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New fossils from Tadkeshwar Mine (Gujarat, India) increase primate diversity from the early Eocene Cambay Shale

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ABSTRACT

Several new fossil specimens from the Cambay Shale Formation at Tadkeshwar Lignite Mine in Gujarat document the presence of two previously unknown early Eocene primate species from India. A new species of *Asiadapis* is named based on a jaw fragment preserving premolars similar in morphology to those of *A. cambayensis* but substantially larger. Also described is an exceptionally preserved edentulous dentary (designated cf. *Asiadapis*, unnamed sp. nov.) that is slightly larger and much more robust than previously known Cambay Shale primates. Its anatomy most closely resembles that of Eocene adapoids, and the dental formula is the same as in *A. cambayensis*. A femur and calcaneus are tentatively allocated to the same taxon. Although the dentition is unknown, exquisite preservation of the dentary of cf. *Asiadapis* sp. nov. enables an assessment of masticatory musculature, function, and gape adaptations, as well as comparison with an equally well-preserved dentary of the asiadapid *Marcgodinotius indicus*, also from Tadkeshwar. The new *M. indicus* specimen shows significant gape adaptations but was probably capable of only weak bite force, whereas cf. *Asiadapis* sp. nov. probably used relatively smaller gapes but could generate relatively greater bite forces.

1. Introduction

The early Eocene primate fauna of India is known so far only from the Cambay Shale Formation, which is exposed in open-cast lignite mines in Gujarat, west central India. Our understanding of these Indian primates has been based almost entirely on the extensive sample from Vastan Lignite Mine, which includes about 100 specimens (dental and postcranial) representing at least four taxa—the asiadapid adapoids *Marcgodinotius indicus* and *Asiadapis cambayensis*, and the omomyids *Vastanomys gracilis* and *V. major* (Bajpai et al., 2005; Rose et al., 2007, 2009; Dunn et al., 2016). Recently we reported a small number of primates from the Cambay Shale at Tadkeshwar Lignite Mine, about 10 km southwest of Vastan Mine (Smith et al., 2016). These fossils, from two stratigraphic levels, were referred to *M. indicus* (two tooth-bearing dentaries) and cf. *Asiadapis cambayensis* (an edentulous dentary). Notably, one of the jaws of *M. indicus* comes from the lower level, stratigraphically slightly higher and thus probably slightly younger than the Vastan fossils, whereas the second comes from the higher level, about 12 m above the lower level and therefore certainly younger, although how much younger is still unknown and controversial. Both specimens of *Marcgodinotius* are close enough morphologically to the Vastan sample to justify allocation to the same species, although the higher specimen is derived in showing slight compression and a possible reduction in number of anterior premolars.

Here we describe several new primate specimens from Tadkeshwar mine, which indicate the presence of two previously unrecognized primate species from the Cambay Shale. This increase in diversity is further evidence that India played an important role in the evolution of primates early in their history.

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2. Materials and methods

Institutional abbreviations:

ACQ—Ancienne Collection de Quercy, Université de Montpellier II, Montpellier, France
DPC—Fossil Primate Center, Duke University, Durham, North Carolina
IVPP—Institute of Vertebrate Paleontology and Paleoanthropology, Beijing, PRC
GU/RSR/TAD, GU/RSR/VAS—Department of Geology (Tadkeshwar collection, Vastan collection), H.N.B. Garhwal University, Srinagar, Uttarakhand, India
MCZ—Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts
QW—Quercy Collection, Naturhistorisches Museum, Basel, Switzerland
UM PAT—Collection Palette, Université de Montpellier II, Montpellier, France
USNM—National Museum of Natural History (NMNH), Smithsonian Institution, Washington, D.C. (USNM V, Department of Paleobiology; USNM-M, Department of Mammalogy)
WIF/A—Wadia Institute of Himalayan Geology, Dehradun, Uttarakhand, India

Images of the new fossils, as well as most of the comparative taxa presented here, were taken from digital surface models created from high-resolution micro-CT scans of the original fossils, performed at the Duke University Shared Materials Instrumentation Facility (SMIF). Scans of some of the comparative taxa were obtained from MorphoSource (morphosource.org) or MorphoMuseuM (morphomuseum.com). Some comparative fossil specimens were imaged by conventional digital photography. A complete list of images reproduced here with links to these images is presented in Table 1.

Because of the fragmentary and incomplete condition of the fossils reported, we consider it premature to employ computer-based phylogenetic methods to attempt to analyze their relationships.

This publication and the nomenclatural acts it contains have been registered with Zoobank: http://zoobank.org/References/093FDF7A-743A-4184-B0D9-8F68A91E4C17.

