

LIMB PROPORTIONS IN TERRESTRIAL MAMMALS

by

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SUMMARY

A large sample of terrestrial mammals (Primates excluded) was used to investigate the relative proportions between the lengths of the long bones. In a more reduced number of species, regressions between limb length against body mass, diameters of proximal and distal bones, and metapodial lengths, were calculated. There appears a strong tendency towards isometry, in cases where lengths or diameters are compared. The limb length scales against body mass with an exponent close to that previously postulated (0.34).

Keywords : Limb bones, proportions, mammals, limb length.

INTRODUCTION

Controversies about the exact explanation of the scaling of the skeleton have produced a very important amount of literature on the relationships between diameter and length of the long bones in different groups of mammals and of each one of those parameters to body mass, namely, dogs (CASINOS *et al.* 1986), insectivores and rodents (BOU *et al.* 1987), primates (AIELLO 1981), ungulates (ALEXANDER 1977; McMAHON 1975), generality of mammals (ALEXANDER *et al.* 1979). Nevertheless, other kind of relationships have been almost untouched. For example, only AIELLO (1981) refers to the relative length of the limb bones in primates.

This paper tries to show a comprehensive view of the proportions between the length of the bones of the fore and hindlimbs (including metapodials) and among their diameters in a large sample of terrestrial mammals. In two special cases (insectivores and rodents) body masses were available and the analysis is more extensive.

Consider a strictly quadrupedal mammal. In principle, we may imagine it as an animal with a horizontal vertebral column supported by both girdles and the two

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pairs of limbs. For that kind of mammal, we formulated the following hypotheses to be tested :

- 1) In both the fore and hind legs, the proximal long bone scales against the distal long bone in an isometric way.
- 2) Any bone of the forelimb (proximal, distal or the metapodial) is directly proportional to its homologue of the hind limb.
- 3) Humerus + ulna must be directly proportional to femur + tibia.
- 4) We may suppose that stresses on midshaft of the proximal bone of each limb equal stresses on the same place in the distal bone. In this case, and taking into account that, according to ALEXANDER (1983), the bending moment on a beam is proportional to the second moment of the area, the latter being proportional to the radius, the regression between the midshaft anteroposterior diameters of both the proximal and distal bones must be isometric.

5) If animals are geometrically similar, any linear dimension must scale with the cube root of body mass. Therefore, the addition of both the long bones of a leg (humerus + ulna or femur + tibia) have to be proportional to $M^{0.33}$. Nevertheless, ALEXANDER *et al.* (1979) found an exponent value of 0.34.

In our sample, not strictly quadrupedal mammals were also included. The idea was to see in which way a particular type of locomotion could modify the results obtained with quadrupedal animals.

HOWELL (1944) carried out a similar kind of research, from a generic point of view, but his data were treated as indices and nothing about scaling can be concluded. Moreover, as AIELLO (1981) says, the use of indices is only correct when both variables comprising it change isometrically.

MATERIAL AND METHODS

The leg bone length of 396 specimens of terrestrial mammals was measured. They were from 119 different species, belonging to 13 orders. The body mass of 96 of those specimens (25 species) was known. All of them were insectivores or rodents. The anteroposterior diameter, at midshaft of the long bones, was available from 236 specimens (36 species). Finally, the length of the longest metacarpal and metatarsal in 74 specimens (31 species) was used. The species were :

O. Monotremata

F. Tachyglossidae

Tachyglossus aculeatus (SHAW and NODDER, 1792) (1)

F. Ornithorhynchidae

Ornithorhynchus anatinus (SHAW and NODDER, 1799) (1)

O. Marsupialia

F. Didelphidae

Didelphis marsupialis LINNAEUS, 1758 (1)

- F. Thylaccinidae
Thylacinus cynocephalus (HARRIS, 1808) (1)
- F. Notoryctidae
Notoryctes typhlops (STIRLING, 1889) (1)
- F. Phascolarctidae
Phascolarctos cinereus (GOLDFUSS, 1817) (1)
- F. Vombatidae
Vombatus ursinus (SHAW, 1800) (1)
- O. Edentata
 - F. Myrmecophagidae
Myrmecophaga tridactyla LINNAEUS, 1758 (1)
 - F. Bradypodidae
Bradypus tridactylus LINNAEUS, 1758 (1)
- O. Insectivora
 - F. Chrysochloridae
Chrysoxalax trevelyani (GUNTHER, 1875) (3)
Chrysochloris sp. LACÉPÈDE, 1799 (3)
 - F. Erinacidae
Erinaceus sp. LINNAEUS, 1758 (5)
 - F. Soricidae
Crocidura russula (HERMANN, 1780) (5)
Sorex araneus LINNAEUS, 1758 (5)
Sorex minutus LINNAEUS, 1766 (4)
Suncus etruscus (SAVI, 1822) (2)
 - F. Talpidae
Galemys pyrenaicus (GEOFFROY, 1811) (4)
Talpa europaea LINNAEUS, 1758 (5)
- O. Carnivora
 - F. Canidae
Canis lupus LINNAEUS, 1758 (12)
Canis lupus (familiaris) LINNAEUS, 1758 (149)
Canis mesomelas SCHREBER, 1778 (1)
Vulpes vulpes (LINNAEUS, 1758) (1)
 - F. Ursidae
Ursus americanus PALLAS, 1780 (1)
Ursus arctos LINNAEUS, 1758 (2)
 - F. Mustelidae
Mustela putorius LINNAEUS, 1758 (1)
 - F. Viverridae
Genetta genetta (LINNAEUS, 1758) (1)
 - F. Herpestidae
Ichneumia albicauda (CUVIER, 1829) (1)

- F. Hyaenidae
 - Crocuta crocuta* (ERXLEBEN, 1777) (1)
- F. Felidae
 - Acinonyx jubatus* (SCHREBER, 1776) (1)
 - Felis silvestris* SCHREBER, 1777 (1)
 - Lynx lynx* (LINNAEUS, 1758) (1)
 - Panthera leo* (LINNAEUS, 1758) (3)
 - Panthera pardus* (LINNAEUS, 1758) (1)
 - Panthera tigris* (LINNAEUS, 1758) (1)
- O. Proboscidea
 - F. Elephantidae
 - Elephas maximus* LINNAEUS, 1758 (2)
 - Loxodonta africana* (BLUMEMBACH, 1797) (3)
- O. Perissodactyla
 - F. Equidae
 - Equus caballus* LINNAEUS, 1758 (2)
 - Equus hemionus* PALLAS, 1775 (1)
 - Equus grevyi* OUSTALET, 1882 (1)
 - Equus quagga* GMELIN, 1788 (1)
 - F. Tapiridae
 - Tapirus indicus* DESMAREST, 1819 (1)
 - F. Rhinocerotidae
 - Diceros bicornis* (LINNAEUS, 1758) (1)
- O. Tubulidentata
 - F. Orycteropodidae
 - Orycteropus afer* (PALLAS, 1766) (1)
- O. Artiodactyla
 - F. Suidae
 - Phacochoerus aethiopicus* (PALLAS, 1767) (2)
 - Potamochoerus porcus* (LINNAEUS, 1758) (1)
 - Sus salvanius* (HODGSON, 1847) (1)
 - Sus scrofa* LINNAEUS, 1758 (1)
 - F. Tayassuidae
 - Tayassu tajacu* (LINNAEUS, 1758) (1)
 - F. Hippopotamidae
 - Hippopotamus amphibius* LINNAEUS, 1758 (1)
 - F. Camelidae
 - Camelus dromedarius* LINNAEUS, 1758 (1)
 - Camelus bactrianus* LINNAEUS, 1758 (1)
 - F. Cervidae
 - Alces* sp. Gray, 1821 (1)
 - Capreolus capreolus* (LINNAEUS, 1758) (1)

