



## EARLIEST CENOZOIC FROGS FROM THE INDIAN SUBCONTINENT: IMPLICATIONS FOR OUT-OF-INDIA HYPOTHESIS

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### ABSTRACT

This paper describes the earliest Cenozoic anurans from the Indian subcontinent, recovered from the early Eocene Cambay Shale deposits (~53.5 Ma) of the Vastan Lignite Mine, Gujarat, western India. The fauna comprises representatives of three distinct groups with Laurasian (Discoglossidae) and Gondwanan (Ranoidea and Leptodactylidae) affinities. The ranoids, previously recorded from the terminal Cretaceous of peninsular India, are particularly significant as they support an Out-of-India dispersal.

**Keywords:** Anura, Cenozoic, early Eocene, India, Out-of-India dispersal

### INTRODUCTION

Most palaeogeographic reconstructions suggest that after the Late Cretaceous (around 85-90 Ma) break-up from Madagascar, the Indian landmass drifted northwards in complete isolation from other landmasses until it collided with the Asian mainland in the early Eocene (Powell, 1979; Besse and Courtillot, 1988; Smith *et al.*, 1994; Hay, *et al.*, 1999; Zhu *et al.*, 2004). The ca. 55 Ma collision age is currently the most widely accepted one, although estimates vary from ~65 Ma (e.g. Klootwijk *et al.*, 1992; Yin and Harrison, 2000) to a much younger collision age of about 35 Ma (Aitchison *et al.*, 2007). Accepting an early/middle Eocene age collision age implies that India remained physically isolated for 30-35 m.y. During such a long period of isolation, landmasses are expected to develop endemic fauna and flora. To evaluate the nature of biota (endemic or non-endemic) during India's northward flight, the fossil record from the Late Cretaceous-early Eocene continental strata of India is crucial. The diversity, evolution, and biogeographic affinities of Late Cretaceous biota of India have received considerable attention in recent years (e.g. Jaeger *et al.*, 1989; Prasad and Rage, 1991, 1995; Sahni and Bajpai, 1991; Krause *et al.*, 1997; Prasad and Sahni, 1999; Khosla and Sahni, 2003 and references therein). These studies led to the belief that the Late Cretaceous biota of India includes both Laurasian and Gondwanan elements. Among the Laurasian elements, the discoglossid frogs and paleoryctid mammals are now considered more important, and the Gondwanan forms mainly include abelisaurid dinosaurs and sudamericid (gonwanathere) mammals. More recently, however, in a series of papers (Whatley and Bajpai, 2006 *et seq.*), it has been demonstrated for the first time that India's freshwater ostracod fauna was highly endemic at the species level, without any close relationships to faunas from the surrounding landmasses. Whatley and Bajpai (2006) interpret this extensive (near 100%) ostracod endemism as indicating India's considerable geographic isolation during the terminal Cretaceous, before it collided with Asia.

As compared to the Late Cretaceous record, India's fossil record is blank for the continental Palaeocene. For the early Eocene too, the terrestrial record was virtually non-existent

until a few years ago. However, recent discoveries of various vertebrate groups, particularly mammals, from the early Eocene Cambay Shale of the Vastan Lignite Mine in Surat District, Gujarat, western India have gone a long way in filling this major gap (Bajpai *et al.*, 2005a, b, c; 2006; 2007a, b; Smith *et al.*, 2007; Rose *et al.*, 2008). The vertebrate-yielding horizons of the Vastan Lignite Mine occur intercalated between the two main lignite seams. Based on benthic foraminifers and dinoflagellates, the Vastan vertebrates have been dated as early Ypresian (~ 53.5 Ma) (see Bajpai *et al.*, 2007a for details of locality and section).

