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An osteometric study of the hind limb of the Galagidae

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INTRODUCTION

Among the Lorisoidea are found two distinct modes of progression, the slow cautious hand over hand climbing movements of the lorises (Hill, 1953) and the saltatory gait of the galagos. However, despite the fact that the gait of galagos was known to Geoffroy (1796) who first described the species, Murie & Mivart (1872) appear to have been unaware of it when they read their paper 'On the Anatomy of the Lemuroidea' to the Zoological Society in 1886. In this paper they note that 'certain genera (e.g. *Galago* and *Tarsius*) present an elongation of the tarsal part of the leg which is altogether peculiar' and make no further comment on the significance of this fact. But in a footnote to the published version they record that the existence of this elongation seemed an inexplicable puzzle until they received a letter from A. D. Bartlett the then Superintendent of the Society's Gardens. In this letter Bartlett described a Garnett's *Galago* as 'jumping about upright like a kangaroo'. In a subsequent paper Mivart (1873) gives comparative osteometric data from the Lemuroidea which clearly demonstrate this tarsal elongation among the Galagidae.

Morton (1924) in his work on the evolution of the human foot makes a more functional appreciation of the primate foot. He introduces the terms 'tarsi-fulcrumating' and 'metatarsi-fulcrumating'. He associates 'tarsi-fulcrumation' with arboreal creatures having a foot that is required to maintain a firm grasp and infers that any lengthening of the foot, as in *Galago* and *Tarsius*, will appear in the anterior tarsal segment. In terrestrial jumpers such as the kangaroo and jerboa the the lengthening occurs in the metatarsal segment and both the pentadactyl form and the ability to grasp are lost in the pes.

Both Nayak (1933) and Le Gros Clark (1959) consider that the elongation of the tarsus found in *Galago* is a specialization that can be correlated with its saltatory gait. Nayak (1933) also notes that the shortness of the fore-limbs makes *Galago* a poor walker or runner. Hill (1953) says that, in leaping, the Galagidae use their elongated hind limbs to obtain the initial momentum.

While it seems, from these observations, that there is an association of an elongated tarsus and hind limb with the ability of *Galago* to jump, no clear picture of the reason why these features may be of advantage emerges. This paper sets out to explore osteometrically the relationships of the different segments of the hind limb in the Galagidae and, in view of Hill's (1953) assumption that this limb is elongated, to decide whether it is in fact relatively longer than those of comparable primates. An attempt is also made to assess what role the relationships found may have in the mechanism of the gait of *Galago*. Comparisons are made possible with the slow moving *Loris* and *Perodicticus* from the Lorisidae and with another saltatory primate, *Tarsius*.

MATERIAL AND METHODS

A list of the skeletons studied and the sources from which they were obtained is given in Table 1.

Table. 1. *Source and number of skeletons examined*

Specimen	Number	Source
Galagoides demidovii	2	B.M.
Galago senegalensis	8	B.M., M.C.
Galago crassicaudatus	11	M.C., C.M.
Euoticus elegantulus	5	B.M.
Perodicticus potto	7	B.M., M.C., C.M., U.C.L.
Loris tardigradus	4	B.M.
Tarsius spectrum	4	B.M., R.F., U.C.L., B.C.

B.M. = British Museum; M.C. = Makerere University College; C.M. = Coryndon Museum, Nairobi; R.F. = Royal Free Hospital School of Medicine; U.C.L. = University College London; B.C. = Bedford College for Women.

From each skeleton the humerus and radius of one fore-limb and the femur, tibia, calcaneus and cuboid of one hind limb were studied. As some of the skeletons were incomplete this procedure allowed the greatest number of individuals to be compared from the material available. In all bones used the proximal and distal epiphyses had fused to the shaft. The maximum lengths of the bones were recorded since these were the easiest, and most accurate to determine on the small bones involved.

The majority of the measurements were obtained by the use of a miniature osteometric board specially constructed for the purpose. This was similar in operation to the normal instrument but was accurately machined from brass and incorporated a machine engraved rule. However, some measurements had to be made with sliding calipers, as the skeletons were articulated and mounted, or were ligamentous. The dimensions recorded in this manner were therefore not strictly speaking maximum lengths but maximum measureable lengths. All measurements were made to the nearest 0·05 cm.

