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With six plates and eight figures in the text

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The early Miocene hylobatine genus, *Limnopithecus*, was first described by Hopwood (1933) on the basis of very fragmentary remains of the mandible and lower dentition discovered in lacustrine deposits at Koru in Kenya. Hopwood gave the trivial name *legetet* to the form represented by these fragments. Other portions of the mandible and lower dentition of the same species were later described by MacInnes (1943) from a Miocene site at Songhor, a few miles north of Koru. Further discoveries of fossil hominoid material in the Miocene deposits of Kenya produced evidence of a larger species, *L. macinnesi*; they were mainly found on Rusinga Island in the Kavirondo Gulf of Lake Victoria (Le Gros Clark & Leakey, 1951). This second species is distinguished from *L. legetet* not only by its general size, but also by a number of morphological details of the dentition, including the elongation of the buccal cusp in $\mathrm{P}\,\underline{3}$, the strong development and beading of the internal cingulum in the upper molars, the feeble development or absence of the external cingulum in $\mathrm{M}\,\overline{2}$ and $\mathrm{M}\,\overline{3}$, the development of interconnecting crests between the protoconid and metaconid and also between the hypoconulid and entoconid, and the presence of well-marked anterior and posterior foveae in the lower molars. Whereas in the general size of its jaws and teeth *L. legetet* corresponds to the genus *Hylobates*, *L. macinnesi* approximates more closely to the larger genus *Symphalangus*.

On the basis of dental morphology, it is clear that *Limnopithecus* is referable to the Hylobatinae, and is not very dissimilar to *Propliopithecus* of earlier date and *Pliopithecus* of later date. Indeed, in certain features of the dentition the East African genus appears to occupy a morphological position intermediate between these two genera. But, whatever may be their precise relationships, it is evident that they can all be assigned by their dental characters to a common taxonomic group (Le Gros Clark & Leakey, 1951). Hitherto these ancient hylobatine forms have been known only from jaws and teeth (with the possible exception of a metacarpal bone—see footnote, p. 24); no skeletal material has been available to provide information regarding their general build or the anatomy and proportions of their limbs. It was not known, therefore, whether they showed hylobatine features in their anatomy as a whole.

In 1948, Dr. L. S. B. Leakey discovered a number of limb bones in direct association with jaws and teeth of *L. macinnesi* embedded together in a block of red limestone on Rusinga Island. The block—somewhat more than a cubic foot in volume—was situated at site R.3a, close to, and immediately north of, site R.3 (see the map in Le Gros Clark & Leakey, 1951). The block was broken in three parts for transport, and removed to the Coryndon Museum in Nairobi for development and study. The photograph of the limb bones still partly embedded in the block given in Pl. **1**, fig. 1, shows that they were closely packed together. Embedded in the same block there were a right maxilla of an immature individual (374 H), a fine palate and upper dentition of a young adult (374 G1), an isolated incisor (374 J), and an isolated lower molar (374 D). Immediately adjacent to the block were found a mandibular fragment (374 G2), which certainly belongs to the same individual as the adult palate; a fragment of an immature mandible (374 E), which probably belongs to the same individual as the immature maxilla; and a few mandibular fragments and isolated teeth, some of which may also belong to the individuals whose remains were contained in the block. Most of the teeth are excellently preserved, and their morphology conforms precisely with that of the species *L. macinnesi*. Their direct association with the limb bones leaves no doubt that the latter also belong to the same species and, in some cases, to the same individuals. As will be seen, the teeth and jaw fragments probably belong to at least four different individuals, and the limb bones also represent at least four individuals. Some rodent material was also found in the same matrix as the *Limnopithecus* remains, but the immediately surrounding deposits were completely barren of fossils.

We are indebted to Dr. Leakey for information regarding the circumstances of his discovery of the *Limnopithecus* material, and also for giving us the opportunity of studying the specimens.

In the following account, the jaws and teeth will be first described, and then the limb bones.

Jaws and Teeth

Specimen 374 *G*1 (text-figs. 1 & 2, Pl. **1**, figs. 2 & 3). This fine specimen of a palate and the upper dentition was found embedded in the limestone block. All the teeth except the incisors are present, and show only a minor degree of wear. The dimensions of the palate and teeth correspond almost precisely with the weathered specimen (545—1947) from Rusinga Island (site R.106A) previously described (Le Gros Clark & Leakey, 1951). The new specimen includes the lower part of the nasal aperture, from which it is apparent that this region of the aperture is narrower and bounded by more sharply defined margins than are commonly seen in the modern gibbons. The maximum width of the nasal aperture is 12 mm. In the incisor region the alveolar border has been slightly damaged by erosion, but it is clear that the subnasal portion of the premaxilla was relatively short. The facial part of the premaxillary suture is quite evident; it extends up vertically from the anterior margin of the canine socket. At the upper end of its course the suture is approximately

2 mm. from the margin of the nasal aperture. The base of the zygomatic process of the maxilla is present and is situated immediately above the first and second molar teeth.

In comparison with modern gibbons the palate is relatively short and narrow in relation to the size of the maxillary teeth. Its total length is 36 mm., its breadth between the medial margins of the second molar teeth 14 mm. Anteriorly, there is a large and well-defined incisive fossa. The palato-maxillary suture can be defined without difficulty; instead of being transversely disposed as it commonly is in modern gibbons, it forms a sharp angle directed forwards in the mid-line, a disposition sometimes seen in *Hylobates* and also in cercopithecoid monkeys.

The canines are robust but not greatly elongated. The total length of the crown is 11 mm., and thus considerably less than in the maxillary specimen previously reported from Songhor (Sgr. 57—1948) in which the canine was about 15 mm. long. There is a well-marked internal cingulum, and the anterior aspect of the tooth is scored by a pronounced vertical groove. Each canine is separated from the socket for the lateral incisor by an interval of approximately 2 mm. As seen from the front (text-fig. 1), the tips of the canines diverge slightly from each other. The maxillary teeth correspond so closely in their morphological features to those of the specimen 545—1947 previously found on Rusinga Island that they do not require a detailed description. The total length of the premolar-molar series is 27 mm., and the two sides converge slightly in a forward direction. In the anterior premolar, the buccal cusp is sharply pointed and projects well beyond the level of the lingual cusp. In the posterior premolar and in all the molar teeth the internal cingulum is strongly developed. In the third molar, and to a lesser extent in the second, the cingulum is finely crenated. The trigon is well defined, the three cusps in $M \underline{1}$ and $M \underline{2}$ being of approximately equal size. The hypocone in these teeth is smaller; it is broadly continuous with the cingulum posteriorly and is connected with the metacone by a low crest, but it is sharply separated from the protocone in front by a well-defined

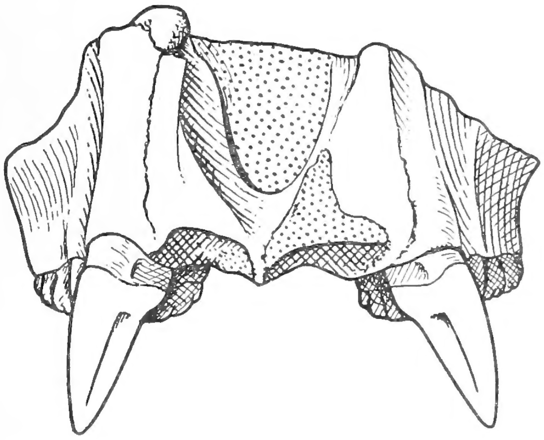

FIG. 1. Anterior aspect of specimen R.374 G1, showing the lower part of the nasal aperture, the premaxillary sutures, and the diverging canine teeth. Defects occupied by matrix are shown in stipple. × 2.

sulcus. In the last molar, the hypocone is practically absent and the metacone much reduced in size.

Specimen 374 *G2* (text-fig. 2 and Pl. **1**, fig. 4).—This specimen consists of the greater part of the body of the mandible of the right side, with the three molar teeth in position and the roots of the canine and premolars, and a portion of the left side with the roots of the premolars. It was found immediately adjacent to the limestone block, and since the molar teeth occlude perfectly with those of the palate just described, and also show the same degree of wear, it is certain that they belong to the same individual. The total length of the premolar-molar series is estimated to have been a little over 30 mm.

In all the molar teeth the cusps are well defined. Low crests connect the protoconid and metaconid, and the hypoconulid and entoconid. There is a well-marked anterior fovea. In the second molar the posterior fovea is also distinct, but in the last molar its development is indeterminate since the medial half of the crown of this tooth is missing. In all the teeth, the external cingulum is rudimentary. The trigonid of the first molar is narrower than the talonid, and the protoconid is slightly in advance of the metaconid. The hypoconulid occupies a median position.

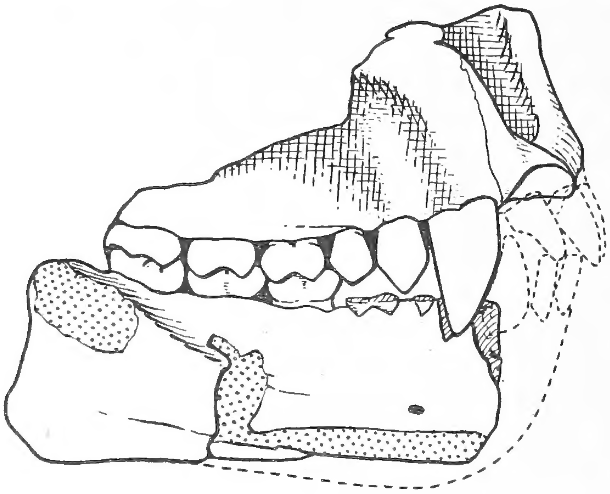

Fig. 2. Lateral aspect of specimens R.374 G1 and R.374 G2, placed in apposition. The outlines of the symphysial region of the mandible and the front teeth have been reconstructed by reference to other specimens of the same species. × 1·5.

In text-fig. 2, specimens 374 G1 and 374 G2 are drawn from the side and slightly from in front, with the teeth in occlusal relationship. The outlines of the incisor teeth, the lower canine, and the symphysial region of the mandible have been reconstructed from other specimens of the same species. The body of the mandible is relatively shallow in contrast with some of the mandibular specimens of the species *L. legetet*. Its height at the level of $M\,\overline{2}$ is 14 mm.

Specimen 374 *H* (text-figs. 3 & 4).—This specimen of an immature individual was found embedded in the limestone block; it consists of the right premaxilla and alveolar region of the maxilla, with the upper dentition. The canine tooth is in process of eruption. The premaxilla has been slightly displaced forwards from its normal position. The lower margin of the nasal aperture near the mid-line can be defined; it is situated about 4 mm. above the alveolar margin of the central incisor.

The two incisor teeth are excellently preserved (text-fig. 4). The central incisor is broad and spatulate. The lateral incisor, also spatulate in form, is considerably narrower. The erupting canine is exposed on its lateral aspect up to the base of the enamel. The total length of the crown is 15 mm. The premolars and the first two molars are in position and very little worn. Except that they are slightly larger, they resemble closely those of specimen 374 G1 in their dimensions and in the details of their cusp pattern. The third molar is missing.

Specimen 374 *E* (Pl. **1**, fig. 5).—This small fragment of the right mandibular ramus with the second molar and the unerupted third molar was found close to the limestone block. Since the second molar occludes perfectly with the corresponding upper tooth the specimen probably belongs to the same individual as the immature maxilla just described.

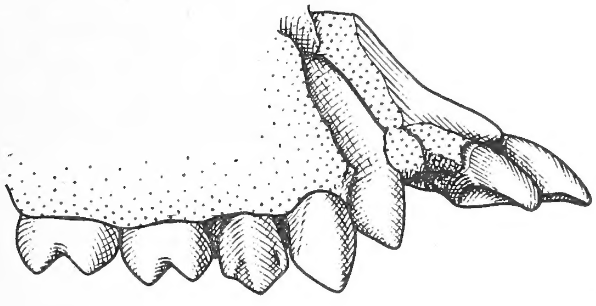

FIG. 3. Lateral view of specimen R.374 H, showing the upper canine tooth in process of eruption. The incisor teeth have been displaced forwards from their natural position. × 2.

