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Early Eocene frogs from Vastan Lignite Mine, Gujarat, India

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The Ypresian Cambay Shale Formation of Vastan Lignite Mine in Gujarat, western India, has yielded a rich vertebrate fauna, including the earliest modern mammals of the Indian subcontinent. Here we describe its assemblage of four frogs, including two new genera and species, based on numerous, diverse and well-preserved ilia and vertebrae. An abundant frog, *Eobarbourula delfinoi* gen. and sp. nov., with a particular vertebral articulation similar to a zygosphenes-zygantrum complex, represents the oldest record of the Bombinatoridae and might have been capable of displaying the Unken reflex. The large non-fossorial pelobatid *Eopelobates*, known from complete skeletons from the Eocene and Oligocene of Europe, is also identified at Vastan based on a single nearly complete ilium. An abundant “ranid” and a possible rhacophorid *Indorana prasadi* gen. and sp. nov. represent the earliest records of both families. The Vastan pelobatids and ranids confirm an early worldwide distribution of these families, and the bombinatorids and rhacophorids show possible origins of those clades on the Indian subcontinent.

Key words: Amphibia, Bombinatoridae, Ranidae, Pelobatidae, Rhacophoridae, Eocene, Vastan, India.

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Introduction

The early Eocene Cambay Shale Formation at Vastan Lignite Mine, located north-east of Surat in Gujarat, western India, has recently received attention for its rich vertebrate assemblage (Rana et al. 2004, 2005; Bajpai et al. 2005; Rose et al. 2006). The terrestrial vertebrates come from continental thin lenses (< 0.5 m thick) of dark, clayey silt and shale with abundant plant matter, situated about 1 m above the lower of the two major lignites (Lignite 2) occurring in the mine (Sahni et al. 2006; Rose et al. 2009a).

The vertebrate-bearing part of the section is estimated to be middle Ypresian in age, corresponding to the shallow benthic zone SBZ 10, based on the large foraminifer *Nummulites burdigalensis* that has been identified about 10 m above the

continental lenses (Rana et al. 2005; Sahni et al. 2006). The co-occurrence of the two subspecies *N. burdigalensis burdigalensis* and *N. burdigalensis kuepperi* at Vastan even suggests the lower part of zone SBZ 10 (Punekar and Saraswati 2010).

The mammal fauna from Vastan has important palaeobiogeographic implications and includes the earliest modern mammals from the Indian subcontinent, with a high diversity of bats (Smith et al. 2007), the first Asian ailuravine rodents (Rana et al. 2008), the oldest lagomorphs (Rose et al. 2008), primitive adapoid and omomyid primates (Rose et al. 2009a), the first Indian tillodont (Rose et al. 2009b), and basal artiodactyls (Kumar et al. 2010). Besides the mammals, other vertebrates include fishes (Rana et al. 2004), snakes (Rage et al. 2008), lizards (Prasad and Bajpai 2008), and birds (Mayr et al.

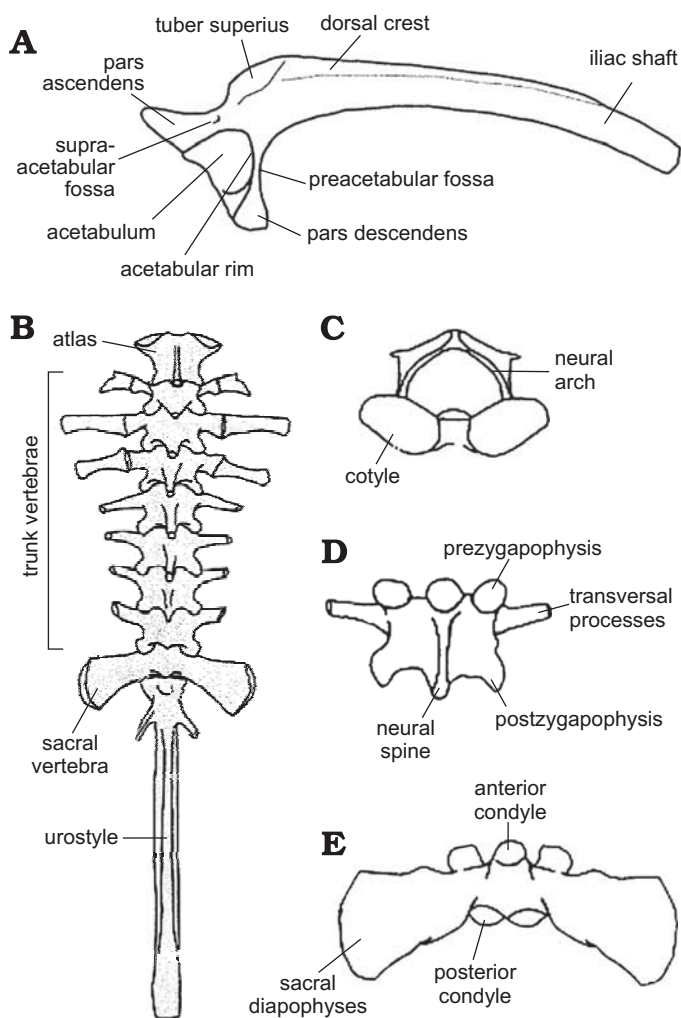


Fig. 1. Nomenclature of anuran ilia and vertebrae used in this work, exemplified by *Discoglossus galganoi* (modified from Sanchiz 1998: figs. 10, 13). **A.** Ilium in lateral view. **B.** General shape of the vertebral column. **C–E.** Vertebral structure. **C.** Atlas in anterior view. **D.** Trunk vertebra (presacral) in dorsal view. **E.** Sacral vertebra in ventral view.

2007, 2010). Amphibians have also been reported (Bajpai and Kapur 2008; Folie et al. 2008) and are here described in detail based on hundreds of very well preserved three-dimensional isolated frog remains including diagnostic ilia and vertebrae; there are no caudates or caecilians.

Institutional abbreviations.—FMNH, Field Museum of Natural History, Chicago, USA; GU/RSR/VAS, H.N.B. Garhwal University, Srinagar, Uttarakhand, India; HLMD, Hessisches Landesmuseum Darmstadt, Germany; IITR/SB/VLM-LV, Vertebrate Paleontology Laboratory, Department of Earth Sciences, Indian Institute of Technology, Roorkee, India; IRSNB, Institut royal des Sciences naturelles de Belgique, Brussels, Belgium; MNHN, Muséum National d’Histoire Naturelle, Paris, France; SMF, Forschungsinstitut Senckenberg, Frankfurt am Main, Germany; TMP, Royal Tyrrell Museum of Palaeontology, Drumheller, Alberta, Canada; UMMZ, University of Michigan Museum of Zoology, Ann Arbor, Michigan, USA.

Other abbreviations.—MP, reference level of the mammalian biochronological scale for the European Paleogene; SBZ, Shallow Benthic Zone.

Systematic palaeontology

Terminology.—The nomenclature of anuran ilia and vertebrae (Fig. 1) is that of Sanchiz (1998). Systematic classification follows Cannatella (2007), who considered Bombinatoridae as a family included in the Discoglossoidea. Pelobatidae is included in the Pelobatoidea, and *Scaphiopus* and *Spea* belong to a separate family Scaphiopodidae. The family “Ranidae” is in quotes to indicate non-monophyly, until a consensus on its definition is reached. The Rhacophoridae is a family in the Ranoidea.

Class Amphibia Linnaeus, 1758

Order Anura Fischer von Waldheim, 1813

Superfamily Discoglossoidea Sokol, 1977

Family Bombinatoridae Gray, 1825

Genus *Eobarbourula* nov.

Etymology: In reference to the extant genus *Barbourula*, associated with the prefix eo-, from Greek *eos*, dawn; referring to the age of the taxon.

Type species: *Eobarbourula delfinoi* sp. nov.; see below.

Diagnosis.—As for the monotypic type species.

Eobarbourula delfinoi sp. nov.

Figs. 2–5.

Etymology: Named for Italian paleontologist Massimo Delfino, who alerted us to the presence of a particular articulation similar to a zygo-sphene-zygantrum complex on the vertebrae of this taxon.

Holotype: GU/RSR/VAS 5001 (Fig. 2A), nearly complete left ilium.

Type locality: Vastan Lignite Mine, Surat District, Gujarat, India.

Type horizon: Cambay Shale Formation, middle Ypresian, lower Eocene.

Referred material.—58 ilia: GU/RSR/VAS 5002 (Fig. 2B), GU/RSR/VAS 5003 (Fig. 2C), GU/RSR/VAS 5004–5059; 129 vertebrae: GU/RSR/VAS 5060–5065 (Fig. 4A–F), GU/RSR/VAS 5066–5188; and 12 urostyles: GU/RSR/VAS 5189 (Fig. 4G), GU/RSR/VAS 5190–5200.