The maximum length of the calcaneus and cuboid when articulated was also recorded and in addition a measurement was taken, with the sliding calipers, from the anterior surface of the calcaneous to the point where the lateral calcaneal articular facet for the talus met the dorsal surface of the bone (distance C, Text-fig. 1). It had been found that this was a well-defined point on the calcaneus, which consistently indicated a vertical projection on to this bone of the axis of the ankle joint. The last two measurements were required in order to obtain the lengths of the anterior and posterior tarsal segments.

The intermembral index was calculated taking the sum of the maximum lengths of the humerus and radius as a percentage of the sum of the maximum lengths of the femur and tibia. A similar index was also calculated in which the length of the anterior tarsal segment was added to the maximum lengths of the femur and tibia.

An index based on lower limb length and body length was used. In this case it was not possible to compare the measured limb lengths with the body lengths of the

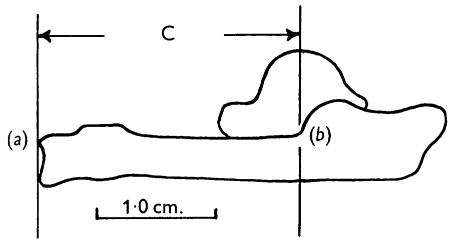
Table 2. *The means and the ranges of the indices calculated*

Specimen	Intermembral index	Intermembral index with ant. tarsal segment included	Lower limb: body length index	Ant. tarsal segment: lower limb length index	Foot-lever index
Galagoides	65·2 (2) (64·5–65·8)	52·5 (2) (51·8–53·1)	—	24·2 (2) (23·9–24·5)	20·0 (2) (18·9–21·1)
Galago senegalensis	51·9 (8) (47·0–60·6) S.D. = ±3·85, S.E. = ±1·36	43·2 (8) (39·0–50·0) S.D. = ±3·06, S.E. = ±1·08	79·3	20·1 (8) (18·7–21·2) S.D. = ±0·75, S.E. = ±0·26	32·9 (8) (29·3–36·5) S.D. = ±2·36, S.E. = ±0·84
Galago crassicaudatus	66·5 (11) (64·7–71·8) S.D. = ±2·10, S.E. = ±0·63	56·4 (11) (55·0–60·2) S.D. = ±1·67, S.E. = ±0·50	—	17·9 (11) (17·2–19·2) S.D. = ±0·86, S.E. = ±0·26	36·2 (11) (33·9–40·4) S.D. = ±2·02, S.E. = ±0·61
Euoticus elegantulus	62·7 (5) (62·2–63·7) S.D. = ±0·56, S.E. = ±0·25	54·5 (5) (53·9–55·7) S.D. = ±0·73, S.E. = ±0·32	62·4	15·1 (5) (14·4–15·7) S.D. = ±0·56, S.E. = ±0·25	39·6 (5) (38·1–41·5) S.D. = ±1·25, S.E. = ±0·56
Loris tardigradus	90·7 (4) (86·4–94·4) S.D. = ±3·29, S.E. = ±1·65	—	70·5	—	—
Perodicticus potto	87·3 (7) (85·3–88·2) S.D. = ±1·07, S.E. = ±0·40	82·2 (5) (81·4–83·4) S.D. = ±0·80, S.E. = ±0·36	54·0	7·05 (5) (6·23–8·08) S.D. = ±0·65, S.E. = ±0·29	79·6 (5) (72·7–90·5) S.D. = ±7·48, S.E. = ±3·35
Tarsius spectrum	52·9 (3) (52·7–53·1) S.D. = ±0·14, S.E. = ±0·08	44·3 (3) (44·2–44·4) S.D. = ±0·04, S.E. = ±0·02	102·1	19·3 (4) (19·1–19·5) S.D. = ±0·15, S.E. = ±0·07	25·7 (4) (24·0–27·7) S.D. = ±1·91, S.E. = ±0·95

same specimens. Instead, the mean of the figures obtained for the sum of the maximum lengths of the femur and tibia were expressed as a percentage of figures for body weights of the appropriate species obtained from other sources. That used for *Galago senegalensis* was obtained from seventeen of the author's specimens. Those given by Hill (1953, 1955) were used in the case of other species.

The anterior tarsal segment was taken as a percentage of the sum of the maximum lengths of the femur and tibia to give an anterior tarsal segment: lower limb length index.

