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.*

INTRODUCTION

Prosimian primate fossils were first discovered in Miocene Siwalik sediments of India and Pakistan some 50 years age. 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

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

Indraloris himalayensis (Pilgrim), 1932

Sivanasua 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

Sivanasua (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

Sivanasua 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

Sivanasua 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.

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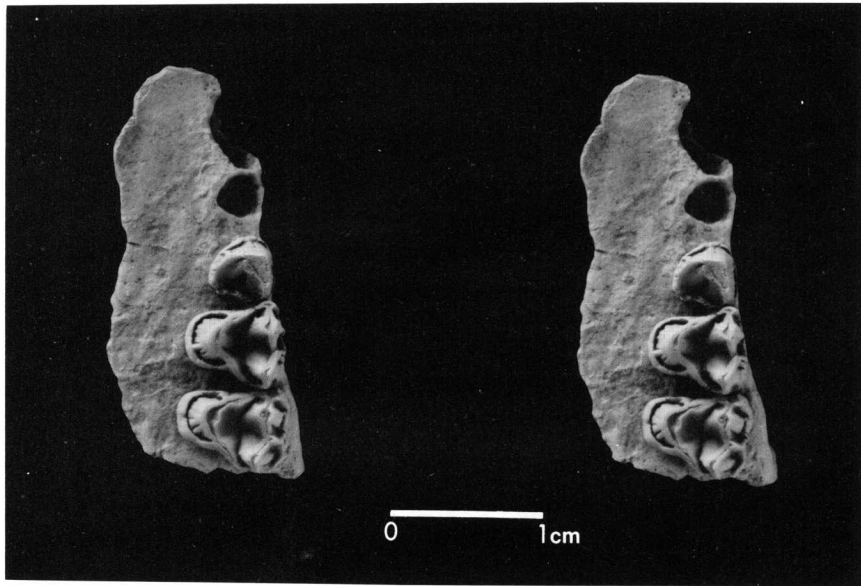
Fig. 1. Left maxilla of *Sivaladapis nagrii* (LUVP 14506) in occlusal view, with alveoli for C^1 and P^2 and crowns of $P^{3-4}M^1$ intact.

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)[a]

Measurement	N	OR	$\bar{X}$	SD	V
Upper permanent dentition					
P^3L	2	4.4–4.6	4.50	—	—
W	2	4.5–4.9	4.70	—	—
P^4L	1	5.7	—	—	—
W	1	6.5	—	—	—
M^1L	3	5.7–6.1	5.90	0.20	3.4
W	3	7.3–7.5	7.37	0.12	1.6
M^2L	3	6.0–6.4	6.17	0.21	3.4
W	3	7.4–8.0	7.80	0.35	4.4
M^3L	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_1L	1	2.4	—	—	—
W	1	1.7	—	—	—
C_1L	2	4.2–4.9	4.55	—	—
W	2	3.3–3.8	3.55	—	—
P_2L	1	4.4	—	—	—
W	1	3.3	—	—	—
P_3L	1	5.2	—	—	—
W	1	3.9	—	—	—
P_4L	4	5.9–6.2	6.05	0.13	2.1
W	4	4.5–4.7	4.60	0.12	2.5
M_1L	6	5.5–5.9	5.65	0.16	2.9
W	6	4.3–4.6	4.47	0.10	2.3
M_2L	4	5.9–6.3	6.05	0.19	3.2
W	4	4.9	4.90	—	—
M_3L	2	6.7–6.9	6.80	—	—
W	2	4.6	4.60	—	—
Mandibular depth below M_1					
MD	4	10.2–12.3	11.15	1.06	9.5
Lower deciduous dentition					
dP_3L	1	4.6	—	—	—
W	1	2.8	—	—	—
dP_3L	1	6.8	—	—	—
W	1	4.1	—	—	—

