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SCALING OF SKELETAL ELEMENT MASS IN BIRDS

by

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SUMMARY

The dry mass from different skeletal elements of 63 specimens belonging to 49 species of birds was measured. The body mass range was 5.7 g-98 kg. Correlations of the mass of the skeletal elements to body mass were established by means of Model II of regression. Positive allometry was found in the case of the femur, tibiotarsus-fibula, tarsometatarsus, synsacrum and thoracic vertebrae, while the skull and sternum showed negative allometry. For a given body mass, a larger mass of avian humerus, ulna-radius and tibiotarsus-fibula can be expected, in comparison with the corresponding bones in mammals. Finally, some species displayed special values for some of their skeletal elements. For example, two orders (Galliformes and Columbiformes) displayed a tendency to lighter skeletal structures.

Keywords : Allometry, adaptation, birds, locomotion.

INTRODUCTION

In recent years several papers dealing with the problems of the scaling of the skeletal mass to the body mass of animals, mainly vertebrates, have been published ; for example, REYNOLDS and KARLOTSKI (1977) and CASADEVALL *et al.* (1990) on teleosteans, LECLAIR *et al.* (1993) on amphibians, PRANGE *et al.* (1976) on reptiles, BOU and CASINOS (1985) on insectivores and rodents, ROBINEAU and DE BUFFRÉNIL (1993) on cetaceans, POTTER (1986) on primates, PRANGE *et al.* (1979) comparing birds and mammals, REYNOLDS (1977) on vertebrates in general, and ANDERSON *et al.* (1979) on animal skeletons in general. With the exception of BOU and CASINOS (1985) and CASADEVALL *et al.* (1990) all the papers cited refer to the whole skeleton. Nevertheless, some of the results for the masses of separate skeletal elements seem to indicate that some particular characteristics may be a response to environmental pressures.

The only paper referring to birds (PRANGE *et al.*, 1979) shows that similar allometries of skeletal mass exist in birds and mammals when entire skeletons are considered. Consequently, the present research had two main aims. First, to study the scaling of the different skeletal elements of birds to body mass, comparing results for long bones and the skull with those previously found by Bou and Casinos (1985) for the same structures in insectivores and rodents. Second, to discuss possible adaptative reasons for particular values of some skeletal structures.

MATERIAL AND METHODS

Some 63 specimens from 49 different species were studied, although the size of the sample varies according to the structure studied. The maximum corresponds to the skull and the minimum (30 specimens and 20 species) to the cervical and thoracic vertebrae. The species were namely :

Order Gaviiformes
  Family Podicipedidae
    Rollandia rolland (Quoy and Gaimard, 1824) (1)
Order Palaeognathiformes
  Family Struthionidae
    Struthio camelus Linnaeus, 1758 (1)
Order Ciconiformes
  Family Ardeidae
    Ardea cinerea Linnaeus, 1758 (1)
    Bubulcus ibis (Linnaeus, 1758) (1)
    Egretta garzetta (Linnaeus, 1766) (1)
  Family Threskiornithidae
    Plegadis chihi (Vieillot, 1817) (1)
Order Falconiformes
  Family Strigidae
    Tyto alba (Scopoli, 1769) (2)
  Family Accipitridae
    Buteo buteo (Linnaeus, 1758) (2)
    Circus cinereus Vieillot, 1816 (1)
    Milvago chimachima (Vieillot, 1816) (1)
    Milvus migrans (Boddaert, 1783) (1)
Order Anseriformes
  Family Anatidae
    Aix sponsa (Linnaeus, 1758) (1)
    Cairina mostacha Fleming, 1822 (1)
    Coscoroba coscoroba (Molina, 1782) (1)
    Cygnus olor (Gmelin, 1789) (1)
    Netta rufina (Pallas, 1773) (1)
Order Galliformes
  Family Opisthocomidae
    Guira guira (Gmelin, 1788) (1)
  Family Megapodiidae
    Gallus sonnerati Temminck, 1813 (1)

Family Numididae
Numida meleagris (Linnaeus, 1758) (1)

Family Phasianidae
Alectoris rufa (Linnaeus, 1758) (2)
Phasianus colchicus Linnaeus, 1758 (2)

Order Gruiformes

Family Rallidae
Fulica leucoptera Vieillot, 1817 (1)

Order Charadriiformes

Family Sternidae
Sterna albifrons Pallas, 1764 (3)

Family Laridae
Larus argentatus Pontoppidan, 1763 (1)
Larus ridibundus Linnaeus, 1766 (1)

Family Recurvirostridae
Himantopus himantopus (Linnaeus, 1758) (1)
Recurvirostra avosetta Linnaeus, 1758 (1)

Family Charadriidae
Charadrius alexandrinus Linnaeus, 1758 (2)
Vanellus chilensis (Molina, 1782) (1)