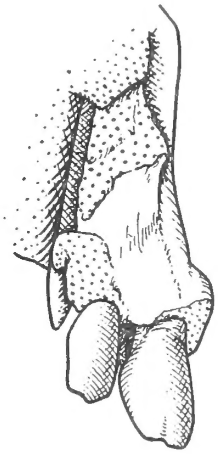

FIG. 4. Anterior aspect of specimen R.374 H, showing the details of the upper incisor teeth. ×2.

The details of the cusp pattern of these two teeth are particularly well shown (see Pl. **1**, fig. 5). In both teeth the anterior and posterior foveae are conspicuous features. The sharply defined conical cusps surround an excavated talonid basin. A crista transversa unites the protoconid and metaconid, and the entoconid and hypoconulid are similarly united by a ridge. The external cingulum is only feebly developed. The hypoconulid is situated slightly lateral to the median axis of the crown, and in the third molar it is almost in line with the protoconid and hypoconid. The narrowing of the talonid portion of the third molar gives the occlusal surface of the crown a triangular contour.

Specimen 374 *F*.—This is the crown of an unerupted third upper molar of the right side, found near the limestone block. Almost certainly it belongs to the immature maxilla 374 E. It shows the characteristic features of the third upper molar of *L. macinnesi*—a well-defined trigon, reduction of the metacone and hypocone (particularly the latter), and a strongly developed crenate internal cingulum.

Specimen 374 *J*.—This isolated left upper central incisor, found in the limestone block, is a perfect match to the right central incisor in the immature maxilla; it can thus with confidence be assigned to the same individual.

Specimen 374 *C*.—This is a right upper central incisor found near the block. It is closely similar to the previous specimen in its general shape and dimensions, but shows a slightly greater degree of wear on its biting edge. Possibly it is one of the missing incisors of specimen 374 G1. All the central incisors in this collection are narrower than that previously described from the specimen Sgr. 57—1948, found at Songhor (Le Gros Clark & Leakey, 1951).

Specimen 374 *I*.—This first left lower molar embedded in a fragment of alveolus was found near the limestone block. It is practically unworn and may possibly belong to the same individual as specimen 374 H. It is larger than the corresponding tooth in the mandibular specimen 374 G2. The protoconid is slightly in front of the transverse level of the metaconid, and these two cusps are placed much closer together than the hypoconid and entoconid, a primitive disposition of the cusps characteristic of the lower first molars of *Limnopithecus*. The posterior fovea is well developed.

Specimen 374 *D*.—This isolated tooth, a second lower molar of the left side, was found embedded in the limestone block. It is in an advanced stage of wear. The anterior and posterior foveae are quite distinct, but there is no more than a rudimentary external cingulum.

Specimen 374 *B*.—This specimen is also a left second lower molar, of which the crown is partly broken. It is moderately worn and badly weathered, and almost certainly does not belong to any of the individuals represented by the specimens already described.

Specimen 374 *A*.—This specimen was found with the former one (374 B) near the limestone block. It is a small fragment of the body of the left side of the mandible with a lower molar tooth (? $\overline{\text{M 1}}$) in position. The tooth is moderately worn and badly weathered. Probably it belongs to the same individual as specimen 374 B.

The above descriptions prove that at least four individuals of *L. macinnesi* are represented by specimens of jaws and teeth. Specimens 374 G1 and 374 G2 (and possibly 374 C) evidently belonged to a young adult, in which the permanent dentition had completed its eruption but the teeth were very little worn. Specimens 374 H, 374 E, 374 F, 374 J (and possibly 374 I) almost certainly belonged to another individual, an immature animal in which the canine was in process of eruption and the last molars were still embedded in the alveolus. From its advanced state of wear, specimen 374 D clearly belonged to an old adult. Lastly, specimens 374 A and 374 B appear to represent a fourth individual, a mature adult in which the teeth were moderately worn.

The antero-posterior and transverse measurements and the length-breadth indices of all the premolars and molars which can be accurately measured are shown in Table 1. All measurements are given in mm.

Limb Bones

The limb bones were all found embedded in the limestone block and closely packed together (Pl. **1**, fig. 1). As previously noted, they belong to at least four individuals, presumably those represented by the jaws and teeth just described.

TABLE 1

UPPER DENTITION

	P $\underline{3}$			P $\underline{4}$			M $\underline{1}$			M $\underline{2}$			M $\underline{3}$		
	a.p.	*tr.*	*ind.*	*a.p.*	*tr.*	*ind.*	*a.p.*	*tr.*	*ind.*	*a.p.*	*tr.*	*ind.*	*a.p.*	*tr.*	*ind.*
374 G1*	4·0	6·6	165	3·8	6·4	168	5·6	7·3	130	6·3	8·0	127	6·4	7·6	119
374 H	4·6	6·8	148	4·2	7·2	171	5·9	7·5	127	6·8	8·2	121	—	—	—
374 F	—	—	—	—	—	—	—	—	—	—	—	—	6·0	7·2	120

* The measurements of the teeth in specimen 374 G1 are the means of the two sides.

LOWER DENTITION

	M $\overline{1}$			M $\overline{2}$			M $\overline{3}$		
	a.p.	*tr.*	*ind.*	*a.p.*	*tr.*	*ind.*	*a.p.*	*tr.*	*ind.*
374 G2	5·8	5·1	88	6·8	5·9	87	—	—	—
374 I	7·0	5·4	77	—	—	—	—	—	—
374 D	—	—	—	7·4	6·3	85	—	—	—
374 H	—	—	—	8·0	6·1	76	8·1	6·0	74

The Bones of the Fore-limb

The fore-limb is represented by a humerus (complete except for the proximal extremity) and the proximal portions of the radius and ulna. Their position in the matrix, together with the fact that they are all of the right side and conform closely in size and articular apposition, makes it reasonably certain that they belong to one individual. They have been compared with the corresponding bones of *Hylobates* and *Symphalangus*, with a number of cercopithecid monkeys in which the limbs appeared to be of about the same size as those of *Limnopithecus*, and with *Ateles*. This last genus was chosen because in general build, as well as in a number of structural details, its limb bones, particularly those of the fore-limb, bear a rather close resemblance to the fossils.

The Humerus (Pl. **2**, fig. 6*c*; **3**, fig. 7*c*; **4**, fig. 8; **5**, fig. 9).—The humerus is the best preserved of all the limb bones in the collection. The proximal articular extremity is missing, but the base of the lesser tuberosity and part of the greater tuberosity are present. It is reasonably certain that, on the posterior aspect of the bone, the neck is preserved up to the level of the lower lip of the missing articular surface.

The shaft of the humerus of *Limnopithecus* resembles that of the gibbons in its straightness and relative slenderness, and also in the absence of pronounced muscular ridges and eminences: in these characters it contrasts strongly with the Cercopithecidae, but it is shorter and more robust than the humeral shaft of Recent Hylobatinae. The total length of the fossil humerus has been estimated by comparing the proportionate length measured from points preserved intact at the proximal extremity with corresponding proportionate lengths in *Hylobates*, *Symphalangus*, and *Ateles*. Three points were selected and their distance from the most distal point of the medial margin of the trochlea measured directly; these were (*a*) the mid-point of the base of the lesser tuberosity, (*b*) a point at the upper end of the posterior aspect of the neck of the humerus where this approximates to the lower margin of the articular head, and (*c*) a point marking the maximum lateral convexity of the greater tuberosity. These points can be located on the fossil humerus with reasonable accuracy—certainly to within one or two millimetres. In Table 2, the estimated total length of the humerus is given by reference to these three points as based on corresponding measurements of a series of humeri of modern species. The estimates are reasonably consistent, the means based on each series of measurements showing a range of 190 mm. to 193 mm. Probably, therefore, the total length of the fossil humerus did not significantly exceed 193 mm. In Table 3, the estimated total length and the diameters at the mid-point of the shaft of the fossil humerus are compared with those of a number of modern species, as well as robusticity indices based on the formula: $\frac{\text{circumference at mid-point of shaft} \times 100}{\text{total length}}$ equivalent to the "Stärkeindex" of Duerst.

TABLE 2

Species on which proportionate length of *Limnopithecus* humerus was based	Total length in mm. of *Limnopithecus* humerus estimated by reference to:		
	Point *a*	Point *b*	Point *c*
Hylobates concolor . . .	189	191	193
Hylobates hoolock . . .	191	195	194
Hylobates leuciscus. . .	189	192	194
Hylobates lar. . . .	188	191	192
Symphalangus syndactylus .	189	192	192
Symphalangus syndactylus .	192	195	195
Ateles geoffroyi . . .	192	195	193
Ateles paniscus . . .	190	194	193
Mean .	190	193	193

From Table 3 it is apparent that in its robusticity the shaft of the *Limnopithecus* humerus approximates to that of *Ateles* and occupies a position intermediate between the Recent gibbons and those cercopithecids of equivalent limb-size with which comparisons were made. The fossil humerus is considerably shorter in absolute length than that of either *Symphalangus* or *Hylobates*, though it is evident from a study of the limb bones as a whole, and also of the jaws and teeth, that *Limnopithecus* was certainly much more stoutly built than *Hylobates*. By itself, therefore, the shaft of the humerus suggests that *Limnopithecus* did not present the specialized proportions of the fore-limb characteristic of the modern Hylobatinae. This inference is supported by certain of the structural details of the humerus.

TABLE 3

	Total length of humerus	Diameters at mid-point of shaft		Robusticity index
		ant. post.	trans.	
H. concolor	228	10·2	11·4	14·9
H. hoolock	230	9·5	10·0	13·9
H. leuciscus	224	8·9	9·3	13·8
H. lar	228	8·8	10·4	14·0
S. syndactylus	259	12·2	9·9	14·3
S. syndactylus	263	12·0	11·4	14·2
Macaca nemestrina	176	13·0	14·0	25·0
Macaca pileata	171	12·2	12·0	22·8
Presbytis priamus	169	12·2	13·8	24·8
Rhinopithecus roxellanae	197	12·5	13·1	25·9
Colobus satanas	168	11·0	11·5	22·6
Semnopithecus chrysomelas	140	9·0	8·9	21·1
A. geoffroyi	198	11·0	10·8	18·2
A. paniscus	234	11·6	11·8	16·6
Limnopithecus macinnesi	193 (estimated)	10·6	11·0	19·3

The lower articular extremity of the fossil humerus is in a good state of preservation (Pl. 5, fig. 12). The trochlea has a well-defined medial lip, but this does not extend distally to form the sharp projecting rim commonly seen in the cercopithecid humerus. In this respect it more closely resembles the modern gibbons, although it differs from them in having a less pronounced lateral lip, and the anterior surface of the trochlear facet is not so deeply grooved. The capitellum is globular in shape as in the gibbon; this might be taken to indicate an equivalent degree of pronation and supination of the forearm, but such an inference is apparently contradicted by certain details of the head of the radius. On the lateral aspect of the capitellum is a sharply defined pit for the attachment of a strong lateral ligament of the elbow joint. The radial fossa is moderately developed, but the coronoid fossa is very indistinct and contrasts with the well-marked coronoid fossa in the humerus of Recent hylobatines. On the posterior aspect of the lower extremity of the fossil humerus, the olecranon fossa (which is partly filled with matrix) is relatively a little broader than in the gibbon humeri with which it was compared. The medial epicondyle is prominent and relatively stout, and projects directly medially. In Table 4 are comparative data showing the maximum width of the trochlear facet anteriorly, the epicondylar width of the lower extremity of the humerus measured between the maximum convexities of the epicondyles, and the relation of this width to the total length of the humerus. This table indicates that the lower extremity of the humerus of *Limnopithecus* is proportionately broader than the humerus of the modern hylobatine species examined, and that it is more directly comparable with the Cercopithecidae and *Ateles*, particularly the latter. The supinator crest in the fossil humerus is strongly developed in comparison with modern gibbons and the spider monkey. It can be traced upwards almost to the junction of the upper and middle thirds of the shaft of the bone, which is relatively straight and smooth. The delto-pectoral crest is but weakly developed, approaching the hylobatine humerus in this respect, and contrasting with the cercopithecid humerus in which the usually strongly developed crest contributes to the markedly angulated appearance of the shaft (Pls. **2, 3,** figs. 6 & 7). The bicipital groove on the shaft is very shallow, another resemblance to the modern gibbons, but its medial lip is more sharply defined and shows some approach to the Cercopithecidae.