Diagnosis.—Differs from the other Bombinatoridae by having less laterally expanded sacral diapophyses on the vertebrae (antero-posterior/lateral length ratio, 1.1) and by having the tuber superius more developed dorsally, more asymmetric in lateral view and placed more anteriorly compared with the acetabulum. Differs further (in adults) from *Bombina* by being about twice as large, and by having a tuber superius situated anteriorly to the acetabulum; from *Barbourula* by being 1.5 times smaller and in having a more developed tuber superius.

Description.—In lateral view, the iliac shaft is almost straight and lacks a dorsal crest (Fig. 2A). The tuber superius is a long, prominent, asymmetric and slightly anterodorsally oriented tubercle, anteriorly situated with respect to the acetabulum (Fig. 3D). The junction between the acetabular area and the

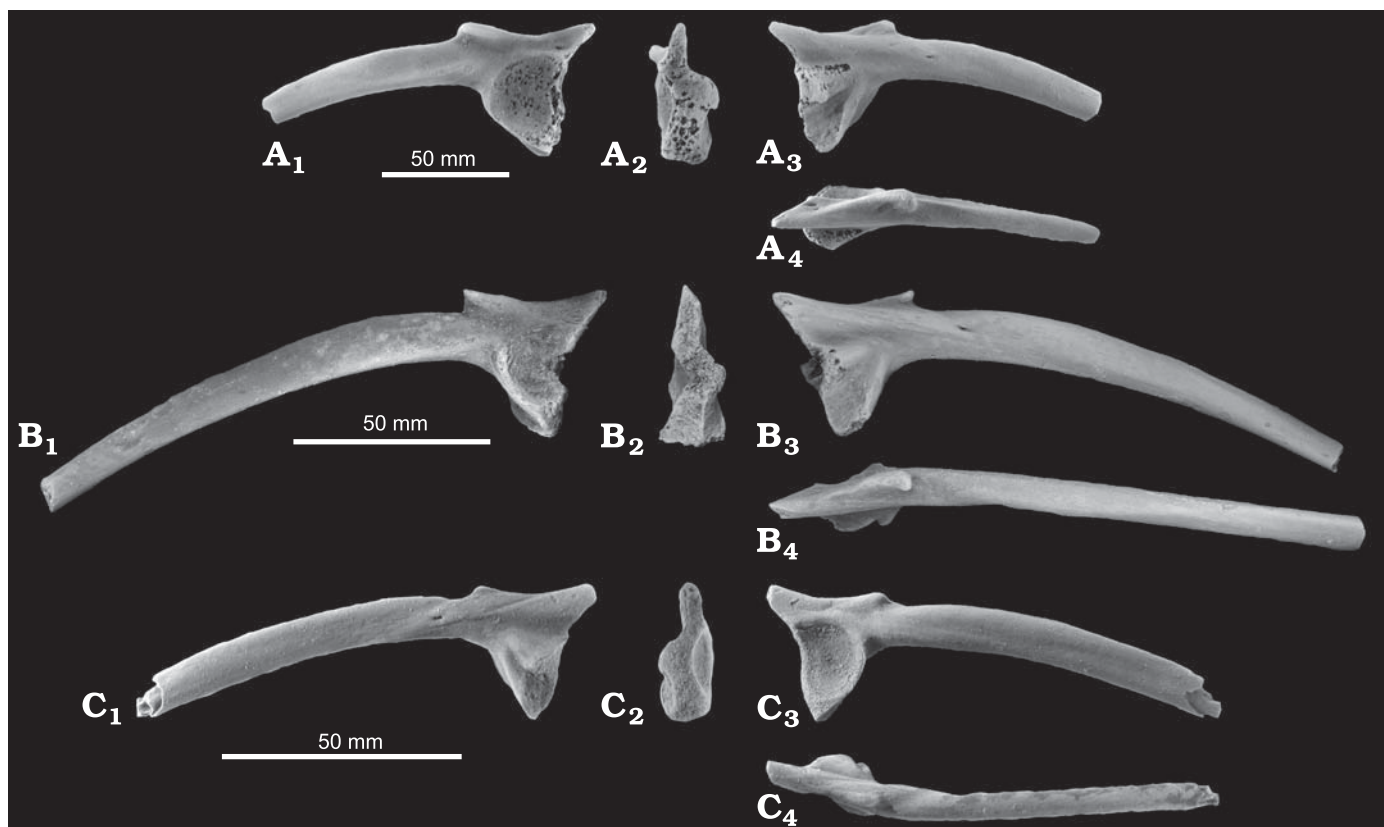


Fig. 2. Nearly complete ilium of frog *Eobarbourula delfinoi* gen. et sp. nov., early Eocene, Vastan Lignite Mine, Gujarat, India. A. GU/RSR/VAS 5001, holotype, left ilium in lateral (A₁), posterior (A₂), medial (A₃), and dorsal (A₄) views. B. GU/RSR/VAS 5002, left ilium in lateral (B₁), posterior (B₂), medial (B₃), and dorsal (B₄) views. C. GU/RSR/VAS 5003, right ilium in medial (C₁), posterior (C₂), lateral (C₃), and dorsal (C₄) views.

shaft is only slightly constricted. There is no subacetabular or supraacetabular fossa. The pars ascendens is short and posteriorly oriented. It forms an open angle (about 160°) with the tuber superius. The pars descendens is slightly developed and is obscured by the large acetabulum, which extends onto the pars descendens ventrally. The acetabulum is deep, slightly bell-shaped and bordered by a sharp rim. A shallow but well-marked protuberance is present near the anterior border of the acetabulum. In medial view, the acetabular area is bordered by shallow ridges. Between them, a triangular and medially prominent interiliac tubercle is developed. In dorsal view, the medial part of the acetabular area is prominent and the tuber superius projects laterally. This general shape is also visible on specimens that are nearly half the size of the first specimens (Fig. 2C). However, in lateral view, they differ from the first specimens by both less well-marked tuber superius and weaker protuberance near the anterior border of the acetabulum. The junction between the acetabular area and the shaft is slightly more constricted. In medial view, the interiliac tubercle is less developed. In dorsal view, the tuber superius is less laterally projected (Fig. 2A₄, B₄, C₄). Other specimens with the same morphology and presenting intermediate sizes between these two extreme sizes (Fig. 2B) are attributed to the same single taxon.

The vertebrae (Fig. 4) are imbricate (the elongate posterior part of the neural arch overlaps the anterior border of the

subjacent vertebra like tiles on a roof), opisthocoelous, and present a particular articulation similar to the zygosphenozygantrum complex of snake vertebrae (Fig. 5). The zygosphenozygantrum articulation was defined by Romer (1956) as an accessory articulation composed of a dorsally tapered wedge of bone bearing articular surfaces on either side (zygosphenone) that projects forward from the neural arch into a corresponding wedge-shaped cavity (zygantrum). However, on the Vastan specimens, the structure resembling the zygosphenone looks like a pair of anterior processes separated by a notch and well differentiated from the neural arch (Fig. 5A) and the zygantrum is the corresponding cavity (Fig. 5B). Such a structure can also be found in the anuran *Bombina*, the salamander *Salamandrina* and some lacertilians such as lacertid, teiid, and cordylid lizards (Sanchiz 1988). A similar structure, the hyposphene-hyantrum complex, is also present in some dinosaurs and on cervical vertebrae of primitive birds (Rauhut 2003). The atlas of the Vastan taxon is fused with V2 and presents two large reniform cotyles narrowly separated and forming two distinct articular surfaces. This morphology is characteristic of type II of Lynch (1971). Posteriorly, a zygantrum-like cavity is slightly developed on V2, and the neural arch is postero-dorsally elongated and ends with three expansions or spikes, the medial one being the spinous process, and the two lateral expansions being the postzygapophyses (Fig. 4A₃–A₅). From the atlas to the fourth vertebra (Fig. 4B, C), the neural