- Cervus dama* LINNAEUS, 1758 (1)
Cervus elaphus LINNAEUS, 1758 (1)
Rangifer tarandus (LINNAEUS, 1758) (1)

F. Giraffidae

- Giraffa camelopardalis* (LINNAEUS, 1758) (1)

F. Bovidae

- Addax nasomaculatus* (BLAINVILLE, 1816) (1)
Aepyceros melampus (LICHTENSTEIN, 1812) (1)
Antidorcas sp. SUNDEVALL, 1847 (1)
Bison bison (LINNAEUS, 1758) (1)
Bos frontalis LAMBERT, 1804 (1)
Bos javanicus D'ALTON, 1823 (1)
Boselaphus tragocamelus (PALLAS, 1766) (1)
Bubalus bubalis (LINNAEUS, 1758) (1)
Bubalus depressicornis (H. SMITH, 1827) (1)
Capra hircus (LINNAEUS, 1758) (1)
Capra ibex LINNAEUS, 1758 (1)
Connochaetes gnou (ZIMMERMANN, 1780) (2)
Connochaetes taurinus (BURCHELL, 1824) (1)
Gazella granti BROOKE, 1872 (2)
Gazella thomsoni GUNTHER, 1884 (1)
Hippotragus equinus (DESMAREST, 1804) (1)
Hippotragus niger (HARRIS, 1838) (1)
Kobus ellipsiprymus (OGILBY, 1833) (1)
Kobus kob (ERXLEBEN, 1777) (1)
Litrocanius walleri (BROOKE, 1879) (1)
Madoqua kirki (GUNTHER, 1880) (2)
Oryx dammah (CRETZSCHMAR, 1826) (1)
Oryx gazella (LINNAEUS, 1758) (1)
Ovis aries LINNAEUS, 1758 (1)
Rupicapra rupicapra (LINNAEUS, 1758) (1)
Saiga sp. GRAY, 1843 (1)
Syncerus caffer (SPARRMAN, 1779) (1)

O. Pholidota

F. Manidae

- Manis tricuspis* RAFINESQUE, 1821 (1)

O. Rodentia

F. Sciuridae

- Cynomys* sp. RAFINESQUE, 1817 (2)
Iomys horsfieldii (WATERHOUSE, 1838) (1)
Marmota marmota (LINNAEUS, 1758) (5)
Petinomis vordermanni (JENTIK, 1890) (4)
Sciurus vulgaris LINNAEUS, 1758 (2)
Spermophilopsis leptadactylus (LICHTENSTEIN, 1823) (1)

- F. Geomyidae
Geomys sp. RAFINESQUE, 1817 (1)
- F. Castoridae
Castor canadiensis KUHL, 1820 (2)
Castor fiber LINNAEUS, 1758 (2)
- F. Pedetidae
Pedetes capensis (FORSTER, 1778) (1)
- F. Cricetidae
Cricetomys gambianus WATERHOUSE, 1840 (5)
Meriones sacramenti THOMAS, 1922 (5)
Mesocricetus auratus (WATERHOUSE, 1839) (5)
- F. Spalacidae
Spalax sp. GUNDENSTAEDT, 1770 (5)
- F. Rhizomyidae
Rhizomys sp. GRAY, 1831 (2)
- F. Arvicolidae
Arvicola sapidus MILLER, 1908 (5)
Arvicola terrestris (LINNAEUS, 1758) (5)
Clethrionomys sp. TILESIIUS, 1850 (5)
Pitymys duodecimcostatus (S-LONGCHAMPS, 1839) (5)
- F. Muridae
Acomys cahirinus (DESMAREST, 1891) (1)
Apodemus sylvaticus (LINNAEUS, 1758) (1)
Mus musculus LINNAEUS, 1766 (5)
Rattus norvegicus (BERKENHOUT, 1769) (5)
Rattus rattus (LINNAEUS, 1758) (5)
- F. Gliridae
Eliomys quercinus (LINNAEUS, 1766) (5)
Myoxus glis LINNAEUS, 1766 (3)
- F. Caviidae
Cavia porcellus (LINNAEUS, 1758) (5)
Dolichotes patagonum (ZIMMERMANN, 1780) (4)
- F. Hydrochaeridae
Hydrochaeris hydrochaeris (LINNAEUS, 1766) (1)
- F. Dasyproctidae
Dasyprocta leporina (LINNAEUS, 1758) (3)
Myoprocta acouchy (ERXLEBEN, 1777) (4)
- O. Lagomorpha
- F. Leporidae
Lepus capensis LINNAEUS, 1758 (1)
Oryctolagus cuniculus (LINNAEUS, 1758) (2)

O. Macroscelida

F. Macroscelididae

Rhynchocyon chrysopygus GUNTHER, 1881 (1)

The data on insectivores and rodents and dog breeds had already been used in other researches (BOU *et al.* 1987; CASINOS *et al.* 1986). See this second paper for a detailed list of the dog breeds. The name of every species is followed by the number of specimens studied in parentheses.

Vernier callipers were used for measuring. The length was always the functional one (i.e., the distance between the middle points of the two opposite articulations). Regression coefficients were calculated by means of Model II or reduced major axis method. When comparisons with theoretical exponents were required, Student *t*-tests were used. For more details about the mathematical methodology see BOU *et al.* (1987). Separate allometric equations were calculated for the different orders, namely Marsupialia, Insectivora, Carnivora, Proboscidea, Perissodactyla, Artiodactyla and Rodentia. Moreover, for Carnivora a separate equation was calculated for the genus *Canis*, because of the large size of the sample. For Monotremata, Edentata, Tubulidentata, Pholidota and Lagomorpha, individual equations were not calculated because the minimum number of five specimens, considered indispensable for calculations, was not available. Those data were only used for calculations of general correlations of all mammals. The only big major order that was not studied was that of Primates. Results of AIELLO (1981) were considered sufficient.