Lastly, by expressing the posterior tarsal segment as a percentage of the anterior tarsal segment an index named the foot-level index was calculated. The indices



Text-fig. 1. A tracing of the talus and calcaneus of *Galago crassicaudatus* showing the distance C measured between the distal end of the calcaneus (*a*) and the point where the lateral facet on the calcaneus meets the dorsal surface of the body (*b*).

involving the anterior tarsal segment were not calculated for *Loris* owing to the specialized nature of the calcaneus in this genus.

RESULTS

The means of the indices calculated are shown in Table 2. The figure in brackets which follows the mean indicates the number of specimens for which the index was calculated and this is followed by the range of the values obtained.

DISCUSSION

A comparison can be made between the limb lengths of different species only by relating them to some other dimension common to both. It must be borne in mind, however, that this dimension may in turn be influenced by factors which differ in each species. The intermembral index, which relates fore-limb to hind-limb length, shows that among the Galagidae there exists a gross disproportion between these lengths which is most pronounced in *Galago senegalensis*. Here, as in *Tarsius*, the hind limb is seen to be nearly twice as long as the fore-limb. In the slow-moving *Loris* and *Perodicticus*, however, the limbs are shown to be almost equal in length. Because it has been shown by photographic methods (Hall-Craggs, 1964) that in the jump of *Galago senegalensis* the length of the anterior tarsal segment is added to the functional length of the hind limb (Pl. 1, figs. 1 and 2), the intermembral index has also been calculated with the length of this segment included in the lower limb length. While this index shows a relatively small change in *Perodicticus* it is markedly reduced in the saltatory animals. Despite this the possibility that much of the disproportion is due to an excessive shortness of the fore-limbs cannot be excluded.

Perhaps a better indication of limb length is given by the lower limb length: body length index. Although the data on which it is based is not altogether satisfactory, the fact that the index for *Loris* lies between those for *Galago senegalensis* and *Euoticus elegantulus* suggests that a hind limb that is long relative to body length is not necessarily to be associated with jumping or speed of movement. The explanation may lie in the use which is made of this length. Gray (1953) points out that it is the ability to extend the limb to a greater length that is advantageous in jumping, Long legs in themselves are of no value. It is the distance moved in the direction of the jump by the top of the limb while the foot is in contact with the ground that is important, for, in a bi-pedal jump, the acceleration required to make a jump of a given height varies inversely with this distance. That *Galago senegalensis* makes full use of the length of its hind limb has also been demonstrated photographically. Prior to jumping the limb is acutely flexed at hip, knee and ankle joints but at the moment of take-off the body, thigh, leg and foot lie almost in a straight line (Pl. 1. fig. 2).

The anterior tarsal segment: lower limb length index shows that the anterior tarsal segment of the Galagidae and *Tarsius* is long relative to the lower limb length when compared with that of *Perodicticus*. The foot-lever index again clearly separates these two groups and shows that the lengthening of the anterior tarsal segment is not accompanied by a proportionate increase in the length of the posterior tarsal segment. Not only is the index low among the jumpers but its value tends to decrease within this group as the ability to jump increases. Schultz (1963) in a study of the primate foot has devised a 'power arm: load arm' index in which the length of the third metatarsal is included in the length of the load arm. This index has been applied to tarsi-fulcrumating and metatarsi-fulcrumating types alike, thus obscuring the very considerable differences between the true load arms in *Galago* and *Perodicticus*. The fall demonstrated in the foot-lever index indicates a worsening of the mechanical advantage of the plantar-flexors of the ankle joint and this would seem, at first sight, to have no obvious advantage to a saltatory animal. It seems likely that it is in the physiological properties of the muscle that the reason for this apparent anomaly is to be found.

The optimum speed of a muscle is 20–30 % of the maximum speed at which it can shorten under zero load (Hill, 1956). At lower or higher speeds of shortening, efficiency and power output decrease. Force-velocity and power-velocity curves plotted for both the quadriceps femoris and triceps surae muscles (Hall-Craggs, unpublished data) have confirmed that this is so in *Galago senegalensis*. The muscle groups used for jumping are also used for performing slower movements and to maintain posture. This means that extremes of speed of shortening are required of the same muscles. Any arrangement whereby the maximum speed of shortening can be reduced will allow a more efficient compromise to be made.