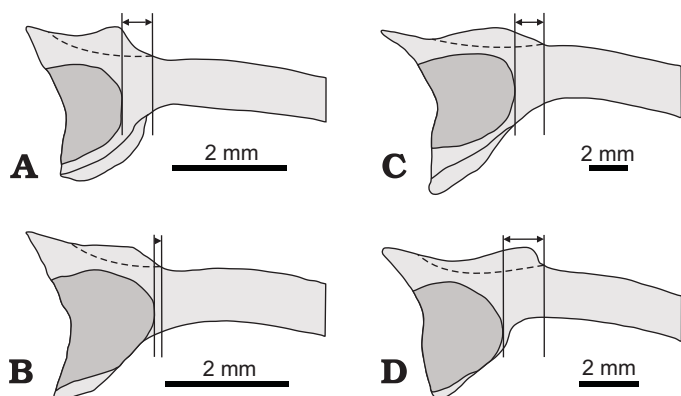


Fig. 3. Comparative drawings of bombinatorid ilia in lateral view. **A.** *Bombina bombina* (Linnaeus, 1761), specimen UMMZ 152271, Recent, Germany (modified from Gardner 2010). **B.** *Bombina orientalis* (Boulenger, 1890), specimen TMP 2010.30.21, Recent, captive raised specimen (modified from Gardner et al. 2010). **C.** *Barbourula busuagensis* Taylor and Noble, 1924, specimen FMNH 50999, Recent, Philippines (modified from Clarke 1987). **D.** *Eobarbourula delfinoi* gen. et sp. nov., specimen GU/RS/VAS 5001, early Eocene, Vastan Lignite Mine, Gujarat, India. Arrows represent the distance between the anterior border of the acetabulum and the inflexion point where the tuber superius starts anteriorly.

canal decreases in diameter, the transverse processes become more strongly developed, and the neural arch becomes flatter but is posteriorly well developed, presenting an acute spinous process. The neural arches of the other vertebrae up to the sacral are shorter posteriorly and become more rectangular in

dorsal view (Fig. 4D, E). The sacral vertebra is biconvex and the sacral diapophyses are dorsoventrally flattened and moderately expanded laterally (Fig. 4F₄). The urostyle presents an anterior cotyle, a low dorsal crest, and two laterally and slightly anteroposteriorly elongated transversal processes (Fig. 4G; see Table 1).

Discussion.—All the bones described above are grouped together based on their morphology, size and relative abundance. The small form of ilium (Fig. 2C) is here interpreted as a juvenile stage of the larger form (Fig. 2A). Iliia of intermediate size, such as GU/RSR/VAS 5061 (Fig. 2B), are also present, supporting the interpretation of these as ontogenetic stages of the same species. The morphological characters of all these ilia are the same, with the exception of the tuber superius, which shows ontogenetic variability by being better developed and slightly inclined laterally in adult forms than in the juvenile forms, as can be seen in the posterior view of GU/RSR/VAS 5060 (Fig. 2A₄, B₄, C₄).

The presence of an open angle between the tuber superius and the pars ascendens (Rage and Hossini 2000) and the imbricate vertebrae indicate that the Vastan taxon belongs to “Archaeobatrachia” and/or “Mesobatrachia” because they are only known in these groups (Prasad and Rage 2004). However, it does not belong to the most common “*Discoglossus* group”, including the genera *Discoglossus*, *Eodiscoglossus*, *Paradiscoglossus*, *Latonia*, and *Paralatonia* (Duffaud and Rage 1999; Rage and Hossini 2000) because the Vastan taxon lacks the dorsal crest on the iliac shaft (Rage and Hossini

Table 1. Character matrix and description of characters studied on ilia and vertebrae of the four anuran taxa from Vastan Lignite Mine, Gujarat, India.

Characters	<i>Eobarbourula delfinoi</i>	<i>Eopelobates</i> sp.	“Ranidae” indet.	<i>Indorara prasadi</i>
Iliia				
dorsal expansion of the tuber superius: 0 = not developed, absent; 1 = developed but low; 2 = well-developed	2	0	2	1
asymmetry of the tuber superius: 0 = not asymmetric; 1 = asymmetric; 2 = well-asymmetric	2	–	1	0
position of the tuber superius relative to the acetabulum: 0 = tuber superius anterior to the acetabulum; 1 = at the same level as the acetabulum; 2 = posterior to the acetabulum	2	–	2	2
dorsal crest on the shaft: 0 = absent; 1 = well-developed	0	0	1	0
constriction of the area between the shaft and the acetabular area: 0 = not constricted; 1 = constricted	1	0	1	0
supraacetabular fossa: 0 = absent; 1 = present	0	0	1	0
subacetabular fossa: 0 = absent; 1 = present	0	0	0	0
angle between the pars ascendens and the tuber superius: 0 = open (160 to 180°); 1 = closed (around 90°)	0	0	1	0
pars descendens: 0 = absent; 1 = present	1	1	1	1
acetabulum: 0 = restricted; 1 = expended, covering a huge part of the acetabular area and the pars descendens	1	0	0	0
interiliac tubercule: 0 = absent; 1 = present	1	1	0	0
Vertebrae				
imbricate: 0 = no; 1 = yes	1	?	0	?
shape of the presacral vertebrae: 0 = procoelous; 1 = amphicoelous; 2 = opisthocelous	2	?	0	?
sacro-urostyler articulation: 0 = monocondylar 1 = bicondylar	0	?	1	?
ratio of the expansion of the sacral diapophyses	1.1	?	?	?
“zygosphenes-zygantrum” articulation: 0 = absent; 1 = present	1	?	0	?