According to the hypotheses assumed (see above), the following regressions were estimated: length of the humerus to length of the ulna; length of the femur to length of the tibia (in both cases the independent variable was always the proximal bone); length of the femur to length of the humerus; length of the tibia to length of the ulna; length of femur + tibia to length of humerus + ulna; length of the longest metatarsal to length of the longest metacarpian (in those cases the hindlimb bone (or bones) was the independent variable); body mass to length of humerus + ulna, and femur + tibia (body mass as independent variable); diameter of the humerus to diameter of the ulna; diameter of the femur to diameter of the tibia (the diameter of the proximal bone was taken in all cases as independent variable).

RESULTS

Results are given separately for each kind of regression.

Relative proportions between the forelimb long bones. — Separate equations were calculated for all the mammal groups quoted above and the whole sample. They are shown in Table 1. Taking into account that according to our first hypothesis the isometric condition was considered the most logical in a perfect quadrupedal mammal, the exponents of the equation were compared to the theoretical slope of 1. In three cases (Marsupialia, *Canis* sp., Artiodactyla and all mammals) the calculated exponents differ significantly from 1. The only case in

which the correlation coefficient is not really high is in the order Perissodactyla. The dispersion of values is caused by the separation between the Equidae and the other two species (*Tapirus indicus* (TI) and *Diceros bicornis* (DB)) (Fig. 1).

TABLE 1

Allometric equations for the relationship between humerus and ulna. r , correlation coefficient; n , number of specimens; D and E , mean « different » and « equal » to the theoretical exponent, respectively.

		r	n	
Marsupialia	$y = 0.66 x^{1.19}$	0.997	5	DP < 0.05
Insectivora	$y = 1.01 x^{0.89}$	0.942	36	EP > 0.05
Carnivora	$y = 1.07 x^{0.98}$	0.988	20	EP > 0.05
<i>Canis</i> sp.	$y = 0.74 x^{1.12}$	0.989	158	DP < 0.05
Proboscidea	$y = 0.40 x^{1.15}$	0.982	5	EP > 0.05
Perissodactyla	$y = 1.36 x^{0.95}$	0.678	8	EP > 0.05
Artiodactyla	$y = 0.67 x^{1.19}$	0.893	45	DP < 0.05
Rodentia	$y = 0.99 x^{1.02}$	0.984	110	EP > 0.05
Mammalia	$y = 0.98 x^{1.02}$	0.993	396	DP < 0.05

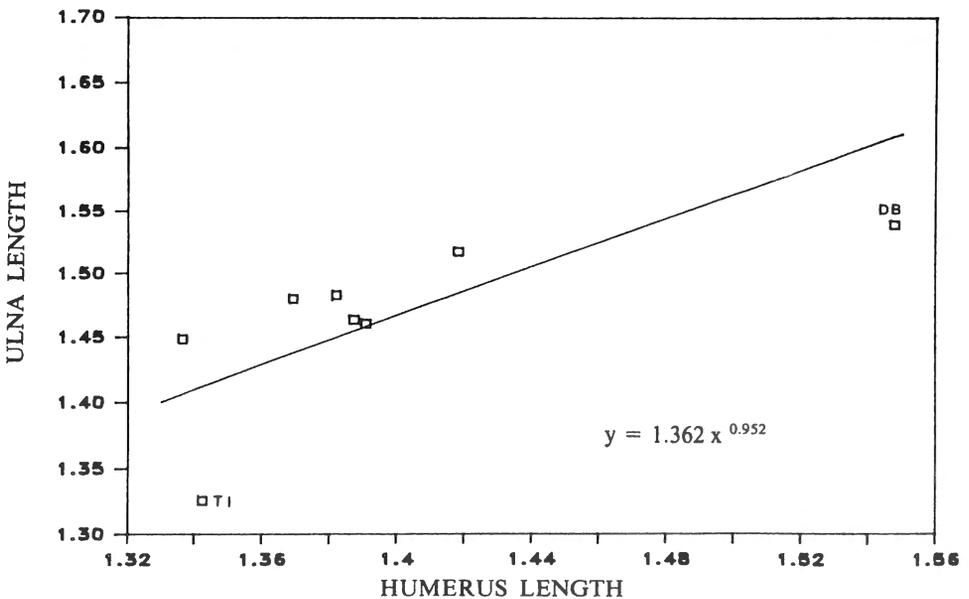


Fig. 1. — Graph of logarithmic coordinates of ulnar length against humeral length for Perissodactyla. DB, *Diceros bicornis*; TI, *Tapirus indicus*.

Relative proportions between the hindlimb long bones. — In Table 2 the equations calculated for the different groups and for the whole sample are shown. In four cases (Insectivora, Carnivora, *Canis* sp. and the general regression) the achieved slopes are different from 1. Again the Perissodactyla have the lowest correlation coefficient. Their points are distributed in a similar way to that which we have seen before.

TABLE 2

Allometric equations for the relationship between femur and tibia.
See table 1 for abbreviations.

		<i>r</i>	<i>n</i>	
Marsupialia	$y = 0.84 x^{1.02}$	0.992	5	EP > 0.05
Insectivora	$y = 1.43 x^{0.82}$	0.889	36	DP < 0.05
Carnivora	$y = 1.49 x^{0.83}$	0.986	20	DP < 0.05
<i>Canis</i> sp.	$y = 0.91 x^{1.04}$	0.991	158	DP < 0.05
Proboscidea	$y = 0.57 x^{1.01}$	0.943	5	EP > 0.05
Perissodactyla	$y = 2.97 x^{0.66}$	0.729	8	EP > 0.05
Artiodactyla	$y = 1.42 x^{0.92}$	0.925	45	EP > 0.05
Rodentia	$y = 1.14 x^{1.02}$	0.987	110	EP > 0.05
Mammalia	$y = 1.29 x^{0.91}$	0.991	396	DP < 0.05

TABLE 3

Allometric equations for the relationship between humerus and femur.
Abbreviations as in table 1.

		<i>r</i>	<i>n</i>	
Marsupialia	$y = 0.94 x^{0.94}$	0.999	5	DP < 0.05
Insectivora	$y = 0.91 x^{1.05}$	0.991	36	DP < 0.05
Carnivora	$y = 0.94 x^{0.98}$	0.998	20	EP > 0.05
<i>Canis</i> sp.	$y = 1.05 x^{0.95}$	0.994	158	DP < 0.05
Proboscidea	$y = 0.40 x^{1.16}$	0.994	5	EP > 0.05
Perissodactyla	$y = 0.45 x^{1.15}$	0.974	8	EP > 0.05
Artiodactyla	$y = 0.73 x^{1.03}$	0.975	45	EP > 0.05
Rodentia	$y = 0.87 x^{1.01}$	0.989	110	EP > 0.05
Mammalia	$y = 0.87 x^{1.00}$	0.996	396	EP > 0.05

Relative proportions between the proximal long bones. — Only three of the nine equations show slopes different from the isometric condition (Marsupialia, Insectivora and *Canis* sp.) (Table 3) although in the first two cases the results of the Student-t tests are in the limit. In the general plot for all the studied mammals, values

from two species (*Pedetes capensis* (PE) and *Bradypus tridactylus* (BT)) are really distant from the general regression line (Fig. 2).