Family Scolopacidae
Calidris alpina (Linnaeus, 1758) (2)
Calidris ferruginea (Pontoppidan, 1763) (2)
Calidris minuta Leisler, 1812 (1)
Tringa erythropus (Pallas, 1764) (1)

Order Columbiformes

Family Columbidae
Columba livia Gmelin, 1789 (2)
Columba palumbus Linnaeus, 1758 (1)

Order Psittaciformes

Family Psittacidae
Amazona aestiva (Linnaeus, 1758) (1)
Myopsitta monachus (Boddaert, 1783) (1)
Poicephalus senegalus (Linnaeus, 1766) (1)

Order Piciformes

Family Picidae
Melanerpes candidus (Otto, 1796) (1)

Order Passeriformes

Family Prunellidae
Prunella modularis (Linnaeus, 1758) (1)

Family Muscicapidae
Erithacus rubecula (Linnaeus, 1758) (2)
Turdus philomelos Brehm, 1831 (3)
Sylvia atricapilla (Linnaeus, 1758) (1)

Family Certhiidae
  Certhia brachydactyla Brehm, 1870 (1)
Family Corvidae
  Corvus corone Linnaeus, 1758 (1)
  Cyanocorax caeruleus (Vieillot, 1818) (1)
Family Fringillidae
  Carduelis carduelis (Linnaeus, 1758) (1)
  Fringilla coelebs Linnaeus, 1758 (2)
  Serinus serinus (Linnaeus, 1766) (1)

The systematic scheme is that of CRACRAFT (1981). The number of specimens studied is given in brackets. From some species not all the the skeletal elements were available. This is the origin of the variability in the samples (Table 1).

The sample was obtained from the Barcelona Zoological Garden and several Spanish natural parks. Some of the skulls, belonging to neotropical species, correspond to material studied by one of us (A.C.) some years ago in the museum of Mar del Plata (Argentina). For preparation, hot water and a drying-chamber were used (BOU and CASINOS, 1985). Regression of the individual skeletal elements against body mass were calculated by means of Model II. The calculation of confidence intervals enabled comparison with the corresponding values for insectivores and rodents to be made (BOU and CASINOS, 1985).

RESULTS

In Table 1 the different equations calculated, the size of the samples, the correlation coefficients and the confidence intervals are shown.

In two cases (skull and sternum) a clear negative allometry appears, since the confidence intervals of b (the exponent) exclude the isometric value (slope 1). In the case of the skull, this is not very surprising, because brain mass also scales with negative allometry. Inversely, the femur, tibiotarsus and fibula, tarsometatarsus, synsacrum and thoracic vertebrae scale with positive allometry, the confidence intervals also excluding the isometric value for b.

It is known that wing length scales with positive allometry. Therefore it can be expected that wing bone mass does likewise. When comparisons with long bones of insectivores and rodents are established, the humerus and ulna-radius scale with exponents significantly different from those of mammals and in all cases, except femur, the y-interceptions (Table 1, a) are higher than the corresponding values for insectivores and rodents and the confidence intervals calculated for birds exclude mammalian values. The femur is the only long bone for which a similar mass can be expected in both birds and mammals. Finally, the avian skull scales slower than the mammalian skull and the confidence intervals of exponent (Table 1, b) in the case of birds exclude those calculated for insectivores and rodents (BOU and CASINOS, 1985) whether the calculation is made with the least-square system (as was originally the case) or model II.

TABLE 1

Equations calculated for the regressions of the different skeletal elements to body mass. Confidence intervals for both the y-interception (a) and the slope (b) are shown. Abbreviations : n, size of the sample ; r, correlation coefficient.

Skeletal element	Equation	n	r	a Confidence interval	b Confidence interval
Skull	$y = 0.0194 * x^{0.805}$	61	0.941	0.0286-0.0131	0.876-0.734
Humerus	$y = 0.0034 * x^{1.007}$	53	0.979	0.0046-0.0025	1.064-0.949
Ulna-radius	$y = 0.0034 * x^{0.990}$	52	0.955	0.0053-0.0022	1.073-0.907
Femur	$y = 0.0008 * x^{1.151}$	53	0.993	0.0009-0.0006	1.188-1.113
Tibiotarsus + fibula	$y = 0.0015 * x^{1.126}$	51	0.984	0.0021-0.0011	1.183-1.068
Tarsometatarsus	$y = 0.0007 * x^{1.159}$	52	0.971	0.0011-0.0005	1.238-1.080
Clavicle	$y = 0.0007 * x^{1.024}$	31	0.945	0.0013-0.0003	1.151-0.897
Scapula + coracoid	$y = 0.0018 * x^{1.008}$	32	0.992	0.0023-0.0014	1.056-0.960
Sternum	$y = 0.0046 * x^{0.950}$	33	0.992	0.0059-0.0036	0.993-0.907
Synsacrum	$y = 0.0021 * x^{1.114}$	33	0.995	0.0027-0.0016	1.156-1.072
Cervical vertebrae	$y = 0.0026 * x^{1.047}$	30	0.975	0.0044-0.0015	1.137-0.957
Thoracic vertebrae	$y = 0.0010 * x^{1.077}$	30	0.991	0.0014-0.0008	1.131-1.023
Caudal vertebrae	$y = 0.0005 * x^{1.008}$	31	0.959	0.0011-0.0003	1.117-0.899