The length-tension diagrams of isolated frog muscle fibres prepared by Ramsay & Street (1940) show that for this animal the additional tension developed on stimulation is maximum at the resting length of the fibre and decreases with stretch or shortening. More recently Alder, Crawford & Edwards (1958) have shown that a similar length tension relationship is found in rabbit tibialis anterior. In their experiments the tension exerted by the belly when at its minimum length in the body was only 62 % of the maximum isometric tetanic tension recorded, which in turn is exerted when the belly length is about 93 % of its maximum length in the body. These findings suggest that a reduction of the distance that a muscle is required to depart from its resting length in order to produce a full excursion of the joint at which it acts may be advantageous in that near maximum tensions may be maintained. In the case of the plantar-flexors of the foot this occurs if the velocity ratio (distance moved by effort/distance moved by load) of the lever at the ankle joint is decreased.

In the Galagidae and *Tarsius* the presence of an elongation of the tarsus that is relatively greater in the anterior than the posterior segment allows a reduction both in the range of speeds of shortening required of the plantar-flexor muscles and in the velocity ratio at the ankle joint while at the same time creating an increased functional limb length. Although these features have been shown to have possible advantages they can only be enjoyed at the expense of the mechanical advantage of the lever at the ankle joint and mean that relatively greater tensions must be developed by the muscle groups concerned. That an efficient balance is struck between these competing factors is judged by the great facility with which the Galagidae jump.

SUMMARY

1. An osteometric study has been made of the relationships of the different segments of the hind limb of the saltatory Galagidae and allied prosimian species.

2. Particular attention has been paid to the significance in jumping of leg length and leverage at the ankle joint.

3. Gross disproportion was found between the fore-limbs and hind limbs of the saltatory animals but their hind limbs were not found, in all species, to be longer relative to body length than those of more slowly moving types.

4. It is shown how the finding of an elongation of the tarsus may be advantageously related to the speed of shortening and the optimum length of the plantar-flexors of the ankle joint despite the reduction of the mechanical advantage at the joint which accompanies this elongation.

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REFERENCES

ALDER, A. B., CRAWFORD, G. N. C. & EDWARDS, R. G. (1958). The growth of the muscle tibialis anterior in the normal rabbit in relation to the tension-length ratio. *Proc. roy. Soc. B*, **148**, 207–216.

CLARK, W. E. LE GROS (1959). *The Antecedents of Man.* Edinburgh University Press.

GEOFFROY ST. HILAIRE, E. (1796). Mémoire sur les rapports naturels des *Makis Lemur*, L. et description d'une espèce nouvelle de mammifère. *Magasin encyclop.* **1**, 20–50.

RAY, J. (1953). *How Animals Move.* Cambridge University Press.

HALL-CRAGGS, E. C. B. (1964). The jump of the Bush Baby—A photographic analysis. *Med. biol. Ill.* **14**, 170–174.

HILL, A. V. (1956). The design of muscles. *Brit. med. Bull.* **12**, 165–166.
HILL, W. C. O. (1953). *Primates*, vol. I. Edinburgh University Press.
HILL, W. C. O. (1955). *Primates*, vol. II. Edinburgh University Press.
MIVART, ST. G. (1873). On *Lepilemur* and *Cheirogaleus* and on the zoological rank of the Lemuroidea. *Proc. zool. Soc. Lond.* 1873, 484–510.
MORTON, D. J. (1924). Evolution of the human foot, II. *Amer. J. phys. Anthrop.* **7**, 1–52.
MURIE, J. & MIVART, ST. G. (1872). On the anatomy of the Lemuroidea. *Trans. zool. Soc. Lond.* **7**, 1–114.
NAYAK, U. V. (1933). A comparative study of the Lorisinae and Galaginae. Ph.D. Thesis, London University.
RAMSAY, R. W. & STREET, S. F. (1940). The isometric length-tension diagram of isolated skeletal muscle fibres of the frog. *J. cell. comp. Physiol.* **15**, 11–34.
SCHULTZ, A. H. (1963). Relations between the lengths of the main parts of the foot skeleton in primates. *Folia primat.* **1**, 150–171.

EXPLANATION OF PLATE

Photographs taken at two different stages in the jump of *Galago senegalensis*.

Fig. 1. The limbs and trunk are partially extended. The tips of the digits and the metatarsal region are applied to the ground and the tarsal region has been raised off it.

Fig. 2. Just before the moment of take-off the trunk, thigh, leg and anterior tarsal segment lie almost in a straight line.

Plate 1