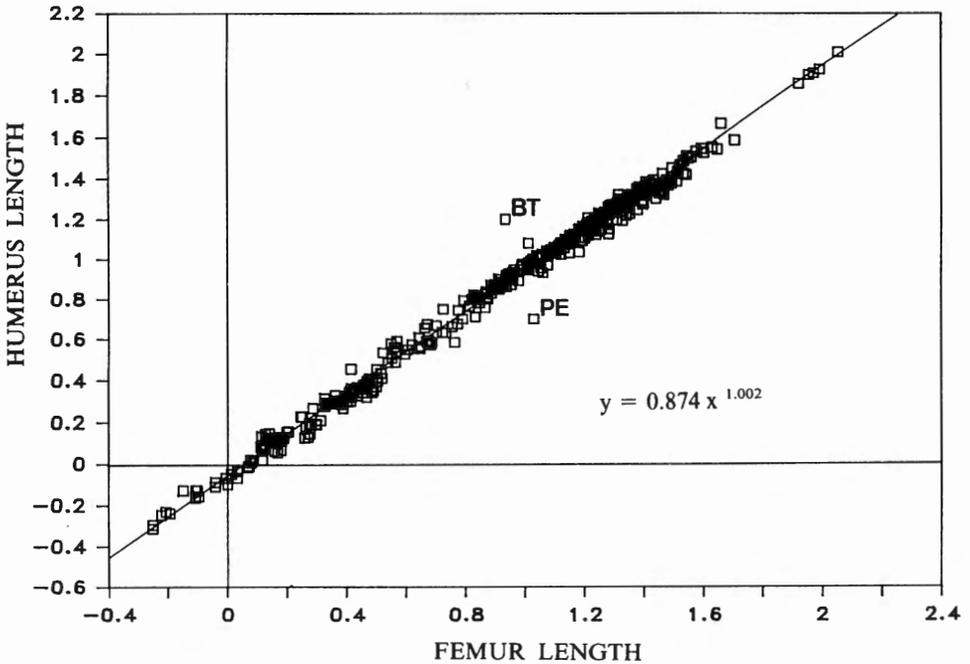


Fig. 2. — Graph of logarithmic coordinates of humeral length against femoral length for all the studied species. BT, *Bradypus tridactylus*; PE, *Pedetes capensis*.

TABLE 4

Allometric equations for the relationship between ulna and tibia.
Abbreviations as in table 1.

		<i>r</i>	<i>n</i>	
Marsupialia	$y = 0.74 x^{1.09}$	0.989	5	EP > 0.05
Insectivora	$y = 0.61 x^{1.14}$	0.977	36	DP < 0.05
Carnivora	$y = 0.64 x^{1.14}$	0.986	20	DP < 0.05
<i>Canis</i> sp.	$y = 0.86 x^{1.02}$	0.991	158	DP < 0.05
Proboscidea	$y = 0.29 x^{1.32}$	0.927	5	EP > 0.05
Perissodactyla	$y = 0.10 x^{1.65}$	0.978	8	DP < 0.05
Artiodactyla	$y = 0.29 x^{1.33}$	0.961	45	DP < 0.05
Rodentia	$y = 0.71 x^{1.01}$	0.983	110	EP > 0.05
Mammalia	$y = 0.64 x^{1.12}$	0.944	396	DP < 0.05

Relative proportions between the distal long bones. — Only three of the exponents, those of Marsupialia, Proboscidea and Rodentia, are not significantly different from 1 (Table 4). The correlation coefficients are always very high. Again, in the general plot for all the mammals the values of *Pedetes capensis* and *Bradypus tridactylus* are placed below and above the regression line, respectively : this means that, while the former species has a relatively shorter ulna than the general tendency, that of the latter is longer.

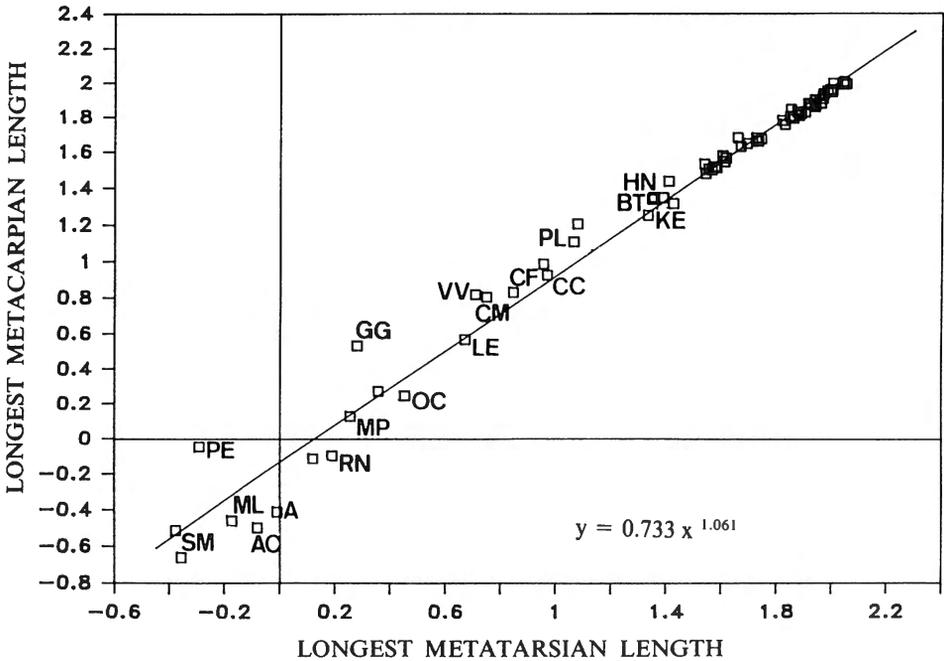


Fig. 3. — Graph of logarithmic coordinates of the longest metacarpian length against the longest metatarsian length for all the studied species.

Symbols other than that used previously : A, *Apodemus sylvaticus*; AC, *Acomys cahirinus*; BT, *Boselaphus tragocamelus*; CC, *Crocota crocuta*; CF, *Castor fiber*; CM, *Canis mesomelas*; GG, *Genetta genetta*; HN, *Hippotragus niger*; KE, *Kobus ellipsiprymus*; LE, *Lepus capensis*; ML, *Mus musculus*; MP, *Mustela putorius*; OC, *Oryctolagus cuniculus*; PL, *Panthera leo*; RN, *Rattus norvegicus*; SM, *Sorex minutus*; VV, *Vulpes vulpes*.