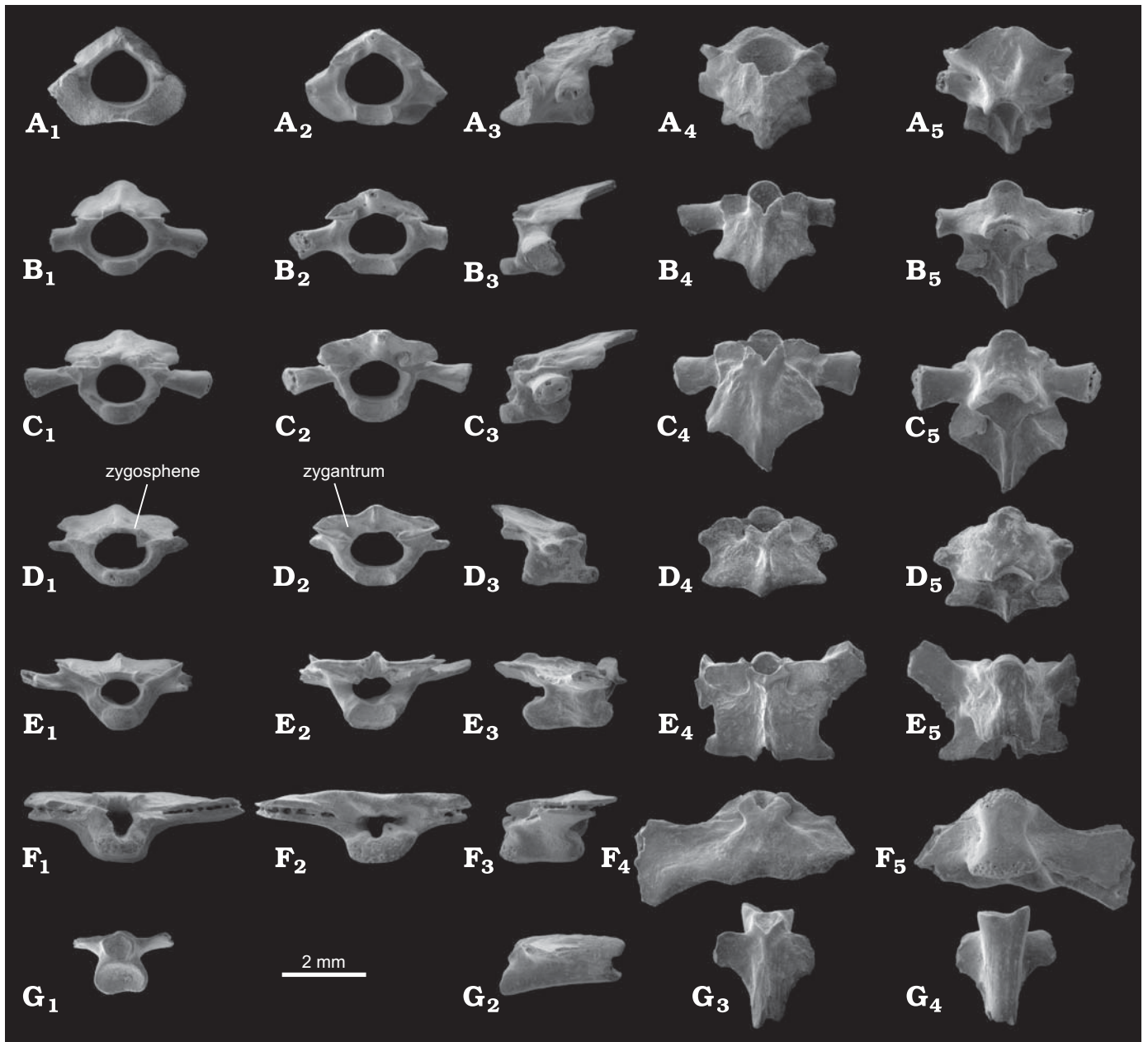


Fig. 4. Vertebrae of frog *Eobarbourula delfinoi* gen. et sp. nov., early Eocene, Vastan Lignite Mine, Gujarat, India. **A.** GU/RSR/VAS 5060, atlas in anterior (A₁), posterior (A₂), left lateral (A₃), dorsal (A₄), and ventral (A₅) views. **B.** GU/RSR/VAS 5061, anterior trunk vertebra in anterior (B₁), posterior (B₂), left lateral (B₃), dorsal (B₄), and ventral (B₅) views. **C.** GU/RSR/VAS 5062, trunk vertebra in anterior (C₁), posterior (C₂), left lateral (C₃), dorsal (C₄), and ventral (C₅) views. **D.** GU/RSR/VAS 5063, trunk vertebra in anterior (D₁), posterior (D₂), right lateral (D₃), dorsal (D₄), and ventral (D₅) views. **E.** GU/RSR/VAS 5064, presacral vertebra in anterior (E₁), posterior (E₂), right lateral (E₃), dorsal (E₄), and ventral (E₅) views. **F.** GU/RSR/VAS 5065, sacral vertebra in anterior (F₁), posterior (F₂), left lateral (F₃), dorsal (F₄), and ventral (F₅) views. **G.** GU/RSR/VAS 5189, fragmentary urostyle in anterior (G₁), left lateral (G₂), dorsal (G₃), and ventral (G₄) views.

2000) and the bicondylar sacro-urostyler articulation (Clarke 1987). It is similar to gobiatids, including the ilium attributed to ?Gobiatinae from the Late Cretaceous intertrappean beds of Naskal, India (Prasad and Rage 2004: fig. 1D), in having an asymmetric tuber superius (Roček and Nessov 1993: fig. 25). However, gobiatids present an acetabulum not extending over the pars descendens on the ilium and amphicoelous vertebrae (Roček and Nessov 1993; Prasad and Rage 2004), whereas the Vastan species presents a ventrally extensive acetabulum that

observes the pars descendens on the ilium and has opistho-coelous vertebrae.

Within the Discoglossoidea, the Vastan species closely resembles the Bombinatoridae. This family includes only the genera *Bombina* and *Barbourula* (Cannatella 2007). The presence of an articulation similar to a zygosphene-zygantrum complex and an interiliac tubercle are resemblances to *Bombina* (Sanchiz 1988; Gardner et al. 2010). However, in *Bombina orientalis* and *Bombina bombina*, the tuber superius

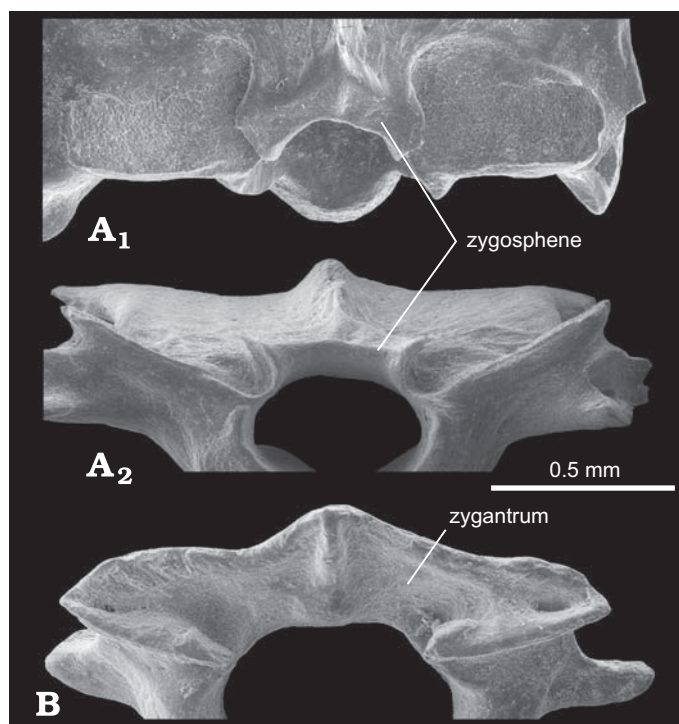


Fig. 5. Close up views of vertebrae of frog *Eobarbourula delfinoi* sp. nov., early Eocene, Vastan Lignite Mine, Gujarat, India. **A.** GU/RSR/VAS 5064, presacral vertebra in dorsal (A_1) and anterior (A_2) views. **B.** GU/RSR/VAS 5063, trunk vertebra in posterior view.

is situated above the acetabulum (the anterior border of the acetabulum extends further to the anterior border of the tuber superius; Nokariya 1983a; Gardner et al. 2010; Fig. 3A, B), than in *E. delfinoi* in which case the anterior border of the acetabulum reaches only a third to a half of the length of the tuber superius (Fig. 3D). Moreover, the adult size of the ilium of *E. delfinoi*, measured at the level of the posterior suture with the ischium and pubis, is about twice that of *B. orientalis* (Nokariya 1983a) or *B. bombina* (Gardner et al. 2010). Little osteological information is available about the extant genus *Barbourula*. The Vastan specimens are close to *Barbourula busuangensis* in the general shape of the ilia and vertebrae (Clarke 1987; Prikryl et al. 2009). Indeed, both taxa have an ilium without a dorsal crest, a long prominent tuber superius, imbricate and opisthocoelous vertebrae, neural spines decreasing posteriorly in height, a monocondylar sacro-urostylar articulation, and a pair of well-developed transverse processes on the urostyle. However, the ilia of adult *E. delfinoi* are about 1.5 times smaller than those of *B. busuangensis* (Clarke 1987). Finally, the Vastan bombinatorid differs from both *Bombina* and *Barbourula* in having the tuber superius situated above the acetabulum (the anterior border of the acetabulum extends further to the anterior border of the tuber superius; Nokariya 1983a; Gardner et al. 2010; Fig. 3A–C), than in *E. delfinoi* in which case the anterior border of the acetabulum reaches only a third to a half of the length of the tuber superius (Fig. 3D). Moreover, in *E. delfinoi*, the tuber superius is more developed dorsally and more asymmetric

in lateral view on the ilium and have sacral diapophyses that were likely less dilated laterally, like butterfly wings, than in *Bombina* and *Barbourula* (Clarke 1987; Gardner et al. 2010; Prikryl et al. 2009; Nokariya 1983a). In *Barbourula busuangensis* (Clarke 1987), the ratio of antero-posterior to lateral length in the sacral diapophyses is 2.1; in *Bombina orientalis* (Nokariya 1983a), the ratio is 2.2, and in *E. delfinoi*, 1.1. Based on these comparisons, the Vastan taxon closely resembles the extant genus *Barbourula*.

The morphologies of the ilia and vertebrae correspond also exactly to those described from Vastan by Bajpai and Kapur (2008) as *Discoglossidae* indet. Indeed, the ilia IITR/SB/VLM-LV/203–204 show the tuber superius as a swelling of the dorsal margin of the iliac shaft, the ventral margin of the acetabulum overhanging the pars descendens, and medially, the ilium bears an interiliac protuberance. The vertebra IITR/SB/VLM-LV/208 is similar to the anterior trunk vertebra VAS 5061 in being opisthocoelous, bearing a dorso-ventrally flattened centrum, and presenting three posterior spikes on the neural arch. The same may be concluded for ilium IITR/SB/VLM-LV/209 described from Vastan by Bajpai and Kapur (2008) and attributed to *Leptodactylidae* indet. based on general resemblances with the genera *Telmatobius*, *Lymnodynastes*, *Kyarranus*, and *Phyloria*.

It is noteworthy that similarities were also observed with the genus *Hatzegobatrachus* from the latest Cretaceous of the Hațeg Basin, Romania, and this has been already compared with bombinatorids (Venczel and Csiki 2003). They both share “a well-developed and undivided dorsal prominence” and a small pars descendens, but *Hatzegobatrachus* shows a thicker dorso-lateral margin and it also lacks “any waisting between the acetabular region and the iliac shaft”. Therefore, the Vastan taxon cannot be attributed to the Romanian genus *Hatzegobatrachus*.

Stratigraphic and geographic range.—Type locality and horizon locality only.

Superfamily Pelobatoidea Bolkay, 1919

Family Pelobatidae Bonaparte, 1850

Genus *Eopelobates* Parker, 1929

Type species: *Eopelobates anthracinus* Parker, 1929, latest Oligocene, MP 30, Rott, Germany.

