

## Dentition of *Sivaladapis nagrii* (Adapidae) from the Late Miocene of India

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*Two genera and three species of adapid primates are known from the middle and late Miocene of India and Pakistan. Most fossil specimens are fragmentary, but the best-known species, Sivaladapis nagrii, is now represented by enough specimens to permit composite reconstruction of much of the dentition. The incisors of Sivaladapis have spatulate crowns, and the canines are large, projecting teeth. Premolars and molars exhibit complex occlusion involving simultaneous approximation of pointed leading cusps on upper and lower molars, with linear trailing lophs. The premolar eruption sequence in Sivaladapis appears to be  $P_2$ - $P_4$ - $P_3$ , as in most extant prosimians. Symphyseal fusion of the mandibular rami occurred early in ontogeny, before the eruption of any of the anterior permanent teeth. We interpret Sivaladapis to have been a specialized arboreal folivore that became extinct near the end of the Miocene, when the distribution of forests was increasingly restricted and colobine monkeys first invaded South Asia.*

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**KEY WORDS:** *Sivaladapis*; Adapidae; Miocene primates; tooth eruption; symphyseal fusion.

### INTRODUCTION

Prosimian primate fossils were first discovered in Miocene Siwalik sediments of India and Pakistan some 50 years ago. The initial finds were

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**Table I.** Systematic Listing of Valid Species of Miocene Adapidae (boldface), with Principal Synonyms and References<sup>a</sup>

Family **ADAPIDAE** Trouessart, 1879

Subfamily **SIVALADAPINAE** Thomas and Verma, 1979

**SIVALADAPINAE** Thomas and Verma, 1979, p. 833 (published November 12, 1979).  
**INDRALORISINI** Szalay and Delson, 1979, p. 143 (published December 31, 1979).

**Indraloris** Lewis, 1933

*Sivasua* (in part), Pilgrim, 1932, p. 52.  
*Indraloris* Lewis, 1933, p. 135.

**Indraloris himalayensis** (Pilgrim), 1932

*Sivasua himalayensis* Pilgrim, 1932, p. 59, Pl. 2, Fig. 13.  
*Indraloris lulli* Lewis, 1933, p. 135, Figs. 1, 2. Tattersall, 1968, p. 2, Figs. 1a-c.  
*Indraloris himalayensis*, Gingerich and Sahni, 1979, p. 415, Figs. 1a, b.

Type specimen: Geological Survey of India (Calcutta) No. D.237, right mandibular ramus with  $M_1$ , collected in Nagri beds near Haritalyangar, India.

Type of synonym: Yale University (New Haven) No. 13802, crown of isolated left  $M_1$ , collected in Nagri beds near Haritalyangar, India.

**Sivaladapis** Gingerich and Sahni, 1979

*Sivasua* (in part), Pilgrim, 1932, p. 52. Prasad, 1963, p. 95; 1970, p. 17.  
*Indraloris* (in part), Tattersall, 1968, p. 4. Chopra and Vasishat, 1980a, p. 129.  
*Sivaladapis* Gingerich and Sahni, 1979, p. 415. Thomas and Verma, 1979, p. 833.  
*Indoadapis* Chopra and Vasishat, 1980b, p. 511.

**Sivaladapis palaeindicus** (Pilgrim), 1932

*Sivasua palaeindica* Pilgrim, 1932, p. 56, Pl. 2, Figs. 10-12.  
*Indraloris* cf. *lulli*, Tattersall, 1968, p. 4, Figs. 1d, 2.  
*Sivaladapis palaeindicus*, Gingerich and Sahni, p. 415, Fig. 1e. Thomas and Verma, 1979, p. 833, Fig. 1.

Type specimen: Geological Survey of India (Calcutta) No. D. 224, associated right,  $P_4$  and  $M_{1-2}$  or  $M_{2-3}$ , collected in beds of "Chinji" age near Chinji, Pakistan.

