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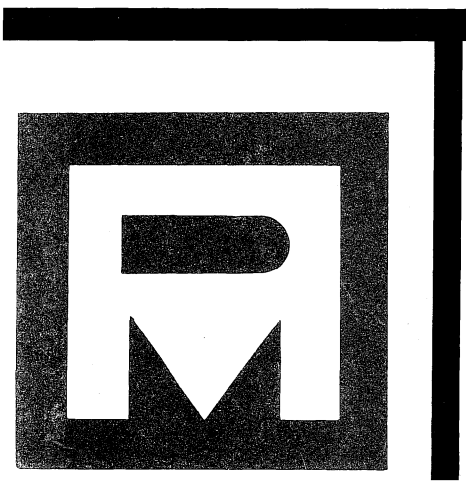

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A MANDIBLE OF INDRALORIS (PRIMATES, LORISIDAE) FROM THE MIOCENE OF INDIA

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ABSTRACT

A partial mandible of a large lorisid primate is described. The specimen (YPM 19134) comes from probable late Miocene deposits in northeastern India and consists of a fragment of a left mandibular ramus containing M_3, the roots of M_2 and the posterior root of M_1. The third molar resembles the M_3 of modern *Nycticebus coucang borneanus;* the specimen is referred to *Indraloris* cf. *lulli*. Unfotunately, because of its specialized nature, YPM 19134 affords no clue as to lorisid ancestry.

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THE TYPE SPECIMEN OF *Indraloris lulli* Lewis (YPM[1] 13802)

In the first of his long series of papers on the mammalian fossils collected during 1932 and 1933 by the Yale North India Expedition, G. Edward Lewis (1933) described a new genus and species of lorisid, *Indraloris lulli*. This taxon was based on a single tooth, a left M_2 now in the Peabody Museum of Natural History, Yale University. This tooth (Fig. 1) was recovered from a locality near Hari-Talyangar villages, northeastern Bilaspur, in the Simla Hills of northern India. This locality has been referred to the Nagri (Lower Middle Siwalik) horizon of the Siwalik series, which would give the fossil a probable early Pliocene date. Lewis (1933, p. 135) diagnosed the new genus as follows:

> Lorisidae of relatively large size. The several molar cusps are sub-equal; there is relatively little differentiation between the anterior and posterior moieties of the crown, and is confined to the degree of robustness of their bases, the hypoconid and entoconid having more robust bases than the protoconid and metaconid. The cusps are quite high. Although the crests of the protoconid and hypoconid are more anteriorly placed than those of the metaconid and entoconid respectively, the general outline of the superior aspect of the crown is sub-rectangular. There is an external cingulum confined to the buccal faces of the protoconid and hypoconid. A well-developed fovea anterior and a relatively low breadth index are characteristic.

Lewis further provided a minutely detailed description of the specimen, in which he pointed out a variety of resemblances to the modern lorisine *Nycticebus borneanus* Lyon. (This form is now generally placed as a subspecies of *Nycticebus coucang* Boddaert. The genus is now considered to contain only two species: *N. coucang,* the slow loris, and *N. pygmaeus,* the lesser slow loris. All comparisons in this paper are with *N. coucang*). The presence of a well-defined external cingulum and the great height of the cusps he

[1] The following abbreviations are used in this paper:

AMNH = American Museum of Natural History
GSI = Geological Survey of India
YPM = Peabody Museum of Natural History, Yale University