TABLE 4

	Anterior trochlear width	Epicondylar width	Epicondylar width × 100 / Total humeral length
H. concolor	8·4	29·5	12·9
H. hoolock	8·6	27·2	11·8
H. leuciscus	8·4	26·4	11·3
H. lar	8·8	27·2	11·4
S. syndactylus	9·4	32·2	12·4
S. syndactylus	9·4	32·4	12·3
M. nemestrina	9·2	34·4	19·4
M. pileata	7·2	33·0	19·3
P. priamus	8·4	31·8	18·8
R. roxellanae	9·2	33·0	16·8
C. satanas	8·8	36·0	21·4
S. chrysomelas	6·6	24·5	17·5
A. geoffroyi	7·2	32·2	16·3
A. paniscus	8·4	31·0	13·2
L. macinnesi	9·4	31·8	16·6

The tuberosities at the upper extremity of the fossil bone are not sufficiently preserved to allow their size to be estimated or their details to be studied. On the other hand, the neck of the humerus is almost intact, and presents certain interesting features. A rounded longitudinal ridge on the posterior aspect curves backwards at its upper end to a level which must practically have reached the lower lip of the articular surface. This ridge, a common feature in mammalian humeri, forms a flange which provides a bracket-like support for the head of the bone. A study of a number of humeri of Recent primates shows that the median axis of the ridge bears a sufficiently close relationship to the median vertical axis of the articular head to permit its use in determining the orientation of the latter, and thus to obtain information regarding the torsion of the humerus in *Limnopithecus*. Since there is some evidence (Evans and Krahl, 1945) that the modern hylobatine humerus is distinguished from the cercopithecid humerus by a more medial orientation of the head, and since this may be in part related to posture and gait, it is clearly of some importance to determine the condition in the fossil bone. Comparative observations were therefore made on the orientation of the ridge on the humeral neck in relation to the transverse axis of the lower articular extremity of the bone in a number of gibbon and monkey humeri. In order to do this, an apparatus was devised consisting of a metal cylinder fitted with rotating caps at either end. At the "distal" end, the cap was circular and provided with a transverse cross-wire. At the "proximal" end, the cap was cylindrical, having a transverse cross-wire as at the other end, and a window cut in one side fitted with a longitudinal cross-wire. In each humerus the median axis of the summit of the ridge on the neck was first marked with a line. The humerus was then placed centrally in the cylinder and aligned so that the axis of the ridge coincided with the longitudinal cross-wire at the proximal end, and the central axis of the neck of the bone with the centre of the transverse cross-wire. The cap at the distal end was then rotated until its transverse cross-wire coincided with the median transverse axis of the lower articular extremity of the humerus. By reference to a scale of degrees marked round the margins of the two extremities of the cylinder, it was then possible to determine the angle between the transverse axis of the lower extremity and a line passing through the centre of the neck of the humerus and the summit of the ridge (text-fig. 5). The torsional angles in a series of modern gibbons and monkeys compared with that of *Limnopithecus* are recorded in Table 5; in *Limnopithecus* the angle of 108° (β in text-fig. 5B) falls within the range of variation, 102°–115°, of the

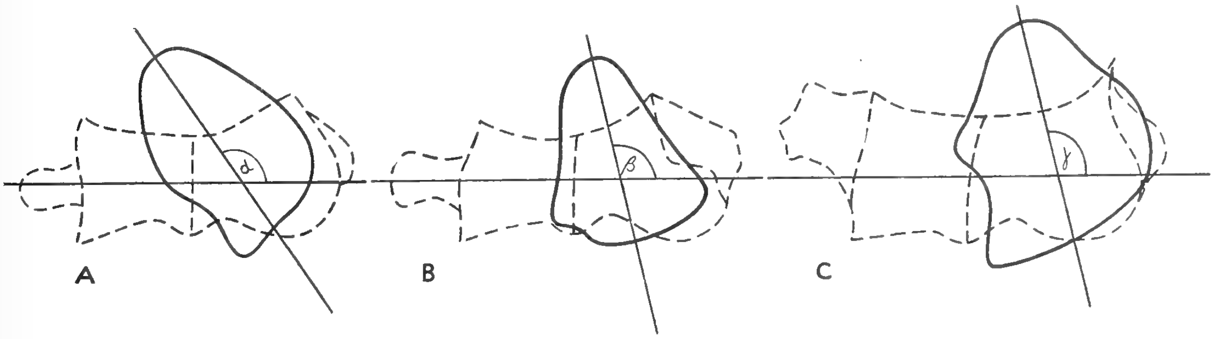

FIG. 5. Outline of a transverse section through the upper end of the shaft of the humerus (continuous line) superimposed on that of the lower extremity (interrupted line), to demonstrate the angle of torsion in the modern gibbons (A), *Limnopithecus macinnesi* (B), and modern cercopithecid monkeys (C). For details, see text.

TABLE 5

	Humeral torsion
H. concolor	128°
H. hoolock	128°
H. leuciscus	133°
H. lar	137°
S. syndactylus	127°
S. syndactylus	124°
M. nemestrina	110°
M. pileata	107°
P. priamus	115°
R. roxellanae	102°
C. satanas	106°
S. chrysomelas	111°
A. geoffroyi	119°
A. paniscus	121°
L. macinnesi	108°

cercopithecid monkeys examined (γ in text-fig. 5C), and is considerably below the range, 124°–137°, in the Recent Hylobatinae (α in text-fig. 5A). It may be inferred, therefore, that the articular head of the humerus in the fossil species was orientated almost directly backwards, as in the modern catarrhine monkeys, and, further, that in its posture and gait *Limnopithecus* resembled the quadrupedal monkeys rather than the brachiating gibbons. In strong contrast to *Limnopithecus*, the angle of torsion of the humerus of the spider monkey shows a remarkable approach to that of the modern gibbon.

To sum up; as compared with that of other catarrhine primates the humerus of *Limnopithecus* shows pronounced hylobatine features in the relative length, straightness, and slenderness of the shaft; in the lack of pronounced muscular ridges, particularly the feeble development of the delto-pectoral crest; and in certain features of the lower articular extremity. On the other hand, it also presents a number of primitive characters representing a cercopithecid level of development; among them are the backward orientation of the articular head, the well-developed supinator crest, the feebly marked coronoid fossa, and the weak lateral lip of the trochlear facet on its anterior aspect. This combination of characters suggests that *Limnopithecus* represents an early phase of hylobatine evolution in which quadrupedal habits had not yet been replaced by brachiating habits. The resemblance to *Ateles* in certain of the structural details of the humerus and some of the other limb bones is remarkable. An exception, however, is found in the inclination of the articular head. A study of the humerus by itself suggests that *Limnopithecus* was a lightly built and active arboreal creature resembling the cercopithecid monkeys far more closely than the modern gibbons in its mode of progression.

Radius (Pl. **4**, fig. 9; **5**, fig. 11).—The upper extremity and the proximal part of the shaft of this bone are preserved. The length of the specimen is 125 mm. The radial shaft is slender and rounded in cross-section, and is very similar to that of the modern gibbons in general appearance and in the absence of strong muscular markings. Comparative data for the diameter of the head and shaft are shown in Table 6, from which it will be seen that in these measurements *Limnopithecus macinnesi* compares closely with the Hylobatinae. The upper articular surface of the head has a pronounced slope downwards and forwards (Pl. **5**, fig. 11). In this respect it differs rather markedly from *Hylobates* and *Symphalangus*, where this surface is approximately horizontal with reference to the long axis of the bone, and resembles the condition commonly present in the cercopithecid radius. Possibly it indicates less free and complete movements of pronation and supination than in the Recent Hylobatinae The neck of the fossil radius is constricted by a marked depression on its medial aspect between the head and the tuberosity. This depression finds an approximate parallel in *Ateles*, and is also present in some cercopithecid radii to a moderate degree. It is absent, however, in the modern gibbons, which have the radial neck practically cylindrical in form, though in some specimens there is a slight medio-lateral flattening. The neck is relatively long, and so approaches the characteristic condition of the modern gibbons and of *Ateles*. In Table 7, comparative data are provided for the length of the neck measured between the distal margin of the articular head and the proximal margin of the radial tuberosity, and the relation of this length to the maximum diameter of the head.

TABLE 6

	Diameters of radial head		Diameters of radial shaft (approximately at mid-point)	
	ant. post.	trans.	ant. post.	trans.
H. concolor	13·4	13·0	8·0	5·6
H. hoolock	12·2	12·0	7·6	6·4
H. leuciscus	12·2	12·1	6·8	5·2
H. lar	12·7	12·2	7·2	5·8
S. syndactylus	14·2	14·7	8·0	6·3
S. syndactylus	15·0	15·6	8·2	6·4
M. nemestrina	14·0	13·8	7·4	12·0
M. pileata	15·0	13·7	7·9	9·6
P. priamus	15·4	13·4	8·8	10·0
R. roxellanae	16·0	16·0	7·8	9·2
C. satanas	13·2	12·2	7·2	8·8
S. chrysomelas	12·0	10·8	6·2	6·0
A. geoffroyi	13·6	13·4	9·1	8·0
A. paniscus	13·4	13·0	8·4	7·8
L. macinnesi	11·6	12·8	6·8	7·6

TABLE 7

	(*a*) Length of neck of radius	(*b*) Maximum diameter of head of radius	$\frac{a}{b}$
H. concolor	14·4	13·4	1·08
H. hoolock	14·2	12·2	1·16
H. leuciscus	14·2	12·2	1·16
H. lar	17·0	12·7	1·34
S. syndactylus	22·0	14·7	1·50
S. syndactylus	25·2	15·6	1·62
M. nemestrina	7·0	14·0	0·50
M. pileata	6·2	15·0	0·41
P. priamus	5·4	15·4	0·35
R. roxellanae	8·0	16·0	0·50
C. satanas	5·2	13·2	0·39
S. chrysomelas	7·0	12·0	0·58
A. geoffroyi	15·0	13·6	1·10
A. paniscus	16·0	13·4	1·19
L. macinnesi	12·0	12·8	0·94

The radial tuberosity for the insertion of the biceps tendon is prominent and well defined. To the lateral side of it is a shallow groove, about 10 mm. long. Such a groove is developed to a certain degree in the cercopithecid radius, but is absent from all the specimens of Recent Hylobatinae available for comparison. The shaft of the fossil radius is somewhat flattened anteriorly, and in this feature shows some resemblance to the Cercopithecidae. The anterior surface is rounded in the modern gibbons.

Attempts to estimate the total length of the radius of *Limnopithecus* proved to be more difficult than was at first anticipated, but was done by reference to length ratios in modern hylobatine radii, a comparison justified by the general hylobatine proportions of the preserved part of the fossil. Fortunately a sufficient length of the bone is preserved to include the maximum lateral convexity of the shaft. By determining the position of the point of maximum convexity in relation to the total length of the radius in *Hylobates* and *Symphalangus*, a ratio was calculated which could then be applied to *Limnopithecus*. Similar estimates were made by calculating the ratio of the distance between the most proximal point of the head of the radius and the proximal extremity of the tuberosity to the total length of the bone. In each case the average of the estimates based on these two methods was taken. They are shown in Table 8.

TABLE 8

	Length of radius	Estimated length of *Limnopithecus* radius based on position relative to total length of tuberosity and maximum convexity of shaft
H. concolor	253	197
H. hoolock	239	199
H. leuciscus	263	201
H. lar	250	213
S. syndactylus	305	206
S. syndactylus	292	184

From these data, it appears probable that the total length of the complete radius of *Limnopithecus macinnesi* did not significantly exceed 200 mm., and thus was considerably shorter than any of the specimens of *Hylobates* and *Symphalangus* which were examined.