Relative proportions between among metapodials. — Only one equation was calculated- that of the whole sample (Table 5). Although the achieved exponent (1.06) is very close to 1, they are statistically different. In figure 3 it is shown that the dispersion of values is particularly important in the smallest range of sizes, while for big body masses, values are remarkably united.

TABLE 5

Allometric equations for all the sample for the relationship between the longest metapodials. Abbreviations are the same that used in table 1.

		<i>r</i>	<i>n</i>
Insectivora			2
Carnivora (including <i>Canis</i> sp.)			52
Proboscidea			1
Artiodactyla			10
Rodentia			6
Lagomorpha			3
Mammalia	$y = 0.73 x^{1.06}$	0.991	74

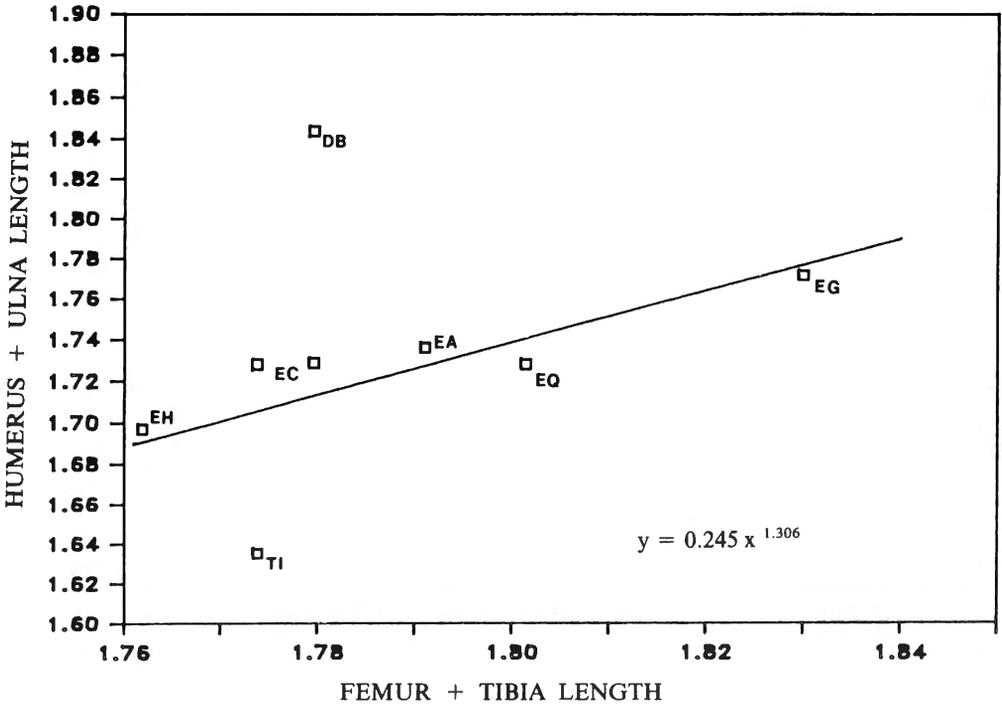


Fig. 4. — Graph of logarithmic coordinates of the forelimb (humerus + ulna) length against the hindlimb (femur + tibia) length for Perissodactyla. Symbols other that used before : EA, *Equus asinus*; EC, *Equus caballus*; EH, *Equus hemionus*; EG, *Equus grevyi*; EQ, *Equus quagga*.

Relative proportions between the fore and hindlimbs. — Five of the slopes differ significantly from 1 ; other five can be considered equal (Table 6). The different

plots were remarkably uniform with the only exception of *Perissodactyla* (Fig. 4). Among the values of this order of mammals, *Diceros bicornis* (DB) has an extremely long forelimb (humerus + ulna) while that *Tapirus indicus* (TI) is rather short. The general regression line for all the sample appears very similar to that of figure 2, with the same relative positions as that of *Pedetes capensis* and *Bradypus tridactylus*.

TABLE 6

Allometric equations for the relationship humerus + ulna and femur + tibia.
See table 1 for abbreviations.

		<i>r</i>	<i>n</i>	
Marsupialia	$y = 0.82 x^{1.01}$	0.997	5	EP > 0.05
Insectivora	$y = 0.67 x^{1.12}$	0.991	36	DP < 0.05
Carnivora	$y = 0.76 x^{1.05}$	0.996	20	DP < 0.05
<i>Canis</i> sp.	$y = 0.96 x^{0.99}$	0.995	158	EP > 0.05
Proboscidea	$y = 0.27 x^{1.25}$	0.992	5	EP > 0.05
Perissodactyla	$y = 0.24 x^{1.30}$	0.972	8	DP < 0.05
Artiodactyla	$y = 0.41 x^{1.18}$	0.977	45	DP < 0.05
Rodentia	$y = 0.76 x^{1.01}$	0.988	110	EP > 0.05
Mammalia	$y = 0.71 x^{1.06}$	0.996	396	DP < 0.05

TABLE 7

Allometric equations obtained from the correlation of body mass against humerus + ulna or femur + tibia. F and H mean forelimb and hindlimb, respectively.

For other abbreviations, see table 1.

			<i>r</i>	<i>n</i>	
Insectivora	F	$y = 0.76 x^{0.32}$	0.960	25	EP > 0.05
	H	$y = 1.16 x^{0.28}$	0.973	25	DP < 0.05
Rodentia	F	$y = 0.78 x^{0.35}$	0.930	71	EP > 0.05
	H	$y = 1.02 x^{0.35}$	0.915	71	EP > 0.05

Scaling of the limb length to body mass. — The body mass was only available from insectivores and rodents. In this case the achieved exponents were tested against the theoretical value (0.34) postulated by ALEXANDER *et al.* (1979) (see above). Only the slope corresponding to the insectivore hindlimb is different from 0.34 (Table 7). The exceptions to the general tendency often appears as equal in both orders. That is to say, in insectivores *Talpa europea* (T) shows both legs shorter than expected (Fig. 5). Among rodents, the flying squirrels (*Iomys horsfieldii* (I),

