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Indraloris and Sivaladapis: Miocene adapid primates from the Siwaliks of India and Pakistan

THE primate family Adapidae underwent a major radiation during the Eocene in Europe^{1,2} and North America^{3,4}. Asian and African Eocene mammalian faunas are still poorly known, but there is sufficient evidence to indicate at least a modest radiation of Eocene adapids in Asia^{5,6} and probably also in Africa². Apart from possible lemuriform and anthropoid primate derivatives, the family Adapidae was thought to have become extinct at the end of the Eocene (middle Tongrian, ~37 Myr (refs 2, 7, 8)). We present here new evidence which indicates that at least two genera of adapid primates, *Indraloris* and *Sivaladapis* (*gen. nov.*), survived into the late Miocene of India and Pakistan. These genera are little advanced over Eocene Adapidae in terms of dental adaptations and are apparently south Asian relicts of a much earlier radiation.

The history of species here placed in *Indraloris* and *Sivaladapis* is complex (Table 1). Pilgrim⁹ first proposed the genus *Sivanasua* in a footnote as a replacement for the preoccupied name *Ailuravus* Schlosser¹⁰. The type species of *Sivanasua* is thus the European procyonid carnivore *Ailuravus viverroides*. Pilgrim¹¹ later named two Asian species of *Sivanasua*: *S. palaeindica*, from Chinji beds near Chinji, Pakistan, and *S. himalayensis* from Nagri equivalent beds near Haritalyangar, India. Lewis¹² then named *Indraloris lulli* from Haritalyangar. Pilgrim regarded his Asian species of *Sivanasua*

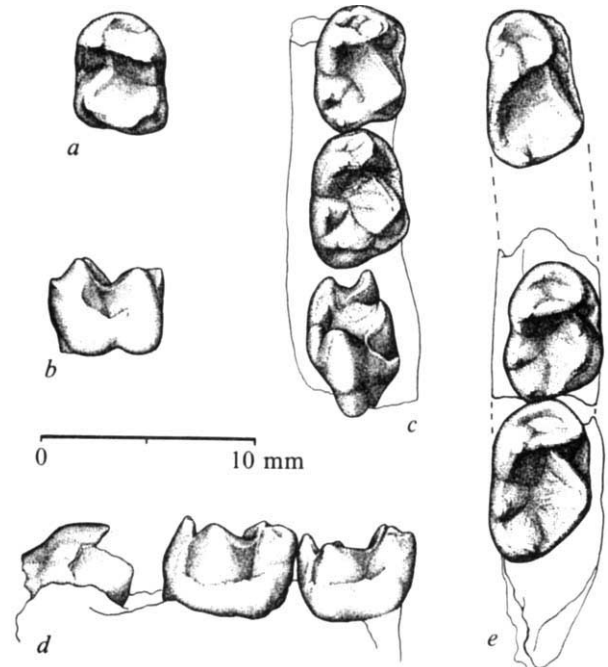


Fig. 1 Comparison of type specimens of *Indraloris* and *Sivaladapis*. a, b, *Indraloris lulli* (now placed in *I. himalayensis*), YPM 13802, left M₁ in occlusal and lateral view. c, d, *Sivaladapis nagrii*, GSI 18093, right mandible with M₁₋₂ and impacted M₃ in occlusal and lateral view. e, *Sivaladapis palaeindicus*, GSI-D224, right P₄ and M₂₋₃ in occlusal view. Note elongated molars with very large hypoconulids distinguishing *Sivaladapis* from *Indraloris*.

as carnivores, and Lewis regarded *Indraloris* as a lorisid primate "easily derived from the Adapidae", but the specimens available to these authors were insufficient for unequivocal systematic placement. Tattersall¹³ later suggested that the type specimens of *S. himalayensis* (now lost) and *I. lulli* (Fig. 1a, b) are identical, and he regarded both as lorisid. Subsequently, *Indraloris* has usually been classified in Lorisidae¹⁴⁻¹⁶ or tentatively with Adapidae^{6,17}.