In summary, the general hylobatine appearance of the radius of *Limnopithecus* should be emphasized, particularly the slenderness and smoothness of the shaft. Other hylobatine features are the relatively small size of the articular head, and the length of the neck. Characters indicating a more primitive, or cercopithecid, level of evolution are the shape and slope of the articular head, the lateral flattening of the neck, and the evidence that the shaft was much shorter than that of the modern gibbons.

Ulna (text-fig. 6, Pl. **4**, fig. 9; **5**, fig. 10).—This bone is represented by the upper extremity and the proximal part of the shaft. The length of the specimen is 134 mm. The general appearance of the ulna, as of the radius, is strikingly hylobatine in its slenderness and in the absence of the strong muscular impressions commonly characteristic of cercopithecid ulnae of comparable size. In two significant features, however, the ulna of *Limnopithecus* contrasts rather strongly with that of the modern gibbons, namely in the shape of the trochlear surface and in the proximal prolongation of the olecranon process. The upper half of the trochlear facet is missing, but its lower half, where it forms the upper surface of the coronoid process, is preserved. Here it forms a flattened surface, slightly and evenly concave from side to side. It slopes forwards and downwards to terminate anteriorly in a lip which is similarly concave in a medio-lateral direction. In the modern gibbons the lower half of the trochlear facet is very different, for it has a strongly developed median keel, and curves directly forwards to terminate anteriorly in a lip with a marked upward convexity. In the details of the trochlear surface *Limnopithecus* is closely paralleled by *Ateles*, and to a somewhat less extent by cercopithecid monkeys. So far as catarrhine primates alone are concerned, this feature of *Limnopithecus* resembles the Cercopithecidae more closely than *Hylobates* and *Symphalangus*. The flattened contour of the trochlear facet is correlated with the flattened contour of the corresponding facet of the humerus on its anterior aspect.

The olecranon process in the fossil bone is incomplete, but it is sufficiently preserved to show that proximally it was prolonged well beyond the level of the trochlear articular surface. Although the upper part of the articular surface is broken away its upper limit can be determined by articulating the ulna with the humerus. This upward prolongation of the olecranon process is a typical cercopithecid character which contrasts rather strongly with the condition in the modern gibbons (text-fig. 6). The upper end of the shaft of the ulna, at the level of the coronoid process, is marked by broad grooves on its medial and lateral aspects. The medial groove is not developed to the same extent in any of the available specimens of modern gibbons, though it can be paralleled in some cercopithecid ulnae. The upper part of the shaft of the ulna is strongly compressed from side to side, closely resembling *Ateles* and contrasting with the modern gibbons, in which the shaft at this level is more triangular in cross-section.

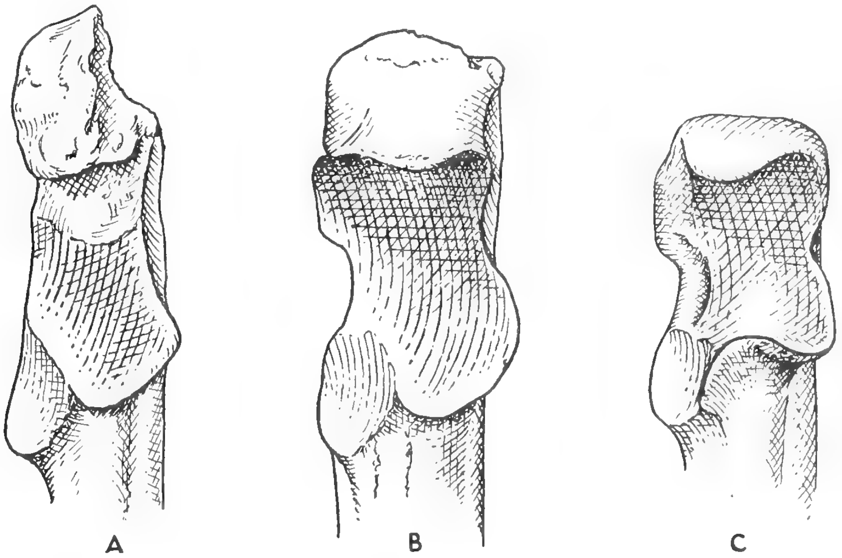

FIG. 6. Anterior aspect of the upper extremity of the ulna of (A) *L. macinnesi*, (B) *Ateles*, and (C) *Hylobates*. × 2.

The estimated total length of the complete ulna in *Limnopithecus macinnesi* is based on the position of the nutrient foramen relative to the total length of the bone in modern species, since this foramen can be identified on the fossil bone 59 mm. from the tip of the olecranon process. This method can of course only give very approximate results. The relevant data are recorded in Table 9. As might be expected these data show a rather wide scatter, but their mean value conforms reasonably well with the estimated length (200 mm.) of the radius. For, since the distance between the level of the upper extremity of the radius and the tip of the olecranon process was estimated to have been at least 18 mm., the total length of the ulna, on the basis of the estimated radial length, must have been in the neighbourhood of 218 mm. This last figure is similar to the estimate based on the relative position of the nutrient foramen in *Ateles*, an estimate which is perhaps more reliable because of the close similarity in proportions and details of the upper part of the ulna between *Limnopithecus* and the spider monkey.

TABLE 9

	Total length of ulna	Distance from olecranon to nutrient foramen	Estimated length of *Limnopithecus* ulna based on position of nutrient foramen
H. concolor	259	64	239
H. hoolock	248	67	218
H. leuciscus	271	70	228
S. syndactylus	312	106	174
S. syndactylus	292	96	180
A. geoffroyi	229	62	218
A. paniscus	240	66	215

In summary, the ulna of *Limnopithecus macinnesi* is hylobatine rather than cercopithecid in the slender and smooth character of the shaft, but resembles the Cercopithecidae in the details of the trochlear facet and in the proximal extension of the olecranon process. In its total length it appears to occupy a position intermediate between the cercopithecid monkeys and the modern gibbons. In its general character, and also in some of its structural details, the ulna shows rather close similarities to that of *Ateles*.

The proportions of the fore-limb.—One of the characteristics of the anthropoid apes, as compared with cercopithecid monkeys, is the relative elongation of the forearm. The brachial index, i.e. the relation of radial to humeral length, has been computed by Schultz (1930) in twelve specimens of catarrhine monkeys belonging to five genera to show an average of 100·8 (maximum 110·1). On the other hand, he found the average in twenty-four adult specimens of *Hylobates* to be 113·3 (minimum 107·8), and in thirteen adult specimens of *Symphalangus syndactylus* 111·3 (minimum 106). In *Limnopithecus macinnesi*, assuming the probable total length of the humerus to be 193 mm., and that of the radius 200 mm., the index is 103·6. Thus it appears that *Limnopithecus* may have approximated more closely to the primitive cercopithecid ratio than to that of the modern gibbons. The inference follows that this early Miocene genus had not yet developed the specialized brachiating habits characteristic of Recent Hylobatinae. Such a conclusion is reinforced by a number of morphological details already mentioned, particularly by the orientation of the articular head of the humerus, the conformation of the trochlear facets of the humerus and ulna, and by the slope of the head of the radius.

The Bones of the Hind-limb

The hind-limb of *Limnopithecus macinnesi* is represented by incomplete shafts of four femora and one tibia, the detached head of a femur, a fragment of a fibula, an incomplete calcaneum, and part of a talus. These specimens were compared with the corresponding elements of the skeletons utilized in preparing the account of the fore-limb, but they did not prove to be so informative as the bones of the fore-limb, since, apart from the isolated femoral head, none of the articular extremities is preserved.

The Femur (Pl. **6,** figs. 13, 14).—Of the four femoral shafts one (No. 4) is judged by its small size to belong to a young individual, and may probably be associated with the immature maxilla and the mandibular fragment containing an unerupted third molar. Specimen 1 is the most complete and includes the lesser trochanter at the upper end of the shaft. The lower end of the shaft of this femur is represented by a small detached fragment which does not extend down to the level of the epicondyles, neither does it make a direct contact with the main part of the shaft; but the association of the two is rendered reasonably certain by the conformity in size, and by the precise similarity in the texture of the bone and in the appearance of the matrix which fills the medullary space. By reference to the diverging lines of the supracondylar ridges the interval between the main shaft and the lower fragment can be estimated to be about 3 mm. Specimens 2 and 3 are lower portions of the shafts of two femora, probably both of the right side; their diameters are approximately similar and slightly less than that of specimen 1. There is no evidence to show to which specimen the detached femoral head belongs. The femoral specimens belong to at least four individuals—presumably the same four as those represented by the jaws and teeth.

A notable feature of the femur of *Limnopithecus macinnesi* is its straightness and evenly cylindrical form (particularly evident in specimens 1 and 4), features which by themselves suggest hylobatine affinities, for in the cercopithecid material examined the femoral shaft shows varying degrees of curvature. The lesser trochanter is relatively strongly developed and the oval facet on its summit faces directly medially. In this respect it resembles the gibbons, and contrasts with the cercopithecid monkeys in which the facet is characteristically directed upwards at a marked angle. Comparison with Recent catarrhine primates also shows that in the details of its contour the lesser trochanter rather closely resembles that of the modern Hylobatinae, more particularly of *Symphalangus*. Strictly speaking there is no linea aspera, for the ridges on the back of the shaft which form a continuation downwards of the spiral line and the line of the gluteal ridge do not join, but are separated by an interval of about 4 mm. in the middle of the shaft. As may be seen in specimen 1, these ridges are more strongly developed than in the femora of the Recent Hylobatinae examined.

In Table 10 the antero-posterior and transverse diameters (at or near the middle) of the femoral shaft of *Limnopithecus* and of a number of Recent hylobatines and cercopithecids are given. In these dimensions specimen 1 exceeds the range of the modern gibbons; but in each specimen of *Limnopithecus* the diameters are less than those of the cercopithecid femora measured, except that of *Semnopithecus*. The width of the popliteal surface immediately proximal to the condyles is estimated to have been 25 mm. in specimen 2, and this falls well within the range of the modern gibbons. On the other hand, except for the specimen of *S. chrysomelas* in which the corresponding width is 25·4 mm., it is below the range found in the cercopithecids examined, and in the specimens of *Ateles*. In its general shape and proportions the lower end of the femur of *S. chrysomelas* bears rather a striking resemblance to *L. macinnesi* as shown in specimens 2 and 3.

TABLE 10

	Diameter of femoral shaft	
	ant. post.	trans.
H. concolor	10·4	10·3
H. hoolock	9·6	10·2
H. leuciscus	9·0	9·8
H. lar	9·9	10·0
S. syndactylus	10·4	10·6
S. syndactylus	11·0	12·2
M. nemestrina	12·0	14·0
M. pileata	14·0	13·6
P. priamus	14·0	14·8
C. satanas	13·2	12·8
S. chrysomelas	10·6	11·2
A. geoffroyi	11·4	13·4
A. paniscus	14·2	15·0
L. macinnesi	12·4	12·0
L. macinnesi	10·3	10·0
L. macinnesi	10·0	11·2

The detached head of a femur found with the other specimens is too incomplete to yield useful information: it has a maximum diameter of 15·8 mm., and comes within the range of variation of Recent Hylobatinae and Cercopithecidae. There is a well-defined foveal depression at the summit of the head.

