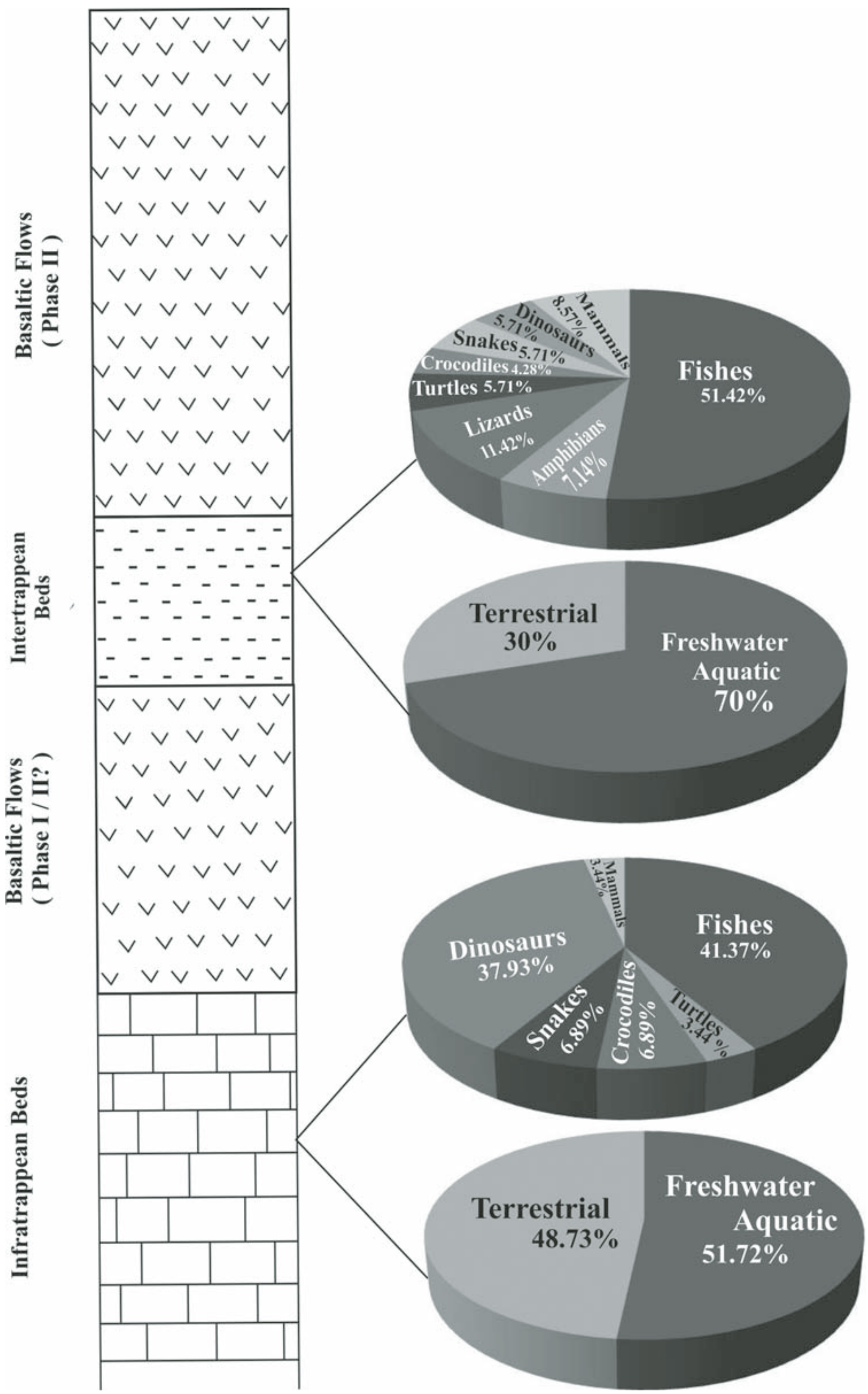

Figure 5. Relative composition of freshwater aquatic and terrestrial vertebrates of the infratrappean and intertrappean beds.

infratrappean and intertrappean beds revealed that many freshwater taxa survived the first phase of Deccan volcanism. The reasons one could offer for their survival are: (1) ability of the fauna to bounce back during the quiescent periods of volcanism; (2) the different feeding strategies adapted by freshwater and terrestrial communities; or (3) sampling bias—the observed increase in the vertebrate diversity from the infratrappean to intertrappean beds could be a consequence of limited sampling from the infratrappean beds in comparison to large-scale screen-washing of intertrappean sediments. If Deccan volcanism had any impact on life, it was possibly during the second phase, when 80% of the total volume erupted. Although a linkage has been suggested between Deccan volcanism and foraminiferal extinction in Cretaceous-Paleogene boundary subsurface sections of ONGC wells in the Krishna-Godavari Basin (Keller et al., 2011, 2012) and in the Um Sohryngkew section of Meghalaya, ~800 km northeast of the main Deccan volcanic province (Gertsch et al., 2011), so far no well-defined Cretaceous-Paleogene boundary section has been discovered in continental outcrops of the main Deccan volcanic province. Therefore, future studies should focus on identifying clearly marked Cretaceous-Paleogene boundary sections in the main Deccan volcanic province outcrops in order to understand the effects of volcanism on physical environments and biota in a terrestrial environment.

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