

= Indraloris =

Indraloris is a fossil primate from the Miocene of India and Pakistan in the family Sivaladapidae . Two species are now recognized : *I. himalayensis* from Haritalyangar , India ( about 9 million years old ) and *I. kamliensis* from the Pothohar Plateau , Pakistan ( 15 @. @ 2 million years old ) . Other material from the Potwar Plateau ( 16 @. @ 8 and 15 @. @ 2 million years old ) may represent an additional , unnamed species . Body mass estimates range from about 2 kg ( 4 @. @ 4 lb ) for the smaller *I. kamliensis* to over 4 kg ( 8 @. @ 8 lb ) for the larger *I. himalayensis* .

Indraloris is known from isolated teeth and fragmentary lower jaws . The jaw is deep under the last premolars , but becomes shallower towards the front . The lower premolars are elongate . The lower molars are shorter and broader than those of *Sivaladapis* . Indraloris may have been arboreal and at least partly frugivorous . When the first Indraloris fossils were discovered in the early 1930s , one was misidentified as a carnivoran and the other as a loris . The carnivoran identification was corrected in 1968 , and in 1979 Indraloris and the related *Sivaladapis* were identified as late survivors of Adapiformes , an archaic primate group .

= = Taxonomy = =

Currently , Indraloris is considered to be a valid genus within the family Sivaladapidae , containing two named species : *I. himalayensis* from India and *I. kamliensis* from Pakistan . A third species may be represented in the Pakistani material of Indraloris . However , Indraloris has had a complicated taxonomic history , and some of the known material was misidentified as members of other mammalian groups for decades .

In 1932 , British paleontologist Guy Pilgrim described two species from the Miocene of what is now India and Pakistan , *Sivasua palaeindica* from Chinji ( Pakistan ) and *Sivasua himalayensis* from Haritalyangar ( India ) . He attributed both to *Sivasua* , a carnivoran genus otherwise known from Europe . The next year , American scientist G. Edward Lewis described the new genus and species *Indraloris lulli* from Haritalyangar , which he provisionally allocated to the family Lorisidae . The generic name , Indraloris , combines the name of the god Indra with the generic name Loris , and the specific name , lulli , honors Richard Swann Lull , at the time director of the Peabody Museum of Natural History . It was not until 1968 that American anthropologist Ian Tattersall noted that Pilgrim 's *Sivasua* species had been misidentified ; he suggested that *Sivasua himalayensis* was probably the same as *Indraloris lulli* , but left the affinities of *Sivasua palaeindica* open . Tattersall , who also described additional material of Indraloris , continued to regard the animal as a lorisid .

Lewis had suggested that Indraloris might derive from the Adapidae , a primitive group of primates , and in the 1970s some authors provisionally placed Indraloris among the Adapidae . In 1979 , American and Indian paleontologists Philip Gingerich and Ashok Sahni reviewed Indraloris and the Indo @-@ Pakistani " *Sivasua* " species . They recognized *Sivasua himalayensis* and *Indraloris lulli* as representing the same species , *Indraloris himalayensis* , and created the new genus *Sivaladapis* for *Sivasua palaeindica* and another species that had been named later , *Sivasua nagrii* . Gingerich and Sahni considered both Indraloris and *Sivaladapis* to be adapids .

Several other authors suggested similar taxonomic rearrangements around the same time . In 1979 , Herbert Thomas and Surinder Verma agreed that Indraloris and *Sivaladapis* were adapids , but placed them in a subfamily of their own , Sivaladapinae . Also in 1979 , Frederick Szalay and Eric Delson placed Indraloris in its own tribe , Indralorini , within Adapidae . In 1980 , Indian paleontologists S.R.K. Chopra and R.N. Vasishat placed both of Pilgrim 's *Sivasua* species in Indraloris and argued that Indraloris lulli , *Sivasua himalayensis* and *Sivasua nagrii* all represented the same species ? *Indraloris himalayensis* . They listed *Sivasua palaeindica* as a second Indraloris species , *I. palaeindica* , and continued to regard Indraloris as a lorisid . Gingerich and Sahni published in more detail on *Sivaladapis* in 1984 . They then placed the two genera in a separate subfamily of Adapidae , called Sivaladapinae because that name was published two months before Indralorini . In 1985 , Vasishat continued to classify Indraloris and *Sivaladapis* in a

single genus , and *Indraloris himalayensis* and *Sivaladapis nagrii* in a single species , but other authors have not followed this classification .