An attempt was made to estimate the total length of specimen 1, in order to calculate the robusticity index of the shaft as well as the humero-femoral index. The position of the detached lower fragment of this specimen can be determined with reasonable accuracy by noticing the alignment of the diverging supracondylar ridges. The total length of specimen 1, with the lower detached fragment in position, is 177 mm. In this specimen the lesser trochanter is preserved at the upper end; the lower end, however, only includes the upper part of the popliteal surface. The total extent of the latter down to the level of the epicondyles was estimated by comparison with specimen 3, in which the lower end of the shaft as far as the level of the medial epicondyle has been preserved (Pl. **6**, fig. 14*b*). The general dimensions of the lower end of the shaft of specimen 3 are closely similar to those of specimen 1, and by comparing the angle of divergence of the supracondylar ridges in the two specimens, the latter can readily be placed in the same position relative to their total length. Thus, by reference to specimens 1 and 3, it is possible to get an estimate of the length of the more complete specimen 1 from the mid-point of the summit of the lesser trochanter above to the level of the medial epicondyle below. This estimate is 170 mm. Next, in order to obtain an estimate of the total length of the intact femur represented by specimen 1, including the two articular extremities, the relation between the total length and the distance between the lesser trochanter and the medial epicondyle was calculated in a number of femora in modern gibbons, cercopithecids and spider monkeys, and the relationships applied to specimen 1 of *L. macinnesi*. The results, which are given in Table 11, show that the estimates for the total length of the femur of *L. macinnesi*, as represented by specimen 1, range from 205 mm. to 226 mm., with a mean of 214 mm. The lowest estimate (205 mm.) is greater than the highest estimate for the humeral length (195 mm.), and even if these extreme figures are taken, the humero-femoral index is only 95. This ratio contrasts strongly with that of Recent Hylobatinae in which it has been shown to vary from 108 to 142 (Mollison, 1911). Although there is no certainty that the femoral specimen 1 belongs to the same individual as the humerus, there is some probability that this may be so. They are both bones (of the right side) of a fully mature creature, and they were embedded in the limestone matrix in close juxtaposition, lying within 3 cm. of each other. Thus there is some reason to accept the estimated humero-femoral index as a near approximation to the true value, particularly as it conforms well with expectations based on the general proportions of the femur considered in relation to those of the bones of the arm and forearm. Nevertheless, in the absence of more complete material, conclusions based on the estimated humero-femoral index must be regarded as provisional only, even though there is a high degree of probability that the index was considerably less than in the modern gibbons.

TABLE 11

	(*a*) Distance from lesser trochanter to medial epicondyle	(*b*) Total length of femur	Total length of femur of *L. macinnesi* estimated from the ratio $\frac{a}{b}$
H. concolor	164	202	209
H. hoolock	155	197	216
H. leuciscus	157	194	210
H. lar	169	208	209
S. syndactylus	161	204	215
S. syndactylus	161	206·5	218
M. nemestrina	135	179·5	226
M. pileata	185	228	209
P. priamus	179	222	215
R. roxellanae	169	221	222
C. satanas	180	224	212
S. chrysomelas	170	205	205
A. geoffroyi	161	206	216
A. paniscus	179	230	218

The robusticity index of the femoral shaft of *L. macinnesi* has been calculated on the basis of the mean estimated total length of specimen 1, i.e. 214 mm. In Table 12, the index is compared with that of modern gibbons, cercopithecids and *Ateles*. In its robusticity the femur of *Limnopithecus* exceeds the range found in the specimens of Recent Hylobatinae examined, and approximates more closely to the cercopithecids and *Ateles*. The relatively low index in *S. chrysomelas* reflects the similarity in general build between the femur of this species and that of *L. macinnesi*. Visual comparison suggests that the robusticity of the femoral specimens 2 and 3 may have been rather less than that of specimen 1, but the similarity in morphological detail between them and the equivalent part of the femur in *S. chrysomelas* indicates a close resemblance in general build. Specimen 4, as already noted, probably belongs to an immature individual; the shaft of this bone is remarkable for its straight cylindrical character, but unfortunately it presents no features of morphological detail for comparative study.

TABLE 12

	Circumference of femoral shaft at mid-point	Robusticity Index of Femur $\frac{\text{Circumference} \times 100}{\text{Total length}}$
H. concolor	34·9	17·0
H. hoolock	33·5	17·0
H. leuciscus	31·5	16·2
H. lar	33·0	15·9
S. syndactylus	33·0	16·2
M. nemestrina	44·0	24·5
M. pileata	45·0	19·8
P. priamus	49·0	22·1
R. roxellanae	47·0	21·3
C. satanas	43·0	19·2
S. chrysomelas	36·5	17·8
A. geoffroyi	41·0	19·9
A. paniscus	46·0	20·0
L. macinnesi	40·0	18·7

The Tibia (Pl. **6,** fig. 15). The tibia of *L. macinnesi* is represented by the major part of a shaft lacking the head and the distal end. The total length of the specimen is 163 mm. It is considerably stouter in build than the tibia of modern gibbons and, indeed, shows no close resemblance to the latter. On the other hand, in its general build it is remarkably like the tibia of *S. chrysomelas*, and from a comparison with that species one may infer that the total length of the intact bone was about 190–200 mm. Comparison with the tibia of other cercopithecids and of modern gibbons, in which the distance between the tubercle above and the level at which the anterior crest flattens out below was related to the total length of the bone appears to confirm this estimate, which, however, can only be regarded as an approximation.

The fossil tibia is of the right side. Proximally the lower part of the tibial tubercle is preserved, but above this the head is missing. Distally the shaft is preserved down to the level where it commences to broaden towards the lower articular extremity. The shaft is flattened from side to side. At the level of the lower end of the tubercle the antero-posterior diameter is 18·4 mm., and the maximum transverse diameter 13·0 mm. At the middle of the shaft the corresponding measurements are 13·8 mm. and 7·8 mm., and in Table 13 these are compared with modern gibbons. From the tibial tubercle a rounded crest extends downwards on the anterior aspect of the shaft. About 25 mm. below the tubercle this crest shows a slight roughening such as is commonly seen in cercopithecid monkeys, where it is usually more pronounced. On the other hand, it is absent, or only very faintly indicated, in the hylobatine tibiae examined. The medial surface of the tibia is evenly convex, except for its upper end where it is slightly hollowed. The lateral surface shows a pronounced concavity at the level of the tubercle, and in a downward direction this gradually fades out at about the middle of the shaft. The posterior surface of the shaft is narrow and rounded. In its middle third it is marked by a rather well-defined vertical ridge, presumably marking the attachment of the tibialis posterior muscle. Such a ridge is commonly present in cercopithecid tibiae, but we have not found it in any of the modern gibbons. The whole shaft shows a very slight anterior curvature.

TABLE 13

	Total length of tibia	Diameters at mid-point	
		ant. post.	trans.
H. concolor	176	10·8	7·2
H. leuciscus	178	10·0	7·1
H. lar	169	12·2	6·0
S. syndactylus	180	10·4	7·0
S. syndactylus	177	10·6	7·4
L. macinnesi	190–200	13·8	7·8

The Fibula.—This bone is represented by a fragment of a shaft 84 mm. in length. It is straight, regularly cylindrical in form, and bears a close resemblance to the fibular shaft of a specimen of *S. chrysomelas,* in which the maximum diameter at the middle is 4·9 mm. The maximum diameter at a level which probably corresponds to the middle of the intact shaft is 4·6 mm.

In general, the long bones of the hind-limb present some interesting contrasts. For whereas the femur shows obvious resemblances to the modern gibbons, in its straight cylindrical character of the shaft, in the absence of pronounced muscular ridges and in the details of the lesser trochanter, so that, by themselves, the fossil femora would probably be referred to a hylobatine type by most comparative anatomists, the tibia, very different in several respects, approximates more closely to that of the cercopithecids. This combination of morphological characters confirms the implications of the anatomy of the fore-limb, namely, that *Limnopithecus* had not acquired the extreme arboreal specialization of the modern gibbons and that it was still capable of quadrupedal activities similar to those of the modern cercopithecid monkeys.

The Calcaneum (text-fig. 7).—An almost complete right calcaneum was among the specimens embedded in the limestone block. The bone was broken through the middle, but the two parts can be placed in perfect apposition except over the talar facet. The sustentaculum tali is missing as the result of weathering, and there is a defect in the upper surface of the heel process. The total length of the bone exceeds that of the specimens of *Hylobates* and *Syndactylus* available for examination, and approximates in some degree to cercopithecids of comparable limb size (see Table 14).

The talar facet is evenly curved in an antero-posterior direction and forms a relatively narrow oval (maximum length 11·6 mm., maximum width 7·6 mm.). In front of it the upper surface of the bone is broad and roughened. On the plantar aspect is an elongated anterior tubercle which extends back approximately to the level of the posterior border of the attached margin of the sustentaculum tali. The facet for the cuboid bone is flattened above, but hollowed out below into a circumscribed cup-shaped depression in which is a pit for a ligamentous attachment. In this character the facet presents a somewhat closer approach to the cercopithecid condition than to that of the modern gibbons in which the concavity of the facet is shallower, presumably in relation to a greater degree of mobility at the calcaneo-cuboid joint.

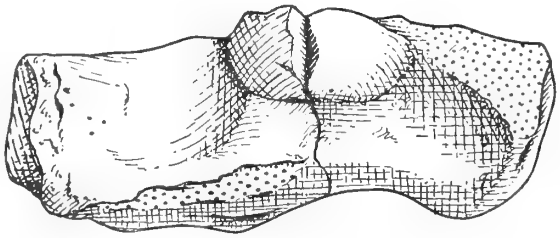

FIG. 7. The right calcaneum of *L. macinnesi* viewed from a medial and superior aspect. × 2.

TABLE 14

	Total length of calcaneum	Distance from facet to post. extremity (*a*)	Distance from facet to ant. border (*b*)	$\frac{a}{b}$
H. concolor	30·0	7·6	18·6	0·41
H. hoolock	28·6	7·6	18·2	0·42
H. lar	28·2	7·4	17·8	0·42
H. sp?	27·4	7·0	18·8	0·37
S. syndactylus	29·0	7·4	19·0	0·39
M. nemestrina	40·0	13·0	23·2	0·56
M. pileata	44·0	13·2	24·8	0·53
R. roxellanae	43·8	13·2	26·0	0·51
C. satanas	39·6	11·0	23·2	0·47
A. geoffroyi	37·4	11·0	25·0	0·44
A. paniscus	40·2	10·8	24·2	0·45
L. macinnesi	34·9	9·4	23·6	0·40

To determine the relative length of the heel process, measurements were taken from the posterior border of the talar facet to the posterior surface of the heel process and to the anterior extremity of the bone in the fossil as well as in a number of Recent species, and the ratio between the two calculated. The results in Table 14 show that, in the relative shortness of the post-talar part of the bone, the calcaneum of *L. macinnesi* approximates to the modern gibbons rather than the cercopithecids.

The Talus.—The talar fragment consists of the greater part of the body which, however, is considerably weathered. The head and neck are missing. The bone is from the right side and probably belongs to the same individual as the calcaneum. This probability is increased by the approximate correspondence of the dimensions of the main calcaneal facet (maximum length 11·6 mm., maximum width 6 mm.) with those of the talar facet on the calcaneum.

The superior facet is evenly concave from side to side and relatively shallow. The lateral and medial margins are of approximately equal height, in which it resembles the modern gibbons rather than the cercopithecids, for in the latter the lateral margin is characteristically much more prominent than the medial. In the cercopithecids, also, the concavity of the superior facet is usually deeper. Since the anterior part of the lateral margin of the superior facet is missing, and the whole facet has been affected by a considerable degree of weathering, it is not possible to take satisfactory measurements except for width midway between the anterior and posterior margin (10·4 mm.). The tibial malleolar facet is missing. The fibular facet is present and shows a maximum height of 8·0 mm.

