

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.

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^a

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_{1-3} , 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.

^aPublications 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