DISCUSSION

According to the results found in this research, it seems very clear that for a given body mass, larger masses in avian humerus, ulna-radius and tibiotarsus and fibula than for the corresponding bones of insectivores and rodents (tibia and fibula instead of tibiotarsus and fibula) can always be expected. The femur is the exception. As noted above, a similar femur mass can be expected for birds and mammals. In fact, the femur is the most constant bone within mammals (Bou *et al.*, 1991 ; Casinos *et al.*, 1993) both from a mechanical and a biometrical point of view. At the same time the variation in the mechanical behaviour of the avian and mammalian femur, both as regards bending and twisting, seems to be minimal (Bou *et al.*, 1991). Since the avian femur is at the same time shorter and thicker (Alexander *et al.*, 1979, Maloiy *et al.*, 1979, and unpublished data from Olmos, 1988), possibly there exists a compensation, in which case the similarity of mass between bird and mammal femur would not be surprising.

We can wonder about the reason for the greater mass in most avian long bones compared with the same bones in mammals. One reason could be biometrical : in general long bones scale faster in birds than in mammals, according to the equations of Alexander *et al.* (1979) and unpublished data from Olmos (1988). For example, the slope of the avian humerus length against body mass is 0.43, while it is only 0.36 in the case of the mammalian humerus. But the y-interceptions are very

TABLE 2

Theoretical masses (in grams), calculated by means of the predictive value of the equations obtained in this study, for birds of 100 g, 1,000 g and 10,000 g of body mass, respectively.

	100 g	1,000 g	10,000 g
Humerus mass	0.351	3.568	36.264
Ulna-radius mass	0.325	3.173	31.008
Femur mass	0.160	2.270	32.143
Tibiotarsus + fibula mass	0.268	3.582	47.873
Tarsometatarsus mass	0.146	2.099	30.276