During the course of the work at Songhor in 1949, Dr. Leakey found a more complete *Limnopithecus* talus (Sgr. 218), and a description of this important specimen is included here (text-fig. 8). It was discovered at a site which had also yielded many teeth of *Limnopithecus*. On the other hand, no remains of *Mesopithecus* (the only other primate known from the Miocene deposits in Kenya to which the talus could possibly be attributed) have been found in this particular area. Apart from such general considerations, however, the precise correspondence between the absolute dimensions and morphological details of this specimen and those of the talar fragment found in the limestone block on Rusinga Island leaves no doubt that it is a talus of *L. macinnesi*. The Songhor talus (which is of the left side) is complete except for some degree of erosion of the neck, the margins of the articular head, and the medial margin of the lower surface of the body. The main dimensions are as follows: Total length, 26 mm.; length of median axis of superior facet, 13·4 mm.; width of anterior margin of superior facet, 13·4 mm.; width of superior facet at the middle of its length, 9·4 mm.; width of posterior margin of superior facet, 7·4 mm.; maximum height of lateral malleolar facet, 9·6 mm.; maximum length of the main calcaneal facet, 12·0 mm. (est.); maximum width of main calcaneal facet, 7·4 mm. (est.). The most

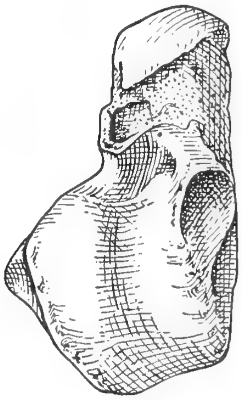

FIG. 8. Dorsal view of the left talus of *L. macinnesi* (Sgr. 218, '49), × 2. The eroded area on the neck and articular head of the bone is indicated by stippling. Note particularly the cup-shaped hollow in the anterior part of the medial malleolar facet, and the well-developed "dorsal tubercle" on the dorsal aspect of the neck of the bone.

striking features of the bone are the relative length of the neck, the presence of a cup-shaped hollow at the anterior end of the medial malleolar facet, and the strong development of the dorsal tubercle of the neck. In the last two characters particularly, the talus of *Limnopithecus* contrasts strongly with that of Recent Hylobatinae and resembles the cercopithecid talus. The significance of the cup-shaped hollow of the medial malleolar facet and the dorsal tubercle has been discussed elsewhere (Le Gros Clark & Leakey, 1951); they are evidently related to a "locking" action of the ankle joint in extreme dorsi-flexion, which permits of rapid springing movements from this position. Other noteworthy features of the *Limnopithecus* talus are a narrow and well-defined sinus tarsi, and the presence of two deep circumscribed fossae for ligamentous attachments. One fossa, presumably for the attachment of a strong talo-fibular ligament, is situated close to the posterior margin of the lateral malleolar facet, and the other, presumably for a strong talo-calcaneal ligament, is placed on the infero-lateral aspect of the neck immediately behind the articular head. These fossae are only weakly developed in the talus of modern gibbons. On the other hand, they are striking features of the cercopithecid talus. They appear to indicate a firmly knit ligamentous mechanism such as would be required to resist the strains associated with the active quadrupedal mode of progression characteristic of the Cercopithecidae in general.

The talus and calcaneum of *L. macinnesi* clearly provide information of considerable interest. Whereas in certain features, the contour of the superior facet of the talus and the relative shortness of the heel process of the calcaneum, for example, they appear to be somewhat hylobatine in type, both bones show a preponderating resemblance to the corresponding tarsal bones of the Cercopithecidae in their morphological details. The evidence which they provide is thus entirely confirmatory of the functional implications of the rest of the limb skeleton—that is, that *Limnopithecus* was not specialized for a brachiating mode of life as are the modern gibbons, but was adapted for the more primitive quadrupedal habits still retained by the modern cercopithecid monkeys.

Other skeletal fragments.—Associated with the limb bones in the limestone block, there were a number of small fragments of the skeleton too incomplete to yield data of any significance. These fragments include pieces of a rib, a badly damaged portion of a humeral shaft, part of a fibula, a small length of a metacarpal bone, and a few fragments of (possibly) a clavicle.

Conclusions

The discovery of teeth and jaws of *Limnopithecus macinnesi* in direct association with limb bones is of outstanding importance. It has provided the first information on the limb character and proportions of one member of a group of early hylobatine apes hitherto known only from their dentition and jaws. This group comprises the genera *Propliopithecus*, *Limnopithecus*, and *Pliopithecus*.* On the basis of dental

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* Since the manuscript of this paper was completed, our attention was drawn by Professor G. von Koenigswald to a report by C. Depéret in 1887 (*Arch. Mus. Hist. Nat. Lyon*, **4**: 45) on fossil material from middle Miocene deposits of the Rhone basin. In this report, Depéret described a first metacarpal

morphology the three genera, though not of the same geological age, appear to show rather close affinities, and it is primarily on the criteria of the dentition that they have been assigned to the subfamily Hylobatinae which includes the modern gibbons. It is particularly interesting to note, therefore, that this conclusion is consistent with a number of features of the limb bones of *Limnopithecus*, in which they resemble the bones of *Hylobates* and *Symphalangus*.

When the limb bones of *L. macinnesi* are compared with those of Recent catarrhine primates, the resemblances to the gibbon are obvious. They are to be seen mainly in the straight, slender, and cylindrical character of the shafts of the long-bones (particularly the humerus and femur), and the lack of strong muscular markings. They are also evident in some of the structural details such as those of the lower extremity of the humerus, the neck of the radius, the lesser trochanter of the femur, and the upper articular surface of the talus. With these characters are combined others which presumably reflect a more primitive phase of the evolution of the limbs associated with a quadrupedal type of activity. Thus, the limb proportions approximate more to those of the Cercopithecidae, as do also structural details such as the orientation of the head of the humerus, the well-developed supinator ridge, the slant of the radial head, the upward prolongation of the olecranon process and the contour of the articular surface of the upper end of the ulna, the facet on the calcaneum for the cuboid, and so forth.

The remarkable combination of anatomical characters presented by the limb bones of *Limnopithecus* makes it certain that the limb proportions were very different from those of the modern gibbons, and that this Miocene genus had not developed the arboreal specializations so characteristic of *Symphalangus* and *Hylobates*. In other words, *Limnopithecus* was not a brachiating animal like the modern gibbons. Though it may well have been arboreal in its habits, its activities were presumably much more akin to those of some of the modern cercopithecid monkeys.

The striking resemblance between some of the details of the fossil limb bones and those of *Ateles* is particularly interesting, for it is well recognized that the spider monkey of the New World shows certain structural modifications which parallel the line of development followed by the gibbons of the Old World. Thus if, as now appears, *Limnopithecus* is to be regarded as a gibbon "in the making", it is not surprising that it should display these resemblances to the spider monkey. On the other hand, it shows a significant difference from *Ateles* in the orientation of the head of the humerus, wherein it approximates more closely to the relatively more generalized cercopithecid skeleton.

The anatomical characters of *Limnopithecus*, both of the dentition and of the limb bones, appear to be quite consistent with theoretical postulates for representatives of the Hylobatinae at a period so far back as the early Miocene. It is generally agreed that the hylobatine sequence of evolution was initially derived from a generalized

bone found in association with a mandibular fragment of *Pliopithecus antiquus*. He was evidently puzzled by his observations that, although no other remains of apes or monkeys had been found at the site, the bone resembled in its proportions that of *Macaca* or *Semnopithecus* rather than the metacarpal bone of a gibbon. He concluded that, if the bone really belonged to *Pliopithecus*, " il faudrait admettre l'existence à l'époque du Miocène moyen, d'un Singe ayant les mains de Semnopithèque ou de Macaque avec les molaires de Gibbon." A similar comment might be made in reference to the general implications of the limb skeleton of *Limnopithecus macinnesi*.

catarrhine stock which also gave rise to the cercopithecoid sequence. One would expect therefore that the earliest representatives of the hylobatine sequence would present primitive limb characters corresponding to those still retained by the modern catarrhine monkeys, and that in the course of later adaptation to brachiating habits they would become highly specialized. There is also evidence which indicates that the cercopithecoid and hominoid sequences began to separate probably during the Oligocene period, and that by the early Miocene they had become clearly segregated. However, the early Miocene genus *Limnopithecus* still retained a number of primitive dental features not found in the modern Hylobatinae, and it now appears that the limb skeleton was also more primitive than that of the Recent species.

The discovery of early transitional forms such as *Limnopithecus* inevitably raises problems of taxonomic definition. It may even be suggested that, since the term "anthropoid ape" is commonly assumed to refer to catarrhine primates with the specialized proportions of the limbs which have been developed in the modern apes, it is not appropriate to call *Limnopithecus* an anthropoid ape. But such an argument might also be applied to *Proconsul,* and perhaps to Miocene and Pliocene genera such as *Dryopithecus* and *Sivapithecus*. However, it has now been established on the criteria of dental morphology that the catarrhine primates had become sharply differentiated into two groups by the early Miocene, one group characterized by a dentition of somewhat specialized type corresponding to that of the Cercopithecoidea, and the other showing dental characters which are morphologically quite similar to those of the modern anthropoid apes. The second group includes the genus *Limnopithecus* and, even though it is now evident that the limb characters of *Limnopithecus* still retained primitive features corresponding to a cercopithecoid level of evolution, this does not seem to us to provide adequate grounds for excluding it from the family Pongidae, and therefore from the category of anthropoid apes. If the factor of evolutionary development is given due consideration in the taxonomic definition of the Pongidae, the latter must surely be taken to refer not only to the terminal products of their evolution, that is, the modern anthropoid apes, but to all those intermediate forms which have come into existence since the anthropoid ape sequence first became segregated from the common stock which also gave rise to the Cercopithecoidea. In some of their anatomical characters, the earlier representatives of the anthropoid ape sequence may well have resembled the modern cercopithecid monkeys more closely than the modern anthropoid apes. This was certainly true of *Limnopithecus,* but at the same time this genus had already developed features of the dentition and of the limb skeleton which clearly indicate that it represents an early phase in the course of evolutionary development that finally culminated in the hylobatine members of the modern anthropoid apes. It may therefore legitimately be termed a primitive gibbon.

ACKNOWLEDGMENTS

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REFERENCES

EVANS, F. G. & KRAHL, V. E. 1945. The Torsion of the Humerus. A Phylogenetic Survey from Fish to Man. *Amer. J. Anat.*, Baltimore, **76**: 303–337.

HOPWOOD, A. T. 1933. Miocene Primates from Kenya. *J. Linn. Soc. Zool.*, London, **38**: 437–464.

LE GROS CLARK, W. E. & LEAKEY, L. S. B. 1951. *Fossil Mammals of Africa*, **1**. *The Miocene Hominoidea of East Africa*, 117 pp., 9 pls. Brit. Mus. (Nat. Hist.), London.

MACINNES, D. G. 1943. Notes on the East African Miocene Primates. *J. E. Afr. Ug. Nat. Hist. Soc.*, **17**: 141–181.

MOLLISON, T. 1911. Die Körperproportionen der Primaten. *Morph. Jb.*, Leipzig, **42**: 79–304.

SCHULTZ, A. H. 1930. The Skeleton of the Trunk and Limbs of the Higher Primates. *Hum. Biol.*, Baltimore, **2**: 303–438.

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EXPLANATION OF PLATES

PLATE 1

EXPLANATION OF PLATE 1

FIG. 1. Photograph of the limb bones of *L. macinnesi* showing their position while still partly embedded in the block of red limestone. Below is the humerus, and immediately above it the shaft of a femur of a young individual. Above this, again, is a radius and (parallel to it and still further up) the shaft of another femur. To the right, sloping obliquely downwards, are the shafts of a tibia and a third femur. × $\frac{1}{3}$ approx.

,, 2. The palatal aspect of specimen R.374 G1. The incisor teeth are missing. The palatal suture has been outlined in order to make it apparent. × 2 approx.

,, 3. Specimen R.374 G1 viewed from the left side. × 2 approx.

,, 4. Specimen R.374 G2 viewed (a) from the lateral aspect and (b) from above. The medial half of M $\overline{3}$ is missing. × 2 approx.

,, 5. The second (a) and third (b) right lower molar teeth of specimen R.374 E, viewed from the occlusal aspect. The third molar in this specimen was unerupted and still embedded in the alveolus. Note the strong development of the anterior and posterior foveae, and the rudimentary external cingulum. × 3.