**Sivaladapis nagrii** (Prasad), 1970

*Sivasua nagrii* Prasad, 1963, p. 95 (*nomen nudum*); 1970, p. 17, Pl. 4, Figs. 10, 11.  
*Sivaladapis nagrii*, Gingerich and Sahni, 1979, p. 415, Figs. 1c, d.  
*Indraloris himalayensis*, Chopra and Vasishat, 1979, p. 144; 1980a, p. 130, Pl. 1, Figs. a-f.  
*Indoadapis shivaii* Chopra and Vasishat, 1980b, p. 512, Pl. 1, Figs. 1, 2, Pl. 2 Figs. 1, 2.  
Type specimen: Geological Survey of India (Calcutta) No. 18093, right mandibular ramus with  $M_{1-2}$ , from "Nagri beds of Haritalyangar," India.  
Type of synonym: Panjab University Anthropology (Chandigarh) No. 79-P, right maxilla with  $C^1-M^2$ , from "Nagri" beds 250 m east of Haritalyangar, India.

<sup>a</sup>Publications by Chopra and Vasishat are dated 1980a and 1980b, respectively, conforming to the order in which they were submitted for publication rather than the order in which they were actually published.

fragmentary, and for many years these were misinterpreted as coati-like procyonid carnivores (Pilgrim, 1932). One specimen found later, an isolated lower molar, was described as a primitive lorisid (Lewis, 1933), a designation consistent with the distribution of extant prosimians in southern Asia today. However, more complete specimens collected in recent years indicate that all these early finds probably represent archaic lemuriform primates of the family Adapidae (Gingerich and Sahni, 1979). True Lorisidae have been discovered in Miocene Siwalik sediments in recent years (Jacobs, 1981), but these are virtually modern in form and differ markedly from the adapids discussed here.

Two genera and three species of Miocene Adapidae are known from southern Asia, and their taxonomic history is complex (see Table I). *Sivaladapis palaeindicus* is found in the middle Miocene Chinji faunal zone (dated at about 13–14 Ma), while *Sivaladapis nagrii* and *Indraloris himalayensis* are found in the late Miocene Nagri faunal zone (ca. 9 Ma). The stratigraphy and succession of Siwalik faunas in India are discussed by Prasad (1970) and Johnson and Vondra (1972). Ages of successive Siwalik faunas are documented in Pakistan by Barry *et al.* (1982). At present only one species, *Sivaladapis nagrii*, is known from specimens adequate to distinguish it with certainty from prosimians of modern aspect, and its distinctive features are emphasized in the following discussion. The other two species, *S. palaeindicus* and *I. himalayensis*, are referred to Adapidae on the basis of overall similarity to *S. nagrii*.

Abbreviations used in the text and figure captions are as follows: LUVU, Lucknow University Department of Geology (Vertebrate Paleontology), Lucknow, India; and UM, University of Michigan Museum of Paleontology, Ann Arbor, Michigan.

### DENTITION OF *SIVALADAPIS*

The full dental formula of *Sivaladapis nagrii* is  $2/2 \cdot 1/1 \cdot 3/3 \cdot 3/3$ . Upper incisors are not yet known, and the upper canine is known in only one specimen. Judging from Plate 2, Fig. 2, of Chopra and Vasishat (1980b), the upper canine is a large, vertically implanted tooth with a simple, projecting, pointed crown interlocking in occlusion with the lower canine and  $P_2$ . Upper premolars are progressively more molarized from front to back (Fig. 1).  $P^2$  is single-rooted, with a simple conical cusp.  $P^3$  is larger and double-rooted, and it too has a simple crown with one principal cusp, apparently a serial homologue of the paracone. Two prominent crests curve medially and posteriorly, respectively, from the paracone, enclosing a rudimentary trigon basin.  $P^4$  is three-rooted and fully molarized. It is