[a]Abbreviations: L, crown length; W, crown width; N, sample size; OR, observed range; X, mean; SD, standard deviation; V, coefficient of variation.
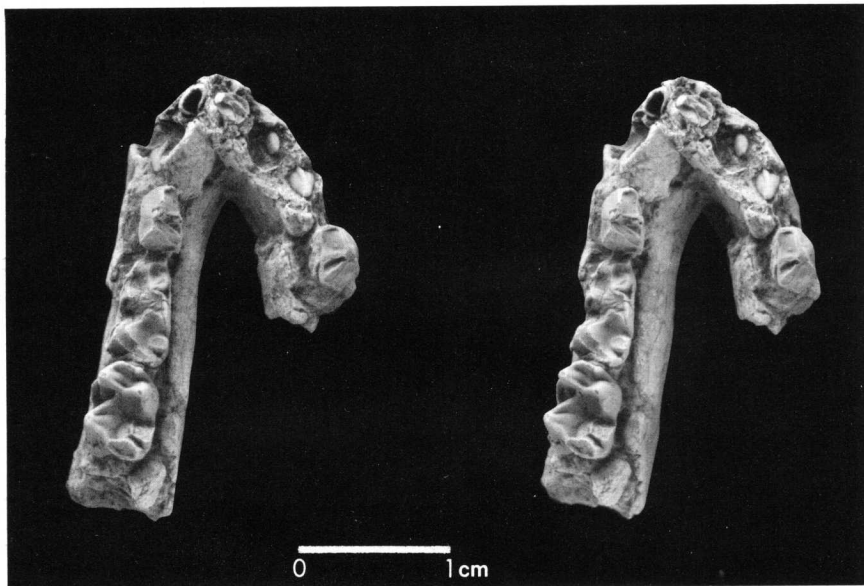
Fig. 2. Partial mandible of subadult *Sivaladapis nagrii* (LUVP 14505) in occlusal view, with left and right I$_1$ erupting and crowns of left and right dP$_3$, left dP$_4$, and left M$_1$ in place. Mandibular symphysis of this specimen is fully fused.