3. Occurrence

The new fossils reported here come from two different stratigraphic levels in the early Eocene Cambay Shale Formation at Tadkeshwar Lignite Mine (Supplementary Online Material [SOM] Fig. S1), the lower one designated TAD-1 and the higher one TAD-2. TAD-1 is situated about 4–5 m above Lignite 2, the lower of two major lignites excavated at Tadkeshwar, Vastan, and neighboring mines. TAD-2 is about 12 m higher than TAD-1, and about 4 m below Lignite 1 (see SOM Fig. S2 and Smith et al., 2016, for details of the stratigraphy and sedimentation of Tadkeshwar). Thicknesses of sediments vary between Tadkeshwar and Vastan mines, and even in different parts of each mine, making precise correlation and age-determination challenging. However, based on the position of the fossiliferous levels at Tadkeshwar relative to Lignite 2, it is reasonable to conclude that both Tadkeshwar levels (TAD-1 and TAD-2) are at least slightly younger than the productive layer at Vastan (1–2 m above Lignite 2), which appears to be ~54.5 Ma based on carbon isotope stratigraphy (Clementz et al., 2011; Samanta et al., 2013; Adatte et al., 2014) and dinoflagellates (Garg et al., 2008). The asiadapid primate *Marcgodinotius indicus*, first described from Vastan Mine, has been found at both TAD-1 and TAD-2, although, as noted above, differences in the TAD-2 specimen suggest it is slightly more derived. In addition, two other mammal species from Vastan (*Indohyaenodon raoi* and *Cambaytherium thewissi*) are recorded from TAD-2. Thus the fossil mammals reported so far from the two levels at Tadkeshwar differ only in minor ways, suggesting age difference in the tens to hundreds of thousands of years (Smith et al., 2016).

Table 1
List of euprimate fossils from Tadkeshwar Mine and comparative specimens, including links and DOIs for 3D models and scan data.

Element	Number	Taxon	Side	Figure	File description	DOI/Link
Tadkeshwar Fossil Primates						
Dentary	GU 9239	*Asiadapis tapiensis* sp. nov.	R	1, 2	Zipped .tiff stack	https://doi.org/10.17602/M2/M39123
					3D mesh, .ply	https://doi.org/10.17602/M2/M39100
Dentary	GU 9004	cf. *Asiadapis* sp.	R	2, 3, 4, 5, SI 3	Zipped .tiff stack	https://doi.org/10.17602/M2/M39121
					3D mesh, .ply	https://doi.org/10.17602/M2/M39102
Dentary	GU 9014	cf. *Asiadapis* sp.	R	2, 3, 4, 5, 6, 7, 8, 11, 12, SOM 3	Zipped .tiff stack	https://doi.org/10.17602/M2/M39122
					3D mesh, .ply	https://doi.org/10.17602/M2/M39103
Femur, without head	GU 9012	cf. *Asiadapis* sp.	L	SOM 4A and B	Zipped .tiff stack	https://doi.org/10.17602/M2/M39119
					3D mesh, .ply	https://doi.org/10.17602/M2/M39105
Femoral head	GU 9012	cf. *Asiadapis* sp.	L		Zipped .tiff stack	https://doi.org/10.17602/M2/M39120
					3D mesh, .ply	https://doi.org/10.17602/M2/M39118
Reconstructed femur	GU 9012	cf. *Asiadapis* sp.	L	9, 10	3D mesh, .ply	https://doi.org/10.17602/M2/M39104
Dentary	WIF/A 2334	*Marcgodinotius indicus*	R	2, 3, 4, 5, 7, 12, SOM 3	Zipped .tiff stack	https://doi.org/10.17602/M2/M39125
					3D mesh, .ply	https://doi.org/10.17602/M2/M39101
Comparative Fossil Specimens						
Dentary	GU 745	*Asiadapis cambayensis*	L	7	Zipped .tiff stack	https://doi.org/10.5072/FK2/M39722
					3D mesh, .ply	https://doi.org/10.5072/FK2/M39723
Dentary	DPC 12437	*Aframonius diedes*	R	11	3D mesh, .ply	https://doi.org/10.17602/M2/M11995
Dentary	DPC 13596	*Apidium phiomense*	L	11	3D mesh, .ply	M8767-11600
Dentary	DPC 10994	*Babakotia radofilai*	R	8	.jpg image	Digital image taken by JMGP
Dentary	DPC 7342	*Catopithecus browni*	L	11	3D mesh, .ply	M15610-28845
Dentary	UM PAT 17	*Donrussellia magna*	L	7	3D mesh, .ply	https://doi.org/10.18563/m3.sf17
Dentary	ACQ 6397	*Leptadapis magnus*	L	8	.jpg image	Digital image taken by JMGP
Dentary	QW 620a	*Adapis parisiensis*	L	8	.jpg image	Digital image taken by JMGP
Dentary	USNM V21864	*Notharctus tenebrosus*	R	7	Zipped .tiff stack	M2784
Dentary	USNM V21815	*Smilodectes gracilis*	R	7	Zipped .tiff stack	M5972
Dentary	USNM V21815	*Smilodectes gracilis*	L	7	Zipped .tiff stack	M5972
Comparative Extant Specimens						
Dentary	DPC 1232	*Lemur catta*	R	11	Zipped .tiff stack	M647-556h
Dentary	MCZ 16375	*Propithecus verreauxi*	L	11	Zipped DICOM stack	https://doi.org/10.17602/M2/M2724

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