Eopelobates sp.

Fig. 6.

Material.—GU/RSR/VAS 5201 (Fig. 6), a nearly complete right ilium.

Description.—Only the proximal (= anterior) part of the shaft and the ventral extremity of the pars descendens are missing. In medial and dorsal views, a partial dorsal crest extends onto the anterior half of the bone. There is no tuber superius, but a thin ridge bordered by two shallow spiral grooves extends posterolaterally-anteromedially. The junction between the acetabular area and the shaft is not constricted. There is no fossa around the acetabulum. The angle

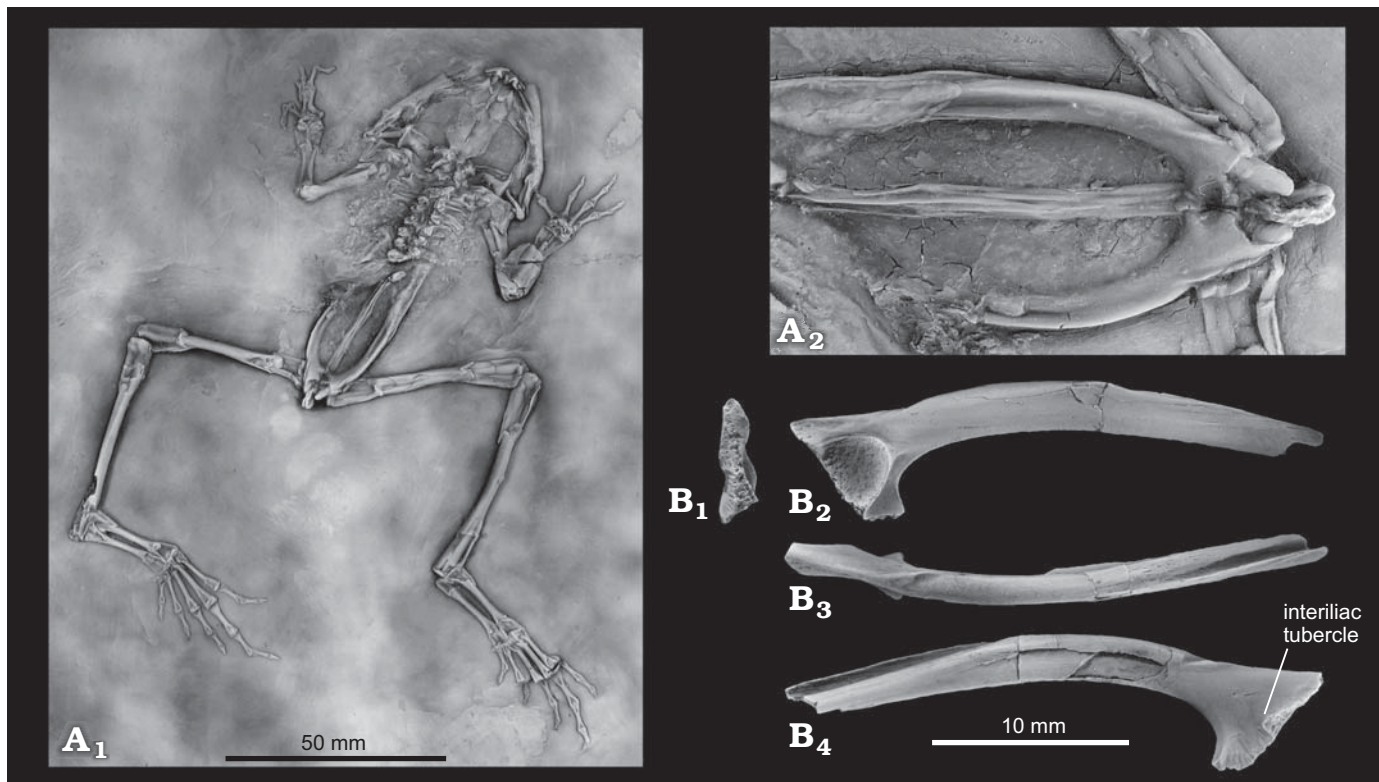


Fig. 6. Pelvic girdle of frog *Eopelobates*. **A.** *Eopelobates wagneri* (Weitzel, 1938), middle Eocene, Messel, Germany. Specimen IRSNB A 2 (field number BE 2-126), complete skeleton in dorsal view (A₁); pelvic girdle in mediadorsal view showing anatomical characters of ilia (A₂). **B.** *Eopelobates* sp., early Eocene, Vastan Lignite Mine, Gujarat, India. GU/RSR/VAS 5201, nearly complete right ilium in posterior (B₁), lateral (B₂), dorsal (B₃), and medial (B₄) views.

between the pars ascendens and the shaft is close to 180°. The pars ascendens is short. The pars descendens is broken but was likely flared. The acetabulum is oval and its border is very well marked. The angle between the shaft and the pars descendens is close to 90°. In medial view, an interiliac tubercle is well developed. Below this latter, a striated scar indicates that the contact between the two ilia was extensive (see Table 1).

Discussion.—The morphology of this ilium is reminiscent of Pelobatidae. This family includes only the living genus *Pelobates* and the fossil genera *Elkobatrachus* (middle Eocene, Elko Formation, Nevada, USA; Henrici and Haynes 2006) and *Eopelobates* (see distribution below). Pelobatid ilia are characterized by the absence of the dorsal crest, the tuber superius and the subacetabular and supraacetabular fossae (Rage and Hossini 2000) and by the presence of an oblique spiral groove on the middle surface (Evans and Milner 1993). All these characters are visible in the Vastan specimen. The Miocene specimens of *Pelobates* and *Eopelobates* have a small interiliac tubercle whereas the Recent specimens of *Pelobates* do not (Rage and Hossini 2000). Moreover, following Rage and Hossini (2000), the presence of striated scars on the postero-mesial border of the ilia is indicative of the genus *Pelobates*. However, striated scars are also present in *Eopelobates* (personal observation on specimens of *E. wagneri*, SMF Me-11262a and 2795). In addition, there

is a partial dorsal crest extending on the anterior half of the bone, which is only known in the genus *Eopelobates*. For these reasons, the ilium GU/RSR/VAS 5201 from Vastan is here attributed to the genus *Eopelobates*. The type species of the latter genus, *E. anthracinus* from the latest Oligocene of Rott (MP30), Germany, differs from all the other *Eopelobates* species by being about half the size of the other species (Roček and Rage 2000). Following Rage and Roček (2003), three other species are recognized in the genus. Two species are known from the middle Eocene of Germany, *E. wagneri* from Messel (MP11) and *E. hinschei* from Geiseltal (MP13), the latter possibly a synonym of *E. wagneri* (Roček and Rage 2000). The third species is *E. bayeri* from the late Oligocene of Bechlejovice, Czech Republic, which is smaller than *E. wagneri* (Roček and Rage 2000) and bigger than *E. anthracinus* (Estes 1970).

The identification of the different species of *Eopelobates* is based on cranial characters, especially the frontoparietal; whereas ilia of *Eopelobates* are not diagnostic enough for determination below the genus level (Evans and Milner 1993; Rage and Roček 2003). Nevertheless, the single ilium from Vastan was compared with IRSNB A 2 (field number BE 2-126), an exceptionally well preserved specimen of *Eopelobates wagneri* from the middle Eocene of Messel, which preserves the two ilia in dorsomedial view (Fig. 6A). The ilia of both the Indian and German specimens are very close in size and morphology (Fig. 6A₂, B). They share a similar aceta-

bular area, the presence of a thin ridge instead of the tuber superius, a dorsal crest extending on the anterior half of the bone, and a well-developed interiliac tubercle. Comparisons with other specimens attributed to *Eopelobates wagneri* (HLMD-Be-171 and SMF Me-11262a, SMF Me-2795, SMF Me-2562, SMF Me-189) confirm these observations. The vertebrae, cranial bones and other skeletal elements of this Indian taxon are unknown. It is therefore not possible to give a more precise identification of the Vastan pelobatid frog until a revision of *Eopelobates* is undertaken.

Superfamily Ranoidea Rafinesque, 1814

Family “Ranidae” Rafinesque, 1814

“Ranidae” indet.

Figs. 7, 8.

Material.—Eight nearly complete ilia: GU/RSR/VAS 5202 (Fig. 7), GU/RSR/VAS 5203–5209); seven vertebrae: GU/RSR/VAS 5210–5212 (Fig. 8A–C), GU/RSR/VAS 5213–5216; and two urostyles: GU/RSR/VAS 5218 (Fig. 8D), GU/RSR/VAS 5217.