Sivanasua nagrii, described by Prasad¹⁸, is critical for understanding the systematic relationships of *Indraloris* and *Sivanasua*. The holotype of *S. nagrii* (Fig. 1c, d) is the first specimen to show unequivocally the presence of three molars in the lower dentition, ruling out any close relationship with procyonid carnivores such as European *Sivanasua* (Prasad orientated this specimen back to front and misidentified the impacted M₃ as P₄, but further preparation confirms that three molars are present). *Sivanasua nagrii* is the only described specimen of Asian *Sivanasua* preserving the lower first molar (M₁), permitting the first direct comparison with the holotype of *I. lulli*. Judging from molar structure, species of *Indraloris* and Asian 'Sivanasua' are related, but they clearly represent two different genera.

No generic name is available for Asian species of 'Sivanasua'. New specimens from Haritalyangar mentioned below indicate that these species are adapid primates, and we here propose the new name *Sivaladapis* to include the Haritalyangar species *S. nagrii* (Prasad) and the Chinji species *S. paleindicus* (Pilgrim). The holotype of 'Sivanasua' *himalayensis* is probably a lower second molar (M₂) of the same species represented by the type specimen of *Indraloris lulli* (an M₁), and the correct name for this Haritalyangar species is thus *Indraloris himalayensis* (Pilgrim). The mandible with M₃ described by Tattersall¹³ is probably a specimen of *Sivaladapis palaeindicus*, as it comes from Chinji and has the morphology of this species.

Sivaladapis differs from *Indraloris* principally in having longer, relatively narrower lower molars, with a much larger hypoconulid (Fig. 1). The hypoconulid in *Sivaladapis* is twinned with the entoconid, and these two cusps are separated by a deep

Table 1 Named species of *Sivanasua* and *Indraloris* from the Miocene of India and Pakistan

Species	Type locality	Associated fauna ²² (European equivalent)
(1) ' <i>Sivanasua</i> ' <i>palaeindica</i> Pilgrim, 1932 (now placed in <i>Sivaladapis</i>)	Chinji (Pakistan)	Chinji (Astaracian)
(2) ' <i>Sivanasua</i> ' <i>himalayensis</i> Pilgrim, 1932 (now placed in <i>Indraloris</i>)	Haritalyangar (India)	Upper Nagri (Late Vallesian)
<i>Indraloris lulli</i> Lewis, 1933 (conspecific with <i>S. himalayensis</i>)	Haritalyangar (India)	Upper Nagri (Late Vallesian)
(3) ' <i>Sivanasua</i> ' <i>nagrii</i> Prasad, 1970 (type species of <i>Sivaladapis</i>)	Haritalyangar (India)	Upper Nagri (Late Vallesian)

Valid species are numbered in the order in which they were described.

notch. The trigonids of *S. nagrii* are narrower than those in *I. himalayensis*, and the buccal cingulid is better developed. *Sivaladapis nagrii* also differs from *S. palaeindicus* in the latter two characteristics (Fig. 1). *Sivaladapis* and *Indraloris* are sufficiently similar that there is little doubt that both belong in the same family.

We are preparing a detailed description of the dentition of *Sivaladapis nagrii*, based on new specimens collected by S. Khare from the vicinity of Haritalyangar¹⁹, but the main points of interest are outlined here. *Sivaladapis* had an upper and lower dental formula of 2.1.3.3. The mandibular rami were solidly co-ossified at the symphysis early in life. The incisors are slightly procumbent, but have spatulate crowns and no indication of a dental scraper or tooth comb. This effectively rules out any close relationship to extant Asian lorises. The canines are relatively large and projecting, with a well developed dental hone on P₂ sharpening the back of the upper canine. The upper and lower fourth premolars are highly molarised. Upper molars have mesostyles and no hypocone. Average body size of *Sivaladapis nagrii*, estimated from tooth size²⁰, was about 5–6 kg. The highly crested crown morphology of the molars and molarised premolars, together with body size²¹, indicate that *Sivaladapis* was probably predominantly folivorous. *Indraloris*, by comparison, has less sharply crested molars and probably included relatively more fruit in its diet. A fused mandibular symphysis, spatulate incisors and projecting interlocking canine teeth honed by P₂ are adapid characteristics. *Sivaladapis* lacked the tooth comb characteristic of Lorisioidea and Lemuroidea. The cheek teeth of *Indraloris* and *Sivaladapis* resemble those of loriseid and lemuroid primates (such as *Hapalemur*) as well as most Adapidae, but the presence of a distinct hypoconulid twinned with the entoconid is found among lemuriform primates only in adapids such as *Hoanghoni* and *Oligopithecus*. Taken together, these dental characteristics leave little doubt that *Sivaladapis* and *Indraloris* belong to the family Adapidae.