Here, we describe the early Eocene anuran fauna from the Vastan Lignite Mine. These fossils represent the oldest known Cenozoic frogs of South Asia. Prior to this work, Cenozoic anuran remains were reported from the middle Eocene Kuldana Formation of Pakistan (Rage, 1987) and the Siwalik deposits of India (Rage *et al.*, 2001). The anuran fauna of the present collection includes well-preserved ilia, humeri, radio-ulnae, vertebra, and partially preserved urostyles. The ilia, which are taxonomically more diagnostic, indicate the presence of at least three groups of anurans namely, Discoglossidae, Ranoidea, and Leptodactylidae. These fossils have important palaeobiogeographic implications in the context of India's geodynamic framework around the time of its collision with Asia.

The specimens are housed in the Vertebrate Palaeontology Laboratory, Department of Earth Sciences, Indian Institute of Technology, Roorkee under the acronym IITR/SB/VLM-LV.

### SYSTEMATIC PALEONTOLOGY

#### Ranoidea Bonaparte, 1845

(Pl. I, figs. a-d)

*Description:* Two ilia (IITR/SB/VLM-LV/ 201- 202) are referred to this group. In these ilia, a distinct dorsal crest is present. The *tuber superius* is formed by the thickening of posterior end of the dorsal crest. Posteriorly, the *tuber superius* terminates at the anterodorsal margin of the acetabulum. The posterior face of the *tuber superius* descends steeply into the supra-acetabular area making an open angle with it, whereas its anterior face slopes gently and continues with the dorsal crest. It does not project above the dorsal crest. The *tuber*

*superius* is tear-drop shaped with a blunt posterior and pointed anterior end raised above the lateral face of the ilia. Its long axis forms an acute angle with the ilial shaft. A depressed area separates the *tuber superius* from the ilial shaft anteroventrally. The acetabulum is large and suboval in outline with an expanded ventral rim. The ventral acetabular rim is markedly raised above the pre-acetabular zone. The anterior end of the acetabular rim is in line with the ilial shaft. The supra-acetabular and pre-acetabular fossae are absent. The supra-acetabular expansion is incompletely preserved. The pre-acetabular area forms an open angle with the ventral border of the iliac shaft. No inter-iliac tuber is present. The iliac shaft is ovoid in cross section.

**Remarks:** IITR/SB/VLM-LV/201 and 202 resemble the ilia from the Upper Cretaceous intertrappean beds of Naskal (India) referred to ?Leptodactylidae or Hemisotidae (Prasad and Rage, 2004, fig.1 E-G) in having a *tuber superius* steeply sloping posteriorly and gently sloping anteriorly. But unlike in the latter ilia, the *tuber superius* of the Vastan specimens does not project dorsally above the dorsal iliac crest and also lacks the supra-acetabular fossa. In fact, the Vastan ilia compare very well with those of Ranoidea in the presence of a dorsal crest, mediolaterally flattened iliac shaft, *tuber superius* forming as a posterior thickening of the dorsal crest with broad posterior and tapering anterior ends, not projecting above the dorsal crest, absence of supra-acetabular fossa, acetabulum with a flared ventral rim which is raised above the pre-acetabular zone and the absence of inter-iliac tuber. As in ranoids and unlike in leptodactylids, the anterior face of *tuber superius* descends gradually with a gentle slope and continues anteriorly with the dorsal crest. The Vastan ilia differ from the one referred to Ranoidea from the Upper Cretaceous intertrappean beds of Naskal, India (Prasad and Rage, 2004, fig.2) in having a steeply sloping posterior face of the *tuber superius*. These ilia are more like those of *Rana pipiens* and *Rana esculenta* in the development of *tuber superius*, supra-acetabular expansion, pre-acetabular area and the dorsal iliac crest. However, the Vastan ilia lack the supra-acetabular fossa of these two species.