edge of each crown wrapping around a triangular central basin both medially and laterally. Judging from the size of roots preserved in LUVP 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 LUVP 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 LUVP 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
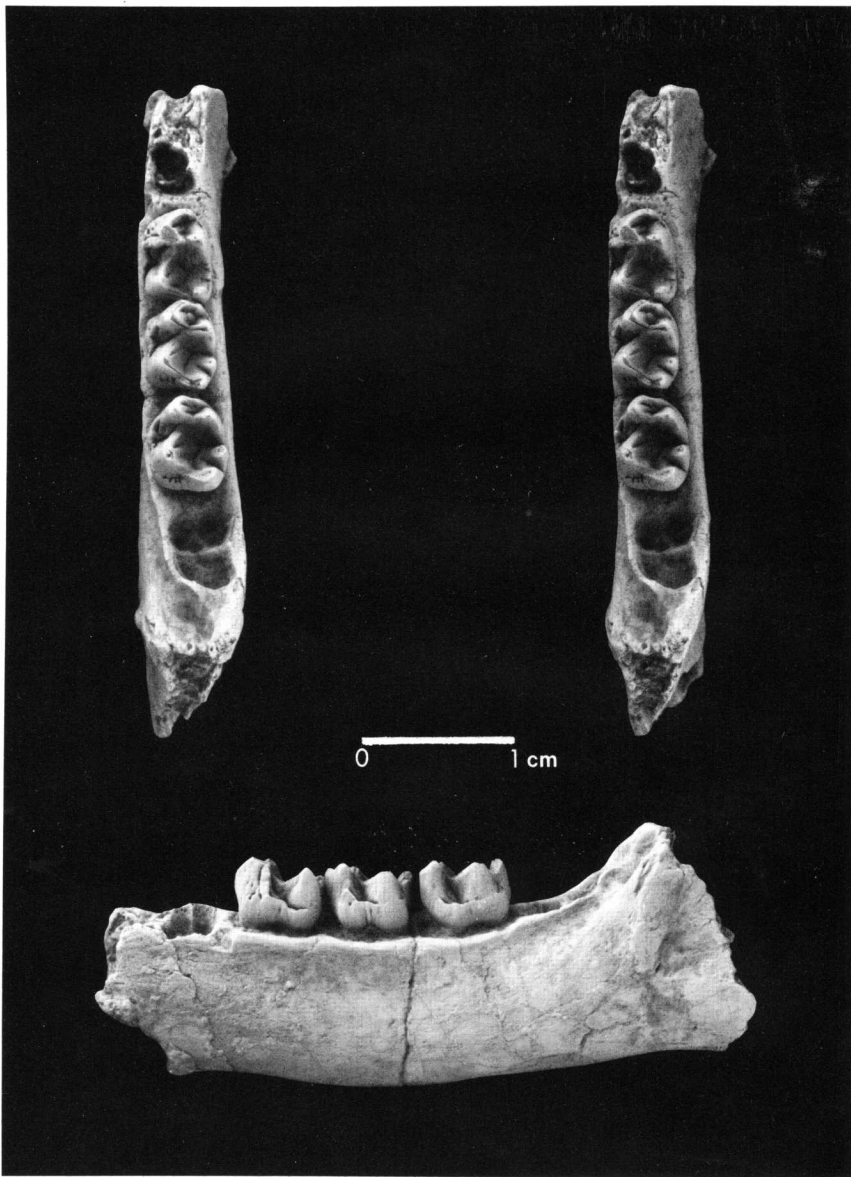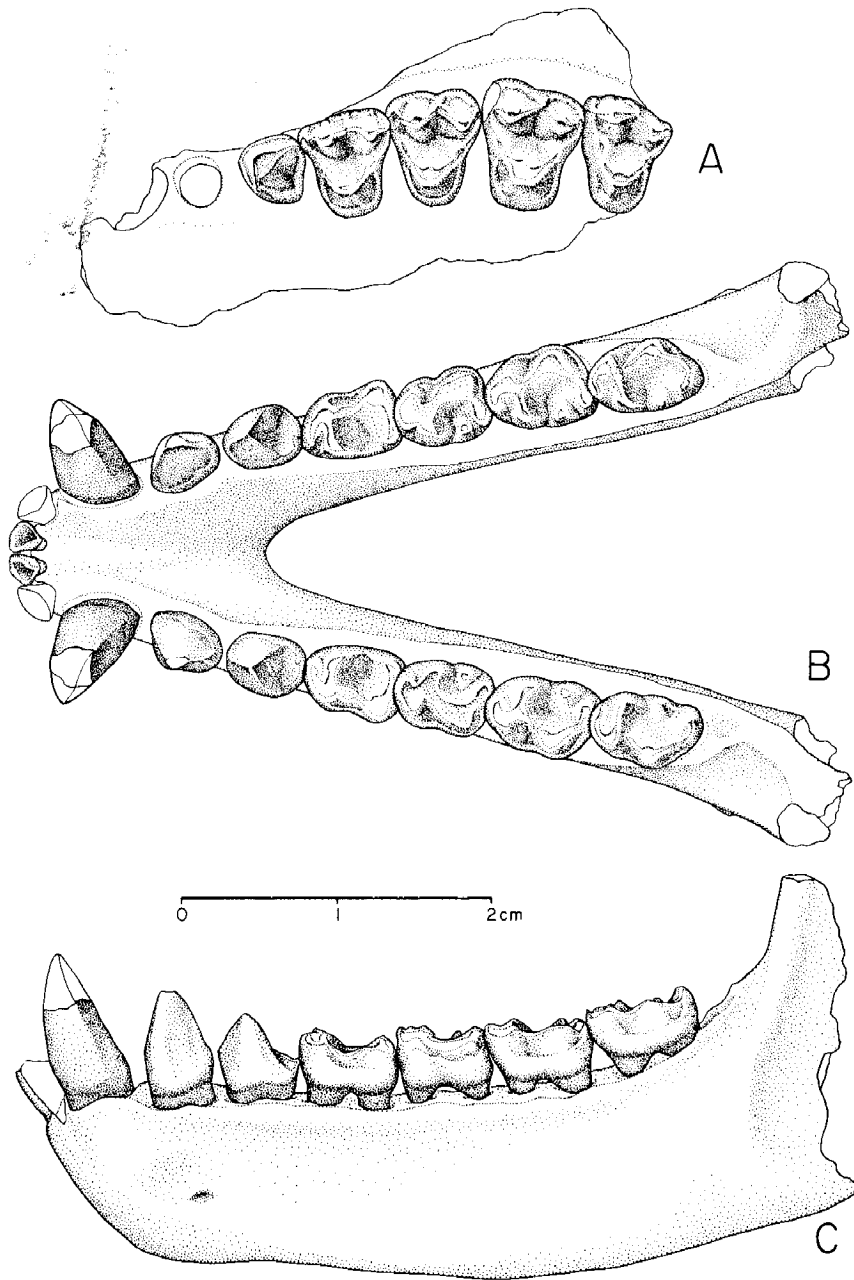
Fig. 3. Left dentary of *Sivaladapis nagrii* (UM 71837) in occlusal view, with alveoli for P$_3$, crowns of P$_4$M$_{1-2}$, and alveoli for M$_3$. Note the large distinct entoconids on M$_{1-2}$.