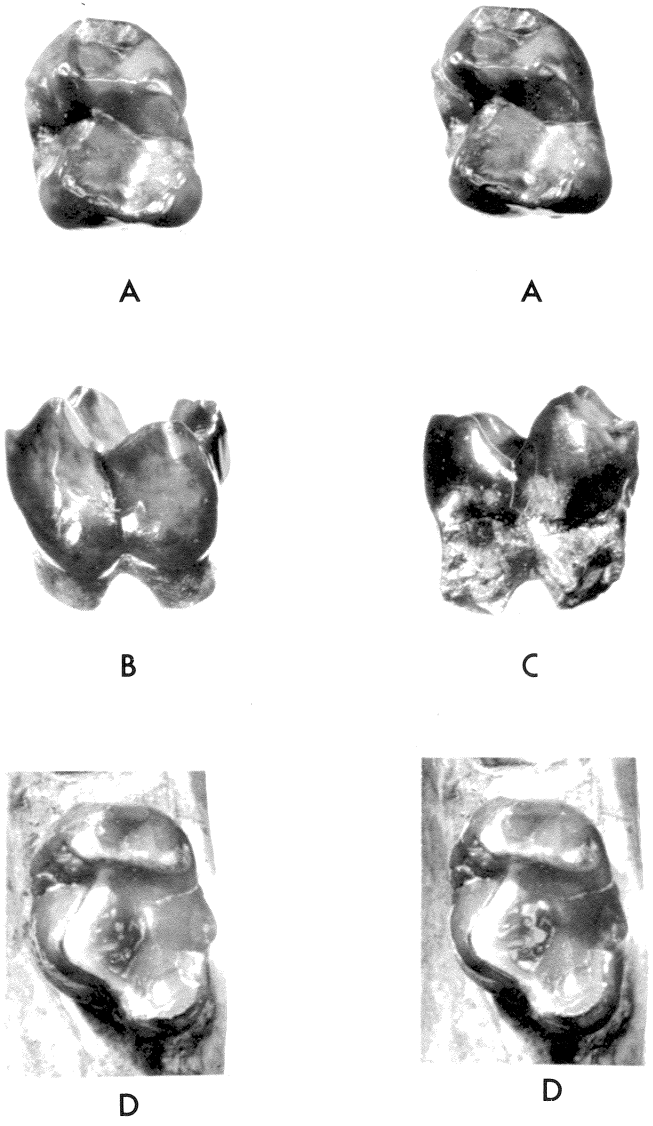

FIG. 1. YPM 13802 (holotype of *Indraloris lulli* Lewis) M_2. A) Stereophotograph, occlusal view; B) buccal view; C) lingual view. D) YPM 19134 (*I.* cf. *lulli*) M_3, stereophotograph, occlusal view. (All $\times$ 5).

considered to be primitive characters, but the cusp height, at least, can be matched among individuals of *Nycticebus*.

A New Mandible of *Indraloris* (YPM 19134)

Among the collections of the Peabody Museum of Natural History, Dr. J. A. Hopson has recently found a fragment of an individual referable to *Indraloris*.[2] He has kindly allowed me to describe this specimen, which consists of a fragment of a left mandibular ramus containing M_3, the roots of M_2 and the posterior root of M_1. It was collected by Lewis in May 1932 at a locality two or three miles southwest of Chinji, in the Salt Range, Attock District of the Punjab. The locality is given as of Chinji (Upper Lower Siwalik) age. The stratigraphy of the area is poorly understood, but a late Miocene age is at present most likely for this fossil.

M_3, the sole remaining tooth, is very large, measuring 6.6 mm mesiodistally and 5.0 mm buccolingually. The length of M_2 is estimated to have been 6.75 mm; YPM 19134 is therefore likely to be from a larger individual than is the type tooth, which measures 5.5 mm mesiodistally. Lewis (1933, p. 135) remarked that a "relatively low breadth index . . . [is] . . .characteristic" of the *Indraloris lulli* M_2. Table 1 shows, however, that the breadth index of YPM 13802 falls well within the range of variation of the sample of *Nycticebus coucang*. On the other hand, the same table shows that the length/breadth ratio of YPM 19134 is in all probability significantly higher than it is in the *Nycticebus coucang* sample. It is unfortunate that there exists at present no statistical method for calculating reliable confidence limits on ratios, at least as far as small samples are concerned.