In a 1998 review , primatologist Marc Godinot recognized Sivaladapidae as a separate family within the Adapiformes , and this classification has been followed since then . Several genera in addition to *Indraloris* and *Sivaladapis* are now allocated to Sivaladapidae , which is known from the Eocene through the Miocene of China , Thailand , Myanmar , India , and Pakistan . Sivaladapids are notable for including by far the youngest adapiforms ; members of this group are otherwise known mostly from the Eocene , but several sivaladapids occurred during the Miocene .

Despite these taxonomic changes , *Indraloris* remained known from only two specimens ( the holotypes of *Indraloris lulli* and *Sivanasua palaeindica* ) until 2005 . Both of those specimens ? an isolated first lower molar ( m1 ) and a mandible ( lower jaw ) fragment with m1 , respectively ? come from Haritalyangar in the Nagri Formation . In 2005 , however , American paleontologists Lawrence Flynn and Michèle Morgan described five teeth of *Indraloris* from fossil sites in the older Kamliyal Formation as a second species in the genus , *Indraloris kamliyalensis* . The species was named after the Kamliyal Formation . In addition , they suggested that two lower jaw fragments from the Kamliyal Formation represented a third , larger species of *Indraloris* .

= = Description = =

*Indraloris* is known only from isolated teeth and fragments of the mandible . These show that *Indraloris* was a medium @-@ sized sivaladapid , somewhat smaller than *Sivaladapis* . In 1982 , Gingerich and colleagues estimated that *Indraloris himalayensis* may have weighed 3 @.@ 7 to 4 @.@ 3 kg ( 8 @.@ 2 to 9 @.@ 5 lb ) on the basis of allometric scaling of tooth size ; Flynn and Morgan estimated a body size of about 2 kg ( 4 @.@ 4 lb ) for *I. kamliyalensis* . In general , the cingula ( shelves ) on the margins of the cheekteeth are weak in *Indraloris* . Among the two named species , *I. kamliyalensis* is about 20 % smaller than *I. himalayensis* . The unnamed large *Indraloris* is similar in size to *I. himalayensis* .

The mandible is best represented by YGSP 32727 , one of two specimens of the unnamed large species of *Indraloris* . It preserves both the right and left sides of the dentary , back to the level of the fourth lower premolars ( p4 ) , but is also damaged at the front . The jaw is deep below p4 , but rapidly becomes shallower further to the front . The roots of two lower incisors and a much larger canine are preserved ; the three roots cluster together , with the canine root above the incisor roots , suggesting that these teeth shared some function . The mental foramen , an opening in the jawbone , is below p4 . A root for the deciduous second premolar ( dp2 ) is preserved on both the left and right sides , but the tooth itself is not and it is not possible to determine whether dp2 had one or two roots . The right permanent second premolar ( p2 ) is unerupted , but partially visible ; it is a blade @-@ shaped cutting tooth . The p3 bears a single cusp , somewhat anterior to the middle of the tooth , with crests descending from it towards the front and back , and weak cingula on the inner and outer sides . It is supported by two roots , which are close together .

Isolated lower premolars are known from *I. kamliyalensis* . A p3 , YGSP 33157 , resembles that of YGSP 32727 in possessing a single large cusp connected to crests at the front and back . A heel is present at the back , part of a small talonid . The tooth has two roots . The p4 , represented by YGSP 24338 , is an elongate , two @-@ rooted tooth with a distinct trigonid at the front and talonid at the back . The protoconid is the highest cusp of the trigonid . Two crests descend from it at right angles in a lingual direction ( towards the inner side of the tooth ) : the protolophid towards the front , ending at the low paraconid , and the metalophid towards the back , reaching the elongate metaconid . The talonid basin is open lingually ; on the labial side , the hypoconid cusp is present . A crest , the cristid obliqua , reaches from the hypoconid forward towards the trigonid . No other cusps are visible in the talonid , but the specimen is worn and poorly preserved ; the posterolophid , a crest descending from the hypoconid , may end in a small hypoconulid . A weak cingulum is present on the labial side of the tooth between the protoconid and hypoconid . Another tooth , YGSP 32151 , is interpreted as a dp4 . It has a more closed trigonid ( with the protolophid and metalophid making a more acute angle ) , the protolophid is shorter , and the paraconid is indistinct . In the talonid , the

hypoconulid and entoconid are distinct . The labial cingulum is strong .