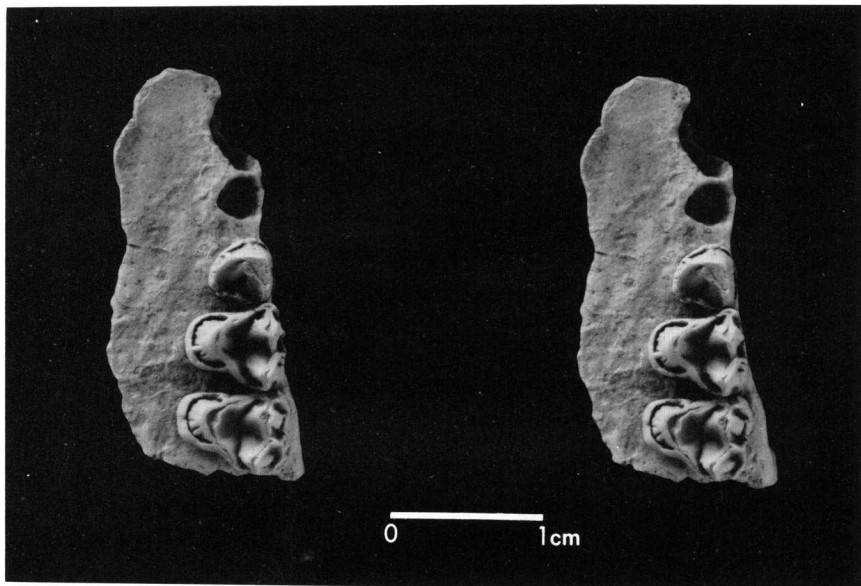


Fig. 1. Left maxilla of *Sivaladapis nagrii* (LUVP 14506) in occlusal view, with alveoli for  $C^1$  and  $P^2$  and crowns of  $P^3-4$  and  $M^1$  intact.

slightly smaller and has the mesostyle less well developed, but otherwise it closely resembles the following molars.

Among upper molars,  $M^1$  and  $M^2$  differ slightly in size, but they are otherwise identical. The protocone, paracone, and metacone are prominent, enclosing a large, basined trigone that is completely enclosed by the preprotocrista, the postprotocrista, and a sharp ectoloph. The paraconule is moderately developed on unworn molars but it is usually obscured by wear. There are a distinct parastyle and mesostyle on the upper molars, connected by a labial cingulum. A prominent lingual cingulum surrounds the protocone. There is no hypocone or pericone on this lingual cingulum. The crown of  $M^3$  differs from that of  $M^1$  or  $M^2$  in being slightly less symmetrical, with the metacone located relatively closer to the protocone. All of the upper cheek teeth have high, sharp cusps when freshly erupted, but these were rapidly worn to create a crown of less relief, with considerable dentine exposed at the apices of cusps and crests. Measurements of upper teeth of *Sivaladapis nagrii* are summarized in Table II.

Crowns of the lower central incisors are preserved in one specimen, LUVP 14505 (Fig. 2). They are small, spatulate, and vertically implanted. The incisors are distinctive in being high-crowned, with the worn occlusal

**Table II.** Statistical Summary of Measurements of Upper and Lower Teeth of *Sivaladapis nagrii*, Based on Specimens at the Geological Survey of India (Calcutta), Lucknow University (Lucknow), and University of Michigan (Ann Arbor)<sup>a</sup>

Measurement	<i>N</i>	OR	$\bar{X}$	SD	<i>V</i>
Upper permanent dentition					
P <sup>3</sup> L	2	4.4-4.6	4.50	—	—
W	2	4.5-4.9	4.70	—	—
P <sup>4</sup> L	1	5.7	—	—	—
W	1	6.5	—	—	—
M <sup>1</sup> L	3	5.7-6.1	5.90	0.20	3.4
W	3	7.3-7.5	7.37	0.12	1.6
M <sup>2</sup> L	3	6.0-6.4	6.17	0.21	3.4
W	3	7.4-8.0	7.80	0.35	4.4
M <sup>3</sup> L	3	5.3-5.7	5.50	0.20	3.6
W	3	7.1-7.3	7.20	0.10	1.4
Lower permanent dentition					
I <sub>1</sub> L	1	2.4	—	—	—
W	1	1.7	—	—	—
C <sub>1</sub> L	2	4.2-4.9	4.55	—	—
W	2	3.3-3.8	3.55	—	—
P <sub>2</sub> L	1	4.4	—	—	—
W	1	3.3	—	—	—
P <sub>3</sub> L	1	5.2	—	—	—
W	1	3.9	—	—	—
P <sub>4</sub> L	4	5.9-6.2	6.05	0.13	2.1
W	4	4.5-4.7	4.60	0.12	2.5
M <sub>1</sub> L	6	5.5-5.9	5.65	0.16	2.9
W	6	4.3-4.6	4.47	0.10	2.3
M <sub>2</sub> L	4	5.9-6.3	6.05	0.19	3.2
W	4	4.9	4.90	—	—
M <sub>3</sub> L	2	6.7-6.9	6.80	—	—
W	2	4.6	4.60	—	—
Mandibular depth below M <sub>1</sub>					
MD	4	10.2-12.3	11.15	1.06	9.5
Lower deciduous dentition					
dP <sub>3</sub> L	1	4.6	—	—	—
W	1	2.8	—	—	—
dP <sub>3</sub> L	1	6.8	—	—	—
W	1	4.1	—	—	—