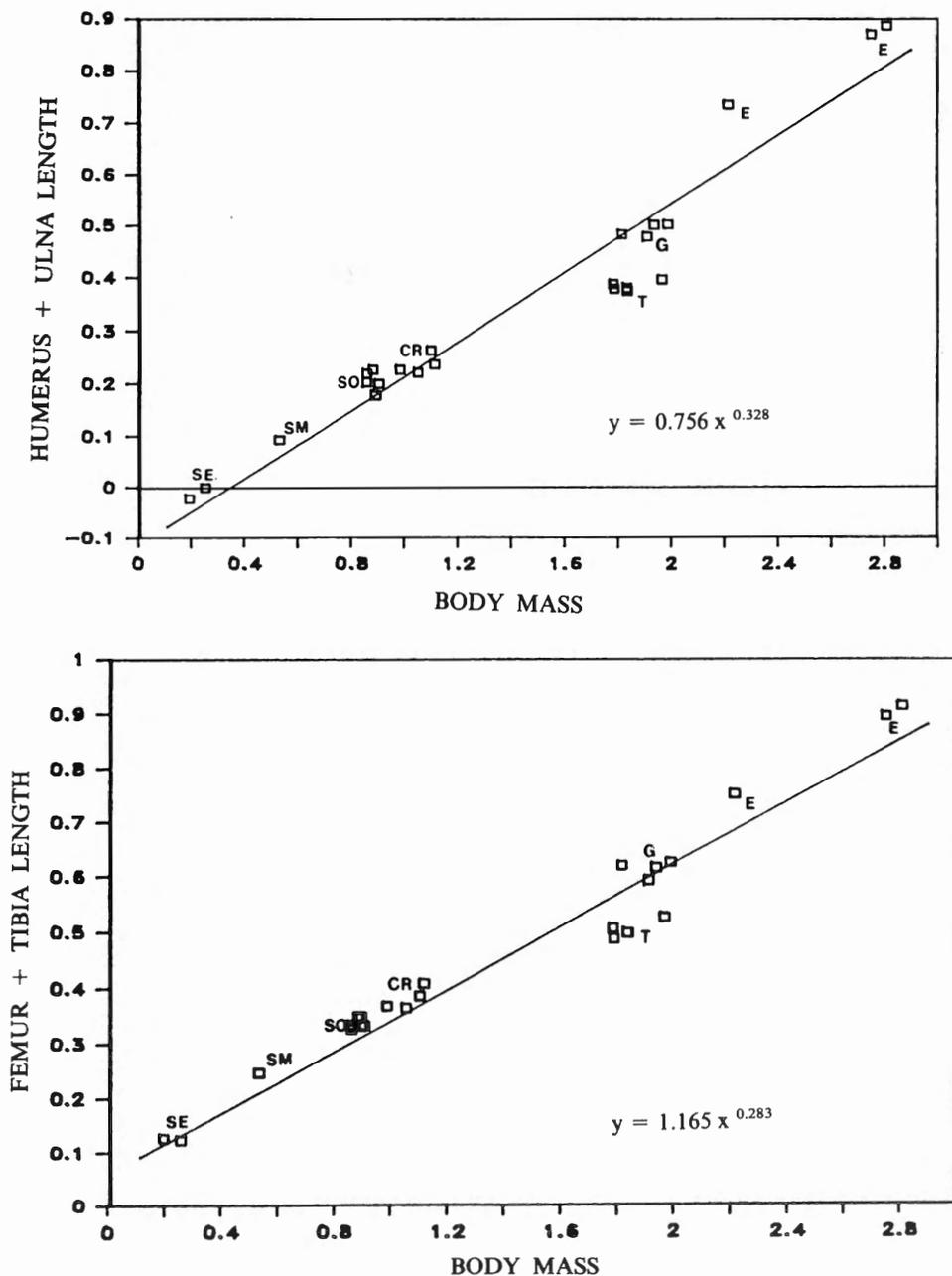


Fig. 5. — Graph of logarithmic coordinates of the forelimb (humerus + ulna) length against body mass (A) and of the hindlimb (femur + tibia) length against body mass (B), both for insectivores.

Symbols other than those used above: CR, *Crocidura russula*; E, *Erinaceus* sp.; G, *Galemys pyrenaicus*; SE, *Suncus etruscus*; SM, *Sorex minutus*; SO, *Sorex araneus*; T, *Talpa europaea*.

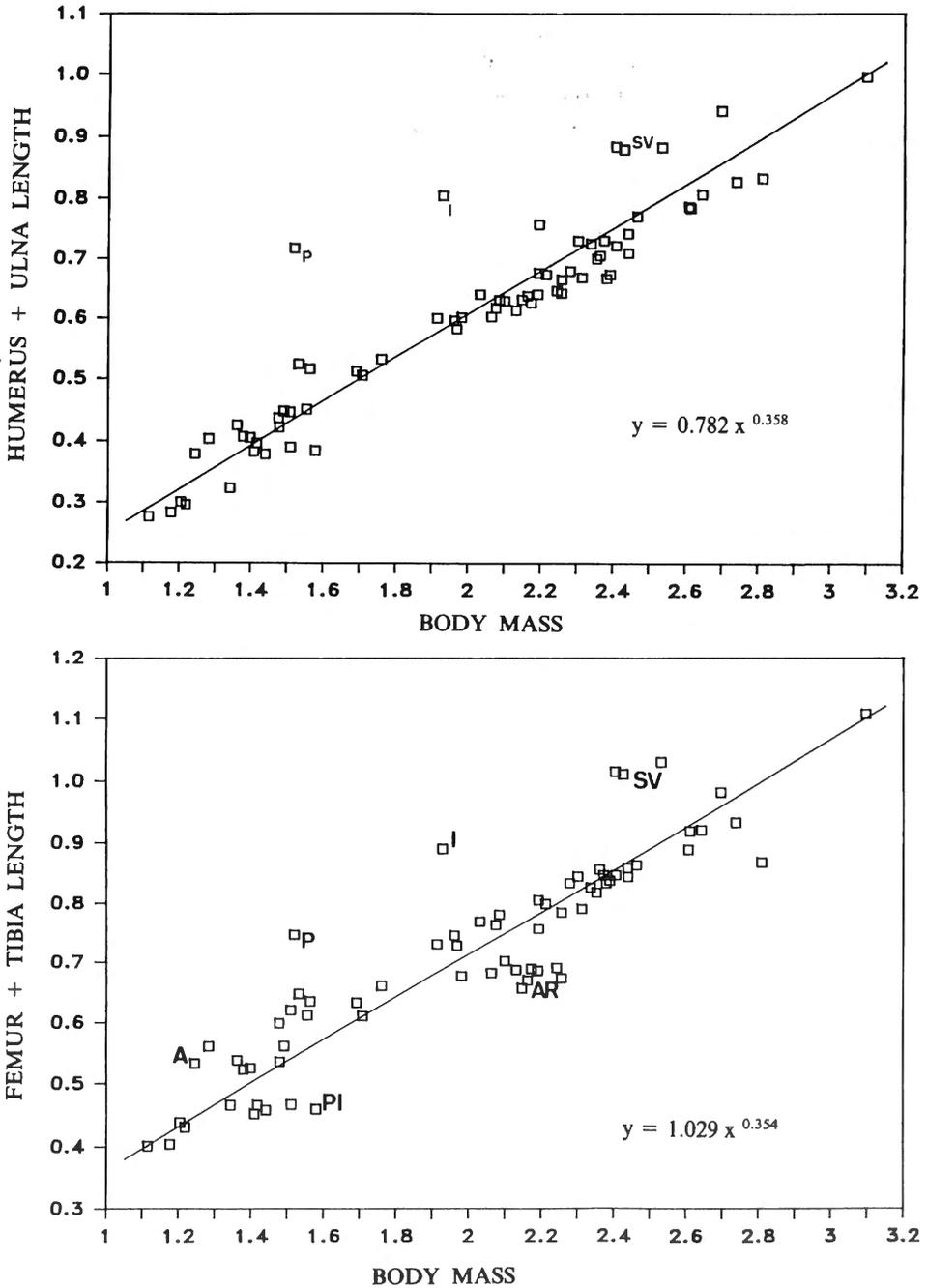


Fig. 6. — Graph of logarithmic coordinates of the forelimb (humerus+ulna) length against body mass (A) and of the hindlimb (femur+tibia) length against body mass (B), both for rodents.