[2] The possibility has been considered that the affinities of this fossil may lie with Carnivora rather than with Primates, but on present evidence this seems unlikely. The Siwalik fossils most closely resembling the *Indraloris* material are the type specimens of the two Indian species of the supposed procyonid genus *Sivanasua, S. palaeindica* Pilgrim 1932 (p. 56) and *S. himalayensis* Pilgrim 1932 (p. 59). The type specimen of the latter species (GSI D237) appears identical with the type specimen of *I. lulli* (YPM 13802) and is undoubtedly lorisid; the type specimen of *S. palaeindica* (GSI D224), a right last lower molar, differs in a number of features from YPM 19134; notably, it possesses a more expanded trigonid, with a small paraconid present. The systematic position of the Indian species of *Sivanasua* will be dealt with in a later publication.

TABLE 1. Measurements of second molar of *Indraloris lulli,* third molar of *Indraloris* cf. *lulli,* and second and third molars of *Nycticebus coucang* (in millimeters).

		L	B	100 B/L	L	B	100 B/L
		M_2			M_3		
Indraloris lulli	YPM 13802	5.5	4.3	78.1	—	—	—
I. cf. *lulli*	YPM 19134	—	—	—	6.6	5.0	75.7
Nycticebus	YPM 992	3.0	2.3	78.3	3.3	1.9	58.2
coucang	YPM 998	3.2	2.6	80.0	3.5	2.3	67.1
	AMNH 60766	3.6	2.8	76.7	3.1	2.2	69.8
	AMNH 87279	3.9	3.1	79.5	3.0	2.5	62.5
	AMNH 165656	3.9	3.1	79.5	3.7	2.5	66.6

L = length
B = breadth

THE THIRD MOLAR

The M_3 of YPM 19134 is severely worn, and has also suffered some post-mortem damage. Its dentine is exposed by wear in a wide band originating high on the buccal aspect of the hypoconulid, and traversing the depression between this cusp and the hypoconid, which is almost entirely obliterated. Exposure of the dentine continues uninterrupted to a point about halfway up the posterior face of the protoconid, and is renewed at the apex of this cusp. The talonid basin has been enlarged by the development of facets of occlusal wear on the internal surfaces of the lingual cusps, as well as by the removal of most of the hypoconid.

Post-mortem damage to the tooth is not inconsiderable. The enamel has been broken along the ridge between the hypoconid and hypoconulid. The tip of the entoconid has been broken off, exposing the dentine; this damage extends some distance down the lingual slope of the cusp. The dentine has also been exposed by breakage at the apex of the metaconid and on the anterolingual aspect of this cusp. The greatest damage occurs on the protoconid; breakage and wear have combined to expose the dentine at the apex and on the buccal surface of the cusp. Internal to this, break-