#### **Discoglossidae** Gunther, 1858

(Pl. I, figs. e-l)

##### *Description:*

**Ilia:** IITR/SB/VLM-LV/203 is characterized by the absence of dorsal iliac crest. The *tuber superius* occurs as a swelling of the dorsal margin of the iliac shaft slightly anterior to the anterior

acetabular rim. The *tuber superius* is laterally flattened and continues posteriorly with the supraacetabular expansion in a straight line. The supra-acetabular expansion is long and dorsally curved at its posterior end. The supra-acetabular and pre-acetabular fossae are absent. The acetabulum is hemispherical in outline and has a raised ventral margin that overhangs the pre-acetabular area. The pre-acetabular area forms an obtuse angle with the ventral margin of iliac shaft. Medially, the ilium bears inter-iliac protuberance. The iliac shaft has an ovoid cross section.

IITR/SB/VLM-LV/204 lacks the dorsal iliac crest. The *tuber superius* lies on the dorsal margin of the iliac shaft above the anterior part of acetabular rim and is medio-laterally compressed. It has gently sloping anterior and posterior faces. There are no supra-acetabular and pre-acetabular fossae. The supra-acetabular expansion is posteriorly elongated and the posterior face of *tuber superius* merges with the supra-acetabular expansion almost in a straight line. The acetabulum rim is broken ventrally and hence the outline of acetabulum is difficult to infer. Medially, the posteroventral part of the ilium is broken but its medial surface is flat indicating that there is no inter-iliac tuber medially. The iliac shaft is subcylindrical and has an ovoid cross section.

**Humeri:** There are three relatively well preserved (IITR/SB/VLM-LV/205-207) and three fragmentary humeri in the present collection. Of these, IITR/SB/VLM-LV/205 is a complete left humerus possessing both proximal and distal ends whereas IITR/SB/VLM-LV/206 and 207 do not preserve the proximal ends. In IITR/SB/VLM-LV/205, *eminencia capitata* or the humeral condyle is spherical in shape, large occupying about 75% of the distal humeral width. Although the humeral condyle is in line with the humeral shaft, it is slightly offset to the radial side. The *epicondylus radialis* or the radial epicondyle is distinct but less developed. The *epicondylus ulnaris* or ulnar epicondyle is more strongly developed than the radial epicondyle. The *fossa cubitalis ventralis* is deep and crescentic in outline and it does not extend proximally. A weakly developed *crista lateralis* is present but the *crista medialis* is absent. This suggests that all these humeri belong to females as males only develop *crista medialis* and a strong *crista lateralis*. In IITR/SB/VLM-LV/205, the *crista ventralis* is a high crest extending more than half the length of the humerus and proximally curved in a 'S'-like shape. Proximally, a less distinct *crista paraventralis* extends to a point where *crista ventralis* is very high. The *crista paraventralis* is also present on IITR/

### **EXPLANATION OF PLATE I**

(Anurans from the early Eocene of Vastan)

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|--|---|
| a. <b>Ranoidea</b> indet., right ilium (IITR/SB/VLM-LV/ 201), lateral view       | i. <b>Discoglossidae</b> indet., humerus (IITR/SB/VLM-LV/ 206), ventral view      |
| b. <b>Ranoidea</b> indet., right ilium (IITR/SB/VLM-LV/ 201), medial view        | j. <b>Discoglossidae</b> indet., humerus (IITR/SB/VLM-LV/ 207), ventral view      |
| c. <b>Ranoidea</b> indet., left ilium (IITR/SB/VLM-LV/ 202), lateral view        | k. <b>Discoglossidae</b> indet., humerus (IITR/SB/VLM-LV/207), dorsal view        |
| d. <b>Ranoidea</b> indet., left ilium (IITR/SB/VLM-LV/ 202), medial view         | l. <b>Discoglossidae</b> indet., vertebra (IITR/SB/VLM-LV/208), dorsal view       |
| e. <b>Discoglossidae</b> indet., left ilium (IITR/SB/VLM-LV/ 203), lateral view  | m. <b>Leptodactylidae</b> indet., right ilium (IITR/SB/VLM-LV/ 209), lateral view |
| f. <b>Discoglossidae</b> indet., left ilium (IITR/SB/VLM-LV/ 203), medial view   | n. <b>Leptodactylidae</b> indet., right ilium (IITR/SB/VLM-LV/ 209), medial view  |
| g. <b>Discoglossidae</b> indet., right ilium (IITR/SB/VLM-LV/ 204), lateral view | o. <b>Anura</b> indet., radioulna (IITR/SB/VLM-LV/ 211), lateral view             |
| h. <b>Discoglossidae</b> indet., right ilium (IITR/SB/VLM-LV/ 204), medial view  |   |