Fig. 4. Composite reconstruction of upper and lower dentition of *Sivaladapis nagrii,* based on LUVP 14501-14507. A and B, occlusal view; C, left lateral view. Note the large caniniform crown of P_2.

anterior part of the protolophid is supported by the hypoconulid of the preceding molar. The hypoconid and associated crests comprise a less prominent hypolophid. The paraconid is reduced and crest-like on the trigonid of each molar, but the entoconid is a prominent pointed cusp on the talonid. As in the upper dentition, the lower cheek teeth appear to have thin enamel and to have worn rapidly, exposing dentine at the apices of cusps and crests. Measurements of the lower teeth of *Sivaladapis nagrii* are summarized in Table II. A composite drawing of the upper and lower dentition of *Sivaladapis nagrii,* based on LUVP specimens, is illustrated in Fig. 4.

MOLAR OCCLUSION

Sivaladapis has a number of very distinctive morphological features on both the upper and the lower molars. Upper molars are unusual in having a prominent parastyle and mesostyle on the ectoloph, a reduced paraconule and no metaconule, and a prominent lingual cingulum but no hypocone. Lower molars are unusual in being so sharply crested and in having very distinct, pointed entoconids.

The functional relationships of molar cusps and crests during occlusion are shown diagrammatically in Fig. 5. We attempted to orient upper and lower cheek teeth as they function in the dominant phase of occlusion [the buccal phase, or Phase I of Kay and Hiiemäe (1974)]. This is complicated because the paths of movement of the upper and lower cheek teeth relative to each other are curvilinear, and projection of this onto any single plane for analysis necessarily leads to some distortion. Nevertheless, the principal relationships of most functional elements can be recognized. Both cheek tooth series are shown in Fig. 5, with the leading occlusal edge forward in the drawings. This allows individual structural elements to be viewed as functional groups, and upper and lower functional groups to be approximated.

In the upper dentition of *Sivaladapis,* the leading functional elements are parastyles and mesostyles. These appear in occlusal orientation as points (filled circles in Fig. 5B). The next series of functional elements in the upper dentition is a series of cusps (paracone and metacone; open circles with dots in Fig. 5B). supporting an associated series of serrated crests that together comprise the upper molar ectolophs. The final functional elements are larger crests or lophs (pre- and postprotocristae) associated with the protocones (open circles in Fig. 5B). Thus there is a progression from puncturing points to small shearing crests to larger shearing crests on the upper cheek teeth, all associated with the buccal phase of occlusion.