Symbols not used before : AR, *Arvicola terrestris*; I, *Iomys horsfieldii*; P, *Petinomys vordermanni*; PI, *Pitymys duodecimcostatus*; SV, *Sciurus vulgaris*.

Petinomis vondermanni (P) and *Sciurus vulgaris* (SV) are clearly above the regression lines of both legs, while *Pitymys duodecimcostatus* (PI) and *Arvicola terrestris* (AR) have all their values below the hindlimb regression line (Fig. 6). Similar results had been achieved previously for individual bones (BOU *et al.* 1987).

TABLE 8

Allometric equations achieved from the relationship between the diameters of the fore and hindlimb long bones. Abbreviations as in table 7.

			<i>r</i>	<i>n</i>	
Insectivora	F	$y = 0.75 x^{0.86}$	0.975	30	DP < 0.05
	H	$y = 0.84 x^{0.99}$	0.939	30	EP > 0.05
<i>Canis</i> sp.	F	$y = 0.45 x^{1.04}$	0.864	135	EP > 0.05
	H	$y = 1.06 x^{0.96}$	0.957	135	EP > 0.05
Rodentia	F	$y = 0.85 x^{0.95}$	0.914	71	EP > 0.05
	H	$y = 0.83 x^{1.10}$	0.987	71	DP < 0.05

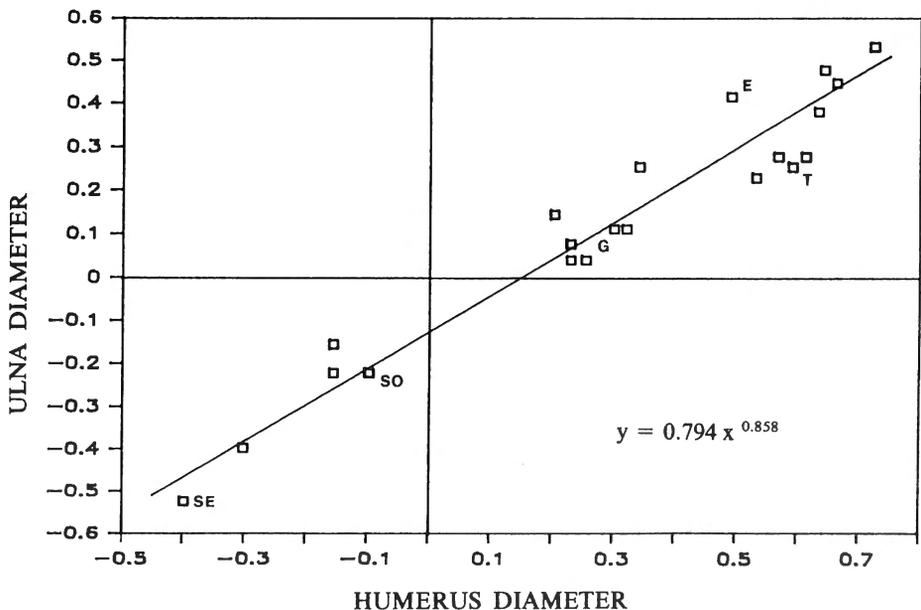


Fig. 7. — Graph of logarithmic coordinates of the ulnar diameter against humeral diameter for insectivores.

Relative proportions between diameters of the long bones. — Separated comparisons were established between the foreleg long bones (humerus + ulna) and the

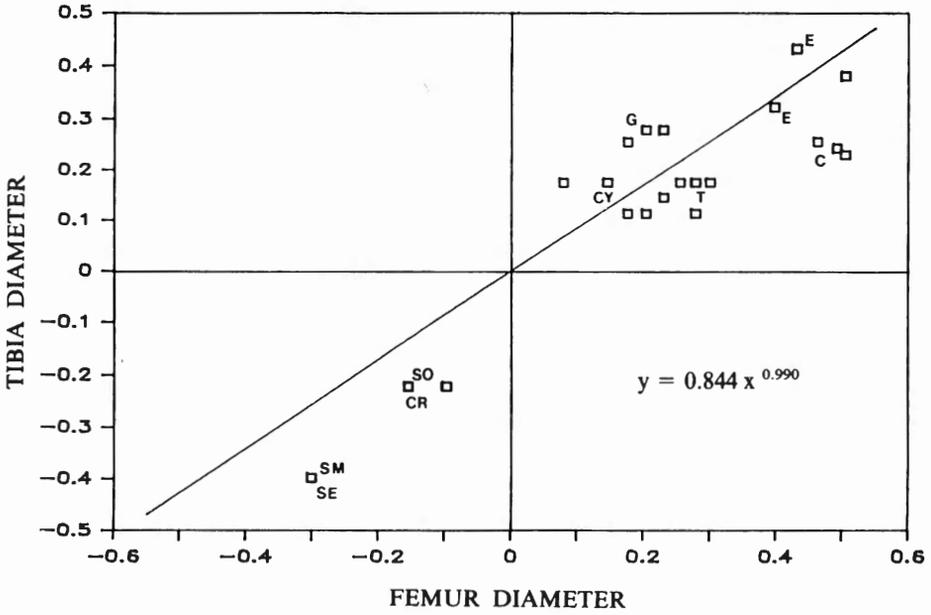


Fig. 8. — Graph of logarithmic coordinates of the tibial diameter against femoral diameter for insectivores.

Symbols not used before : C, *Chrysospalax trevelyani* ; CY, *Chrysochloris* sp.