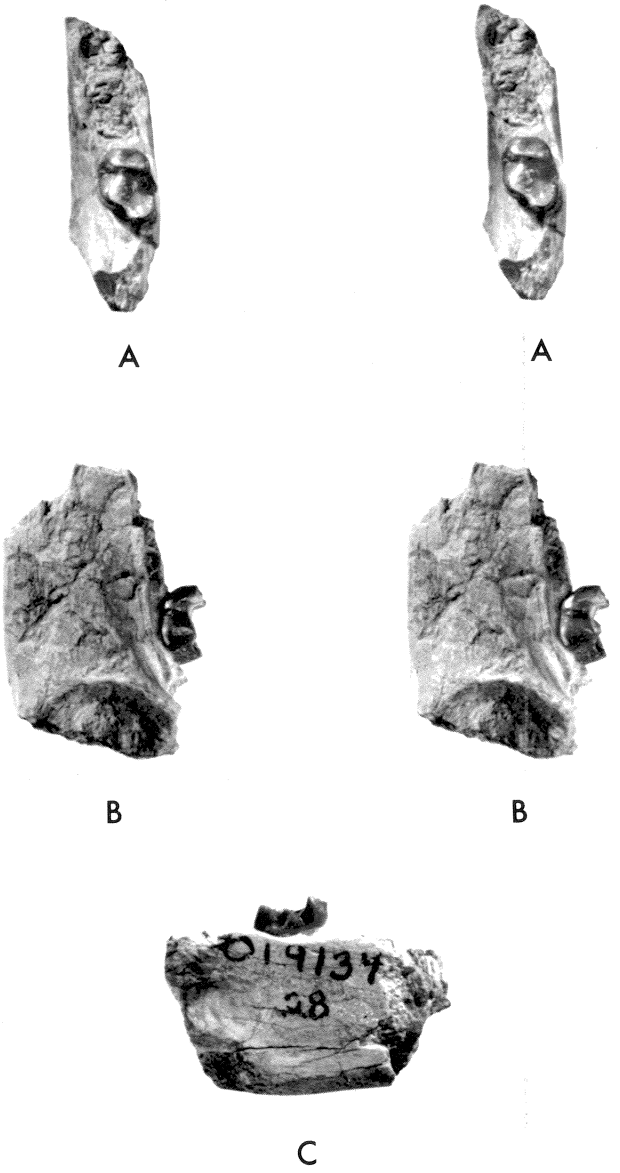

FIG. 2. YPM 19134 (*Indraloris* cf. *lulli*). A) stereophotograph, superior view; B) stereophotograph, external view; C) internal view. (All × 5).

age extends a short way along the paraconid-metaconid crest, and also encroaches upon the highest point of the narrow ridge which represents all that remains of the paraconid.

With its less than perfect condition in mind, we may now briefly describe the tooth, which, apart from its size, bears a strong resemblance to the M_3 of *Nycticebus coucang*. As in the latter species, the trigonid is only slightly higher but is more sharp-cusped than the talonid, the metaconid being the higher anterior cusp, though by no great margin. Of the three posterior cusps, the hypoconid, now badly worn, would originally have been the largest, although the hypoconulid is well-developed; the entoconid is small, and, as is the hypoconulid, slightly more lingually placed than in the majority of individuals of *N. coucang* examined. Otherwise, the disposition of the cusps is precisely that seen in most *N. coucang,* the protoconid being slightly anterior to the metaconid, and the entoconid fractionally anterior to the hypoconid. A small triangular external cingulum lies low at the base of a deep groove which originates at approximately the center of the posterior face of the protoconid, and runs steeply inferiorly to form a large cleft between the buccal aspects of the protoconid and hypoconid. The cingulum lies close to the base of the tooth, and is bisected by a shallow groove; it is also clearly demarcated from the bases of the protoconid and hypoconid by grooves which radiate from the base of the cleft. The whole cingular area is moderately crenulated. No such cingulum was observed in the *N. coucang* specimens, although the bases of the protoconid and hypoconid are well differentiated in this form. A tiny cingulum, however, is infrequently present in *Loris*.

The paraconid in YPM 19134 has been reduced to a narrow shelf originating low on the buccal side of the anterior face of the metaconid, and running buccally and superiorly to terminate at a point high on the midline of the anterior face of the protoconid. A shallow groove runs down between the protoconid and metaconid to meet this shelf at its most inferior point. The lack of a distinct paraconid on the lower molars is a lorisid characteristic (Simpson, 1967); its expression in *Indraloris,* however, differs from that in *Nycticebus*. In the latter the paraconid shelf tends to be relatively broad, and runs more or less horizontally.

The demarcation between the metaconid and entoconid of YPM 19134 is sharply delineated by a deep groove originating at

the basal midpoint of the posterior face of the metaconid and running lingually and inferiorly between the two cusps to terminate at a point almost at the base of the lingual aspect of the crown. The entoconid and hypoconulid are similarly, though less sharply, differentiated. The posterior aspect of the hypoconulid is heavily wrinkled, a deep external groove between the hypoconid and hypoconulid being the most conspicuous feature in this area.

