Research paper

New early Eocene vertebrate assemblage from western India reveals a mixed fauna of European and Gondwana affinities

CrossMark

Thierry Smith [a,*], Kishor Kumar [b], Rajendra S. Rana [c], Annelise Folie [d], Floréal Solé [a], Corentin Noiret [e], Thomas Steeman [f], Ashok Sahni [g], Kenneth D. Rose [h]

[a] Directorate Earth and History of Life, Royal Belgian Institute of Natural Sciences, 29 rue Vautier, B-1000, Brussels, Belgium
[b] Wadia Institute of Himalayan Geology, 33 General Mahadeo Singh Road, Dehradun, 248001, Uttarakhand, India
[c] Department of Geology, H.N.B. Garhwal University, Srinagar, 246175, Uttarakhand, India
[d] Scientific Heritage Survey, Royal Belgian Institute of Natural Sciences, 29 rue Vautier, B-1000, Brussels, Belgium
[e] Department of Geology, University of Namur, 61 rue de Bruxelles, B-5000, Namur, Belgium
[f] Research Unit Palaeontology, Ghent University, Krijgslaan 281, S8, B-9000, Ghent, Belgium
[g] Centre of Advanced Study in Geology, Panjab University, Chandigarh, 160014, India
[h] Center for Functional Anatomy and Evolution, Johns Hopkins University School of Medicine, Baltimore, MD, 21205, USA

A B S T R A C T

The Ypresian Cambay Shale Formation at Vastan and Mangrol lignite mines in Gujarat, western India, has yielded a rich vertebrate fauna with numerous taxa of European affinities. Here we report a new, approximately contemporary vertebrate assemblage from two fossiliferous layers in the nearby mine of Tadkeshwar. These layers have yielded a similar mammal fauna with the co-occurrence of the perissodactyl-like cambaytheriid *Cambaytherium thewissi*, the adapoid primates *Marcgodinotius indicus* and cf. *Asiadapis cambayensis*, and the hyaenodontid *Indohyaenodon raoi*. The presence of these species in both Vastan and Tadkeshwar mines and at different levels suggests that the deposits between the two major lignite seams represent a single land mammal age. Apart from the aforementioned species there is a new, smaller species of *Cambaytherium*, and a new genus and species of esthonychid tillodont. This fauna also contains the first large early Eocene vertebrates from India, including an unidentified *Coryphodon*-like pantodont, a dyrosaurid crocodyliform and a new giant madtsoiid snake. Among the Tadkeshwar vertebrates several taxa are of Gondwana affinities, such as Pelomedusoides turtles, dyrosaurids, and large madtsoiids, attesting that the early Eocene was a crucial period in India during which Laurasian taxa of European affinities co-existed with relict taxa from Gondwana before the India-Asia collision. Our results suggest that terrestrial faunas could have dispersed to or from Europe during episodes of contact between the Indian subcontinent and different island blocks along the northern margin of the Neotethys, such as the Kohistan—Ladakh island-arc system. Gondwana taxa might represent remnants of ghost lineages shared with Madagascar, which reached the Indian subcontinent during the late Cretaceous; alternatively they might have come from North Africa and passed along the southern margin of the Neotethys to reach the Indian subcontinent. These dispersals would have been possible as a result of favourable paleogeographic conditions such as the particular Neotethys conformation during the beginning of the early Eocene.

© 2016, China University of Geosciences (Beijing) and Peking University. Production and hosting by Elsevier B.V. This is an open access article under the CC BY-NC-ND license (http://creativecommons.org/licenses/by-nc-nd/4.0/).

1. Introduction

The Cambay Shale Formation, exposed at the Vastan open cast lignite mine near the Vastan village about 40 km northeast of Surat, Gujarat, western India (Fig. 1), is known since 2004 for its well-preserved diverse fauna of terrestrial mammals as well as other vertebrates (e.g., Rana et al., 2004, 2005; Bajpai et al., 2005a, 2009;
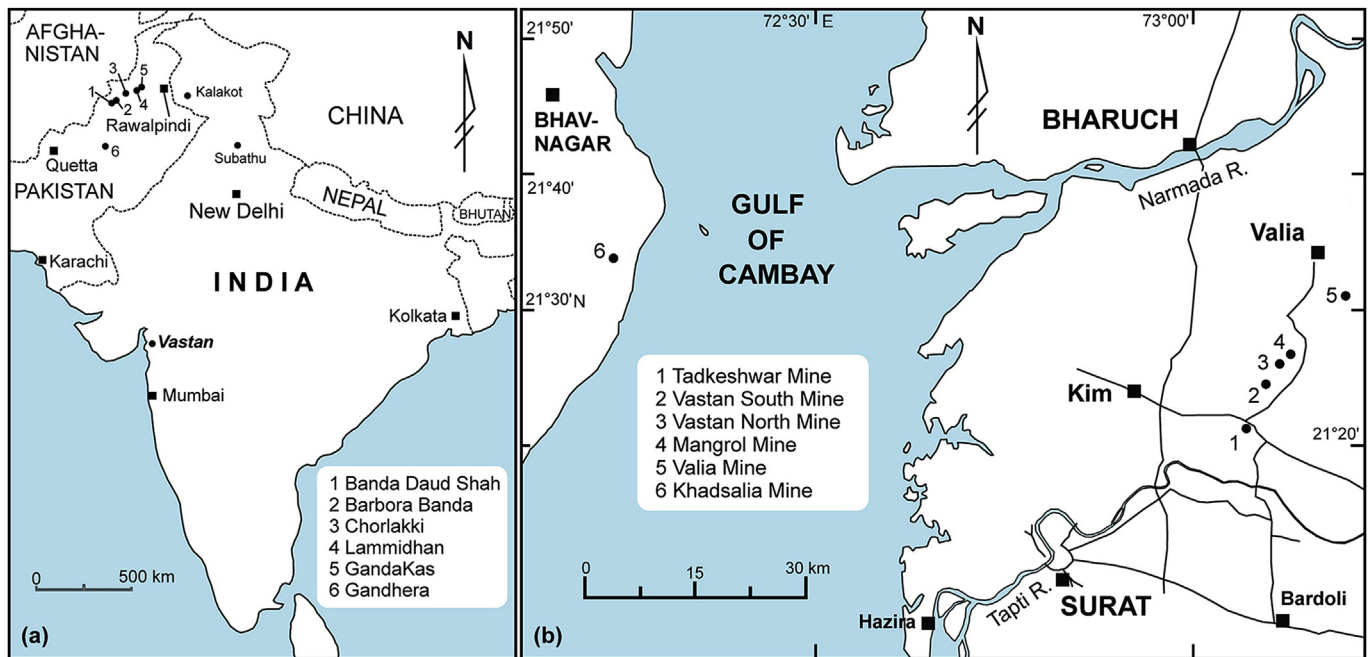
Figure 1. (a) Map of Indian subcontinent showing the location of early and middle Eocene terrestrial vertebrate localities including Vastan Lignite Mine. Squares represent major cities and black dots vertebrate localities. (b) Location map of the area around Vastan Lignite Mine, Surat District. Squares represent major cities and black dots lignite mines. Localities 1, 3, and 4 yielded terrestrial vertebrates.

Rose et al., 2006; Sahni et al., 2006; Bajpai and Kapur, 2008). The mammalian fauna of the Cambay Shale Formation includes the earliest modern mammals from the Indian subcontinent—with the highest diversity of early bats (Smith et al., 2007), the oldest lagomorph (Rose et al., 2008), the first Asian ailuravine rodent (Rana et al., 2008), primitive adapoid and omomyid primates (Bajpai et al., 2005b; Rose et al., 2007, 2009a), primitive artiodactyls (Kumar et al., 2010), the earliest Indian tapiroid (Smith et al., 2015), endemic perissodactyl-like cambaytheriid mammals (Bajpai et al., 2005a; Rose et al., 2014) — as well as more archaic groups, such as the first Indian tillodonts (Rose et al., 2009b, 2013) and basal hyaenodontid "creodonts" (Bajpai et al., 2009; Rana et al., 2015).

Other vertebrates include marine and non-marine fish (Rana et al., 2004; Nolf et al., 2006), the oldest birds of the Indian subcontinent (Mayr et al., 2007, 2010), a high diversity of terrestrial and aquatic snakes (Rage et al., 2008) and acrodontan lizards (Prasad and Bajpai, 2008; Rana et al., 2013), and the earliest ranid and bombinatorid frogs (Folie et al., 2013).

During the last decade our Indian-American-Belgian team has explored other lignite mines hoping to discover other vertebrate fossils in order to increase our knowledge of the early Paleogene faunas of the Indian subcontinent. In this pursuit, terrestrial vertebrates have also been found in the Mangrol lignite mine situated north of Vastan and in continuity with the same deposits. Here we describe the first vertebrate discoveries from the Tadkeshwar mine south of Mangrol and Vastan (Fig. 1). While the general lithology and the first discovered vertebrate remains from the Tadkeshwar mine present similar aspects to those of Vastan and Mangrol, with taxa of European affinities, several new taxa, especially among large non-mammalian vertebrates, indicate Gondwana affinities as well.

2. Material and methods

All the fossil vertebrate specimens from the Tadkeshwar lignite mine described in this paper were recovered from two horizons by quarrying the subsurface strata exposed by open-pit mining operations. These fossiliferous continental sediments were also subjected to preliminary screen-washing through mesh of 1.5 mm.

Smaller remains were picked out and sorted in the laboratory under a binocular microscope. The material is composed of dental specimens and postcranial bones. All specimens from the upper fossiliferous horizon are originally brownish or dark in colour while specimens from the lower fossiliferous horizon vary from pale to dark in colour. To avoid oxidation and especially deterioration due to pyritization specimens have been coated with an acrylic resin (Paraloid B72) mixed with ethyl acetate solvent.

Larger specimens were coated (whitened) with ammonium chloride for digital imaging. Smaller specimens were photographed with an FEI Quanta 200 environmental scanning electron microscope at the Royal Belgian Institute of Natural Sciences in Brussels.

The present figured specimens are stored in the collections of the Wadia Institute of Himalayan Geology in Dehradun, and the H.N.B. Garhwal University in Srinagar, both in Uttarakhand state, India.

Abbreviations

AV: Avenay, MNHN collections, France.
CGM: Egyptian Geological Museum, Cairo, Egypt.
GSI/PAL/CR: Geological Survey of India, Kolkata, India.
GU/RSR: H.N.B. Garhwal University, Srinagar, Uttarakhand, India.
MNHN: Muséum National d'Histoire Naturelle, Paris, France.
MRAC: Musée Royal d'Afrique Centrale, Tervuren, Belgium.
OCP DEK-GE: Office Chérifien des Phosphates, Direction de l'Exploitation de Khouribga, Geologie-Exploitation, Khouribga, Morocco.
TAD: Tadkeshwar locality (2 levels, TAD-1 corresponding to the lower level and TAD-2 corresponding to the upper level).
UM: University of Michigan Museum of Paleontology, Ann Arbor, Michigan, USA.

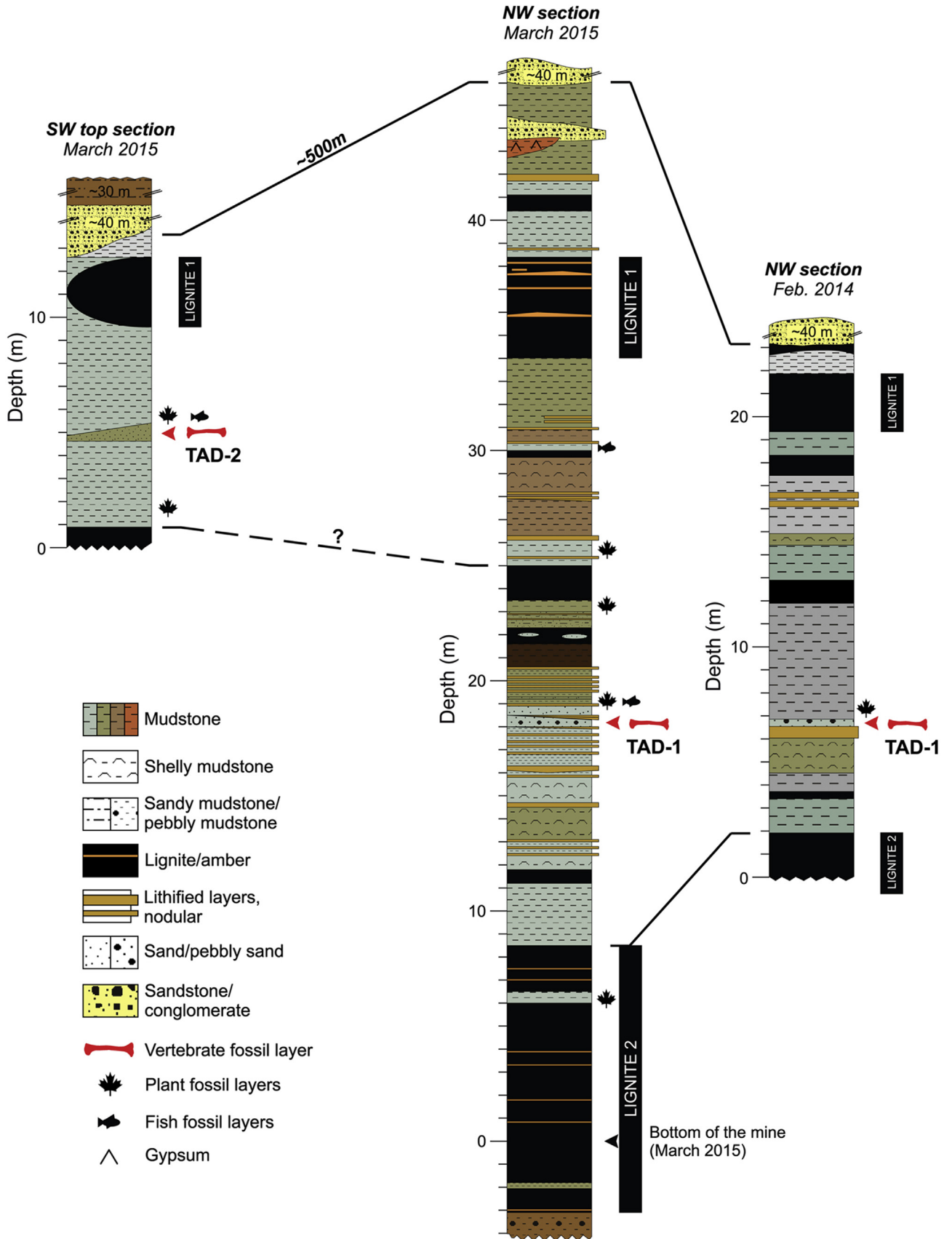**Figure 2.** Stratigraphic section through the lower Eocene Cambay Formation in Tadkeshwar Mine. Section shows position of the vertebrate-producing layers TAD-1 and TAD-2 relative to the two principal lignites (Lignite seam 1 and Lignite seam 2).

USGS: United States Geological Survey, Denver, Colorado; collection now at USNM.

USNM: United States National Museum of Natural History, Smithsonian Institution, Washington, D.C., USA.

WIF/A: Wadia Institute of Himalayan Geology, Dehradun, India.

3. Geological setting

The Paleogene deposits in the Cambay Basin are characterized by the occurrence of several laterally and vertically extensive lignite seams. Over the years extensive research has been carried out, including the drilling of numerous exploratory bore wells, to assess the hydrocarbon source rock potential of the lignite beds, as well as their ongoing and future exploitation (Shanmukhappa, 2011). Consequently, there is considerable information on the subsurface occurrence and continuity of these beds. At Tadkeshwar mining site (GPS coordinates 21°21′50″N to 21°20′20″N and 73°03′30″E to 73°05′00″E), located roughly along strike of the Vastan-Mangrol mining complex (Fig. 1), two lignite seams are present (Figs. 2 and 3): a thick one of 7−12 m (Lignite 2) at the base of the studied section, and a 3−4 m thick seam (Lignite 1) about 15−25 m above the top of Lignite 2. There is substantial variation in thickness of the layers laterally.

The section measured at Tadkeshwar in March 2015 by two of us (C.N. and T.S.) showed a thickness of 25.5 m between the top of Lignite 2 and the base of Lignite 1. Lignite 2 is more than 12 m thick and Lignite 1 is 4.5 m thick, but thins in the southwest part of the mine. Above Lignite 1 are 70 m of sandy to conglomeratic sediments, overlain by nummulitic clays. Previous studies of Tadkeshwar mine reported thicknesses that are substantially lower than the section logged in 2015. A preliminary section measured by our team (K.K. and R.S.R.) in February 2014 recorded about 16.5 m between Lignite 1 and Lignite 2 (Fig. 2). Adatte et al. (2014) reported a similar thickness for the section of about 15 m between Lignite 1 and Lignite 2. Singh et al. (2014) noted a thickness of around 75 m from the Deccan traps to the alluvial lateritic bed. Our more recent Tadkeshwar section from the bottom of Lignite 2 to the lateritic bed was about 70 m, although the Deccan traps were not evident at the floor of the mine.

The general stratigraphic framework of the Tadkeshwar section closely resembles that observed in the more extensively studied Vastan section roughly north of Tadkeshwar (Fig. 1; e.g., Sahni et al., 2006; McCann, 2010; Prasad et al., 2013) and is characterized by an, at times, almost cyclic appearing alteration of mostly muddy shale deposits with varying colour and carbon content (Figs. 2 and 3). At Vastan these are interpreted as sediments deposited in a shallow, restricted bay environment that was flanked by a salt, fresh to brackish water marsh complex cut by several freshwater and tidal creeks and channels (Prasad et al., 2013). Pollen assemblages recovered from the Tadkeshwar deposits (Singh et al., 2014) closely resemble those known from the Vastan Mine (Rao et al., 2013).

One of the major differences between the two mining sites (Vastan and Tadkeshwar) is the presence of intercalated erosional sandy channels at Tadkeshwar, which are absent from the Vastan succession (Prasad et al., 2013). It is from these channels that some of the vertebrate remains were recovered at Tadkeshwar (Fig. 4). The lower vertebrate-bearing horizon from the Tadkeshwar mine (TAD-1: GPS coordinates 21°21′08″N and 73°04′04″E; Figs. 2−4), situated about 4−5 m above Lignite 2, is a sandy channel, with a sporadic conglomeratic, erosional base (Figs. 2 and 4), which extends laterally for about 96 m and has a thickness that can reach up to 60 cm. The sediment is also less dark, less clayey and less rich in plant material than the vertebrate-bearing lenses at Vastan (Sahni et al., 2006; McCann, 2010). The occasionally conglomeratic, erosional base and general sandy nature of the channel indicates a fluviatile depositional environment, while above and below the mammal-bearing layer a near-shore environment is inferred by the
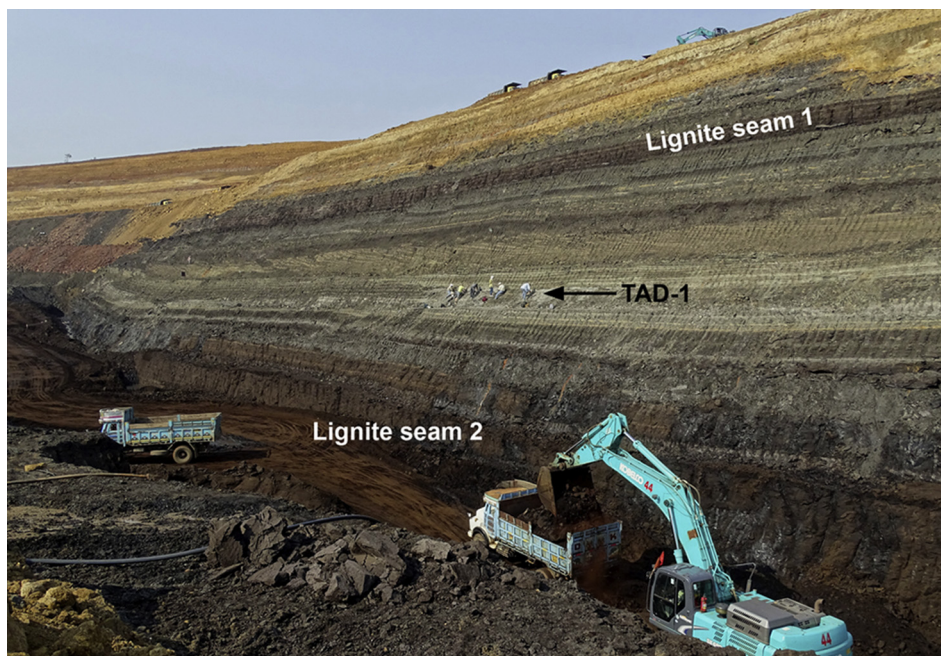

Figure 3. Outcrop of the Cambay Formation in Tadkeshwar Mine showing the position of the vertebrate-producing layer TAD-1 relative to the two major lignite seams (Lignite 1 and Lignite 2).
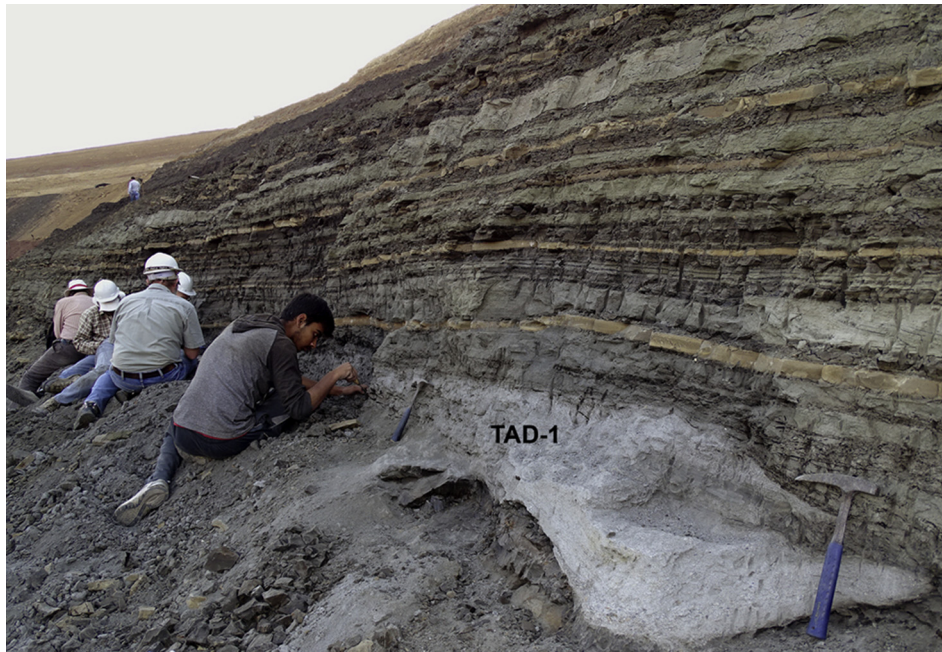
Figure 4. Fluvial lenticular sandy layer of Tadkeshwar vertebrate site TAD-1 below a shallow marine dark grey limestone.

presence of marine shell beds. The higher fossiliferous horizon (TAD-2: GPS coordinates 21°20′48″N and 73°04′05″E; Figs. 2, 5 and 6), situated about 3—4 m below Lignite 1, clearly differs sedimentologically from TAD-1. TAD-2 is a lenticular, dark, sandy deposit about 30 cm thick and 4 m in extension, rich in organic matter and similar to the lenses at Vastan. It tops a channel that extends laterally for about 35 m and has a thickness reaching a maximum of 1 m, which again seems to cut into the layers beneath, signalling a fluviatile depositional environment.

The syn-rift deposits of the lower Eocene Cambay Shale Formation show various lithofacies attributed to specific depositional environments: shell carbonates (open bay), greenish-grey shale (restricted bay), carbonaceous shale (creek and channel) or lignite (coastal marshes) (McCann, 2010; Prasad et al., 2013). The long-term transgressive system in the Vastan mine, as for the Tadkeshwar mine, is punctuated by short-term regressions due to high rates of sediment supply. The thickness of these transgressive deposits is controlled by sedimentation rate, accommodation space or relative sea-level changes (e.g., Samanta et al., 2016). Fluctuations in depositional environments and accommodation space could explain such thickness variations and lateral facies changes in the Tadkeshwar mine (e.g., Cattaneo and Steel, 2003).
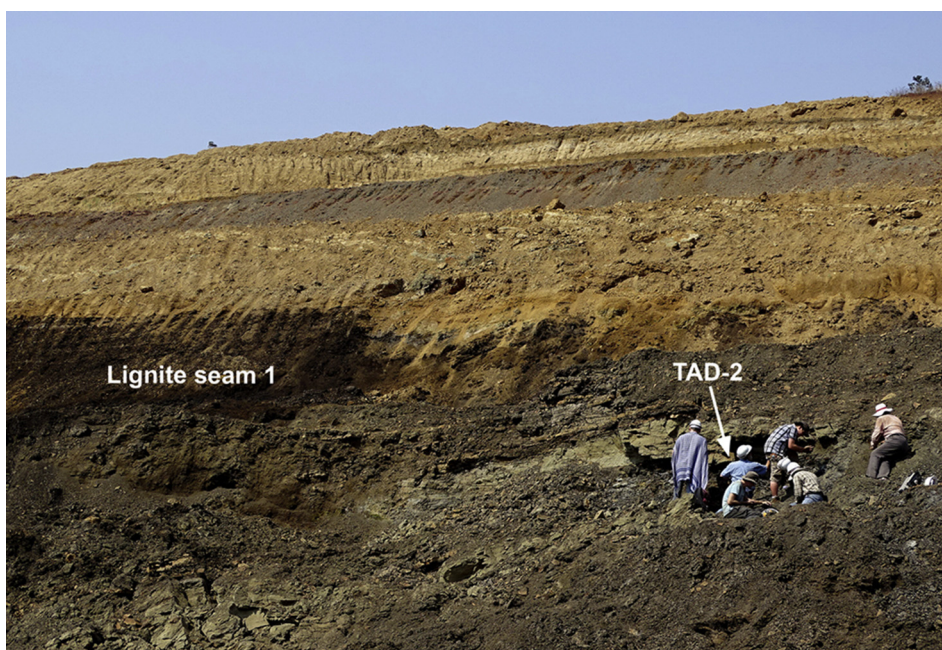

Figure 5. Outcrop of the Cambay Formation in Tadkeshwar Mine showing the position of the vertebrate-producing layer TAD-2 relative to Lignite seam 1.
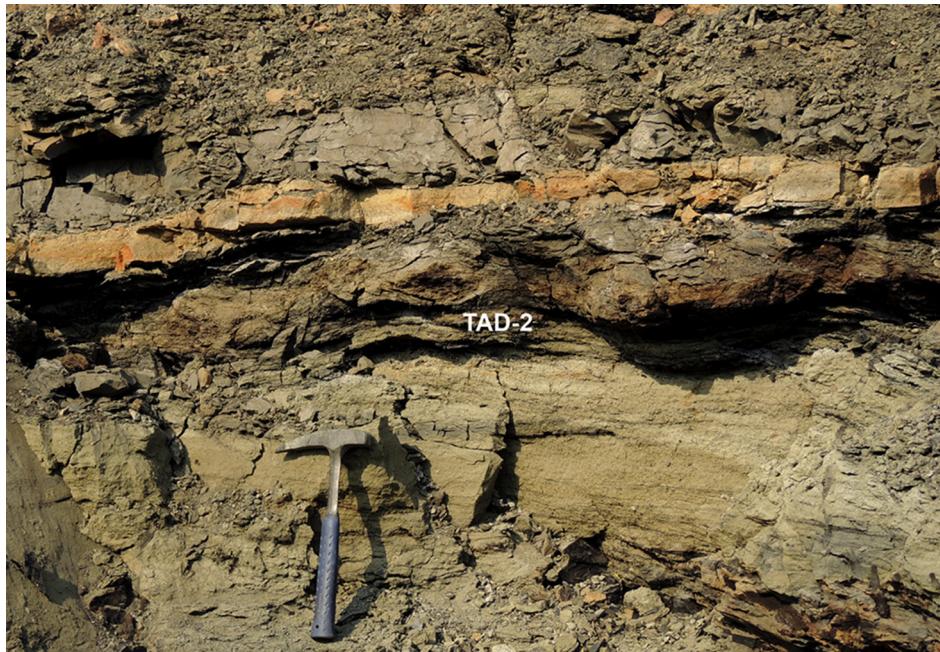
Figure 6. Lens very rich in organic matter of Tadkeshwar vertebrate site TAD-2 below Lignite 1.