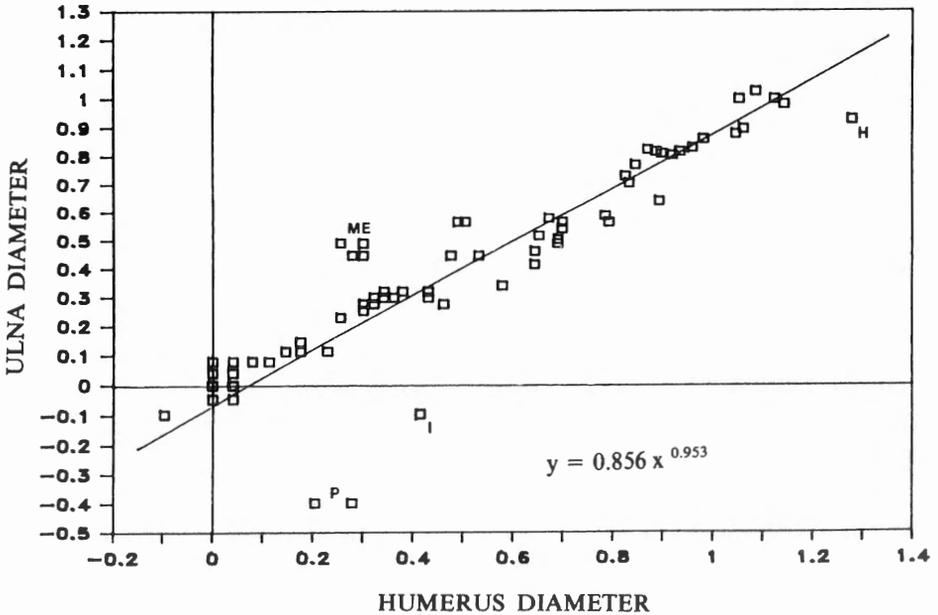


Fig. 9. — Graph of logarithmic coordinates of the ulnar diameter against humeral diameter for rodents.

Symbols not used previously : H, *Hydrochaeris hydrochaeris* ; ME, *Mesocricetus auratus*.

hindleg long bones (femur + tibia) for specimens of insectivores, *Canis sp.* and rodents. That is to say for the groups from which the diameters were available. The hypothetical condition, according to hypothesis number 4 was isometry. Table 8 shows that the exponents for the insectivore forelimb and the rodent hindlimb are significantly different from 1. In the first case the reason is possibly the position of the values of *Talpa europaea* (T), with a humerus wider than the ulna (Fig. 7). The small insectivores, like *Sorex araneus* (SO), *Crocidura russula* (Cr), *Sorex minutus* (SM) and *Suncus etruscus* (SE) have a remarkably slender tibia (Fig. 8). In a similar way, the flying squirrels *Petinomys vondermanni* (P) and *Iomys horsfieldii* (I) show a diameter decreasing from humerus to ulna (Fig. 9), which had been previously expected (BOU *et al.* 1987).

DISCUSSION

In general, in all the cases in which different lengths or diameters were compared, there is a tendency towards isometry. Species that appear far from the normal tendency show very particular kinds of locomotion, like *Pedetes capensis*, a very specialized jumping rodent (OFFERMANS and DE VREE 1988), with hindlegs very much longer than forelegs, and *Bradypus tridactylus* (Edentata), a typical arboreal species, in which case it is not surprising that it shows a reverse leg adaptation, according to previous results (BOU *et al.* 1987). For lengths, perhaps it is in Proboscidea, Perissodactyla and Artiodactyla where that tendency is less evident. In all the correlations calculated, one or more of those three orders shows the strongest positive or negative allometries. In Perissodactyla the positions of *Diceros bicornis* and *Tapirus indicus* are the most interesting. We have seen that the rhino has a relatively longer forelimb, while that of tapir is relatively short. But both species have shorter ulnae in comparison with the humeri. All this seems to indicate that the rhino has either a long humerus or a short hindlimb, according to its size, but unfortunately no data are available about this. The rhino has the head closer to the ground than the tapir, because of feeding habits, and that can mean a lowering of the center of mass. In general, it seems that the heavier the skull, the longer the forelimb is, taking into account the results of Proboscidea for the scaling of the forelimb against the hindlimb, which show a relatively important positive allometry (slope equals to 1.25; see Table 6). This can be an example that other functions than locomotion can exert their selective pressure on the limb design.

Because of the reduced size of the sample in Proboscidea and Perissodactyla, some mathematical artefact could be thought to be the cause of the allometries, but this is not the case in the Artiodactyla, where the number of studied specimens is very much more important. Thus, the different adaptations seem to act mainly on the long bone of the big mammals, while in the case of small mammals the selective pressure seems to be exerted mainly on the metapodial bones (Fig. 3). On the other hand, it seems that the proportionality is more constant between the forelimb long bones than between the hindlimb ones, and the relative lengths of humerus and femur are more similar than those of ulna and tibia. If the whole legs are compared,

there appears a slight tendency to have a humerus + ulna longer than femur + tibia. In comparison to the data on the only big order of terrestrial mammals not studied here (Primates), the main disagreement with the results of AIELLO (1981) concerns the slope for the correlation between the lengths of both legs. Primates show a slightly negative allometry (0.95), while in the other orders of terrestrial mammals studied (see table 6) the relationship is isometric or positively allometric, except for *Canis* sp. About the relationship between diameters, only in two cases, the forelimb of dogs and the hindlimb of rodents, the diameters of the distal bones seem to scale faster than those of the proximal bones. Supposing that diameters are proportional to the strength of bones (see above), it appears that proximal and distal bones are submitted to more or less equivalent stresses. Something similar was assumed by means of experimental work on bending and twisting strength in small mammals and birds (BOU *et al.*, accepted).

According to the terminology and distinction introduced by JENKINS (1971), in the sample used in this study there are cursorial and non-cursorial mammals. However, it seems that no important difference exists from the point of view of limb proportions between those two types of quadrupeds, except the already commented characteristic of more variability within the metapodials than in long bones in small mammals, although no direct relationship appears.

Another question concerns the way in which we recognized the homologous structures in both limbs. As frequently happens in morphology, two possibilities exist : the structural and the functional. From a structuralistic approach, our comparisons are correct. But we cannot forget the different role of the two girdles in mammals : the main element of the pectoral girdle, the scapula, is capable of forwards and backwards oscillations. This fact and the fact that in some mammals (for instance, the cat) the motor pattern of the scapula long muscles and that of the muscles of the femoral region are identical, induce some morphologists to think of a functional « homology » between the scapula and the femur (Jean-Pierre Gasc, personal communication). If that point of view is right, a comparison between the lengths of the humerus and the tibia would seem reasonable. Let's do this comparison. According to our results for all the sample

$$\text{ulna} \propto (\text{humerus})^{1.02}$$

and

$$\text{ulna} \propto (\text{tibia})^{1.12}$$

Therefore

$$(\text{humerus})^{1.02} \propto (\text{tibia})^{1.12}$$

or

$$\text{humerus} \propto (\text{tibia})^{1.12/1.02} \propto (\text{tibia})^{1.098}$$

So, whether the comparison of the tibia is established with its structural (ulna) or functional (humerus) homologue, the result is a slightly positive allometry. That means that in all cases the forelimb bone scales faster than the hind limb bone.

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