SB/VLM-LV/206 and 207. The olecranon scar (*impressio olecraneana*) is large and its proximal end points more towards the lateral margin of the humerus.

**Vertebra:** IITR/SB/VLM-LV/208 is a well preserved, opisthocoelous presacral vertebra. It is characterized by dorsoventrally flattened centrum which results in a subrectangular outline of the anterior condyle and posterior cotyle. In ventral view, the centrum is nearly as wide as long. The neural canal is elliptical to subspherical in shape and higher than the centrum. The neural spine is a narrow, convex ridge slightly raised above the neural arch and projects posteriorly in a pointed ridge beyond the postzygapophyseal facets. On the posteroventral face of neural arch, a narrow crest extends from the anterolateral margin of each postzygapophyseal facet and these crests merge medially at the level of postzygapophyses and continue posteriorly to the tip of neural spine as a narrow ridge. The transverse processes are slender, broken slightly lateral to the prezygapophyses, and ovoid to cylindrical in cross section.

**Remarks:** The ilia exhibit morphological features characteristic of discoglossids such as the absence of a dorsal iliac crest, posterodorsally extended supra-acetabular expansion, and the *tuber superius* occurring as a dorsal swelling of iliac shaft dorsal to the acetabular rim. In IITR/SB/VLM-LV/203, the *tuber superius* occurs as a small dorsal swelling of the posterior part of the ilium and continues with the supra-acetabular expansion posteriorly in a straight line as in *Alytes* and in contrast to a better developed *tuber superius* making an open angle with the supra-acetabular expansion in "*Discoglossus*". A reduced inter-iliac tuber is known to occur in discoglossids as in IITR/SB/VLM-LC/203. This character is generally present in primitive or aquatic taxa (Prasad and Rage, 2004). IITR/SB/VLM-LV/204 is also comparable to discoglossids in the absence of dorsal crest, posteriorly extended supra-acetabular expansion and the tuber superius continuing with the supra-acetabular expansion in a straight line. As the ventral acetabular rim and pre-acetabular rim are not preserved, IITR/SB/VLM-LV/204 is tentatively assigned to the family Discoglossidae. In having a distinct opisthocoelous vertebra with distinct neural crest that is prolonged and pointed posteriorly, and cylindrical to ovoid transverse processes, IITR/SB/VLM-LV/208 is more closely comparable to the presacral vertebrae of *Discoglossus* than to any other taxon. Opisthocoelous vertebrae occur in Discoglossidae, Pipidae and Rhinophrynidae. As the anuran material from Vastan contains no bones referable to the latter two families, here we assign the vertebra to Discoglossidae. Further, the vertebral morphology of IITR/SB/VLM-LV/208 is reminiscent of the extant *Discoglossus*. Humeri with distinct *crista paraventralis* (IITR/SB/VLM-LV/205-207) are also characteristic of discoglossid frogs. Therefore, the presence of opisthocoelous vertebra and humeri with *crista paraventralis* confirm the presence of discoglossid frogs in the early Eocene vertebrate assemblage of Vastan.