For now it seems that the earliest lignite deposits observed in the Cambay Basin are Paleocene in age, while the youngest lignite deposits are considered to be early Eocene or younger (Shanmukhappa, 2011). Ostracod assemblages recovered from the nummulitic limestone and marl deposits above Lignite 1 at Tadkeshwar appear to be middle Eocene in age (Nagori et al., 2013). This suggests that the deposits down section are at least as old as middle Eocene and likely older. The section measured at Tadkeshwar in March 2015 indeed showed about 40 m of sandstone-conglomerate channels alternating with clayey beds between the top of Lignite 1 and the 30 m thickness of brownish nummulitic clays. All these observations are consistent with the inferred early Eocene age for the deposits between the two major lignite seams at the Vastan mine, based on the presence of *Nummulites burdigalensis burdigalensis* (Sahni et al., 2006; Punekar and Saraswati, 2010), a stratigraphic marker for the early Eocene. The *Nummulites* assemblages at Tadkeshwar are yet to be properly assessed; however, other proxies also suggest an early Eocene age (Adatte et al., 2014; Singh et al., 2014; Samanta et al., 2016).

4. Systematic paleontology of the vertebrates from Tadkeshwar

This published work and the nomenclatural acts it contains have been registered in Zoobank (http://zoobank.org), the online registration system for the International Code of Zoological Nomenclature. The LSID for this publication is: urn:lsid:zoobank.org:pub:36C62466-3283-468E-8DC2-20EA18001748.

The diversity of the terrestrial vertebrate fauna from the Tadkeshwar mine is indicated in Table 1. Most of the taxa occur in both levels TAD-1 and TAD-2.

Vertebrata Lamarck, 1801
Pisces Linnaeus, 1758
Chondrichthyes Huxley, 1880
Carchariniformes Compagno, 1977
Carcharhinidae Jordan and Evermann, 1896
Physogaleus sp.

Referred material: WIF/A 2339, upper antero-lateral tooth (from level TAD-1).

Comments

This specimen is the only shark tooth found at Tadkeshwar (Fig. 7A–B). It measures 10 mm wide and 6 mm high. The tooth has a moderately thick root and is strongly mesio-distally compressed with the mesial cutting edge nearly smooth and bearing only one tiny serration. The distal shoulder bears five coarse serrations. A transverse groove is present. These typical carchariniform characters conform well with the genus *Physogaleus*. By comparison with *Physogaleus secundus* from the Ypresian of the Ouled Abdoun Basin, Morocco, the specimen would correspond to an antero-lateral tooth of the upper jaw (Cappetta, 1980).

Myliobatiformes Compagno, 1973
Myliobatidae Bonaparte, 1838
Myliobatis sp.
Referred material: WIF/A 2282, WIF/A 2283, WIF/A 2317, WIF/A 2338, GU/RSR/TAD 9552, median teeth (all from TAD-1).

Comments

Five ray teeth have been found in Tadkeshwar. They all belong to the same genus of the eagle ray, *Myliobatis*, which is characterized by dental plates with occlusal surface flat, wide roots with block-like laminae and shallow, narrow grooves between laminae (Fig. 7C). All these teeth are much wider than long, with a hexagonal contour, and they correspond to median teeth (Cappetta, 1987).

Osteichthyes Huxley, 1880
Actinopterygii Cope, 1887
Teleostei Müller, 1846
Tetraodontiformes Berg, 1940
Tetraodontiformes indet.
Referred material: WIF/A 2340, fused jaws with teeth (TAD-1).

Table 1
Preliminary list of vertebrates in the Tadkeshwar assemblage.

Chondrichthyes
　Carcharhiniformes
　　Carcharhinidae
　　　Physogaleus sp.
　Myliobatiformes
　　Myliobatidae
　　　Myliobatis sp.
Osteichthyes
　Tetraodontiformes
　　Tetraodontiformes indet.
Amphibia
　Anura
　　?Pelobatidae
　　　cf. *Eopelobates* sp.
　　Ranoidea
　　　"Ranidae" indet.
Testudinata
　Pleurodira
　　Pelomedusoides
　　　Pelomedusoides indet.
　Cryptodira
　　Trionychoidea
　　　Carettochelyidae indet.
　　　Trionychidae indet.
Squamata
　Lacertilia
　　Agamidae
　　　Tinosaurus indicus
　Serpentes
　　Madtsoiidae
　　　Platyspondylophis tadkeshwarensis, gen. et sp. nov.
　　　Madtsoiidae indet.
　　Palaeophiidae
　　　Palaeophis vastaniensis
　　Boidae
　　　Boidae indet.
　　Colubroidea indet.
　　　Procerophis sahnii
　　Caenophidia incertae sedis
　　　Thaumastophis missiaeni
Crocodylomorpha
　Mesoeucrocodylia
　　Dyrosauridae
　　　cf. *Congosaurus* sp.
Aves
　?Psittaciformes
　　Vastanavidae
　　　Vastanavis sp.
　Aves indet.
Mammalia
　Pantodonta
　　cf. Coryphodontidae, indet.
　Tillodontia
　　Esthonychidae
　　　Indoesthonyx suratensis, gen. et sp. nov.
　　　cf. *Indoesthonyx suratensis*
　Rodentia
　　Ischyromyidae
　　　cf. *Meldimys* sp.
　Chiroptera
　　Microchiropteramorpha
　　　"Eochiroptera" indet. 1
　　　"Eochiroptera" indet. 2
　Primates
　　Asiadapidae
　　　Marcgodinotius indicus
　　　cf. *Asiadapis cambayensis*
　Hyaenodonta
　　Hyaenodontidae
　　　Indohyaenodon raoi
　Ungulata
　　Cambaytheriidae
　　　Cambaytherium thewissi
　　　Cambaytherium gracilis, sp. nov.

Comments

This very well-preserved jaw is attributed to a bony fish by the fibrous aspect of the bone and the numerous rounded trituration teeth (Fig. 7D—E). The jaw is distinctive as it results from the fusion of the right and left sides as in some tetraodontiforms. The modified teeth incorporated into a "beak" suggest that this taxon could be a member of an early gymnodont clade of tetraodontiforms (Tyler, 1980). However, the numerous rounded teeth would be unique among gymnodonts, in which only larger and more consolidated trituration plates are known (Tyler and Santini, 2002). If the identification of this specimen is confirmed, this jaw would represent the most plesiomorphic condition known to date for tetraodontiforms.

Amphibia Linnaeus, 1758
Anura Fischer von Waldheim, 1813
?Pelobatidae Bonaparte, 1850
cf. *Eopelobates* sp.
Referred material: WIF/A 2341, tibio-fibula; GU/RSR/TAD 9523, proximal humerus (both from TAD-1).

Comments

A medium-sized frog is represented in Tadkeshwar by a long tibio-fibula of 43 mm (Fig. 8A—B). Both proximal and distal ends are missing, which indicates that the bone was about 5 cm long. A comparison with the Vastan anuran assemblage shows that this bone corresponds to the size of *Eopelobates* sp. (Folie et al., 2013). Comparison with *Eopelobates wagneri* from the middle Eocene of Messel also shows similar proportions. Moreover, a proximal humerus from Tadkeshwar also is comparable in size and proportions to *Eopelobates wagneri*.

Ranoidea Rafinesque, 1814
"Ranidae" Rafinesque, 1814
"Ranidae" indet.
Referred material: WIF/A 2342, femur; WIF/A 2343, surangular; GU/RSR/TAD 9558, presacral vertebra (all from TAD-1).

Comments

Small-sized frogs are also present in Tadkeshwar, based on a complete femur of 13 mm long (Fig. 8C), a nearly complete surangular (Fig. 8D) and an isolated vertebra (Fig. 8E—I). By comparison with the Vastan anuran assemblage these small frog remains correspond in size with the taxon Ranidae indet. or the possible rhacophorid *Indorana prasadi* (Folie et al., 2013). The vertebra from Tadkeshwar can be attributed to a ranoid because it is procoelous with an antero-posteriorly short neural arch, the transversal processes are not situated below the prezygapophyses, the centrum is small, the lateral borders of the neural arch are thin, and a neural crest is present (Bailon, 1999). It presents the same morphology as the last presacral vertebra from Vastan (GU/RSR/VAS 5211), including having transverse processes that are posteriorly oriented. However, it is procoelous which indicates that it is likely one of the last presacral vertebrae but not the last one, which is amphicoelous. Nevertheless, the neural arch is wider at the level of the postzygapophyses, and the shape of the pre- and postzygapophyses is slightly different, which could suggest a taxon different than that from Vastan.

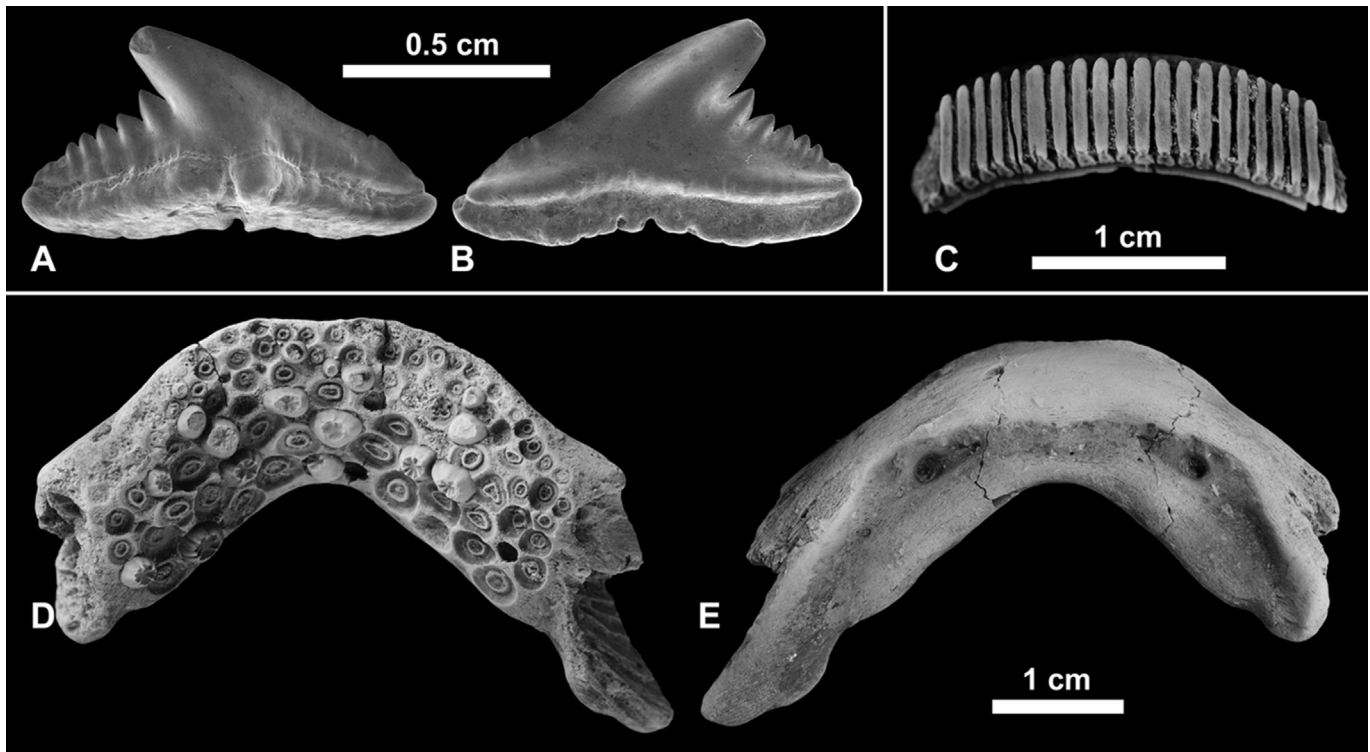Squamata Oppel, 1811
Lacertilia Günther, 1867

Figure 7. Pisces. A–B, *Physogaleus* sp., WIF/A 2339, upper antero-lateral tooth in (A) lingual and (B) labial views. (C) *Myliobatis* sp., WIF/A 2338, median tooth in basal view. (D, E) Tetraodontiformes indet., WIF/A 2340, fused jaws with teeth in (A) occlusal and (B) ventral views.

Iguania Cope, 1864
Acrodonta Cope, 1864
Agamidae Spix, 1825
Tinosaurus indicus Prasad and Bajpai, 2008
Referred material: WIF/A 4286, dentary; WIF/A 2344, dentary fragment; WIF/A 2345, vertebra (all from TAD-1).

Comments

Acrodont dentaries and a typical lizard vertebra have been found in the lower bed at Tadkeshwar. The dentaries belong to agamids and differ from those of priscagamids in having an open

Meckel's canal and lacking a splenial. The specimen WIF/A 4286 (Fig. 9A–C) can be attributed to *Tinosaurus indicus*, which is abundant in the nearby Vastan mine (Prasad and Bajpai, 2008; Rana et al., 2013), by the following characters: long dentary with a heterodont dentition; well-individualized teeth gradually increasing in size posteriorly; posterior tricuspid acrodont teeth with a high central cusp surrounded by lateral smaller cusps; presence of a narrow, cylindrical subdental ridge between the Meckelian fossa and the alveolar border; presence of a nearly horizontal, elliptical, narrow, anteroposteriorly elongated symphysial facet; and closely spaced hatchling teeth versus widely spaced pleuracrodont teeth (Rana et al., 2013). The dentary fragment and the vertebra are
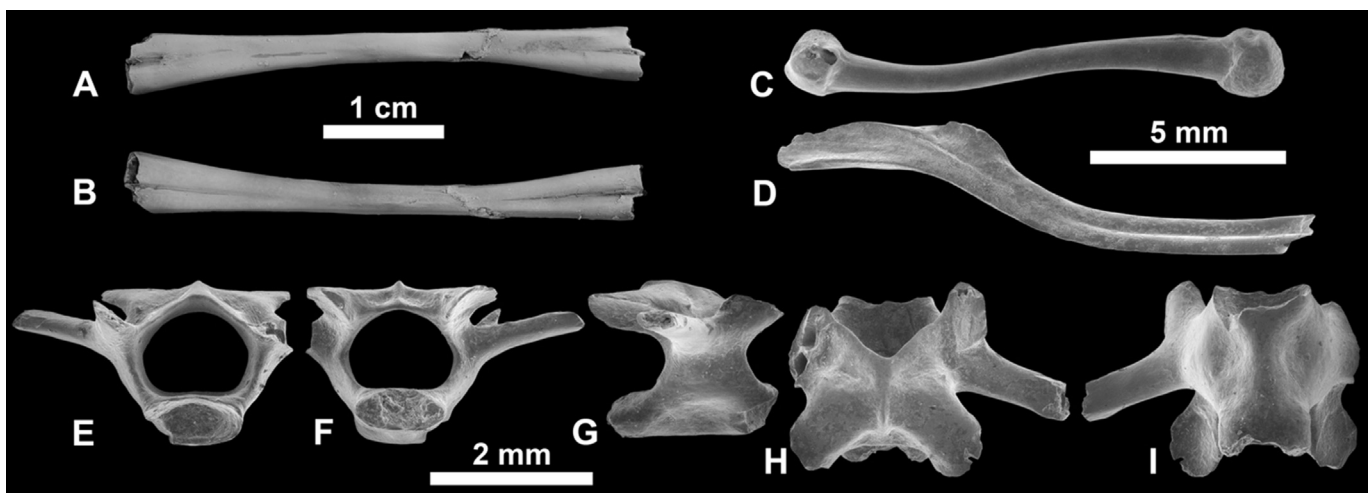

Figure 8. Anura. A–B, cf. *Eopelobates* sp., WIF/A 2341, tibio-fibula in (A) anterior and (B) posterior views. C–I, "Ranidae" indet. (C) WIF/A 2342, femur in anterior view. (D) WIF/A 2343, surangular in dorsal view. E–I, GU/RSR/TAD 9558, presacral vertebra in anterior (E), posterior (F), right lateral (G), dorsal (H), and ventral (I) views.
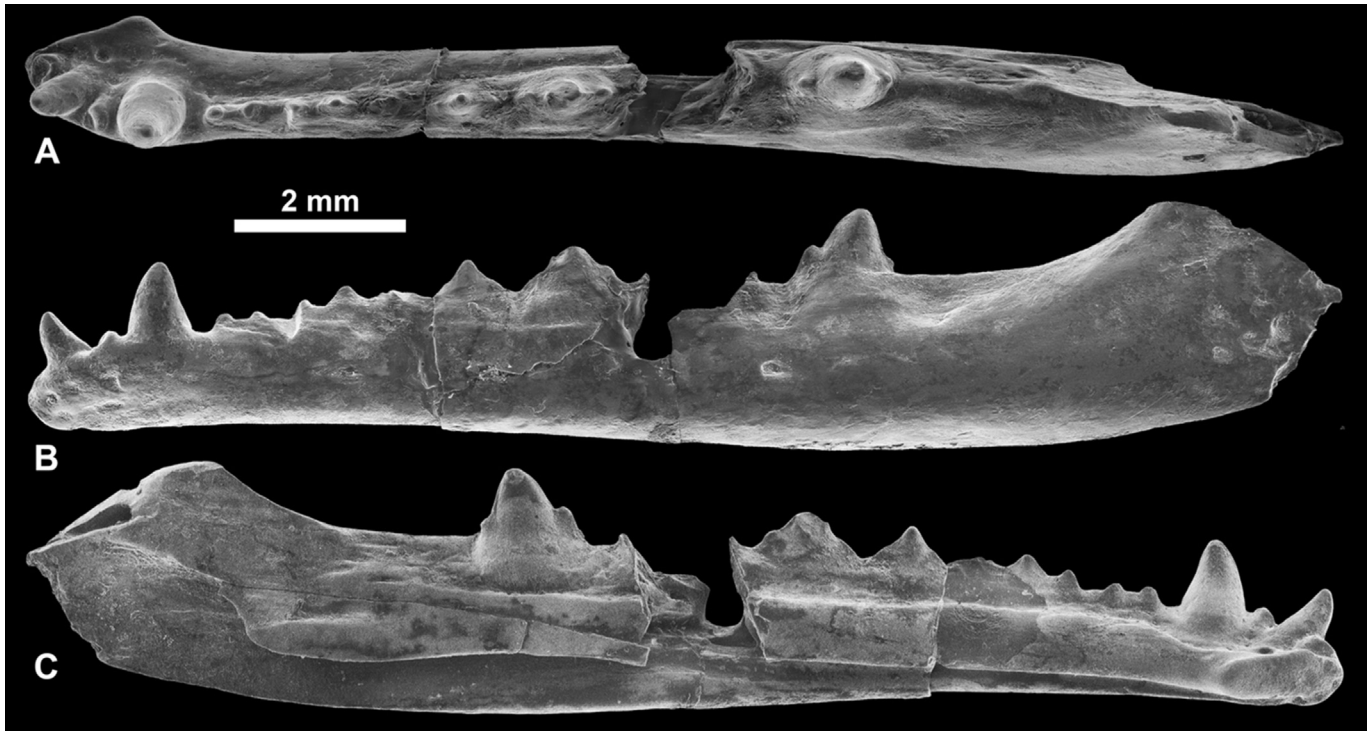
Figure 9. Agamidae, *Tinosaurus indicus*. WIF/A 4286, dentary in (A) occlusal, (B) labial, (C) lingual views.

tentatively assigned here because *T. indicus* is the only lizard known so far from Tadkeshwar.

Testudinata Klein, 1760
Pleurodira Cope, 1864
Pelomedusoides Cope, 1868
Pelomedusoides indet.
Referred material: GU/RSR/TAD 9553, nuchal plate; WIF/A 4288, left epiplastron; WIF/A 4289, costal plate; WIF/A 4290, fragment of left hyoplastron (all from TAD-1).

Comments

Thick fragments of the hyoplastron and epiplastron, as well as a costal plate, belong to an indeterminate pleurodiran turtle. However, a nuchal plate (Fig. 10A), trapezoidal to hexagonal in shape, with very fine ornamentation, and consisting of two cervical scutes and one vertebral scute (broken posteriorly), slightly concave ventrally, suggest that this taxon belongs to the Pelomedusoides group. While a possible pelomedusid has been reported from the middle Eocene of Pakistan (Broin, 1987), this group is mainly represented in the late Cretaceous (Maastrichtian) of India by the bothremydids *Kurmademys* and *Sanchuchemys* (Gaffney et al., 2006).

Cryptodira Cope, 1868
Trionychoidea Fitzinger, 1826
Carettochelyidae Boulenger, 1887
Carettochelyidae indet.
Referred material: WIF/A 2347, fragmentary right epiplastron plate; WIF/A 4291-WIF/A 4294, four peripherals; WIF/A 4295, bridge peripheral; WIF/A 4296, nine small fragments of costal plates; WIF/A 4297, fragment of plastron; GU/RSR/TAD 9563-GU/RSR/TAD 9567, five fragments of plates (all from TAD-1).

Comments

This taxon represents the most abundant turtle from Tadkeshwar. The plastron is relatively thin, and its surface is covered with a fine ornamentation of vermiculated ridges and tubercles typical of a carettochelyid (Fig. 10B). Better preserved specimens from this Tadkeshwar species will be needed for a thorough comparison with other carettochelyids, especially with *Chorlakkichelys shahi* known from the early—middle Eocene Kuldana Formation of Pakistan (Broin, 1987).

Trionychidae Fitzinger, 1826
Trionychidae indet.
Referred material: WIF/A 2346, a fragmentary costal plate (TAD-1).

Comments

A trionychid species is attested by a typical plate, relatively thick (about 6 mm) with strong pits and ridges (Fig. 10C). A taxon referred to Trionychidae gen. et sp. indet. has been reported from the early—middle Eocene Kuldana Formation of Pakistan based on four indeterminate pleural plate fragments (Broin, 1987). Unfortunately, the material from Tadkeshwar is not yet sufficient for any comparisons.

Serpentes Linnaeus, 1758
Alethinophidia Nopcsa, 1923
Madtsoiidae Hoffstetter, 1961
***Platyspondylophis*, gen. nov.**
urn:lsid:zoobank.org:act:2898DE8D-634E-4731-9D22-F96741EA7B81
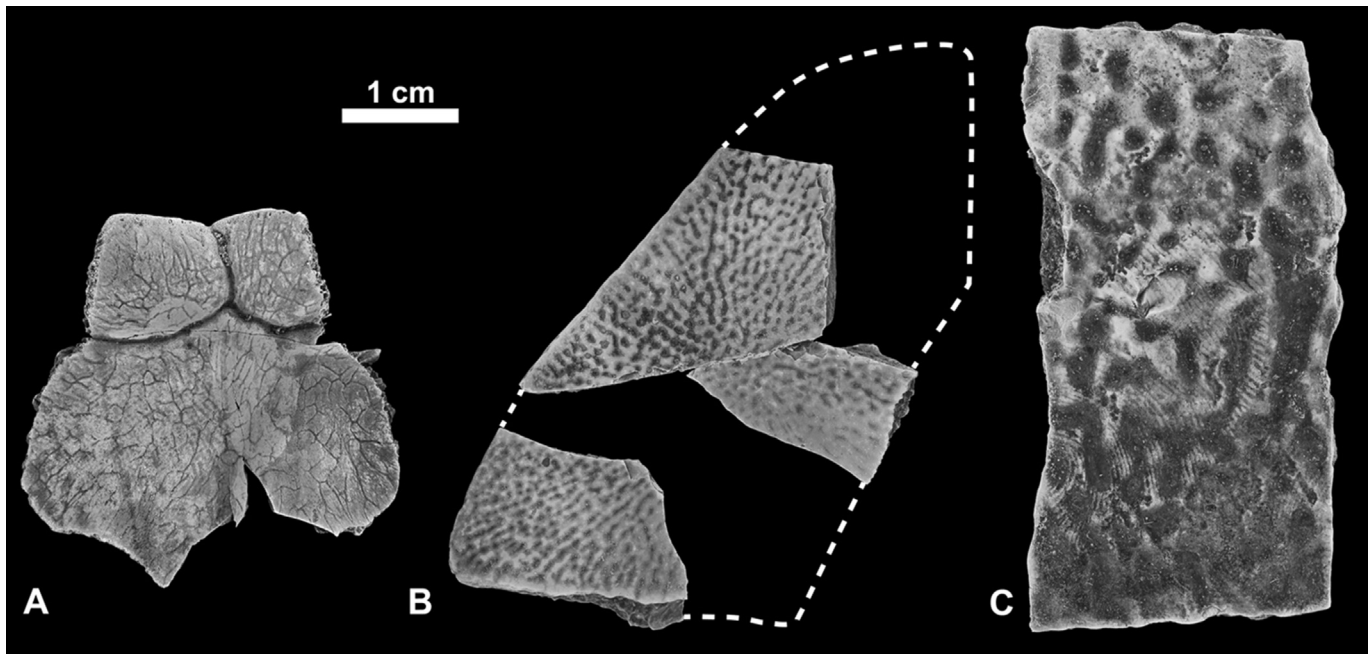***Platyspondylophis tadkeshwarensis*, gen. et sp. nov.**

Figure 10. Testudinata. (A) Pelomedusoides indet., GU/RSR/TAD 9553, nuchal plate in dorsal view. (B) Carettochelyidae indet., WIF/A 2347, fragmentary right epiplastron plate in dorsal view. (C) Trionychidae indet., WIF/A 2346, fragmentary costal plate in dorsal view.

urn:lsid:zoobank.org:act:8E1687DB-97BA-4648-BD1D-951BD0FC0AF9

(Fig. 11A–O)

Etymology: Genus name from Greek *platys*, flat, and *spondyl*, vertebra, referring to the dorso-ventral compression of the cotyle, condyle, and centrum on vertebrae; and species name from Tadkeshwar, the locality where this species was found.

Holotype: WIF/A 2272, posterior trunk vertebra (TAD-1).

Hypodigm: Holotype and WIF/A 2269-WIF/A 2271, WIF/A 2273, GU/RSR/TAD 9503, GU/RSR/TAD 9506, six isolated vertebrae (all from TAD-1).

Horizon and locality: Cambay Shale Formation, Ypresian, lower Eocene, Tadkeshwar Lignite Mine (TAD-1), Surat District, Gujarat, India.