parastyle   mesostyle

A

B

C

D

entoconid
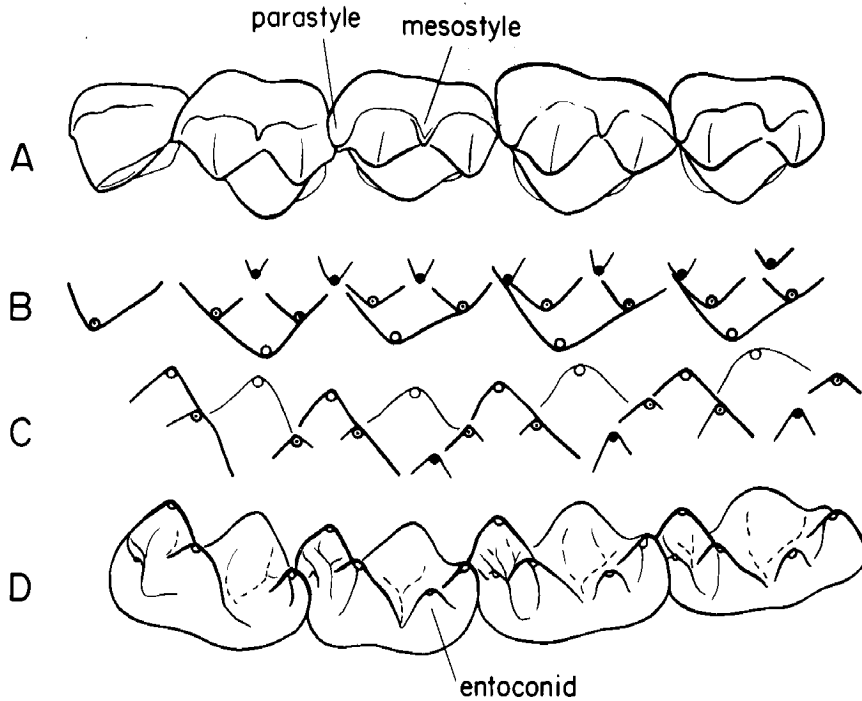
Fig. 5. Diagrammatic representation of upper (A) and lower (D) cheek teeth of *Sivaladapis nagrii* in functional perspective, viewed parallel to the direction of relative movement of each jaw during the buccal phase of occlusion, with the leading edge of each tooth row forward and the trailing edge behind in each drawing. Principal functional elements on upper and lower cheek teeth are identified in B and C, respectively, where filled circles are leading points, open circles with dots are following cusps with associated microshearing crests, and open circles are trailing cusps with larger shearing crests. Note the pattern of reciprocally occluding triangles (heavy lines in B and C). Shearing paraconids and hypoconids (open circles) on lower molars occluded first with puncturing parastyles and mesostyles (filled circles) on upper molars, while simultaneously puncturing entoconids (filled circles) on lower molars occluded with shearing protocones (open circles) on upper molars. Hence well-developed lower molar entoconids are functionally equivalent to upper molar parastyles and mesostyles in *Sivaladapis*.

In the lower dentition of *Sivaladapis*, the leading functional elements are the small, reduced paraconids and larger pointed entoconids (filled circles in Fig. 5C). The next series of functional elements in the lower dentition is a series of cusps (metaconid and hypoconulid; open circles with dots in Fig. 5C) supporting an associated series of crests. The final functional elements are a prominent series of large crests or lophs associated with protoconids (open circles in Fig. 5C) and a lesser series of crests associated with hypoconids. The same progression from puncturing points

to small shearing crests to larger shearing crests seen on the upper cheek teeth is seen on the lower cheek teeth, again associated with buccal-phase occlusion.

Lingual-phase wear facets [Phase II of Kay and Hiiemae (1974)] are present on some teeth, but are never large. Grinding occlusion appears not to have been important in *Sivaladapis*. The absence of hypocones on upper molars is consistent with reduced functional importance of grinding occlusion. Puncturing tooth-food-tooth occlusion may have been important, but no evidence of this is preserved. The dominant functional mode in *Sivaladapis* appears to have been tooth-on-tooth buccal-phase occlusion. Upper and lower cheek teeth are highly specialized for this phase of occlusion, with puncturing elements followed by microshearing elements followed by larger shearing elements. During function, pointed leading cusps on upper cheek teeth occluded with linear trailing crests or lophs on lower cheek teeth and, simultaneously, pointed leading cusps on lower cheek teeth occluded with linear crests or lophs on upper cheek teeth. We interpret the distinct, pointed lower molar entoconids in *Sivaladapis* as puncturing cusps functionally equivalent to upper molar parastyles and mesostyles.