#### Leptodactylidae Werner, 1896

(Pl. I, figs. m-n)

**Description:** The ilium (IITR/SB/VLM-LV/209) is characterized by a long cylindrical shaft regularly curving anteriorly and ventrally. It lacks the dorsal iliac crest. The *tuber superius* occurs along the dorsal margin of the iliac shaft above the anterior end of acetabular rim and its long axis is oriented

parallel to the long axis of the shaft. In lateral view, the *tuber superius* is a symmetrical mound raised above the shaft with gentle anterior and posterior slopes. As the *tuber superius* is parallel to the long axis of iliac shaft, it does not make an angle with the supra-acetabular expansion. The supra-acetabular expansion is broken posteriorly. The acetabulum is subtriangular in outline with its pointed end directed anteroventrally and lying below the ventral margin of iliac shaft. The posterior rim of the acetabulum is raised both dorsally and ventrally. The ventral margin of the acetabulum is also raised above the pre-acetabular zone. The pre-acetabular area is flared ventrally and makes an obtuse angle with the ventral margin of iliac shaft. The supra-acetabular and pre-acetabular fossa are absent. The posterior medial face of the ilium is chipped and hence the presence or absence of inter-iliac tuber is not known. The iliac shaft is ovoid in cross-section.

**Remarks:** IITR/SB/VLM-LV/209 is comparable in general morphology to that of *Telmatobius* in having a *tuber superius* located at the posterodorsal margin of the iliac shaft just above the anterior part of acetabulum and oriented parallel to the long axis of iliac shaft and anteriorly continuing with the supra-acetabular expansion and in the absence of dorsal iliac crest. The supra-acetabular expansion is posteriorly projecting in *Telmatobius* whereas this part of the ilium is broken in IITR/SB/VLM-LV/209. The pre-acetabular area is flared ventrally in both *Telmatobius* and IITR/SB/VLM-LV/209. The *tuber superius* occurs as a mound in lateral view with gently sloping anterior and posterior faces in both taxa. In size and mediolateral compression of the iliac shaft also, the two taxa are similar. However, they differ from each other in the position of anterior rim of the acetabulum. In *Telmatobius*, the anterior rim of acetabulum is in line with the ventral margin of the iliac shaft whereas in IITR/SB/VLM-LV/209 it is slightly ventral to the ventral margin of the iliac shaft. It is generally included in the broad leptodactyloid group often placed within the family Ceratophryidae (Frost *et al.*, 2006). In having anterior acetabular rim slightly below the ventral margin of the iliac shaft and relatively large pre-acetabular expansion, IITR/SB/VLM-LV/209 is comparable to the ilia of *Lymnodynastes tasmaniensis* (Tyler, 1977; fig.2F) and *Kyarranus* (Tyler, 1976; fig.3L). However, unlike in IITR/SB/VLM-LV/209, the *tuber superius* in *L. tasmaniensis* makes an angle of 45° with the supra-acetabular expansion and has a steep anterior face. Further, in a marked contrast to the condition in IITR/SB/VLM/209, the *tuber superius* of *Kyarranus* is located anterior to the anterior rim of acetabulum and is posteroventrally inclined. IITR/SB/VLM-LV/209 is also comparable to the ilium of *Philoria* (Tyler, 1991; fig.1A) in having a lower supra-acetabular expansion, in its *tuber superius* not making a large angle with the supra-acetabular expansion and in the extent of pre-acetabular zone development. However, in *Philoria*, the anterior acetabular rim is slightly above the ventral margin of the shaft and the pre-acetabular area is nearly at right angles with the ventral margin of iliac shaft. On the whole, it appears that the affinities of IITR/SB/VLM-LV/209 lie somewhere within the broad leptodactylid group.

#### Anura indet.

(Pl. I, fig. o)

**Description:** IITR/SB/VLM-LV/210-211 are two well preserved radioulnae. The *capitulum* and *olecranon* present a subrectangular and deeply concave face. The medial margin

of olecranon is thick and raised above the *capitulum*. The *crista radii* is a sharp crest from the distolateral base of the *capitulum* to two-thirds the length of the bone. The *sulcus longitudinalis* separating the ulna from radius extends from the distal end of the bone to its mid-height. In transverse view, the distal end of radioulnae are characterized by distally convex, subspherical facets of radius and ulna. The distal facet of radius is more than twice the size of that of ulna and the two are separated by a deep notch. On IITR/SB/VLM-LV/210, a short crest is present laterally to the radius.