Adapid primates are first known from the early Eocene. Inclusion of *Sivaladapis* and *Indraloris* in the Adapidae extends the latest record of this family from latest Eocene (~37 Myr (ref. 8)) to the late Miocene (~10 Myr (ref. 22)). This 27-Myr extension more than doubles the known stratigraphic range of the family. It also emphasises how little we know of the radiation of primates in Asia. Hyaenodontid creodonts were the dominant carnivorous mammals and adapids were the dominant primates in Eurasia during the Eocene. The last representatives of both these groups are now known from Siwalik faunas, and it is clear that the Indian subcontinent sheltered several archaic faunal elements as relicts through the Miocene.

The final extinction of Adapidae may have coincided with a major faunal turnover on the Indian subcontinent near the end of the Miocene (~8 Myr (ref. 22)). This faunal turnover included the first introduction of leaf-eating cercopithecoid monkeys, identified as *Presbytis sivalensis*. Judging from their teeth, *Sivaladapis* and *Indraloris* may have been the ecological precursors of cercopithecoid monkeys in south Asia, but more detailed stratigraphical and palaeoecological data in Siwalik faunas are required before any specific hypothesis can be advanced to explain the extinction of Adapidae. We now know that this important Tertiary primate family survived much longer than was previously thought.

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Cranial anatomy and implications of *Dolichocebus*, a late Oligocene ceboid primate

THE very scarce fossil record of Cainozoic New World monkeys^{1,2} has contributed little to knowledge of the history of platyrrhine primates, an important element of both the neotropical mammal fauna³ and the pantropical primates, as a whole. Only the affinities of the Middle Miocene Colombian fossils *Neosaimiri*, *Stirtonia* and *Cebupithecia* seem reasonably well established⁴, though not without dissent⁵, and these are clearly linked with the modern squirrel, howler and saki-uakari monkeys, respectively. After completion of a survey of the morphology and interrelationships of the platyrrhines, to be detailed elsewhere (A. L. R., in preparation), it is now possible to discuss the evolutionary implications of the terminal Oligocene *Dolichocebus gaimanensis* of Patagonia, represented by a nearly complete cranium only recently prepared fully, although first described in 1942 (ref. 6). This specimen strongly suggests that *Dolichocebus* is a member of the *Saimiri* lineage, which thus becomes the oldest generic lineage known for the primates, dating from about 25 Myr ago⁷. Its affinities also imply that the two major monophyletic divisions of Ceboidea were already established by late Oligocene times, as were the marmosets and tamarins.

A restoration of the *Dolichocebus* cranium is presented in Fig. 1. It is close in size to the modern middle-sized ceboids *Saimiri*, *Aotus* and *Callicebus* and the late Oligocene–early Miocene *Tremacebus* and *Homunculus*^{8,9}. During fossilisation all permeable cavities were filled with a fine sand that later hardened with the skull into a single mass. Most subsequent damage involved plastic deformation, bilaterally compressing the neurocranial vault asymmetrically above the skull base and partially collapsing the left orbit. The relatively undistorted basicranium affirms Kraglievich's⁹ nominal interpretation of the long, narrow skull. Because essentially all tooth crowns are missing and the posterior dental arch was shorn away bilaterally, the number of molars cannot be counted with certainty. However, the highly compact, alveolar-like texture of the exposed bone suggests that third molars were present in life⁸, contrary to Kraglievich's interpretation⁹.

There are several indications that the masticatory system of *Dolichocebus* was rather lightly built. The anterior and posterior roots of the right zygomatic arch, suggestive of the bending stress imposed by the attached masseter muscles, are quite gracile. Similarly, the pyramidal process of the palatine is slender, providing evidence that the pterygoids were not powerfully developed. The right temporal line is visible along much