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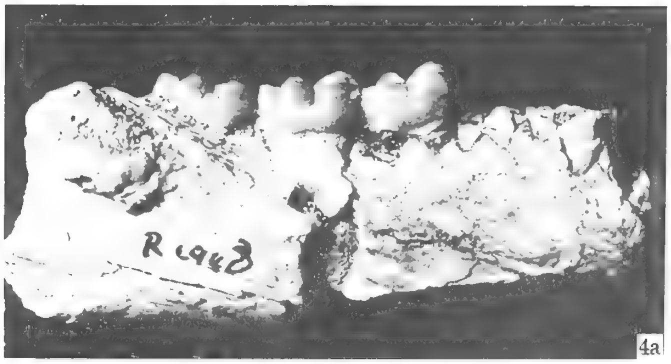

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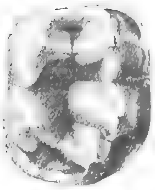

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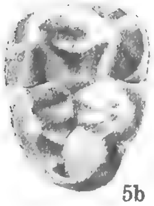

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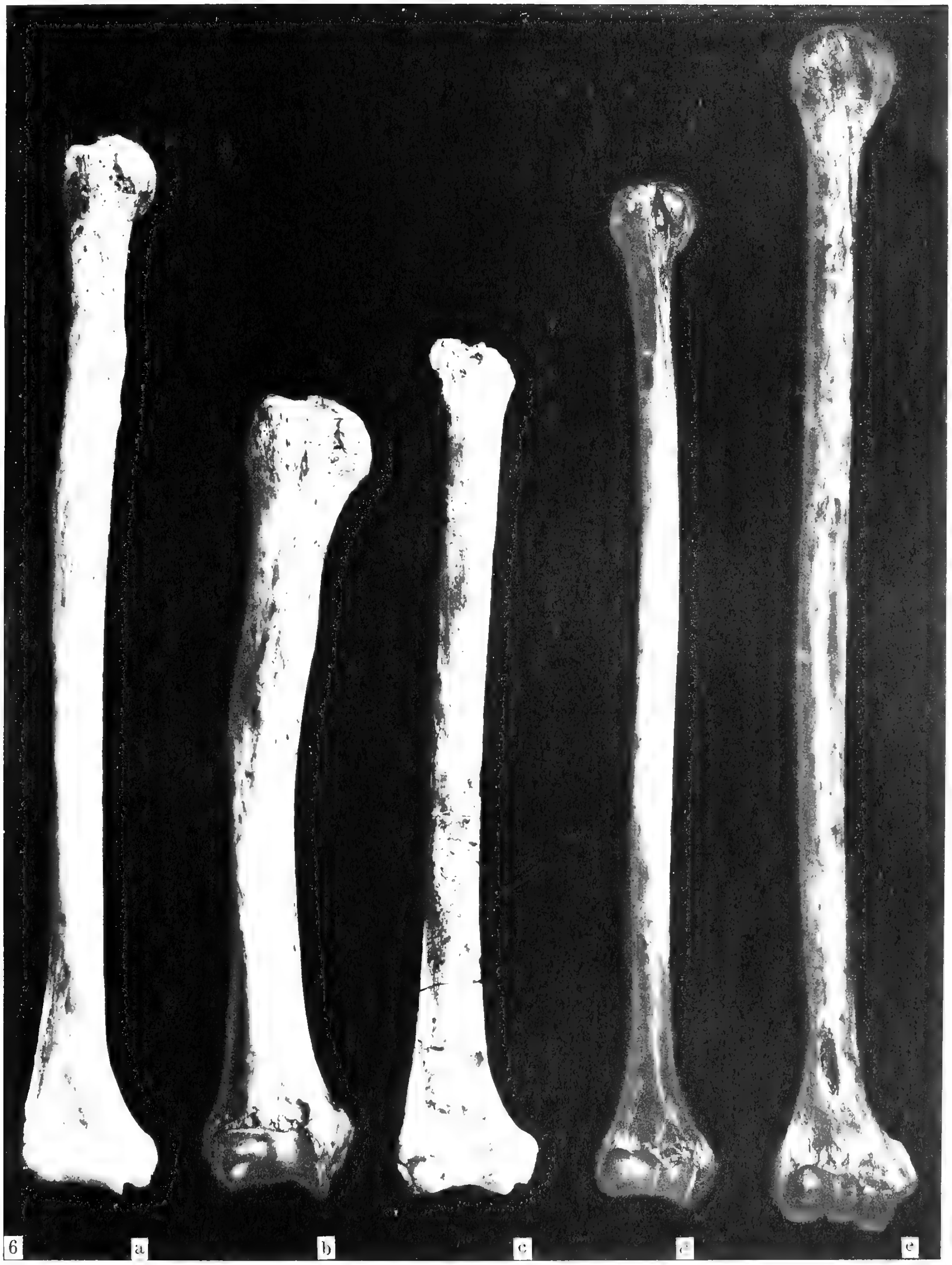
4b

LIMNOPITHECUS MACINNESI

PLATE 2

EXPLANATION OF PLATE 2

Fig. 6. The anterior aspect of the humerus of (a) *Ateles paniscus*, (b) *Macaca nemestrina*, (c) *Limnopithecus macinnesi*, (d) *Hylobates leuciscus*, and (e) *Symphalangus syndactylus*. × 0·7.

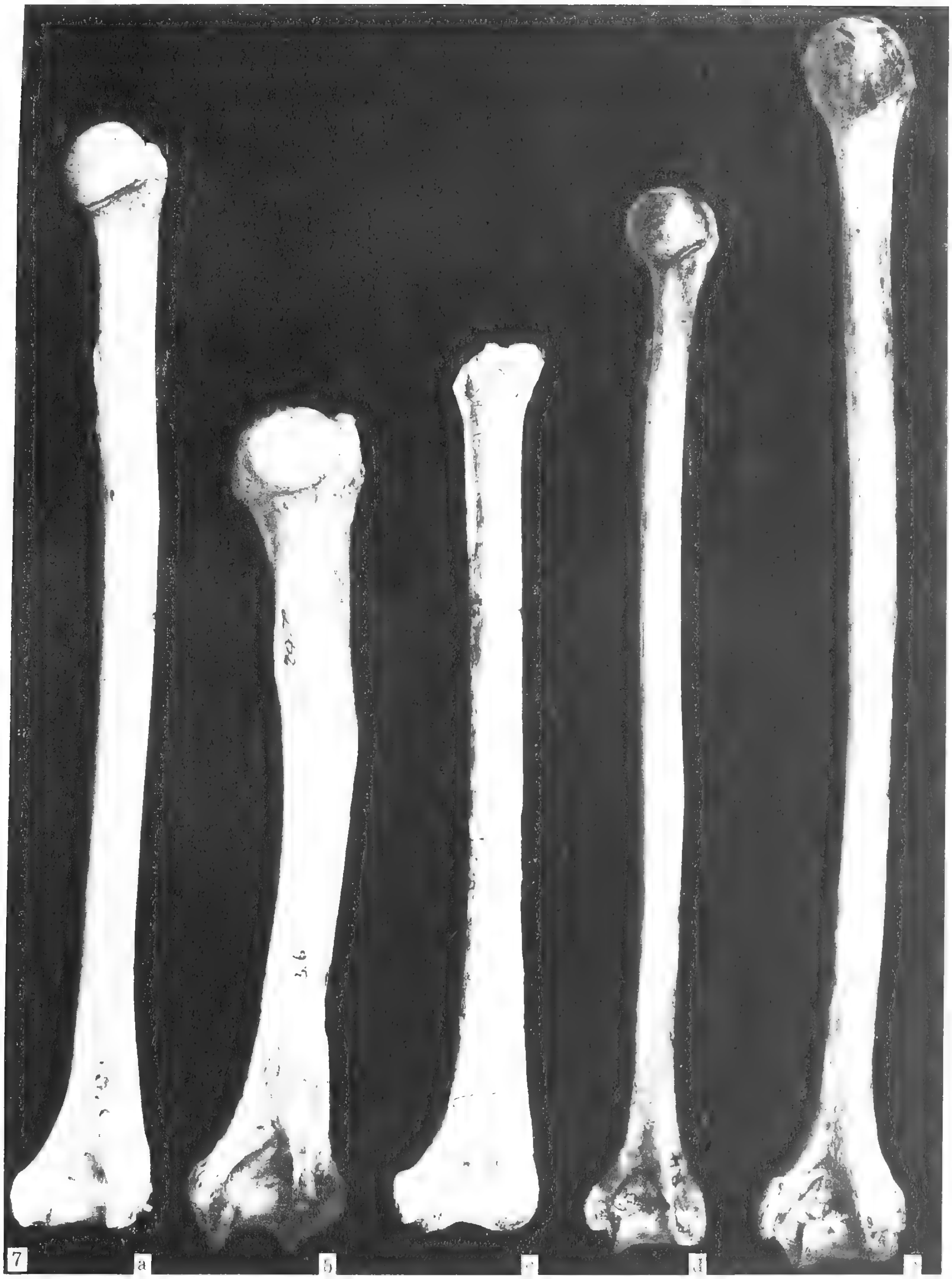


HUMERUS (Various genera: anterior aspect)

PLATE 3

EXPLANATION OF PLATE 3

Fig. 7. The posterior aspect of the humeri shown in Pl. **2**, fig. 6. × 0·7.



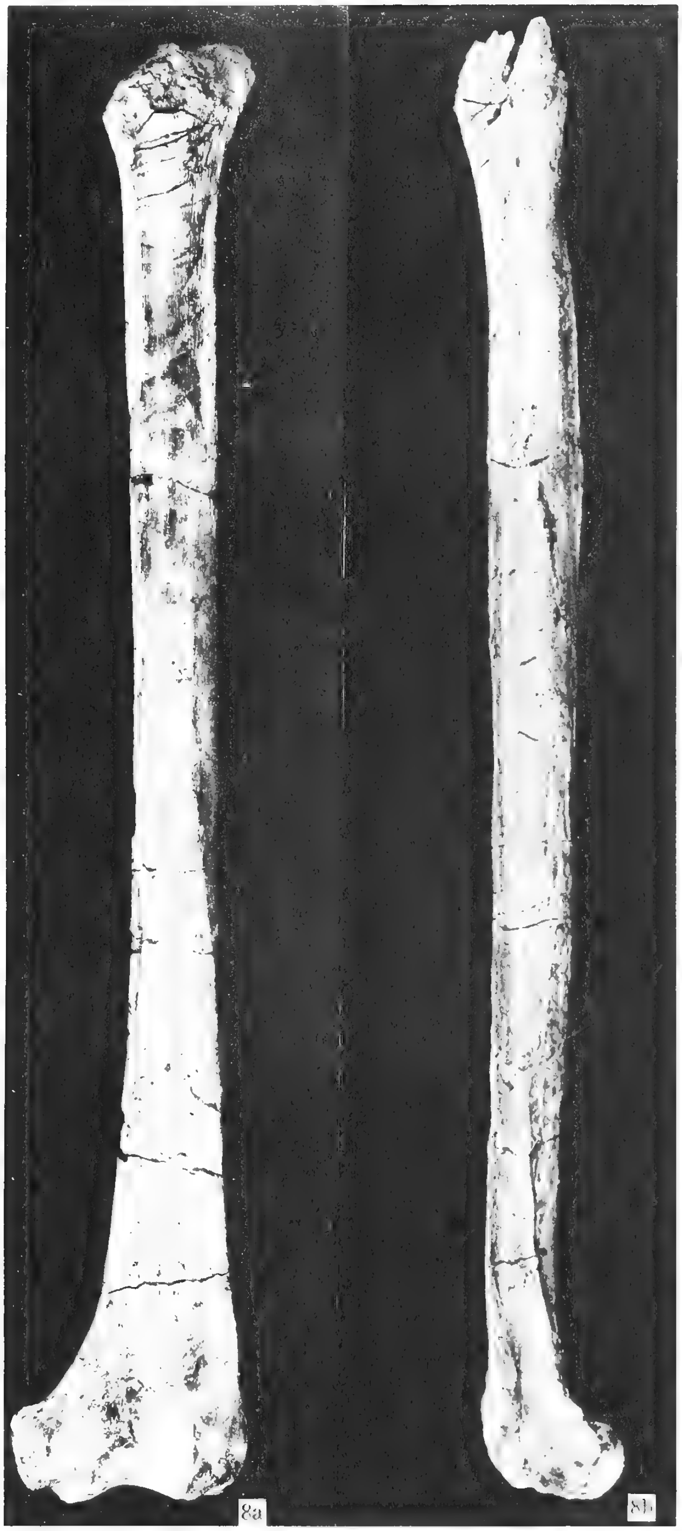
HUMERUS (Various genera: posterior aspect)

PLATE 4

EXPLANATION OF PLATE 4

FIG. 8. The humerus of *L. macinnesi* seen from behind (a) and from the lateral aspect (b). × 1.