Diagnosis: Large madtsoiid differing from the other genera and species by the association of the following characters: wide and dorsoventrally compressed centrum with strongly oval cotyle and condyle (ratio of width/height between 1.30 and 1.54); presence of a deep and wide posterior median notch of the low neural arch; major axis of the prezygapophysis transverse in dorsal aspect and nearly horizontally oriented in anterior and posterior view; wide diapophyses inclined dorso-posteriorly; shallow parazygantral fossae without visible foramina, low and antero-posteriorly short neural spine dorsally or even antero-dorsally oriented. Differs further from *Gigantophis* by having less massively built vertebrae, well-developed hypapophyses on the anterior vertebrae, and a larger neural canal. Differs further from *Madtsoia* by having a sharp internal carina in the neural canal.

Description

The most abundant snake taxon at Tadkeshwar possesses large and massively built vertebrae (antero-posteriorly shorter than wide) with a small, slightly trilobate neural canal. WIF/A 2269 is 43 mm wide across the prezygapophyses (Fig. 11A–E), whereas the other vertebrae, including the holotype, are about 30 mm wide. Based on the precondylar centrum length of 18 mm

for the largest trunk vertebra (WIF/A 2269), we estimate that *Platyspondylophis tadkeshwarensis* was ca. 5 m long (see method in LaDuke et al., 2010). The neural spine is antero-posteriorly short and low in lateral view (maximum height is visible on vertebra WIF/A 2271, Fig. 11F–J), and the low neural arch is evenly curved (vaulted) in anterior and posterior views. In anterior view, the prezygapophyseal processes are lacking, the prezygapophyses are ventrally continuous with large para-diapophyses, the dorso-posteriorly inclined diapophyses extend laterally over the tip of the prezygapophyses, and the para-pophyses project ventrally. The latter lie above the level of the floor of the neural canal and are nearly horizontal. Fossae are developed at the level of the parazygantral and paracotylar foramina, especially on vertebrae WIF/A 2270 and 2272 (Fig. 11K–O). However, foramina that would be expected to be present in these fossae are not visible. The zygosphene is dorso-ventrally low (except on WIF/A 2269 and WIF/A 2271) and transversely narrower than the cotyle. The cotyle and condyle are strongly oval, wider transversely than dorso-ventrally. The ratio of height to width of the cotyle varies from 1.54 for vertebra WIF/A 2269 to 1.30 for vertebra WIF/A 2271. However, the lower ratio of the latter vertebra could be due to erosion. In ventral and dorsal views, the zygapophyses are oval, obliquely oriented, and do not project laterally, so that the interzygapophyseal constriction is not marked. The anterior border of the zygo-sphene is straight and not notched. On WIF/A 2269 and 2271 a hypapophysis is ventrally well-developed on the posterior part of the wide and dorsoventrally compressed centrum. It projects well below the condyle, nearly reaching its posterior part. Its lateral sides are not sharp and the subcentral fossae are shallow. No haemal keel is present on the vertebrae, but two tuberosities are developed at the posterior end of the centrum of posterior trunk vertebrae.

Discussion

The presence of parazygantral and paracotylar foramina and wide diapophyses, together with the absence of prezygapophyseal
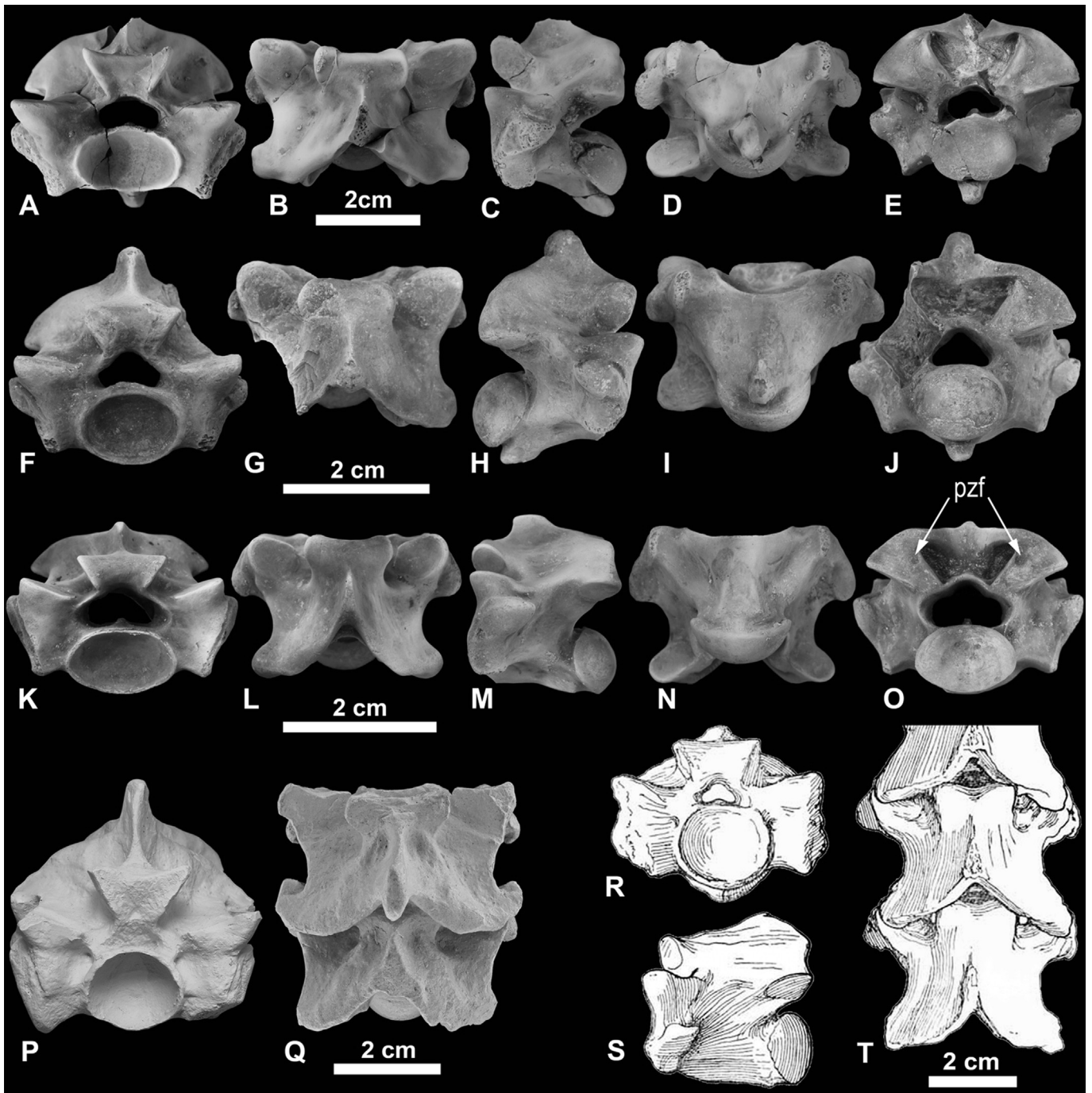
Figure 11. Madtsoiidae, *Platyspondylophis tadkeshwarensis* gen et. sp. nov. A–E, WIF/A 2269, anterior trunk vertebra in (A) anterior, (B) dorsal, (C) left lateral, (D) ventral, and (E) posterior views. F–J, WIF/A 2271, anterior trunk vertebra in (F) anterior, (G) dorsal, (H) right lateral, (I) ventral, and (J) posterior views. K–O, WIF/A 2272, holotype, posterior trunk vertebra in (K) anterior, (L) dorsal, (M) left lateral, (N) ventral, and (O) posterior views. *Madtsoia pisdurensis*, P–Q, 225/GSI/PAL/CR/10, posterior trunk vertebrae in (P) anterior and (Q) dorsal views. *Gigantophis garstini*, R–T, CGM C.10022, vertebrae in (R) ventral, (S) left lateral, and (T) dorsal views (from Andrews, 1901). Abbreviations: pzf, parazygantral fossae.

processes, are considered diagnostic characters for madtsoiids (Rage et al., 2014). The presence of hypapophyses only on anterior trunk vertebrae is also considered a diagnostic character of the family (Scanlon, 2005; Mohabey et al., 2011).

Large Madtsoiidae (*Madtsoia*, *Gigantophis*, *Wonambi* and *Yurlunggur*) form a separate clade based on the presence of parazygantral foramina in fossae, and their large size, which has been recognized as a derived and phylogenetically significant character (Mohabey et al., 2011). The large size of the Tadkeshwar vertebrae and the small neural canal are consistent with large madtsoiids

(Rage et al., 2008). Moreover, large madtsoiids are often described as having parapophyses concave in lateral view, which is the case on the Tadkeshwar specimens. For these reasons, *Platyspondylophis tadkeshwarensis* is here included in the clade of large madtsoiids.

Comparisons indicate that the new Indian vertebrae do not belong to the genera *Wonambi* (Smith, 1976) or *Yurlunggur* (Scanlon, 2006). *Wonambi*, from the Pliocene and Pleistocene of Australia, presents a high postero-dorsally oriented neural spine running from the anteriormost to the posteriormost extremity of the neural arch, the zygosphene is as wide as high, the

zygapophyses are inclined 25° above the horizontal, and a haemal keel is present (Smith, 1976; Scanlon and Lee, 2000). The haemal keel of *Wonambi* ends with two protuberances, as in *Madtsoia* and the Tadkeshwar specimens. However, the shape of the haemal keel changes progressively on the different ventral positions in *Wonambi*, which is a significant difference from *Madtsoia* and the Tadkeshwar specimens. *Yurlunggur* from the Miocene of Australia presents a low neural spine and a trilobate shape of the neural canal (Scanlon, 1992) as in *Platyspondylophis*. However, the neural spine is dorso-posteriorly oriented, the cotyle is about the same width as the zygosphene, the diapophyses do not extend lateral to the prezygapophyses, the posterior median notch of the neural arch is not well-developed, and a haemal keel is present. *Platyspondylophis* differs further from *Wonambi* and *Yurlunggur* by having only one pair of parazygantral foramina instead of two pairs (characters from LaDuke et al., 2010).

Differences between *Madtsoia* and *Gigantophis* are weak and have been debated since Simpson (1933; see Rage et al., 2014, and references therein). Hoffstetter (1961) suggested that *Gigantophis* presents a well-marked haemal keel, whereas *Madtsoia* presents a shallow keel with a pair of small tubercles posteriorly. The two genera are nevertheless still considered as being distinct (LaDuke et al., 2010; Mohabey et al., 2011). An additional character that differentiates *Gigantophis* and *Madtsoia* is the presence of an internal carina in the neural canal, which was illustrated in *Gigantophis* by Andrews (1901, Fig. 1) but mentioned as lacking in *Madtsoia* by Simpson (1933, p. 8).

The original description of the type species *Gigantophis garstini* (Eocene of Egypt) indicates that the cotyle and condyle are oval, the neural spine is short with a flat truncated extremity, and the neural canal has a trilobate form (Andrews, 1901), all as in *Platyspondylophis tadkeshwarensis*. Another shared character is the internal carina in the neural canal, which is well-developed in *P. tadkeshwarensis*. However, the neural spine is very low and the hypapophyses are small in *Gigantophis*, contrasting with relatively well-developed hypapophyses in *Platyspondylophis*. Moreover, Andrews (1901, Fig. 1) showed a massively built vertebra with a high zygosphene (not so massive and high in *Platyspondylophis*), a small neural canal, and a neural spine well-separated anteriorly from the zygosphene (short neural arch with a neural spine ending rather close to the zygosphene in *P. tadkeshwarensis*). A neural spine that does not extend anteriorly onto the zygosphene has recently been confirmed as a diagnostic character of *G. garstini* (McCartney and Seiffert, 2015). With a low neural spine ending rather close to the zygosphene, *P. tadkeshwarensis* clearly differs from *G. garstini*. *Gigantophis* sp. from the late Paleocene of Pakistan (Rage et al., 2014) is the same size as *P. tadkeshwarensis* but differs in having a high zygosphene, a haemal keel, and a thick base of the neural spine.

The original description of the type species of *Madtsoia*, *M. bai* from the Eocene of Patagonia (Simpson, 1933), is very close to the description of *P. tadkeshwarensis*, including a short and wide triangular centrum with a flat ventral side without haemal keel, but presenting two tuberosities at the posterior end of the centrum of posterior trunk vertebrae corresponding to insertions for ligaments (Hoffstetter, 1961); zygapophyses with obliquely oriented oval facets; diapophyses with a convex upper part; and a trilobate neural canal. However, *Madtsoia bai* differs from *P. tadkeshwarensis* in having a high neural spine. *Madtsoia madagascariensis* differs from *P. tadkeshwarensis* in having more rounded cotyle and condyle (Hoffstetter, 1961), a smaller neural canal, and laterally oriented prezygapophyses in dorsal view (LaDuke et al., 2010). *Madtsoia pisdurensis*, described by Mohabey et al. (2011), differs further by having paracotylar foramina placed in deep fossae (shallow fossae in *P. tadkeshwarensis*) and by having para- and diapophyses in the

same nearly vertical axis (diapophyses inclined dorso-posteriorly in *P. tadkeshwarensis*).

Comparison with the middle-size *Sanajeh* from the late Cretaceous of India is limited, as the latter is known from a nearly complete skeleton in sandstone (Wilson et al., 2010) for which the vertebrae are not accessible in all dimensions. However, the available dorsal surface of the vertebrae of *Sanajeh* indicates that the posterior median notch is shallower, with a longer and more developed neural spine.

The middle-size madtsoiids *Menarana* (LaDuke et al., 2010) and *Adinophis* (Pritchard et al., 2014) from the late Cretaceous of Madagascar are clearly different from *Platyspondylophis* by their longer vertebrae and narrower neural canal; but there are also some similarities, such as the low neural spine and the depressed neural arch. Moreover, *Adinophis* has dorsoventrally depressed condyles and cotyles as in *Platyspondylophis*.

The Tadkeshwar specimens differ from those of ?Madtsoiidae indet. from Vastan (Rage et al., 2008) mainly by their much larger size, by having a smaller neural canal and more laterally projecting diapophyses, and by lacking the haemal keel.

The large madtsoiid from Tadkeshwar is thus here referred to a new genus and species based on its important morphological differences from the four already known large madtsoiid genera. Nevertheless, some characters are shared with *Madtsoia*, such as the absence of the haemal keel and the presence of tuberosities on the ventral side of the vertebrae, and with *Gigantophis*, such as the internal carina in the neural canal.

Madtsoiidae indet.
Referred material: WIF/A 2315, GU/RSR/TAD 9504, GU/RSR/TAD 9505, three isolated vertebrae (all from TAD-1).

Comments

This madtsoiid is represented by three massively built isolated vertebrae (Fig. 12), which are about 15 to 25 mm wide across the prezygapophyses. By comparison with *Platyspondylophis tadkeshwarensis* the neural spine is a little higher, the neural canal is larger, and the neural arch presents a bell-shape in posterior view. In anterior and posterior views, there are no prezygapophyseal processes (prezygapophyses are well-separated from the paradiapophyses). The prezygapophyses are slightly inclined above the horizontal. As in *P. tadkeshwarensis*, fossae are developed close to the cotyle and zygantrum, but the parazygantral and paracotylar foramina are not evident. They are, however, assumed to be present based on the fossae, allowing their attribution to madtsoiids. On vertebrae GU/RSR/TAD 9504 (Fig. 12A–E) and 9505, the zygosphene is high and narrow, while it is relatively low on specimen WIF/A 2315 (Fig. 12F–J). This latter vertebra presents two well-developed grooves on the ventral side of its centrum and corresponds to a posterior trunk vertebra, whereas vertebrae GU/RSR/TAD 9504 and 9505 lack these grooves and therefore correspond to more anterior trunk vertebrae. As in *P. tadkeshwarensis*, no haemal keel is present on the ventral side of the centrum, the interzygapophyseal constriction is not marked, and the anterior border of the zygosphene is straight and not notched. However, this taxon differs from *P. tadkeshwarensis* by having round cotyle and condyle, paradiapophyses that are not prominent and do not extend laterally over the tip of the prezygapophyseal processes, and zygapophyses that are elongated and triangular in shape, with a pointed extremity in ventral and dorsal views.

This taxon resembles the ?Madtsoiidae indet. described by Rage et al. (2008) from the early Eocene of Vastan mine. However, the vertebrae described here are larger and lack the haemal keel.
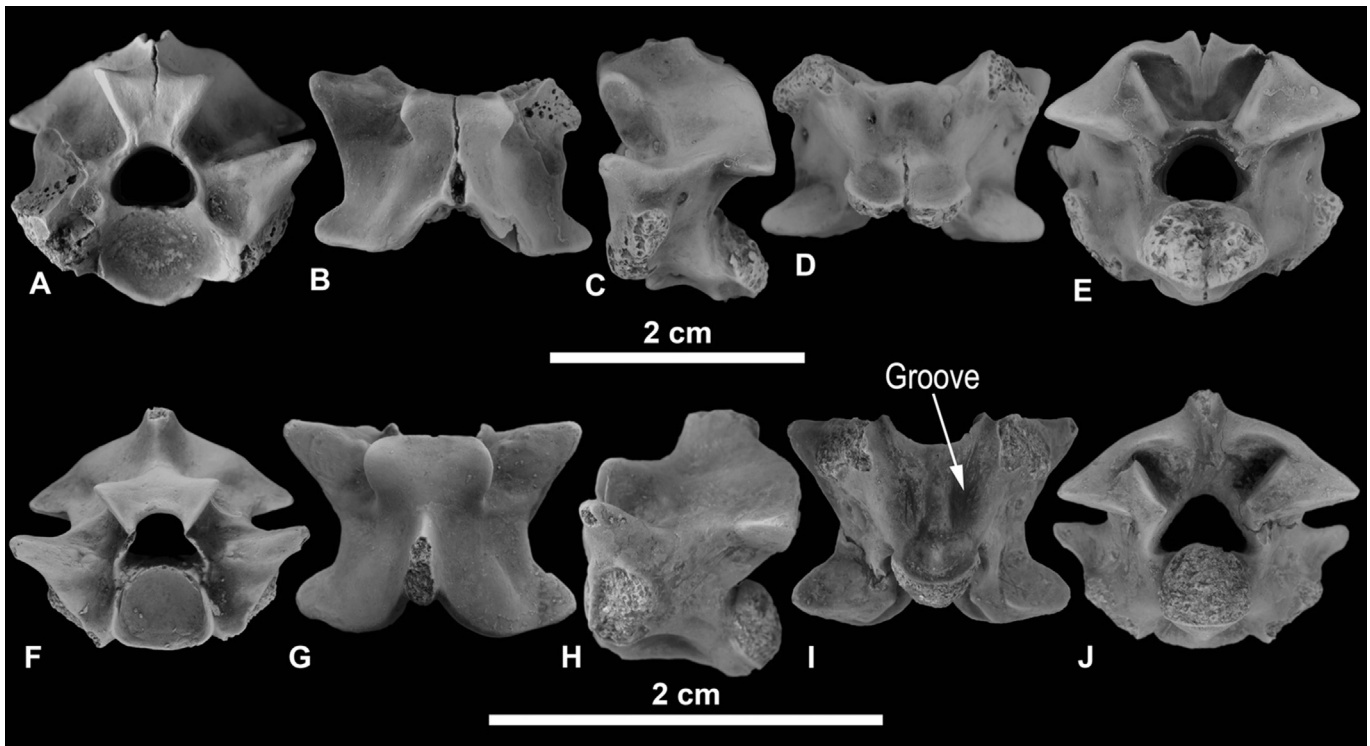
Figure 12. Madtsoiidae indet. A–E, GU/RSR/TAD 9504, mid-trunk vertebra in (A) anterior, (B) dorsal, (C) left lateral, (D) ventral, and (E) posterior views. F–J, WIF/A 2315, posterior trunk vertebra in (F) anterior, (G) dorsal, (H) left lateral, (I) ventral, and (J) posterior views.

Palaeophiidae Lydekker, 1888
Palaeophiinae Lydekker, 1888
Palaeophis Owen, 1841
Palaeophis vastaniensis Bajpai and Head, 2007
Referred material: WIF/A 2348, GU/RSR/TAD 9554–GU/RSR/TAD 9555, three isolated vertebrae (from TAD-1); WIF/A 2349, WIF/A 2350, WIF/A 2356–WIF/A 2360, GU/RSR/TAD 9556, eight isolated vertebrae (from TAD-2).

Comments

This abundant species can be assigned to Palaeophiidae because the vertebrae are laterally compressed with a well-developed hypapophysis. They measure 10 to 17 mm wide across the prezygapophyses.

However, these vertebrae are only slightly modified for an aquatic life (lateral compression weak, pterapophyses low, prezygapophyses not markedly reduced, paradiapophyses not located very low and not distant from the centrum) and thus correspond to the primitive *Palaeophis* grade defined by Rage et al. (2003). Some vertebrae from Vastan, such as GU/RSR/VAS 1007, referred to *Palaeophis* sp. (Rage et al., 2008), probably correspond to the same species. The morphology of vertebra WIF/A 2348 (Fig. 13F–J) corresponds to an anterior trunk vertebra, following Houssaye et al. (2013), and closely resembles the vertebra of *Palaeophis vastaniensis* (IITR/SB/VLM 914) from the Vastan Mine (Bajpai and Head, 2007, fig. 2A) but is 20% smaller. The anterior base of its neural spine also extends horizontally to the zygosphene and an anterior expansion of the haemal keel is present. The vertebra WIF/A 2349 (Fig. 13K–O) is a mid-trunk vertebra that resembles the vertebra figured by Bajpai and Head (2007, fig. 2B) under the same number IITR/SB/VLM 914.

The vertebra WIF/A 2350 is strongly laterally compressed and is the smallest vertebra we refer to *P. vastaniensis* (~1 cm wide across the prezygapophyses), with well-developed pterapophyses and hypapophysis, reduced prezygapophyses, and paradiapophyses low and distant from the centrum (Fig. 13A–E). The base of its neural spine is well separated from the anterior border of the zygosphene, distinguishing it from the genus *Pterosphenus*. In this feature it is closer to the advanced *Palaeophis* grade described by Rage et al. (2003). WIF/A 2350 exhibits an anterior expansion of the haemal keel similar to that of the vertebra GU/RSR/VAS 1037 described from Vastan as *Palaeophis* sp. (Rage et al., 2008, fig. 2B). The morphology of WIF/A 2350 also corresponds to that of *Palaeophis* aff. *typhaeus* (MRAC RG16029), from the Eocene of Landana, Angola, which was interpreted as a very anterior vertebra (Antunes, 1964). Because *P. vastaniensis* is abundant in the Cambay Shale Formation, we tentatively identify WIF/A 2350 as a very anterior vertebra of the same species, rather than referring it to another species of *Palaeophis*.

Henophidia Nopcsa, 1923
Booidea Gray, 1825
Boidae Gray, 1825
Boidae indet.
Referred material: WIF/A 2274, WIF/A 2351, GU/RSR/TAD 9557, three isolated vertebrae (all from TAD-1).

Comments

These vertebrae are about 15 mm wide across the prezygapophyses and are wider than long. The neural spine is low and the neural arch is bell-shaped in posterior view (Fig. 14A–E). The zygosphene is low and wide, and is about the same width as the cotyle. The zygantrum possesses parazygantral foramina. The prezygapophyseal processes are developed and not extended. The prezygapophyses lie above the level of the neural canal floor and are slightly inclined. The paradiapophyses do not extend laterally beyond
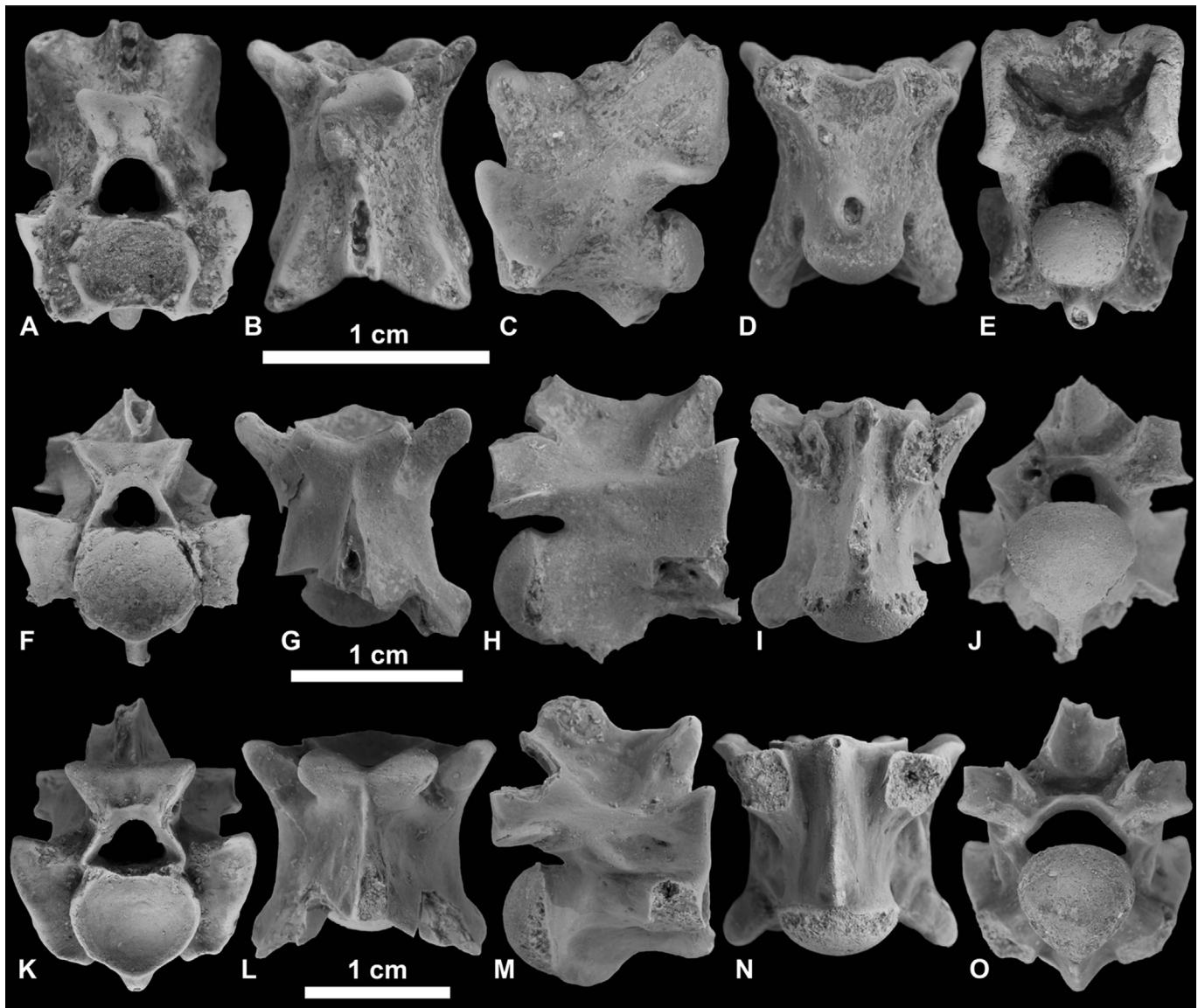
Figure 13. Palaeophiidae, *Palaeophis vastaniensis*. A–E, WIF/A 2350, very anterior trunk vertebra in (A) anterior, (B) dorsal, (C) right lateral, (D) ventral, and (E) posterior views. F–J, WIF/A 2348, anterior trunk vertebra in (F) anterior, (G) dorsal, (H) right lateral, (I) ventral, and (J) posterior views. K–O, WIF/A 2349, mid-trunk vertebra in (K) anterior, (L) dorsal, (M) left lateral, (N) ventral, and (O) posterior views.

the tip of the prezygapophyseal processes, and the diapophyses project slightly ventrally. The cotyle and condyle are somewhat oval in shape (wider transversely than dorso-ventrally). In ventral and dorsal views, the articular surfaces of the zygapophyses are oval and project laterally so that the interzygapophyseal constriction is marked. The prezygapophyseal processes are small and form two protuberances at the extremities of the prezygapophyses. The anterior border of the zygosphene is slightly trilobate and not notched. A weakly developed haemal keel is visible, forming a small projection anteroventral to the condyle. On the vertebra WIF/A 2274 (Fig. 14A–E) the lateral sides are rather sharp and the subcentral fossae are well-marked, suggesting that it is a posterior trunk vertebra.