Description.—In lateral view, the iliac shaft is cylindrical and is separated from a high dorsal crest by a well-marked groove (Fig. 7A). The tuber superius, a thickening of the proximal (= anterior) part of the dorsal crest, is ovoid and projects slightly laterally (Fig. 7D). The junction between the acetabular area and the shaft is constricted. A shallow, small, rounded supraacetabular fossa is present at the proximal (= anterior) base of the tuber superius. The angles between the tuber superius and the pars ascendens and between the shaft and the pars descendens are both close to 90°. The pars ascendens is short. The pars descendens is broken on GU/RSR/VAS 5202, but was likely short and flared. The acetabulum is rounded and its border is accentuated by a sharp rim. There is no subacetabular fossa. In medial view, there is no distinction between the tuber superius and the dorsal crest (Fig. 7C). Two ridges extend along the pars ascendens and pars descendens. Proximally (= anteriorly), the dorsal crest and the iliac shaft are separated by a groove. There is no interiliac tubercle. In dorsal view, the dorsal crest is posterolaterally to anteromedially oriented on the shaft (Fig. 7D).

The posterior part of the presacral region of the vertebral column can be reconstructed. The vertebrae are not imbricate. The presacral vertebrae, except the last one, are procoelous and rather short antero-posteriorly (Fig. 8A); the neural arch bears a strong medial ridge and presents a notch on its anterior border that is anteriorly widened. The last presacral vertebra is amphicoelous, presenting an anterior and a posterior cotyle (Fig. 8B). The sacral vertebra is biconvex with two posterior condyles (Fig. 8C). The sacral diapophyses are well separated from the prezygapophyses, are posteriorly directed and are cylindrical (not laterally or antero-posteriorly expanded). This vertebra is also characterized by a well-developed medial ridge on the neural arch, which is laterally bounded by two well-marked and posteriorly concave ridges. The urostyle is



Fig. 7. Nearly complete right ilium of frog Ranidae indet., early Eocene, Vastan Lignite Mine, Gujarat, India. GU/RSR/VAS 5202, in lateral (A), posterior (B), medial (C), and dorsal (D) views.

free and presents two anterior cotyles and a well-developed dorsal crest (Fig. 8D; see Table 1).

Discussion.—Some ilia of this taxon present a tuber superius that is more elongated and anterodorsally oriented. The supraacetabular fossa is also deeper on some specimens. These differences are interpreted as intraspecific variations.

The presence of a dorsal crest, the acute angle between the tuber superius and the pars ascendens, the tuber superius that is a thickening of the dorsal crest, and the absence of an interiliac tubercle (Prasad and Rage 2004) indicate that these specimens belong to a ranoid frog. These characters are also present in the ilia of Ranoidea indet. (IITR/SB/VLM-LV/201–202) described from Vastan by Bajpai and Kapur (2008), and both probably represent the same taxon.

The bicondylar sacro-urostyler articulation is consistent with a ranoid affinity (Rage and Hossini 2000). This group is considered here to include families “Ranidae”, Rhacophoridae, “Hyperoliidae” and Microhylidae and excludes Dendrobatidae (sensu Cannatella 2007).

The ranoid from Vastan differs from the ranoid described by Prasad and Rage (2004) from the Upper Cretaceous intertrappean beds of Naskal, India, by having a more constricted junction between the acetabular area and the shaft, and by the presence of a supraacetabular fossa. It also differs from the Microhylidae and the Rhacophoridae (except *Mantidactylus*, *Buergeria*, *Chiro-mantis*, *Polypedates*; Liem 1970) and is close to the “Ranidae” and “Hyperoliidae” in the presence of a diplasiocoelous assemblage of the vertebrae (all vertebrae are procoelous, except the last presacral vertebra which is amphicoelous and the sacral vertebra which is biconvex; Liem 1970; Rage and Hossini 2000; Rödel et al. 2009). Moreover, it differs from the rhacophorids *Buergeria*, *Chiro-mantis*, and *Polypedates* by a more developed tuber superius and by a more acute angle between the tuber superius and the pars ascendens. It differs also from the Microhylidae and “Hyperoliidae” by the presence of a well-developed dorsal crest on the iliac shaft (Nokariya 1983a; Scott 2005). Finally, following Rage and Hossini (2000), non-imbricate vertebrae, cylindrical sacral diapophyses and a free urostyle with a

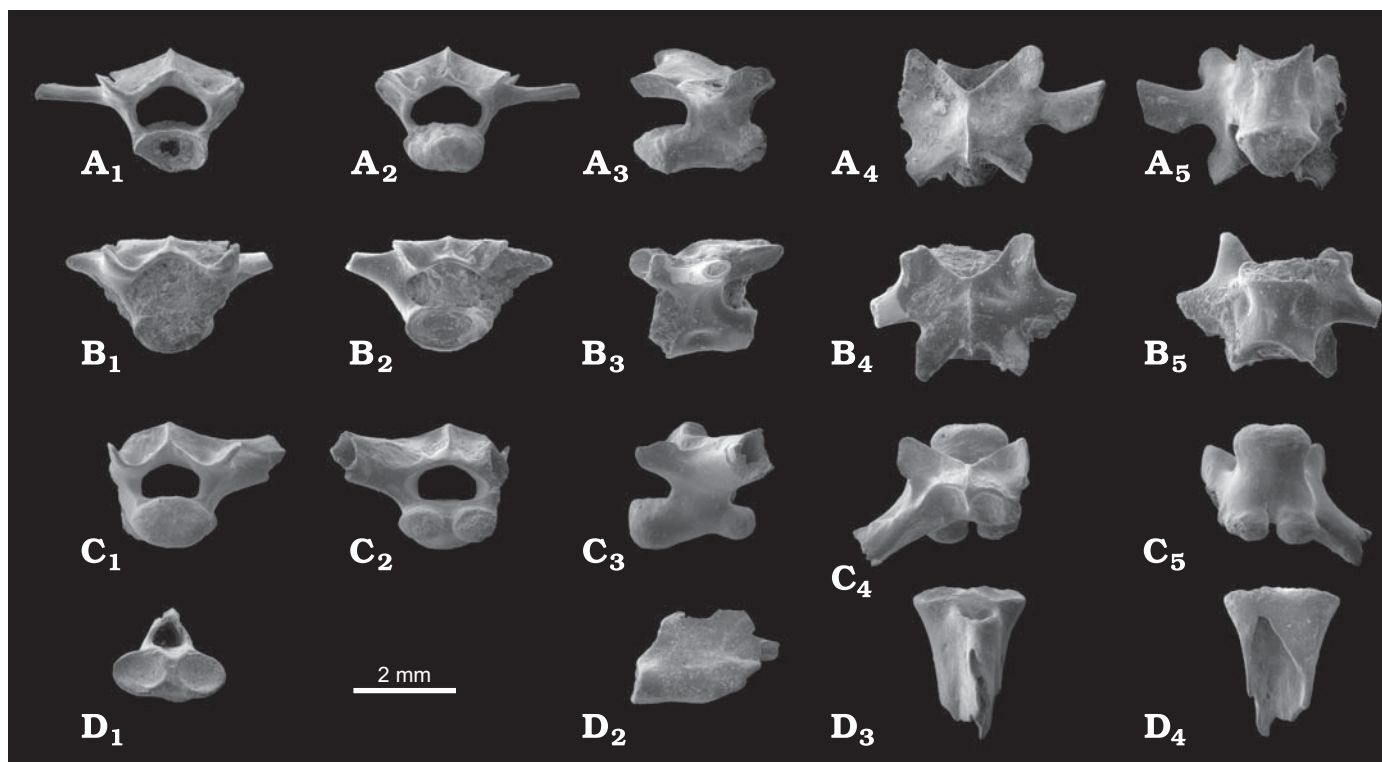


Fig. 8. Vertebrae of frog Ranidae indet., early Eocene, Vastan Lignite Mine, Gujarat, India. **A.** GU/RSR/VAS 5210, presacral vertebra in anterior (A₁), posterior (A₂), left lateral (A₃), dorsal (A₄), and ventral (A₅) views. **B.** GU/RSR/VAS 5211, last presacral vertebra in anterior (B₁), posterior (B₂), left lateral (B₃), dorsal (B₄), and ventral (B₅) views. **C.** GU/RSR/VAS 5212, sacral vertebra in anterior (C₁), posterior (C₂), left lateral (C₃), dorsal (C₄), and ventral (C₅) views. **D.** GU/RSR/VAS 5218, fragmentary urostyle in anterior (D₁), left lateral (D₂), dorsal (D₃), and ventral (D₄) views.

well-developed dorsal crest are a typical character assemblage for the family “Ranidae”. The ilium and vertebrae described above from Vastan can thus be attributed to “Ranidae”. The posterior border of the dorsal crest sloping precipitously into the dorsal acetabular area and the acute angle between the tuber superius and the pars ascendens are similar in general morphology to the green frog *Rana clamitans* (Holman 2003).