,, 9. The medial aspect of the right radius and the lateral aspect of the right ulna of *L. macinnesi.* × 0·9.



LIMNOPITHECUS MACINNESI

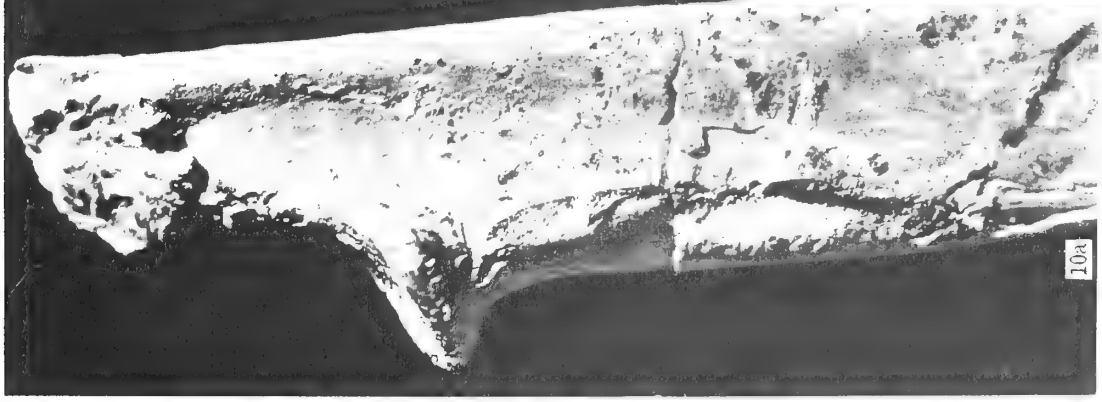
PLATE 5

EXPLANATION OF PLATE 5

FIG. 10. The upper end of the right ulna of *L. macinnesi* viewed from the medial aspect (a) and from in front (b). × 3 approx.

„ 11. The upper end of the right radius of *L. macinnesi* viewed from the postero-medial aspect. × 3·1.

„ 12. The anterior aspect of the lower extremity of the humerus of *L. macinnesi* enlarged to show details. × 2·6.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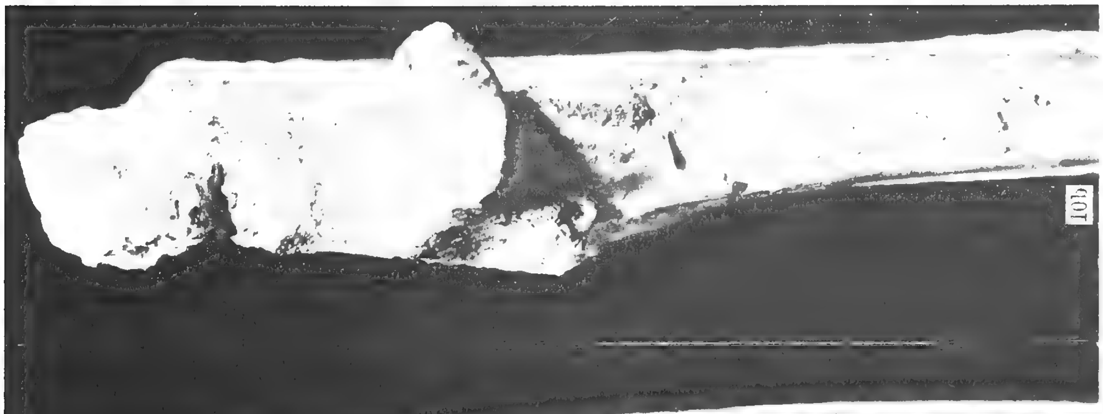
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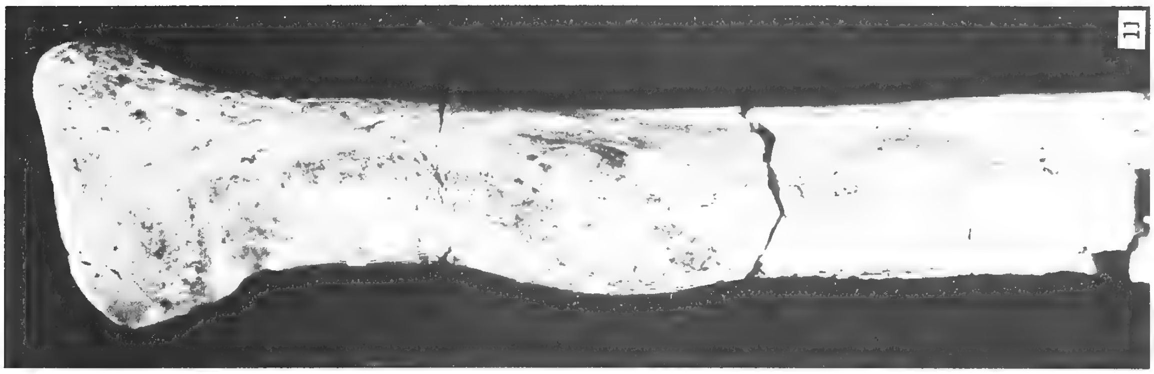
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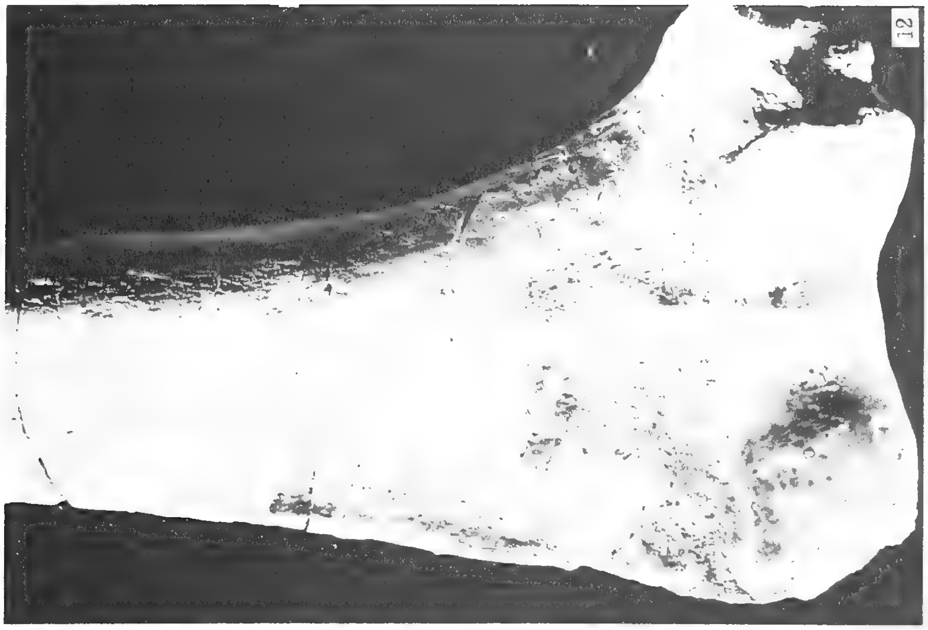
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LIMNOPITHECUS MACINNESI

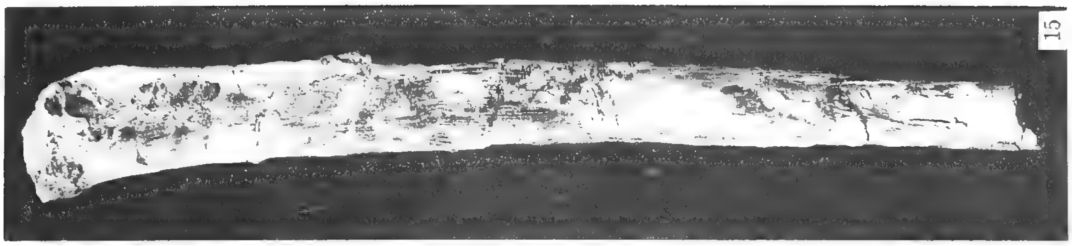
PLATE 6

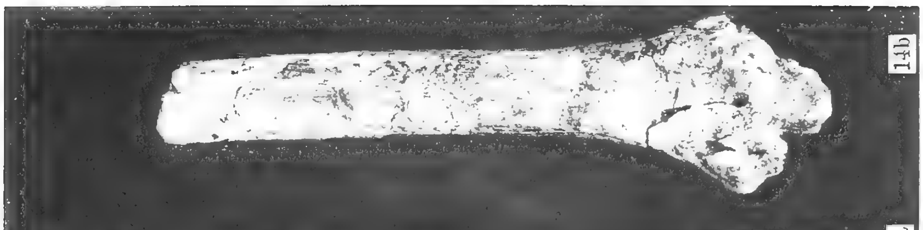
EXPLANATION OF PLATE **6**

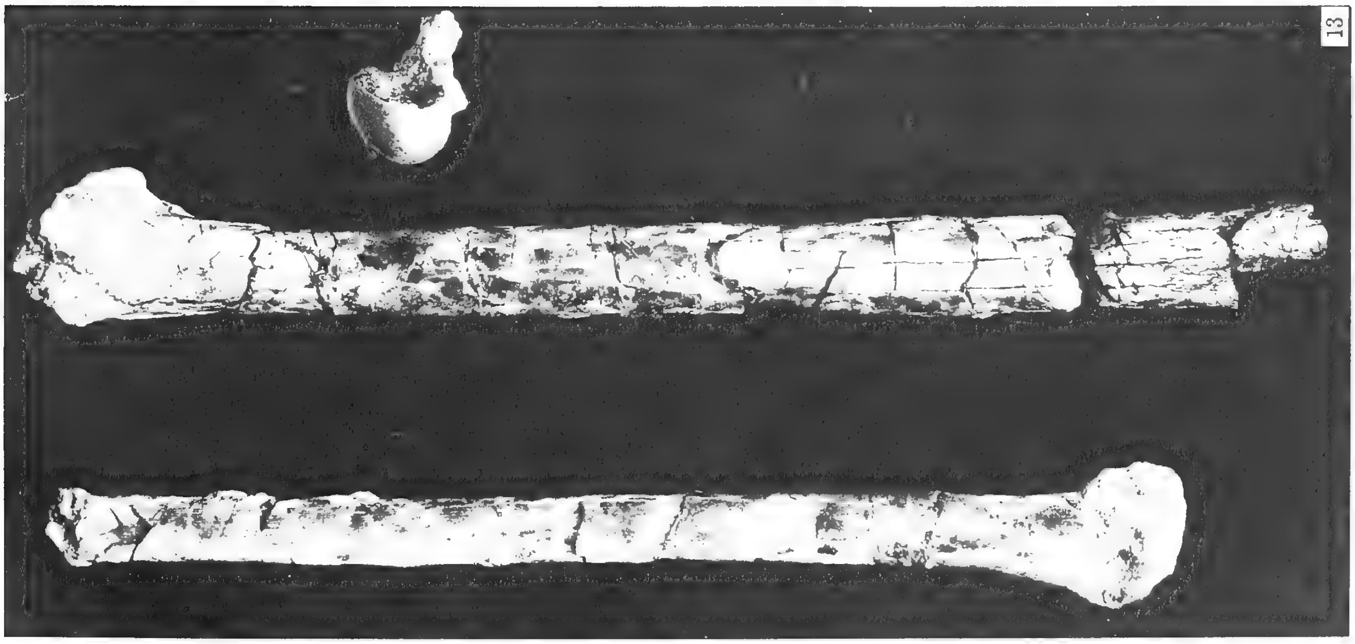
FIG. 13. The shafts of two femora of *L. macinnesi*, (a) specimen 4 and (b) specimen 1, viewed from in front. The isolated femoral head is also shown. × 1.

,, 14. The lower ends of the shafts of two femora of *L. macinnesi*, (a) specimen 2 and (b) specimen 3, viewed from behind. × 1.

,, 15. The right tibia of *L. macinnesi* viewed from the lateral aspect. × 0·8.







LIMNOPITHECUS MACINNESI