Short, wide and massively built vertebrae with short and generally wide centra, small prezygapophyseal processes, and weakly to scarcely subdivided paradiapophyseal surfaces are typical of booid snakes (Rage and Augé, 2010). Within this super-family, xenopeltids are characterized by a well-developed neural spine, bolyeriids by a hypapophysis on each vertebra, and tropidophids by a high neural spine with a well-developed haemal keel

(Rage, 2001). The Tadkeshwar vertebrae lack these characters and therefore do not belong to any of these families. However, they share with boids the presence of reduced prezygapophyseal processes placed below the prezygapophyses (Rage, 2001). Within this family, erycines possess depressed vertebrae with additional apophyses (Szyndlar and Böhme, 1996; Rage, 2001), and pythonines possess an arched neural arch with a high neural spine and a high zygosphene (Szyndlar and Rage, 2003). These characters are absent from the Tadkeshwar vertebrae, which more closely resemble boine vertebrae by the combination of the following characters: the lack of a vertical ridge on the anterior face of the zygosphene; the presence of paracotylar fossae; straight, posteromedially angled interzygapophyseal ridges; and the vaulted, biangled posterior margin of the neural arch (Rage and Danilov, 2008; Head et al., 2009). However, members of this subfamily generally possess paracotylar foramina (Rage, 2001; Head et al., 2009), which are not discernible in the present vertebrae. Nonetheless, it has been demonstrated that paracotylar foramina can be variably present in extant and extinct boines (Rage, 2001).
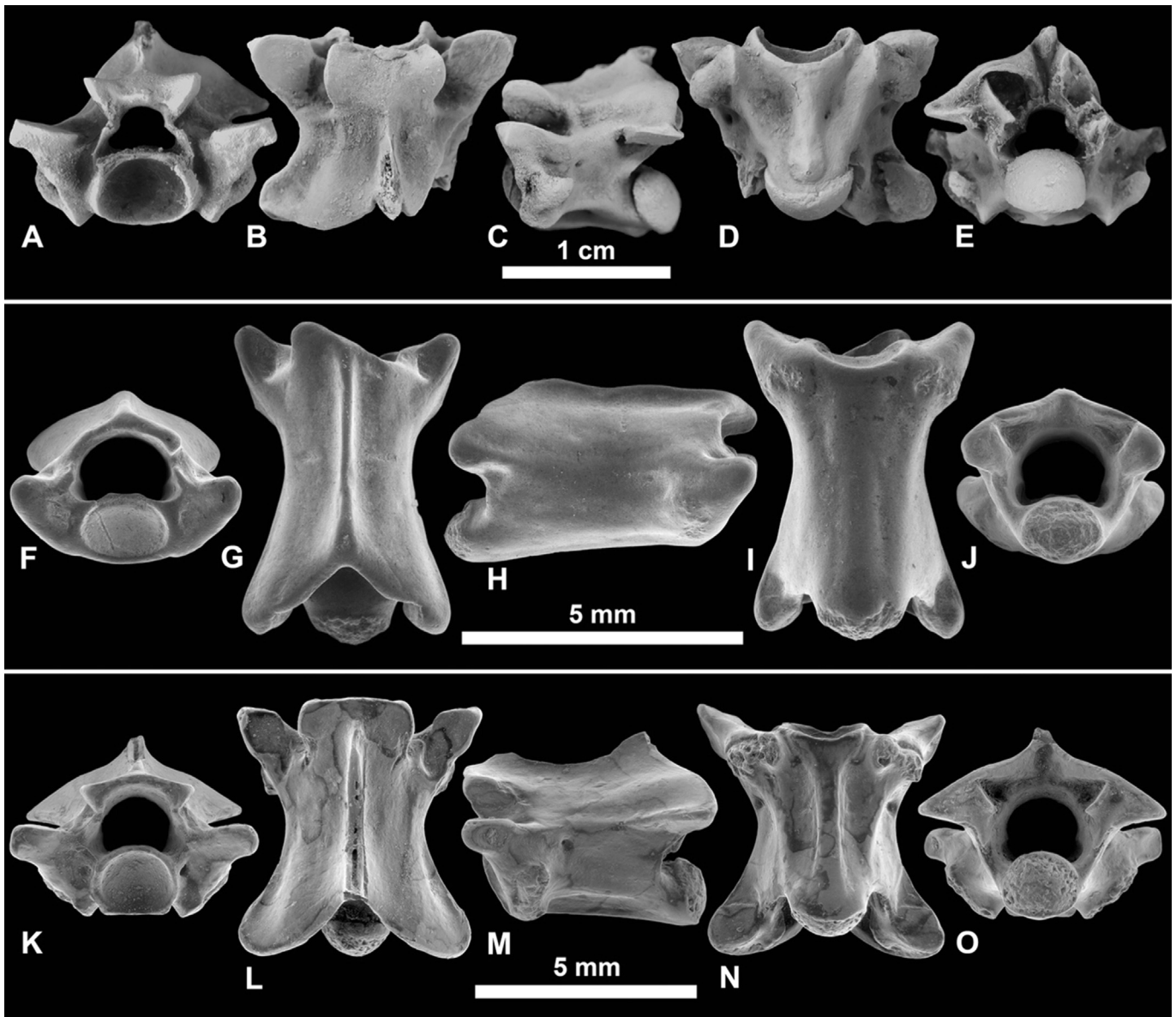
Figure 14. Boidae indet. A—E, WIF/A 2274, vertebra in (A) anterior, (B) dorsal, (C) left lateral, (D) ventral, and (E) posterior views. Colubroidea indet., *Procerophis sahnii*. F—J, GU/RSR/ TAD 9560, vertebra in (F) anterior, (G) dorsal, (H) left lateral, (I) ventral, and (J) posterior views. Caenophidia incertae sedis, *Thaumastophis missiaeni*. K—O, WIF/A 2310, vertebra in (K) anterior, (L) dorsal, (M) left lateral, (N) ventral, and (O) posterior views.

The present vertebrae differ from the Vastan vertebrae referred to Boidae indet. (Rage et al., 2008) in having a more bell-shaped neural arch (more evenly curved on Vastan specimens), a straighter zygosphene in anterior view (more convex on Vastan specimens), and a neural arch that is anteriorly inclined in lateral view (more horizontal on Vastan specimens).

Caenophidia Hoffstetter, 1939
Colubroidea Oppel, 1811
Colubroidea indet.
Procerophis sahnii Rage et al., 2008
Referred material: GU/RSR/TAD 9560, vertebra (from TAD-1)

Comments

The vertebra GU/RSR/TAD 9560 is about 4 mm wide across the prezygapophyses and 6 mm long, and is very lightly built with a wide and thin zygosphene, a bladelike and long neural spine, and

well-marked subcentral ridges (Fig. 14F—J). These characters indicate colubroid affinities. Moreover, this specimen can be attributed to the species *Procerophis sahnii* from Vastan (Rage et al., 2008) by the following diagnostic characters: prezygapophyseal buttresses compressed, forming a vertical ridge, and prolonged by anteriorly oriented prezygapophyseal processes.

Caenophidia incertae sedis
Thaumastophis missiaeni Rage et al., 2008
Referred material: WIF/A 2310, WIF/A 2352, WIF/A 4287, three vertebrae (all from TAD-1).

Comments

These vertebrae are slightly elongated (longer than wide, about 5 mm wide across the prezygapophyses and 5.5 mm long), and are more gracile than those described above. The neural spine is blade-like and the centrum is narrow (Fig. 14K—O). These characters are

reminiscent of colubroids (Rage et al., 2008). We attribute these vertebrae to *Thaumastophis missiaeni*, originally described from the early Eocene of Vastan (Rage et al., 2008), based on their zygapophyseal anatomy. The prezygapophyses are strongly compressed anteroposteriorly below the articular facets, thus forming laminar, deep prezygapophyseal processes that project slightly laterally. In addition, there are distinct diapophyseal and parapophyseal areas.

Crocodylomorpha Walker, 1970
Crocodyliformes Hay, 1930
Mesoeucrocodylia Whetstone and Whybrow, 1983
Neosuchia Benton and Clark, 1988
Dyrosauridae de Stefano, 1903
cf. *Congosaurus* sp.
Referred material: GU/RSR/TAD 9511, right femoral diaphysis; GU/RSR/TAD 9512, partial neural arch; GU/RSR/TAD 9514, right coracoid; GU/RSR/TAD 9516-9521, WIF/A 2265, WIF/A 2355, isolated teeth (all from TAD-1).

Comments

The coracoid (GU/RSR/TAD 9514, Fig. 15A–C) is the most complete bone in our sample. Although the anterior and ventral parts are broken, most of the diagnostic characters are present. The ventral shaft is narrow, with nearly parallel sides, and is relatively circular in cross-section. This differs from Eusuchia and some Mesoeucrocodylia, such as the goniopholid *Goniopholis*, which have a ventral shaft expanding at midshaft to a fan-shaped blade. In this character and in the aspect of the glenoid surface this coracoid resembles that of dyrosaurid neosuchians. Its morphology corresponds better to that of *Congosaurus bequaerti* (MRAC 1811, Fig. 15D–F) from the Paleocene of Landana, Angola (Swinton, 1950; Jouve and Schwarz, 2004), than to that of *Dyrosaurus maghribensis* (OCP DEK-GE 254) from the early Eocene of Ouled Abdoun Basin, Morocco, in having the coracoid foramen closer to the glenoid facet and dorso-ventrally oval (Jouve et al., 2006).
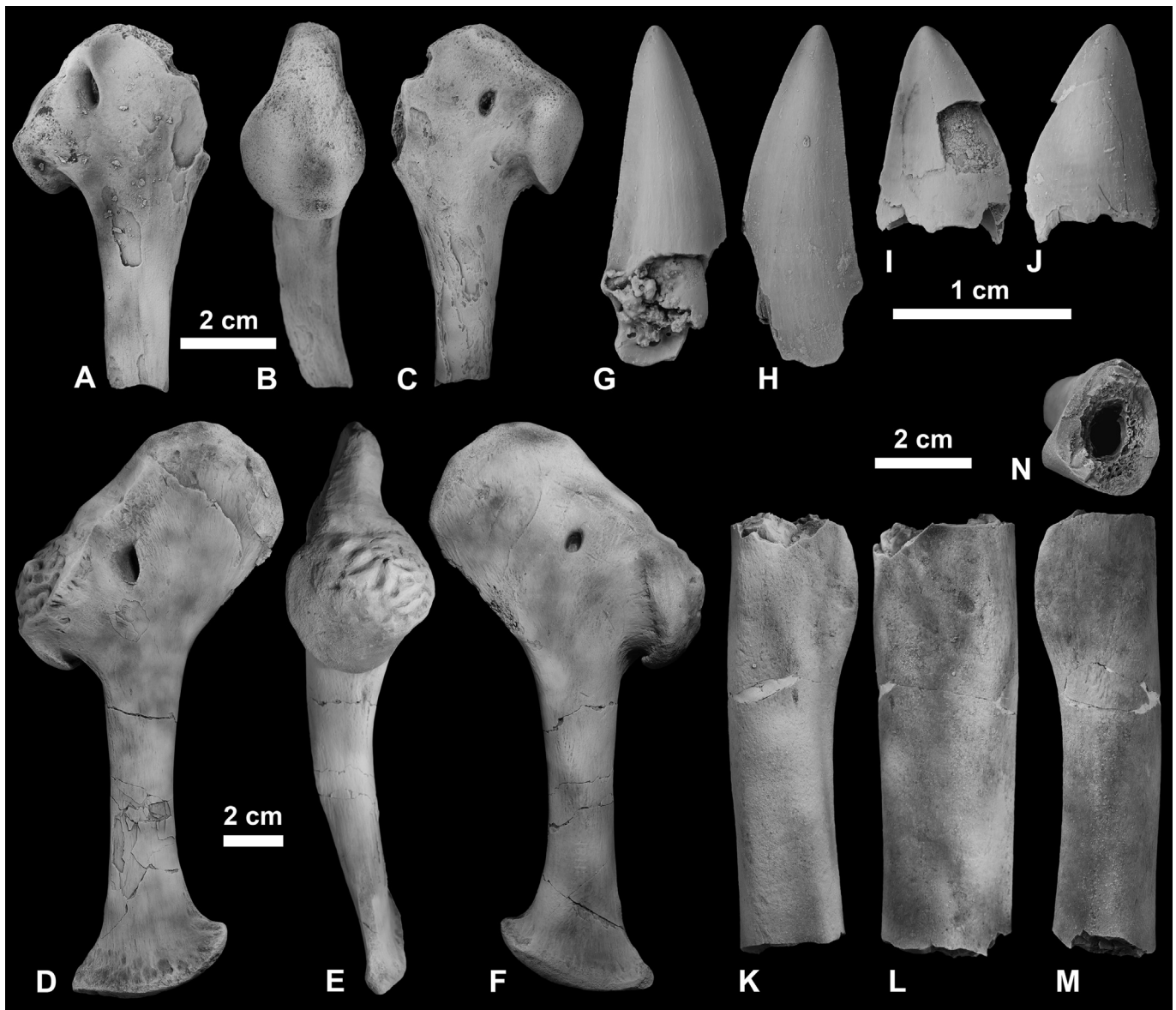
Figure 15. Dyrosauridae. A–C, cf. *Congosaurus* sp., GU/RSR/TAD 9514, right coracoid in (A) lateral, (B) dorsal, and (C) medial views. D–F, *Congosaurus bequaerti*, MRAC 1811, right coracoid in (D) lateral, (E) dorsal, and (F) medial views. G–N, cf. *Congosaurus* sp. G-H, WIF/A 2355, tooth in labial and lingual views. I–J, WIF/A 2265, tooth in labial and lingual views. K–N, GU/RSR/TAD 9511, right femur diaphysis in (K) medial, (L) anterior, (M) lateral, and (N) dorsal views.

Crocodyliform teeth are rare in the Cambay Shale, and the only crocodyliform teeth found in Tadkeshwar mine are elongated teeth with a weak to moderate mediolateral compression, which is characteristic of Dyrosauridae (Fig. 15G–J). However, they differ from the genera *Congosaurus* and *Dyrosaurus* in having weaker (or absent) coronal striae (Jouve and Schwarz, 2004; Jouve, 2005) and sometimes bearing very fine serrations (6 denticles/mm).

A robust part of a diaphysis with a fourth trochanter (GU/RSR/TAD 110) is typical of a crocodyliform femur corresponding in size to the same species (Fig. 15K–N).

Although dyrosaurids are known from very well-preserved comparative material from the early Paleogene of Africa, there are also records of dyrosaurids from the Indian subcontinent. These are represented by isolated vertebrae and teeth, a partial frontal, and a partial mandible from the Cretaceous of India (e.g., Rana, 1987; Prasad and Singh, 1991; Rana and Sati, 2000; Khosla et al., 2009); a nearly complete vertebral column and portions of an associated pelvis and hind limb from the Paleocene of Pakistan (Storrs, 1986); and a supraoccipital bone, a postorbital bone, and small jaw fragments and isolated vertebrae from the Eocene of Pakistan (Buffetaut, 1978b). Unfortunately, none of these specimens contain similar bones to Tadkeshwar specimens for a useful comparison.

Aves Linnaeus, 1758
?Psittaciformes Wagler, 1830
Vastanavidae Mayr et al., 2010
Vastanavis Mayr et al., 2007
Vastanavis sp.
Referred material: WIF/A 2353, complete right humerus (TAD-1).

Comments

The humerus is 74 mm long (Fig. 16A and B), a little longer and slightly wider distally than GU/RSR/VAS1803, a left humerus identified as *Vastanavis* sp. from Vastan mine. Like the Vastan humerus, the shaft is slightly sigmoidally curved in the craniocaudal plane, and its caudal surface is roof shaped (subtriangular in cross section) in the proximal third (Mayr et al., 2013). The crista deltopectoralis is long, extending one-third of the humerus length. The proximal and distal articulations are somewhat eroded on WIF/A 2353 but several characters shared with *Vastanavis* are clearly visible. For example, the ovate attachment scar for musculus latissimus dorsi pars caudalis which is situated next to the fossa pneumotricipitalis is distinct, the fossa musculi brachialis is large, the processus flexorius is very short, and the tuberculum supracondylare ventrale is very large and wide. Both humeri possess similar distal attachment scars, one for the tendon of musculus pronator superficialis and the other for the tendon of musculus extensor carpi radialis, which extends onto the cranial humerus surface.

At present it is not possible to determine if the humerus belongs to *Vastanavis eocaena* or to *V. cambayensis* because these species are differentiated based only on coracoids.

Aves indet.
Referred material: WIF/A 2354, distal right tibiotarsus (TAD-1).

Comments

This bone (Fig. 16C–D) is smaller and more gracile than the tibiotarsus of *Vastanavis* (Mayr et al., 2013). It resembles more the small unidentified slender tibiotarsus GU/RSR/VAS 440 from Vastan (Mayr et al., 2007). However, it differs from the latter by lacking the supratendinal bridge (pons supratendineus) and in having very different proportions of the condylus lateralis and condylus medialis.

Mammalia Linnaeus, 1758
Pantodonta Cope, 1873
cf. Coryphodontidae indet. Marsh, 1876
Referred material: GU/RSR/TAD 9204, right P1 (TAD-2) and, tentatively, GU/RSR/TAD-9501, fragment of a larger tooth (probably a lower right incisor) and GU/RSR/TAD 9515, a rib (both from TAD-1).

Comments

The premolar GU/RSR/TAD 9204 measures 12.20 mm long and 9.78 mm wide (Fig. 17A–C), and is very similar morphologically to P1 of the early Eocene (Wasatchian) pantodont *Coryphodon*. It is about 20% shorter and 10% narrower than P1 in USNM 527729, *Coryphodon* sp., from near the middle of the lower Eocene Willwood Formation of the southern Bighorn Basin, Wyoming (Fig. 17D–E). The tooth is triangular, longer anteroposteriorly than wide, with a modest ectoflexus, slightly more pronounced than that in *Coryphodon*. It is dominated by a central buccal cusp, which forms the vertex of a shallow V-shaped crest, the limbs of which extend anterobuccally and posterobuccally about equal distances to the buccal corners of the tooth. The enamel is worn through to the dentine at the tip of the cusp and along the crests, as is typical in pantodonts. Under the light microscope the margins of the enamel on the occlusal surface of the crests show fine transverse ridges that can be felt with a fingernail. These ridges may be a manifestation of
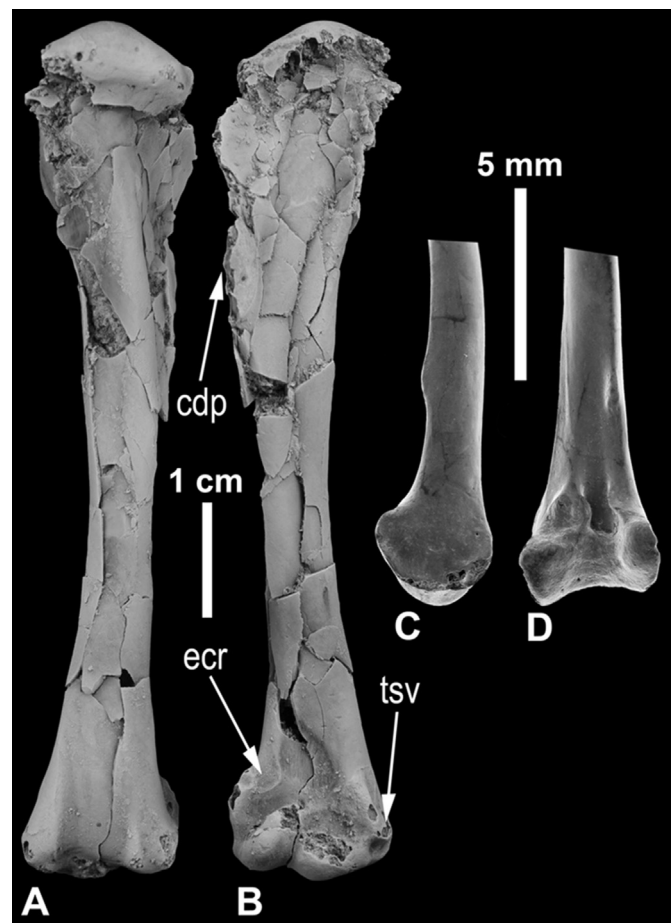

Figure 16. Aves, *Vastanavis* sp. A–B, WIF/A 2353, right humerus in (A) caudal and (B) cranial views. Aves indet. C–D, WIF/A 2354, distal end of right tibiotarsus in (C) cranial and (D) medial views. Abbreviations: cdp–crista deltopectoralis; ecr–attachment scar of the tendon of musculus extensor carpi radialis; tsv–tuberculum supracondylare ventrale.
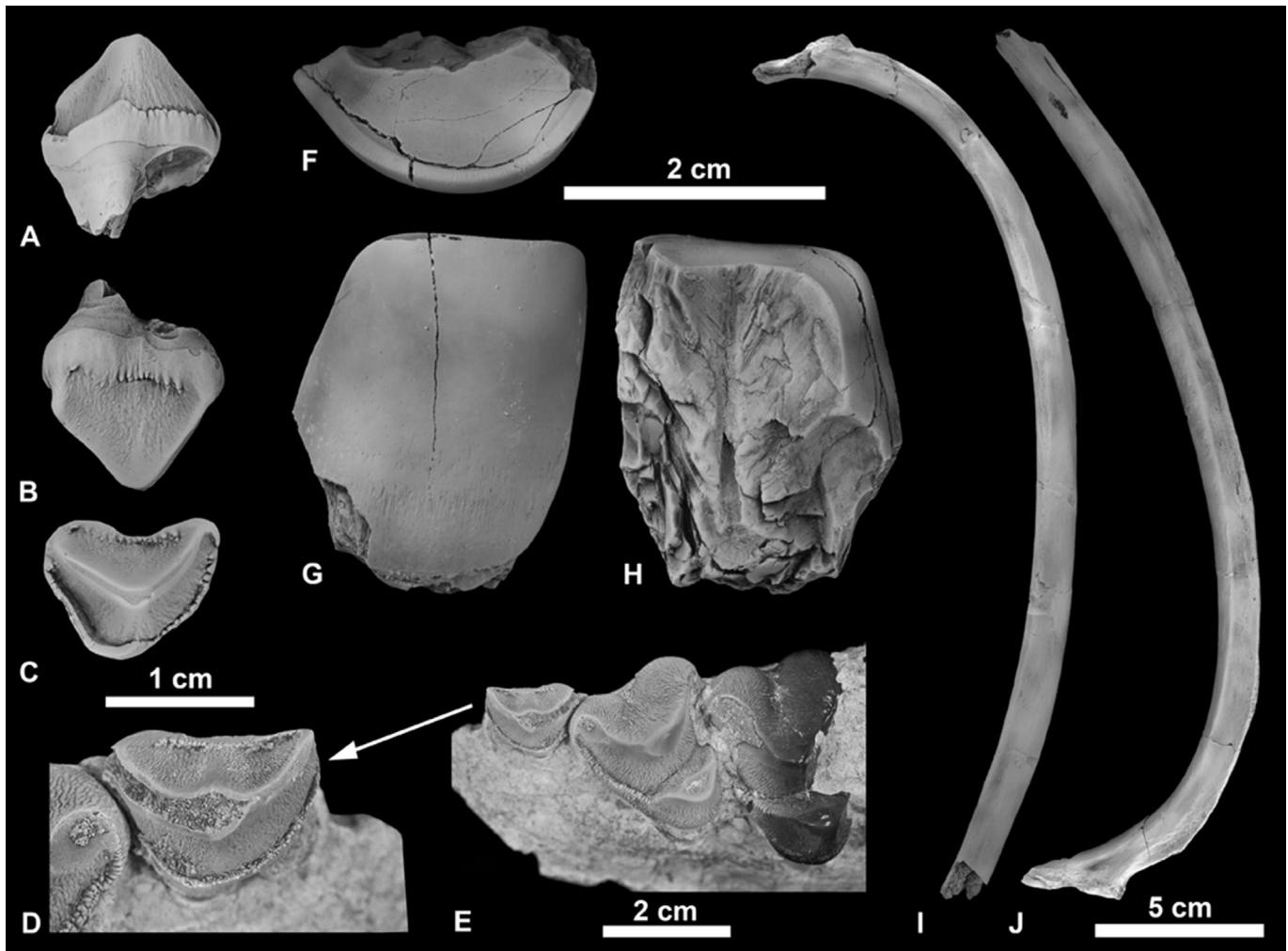
Figure 17. Pantodonta. A–C, cf. Coryphodontidae indet., GU/RSR/TAD 9204, right P1 in (A) lingual, (B) labial, and (C) occlusal views. D–E, *Coryphodon* sp., USNM 527729 (Willwood Formation, Wyoming), left complete maxillary with P1-3 visible (E), and P1 reversed (D) in occlusal views. F–H. cf. Coryphodontidae indet., GU/RSR/TAD 9501, tooth fragment in occlusal (F), lateral (G), and internal (H) views. I–J, GU/RSR/TAD 9515, unidentified rib in anterior (I) and posterior (J) views.

the Hunter-Schreger bands of the enamel, or of an unusual enamel prism arrangement as has been described in *Coryphodon* (Koenigswald and Rose, 2005). The crown is expanded lingually slightly posterior to the middle of the tooth, but neither protocone nor hypocone cusps are evident. There is a weak ectocingulum bearing small digitations of enamel, which fades toward the anterior and posterior ends. A similar rugose anterolingual cingulum is present. Posterolingually the cingulum is better developed, smooth, and slightly expanded into a narrow shelf. The surface enamel between cingula and apex is vertically crenulated. Nearly all of these details are almost precisely mirrored in *Coryphodon*, allowing us to attribute this tooth confidently to Pantodonta. This is the first record of a pantodont from the Indian subcontinent.