It might seem that the quantity and quality of the specimens assembled here should allow us to create a new taxon. However, below the familial level, there are few diagnostic osteological characters of the different “ranid” genera, which are mainly distinguished on external morphological characters. It is thus premature to create a new taxon or to include this material in an already existing taxon until there is a detailed revision of the family “Ranidae” that identifies generically distinctive osteological traits.

Family ?Rhacophoridae Hoffman 1932

Genus *Indorana* nov.

Etymology: In reference to India and *rana*, a suffix for the ranoid taxa.

Type species: *Indorana prasadi* sp. nov.; see below.

Diagnosis.—As for the monotypic type species.

Indorana prasadi sp. nov.

Fig. 9.

Etymology: For Indian paleontologist Guntupalli V.R. Prasad, for his contributions to the knowledge of Indian frogs.

Holotype: GU/RSR/VAS 5220 (Fig. 9A), a nearly complete left ilium associated with the two ischia and pubis.

Type locality: Vastan Lignite Mine, Surat District, Gujarat, India.

Type horizon: Cambay Shale Formation, middle Ypresian, lower Eocene.

Referred material.—GU/RSR/VAS 5219 (Fig. 9B), an incomplete left ilium associated with the pubis, left ischium and half of the right ischium.

Diagnosis.—Ilium differs from *Rhacophorus* and *Polypedates* by a very weak dorsal crest on the iliac shaft, and from *Buergeria buergeri* in having an ossified pubis fused with the ilium and ischium, a wider acetabulum and a thicker iliac shaft.

Description.—In lateral view, the iliac shaft is almost straight and bears a weakly developed elongated tuber superius (Fig. 9A₁). The acetabular area is relatively large dorsoventrally in comparison with the shaft. There is no subacetabular or supraacetabular fossa. The angle between the tuber superius and the pars ascendens is close to 180°, whereas the angle between the shaft and pars descendens is close to 90°. The pars ascendens is short. The extremity of the pars descendens is flared. The acetabulum is deep, slightly bell-shaped, and has a sharp rim. A shallow groove extends from the tuber superius to the anteroventral part of the shaft. The suture with the ischium is nearly dorsoventrally oriented. An ossified pubis is fused with

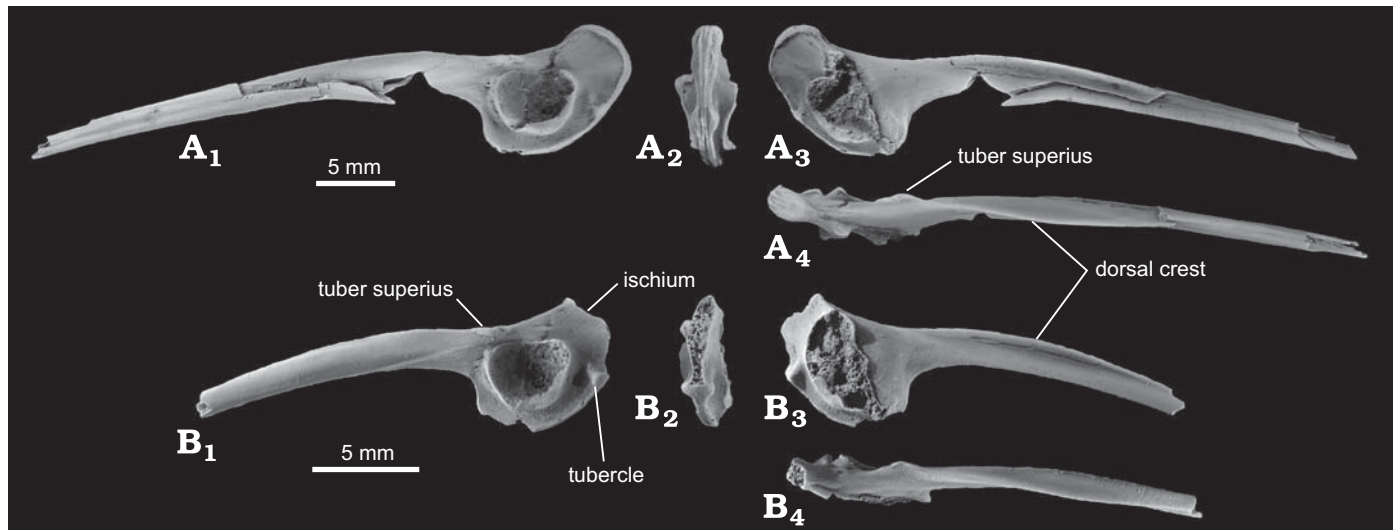


Fig. 9. Pelvic girdle of frog *Indorana prasadi* gen. et sp. nov., early Eocene, Vastan Lignite Mine, Gujarat, India. **A.** GU/RSR/VAS 5220, holotype, nearly complete left ilium with the two ischia and pubis in lateral (A₁), posterior (A₂), medial (A₃), and dorsal (A₄) views. **B.** GU/RSR/VAS 5219, incomplete left ilium with left ischium in lateral (B₁), posterior (B₂), medial (B₃), and dorsal views (B₄).

the ilium and ischium but its limits are not readily visible. The ischium is reniform and its dorsal border is laterally thickened. The acetabulum is deep and presents a rim as sharp as on the ilium. On its posterior border, the ischium bears a tubercle that projects laterally. This structure is clearly visible in posterior view (Fig. 9A₂, B₂). In medial view, there is no ornamentation (e.g., striae or foramina) on the ilium except for a weak dorsal crest (Fig. 9A₃, A₄, B₃, B₄). The latter begins on the dorsal part of the shaft, close to the tuber superius, and extends on the medial side of the shaft. There is no interiliac tubercle. In dorsal view, the iliac shaft is slightly laterally compressed, and the tuber superius, and the dorsal crest project laterally, and medially, respectively (Fig. 9A₃, A₄, B₃, B₄; see Table 1).

Discussion.—This specimen presents features that differ from those of most major groups of frogs. A weak or low dorsal crest is present in some non-ranoid frogs such as Hylidae and Leptodactylidae (Lynch 1971; Holman 2003). However, both families differ from the Vastan taxon by a more developed and globular tuber superius (Bailon 1999).

This taxon does not belong to “Ranidae” or Discoglossidae of the “*Discoglossus* group” because the dorsal crest of the iliac shaft is less developed in particular in the posterior area of the ilium (Rage and Hossini 2000). It most resembles Rhacophoridae (which is here considered a family of the superfamily Ranoidea, sensu Cannatella 2007) in having a weakly developed tuber superius and a relatively elongate pars descendens (Nokariya 1983b: fig. 4.5). The laterally projecting tubercle on the posterior border of the ischium is another character shared with rhacophorids, such as several species of *Rhacophorus* (Nokariya 1983b) and the species *Polypedates leucomystax* (MNHN n°1871–187, Recent, Philippines). Moreover, it resembles the species *Buergeria buergeri* (previously referred to *Rhacophorus*) in having a weak dorsal crest and the anterior border of the acetabulum that extends to half the length of the tuber superius. However, the pubis of the Vastan specimen is

better developed. Indeed, based on Nokariya (1983b: fig. 4.5), the pubis of *B. buergeri* is cartilaginous, whereas it is ossified and fused with the ilium and the ischium in the Vastan taxon. Moreover, the acetabulum is wider, and the shaft is thicker than in *B. buergeri*. These morphological differences and the temporal gap between extant *B. buergeri* and the Vastan form allow us to erect the new name *Indorana prasadi*, gen. and sp. nov., for this early Eocene frog and to tentatively attribute it to the family Rhacophoridae.

Liem (1970) considered the genus *Buergeria* as a primitive rhacophorid frog because it presents several putative plesiomorphies among Asiatic rhacophorids, such as the presence of musculus adductor longus, an arch-shaped anterior horn of the hyoid, and the presence of second and fourth phalangeal slips of the musculus humerodorsalis. Subsequently, Channig (1989) erected the subfamily Buergeriinae for this genus, restricted to Taiwan and Japan, indicating that it is the sister taxon of the other Rhacophoridae. These data are in agreement with the possibility that *Indorana prasadi* represents a primitive rhacophorid.

Stratigraphic and geographic range.—Type locality and horizon only.