THE MANDIBULAR RAMUS OF YPM 19134

The mandibular fragment is robust, but relatively little more so than in large individuals of *Nycticebus coucang*. The masseteric fossa of YPM 19134 is deep and well developed, but, again, *Nycticebus* often shows strong development in this area. The ascending ramus originates in approximately the same position relative to M_3 in both taxa, and the ratio of mandible height to M_3 height is likewise similar, though the crown height of YPM 19134 is relatively slightly greater than that seen in the M_3 of the *Nycticebus* specimens examined. The fossil proved too heavily permineralized and opaque to radiograph satisfactorily, but the exposed posterior root of M_1 suggests that the molar roots penetrate to relatively similar depths in the two forms. The horizontal ramus of YPM 19134 shows the anterior shallowing beneath the molar row characteristic of prosimians.

DISCUSSION

Lewis repeatedly remarked that *Indraloris* is "primitive" compared to *Nycticebus*. The presence of the external cingulum may be a primitive character, but there is otherwise no evidence of primitiveness in the earlier form. Indeed, many of the "advanced" features of modern lorisines cited by Lewis (p. 136) are associated with "the evolutionary tendency to shorten the face." If the inference of this tendency is valid, which it seems to be, then the M_3 of *Indraloris* is more advanced in this respect than that of *Nycticebus* since its breadth index greatly exceeds that of any *Nycticebus* examined. Simpson (1967) has pointed out that (dentally, at least), the known members of the African Miocene lorisid radiation could hardly be termed less specialized than the modern forms. If, as seems reasonable despite the paucity of relevant material, a

similar Miocene-Pliocene radiation of Asian lorisids is postulated, the existence of so large and specialized a lorisid as *Indraloris* in the Chinji and Nagri zones is not surprising. Morphologically, *Indraloris* is extremely similar to *Nycticebus;* this similarity is more plausibly attributed to relative recency of common ancestry than to any linear relationship. That YPM 19134 seems to be from a larger individual than is the later YPM 13802 is probably of no particular significance. Lewis (p. 138) was "impressed . . . by the probability that [*Indraloris*] represents the structural ancestor of the recent Lorisidae [here Lorisinae]." However, it would appear that *Indraloris* itself is too advanced for this role.

Although there are no previously known comparable parts of *Indraloris,* YPM 19134 is referred to this genus because of the common resemblance of the two fossils to *Nycticebus coucang borneanus,* because of their large size, and because of their provenance. The stratigraphy of the Siwalik Hills is, as remarked before, poorly understood, and the temporal relationships of the two specimens are vague. YPM 19134 might be of the very latest Miocene, while YPM 13802 might be of the very earliest Pliocene, in which case the temporal gap could be small. On the other hand, the great thickness of the Nagri and Chinji horizons, implying a long period of deposition, could place the specimens several million years apart. Pending further evidence, YPM 19134 is provisionally referred to *Indraloris* cf. *lulli.*

Lewis suggested that "*Indraloris* could easily be derived from the Adapidae, judging from the limited evidence at hand" (p. 138). Simons (1962) noted that *Pronycticebus* and *Anchomoys* from the late Eocene of Europe show a number of resemblances to lorisoids, but considered that these genera should not be removed from Adapidae "because of many primitive structures also shared with the contemporary *Adapis* and *Protoadapis*" (p. 23). He cautiously concluded, however, that "just possibly these [loris-like features of the genus *Pronycticebus*] can be interpreted as indicating the differentiation of the lorisiform prosimians from the general stock of the Adapidae (s.l.)" (p. 34). Whether or not this is so cannot at present be positively determined for, as Simpson (1967, p. 57) remarked of the African Miocene lorisids, they "do not help to close the gap because in the known parts they are little if any more primitive than some, at least, of the Recent species." Exactly the same must be said of *Indraloris.*

Acknowledgements

The author wishes to thank Dr. E. L. Simons for permission to describe YPM 19134, and the American Museum of Natural History for the loan of specimens of *Nycticebus.*

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