A fragment of a heavily worn larger tooth (GU/RSR/TAD 9501, maximum dimensions 27.7 mm × 21.6 mm; crown height 26 mm) may also belong to a pantodont (Fig. 17F–H). The enamel at the base of the crown is crenulated, as in the premolar, though the rest of the enamel is smooth, as if polished, perhaps from abrasion during transport. Tapering toward the base of the crown suggests that the tooth was rooted. The occlusal surface reveals a large, smooth dentine area enclosed by a curved enamel edge, the surface of which bears transverse ridges as on the premolar. It may be a

part of a large pantodont incisor. No other mammal of comparable size has yet been found in the early Eocene of India.

A rib of about 25 cm length also attests the presence of a *Coryphodon*-size mammal (Fig. 17I–J), although it seems more gracile than in *Coryphodon*. The distal part of the rib is missing but the section and curvature suggest that it was no longer than 30 cm.

Tillodontia Marsh, 1875
Family Esthonychidae Cope, 1883
Esthonychinae Zittel and Schlosser, 1911
***Indoesthonyx*, gen nov.**
urn:lsid:zoobank.org:act:8B2AFE13-A577-4B31-8E76-CED859255039
***Indoesthonyx suratensis*, gen et sp. nov.**
urn:lsid:zoobank.org:act:ECE2B737-D31F-402F-9345-5805E7868E96
(Fig. 18A–F)
Etymology: Genus name refers to India and the allied genus *Esthonyx*. Species name is for the nearby city of Surat, and the Surat District of Gujarat, where Tadkeshwar mine is located.
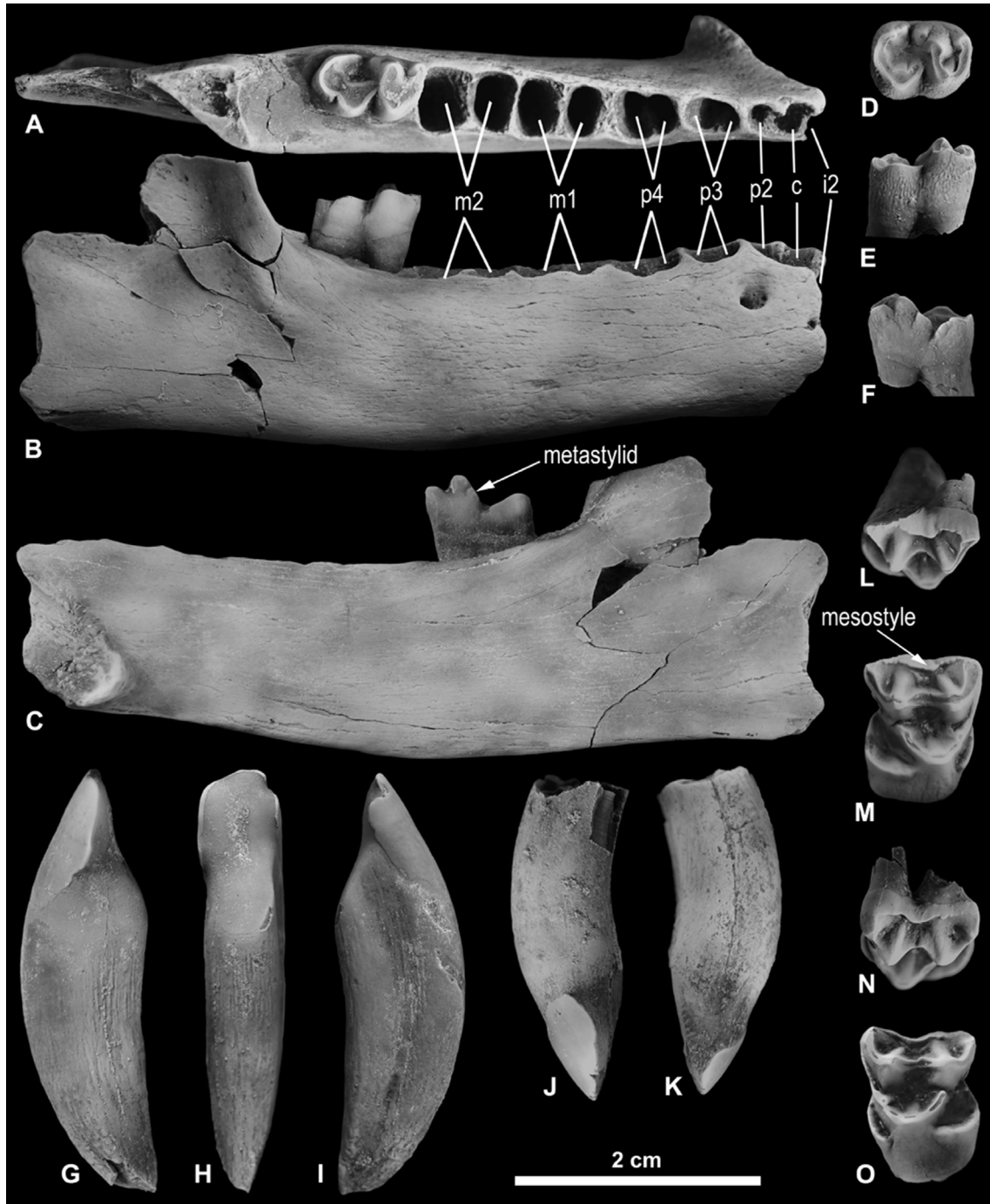Holotype: WIF/A 2333, right dentary with m3 and alveoli for i2–m2 (TAD-1).

Figure 18. Tillodontia. *Indoesthonyx suratensis*, gen et sp. nov. A–C, WIF/A 2333, holotype, right dentary with m3 in (A) occlusal, (B) labial, and (C) lingual views. D–F, WIF/A 4225, right m1 in (D) occlusal, (E) labial, and (F) lingual views. cf. *Indoesthonyx suratensis*, G–I, WIF/A 4230, left i2 in (G) distal, (H) lingual, and (I) mesial views. J–K, WIF/A 4229, left I2 in (J) distal and (K) mesial views. L–M, WIF/A 4227, right M1 in (L) labial and (M) occlusal views. N–O, WIF/A 4226, left M2 in (N) labial and (O) occlusal views.

Hypodigm: Holotype and WIF/A 4225, right m1 (TAD-2).

Horizon and locality: Cambay Shale Formation, Ypresian, lower Eocene, Tadkeshwar Lignite Mine (TAD-1 and TAD-2), Surat District, Gujarat, India.

Diagnosis: Similar to *Esthonyx*, *Azygonyx*, *Plesiesthonyx*, and *Franchaius* in size and general molar morphology. Lower dental formula ?-1-3-3. Symphysis probably unfused, as in *Azygonyx* (and in contrast to *Esthonyx*), and incisors rooted, not ever-growing. Differs from *Azygonyx* and *Esthonyx* in having shorter m3 without an extended third lobe, and p3 and p4 anteroposteriorly compressed with closely appressed bilobed roots. Differs from *Plesiesthonyx* and *Franchaius* in having narrower molars with higher, stronger paraconids.

Description

The holotype is a right dentary with m3 and the alveoli for i2-m2, from the lower fossiliferous horizon TAD-1 (Fig. 18A–C).

The dentary depth is 16.25 mm below the anterior root of m3 and 14.0 mm below the anterior root of m1. The length of the m3 is 8.55 mm and the width is 5.15 mm (trigonid) and 5.0 mm (talonid). Though generally similar to North American *Esthonyx* and *Azygonyx*, it differs in having a distinctly smaller hypoconulid lobe on m3 and much more mesiodistally compressed premolars. The m3 has a slight posterior expansion of the hypoconulid, comparable to that in one specimen of *Plesiesthonyx chardini* figured by Baudry (1992: plate II, 19; MNHN Av 4560), but otherwise smaller than in other Eocene tillodonts. The paraconid is well developed and taller than in the North American and European genera, and the metastylid is low and relatively weak, as in *Azygonyx* and *Plesiesthonyx*, unlike the stronger metastylids of *Esthonyx* and *Franchaius russellonyx*. The p3 and p4, judging from the alveoli, had fused roots and were distinctly shorter than the molars (p3 alveoli <65% as long as m1 or m2 alveoli, p4 alveoli <70% as long as the molar alveoli), whereas both premolars have two separate roots and tend to be less reduced relative to the molars in the North American genera (p3 is 70–89% as long as m1 or m2, and p4 is 84–99% as long as m1 or m2, in several species of *Esthonyx* and *Azygonyx*; Gingerich and Gunnell, 1979). The p2 in the new species was small and had a weakly bilobed root, whereas p2 in *Esthonyx* and *Azygonyx* may have two roots, one root, or a bilobed root. The canine alveolus is slightly larger than that of p2, but much smaller than that of i2, resembling *Azygonyx* but unlike *Esthonyx*, in which the canine is as large as i2 (e.g., Gazin, 1953: Fig. 2). A large alveolus in front of the canine alveolus held the enlarged, slightly procumbent i2. A small indentation buccally between the canine and i2 alveoli may have housed a vestigial i3, but its presence is ambiguous. Gingerich (1989) noted the loss of i3 in some individuals of *Azygonyx*.

The dentary of the holotype is broken medial to the enlarged incisor, and has a small, flattened rugose area at the back of what appears to be an unfused symphysis. If we are correct in inferring an unfused symphysis, this would be a presumably primitive resemblance to *Azygonyx* and a contrast with *Esthonyx* (dentaries of the European species are unknown). However, the apparent symphysis projects more medially than in *Azygonyx*, raising the possibility that it may simply be a fracture in a fused mandibular symphysis or, alternatively, that the symphysis was wider than in *Azygonyx*. The latter interpretation is consistent with the large second incisor alveolus, which appears to be relatively larger than in the North American genera. The seemingly oblique medial border of the symphysis seen in dorsal view (Fig. 18A) is an artifact of breakage more anteriorly. In any case, the symphysis extends posteriorly to the level of the posterior root of p3. A large mental foramen is located beneath the junction of p2 and p3, and a smaller one slightly lower, below the canine alveolus.

A referred m1, WIF/A 4225, found in the upper level (TAD-2) is of appropriate size and morphology to represent *Indoesthonyx suratensis* (Fig. 18D–F). It is relatively short and wide (length = 8.10 mm, width trigonid = 6.50 mm, width talonid = 6.65 mm). Like the m3, it has a relatively tall paraconid. The tooth is relatively unworn, and has a stronger metastylid and a small entoconulid, which is not discernible on the more worn m3 in the holotype. The enamel on its buccal surface is distinctly crenulated, a feature typical of esthonychine tillodonts.

Discussion

The holotype dentary and referred isolated molar show sufficient differences from known tillodonts to warrant allocation of these specimens to a new genus and species that appears to be most similar to the early Eocene North American and European esthonychine tillodonts. It is noteworthy that *Plesiesthonyx chardini* and *Franchaius russellonyx* have recently been considered as synonyms of *Plesiesthonyx munieri* (Hooker, 2010). While the polarity of the small hypoconulid lobe of m3 is ambiguous, the reduced and compacted lower premolars and enlarged i2 of *Indoesthonyx suratensis* appear to be derived states compared to the European and American taxa. Among Asian tillodonts, only early Eocene *Paresthonyx orientalis* (Wutu Formation, China; Tong and Wang, 2006) is close enough in size, morphology, and age to be related to *Indoesthonyx*. *Paresthonyx* is based on upper teeth, however, and cannot be directly compared with *I. suratensis*. Two other esthonychid tillodont species were previously described from the early Eocene of India, both from the Vastan Mine. One is a small esthonychid, *Anthraconyx hypsomylus*, which differs from all other early Eocene tillodonts in being very hypsodont (Rose et al., 2013). The second taxon, based on two isolated teeth, I2 and M3, was identified as cf. *Esthonyx* sp. (Rose et al., 2009b). Although these teeth cannot be directly compared with the new taxon, they appear to be closer in size to *Indoesthonyx suratensis* from Tadkeshwar and may represent the same species (see Discussion in the next section).

cf. *Indoesthonyx suratensis*
Fig. 18G–O
Referred material: WIF/A 4226, left M2; WIF/A 4227, right M1; WIF/A 4228, right m2; WIF/A 4229, left I2; WIF/A 4230, left i2 (all from TAD-2).

Comments

These five isolated esthonychine teeth found at TAD-2 are somewhat larger than the holotype and represent either much larger individuals of *Indoesthonyx suratensis* or possibly a distinct taxon. They include two incisors, an m2, and two upper molars, and are thus not directly comparable to the holotype and referred specimen. The incisors are typically esthonychine in having large roots and enamel limited largely to the labial surface. The upper incisor (WIF/A 4229, crown mesiodistal width = 7.10 mm, crown height = 8.50 mm; Fig. 18J–K) is wider, more gently curved mediolaterally on its labial surface, and lower crowned (possibly due to wear) than the lower i2. It closely resembles I2 in *Esthonyx bisulcatus* (USGS 10258) but is larger. The lower i2 (WIF/A 4230, crown mesiodistal width = 7.20 mm, crown labiolingual width = 10.35 mm, crown height = 12.50 mm; Fig. 18G–I) is a robust tooth, with enamel extending onto the labiomesial and labiodistal surfaces, as in *Esthonyx* and *Azygonyx*. However, the tooth is larger than in specimens of *E. bisulcatus* and even *A. grangeri*, approaching the size of i2 in late early Eocene *Megalesthonyx hopsoni*. It is much larger than the tooth that occupied the alveolus in the holotype of *I. suratensis*, but plausibly represents the same taxon as the upper incisor. A heavily worn isolated right m2 (WIF/A 4228: length = 9.90 mm, width trigonid = 7.60, width talonid = 7.40 mm) is about 20% larger than the holotype and referred m1 of *I. suratensis*. It further differs in having the trigonid and talonid of approximately equal lengths, but this may be exaggerated by the heavy wear. The upper molars are identified as right M1 (WIF/A 4227: L × W = 9.10 mm × 11.95 mm; Fig. 18L–M) and left M2 (WIF/A 4226: L × W = 9.25 mm × 12.60 mm; Fig. 18N–O) based on slight differences in tooth proportions and shape, but they are so close in morphology that both could be M1, and they surely represent the same taxon. They are very similar to molars of *Esthonyx*, differing mainly in having a distinct, crest-like mesostyle (not connected to the centrocrista) on the ectocingulum, a shallower ectoflexus, and a more flaring posterolingual shelf that lacks a distinct hypocone.

Discussion

If the additional isolated teeth from TAD-2 prove to be large individuals of *I. suratensis*, they would provide additional diagnostic criteria for separating this species (e.g., enlarged second incisors, upper molars with cingular mesostyle and flaring posterolingual cingulum). However, until the range of intraspecific variation is better understood, it may be better to interpret these isolated teeth as representing an unidentified esthonychine. The upper molars from TAD-2 are more than 15% larger than *Paresthonyx orientalis* from the early Eocene of China, and further differ in the same traits that separate them from *Esthonyx*, namely a much more expanded posterolingual shelf and a small cingular mesostyle.

As noted above, two isolated upper teeth from Vastan mine, designated cf. *Esthonyx* sp. (Rose et al., 2009b), may be compared with the isolated teeth from TAD-2. The Vastan I^2 (GU/RSR/VAS 1651) is much less worn than the I2 from TAD-2, complicating comparison, but is about 30% narrower. Similarly, the M3 (GU/RSR/VAS 1587) from Vastan, though not directly comparable, is smaller (10—15% narrower and nearly 40% shorter mesiodistally) than the molars from TAD-2. Based on the limited evidence, it seems unlikely that these Vastan teeth belong to the same taxon as the isolated teeth from TAD-2. It is possible that the Vastan teeth pertain to *Indoesthonyx suratensis*, but until teeth are known from the same loci this hypothesis cannot be tested.

Rodentia Bowdich, 1821
Ischyromyoidea Alston, 1876
Ischyromyidae Alston, 1876
Ailuravinae Michaux, 1968
Meldimys Michaux, 1968
cf. *Meldimys* sp.
Referred material: WIF/A 2331, right femur; WIF/A 2276, right distal femur; WIF/A 2278, right tibia (all from TAD-1).

Comments

A 40 mm-long complete tibia (WIF/A 2278) with a large posterior process at the distal end is typical of a rodent (Fig. 19F—J). The shaft is robust and bowed anteriorly in lateral view. The tibial crest extends distally slightly beyond midshaft. A complete short and robust femur (WIF/A 2331) with a shallow and somewhat mediolaterally restricted patellar groove and greater trochanter projecting above the head is also referred to a rodent (Fig. 19A—E). Its length (40 mm) is similar to the tibia and thus it could represent the same species. The morphology of the femur, with a relatively wide and flat distal end and a shallow patellar groove is different from the described early Eocene rodent cf. *Thisbemys* sp., which is almost as wide anteroposteriorly as mediolaterally, with a moderately elevated, narrow, and well-defined patellar groove (Rose and Chinnery, 2004, Fig. 8). The morphology and robustness of the Tadkeshwar bones are comparable to those of extant geomyid and aplodontid rodents (Rose and Chinnery, 2004, Fig. 9), and suggest that they belong to a terrestrial semi-fossorial taxon rather than an arboreal form. However, European *Ailuravus macrurus* from the middle Eocene of Messel, which has been interpreted as arboreal (Wood, 1976), also has a short and robust femur (TS, pers. obs.).

The ailuravine *Meldimys musak* from Vastan mine is the only early Eocene rodent described from the Cambay Shale Formation (Rana et al., 2008; Gupta and Kumar, 2015), consequently we tentatively allocate these bones to *Meldimys*. However, the tibia is notably more robust than two undescribed tibiae (GU/RSR/VAS 795, 796) from Vastan mine that we attribute tentatively to *M. musak*.

Chiroptera Blumenbach, 1779
Microchiropteramorpha Simmons and Geisler, 1998
"Eochiroptera" Van Valen, 1973
"Eochiroptera" indet. 1
Referred material: WIF/A 2330, distal left humerus (TAD-1).

Comments

A small distal humerus with a typical chiropteran morphology, including a rounded capitulum with a reduced medial epicondyle (epitrochlea), documents the presence of a bat (Fig. 19K). Its simple morphology without specialization indicates that it belongs to a primitive "eochiropteran" such as *Archaeonycteris* sp., figured by Russell and Sigé (1970).

"Eochiroptera" indet. 2
Referred material: WIF/A 2316, distal left humerus (TAD-1).
Comments
A distal bat humerus at least 20% wider than WIF/A 2330 presents a slightly damaged trochlea (Fig. 19L). It is generally similar in morphology to WIF/A 2330.

Primates Linnaeus, 1758
Adapoidea Trouessart, 1879
Asiadapidae Rose et al., 2009
Marcgodinotius Bajpai et al., 2005
Marcgodinotius indicus Bajpai et al., 2005
Referred material: WIF/A 2334, right dentary with m2-3 and alveoli for i1-m1 (TAD-1); WIF/A 4231, left dentary with p3-m2 (TAD-2).

Comments

A very well preserved dentary containing m2 (length = 2.50, width trigonid = 1.75, width talonid = 1.80 mm) and m3 (length = 2.40, width trigonid = 1.45, width talonid = 1.35 mm) and all the alveoli for i1 to m1 (WIF/A 2334, Fig. 20A—D) is slightly larger than but similar in morphology to *Marcgodinotius indicus* from Vastan, particularly to the dentary of GU/RSR/VAS 744 and to the molars in GU/RSR/VAS 227 (Rose et al., 2009a). There are two mental foramina, a small one below the canine-p1 junction and a larger one below the posterior alveolus of p2. This is slightly anterior to most other specimens, in which the anterior foramen is usually beneath p1 and the posterior one below p3. GU/RSR/VAS 227, however, differs in having three small foramina, below p1, p2, and p4; hence there is clearly intraspecific variation in position of these foramina. The molars have arcuate paracristids and no trace of a paraconid. The new jaw confirms the lower dental formula of 2-1-4-3, as well as an unfused symphysis. It is distinctive in having the alveoli for p3 larger than those for p4 or m1 (as in GU/RSR/VAS 744), the alveoli for the two-rooted p2 and single-rooted p1 slightly less reduced than in other specimens, and the canine alveolus larger than in other specimens. The large canine suggests the possibility of sexual dimorphism, which has been postulated for other adapoids (see Rose et al., 2009a). The alveoli for the two incisors are small, equal in size, and anteriorly inclined as in GU/RSR/VAS 744 and *Cantius* (Rose et al., 1999). Interestingly, this is the first specimen of *M. indicus* that preserves the complete posterior part of the dentary. It shows a posteriorly inclined coronoid process that differs from the much more vertical coronoid process of most other adapoids including the earliest Eocene *Cantius torresi* from the Willwood Formation of Wyoming (Gingerich, 1995). The angular process is long and very thin, and slightly medially inflected, a condition different from most of the adapoids, which have a dorso-

Figure 19. Rodentia, cf. *Meldimys* sp. A–E, WIF/A 2331, right femur in (A) anterior, (B) posterior, (C) medial, (D) proximal, and (E) distal views. F–J, WIF/A 2278 right tibia in (F) anterior, (G) posterior, (H) medial, (I) distal, and (J) lateral views. Chiroptera. (K) "Eochiroptera" indet. 1, WIF/A 2330, left humerus in anterior view. (L) "Eochiroptera" indet. 2, WIF/A 2316, left humerus in anterior view.

ventrally extended angular process (Szalay and Delson, 1979, Fig. 51; Hooker 2010, text-Fig. 23). The condyle is midway between the top of the coronoid process and the tip of the angular process. This condition, in which the condyle is only slightly higher than the level of the teeth, also differs from most adapoids, in which the condyle is higher and closer to the top of the coronoid process.

A second dentary, from the higher horizon (TAD-2), contains worn p3–m2 (WIF/A 4231, Fig. 20E–G). The measurements (mm) of the teeth are as following: p3 length = 2.0, width = 1.25; p4 length = 2.10, width trigonid = 1.20, width talonid = 1.25; m1 length = 2.25, width trigonid = 1.35, width talonid = 1.60; m2 is damaged and cannot be measured accurately. This dentary is a little smaller than WIF/A 2334 but similar in size and morphology to other specimens of *Marcgodinotius indicus* except that the alveoli for p2 are slightly more compressed and oblique, and the alveolus of p1 is missing and replaced by a diastema. The apparent compression of p2 suggests that p1 was lost during life and its alveolus resorbed. Even

if absence of p1 was real, however, this criterion alone is not adequate justification to separate this jaw specifically, as other early euprimates are known in which presence of p1 varies intraspecifically (e.g., *Teilhardina belgica* and *T. americana*; Bown and Rose, 1987; Smith et al., 2006). The p3 and p4 lack both paraconid and metaconid, like most specimens of *M. indicus*. Several small mental foramina are present, one below p3 and multiple foramina below the front of p2. The specimen is of further interest in showing bite marks on both sides of the dentary.

A complete humerus (GU/RSR/TAD 9005) of appropriate size to represent *M. indicus* was also found at TAD-1. It is very similar in morphology to a euprimate humerus from Vastan mine, GU/RSR/VAS 713 (Rose et al., 2009a: Fig. 16), and will be described in a detailed account of new primate postcrania (Dunn et al., in press).

?*Asiadapis* Rose et al., 2007
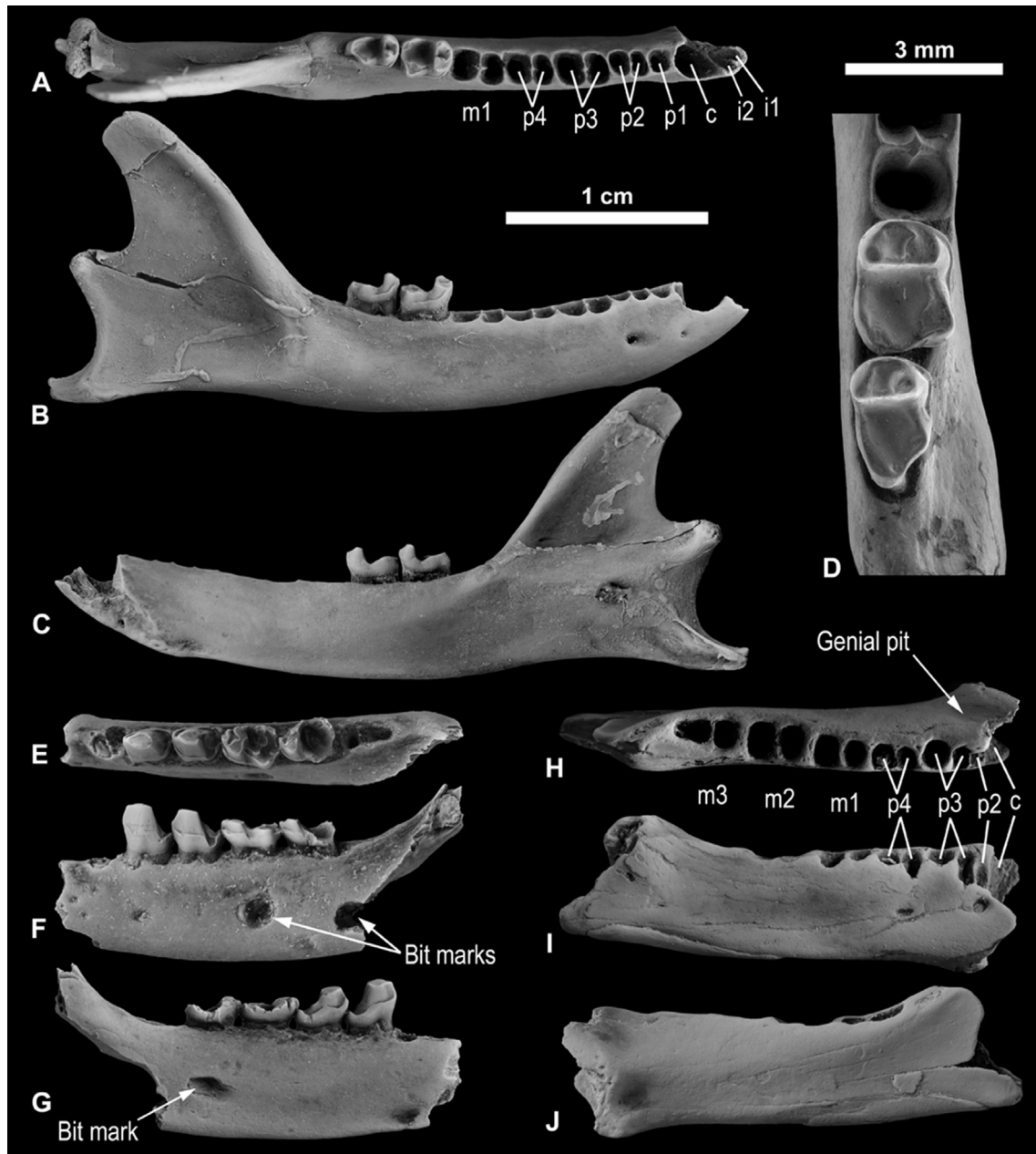cf. *Asiadapis cambayensis* Rose et al., 2007

Figure 20. Primates. *Marcgodinotius indicus.* A–D, WIF/A 2334, right dentary with m2–3 in (A) occlusal, (B) labial, and (C) lingual views, and (D) occlusal close-up. E–G, WIF/A 4231, left dentary with p3–m2 in (E) occlusal, (F) labial, and (G) lingual views. cf. *Asiadapis cambayensis.* H-J, GU/RSR/TAD 9004, edentulous right dentary in (H) occlusal, (I) labial, and (J) lingual views.

Referred material: GU/RSR/TAD 9004, edentulous right dentary with alveoli interpreted as c through m3 (TAD-1).