In addition to the ilia, humeri, vertebra, and radioulnae, a few fragmentary bones of femora and urostyles are also present in the Vastan microvertebrate collection. The fragmentary nature does not permit any taxonomic assignment of these bones.

## DISCUSSION

Until now, the vertebrate fauna recovered from the early Eocene Cambay Shale of the Vastan Lignite Mine was represented by fishes, lizards, snakes, crocodiles, turtles, birds and mammals (Prasad and Bajpai, 2008 and references therein). Published mammal fauna from Vastan includes at least 9 placental orders (Proteutheria, Apatotheria, Insectivora, Artiodactyla, Perissodactyla, Primates, Rodentia, Lagomorpha, and Chiroptera). Overall, the Vastan mammal fauna exhibits holarctic affinities, although it is almost entirely new at the generic level. Apart from mammals, the Vastan vertebrates include aquatic snakes (Bajpai and Head, 2007), lizards (Prasad and Bajpai, 2008) and birds (Mayr *et al.*, 2006).

For over two and a half decades, the Late Cretaceous (Maastrichtian) terrestrial biota of India has been interpreted to have biogeographic affinities with both Gondwanan and Laurasian landmasses (Prasad and Sahni, 1999). However, as mentioned above, a remarkable degree of Maastrichtian faunal endemism in India has also been demonstrated recently, based on nearly a hundred new species of freshwater ostracods from the Deccan intertrappean deposits (Whatley and Bajpai, 2006 and references therein). The extensive ostracod endemism led these authors to support the idea of India's paleogeographic isolation during Maastrichtian, consistent with the geophysical data (see Ali and Aitchison, 2008, for a review of India's plate motion history).

The past few years have also seen the emergence of an interesting "Out-of-India" hypothesis based on molecular phylogeny and divergence timings of modern Asian biota. This hypothesis holds that several modern Asian groups had Gondwanan origin and that these groups were rafted on the northward moving Indian plate before dispersing to Asia as a consequence of India-Asia collision (see Karanth, 2006 for a review). Molecular data on a number of diverse extant groups support this hypothesis: amphibians, particularly ranids (Bossuyt and Milinkovitch, 2001) and caecilians (Gower *et al.*, 2002; Wilkinson *et al.*, 2002), acrodont lizards (Macey *et al.*, 2000); cichlid fishes (Sparks, 2004); ratite birds (Cooper, 2001) and crypteroniaceae plants (Conti *et al.*, 2002; see also Rutschmann, 2004).

Of particular interest to this work are the ranid frogs found in the Western Ghats region of western India. A number of ranid clades documented from this region provide an excellent example of the survival of ancient Gondwanan elements in India's modern biota (Biju and Bossuyt, 2003). The diverse caecilian (Amphibia) fauna of India is also known to include

several taxa which possibly originated during India's geological isolation from Africa and Eurasia, dispersing into South East Asia as a result of India's collision with Asia. The herpetofauna (boid snakes) also provides interesting palaeobiogeographic insights, involving both vicariance and dispersal (Noonan and Chippindale, 2006). Among invertebrates, freshwater snails have also been used in evaluating Out-of-India vs. Into-India hypotheses (Köhler and Glaubrecht, 2007). Botanical evidence is also potentially important in testing Out-of-India dispersal patterns, as suggested by recent phylogenetic analyses and molecular dating estimates based on chloroplast DNA sequences of the Crypteroniaceae (Conti *et al.*, 2002; Rutschmann, 2004).