The conformation of highly specialized puncturing and shearing molar features found in *Sivaladapis* is similar to that found in insectivores that must puncture and shear the chitinous exoskeleton of insects and to that found in folivores that puncture and shear leafy vegetation. The body mass of *Sivaladapis* is inferred from tooth size to have been about 4–7 kg (Gingerich *et al.,* 1982), and thus it is unlikely that *Sivaladapis* fed on insects (Kay, 1975). Judging from body size and dental morphology (Kay and Hylander, 1978), it is almost certain that *Sivaladapis* was predominantly folivorous. The colugo *Cynocephalus* is an extant folivore exhibiting complex dental occlusion similar in function [but not in morphological detail (Rose and Simons, 1977)] to that inferred for *Sivaladapis*.

DECIDUOUS DENTITION AND TOOTH ERUPTION

One specimen, LUVP 14505, is unusual in preserving the deciduous mandibular premolars (dP$_3$ and dP$_4$) in place, with the crowns of developing permanent premolars beneath them. Crowns of the deciduous teeth are illustrated in occlusal view in Fig. 2. Deciduous P$_3$ is smaller and has a relatively narrower crown than permanent P$_3$, but it is otherwise very similar to its permanent successor. The crown of dP$_4$ is highly molarized and resembles that of permanent P$_4$ and M$_1$ in the relative development of most
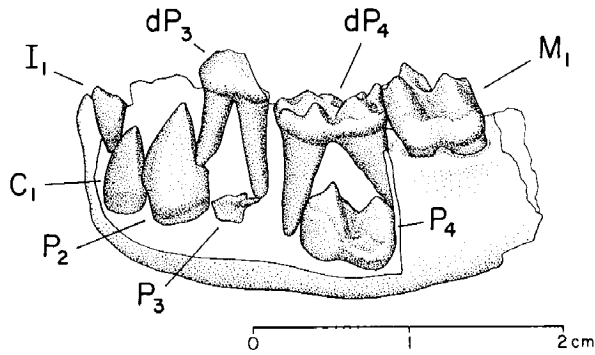
Fig. 6. Partial mandible of subadult *Sivaladapis nagrii* (LUVP 14505) in left lateral view, with cortical bone cut away to show crowns of partially formed and erupting permanent teeth developing in crypts below dP_3 and dP_4. Note the large caniniform crown of P_2 in position to begin eruption, the slightly calcified mass representing the crown of P_3 beneath dP_3, and the well-formed crown of P_4 deep in a crypt below dP_4. The eruption sequence of permanent premolars is inferred to have been P_2-P_4-P_3. The partially calcified crown of the permanent lower canine is visible anterior to that of P_2.

cusps and crests, but it has the longer, relatively narrower crown proportions and thinner enamel characteristic of a deciduous tooth. Deciduous P_4 differs markedly from permanent P_4 in having a distinct entoconid on the talonid. Measurements of dP_3 and dP_4 are listed in Table II.