Comments

An edentulous primate dentary with alveoli for several antemolar teeth (Fig. 20H–J) is distinctly larger and more robust than *Marcgodinotius indicus* and had no more than three premolars; therefore, it may represent *Asiadapis cambayensis* or a closely related adapoid. However, with no teeth preserved and damage at the front of the dentary, the alveoli are open to various interpretations. Most likely is that the alveoli pertain to a canine directly followed by a small, single-rooted p2 and

double-rooted p3–m3, which corresponds to the dental formula of *Asiadapis cambayensis* described from Vastan mine (Rose et al., 2007, 2009a). The size of the dentary is very similar to the holotype GU/RSR/VAS 6, but the jaw is more robust and foreshortened, especially near the unfused symphysis. There are two mental foramina, below the tiny p2 alveolus and below the anterior root of p4, the posterior one slightly farther back than in the holotype and referred specimens of *A. cambayensis*. Inferolingually at the symphysis is a prominent depression (genial pit) presumably for attachment of genioglossus and geniohyoid muscles. This pit is not evident on other specimens of *Asiadapis*, although a similar fossa is present in some specimens of *Cantius* (e.g., USNM 494881, 533559, UM 101958). The

alveoli for p3 are larger than those for p4, as in asiadapids generally. In contrast to the previously described dentaries of *A. cambayensis*, however, the canine alveolus is larger, the p2 alveolus is markedly compressed anteroposteriorly, and the symphysis is deep and robust.

These contrasting traits, when combined with a different interpretation of the anterior alveoli, suggest that, alternatively, GU/RSR/TAD 9004 might represent *Vastanomys major* or a closely related omomyid. This requires interpretation of the large anterior alveolus as that for i1 rather than for the canine. A robust, fore-shortened dentary typifies early Eocene omomyids such as *Tetonius* and *Pseudotetonius*, which have a hypertrophied i1 and reduced, anteroposteriorly compressed teeth between i1 and p4 (Bown and Rose, 1987). These genera also have a very similar genial pit at the back of a robust symphysis. If the large anterior alveolus of GU/RSR/TAD 9004 held an enlarged i1 (and possibly i2 at the back of the same alveolus), followed by a small, anteroposteriorly compressed canine and then two or three premolars (if the anterior premolars were single-rooted), the dental formula and alveolar proportions could be consistent with omomyid affinity. However, the large size of p3, whether double- or single-rooted, is unexpected in an omomyid. Therefore it is more likely that this jaw represents an asiadapid. The modifications at the front of the jaw suggest that it may represent a taxon distinct from *A. cambayensis*, but better specimens are needed to test this hypothesis.

An isolated euprimate calcaneus (WIF/A 2336) from TAD-1 is comparable in size to that of *A. cambayensis* from Vastan mine (GU/RSR/VAS 707 and 716; Rose et al., 2009a: fig. 19). It will be described elsewhere (Dunn et al., in press).

Hyaenodonta Van Valen, 1967
Hyaenodontidae Leidy, 1869
Indohyaenodontinae Solé et al., 2013
Indohyaenodon Bajpai, Kapur, and Thewissen, 2009
Indohyaenodon raoi Bajpai, Kapur, and Thewissen, 2009
Referred material: GU/RSR/TAD 9000, left dentary with m1; WIF/A 4209, right dentary with m2 (both from TAD-2).

Comments

Two jaw fragments found in the upper level TAD-2 belong to a mid-sized hyaenodontid mammal: GU/RSR/TAD 9000 bears m1 (L = 6.0, Wtri = 3.05, Wtal = 2.75 mm, Fig. 21A–C) and WIF/A 4209 contains m2 (L = 7.30, Wtri = 4.25, Wtal = 3.05 mm, Fig. 21D–F). The morphology of the teeth agrees with that of *Indohyaenodon raoi*, a hyaenodontid described based on specimens from Vastan mine (Bajpai et al., 2009; Rana et al., 2015). The new molars notably display the typical features of this species such as the subequal paraconid and metaconid, the open trigonid with the paraconid well mesial to the other cusps, the trigonid considerably taller than the talonid, the small talonid basin surrounded by the three major cusps, and the complete buccal cingulid.

One can note the absence of the first molar in WIF/A 4209, but because the bone of the dentary is remodelled anterior to the m2, the loss of the m1 surely occurred *in vivo*, thus prior to fossilisation. This feature has been observed previously in hyaenodontids (e.g., Lange-Badré, 1979), including *Indohyaenodon raoi* from Vastan mine (GU/RSR/VAS 652; Rana et al., 2015).

The teeth from Tadkeshwar are about 10–15% longer than those from Vastan, but sample sizes are not adequate to assess the significance of this size difference. For the present, therefore, we refer the Tadkeshwar specimens to *Indohyaenodon raoi* rather than to a new species.

Ungulata Linnaeus, 1766
Cambaytheriidae Bajpai et al., 2005
Cambaytherium Bajpai et al., 2005
Cambaytherium thewissi Bajpai et al., 2005
Referred material: GU/RSR/TAD 9002, mandibular symphysis with alveoli for left and right incisors, canines, and p1, and for right p2; GU/RSR/TAD 9202, left maxilla with M1-3, encased in hard matrix; WIF/A 1200, mandible with left p3-4, m2, and symphysis; WIF/A 4217, right maxilla with P4-M2; WIF/A 4219, right M3; WIF/A 4220, right M3; WIF/A 4221, right M3; WIF/A 4222, right m3; WIF/A 4223, left m3; WIF/A 4224, right m2;
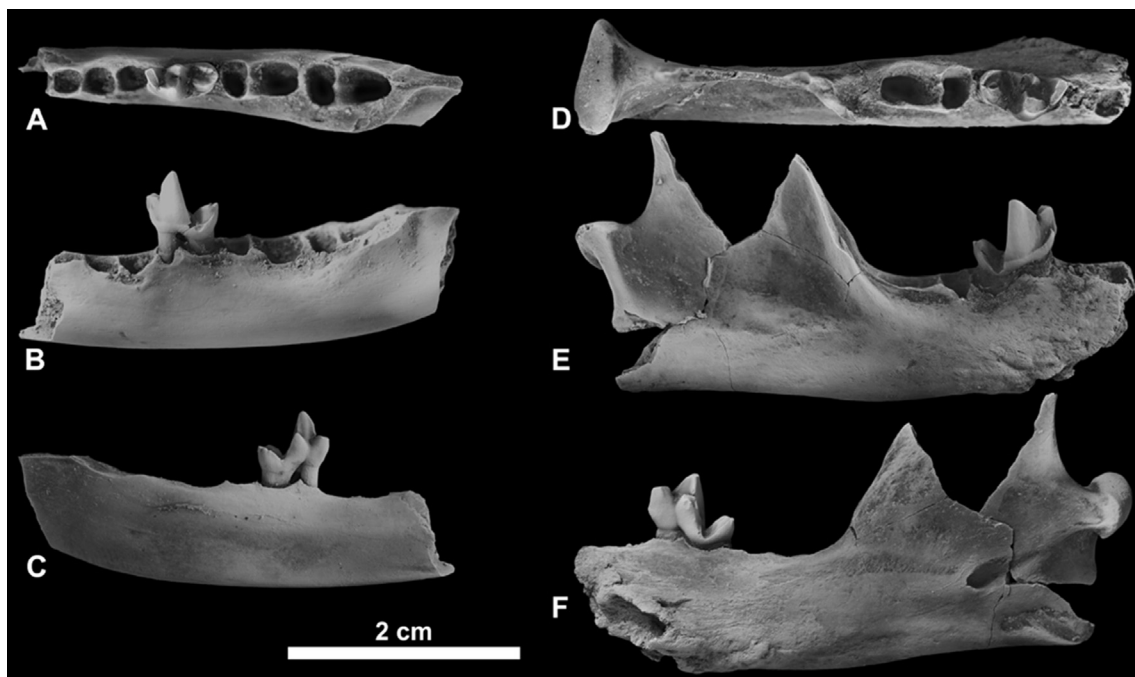

Figure 21. Hyaenodonta, *Indohyaenodon raoi*. A–C, GU/RSR/TAD 9000, left dentary with m1 in (A) occlusal, (B) labial, and (C) lingual views. D–F, WIF/A 4209, right dentary with m2 in (D) occlusal, (E) labial, and (F) occlusal views.

WIF/A 4232, right p2(?); WIF/A 4233, left m1; WIF/A 4234, left dp3; WIF/A 4216, left astragalus; WIF/A 4218, left radius (all from TAD-2).

Comments

Several specimens of *Cambaytherium* from the upper level at Tadkeshwar are similar in size and nearly all aspects of morphology to *C. thewissi* from Vastan (Bajpai et al., 2005a; Rose et al., 2014). The maxilla (WIF/A 4217, Fig. 22C–D) is the same size as GU/RSR/VAS 404 (Rose et al., 2014, Fig. 2), and the isolated teeth have close counterparts in the Vastan *C. thewissi* sample. They differ in a few minor characteristics. Two of the lower teeth, m1 (WIF/A 4233) and one m3 (WIF/A 4223), are about 20% wider than the mean for these teeth in the Vastan sample. The upper molars in WIF/A 4217 are within the size range for *C. thewissi* but differ in having a better

developed accessory cusp posterior to the metaconule and directly buccal to the hypocone. When present in the Vastan sample of *C. thewissi*, this cusp is smaller and more closely twinned with the hypocone. GU/RSR/TAD 9202, however, has a single metaconule, indicating variability in this feature. The three isolated M3s are slightly larger than those in the Vastan sample, and are slightly more expanded posterolingually (though the unusual shape of M3 renders it almost impossible to take consistent, comparable measurements). These minor differences suggest that the TAD-2 sample is slightly derived relative to the Vastan sample and could represent a distinct species, but until the Tadkeshwar sample is better understood, we refrain from separating it specifically from *C. thewissi*.

Cambaytherium gracilis, sp. nov.
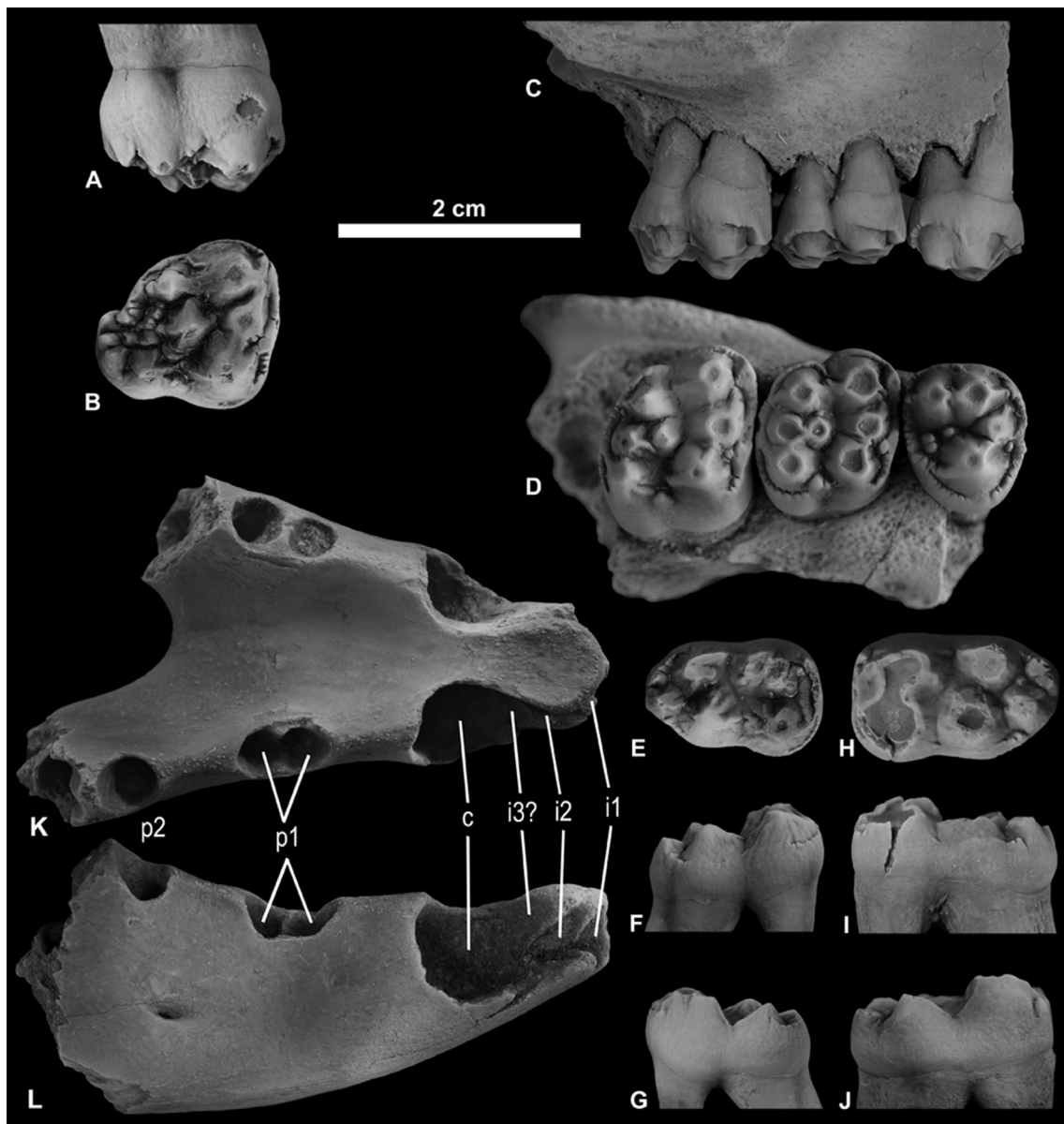urn:lsid:zoobank.org:act:5F9E64E1-EEB4-4BAA-A958-42ACBDDDBD15

Figure 22. Cambaytheriidae, *Cambaytherium thewissi*. A-B, WIF/A 4219, right M3 in (A) labial and (B) occlusal views. C-D, WIF/A 4217, right maxilla with P4-M2 in (C) labial and (D) occlusal views. E-G, WIF/A 4222, right m3 in (E) occlusal, (F) labial, and (G) lingual views. H-J, WIF/A 4223, left m3 in (H) occlusal, (I) labial, and (J) lingual views. K-L, GU/RSR/TAD 9002, mandibular symphysis in (K) occlusal and (L) right lateral views.

Etymology: Gracilis, Latin, slender.

Holotype: GU/RSR/TAD 9001, mandible with left p3-m3, alveoli for left p1–2 and right p1, and symphysis with alveoli for incisors and canines.

Hypodigm: Holotype and the following specimens. From TAD-2: WIF/A 4210, left dentary with p2–m3; WIF/A 4211, right dentary with p4–m1, m3; WIF/A 4212, right dentary with m3; WIF/A 4213, right maxilla with P1–3; WIF/A 4214, left maxilla with P4, M2–3; WIF/A 4215, left P2; WIF/A 4235, right p4; WIF/A 4236, left p4; WIF/A 4237, right m2; WIF/A 4238, right dP4; WIF/A 4239, right P4; WIF/A 4240, left P4; WIF/A 4241, left M2; WIF/A 4242, left M3; WIF/A 4243, right M3; WIF/A 4244, left radius; WIF/A 4245, right ulna; WIF/A 4246, right ulna. From TAD-1: GU/RSR/TAD 9555, right dentary with m2-3; WIF/A 2262, left femur; WIF/A 4207, left femur; WIF/A 4208, right ulna.

Horizon and locality: Cambay Shale Formation, Ypresian, lower Eocene, Tadkeshwar Lignite Mine (TAD-1 and TAD-2), Surat District, Gujarat, India.

Diagnosis: Mean size of cheek teeth at least 20% smaller in linear dimensions than *C. thewissi*. Mandibular symphysis fused, as in *C. thewissi*, but relatively narrower, and canine-p1 diastema
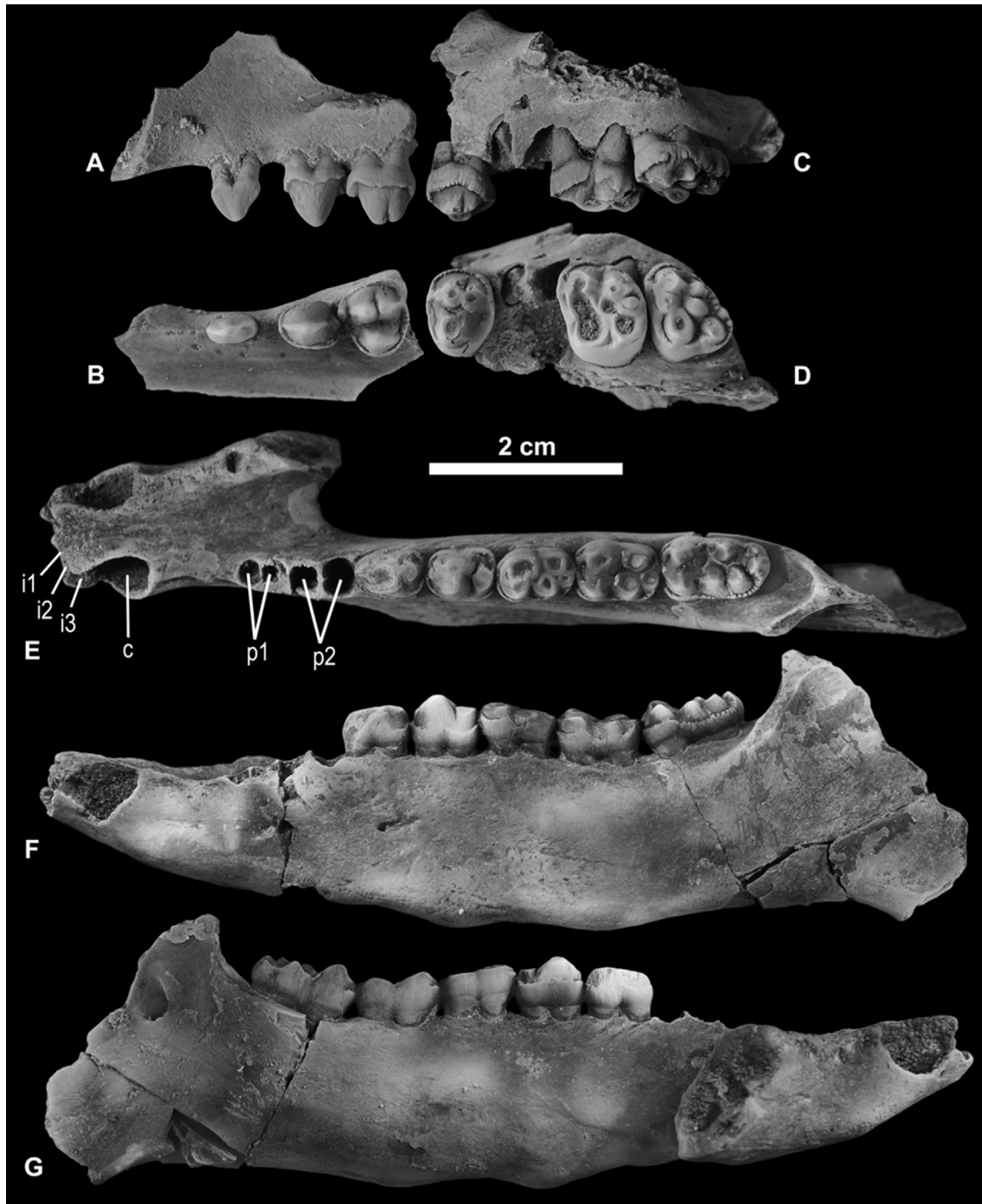

Figure 23. Cambaytheriidae, *Cambaytherium gracilis*, sp. nov. A-B, WIF/A 4213, right maxilla with P1-3 (reversed) in (A) labial and (B) occlusal views. C-D, WIF/A 4214, left maxilla with P4, M2-3 in (C) labial and (D) occlusal views. E-G, GU/RSR/TAD 9001, holotype, mandible with left p3-m3 and symphysis in (E) occlusal, (F) labial, and (G) lingual views.

longer than in *C. thewissi*. Premolars less robust than in *C. thewissi*; p4 with well-developed metaconid.

Description

Cambaytherium gracilis is very similar to *C. thewissi* but significantly smaller (Table 2). All teeth are at least 10% smaller (linear dimensions) than any individual in the *C. thewissi* sample, and all dimensions measured are at least 20% smaller than the mean values for *C. thewissi*, justifying specific separation. The p2 and p3 are even further reduced compared to *C. thewissi* (30−40% smaller than the smallest individuals). Besides these size differences, *C. gracilis* is more derived than *C. thewissi* in the morphology of the mandibular symphysis and p4.

The holotype mandible (Fig. 23E−G) confirms that the dental formula is the same as in *C. thewissi*, 3-1-4-3, with somewhat compressed incisors: the three left incisors are mesiodistally arranged in the holotype, whereas the right incisors are compacted, with two situated labially and one displaced lingual to the other two. The canine alveoli are large, and the symphysis, extending back to p2, is narrow. The diastema between the canine and the two-rooted p1 is almost twice the length of the p1 alveoli, in contrast to *C. thewissi*, in which it is both relatively and absolutely shorter. There are no diastemata separating any of the cheek teeth. The cheek teeth are brachydont and bunodont, with almost no crest development. As in *C. thewissi*, the p2 (WIF/A 4210) is a simple, premolariform tooth with a single primary cusp; but unlike *C. thewissi*, the crown of p2 is distinctly smaller than those of p3 and p4. The p3 is longer than p2, with a primary cusp anteriorly and a single-cusped talonid. The p4 is relatively broad, its trigonid bearing a large, blunt metaconid lingual to the protoconid, and a prominent talonid cusp just buccal to the center. Lingual to the talonid cusp is a well-developed posterolingual cingulum. The lower molars are essentially the same as in *C. thewissi*, including such features as the twinned metaconid and the variable accessory hypoconulid development on m3. Except for their smaller size, no significant differences were observed between upper teeth of

Table 2
Summary measurements (mm) for *Cambaytherium gracilis*, sp. nov.

Dimension	*n*	Mean	Range (mm)
P$_2$L	1	7.35	
P$_2$W	1	4.15	
P$_3$L	2	8.58	8.25−8.90
P$_3$W	2	5.55	5.40−5.70
P$_4$L	5	8.46	8.05−8.90
P$_4$W	5	6.33	5.90−6.65
M$_1$L	3	9.47	9.40−9.50
M$_1$Wtri	3	6.25	6.20−6.35
M$_1$Wtal	3	6.23	6.20−6.30
M$_2$L	3	10.63	10.25−10.90
M$_2$Wtri	3	7.38	7.30−7.50
M$_2$Wtal	3	7.03	6.90−7.25
M$_3$L	4	12.85	12.35−13.30
M$_3$Wtri	4	7.69	7.35−8.20
M$_3$Wtal	4	6.95	6.65−7.20
P^{2}L	2	7.23	7.10−7.35
P^{2}W	2	5.55	5.40−5.70
P^{3}L	1	7.60	
P^{3}W	1	8.30	
P^{4}L	3	7.98	7.65−8.20
P^{4}W	3	9.78	9.70−9.90
M^{1}L	−		
M^{1}W	−		
M^{2}L	2	9.0	8.55−9.45
M^{2}W	2	11.0	10.20−11.80
M^{3}L	3	8.27	8.00−8.70
M^{3}W	3	10.83	10.50−11.20

C. gracilis and those of *C. thewissi*. Like the dentition, the postcrania referred to the new species are conspicuously smaller and more gracile than those of *C. thewissi*. A thorough description of the teeth and postcrania, and comparison to *C. thewissi*, will be presented in a separate study of *Cambaytherium*.

Discussion

The possibility that the sample allocated to *C. gracilis* could represent the females of *C. thewissi* can be rejected for several reasons. The Vastan sample already shows a very broad range of variation, possibly reflecting sexual dimorphism, but in any case certainly encompassing both males and females. Nevertheless, the sample here referred to *C. gracilis* is substantially smaller than even the smallest individuals in the Vastan sample. A conspicuous size gap exists between *C. gracilis* and Tadkeshwar specimens assigned to *C. thewissi*, and there are morphological differences in the antemolar series and symphysis. For these reasons *C. gracilis* can be confidently considered distinct from *C. thewissi*. *Cambaytherium* is very similar to the recently named *Perissobune* Missiaen and Gingerich, 2014, from the lower Eocene Ghazij Formation of Pakistan. Missiaen and Gingerich (2014) considered *Perissobune* to be a bunodont perissodactyl. *Perissobune* differs from *Cambaytherium* in showing incipient cross-lophs on its molars and in having a more molariform p4.

5. Discussion

5.1. Diversity of the Tadkeshwar vertebrate fauna compared to that of Vastan

The Tadkeshwar vertebrate assemblage (Table 1) is mostly similar to the one from the nearby early Eocene Vastan mine. Typical shared taxa are the snakes *Palaeophis vastaniensis* and *Thaumastophis missiaeni*, the bird *Vastanavis* sp., the adapoid primate *Marcgodinotius indicus*, the hyaenodont *Indohyaenodon raoi*, and the cambaythere *Cambaytherium thewissi*. Other taxa that are probably similar in both localities are the frog *Eopelobates* sp., agamid lizards, the tillodont *Indoesthonyx suratensis*, gen. et sp. nov., an *Asiadapis*-like primate, eochiropteran bats, and the ailuravine rodent *Meldimys* sp.

However, some differences exist. Several taxa known from Vastan mine have not been found at Tadkeshwar, such as artiodactyls, insectivorans, and lagomorphs. Also, few bats have been discovered, while they are abundant and diverse in Vastan. But our sample is very small by comparison to the ten years of collecting in Vastan, so little importance should be placed on these absences. Regarding the presence of taxa in Tadkeshwar we can note some large vertebrates that seem to be absent in Vastan. Among them is the large madtsoiid snake *Platyspondylophis tadkeshwarensis*, gen. et sp. nov., which is restricted to the lower level at Tadkeshwar (TAD-1) where it is frequent. Large madtsoiids are particularly interesting for in India they were formerly reported only from the Maastrichtian (Mohabey et al., 2011). Other large vertebrates are the dyrosaurid crocodyliform and the pantodont mammal. The precise identity of the latter is not yet determined but the presence of a tooth crown fragment of about 3 cm indicates for the first time that a large mammal of the size of *Coryphodon* occurred in the early Eocene of India. This constitutes the first record of Pantodonta from the Indian subcontinent. Turtle remains are frequent and relatively diversified in Tadkeshwar, whereas they are extremely rare in Vastan mine. It is noteworthy that they have all been found in the lower level TAD-1. Among the mammals, we described the small cambaythere *Cambaytherium gracilis*, sp. nov., which occurs in both

vertebrate-producing levels at Tadkeshwar (TAD-1 and TAD-2) but is absent from Vastan.

Despite the small collection representing the Tadkeshwar vertebrate assemblage compared to the Vastan assemblage, it appears relatively diverse and contributes to knowledge of the early Eocene fauna of India, especially with large vertebrates that were absent or extremely rare in other previously studied early Eocene Indian localities.