Fossil evidence provides a direct means to test the idea of Out-of-India dispersal. However, fossil data bearing on this hypothesis are scarce, with the notable exceptions of Cretaceous freshwater ostracods (Whatley and Bajpai, 2006), ranoid frogs (Prasad and Rage, 2004), grasses (V. Prasad *et al.*, 2004) and, most recently, agamid lizards (Prasad and Bajpai, 2008). Possible evidence also comes from the recently described oldest known hoofed mammal (condylarth) from the Late Cretaceous of India (Prasad *et al.*, 2007) and the flowering plants belonging to *Lagerstroemia* (crape-myrtle, Lythraceae) (Liu *et al.*, 2007).

As far as the current understanding of biogeographic affinities of Indian terrestrial early Eocene fauna is concerned, it is dominated by holarctic elements although the taxa are largely new at the generic/family level. The Vastan anuran fauna is represented by three distinct groups: Discoglossidae, Leptodactylidae, and Ranoidea. Discoglossidae is a typical Laurasian family not known from other Gondwanan continents prior to the Miocene, with the oldest fossil record coming from the Middle Jurassic of Europe. It has also been recorded from the Late Cretaceous of India (Prasad and Rage, 1995, 2004). In the Late Cretaceous, it is represented by isolated ilia only. The presence of opisthocoelous vertebra and humeri with *crista paraventralis*, in addition to typical ilia, strongly suggests the presence of Discoglossidae in the Early Eocene, when India was probably still not fully docked with Asia.

The presence of Maastrichtian Laurasian elements has long been interpreted as evidence of a terrestrial connection between India and Asia during this interval (e.g. Rage, 2003). Because of their intolerance for salt water, the evidence of frogs (e.g. discoglossids) is considered to be particularly compelling (e.g. Rage, 2003). However, the possibility of such a terrestrial connection has been ruled out recently in a comprehensive analysis of geological and geophysical data by Ali and Aitchison (2008). According to these authors, marine barriers between India and Asia were too wide for such a connection and that the presence of Eurasian elements including discoglossids in the Indian Cretaceous can be better explained in terms of oceanic dispersal. A similar transoceanic dispersal mechanism has been suggested to explain the distribution of amphibians in Africa and Madagascar (Vences, 2004).

The leptodactylid and ranoid frogs represent the Gondwanan component of the Vastan anuran fauna. The presence of ranoid frogs in the Vastan fauna is interesting. As mentioned above, molecular studies on modern ranids indicate that this group had a Gondwanan (? African) origin and that it dispersed to Asia as a consequence of the northward moving Indian plate colliding with Asia (Bossuyt and Milinkovitch, 2001; Bossuyt *et al.*, 2006). The fossil record of ranids is



generally poor. The earliest ranoids come from the Cenomanian (99–93.5 Ma) of Africa (Baez and Werner, 1996). In Europe, their oldest record extends back to the late Eocene and in North America, the oldest ranids are known from the Miocene (Rage and Rocek, 2003). In India, ranoid frogs of ranid- or rhacophorid-like morphology have been described recently from the latest Cretaceous (Maastrichtian) (Prasad and Rage, 2004). There are no known occurrences of pre-Cenozoic ranids in Eurasia. Thus, the presence of ranid frogs in both Cretaceous and the early Eocene of India is consistent with the molecular data that suggest an Out-of-India dispersal of ranids (Bossuyt and Milinkovitch, 2001). It is important to note that agamid lizards, another group of vertebrates from the Vastan Lignite Mine, also support an out-of-India dispersal (Prasad and Bajpai, 2008). Macey *et al.* (2000) suggested that agamid lizards had originated on the former Gondwanaland and later dispersed into Asia via northward drifting Indian plate. Based on the oldest occurrences of agamid lizards (Late Triassic and Jurassic of India) and their presence in the early Eocene of India, Prasad and Bajpai (2008) speculated on the possibility of agamid lizards having been introduced into Eurasia through one of the several trans-Tethyan dispersals phases. It will be of considerable interest to see if the pattern of Out-of-India dispersal is replicated by additional taxa among vertebrates, invertebrates and plants, based on molecular phylogeny, divergence timings, current distribution and critical fossil evidence.

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