The stage of eruption of all teeth in LUVP 14505 is illustrated semidiagrammatically in Fig. 6. Here cortical bone on the labial surface of the mandible has been cut away carefully to expose developing crowns and the roots of the deciduous cheek teeth. From this specimen it is possible to infer part of the sequence of tooth development and a probable sequence of eruption of the preserved permanent teeth. This is interpreted as

$$M_1\text{-}I_1\text{-}P_2\text{-}(C_1, P_4)\text{-}P_3.$$

Obviously, we can say nothing about the relative timing of development or eruption of teeth that are not preserved in LUVP 14505, nor can we be certain that relative development corresponds exactly to erupion sequence. Nevertheless, it appears that I_1 and P_2 develop and erupt before the lower canine, the crown of which is only partially formed in LUVP 14505. Similarly, regardless of the timing of development of the canine relative to P_4, both of these teeth develop (and probably erupt) well before P_3. The

sequence of development and eruption of the permanent lower premolars in *Sivaladapis* appears to be $P_2-P_4-P_3$. This is the sequence of eruption of premolars in living tree shrews (Shigehara, 1980) and most living prosimian primates (Schwartz, 1975), and thus it may be the primitive sequence for prosimians as a whole. Eruption sequences for Eocene adapid primates are not well documented, but premolars appear to have erupted in the sequence $P_4-P_2-P_3$ in *Adapis magnus* and *Adapis parisiensis*. In *Adapis*, P_2 and P_3 erupted at nearly the same time, which may explain why the sequence appears to be $P_4-P_3-P_2$ in a specimen of *A. parisiensis* (Basel QD-72) illustrated by Stehlin (1912).

SEXUAL DIMORPHISM AND SYMPHYSEAL FUSION

The base of the lower canine is preserved in two specimens of *Sivaladapis nagrii*, LUVP 14503 and 14504, and these differ by 15–17% in linear dimensions (Table II). Mandibular depth can be measured on four specimens, and these depth measurements cluster at 10.2 and 12.0 mm, respectively, a difference of 18%. The coefficient of variation of mandibular depth is 9.5 (Table II), a value that may be indicative of moderate body-size dimorphism in living anthropoid primates (Fleagle *et al.*, 1980). The available sample is small, but all of these values taken together suggest the possibility of some body-size and canine dimorphism in *Sivaladapis nagrii*.

Another feature of mandibular morphology preserved in *Sivaladapis* is fusion of the left and right rami at the mandibular symphysis. Three adult specimens show complete symphyseal coossification (LUVP 14502-14504), and the symphysis is also completely fused in the juvenile specimen LUVP 14505 described and illustrated above. Symphyseal fusion evidently occurred well before eruption of any of the anterior permanent teeth in *Sivaladapis*.

All early Eocene Adapidae had unfused mandibular symphyses, but several middle Eocene and later genera exhibit partial to complete symphyseal fusion (Beecher, 1983). The time of fusion during ontogenetic development can be determined in two species of the genus *Adapis, A. magnus* and *A. parisiensis*. In the former species, the symphysis did not fuse until the canine and all cheek teeth were in place. In the latter, smaller species, fusion occurred at the time of eruption of M_2 and before eruption of the lower canine, P_{2-4}, or M_3. *Sivaladapis nagrii* resembles *Adapis parisiensis* in exhibiting complete mandibular fusion at a stage early in ontogeny.

DISCUSSION

The type specimen of *Sivaladapis nagrii*, a fragmentary dentary from Haritalyangar, was initially identified by Prasad (1963, 1970) as a procyonid carnivore and referred to *Sivanasua* for two reasons: (1) an impacted M_3 in the holotype was misinterpreted as P_4, creating an erroneous impression that only two molars were present in the lower dentition, as in procyonids; and (2) among known Siwalik mammals, the specimens described by Prasad most closely resemble those previously referred to *Sivanasua* by Pilgrim. In redescribing the holotype of *Sivaladapis nagrii*, we have shown that the teeth in this specimen are M_{1-3}, removing any special resemblance or suggestion of relationship to procyonid carnivores (Gingerich and Sahni, 1979).

Specimens from Haritalyangar referred to *Indraloris himalayensis* by Chopra and Vasishat (1979, 1980a) have the diagnostic molar structure of *Sivaladapis* and are here regarded as *S. nagrii*. Pilgrim (1932) originally distinguished *Indraloris ("Sivanasua") himalayensis* from *Sivaladapis ("Sivanasua") palaeindicus* by its shorter, relatively broader lower molars, which also lack a hypoconulid. Pilgrim noted that the talonid is approximately equal in size to the trigonid in *I. himalayensis,* whereas it is distinctly longer than the trigonid in *S. palaeindicus. Indraloris himalayensis* resembles *I. lulli* in all of these diagnostic characteristics (hence their proposed synonymy).