5.2. Paleoenvironment and age of Tadkeshwar vertebrate assemblage

Minor differences thus exist between the Vastan and Tadkeshwar faunas, especially with TAD-1. Other minor differences exist between the two levels of Tadkeshwar. TAD-1 and TAD-2 indeed seem to result from different taphonomic conditions. While the lithology of TAD-2 is very similar to that of Vastan, the lithology of TAD-1 corresponds more to an erosive channel deposit with a coarser granulometry probably favouring the concentration of larger vertebrate specimens such as the abundant turtle shell fragments, the large madtsoiid vertebrae, the dyrosaurid coracoid, and the large mammal rib. Nevertheless, TAD-1 also contains some marine forms such as the *Physogaleus* shark tooth, *Myliobatis* ray teeth, cidaroid-like echinoid spines, and probably the tetraodontiform fish jaw. These taxa suggest that TAD-1 was either a brackish channel or has transported/reworked marine forms. This brackish/marine influence is interesting as it could explain the presence of the dyrosaurid, which is considered as a near-shore marine crocodyliform with a freshwater lifestyle of the juveniles (Jouve et al., 2008a). The large madtsoiid snakes are generally considered to have been arboreal and/or semi-aquatic like extant boids or pythonids (LaDuke et al., 2010; Rage et al., 2014). The vertebrae of the new madtsoiid genus *Platyspondylophis* are especially interesting from a functional point of view because they present several burrowing features such as the low neural spine and low neural arch, the oval condyle and cotyle, and the dorso-ventrally compressed centrum (Gasc, 1974). These features are present in burrowing scolecophidian snakes and secretive fossorial anilioid snakes, which suggests that *Platyspondylophis* was fossorial and capable of extensive lateral mobility. Due to its very large size, its behaviour might have been somewhat like that of the anaconda *Eunectes*, which is able to burrow under mats of vegetation. Indeed, the more compressed vertebrae of *Platyspondylophis* suggest that it was a better burrower than *Eunectes*. Like dyrosaurids, madtsoiids such as *Gigantophis* have been reported from coastal deposits of the Oligocene Qasr el Sagha Formation of Fayum in Egypt, the Eocene–Oligocene transitional deposits of Dur At Talah in Libya, and the lower Paleocene Khadro Formation in Pakistan (see Rage et al., 2014). It is noteworthy that the large madtsoiids of Tadkeshwar have been found in association with palaeophiids, which are recognized as aquatic snakes. The last category of vertebrates found in TAD-1 is represented by the mammals and lizards, which are terrestrial.

TAD-2 is stratigraphically higher and therefore certainly younger than TAD-1, but until the sedimentation rate is better understood it is hard to estimate how much younger. Changes in the mammals are minor. Slightly larger teeth in *Indohyaenodon raoi*, and slight morphological differences in *C. thewissi* and in ?*Asiadapis cambayensis*, are consistent with a small age difference, whereas *Marcgodinotius indicus* from this level is essentially indistinguishable from the Vastan sample. Consequently, the age difference between TAD-1 and TAD-2 seems to be in the range of tens of thousands of years to, at most, a few hundred thousand years, but does not justify another land mammal age than the one from Vastan. Terrestrial vertebrates from thin lenses situated 1–2 m above the lower of two major lignites (Lignite 2) at Vastan mine

have an age estimated at 54.5 Myr, based on a consensus established from the results provided by different studies. First, the age is based on the occurrence of the age-diagnostic foraminiferans *Nummulites burdigalensis burdigalensis* and *Nummulites burdigalensis kuepperi* that have been found about 14 m above the vertebrate-bearing lenses at Vastan (Punekar and Saraswati, 2010). These foraminiferans are indicative of Shallow Benthic Zone (SBZ) 10 (Schaub, 1981; Serra-Kiel et al., 1998), which indicates a middle Ypresian age, approximately 53 Ma (Berggren and Aubry, 1998; Luterbacher et al., 2004). Second, dinoflagellate cysts and pollen reported from the Vastan section suggest that the concerned deposits, which extend between the two major lignites (Lignites 1 and 2), range from 52 to 55 Ma and that the vertebrate layer would be an equivalent of the European Sparnacian, 55 to 54 Myr (Garg et al., 2008; Prasad et al., 2013). Third, based on analyses of the dispersed organic carbon (δ^{13}C) from the sediment and strontium isotopes from different proxies, the age of the terrestrial vertebrate level has been estimated at about 54 Myr. This coincides with the second Eocene Thermal Maximum, called ETM2, which has been identified in the Vastan section (Clementz et al., 2011). However, independent carbon isotope, nannofossil, and strontium isotope analyses suggest preservation of all the early Eocene CIE events (PETM, H1/ETM2/ELMO, H2, I1 and I2) in the Vastan section (Samanta et al., 2013) and Tadkeshwar section (Adatte et al., 2014; Samanta et al., 2016). These latter studies based notably on a drill core thus indicate that the early Eocene Vastan and Tadkeshwar lignitic deposits could represent a time span of about 3 Myr, starting within the PETM. Moreover, the carbon isotope stratigraphy further suggests that the terrestrial vertebrate bearing horizon is at least ∼1 Myr younger than the PETM (Samanta et al., 2013).

5.3. Paleobiogeographic origin and affinities of early Eocene Indian vertebrates

The Indian subcontinent had begun its separation from Madagascar during the Coniacian, 88 My ago (Storey et al., 1995). Therefore, the analysis of the latest Cretaceous terrestrial vertebrate taxa on Madagascar that have sister-taxon relationships to Campanian–Maastrichtian (83–66 My ago) taxa of both the Indian subcontinent and the disjunct Gondwanan landmasses of South America revealed long ghost lineages (see Ali and Krause (2011) for an overview). On the other hand, the initial collision of the Indian subcontinent with the Asian continent during the end of the Ypresian around 50 Myr ago resulted in the closure of the Neotethys Ocean and exchanges of Indian and Asian faunas (Krause and Maas, 1990; Macey et al., 2000; Bossuyt and Milinkovitch 2001; Conti et al., 2002; Chatterjee et al., 2013). No Indian terrestrial vertebrate faunas were known between 65 and 50 Myr until the recent discovery of the early Eocene vertebrates from the Cambay Shale Formation at Vastan mine, which represent the time period just before the India-Asia collision. Unexpectedly, the Vastan sediments yielded a vertebrate assemblage mainly composed of taxa with European affinities such as pelobatid frogs (Folie et al., 2013), russellophiid snakes (Rage et al., 2008), vastanavid parrot-like birds (Mayr et al., 2013), hassianycterid, icaronycterid, and archaeonycterid bats (Smith et al., 2007), ailuravine rodents (Rana et al., 2008), adapoid primates (Rose et al., 2009a), diacodexeid artiodactyls (Kumar et al., 2010), and esthonychine tillodonts (Rose et al., 2009b, 2013). A few taxa discovered are considered as endemic to the Indian subcontinent, among which the most remarkable are the cambaytheriid perissodactyl-like mammals (Rose et al., 2014).

While most of the taxa from the new Tadkeshwar fauna are similar to those of Vastan, which confirms faunal exchange with Europe at least 54.5 Myr ago or before, others seem to have for the first time a different geographic origin. Among them are the turtles

of the hyperfamily Pelomedusoides (Gaffney et al., 2006). This group of side-necked turtles is an element of the Gondwana fauna, notably known by the latest Cretaceous Malagasy bothremydid *Kinkonychelys* of Maastrichtian age that is nested within the Indian members of the Kurmademydini tribe (Gaffney et al., 2009). The two other groups of turtles from Tadkeshwar, the Trionychidae and Carettochelyidae, are however present in Laurasia from the early Cretaceous, whereas they are not known before the Miocene in Africa (Joyce, 2014). The madtsoiid snakes from Tadkeshwar are phylogenetically related to Gondwanan snakes. Large madtsoiids are indeed known from the Cretaceous to the Pleistocene in South America, Africa, Madagascar, Pakistan, and India (Scanlon and Lee, 2000; LaDuke et al., 2010; Mohabey et al., 2011; Rage et al., 2014). The presence of the large madtsoiid *Madtsoia pisdurensis* in the late Cretaceous of India (Mohabey et al., 2011) and *Gigantophis* sp. in the early Paleocene of Pakistan (Rage et al., 2014), already attests a dispersal from Africa plus Madagascar to India. The presence of the new large madtsoiid *Platyspondylophis* thus extends the record into the early Eocene of India. The dyrosaurid crocodyliform from Tadkeshwar is another taxon that has a Gondwanan origin. The palaeobiogeographic distribution of this group is mainly concentrated in Africa, and a few taxa are known from North and South America (Jouve et al., 2008b; Hastings et al., 2010). The presence of dyrosaurids in the late Cretaceous of India has already been reported (Rana, 1987; Prasad and Singh, 1991; Khosla et al., 2009); and this presence is here extended to the early Eocene by a typical coracoid morphologically similar to that of *Congosaurus*.

Our results obviously suggest that the early Eocene Tadkeshwar and Vastan vertebrate assemblage represents a mixed fauna of Laurasian and Gondwanan affinities. Taking into account, on one side, the composition of the Paleocene and early Eocene African and Asian faunas, and on the other side, the paleogeographic situation of Africa and Asia before 54.5 Myr ago, the Laurasian taxa might have dispersed between the Indian subcontinent and Europe directly across the Neotethys (Fig. 24). Such a hypothesis has recently been proposed for a dispersal of adapisoriculid mammals around the Cretaceous–Paleogene boundary (Boyer et al., 2010; Prasad et al., 2010; Smith et al., 2010). Adapisoriculids are indeed present in the Maastrichtian of India, the early Paleocene to early Eocene of northwest Europe, and the late Paleocene to early Eocene of northwest Africa (Gheerbrant and Russell, 1989; Gheerbrant, 1993; Prasad et al., 1994; Smith, 1997; De Bast et al., 2012, 2013). The Gondwanan elements of the Tadkeshwar fauna can be explained by two paleobiogeographic hypotheses. The first hypothesis is that this fauna would result from ghost lineages common with Madagascar originally dispersed during the late Cretaceous. This hypothesis would imply that some Tadkeshwar taxa such as the Pelomedusoides, the large madtsoiid, and the dyrosaurid could be the descendants of taxa already present in the Campanian–Maastrichtian of India, which would have survived the Cretaceous–Paleogene crisis and the Paleocene–Eocene event. The second hypothesis is a dispersal of Gondwanan taxa from North Africa along the margins of the Neotethys to the Indian subcontinent. This last hypothesis was originally proposed by Buffetaut (1978a,b) who suggested a late expansion of dyrosaurids along the Tethys margin to explain the presence of the group in the Eocene of Myanmar. It is here strengthened by the fact that Pelomedusoides and madstoiids, like dyrosaurids, are all aquatic or partially aquatic with numerous taxa discovered in shallow marine or brackish deposits. Palaeophiid snakes are aquatic as well and likely lived in marginal marine waters (Parmley and Devore, 2005). Moreover, all these groups are present in the Thanetian–Ypresian marine deposits of the phosphate basins of Morrocco in northwest Africa. However, it is noteworthy that Pelomedusoides and madstoiids are also present in the Maastrichtian of south and eastern Europe (Csiki-Sava et al., 2015). Therefore, a European origin of the Tadkeshwar Pelomedusoides and madtsoiids cannot be excluded. Infrequent, trans-Tethyan dispersals between Africa and Europe, controlled by sea level changes during the late Cretaceous–Paleocene, have already been suggested (Gheerbrant and Rage, 2006). Recently, the presence of Gondwanan faunal elements such as sebecosuchians, a terrestrial crocodyliform group, in the late Cretaceous of southern Europe have suggested that episodic faunal and geographical links were retained between the western Tethyan archipelago and Gondwana during most of the Cretaceous (Rabi and Sebők, 2015). Nevertheless, the Mediterranean Tethys was characterised by a peculiar faunal identity of marine reptiles, illustrating an absence of migration over time despite the apparent lack of barriers (Bardet et al., 2014).

Dispersal between the Indian subcontinent and either Europe or North Africa might have resulted from one single event involving the European archipelago and the Neotethys. However, no members of the clade of large madtsoiids (*Madtsoia*, *Gigantophis*, *Wonambi*, *Yurlungur*) have ever been recorded in Europe. Only small to middle-sized madtsoiids, phylogenetically separated from the large madtsoiids, have been described from Europe (Vasile et al., 2013). Similarly, dyrosaurids have not been reported from Europe with the exception of one possible record in the Cenomanian of Portugal (Buffetaut and Lauverjat, 1978). Similarly, the early Eocene North African mammal fauna is different from the Euro-Indian faunas, with very few orders and families and no genera in common. This suggests that while European continental taxa could have been exchanged during contact of the Indian subcontinent with different island blocks along the northern margin of the Neotethys, the Gondwanan taxa would have passed along the southern margins of the Neotethys to join the Indian subcontinent. Dispersal of Laurasian elements between India and Eurasia across the Kohistan–Ladakh island-arc system at the Indus Suture Zone has been proposed to provide the necessary land passage for the migration of terrestrial vertebrates (Sahni and Bajpai, 1991; Chatterjee et al., 2013). This passage is in agreement with the India–Kohistan collision, which has been shown to predate the accretion of Kohistan–India to the Asian continent (Khan et al., 2009). It is also consistent with the "Greater India Basin," which was occupied by a fluvial-deltaic system (Paleo-Indus) that has been transporting Asian detritus southward across the suture zone and Kohistan–Ladakh arc only since 50 Ma (Zhuang et al., 2015). The latter event implies that the terminal collision between the Indian subcontinent and Asia occurred in the west by 50 Ma (Zhuang et al., 2015).

The dispersals of some European and Gondwanan faunas could have resulted from the favourable paleogeographic conditions due to the Tethys conformation during the beginning of the early Eocene. This paleobiogeographic scenario is supported by the highest diversity of early bats in Europe and Indo-Pakistan with several genera shared in common between the two areas, suggesting the existence of a Europe–western Indian subcontinent faunal province, perhaps including North Africa, that would approximately cover the territory of the Neotethys (Smith et al., 2012). While the direction of dispersal for the Gondwanan taxa is obviously from Africa plus Madagascar to the Indian subcontinent, that for Laurasian taxa is more difficult to determine. In Europe, the earliest faunas with modern mammals such as primates, perissodactyls, and artiodactyls coincide with the Paleocene–Eocene Thermal Maximum, 56 My (Smith et al., 2006), which might suggest that the direction of dispersals was from Europe to India. However, the biogeographic origin of these European modern mammals is still unknown, and until now, no mammal faunas have been discovered before 54.5 My in India.
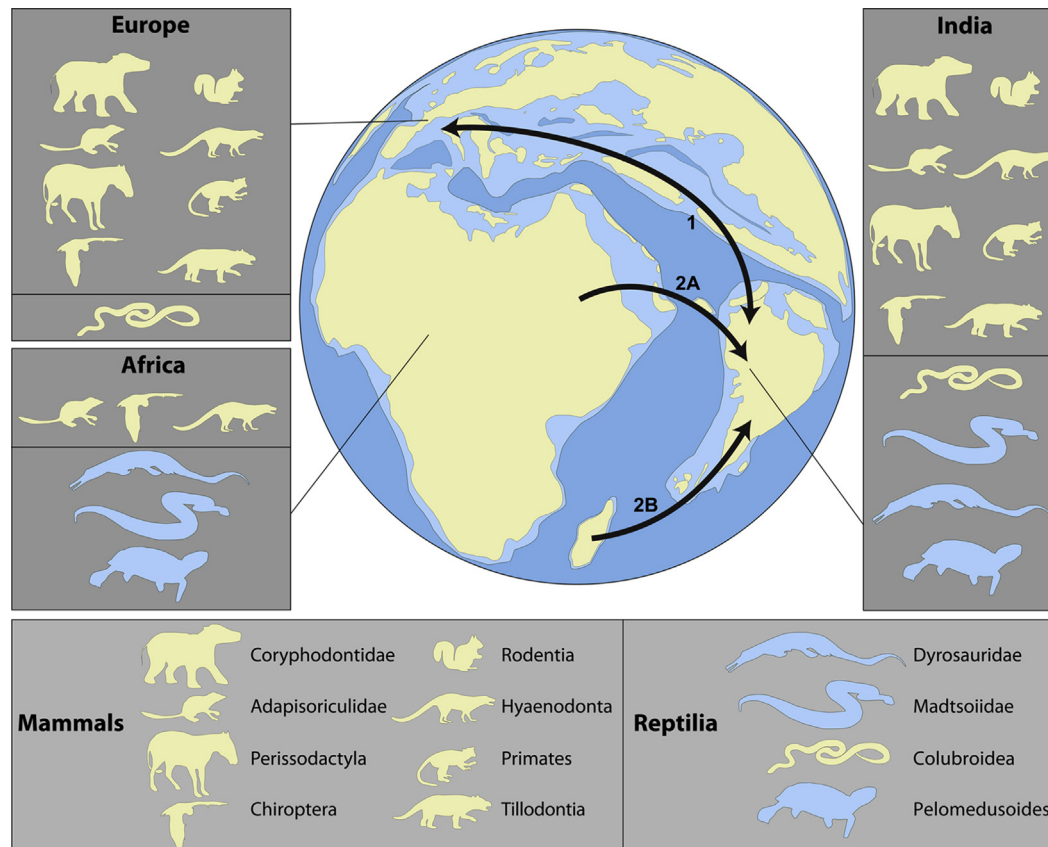
Figure 24. Schematic paleogeographic map showing the hypothetical dispersal routes of vertebrates around 54 My ago (adapted from Scotese, 2013). 1, Dispersal of taxa with European affinities between the Indian subcontinent and Europe across the Neotethys via the Kohistan—Ladakh island-arc system. 2A-B, Dispersal of taxa with Gondwanan affinities to the Indian subcontinent (2A) from Africa along the southern margins of the Neotethys or (2B) from Madagascar (ghost lineages originally dispersed during the late Cretaceous). Pale blue animal outlines represent Gondwanan taxa and pale yellow outlines represent Laurasian taxa.

Thus it cannot be excluded, as initially proposed by Krause and Maas (1990), that some clades of modern mammals were already present on the Indian subcontinent before the Paleocene—Eocene boundary.

6. Conclusions

The new Tadkeshwar vertebrate assemblage from the lower Eocene Cambay Shale Formation originates from two fossil layers that yielded similar faunas to that of the nearby Vastan mine, suggesting that the deposits between the two major lignite seams of both mines represent a single land mammal age. The mammal fauna is characterized by the co-occurrence of the perissodactyl-like cambaytheriid *Cambaytherium thewissi*, the adapoid primates *Marcgodinotius indicus* and ?*Asiadapis cambayensis*, and the hyaenodontid *Indohyaenodon raoi*. For the first time, several vertebrate taxa are of Gondwanan affinities, including a Pelomedusoides turtle, a dyrosaurid crocodyliform, and a large madtsoiid snake; whereas others are Laurasian taxa of European affinities, such as the trionychoid turtles, the bats, the adapoid primates, and the ailuravine rodent. The absence of typical Asian forms in the Tadkeshwar and Vastan vertebrate faunas strongly suggests that, at 54.5 My ago, India had not yet collided with Asia. The Gondwanan affinities of some vertebrates that are known to live partially in coastal marine environments suggest that they result from ghost lineages common with Madagascar, which originally dispersed during the late Cretaceous, or that they passed along the southern margins of the Neotethys to join India. The important European affinities of the majority of these early Eocene Indian faunas suggest a land passage through the Neotethys possibly by the Kohistan—Ladakh island-arc system at the Indus Suture Zone. The direction of the dispersals (out of or into India) cannot yet be determined because although modern mammals are already present in Europe 56.0 My ago, the composition of the Indian terrestrial vertebrate faunas before 54.5 My is not known.

References

Adatte, K.H., Khozyem, H., Spangenberg, J.E., Samant, B., Keller, G., 2014. Response of terrestrial environment to the Paleocene-Eocene Thermal Maximum (PETM), new insights from India and NE Spain. Rendiconti Online della Società Geologica Italiana 31, 5—6.

Ali, J.R., Krause, D.W., 2011. Late Cretaceous bioconnections between Indo-Madagascar and Antarctica: refutation of the Gunnerus Ridge causeway hypothesis. Journal of Biogeography 38 (10), 1855—1872.

Andrews, C.W., 1901. Preliminary note on some recently discovered extinct vertebrates from Egypt (Part II). Geological Magazine 8, 434—444.

Antunes, M.T., 1964. O neocretácico e o cenozóico do litoral de Angola. Junta de Investigações do Ultramar, Lisboa, 254 pp.

Bailon, S., 1999. Différenciation ostéologique des anoures (Amphibia, Anura) de France. In: Desse, J., Desse-Berset, N. (Eds.), Fiches d'ostéologie animale pour l'archéologie, Série C: varia. Centre de Recherches Archéologiques du CNRS, APDCA, Antibes, pp. 1—42.

Bajpai, S., Head, J.J., 2007. An Early Eocene palaeopheid snake from Vastan Lignite Mine, Gujarat, India. Gondwana Geological Magazine 22, 85—90.

Bajpai, S., Kapur, V.V., 2008. Earliest Cenozoic frogs from the Indian subcontinent: implications for out-of-India hypothesis. Journal of the Palaeontological Society of India 53, 65—71.

Bajpai, S., Kapur, V.V., Das, D.P., Tiwari, B.N., Saravanan, N., Sharma, R., 2005a. Early Eocene land mammals from Vastan Lignite Mine, District Surat (Gujarat), western India. Journal of the Palaeontological Society of India 50, 101—113.

Bajpai, S., Kapur, V.V., Thewissen, J.G.M., 2009. Creodont and condylarth from the Cambay Shale (early Eocene, ~55—54 ma), Vastan Lignite Mine, Gujarat, western India. Journal of the Palaeontological Society of India 54, 103—109.

Bajpai, S., Kapur, V.V., Thewissen, J.G.M., Das, D.P., Tiwari, B.N., Sharma, R., Saravanan, N., 2005b. Early Eocene primates from Vastan Lignite Mine, Gujarat, western India. Journal of the Palaeontological Society of India 50, 43—54.

Bardet, N., Falconnet, J., Fischer, V., Houssaye A., ., Jouve, S., Pereda Suberbiola, X., Pérez-García, A., Rage, J.-C., Vincent, P., 2014. Mesozoic marine reptile palaeobiogeography in response to drifting plates. Gondwana Research 26 (3—4), 869—887.

Baudry, M., 1992. Les Tillodontes (Mammalia) de l'Eocène inférieur de France. Bulletin du Muséum national d'histoire naturelle. Section C, Sciences de la terre, paléontologie, géologie, minéralogie 14 (2), 205—243 (in French with English abstract).

Berggren, W.A., Aubry, M.P., 1998. The Paleocene/Eocene Epoch/Series boundary: Chronostratigraphic framework and estimated geochronology. In: Aubry, M.P., Lucas, S., Berggren, W.A. (Eds.), Late Paleocene-Early Eocene Climatic and Biotic Events in the Marine and Terrestrial Records. Columbia University Press, pp. 18—36.

Bossuyt, F., Milinkovitch, M.C., 2001. Amphibians as indicators of Early Tertiary "out-of-India" dispersal of vertebrates. Science 292, 92—95.

Bown, T.M., Rose, K.D., 1987. Patterns of dental evolution in early Eocene anaptomorphine primates (Omomyidae) from the Bighorn Basin, Wyoming. Paleontological Society Memoir 23, 1—162 (Journal of Paleontology 61, supplement to number 5).

Boyer, D.M., Prasad, G.V.R., Krause, D.W., Godinot, M., Goswami, A., Verma, O., Flynn, J.J., 2010. New postcrania of Deccanolestes from the Late Cretaceous of India and their bearing on the evolutionary and biogeographic history of euarchontan mammals. Naturwissenschaften 97, 365—377.

Broin, F. de, 1987. Lower vertebrates from the early-middle Eocene Kuldana Formation of Kohat (Pakistan): Chelonia. Contributions from the Museum of Paleontology, University of Michigan 27 (7), 169—179.

Buffetaut, E., 1978a. A dyrosaurid (Crocodylia, Mesosuchia) from the Upper Eocene of Burma. Neues Jahrbuch für Geologie und Paläontologie, Monatshefte 5, 273—281.

Buffetaut, E., 1978b. Crocodilian remains from the Eocene of Pakistan. Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen 156, 262—283.

Buffetaut, E., Lauverjat, J., 1978. Un crocodilien d'un type particulier dans le Cénomanien de Nazaré. Comptes Rendus Sommaire des Séances de la Société géologique de France 1978 (2), 79—82.

Cappetta, H., 1980. Modification du statut générique de quelques espèces de sélaciens crétacés et tertiaires. Palaeovertebrata 10, 29—42.

Cappetta, H., 1987. Chondrichthyes II. Mesozoic and Cenozoic Elasmobranchii. In: Schultze, H.P. (Ed.), Handbook of Paleoichthyology, vol. 3B. Gustav Fisher Verlag, Stuttgart, pp. 1—193.

Cattaneo, A., Steel, R.J., 2003. Trangressive deposits: a review of their variability. Earth Sci. Rev. 62, 187—228.

Chatterjee, S., Goswami, A., Scotese, C.R., 2013. The longest voyage: tectonic, magmatic, and paleoclimatic evolution of the Indian plate during its northward flight from Gondwana to Asia. Gondwana Research 23 (1), 238—267.

Clementz, M., Bajpai, S., Ravikant, V., Thewissen, J.G.M., Saravanan, N., Singh, I.B., Prasad, V., 2011. Early Eocene warming events and the timing of terrestrial faunal exchange between India and Asia. Geology 39, 15—18.

Conti, E., Eriksson, T., Schönenberger, J., Sytsma, K.J., Baum, D.A., 2002. Early Tertiary out-of-India dispersal of Crypteroniaceae: evidence from phylogeny and molecular dating. Evolution 56, 1931—1942.

Csiki-Sava, Z., Buffetaut, E., Ősi, A., Pereda-Suberbiola, X., Brusatte, S.L., 2015. Island life in the Cretaceous faunal composition, biogeography, evolution, and extinction of land-living vertebrates on the Late Cretaceous European archipelago. ZooKeys 469, 1—161. http://dx.doi.org/10.3897/zookeys.469.8439.

De Bast, E., Sigé, B., Smith, T., 2012. Diversity of the adapisoriculid mammals from the early Palaeocene of Hainin, Belgium. Acta Palaeontologica Polonica 57 (1), 35—52.

De Bast, E., Steurbaut, E., Smith, T., 2013. New mammals from the marine Selandian of Maret, Belgium, and their implications for the age of the Paleocene continental deposits of Walbeck, Germany. Geologica Belgica 16 (4), 236—244.

Dunn, R.H., Rose, K.D., Rana, R.S., Kumar, K., Sahni, A., Smith, T., 2016. New euprimate postcrania from the early Eocene of Gujarat, India, and the strepsirrhine-haplorhine divergence. Journal of Human Evolution (in press).

Folie, A., Rana, R.S., Rose, K.D., Sahni, A., Kumar, K., Singh, L., Smith, T., 2013. Early Eocene frogs from Vastan Lignite Mine, Gujarat, India. Acta Palaeontologica Polonica 58 (3), 511—524.

Gaffney, E.S., Krause, D.W., Zalmout, I.S., 2009. *Kinkonychelys*, a new side-necked turtle (Pelomedusoides: Bothremydidae) from the Late Cretaceous of Madagascar. American Museum Novitates 3662, 1—25.