<sup>a</sup>Abbreviations: L, crown length; W, crown width; *N*, sample size; OR, observed range;  $\bar{X}$ , mean; SD, standard deviation; *V*, coefficient of variation.

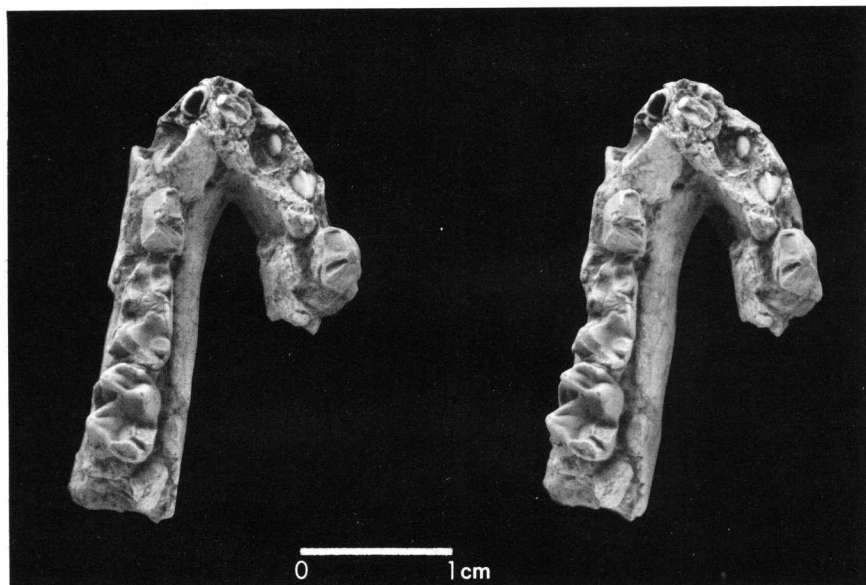


Fig. 2. Partial mandible of subadult *Sivaladapis nagrii* (LUV 14505) in occlusal view, with left and right  $I_1$  erupting and crowns of left and right  $dP_3$ , left  $dP_4$ , and left  $M_1$  in place. Mandibular symphysis of this specimen is fully fused.

edge of each crown wrapping around a triangular central basin both medially and laterally. Judging from the size of roots preserved in LUV 14503 and 14504, the crown of  $I_2$  was slightly larger than that of  $I_1$ . The lower canines have large, straight, projecting crowns in LUV 14503. The crowns are heavily worn along their posterior margin from occlusion with the upper canines.  $P_2$  is single-rooted, high crowned, and caniniform, with a single principal cusp and no accessory cusps. The crown of  $P_2$  in LUV 14504 shows a prominent honing facet for the upper canine along its entire anterior surface.  $P_3$  is double-rooted. It has a single prominent triangular cusp, the protoconid, with an anterior projecting keel or paracristid and separate crests projecting posterolingually and posterolabially. These curve at the base of the crown and border a short, broad talonid. As in the upper dentition, the fourth premolar ( $P_4$ ) is highly molarized (Fig. 3). It differs from the following molars only in having a more open trigonid and in lacking an entoconid on the talonid.

Unworn lower molars of *Sivaladapis nagrii* are high-crowned and almost lophodont (Fig. 3). Each has a large protoconid and metaconid supporting the posterior part of an acutely curved protolophid. The