The lower molar of *Indraloris* is known from four specimens . GSI D237 , an m1 in a piece of jaw , is the holotype of *I. himalayensis* . YPM 13802 , the holotype of *I. lulli* ( = *I. himalayensis* ) was originally identified as an m1 , but Flynn and Morgan suggested in 2005 that it may be an m2 instead .. YGSP 44443 , the holotype of *I. kamliensis* , is either m1 or m2 , but more likely the former . Part of the trigonid is broken off . YGSP 32152 , a very worn m1 in a piece of jaw , represents the unnamed large *Indraloris* . Vasishat suggested in 1985 that these teeth were instead p4s corresponding to molars referable to *Sivaladapis* , but this hypothesis has been disproven by the discovery of p4s referable to *Indraloris* .

*Indraloris* molars are short and organized in two main lobes ( lobes ) . They differ from *Sivaladapis* teeth in being shorter and broader , with a shorter talonid and a smaller hypoconulid . In *Indraloris himalayensis* lower molars , there are four main cusps ( protoconid and metaconid in the trigonid , hypoconid and entoconid in the talonid ) , which give the crown a rectangular aspect , although the labial cusps ( protoconid and hypoconid ) are placed somewhat anterior to their lingual counterparts . In *I. kamliensis* , the entoconid is distinct from the hypoconulid , which is large , but the tooth is otherwise similar . The cusps are high relative to those of extant lorises and approximately equal in height . The cristid obliqua , a crest , descends from the hypoconid to a point on the lingual side of the protoconid . On the hypoconid , this crest forms a right angle with the posterolophid , which runs towards the hypoconulid in the back lingual corner of the tooth . Between the metaconid and entoconid , the talonid basin is open . In *I. himalayensis* at least ( the structure is damaged in the only known lower molar of *I. kamliensis* ) there is a well @-@ developed hollow in the trigonid in front of the protoconid and metaconid . There is a labial cingulum between the protoconid and hypoconid . YGSP 32152 is so worn that little of its structure remains visible . It shows a short trigonid and a distinct entoconid . A small hypoconulid , close to the entoconid , is suggested by an enamel swelling . This specimen is fragmentary enough that it could also represent a catarrhine primate or a carnivoran .

The only known upper tooth of *Indraloris* is an M3 , YGSP 46009 . It is broken at the back labial corner . The main cusp is protocone ; among the other two cusps , the paracone is higher but the metacone larger . There is a spur at the back of the protocone , suggesting a rudimentary hypocone . The protocone is connected to the paracone by a protoloph , which lacks a small cusp ( the paraconule ) . No crest connects the protocone to the metacone , but there is a cingulum at the back margin of the tooth . The tooth bears a strong parastyle ( accessory cusp at the front labial corner ) and has three roots .

= = Distribution and ecology = =

Fossils of *Indraloris* have been found only in the Miocene Siwalik fossil beds of India and Pakistan . *I. himalayensis* is known only from Haritalyangar , a Late Miocene site in the Indian state of Himachal Pradesh . This site has been dated to about 9 million years ago . This site has also yielded *Sivaladapis nagrii* . *Indraloris kamliensis* is known from two sites in the province of Punjab , Pakistan , that are both dated to 15 @.@ 2 million years ago : Y642 and Y682 . *Sivaladapis palaendicus* has also been recorded at both sites , and two lorises are known from Y682 . The unnamed large *Indraloris* is known from Y642 and an older site , Y801 ( 16 @.@ 8 million years old ) . All are in the Potwar Plateau region .

Little is known about sivaladapid ecology . Gingerich and Sahni suggested that *Indraloris* was probably arboreal and that it may have been more frugivorous ( eating fruit ) than *Sivaladapis* , which they interpreted as a folivore ( leaf @-@ eater ) . Flynn and Morgan interpreted *I. kamliensis* as a mixed feeder . The Late Miocene extinction of Indian sivaladapids may be related to a decline in forest cover in Asia and to competition by immigrating colobine monkeys .