Gaffney, E.S., Tong, H., Meylan, P.A., 2006. Evolution of the side-necked turtles: the families Bothremydidae, Euraxemydidae, and Araripemydidae. Bulletin of the American Museum of Natural History 300, 1—698.

Garg, R., Khowaja-Ateequzzaman Prasad, V., Tripathi, S.K.M., Singh, I.B., Jauhri, A.K., Bajpai, S., 2008. Age-diagnostic dinoflagellate cysts from lignite-bearing sediments of the Vastan lignite mine, Surat District, Gujarat, western India. Journal of the Palaeontological Society of India 53, 99—105.

Gasc, J.P., 1974. L'interprétation fonctionelle de l'appareil musculosqueléttique de l'axe vertébral chez les serpents (Reptilia). Mémoires du Muséum National d'Histoire Naturelle, Paris, Série A, Zoologie 83, 1—182.

Gazin, C.L., 1953. The Tillodontia: an early Tertiary order of mammals. Smithsonian Miscellaneous Collections 121 (10), 1—110.

Gheerbrant, E., 1993. Premières données sur les mammifères "insectivores" de l'Yprésien du Bassin d'Ouarzazate (Maroc: site de N'Tagourt 2). Neues Jahrbuch für Geologie und Paläontologie Abhandlungen 187 (2), 225—242.

Gheerbrant, E., Rage, J.C., 2006. Paleobiogeography of Africa: how distinct from Gondwana and Laurasia? Palaeogeography, Palaeoclimatology, Palaeoecology 241, 224—246.

Gheerbrant, E., Russell, D.E., 1989. Presence of the genus *Afrodon* (Mammalia, Lipotyphla (?), Adapisoriculidae) in Europe; new data for the problem of trans-Tethyan relations between Africa and Europe around the K/T boundary. Palaeogeography, Palaeoclimatology, Palaeoecology 76, 1—15.

Gingerich, P.D., 1989. New earliest Wasatchian mammalian fauna from the Eocene of northwestern Wyoming: composition and diversity in a rarely sampled high-floodplain assemblage. University of Michigan Papers on Paleontology 28, 1—97.

Gingerich, P.D., 1995. Sexual dimorphism in earliest Eocene *Cantius torresi* (Mammalia, Primates, Adapoidea). Contributions from the Museum of Paleontology, University of Michigan 29, 185—199.

Gingerich, P.D., Gunnell, G.F., 1979. Systematics and evolution of the genus *Esthonyx* (Mammalia, Tillodontia) in the early Eocene of North America. Contributions from the Museum of Paleontology, The University of Michigan 25, 125—153.

Gupta, S., Kumar, K., 2015. Early Eocene rodents (Mammalia) from the Subathu Formation of type area (Himachal Pradesh), NW sub-Himalaya, India: palaeobiogeographic implications. Journal of Earth System Science 124 (6), 1201—1221.

Hastings, A.K., Bloch, J.I., Cadena, E.A., Jaramillo, C.A., 2010. A new small short-snouted dyrosaurid (Crocodylomorpha, Mesoeucrocodylia) from the Paleocene of northeastern Colombia. Journal of Vertebrate Paleontology 30 (1), 139—162.

Head, J.J., Bloch, J., Hastings, A.K., Bourque, J.R., Cadena, E.A., Herrera, F.A., Polly, P.D., Jaramillo, C.A., 2009. Giant boid snake from the Palaeocene neotropics reveals hotter past equatorial temperatures. Nature 457, 715—718.

Hoffstetter, R., 1961. Nouveaux restes d'un serpent Boïdé (*Madtsoia madagascariensis* nov. sp.) dans le Crétacé Supérieur de Madagascar. Bulletin du Muséum National d'Histoire Naturelle 33, 152—160.

Hooker, J.J., 2010. The mammal fauna of the early Eocene Blackheath Formation of Abbey Wood, London. Monograph of the Palaeontographical Society London 165, 1—162.

Houssaye, A., Rage, J.-C., Bardet, N., Vincent, P., Amaghzaz, M., Meslouh, S., 2013. New highlights about the enigmatic marine snake Palaeophis maghrebianus (Palaeophiidae; Palaeophiinae) from the Ypresian Phosphates (Middle Eocene) of Morocco. Palaeontology 56 (3), 647—661.

Jouve, S., 2005. A new description of the skull of *Dyrosaurus phosphaticus* (Thomas, 1893) (Mesoeucrocodylia: Dyrosauridae) from the Lower Eocene of North Africa. Canadian Journal of Earth Sciences 42, 323—337.

Jouve, S., Schwarz, D., 2004. Congosaurus bequaerti, a Paleocene dyrosaurid (Crocodyliformes; Mesoeucrocodylia) from Landana (Angola). Bulletin de l'Institut Royal des Sciences Naturelles de Belgique 74, 129—146.

Jouve, S., Bardet, N., Jalil, N.-E., Suberbiola, X., Bouya, B., Amaghzaz, M., 2008a. The oldest African crocodylian: phylogeny, paleobiogeography, and differential survivorship of marine reptiles through the Cretaceous-Tertiary boundary. Journal of Vertebrate Paleontology 28 (2), 409—421.

Jouve, S., Bouya, B., Amaghzaz, M., 2008b. A long-snouted dyrosaurid (Crocodyliformes, Mesoeucrocodylia) from the Paleocene of Morocco: phylogenetic and palaeobiogeographic implications. Palaeontology 51, 281—294.

Jouve, S., Iarochene, M., Bouya, B., Amaghzaz, M., 2006. A new species of *Dyrosaurus* (Crocodylomorpha, Dyrosauridae) from the early Eocene of Morocco: phylogenetic implications. Zoological Journal of the Linnean Society 148, 603—656.

Joyce, W.G., 2014. A review of the fossil record of turtles of the Clade Pan-*Careettochelys*. Bulletin of the Peabody Museum of Natural History 55 (1), 3—33.

Khan, S.D., Walker, D.J., Hall, S.A., Burke, K.C., Shah, M.T., Stockli, L., 2009. Did Kohistan—Ladakh island arc collide first with India? Geological Society of America Bulletin 121, 366—384.

Khosla, A., Sertich, J.J.W., Prasad, G.V.R., Verma, O., 2009. Dyrosaurid remains from the intertrappean beds of India and the Late Cretaceous distribution of the Dyrosauridae. Journal of Vertebrate Paleontology 29 (4), 1321—1326.

Koenigswald, W.v., Rose, K.D., 2005. The enamel microstructure of the early Eocene pantodont *Coryphodon* and the nature of the zigzag-enamel. Journal of Mammalian Evolution 12 (3—4), 419—432.

Krause, D.W., Maas, M.C., 1990. The biogeographic origins of late Paleocene—early Eocene mammalian immigrants to the Western Interior of North America. In: Bown, T.M., Rose, K.D. (Eds.), Dawn of the Age of Mammals in the Northern Part of the Rocky Mountain Interior, North America. Geological Society of America Special Paper, pp. 71—105.

Kumar, K., Rose, K.D., Rana, R.S., Singh, L, Smith, T., Sahni, A., 2010. Early Eocene artiodactyls (Mammalia) from western India. Journal of Vertebrate Paleontology 30, 1245—1274.

LaDuke, T.C., Krause, D.W., Scanlon, J.D., Kley, N.J., 2010. A Late Cretaceous (Maastrichtian) snake assemblage from the Maevarano Formation, Mahajanga Basin, Madagascar. Journal of Vertebrate Paleontology 30, 109—138.

Lange-Badré, B., 1979. Les créodontes (Mammalia) d'Europe occidentale de l'Éocène supérieur à l'Oligocène supérieur. Mémoires du Muséum national d'Histoire naturelle C 42, 1—252 (in French with English abstract).

Luterbacher, H.P., Ali, J.R., Brinkhuis, H., Gradstein, F.M., Hooker, J.J., Monechi, S., Ogg, J.G., Powell, J., Rohl, U., Sanfilippo, A., Schmitz, B., 2004. The Paleogene Period. In: Gradstein, F., Ogg, J., Smith, A.G. (Eds.), A Geologic Time Scale 2004. Cambridge University Press, Cambridge, pp. 384—408.

Macey, J.R., Schulte, J.A., Larson, A., Ananjeva, N.B., Wang, Y., Pethiyagoda, R., Rastegar-Pouyani, N., Papenfuss, T.J., 2000. Evaluating trans-tethys migration: an example using acrodont lizard phylogenetics. Systematic Biology 49, 233—256.

Mayr, G., Rana, R.S., Rose, K.D., Sahni, A., Kumar, K., Singh, L., Smith, T., 2010. *Quercypsitta*-like birds from the early Eocene of India (Aves, ?Psittaciformes). Journal of Vertebrate Paleontology 30, 467—478.

Mayr, G., Rana, R.S., Rose, K.D., Sahni, A., Kumar, K., Smith, T., 2013. New Specimens of the Early Eocene Bird *Vastanavis* and the Interrelationships of Stem Group Psittaciformes. Paleontological Journal 47 (11), 1308—1314.

Mayr, G., Rana, R.S., Sahni, A., Smith, T., 2007. Oldest fossil avian remains from the Indian subcontinental plate. Current Science 92, 1266—1269.

McCann, T., 2010. Chenier plain sedimentation in the Palaeogene-age lignite-rich successions of the Surat area, Gujarat, western India. Zeitschrift der Deutschen Gesellschaft für Geowissenschaften 161 (3), 335—351.

McCartney, J.A., Seiffert, E.R., 2015. A late Eocene snake fauna from the Fayum Depression, Egypt. Journal of Vertebrate Paleontology 35 (6). http://dx.doi.org/10.1080/02724634.2015.1029580.

Missiaen, P., Gingerich, P.D., 2014. New basal Perissodactyla (Mammalia) from the lower Eocene Ghazij formation of Pakistan. Contributions from the Museum of Paleontology, University of Michigan 32, 139—160.

Mohabey, D.M., Head, J.J., Wilson, J.A., 2011. A new species of the snake *Madtsoia* from the Upper Cretaceous of India and its paleobiogeographic implications. Journal of Vertebrate Paleontology 31, 588—595.

Nagori, M.L., Khosla, S.C., Jakhar, S.R., 2013. Middle Eocene Ostracoda from the Tadkeshwar lignite mine, Cambay Basin, Gujarat. Journal of the Geological Society of India 81, 514—520.

Nolf, D., Rana, R.S., Singh, H., 2006. Fish otoliths from the Ypresian (early Eocene) of Vastan, Gujarat, India. Bulletin de l'Institut Royal des Sciences Naturelles de Belgique 76, 105—118.

Parmley, D., Devore, M., 2005. Palaeopheid Snakes from the Late Eocene HardieMine Local Fauna of Central Georgia. Southeastern Naturalist 4, 703—722.

Prasad, G.V.R., Bajpai, S., 2008. Agamid lizards from the early Eocene of western India: oldest Cenozoic lizards from South Asia. Palaeontographica Electronica 11, 4a, 19p.

Prasad, G.V.R., Singh, V., 1991. Microvertebrates from the intertrappean beds of Rangareddi District, Andhra Pradesh and their biostratigraphic significance. Bulletin of the Indian geologic Association 24, 1—20.

Prasad, G.V.R., Jaeger, J.-J., Sahni, A., Gheerbrant, E., Khajuria, C.K., 1994. Eutherian mammals from the Upper Cretaceous (Maastrichtian) intertrappean beds of Naskal, Andhra Pradesh, India. Journal of Vertebrate Paleontology 14, 260—277.

Prasad, G.V.R., Verma, O., Gheerbrant, E., Goswami, A., Khosla, A., Parmar, V., Sahni, A., 2010. First mammal evidence from the Late Cretaceous of India for biotic dispersal between India and Africa at the KT transition. Comptes Rendus Palevol 9, 63—71.

Prasad, V., Singh, I.B., Bajpai, S., Garg, R., Thakur, B., Singh, A., 2013. Palynofacies and sedimentology based high resolution sequence stratigraphy of the lignite bearing muddy coastal deposits of early Eocene age, Vastan lignite mine, Gujarat, India. Facies 59, 737—761.

Pritchard, A.C., McCartney, J.A., Krause, D.W., Kley, N.J., 2014. New snakes from the Upper Cretaceous (Maastrichtian) Maevarano Formation, Mahajanga Basin, Madagascar. Journal of Vertebrate Paleontology 34, 1080—1093.

Punekar, J., Saraswati, P.K., 2010. Age of the Vastan Lignite in context of some oldest Cenozoic fossil mammals from India. Journal Geological Society of India 76, 63—68.

Rabi, M., Sebők, N., 2015. A revised Eurogondwana model: Late Cretaceous notosuchian crocodyliforms and other vertebrate taxa suggest the retention of episodic faunal links between Europe and Gondwana during most of the Cretaceous. Gondwana Research 28, 1197—1211.

Rage, J.C., 2001. Fossil snakes from the Palaeocene of São José de Itaboraí, Brazil. Part II. Boidae. Palaeovertebrata 30, 111—150.

Rage, J.C., Augé, M., 2010. Squamate reptiles from the middle Eocene of Lissieu (France). A landmark in the middle Eocene of Europe. Geobios 43, 253—268.

Rage, J.C., Danilov, I.G., 2008. A new Miocene fauna of snakes from eastern Siberia, Russia. Was the snake fauna largely homogenous in Eurasia during the Miocene? Comptes Rendu Palevol 7, 383—390.

Rage, J.C., Bajpai, S., Thewissen, J.G.M., Tiwari, B.N., 2003. Early Eocene snakes from Kutch, Western India, with a review of the Palaeophiidae. Geodiversitas 25, 695—716.

Rage, J.C., Folie, A., Rana, R.S., Singh, H., Rose, K.D., Smith, T., 2008. A diverse snake fauna from the early Eocene of Vastan Lignite Mine, at Gujarat, India. Acta Palaeontologica Polonica 53, 391—403.

Rage, J.C., Métais, G., Bartolini, A., Brohi, I.A., Lashari, R.A., Marivaux, L., Merle, D., Solangi, S.H., 2014. First report of the giant snake *Gigantophis* (Madtsoiidae) from the Paleocene of Pakistan: Paleobiogeographic implications. Geobios 47, 147—153.

Rana, R.S., 1987. Dyrosaurid crocodile (Mesosuchia) from the infratrappean beds of Vikarabad, Hyderabad District, Andhra-Pradesh. Current Science 56, 532—534.

Rana, R.S., Sati, K.K., 2000. Late Cretaceous-Palaeocene crocodilians from the Deccan Trap-associated sedimentary sequences of peninsular India. Journal of the Palaeontological Society of India 45, 123—136.

Rana, R.S., Augé, M., Folie, A., Rose, K.D., Kumar, K., Singh, L., Sahni, A., Smith, T., 2013. High diversity of acrodontan lizards in the Early Eocene Vastan Lignite Mine of India. Geologica Belgica 16 (4), 290—301.

Rana, R.S., Kumar, K., Escarguel, G., Sahni, A., Rose, K.D., Smith, T., Singh, H., Singh, L., 2008. An ailuravine rodent from the lower Eocene Cambay Formation at Vastan, western India, and its palaeobiogeographic implications. Acta Palaeontologica Polonica 53, 1—14.

Rana, R.S., Kumar, K., Singh, H., 2004. Vertebrate fauna from the subsurface Cambay Shale (Lower Eocene), Vastan Lignite Mine, Gujarat, India. Current Science 87, 1726—1732.

Rana, R.S., Kumar, K., Zack, S., Solé, F., Rose, K.D., Missiaen, P., Singh, L, Sahni, A., Smith, T., 2015. Craniodental and postcranial morphology of *Indohyaenodon raoi* from the early Eocene of India, and its implications for ecology, phylogeny, and biogeography of hyaenodontid mammals. Journal of Vertebrate Paleontology 35 (5), e965308. http://dx.doi.org/10.1080/02724634.2015.965308.

Rana, R.S., Singh, H., Sahni, A., Rose, K.D., Saraswati, P.K., 2005. Early Eocene chiropterans from a new mammalian assemblage (Vastan lignite mine, Gujarat, Western Peninsular margin): oldest known bats from Asia. Journal of the Palaeontological Society of India 50, 93—100.

Rao, M.R., Sahni, A., Rana, R.S., Verma, P., 2013. Palynostratigraphy and depositional environment of Vastan Lignite Mine (Early Eocene), Gujarat, western India. Journal of Earth System Science 122 (2), 289—307.

Rose, K.D., Chinnery, B.J., 2004. The postcranial skeleton of early Eocene rodents. Bulletin of Carnegie Museum of Natural History 36, 211—244.

Rose, K.D., DeLeon, V.B., Missiaen, P., Rana, R.S., Sahni, A., Singh, L., Smith, T., 2008. Early Eocene lagomorph (Mammalia) from Western India and the early diversification of Lagomorpha. Proceedings of the Royal Society B 275, 1203—1208.

Rose, K.D., Holbrook, L.T., Rana, R.S., Kumar, K., Jones, K.E., Ahrens, H.E., Missiaen, P., Sahni, A., Smith, T., 2014. Early Eocene fossils suggest that the mammalian order Perissodactyla originated in India. Nature Communications 5, 5570. http://dx.doi.org/10.1038/ncomms6570.

Rose, K.D., Kumar, K., Rana, R.S., Sahni, A., Smith, T., 2013. New hypsodont tillodont (Mammalia, Tillodontia) from the Early Eocene of India. Journal of Paleontology 87 (5), 842—853.

Rose, K.D., MacPhee, R.D.E., Alexander, J.P., 1999. Skull of early Eocene *Cantius abditus* (Primates: Adapiformes) and its phylogenetic implications, with a re-evaluation of "*Hesperolemur*" actius. American Journal of Physical Anthropology 109, 523—539.

Rose, K.D., Rana, R.S., Sahni, A., Kumar, K., Missiaen, P., Singh, L., Smith, T., 2009a. Early Eocene primates from Gujarat, India. Journal of Human Evolution 56, 366—404.

Rose, K.D., Rana, R.S., Sahni, A., Kumar, K., Singh, L., Smith, T., 2009b. First tillodont from India: additional evidence for an early Eocene faunal connection between Europe and India? Acta Palaeontologica Polonica 54, 351—355.

Rose, K.D., Rana, R.S., Sahni, A., Smith, T., 2007. A new adapoid primate from the Early Eocene of India. Contribution from the Museum of Paleontology — The University of Michigan 31 (14), 379—385.

Rose, K.D., Smith, T., Rana, R.S., Sahni, A., Singh, H., Missiaen, P., Folie, A., 2006. Early Eocene (Ypresian) continental vertebrate assemblage from India, with description of a new anthracobunid (Mammalia, Tethytheria). Journal of Vertebrate Paleontology 26, 219—225.

Russell, D.E., Sigé, B., 1970. Révision des chiroptères lutétiens de Messel (Hesse, Allemagne). Palaeovertebrata 3, 83—182.

Sahni, A., Bajpai, S., 1991. Eurasiatic elements in the Upper Cretaceous nonmarine biotas of peninsular India. Cretaceous Research 12 (2), 177—183.

Sahni, A., Saraswati, P.K., Rana, R.S., Kumar, K., Singh, H., Alimohammadian, H., Sahni, N., Rose, K.D., Singh, L., Smith, T., 2006. Temporal constraints and depositional palaeoenvironments of the Vastan Lignite Sequence, Gujarat: Analogy for the Cambay shale hydrocarbon source rock. Indian Journal of Petroleum Geology 15 (1), 1—20.

Samanta, A., Bera, M.K., Sarkar, A., 2016. Climate modulated sequence development in a tropical rift basin during the Late Palaeocene to Early Eocene super greenhouse Earth. Sedimentology 63 (4), 917—939. http://dx.doi.org/10.1111/sed.12243.

Samanta, A., Sarkar, A., Bera, M.K., Rai, J., Rathore, S.S., 2013. Late Paleocene—early Eocene carbon isotope stratigraphy from a near-terrestrial tropical section and antiquity of Indian mammals. Journal of Earth System Science 122, 163—171.

Scanlon, J.D., 1992. A new large madtsoiid snake from the Miocene of the Northern Territory. The Beagle, Records of the Northern Territory Museum of Arts and Sciences 9, 49—60.

Scanlon, J.D., 2005. Australia's oldest known snakes: *Patagoniophis, Alamitophis*, and cf. *Madtsoia* (Squamata: Madtsoiidae) from the Eocene of Queensland. Memoirs of the Queensland Museum 51, 215—235.

Scanlon, J.D., 2006. Skull of the large non-macrostomatan snake *Yurlunggur* from the Australian Oligo-Miocene. Nature 439, 839—842.

Scanlon, J.D., Lee, M.S.Y., 2000. The Pleistocene serpent Wonambi and the early evolution of snakes. Nature 403, 416—420.

Schaub, H., 1981. Nummulites et Assilines de la Tethys Paléogène. Taxonomie, phylogénèse et biostratigraphie. Mémoires suisses de Paléontologie. Bâle, 104-105-106, 236 pp (in French with English abstract).

Scotese, C.R., 2013. The PALEOMAP Project PaleoAtlas for ArcGIS. In: Cenozoic Paleogeographic and Plate Tectonic Reconstructions, vol. 1. PALEOMAP Project, Arlington, Texas.

Serra-Kiel, J., Hottinger, L., Caus, E., Drobne, K., Ferrandez, C., Jauhri, A.K., Less, G., Pavlovec, R., Pignatti, J., Samso, J.M., Schaub, H., Sirel, E., Strougo, A., Tambareau, Y., Tosquella, J., Zakrevskaya, E., 1998. Larger foraminiferal biostratigraphy of the Tethyan Paleocene and Eocene. Bulletin de la Société Géologique de France 169, 281—299.

Shanmukhappa, M., 2011. Source Potential Evaluation of Paleogene-Neogene Sediments in Cambay-Tarapur Area, Cambay Basin, India. AAPG Search and Discovery Article #90118©2011 GEO India 2011, 2nd South Asian Geoscience Conference, Greater Noida, New Delhi, India, 12—14 January 2011.

Simpson, G.G., 1933. A new fossil snake from the *Notostylops* beds of Patagonia. Bulletin of the American Museum of Natural History 67, 1—22.

Singh, H., Samant, B., Adatte, T., Khozyem, H., 2014. Diverse palynoflora from amber and associated sediments of Tarkeshwar lignite mine, Surat district, Gujarat. India Current Science 106 (7), 930—932.

Smith, M.J., 1976. Small fossil vertebrates from Victoria Cave, Naracoorte, South Australia. IV. Reptiles. Transactions of the Royal Society of South Australia 100, 39—51.

Smith, T., 1997. Les insectivores s.s. (Mammalia, Lipotyphla) de la transition Paléocène-Eocène de Dormaal (MP7, Belgique): implications biochronologiques

et paléogéographiques. In: Aguilar, J.P., Legendre, S., Michaux, J. (Eds.), Actes du Congrès BiochroM'97. Mémoires et Travaux de l'Ecole Pratique des Hautes Etudes, Montpellier 21, pp. 687—696.

Smith, T., De Bast, E., Sigé, B., 2010. Euarchontan affinity of Paleocene Afro-European adapisoriculid mammals and their origin in the late Cretaceous Deccan Traps of India. Naturwissenschaften 97, 417—422.

Smith, T., Habersetzer, J., Simmons, N.B., Gunnell, G.F., 2012. Chapter 2. Systematics and paleobiogeography of early bats. In: Gunnell, G.F., Simmons, N.B. (Eds.), Evolutionary History of Bats: Fossils, Molecules and Morphology. Cambridge University Press, Cambridge, pp. 23—66.

Smith, T., Rana, R., Missiaen, P., Rose, K.D., Sahni, A., Singh, H., Singh, L., 2007. High bat (Chiroptera) diversity in the Early Eocene of India. Naturwissenschaften 94, 1003—1009.

Smith, T., Rose, K.D., Gingerich, P.D., 2006. Rapid Asia-Europe-North America geographic dispersal of earliest Eocene primate *Teilhardina* during the Paleocene-Eocene Thermal Maximum. Proceedings of the National Academy of Science 103 (30), 11223—11227.

Smith, T., Solé, F., Missiaen, P., Rana, R., Kumar, K., Sahni, A., Rose, K.D., 2015. First early Eocene tapiroid from India and its implication for the paleobiogeographic origin of perissodactyls. Palaeovertebrata 39 (2), e5. http://dx.doi.org/10.18563/pv.39.2.e5.

Storey, M., Mahoney, J.J., Saunders, A.D., Duncan, R.A., Kelley, S.O., Coffin, M.F., 1995. Timing of hot-spot related volcanism and the breakup of Madagascar and India. Science 267, 852—855.

Storrs, G.W., 1986. A dyrosaurid crocodile (Crocodylia: Mesosuchia) from the Paleocene of Pakistan. Postilla (Peabody Museum of Natural History, Yale University) 197, 1—16.

Swinton, W.E., 1950. On *Congosaurus bequaerti* Dollo. Annales du Musée du Congo Belge, Tervuren (Belgique), Série 8, Sciences Géologiques 4, 1—35 (in French with English abstract).

Szalay, F.S., Delson, E., 1979. Evolutionary History of the Primates. Academic Press, New York, 580 pp.

Szyndlar, Z., Böhme, W., 1996. Redescription of *Tropidonotus atavus* von Meyer, 1855 from the upper Oligocene of Rott (Germany) and its allocation to *Rottophis* gen. nov. (Serpentes, Boidae). Palaeontographica (Abteilung A) 240, 145—161.

Szyndlar, Z., Rage, J.-C., 2003. Non-Erycine Booidea from the Oligocene and Miocene of Europe. Institute of Systematics and Evolution of Animals, Polish Academy of Sciences, Kraków, 111 pp.

Tong, Y.-S., Wang, J-W., 2006. Fossil Mammals from the Early Eocene Wutu Formation of Shandong Province. Palaeontologica Sinica Whole number 192, New Series C, Number 28, 195 pp.

Tyler, J.C., 1980. Osteology, phylogeny, and higher classification of the fishes of the order Plectognathi (Tetraodontiformes). NOAA Technical Report NMFS Circular 434, 1—422.

Tyler, J.C., Santini, F., 2002. Review and reconstructions of the tetraodontiform fishes from the Eocene of Monte Bolca, Italy, with comments on related Tertiary taxa. Studi e Ricerche sui Giacimenti Terziari di Bolca. Museo Civico di Storia Naturale di Verona 9, 47—119.

Vasile, Ş., Csiki-Sava, Z., Venczel, M., 2013. A new madtsoiid snake from the Upper Cretaceous of the Haţeg Basin, Western Romania. Journal of Vertebrate Paleontology 33 (5), 1100—1119.

Wilson, J.A., Mohabey, D.M., Peters, S.E., Head, J.J., 2010. Predation upon hatchling dinosaurs by a new snake from India. PLoS Biology 8 (3), e1000322. http://dx.doi.org/10.1371/journal.pbio.1000322.

Wood, A.E., 1976. The paramyid rodent *Ailuravus* from the middle Eocene of Europe and its relationships. Palaeovertebrata 7 (1—2), 117—149.

Zhuang, G., Najman, Y., Guillot, S., Roddaz, M., Antoine, P.O., Métais, G., Carter, A., Marivaux, L., Solangi, S.H., 2015. Constraints on the collision and the pre-collision tectonic configuration between India and Asia from detrital geochronology, thermochronology, and geochemistry studies in the lower Indus basin, Pakistan. Earth and Planetary Science Letters 432, 363—373.