Chopra and Vasishat (1979, 1980a) follow previous authors in referring specimens of *Indraloris* and *Sivaladapis ("I. himalayensis")* to Lorisidae, but *Sivaladapis* resembles Eocene Adapidae more closely than it does any living or fossil lorisoid. All Lorisoidea (like Lemuroidea) have slender styliform mandibular incisors and canines forming a dental scraper or tooth comb, whereas *Sivaladapis* retains vertical spatulate incisors. The incisors, canines, and fused mandibular symphysis of *Sivaladapis* are characteristics of resemblance to anthropoid primates, but the molar structure of *Sivaladapis* is much more similar to that of Adapidae than it is to the molar structure of any anthropoid. Hence there can be little doubt that *Sivaladapis* is a late surviving adapid, and *Indraloris* is likely to be as well.

The type specimen of *Indoadapis shivaii* described by Chopra and Vasishat (1980b) is a right maxilla with heavily worn teeth from Haritalyangar. It cannot be compared directly with the holotype dentary of *Sivaladapis nagrii,* but comparison of both type specimens to material from Haritalyangar described here leaves little doubt that *Indoadapis shivaii* is a junior synonym of *Sivaladapis nagrii.*

Sivaladapis nagrii has been found only at the type locality near Haritalyangar, where it is associated with *Indraloris himalayensis* (also

restricted to this locality) and a gibbon-sized hominoid (Simons, 1972; Chopra and Kaul, 1979). The rarity of *Sivaladapis* and *Indraloris* in late Miocene faunas in South Asia and their association with a hylobatid (also extremely rare in South Asian late Miocene faunas) suggest that the two adapids may have been members of a poorly sampled forest community. *Sivaladapis* has the large body size and specialized cheek-tooth morphology characteristic of folivorous primates. We speculate that *Sivaladapis* was probably arboreal, and it may have resembled the living arboreal folivore *Indri,* or even *Alouatta,* in habits and habitat. Judging from its dentition, *Indraloris* was probably more frugivorous than *Sivaladapis,* and it too may have been arboreal. Unfortunately, postcranial elements are not known for either genus, and our suggestion that they were arboreal cannot be tested at present.

Most of the known lineages of Adapidae became extinct by the end of the Eocene. Thus it is surprising to find two genera surviving into the late Miocene in South Asia. Other characteristically Eocene and Oligocene mammalian taxa survived into the late Miocene in India and Pakistan as well, and these appear to have belonged to a partially relict fauna. Hyaenodontid Creodonta were important carnivorous mammals during much of the Eocene and Oligocene. The last surviving members of this group have long been known to have survived into the middle Miocene of South Asia, and recently Barry (1980) has described a specimen from the late Miocene at Sethi Nagri in Pakistan. Ctenodactylid Rodentia dominated early and middle Eocene faunas in South Asia (Hartenberger, 1982), and they are last known from late Miocene Nagri faunas as well (Flynn and Jacobs, 1982). Adapids, hyaenodontids, and ctenodactylids appear to have become extinct in South Asia about 8 million years ago. They were undoubtedly affected to some extent by a worldwide trend toward cooler and drier climates and a shift from forests to grasslands over much of India and Pakistan. If our inference that *Sivaladapis* and *Indraloris* were arboreal folivores and/or frugivores is correct, then their extinction may also be related to the immigration of colobine monkeys. Colobines first appear in the fossil record of South Asia in faunas dated at about 7 Ma. Colobines are predominantly arboreal folivores, and it is likely that they would compete directly with relict adapids like *Sivaladapis.* Competitive exclusion is a difficult phenomenon to document in the fossil record, but this remains the most likely explanation for the extinction of *Sivaladapis* and *Indraloris.*

ACKNOWLEDGMENTS

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