Diversity and affinities of Early Eocene Indian frogs

The frog fauna from Vastan is relatively diverse, with at least four families. It includes “Archaeobatrachia” represented by Bombinatoridae, “Mesobatrachia” represented by Pelobatidae, and “Neobatrachia” represented by “Ranidae” and possible Rhacophoridae.

The Bombinatoridae is a primitive Eurasian family of aquatic toads whose only extant representatives are the gen-

era *Barbourula* and *Bombina*. Both are highly toxic and have flattened bodies. *Barbourula* is restricted to Borneo and the Philippine Islands, and no fossil record is known for this genus. *Bombina* occurs mainly in Europe and Eastern Asia, and its earliest record is from the Miocene of Germany (Sanchiz and Schleich 1986). The new species, *Eobarbourula delfinoi* represents the earliest record of the family and marks its first presence on the Indian subcontinent. *Bombina*, also called the fire-bellied toad, can manifest the Unken reflex, like some salamandrids such as *Taricha* or *Salamandrina*, when it is approached by a predator. Two displays can be observed: the animal stays on its belly, arches its back and limbs in order to expose its usually bright and colourful ventral surface (Sanchiz 1988; Zweifel 1998). It can also flip over, arch its back and stretch out its back and forelegs. In the context of these two strategies, the functional role of the vertebral articulation similar to a zygosphene-zygantrum complex is not well understood, but at least in anurans and in the salamander *Salamandrina*, it seems to be related with the Unken reflex by leading to a concave bending of the vertebral column associated with the exhibition of the coloured belly (Sanchiz 1988). The strange articulation similar to a zygosphene-zygantrum complex and the elongated spinal process of the imbricate vertebrae in the new *Eobarbourula delfinoi* would have prevented dorso-ventral movements of the vertebral column, as in *Bombina*, and indicate that this early Eocene bombinatorid frog may have been capable of the Unken reflex.

The Pelobatidae, which are predominantly fossorial (burrowing) frogs (Zweifel 1998), are represented by only one extant genus, *Pelobates*, the spadefoot toad, which is native to Europe and border areas (Cannatella 2007). Pelobatidae have Laurasian affinities (Prasad and Rage 2004) and are recorded in Europe from the early Eocene (Russell et al. 1982; Rage and Hossini 2000). They are also present in the Maastrichtian, based on ilia from the Lance Formation in Montana, North America, and the Deccan Traps of Nagpur, India (Estes and Sanchiz 1982; Sahni et al. 1982). They have been reported from the Cretaceous of central Asia, but this is now considered doubtful: specimens from the Campanian of Khermeen Tsav (Nemegt Basin, Mongolia) referred to the genus *Eopelobates* by Borsuk-Białynicka (1978) were later attributed to the gobiatid *Gobiaties* by Špinar and Tatarinov (1986). Pelobatid characters of *Liaobatrachus grabau* described from the Early Cretaceous of the Yixian Formation, Liaoning Province, China (Ji and Ji 1998), cannot be confirmed following poor preservation of the specimen (Wang and Evans 2006). *Eopelobates* likely had a terrestrial lifestyle because it lacks the burrowing specialization, a bony spade on each hind foot (Henrici and Haynes 2006). Moreover, based on the morphology of the pelvis, it was the only pelobatid frog not able to jump as well as a “ranid” frog (Wuttke 1992). Following Rage and Hossini (2000), it could also be more or less arboreal. By these features, *Eopelobates* could represent the primitive condition in pelobatids. However, burrowing pelobatids were already present in the mid-

dle Eocene of North America. This is especially clear from the skeleton of *Elkobatrachus brocki*, a pelobatid with a bony spade on the hind foot from the Elko Formation of Nevada (Henrici and Haynes 2006).

The “Ranidae”, also called the true frogs, are cosmopolitan in distribution (Rage and Roček 2003; Bossuyt et al. 2006). The oldest “ranids” are from the late Eocene of France and England (Rage 1984; Holman and Harrison 1999). A ranoid has been reported from the Cenomanian of Africa (Báez and Werner 1996) but not described. Another ranoid has been reported from the Maastrichtian Deccan Traps of India (Prasad and Rage 2004). Despite the fact that their geographic origin is not clear, it was recently suggested that the ancestors of at least three clades of “ranids” (ranines, rhacophorines and dicroglossines) reached Eurasia via the Indian subcontinent (Bossuyt et al. 2006). The discovery of the oldest “ranid” in the early Eocene of Vastan is consistent with this dispersal hypothesis.

The Rhacophoridae (here considered a distinct family), also known as shrub frogs or Old World treefrogs, are arboreal and occur in tropical regions of Asia, Africa and the Indo-Australian Archipelago (Rage and Roček 2003). They have been reported from the late Eocene of France (Sanchiz 1998) but not described, and their presence in Europe is regarded as questionable (Rage and Roček 2003). The only fossil record of definitive rhacophorids is from the Pleistocene of Japan (Hasegawa 1980; Nokariya 1983b). Rhacophorids could be related to “ranids” (Rage and Roček 2003) and are considered a subfamily of “ranids” by some authors (Bossuyt et al. 2006). In any case, if the systematic position of the new *Indorana prasadi* is confirmed, it would represent the earliest record of Rhacophoridae.

The composition of the early Eocene Vastan frog fauna is somewhat different from that of the Late Cretaceous of India. The most famous Indian fossil frog, *Indobatrachus pusillus* from the Maastrichtian of Bombay, is represented by complete but poorly preserved skeletons. Moreover, only a few characters are known for its pelvic morphology (Špinar and Hodrova 1985). It was a very small frog of about 20 mm snout-vent length, with an ilium having a slender shaft, a straight pars ascendens, and lacking both a tuber superius and a dorsal crest (Špinar and Hodrova 1985). This does not correspond to the ilia reported here, with the possible exception of *Eopelobates* sp., but its ilium is much larger and has a thicker shaft. Moreover, the rest of the anatomy of the genus *Eopelobates*, based on several complete specimens of *E. wagneri* from the middle Eocene of Messel (Fig. 6A₁), does not fit with that of *I. pusillus*. The genus *Indobatrachus* was attributed to the Myobatrachidae (Lynch 1971; Špinar and Hodrova 1985), but this assignment has been queried. Indeed, among the characters described by Lynch (1971), only the reduced transverse processes of the presacral vertebrae still support this systematic attribution (Roček and Rage 2000). In the Maastrichtian locality of Naskal, Gobiataidae, Ranoidea, and possibly Leptodactylidae have been described (Prasad and Rage 2004). With the exception of the ranoids,

these groups are absent from Vastan. A pelobatid from the Maastrichtian of Nagpur (Sahni et al. 1982) seems to represent a second group that is in common with the early Eocene of Vastan.

Paleobiogeographic affinities of the different groups of anurans suggest that Gobiataidae and Pelobatidae are of Laurasian origin. Gobiataidae are indeed described from the Late Cretaceous of Central Asia (Roček and Nesson 1993) and from the Early Cretaceous Yixian Formation of Liaoning Province, China (Wang and Gao 1999). The early Eocene Vastan fauna does not present typical specimens referable to the family Gobiataidae. Therefore, we can neither confirm nor reject hypothesized dispersal of this family between Eurasia and India during the Maastrichtian. However, the bombinatorid and pelobatid from Vastan support the hypothesis of interchange between Europe and India before or during the early Eocene. This dispersal scenario was already developed for several groups of modern mammals such as bats, rodents, primates, and artiodactyls (Smith et al. 2007; Rana et al. 2008; Rose et al. 2009a; Kumar et al. 2010) and possibly also for some groups of snakes such as colubroids (Rage et al. 2008). The presence of ranoid frogs such as “ranids” and rhacophorids in the early Eocene of Vastan is consistent with a Gondwanan origin of these two groups, with dispersal to Eurasia via India as suggested by the time-calibrated phylogeny coupled with the palaeogeographic framework (Bossuyt et al. 2006).

Despite the evidence of interchange of several modern vertebrate groups between Europe and India, it is difficult to determine whether they dispersed into or out of India. Among amphibians, the absence of fossil and extant caudates in India does not support a Europe to India dispersal scenario. Indeed, caudates are well represented in the Paleocene of Europe (Folie et al. 2009), and if modern vertebrates dispersed from Europe to India it is intriguing why European caudates did not. The apparent absence of bombinatorid, pelobatid, and ranoid frogs, as well as modern mammals, in the Paleocene of Europe could suggest that vertebrates dispersed out of India. However, Indian Paleocene localities are still unknown for continental vertebrates, and Vastan is at present the oldest locality for these groups on the Indian subcontinent. The discovery of a Paleocene continental vertebrate fauna in India should help to resolve this palaeobiogeographic enigma.

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