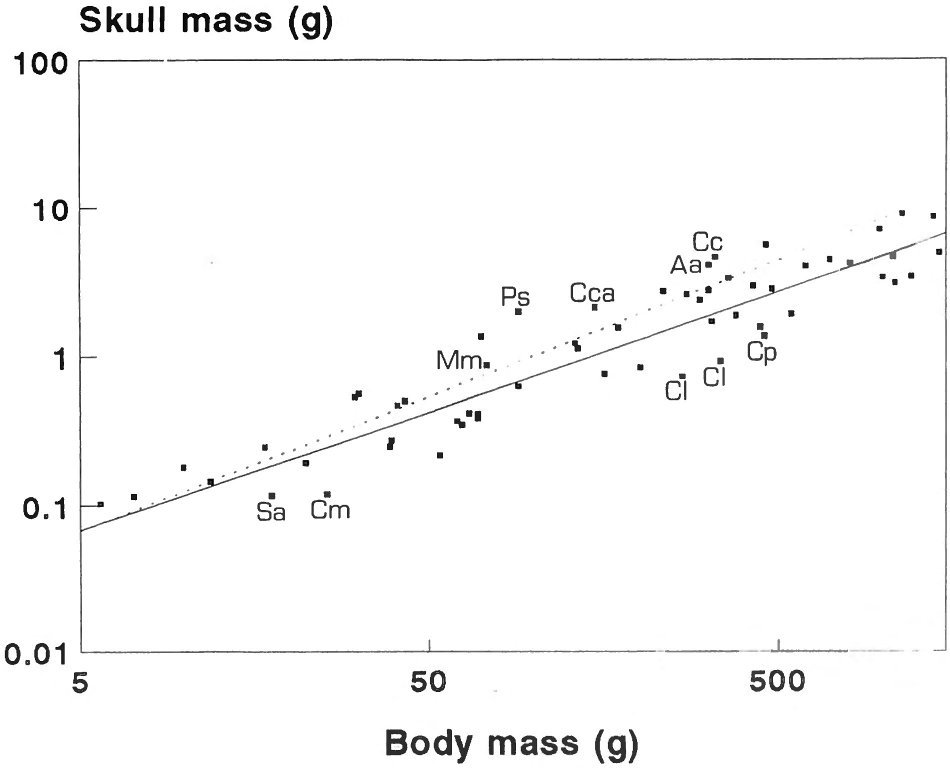

Fig. 1. — Graph on logarithmic coordinates of the skull mass to body mass, both in grammes. Dotted and solid line correspond to mammal and bird regressions, respectively. The points corresponding to *Cygnus olor* and *Struthio camelus* were excluded in all the plotters. Abbreviations : Aa, *Amazona aestiva* ; Cc, *Corvus corone* ; Cca, *Cyanocorax caeruleus* ; Cl, *Columba livia* ; Cm, *Calidris minuta* ; Cp, *Columba palumbus* ; g, grams ; Mm, *Myopsitta monachus* ; Ps, *Poicephalus senegalus* ; Sa, *Sylvia atricapilla.*

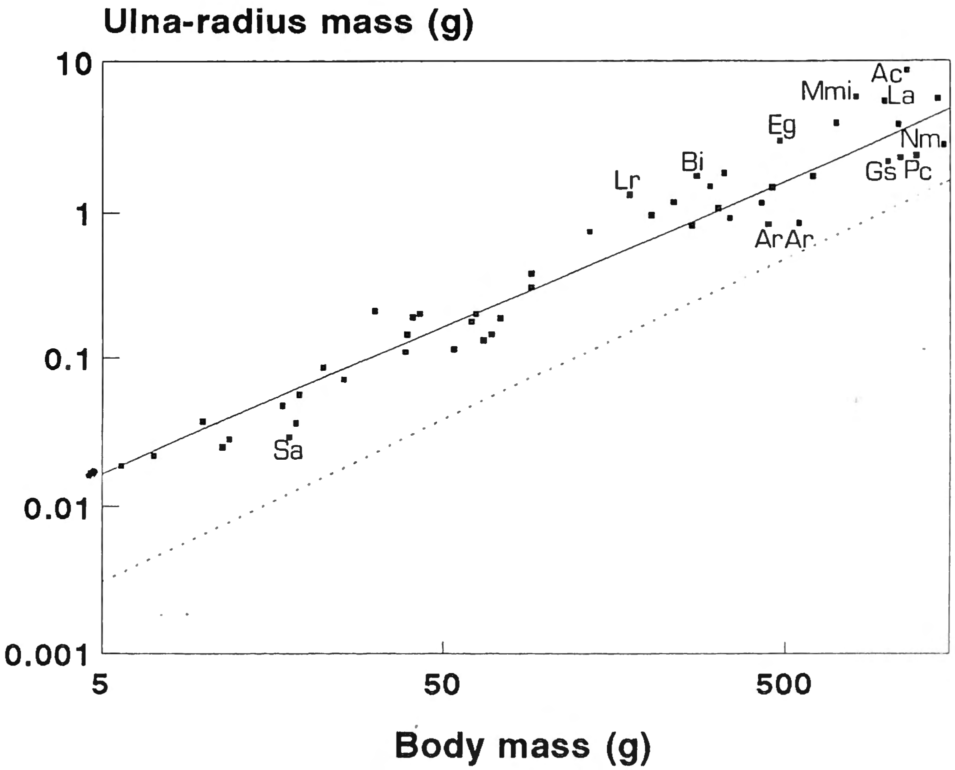

Fig. 2. — Graph on logarithmic coordinates of the ulna-radius mass to body mass, both in grammes. Abbreviations : Ac, *Ardea cinerea*; Ar, *Alectoris rufa*; Bi, *Bubulcus ibis*; Eg, *Egretta garzetta*; Gs, *Gallus sonnerati*; La, *Larus argentatus*; Lr, *Larus ridibundus*; Mmi, *Milvus migrans*, Nm, *Numida meleagris*; Pc, *Phasianus colchicus*. For other abbreviations and details, see figure 1.

close (0.46 and 0.51, respectively). This means that lengths are likely to be very similar for small body masses, but they become far larger in birds than in mammals when the body mass increases. This is not the case for skeletal masses : the slopes for birds and small mammals are practically parallel in such a way that the ratio is constant. In fact, the present results are completely opposed to the generalized assumption that avian skeletal structures are lighter than the corresponding mammalian structures. However, since PRANGE *et al.* (1979) found that the scaling of the mass of the whole skeleton to body mass is not significantly different in birds and mammals, some bony structures other than the skull must be heavier in mammals than in birds. At the same time, the prediction of PRANGE *et al.* (1979) « ...the structural material that is saved in the long pneumatized wing bones has had to be added to the more robust leg bones » would seem to be unjustified. In Table 2 the masses of the different long bones of three hypothetical birds of 100 g, 1,000 g and 10,000 g of body mass, respectively, are shown. These figures have been calculated using the predictive value of the equations obtained in this research (Table 1). It

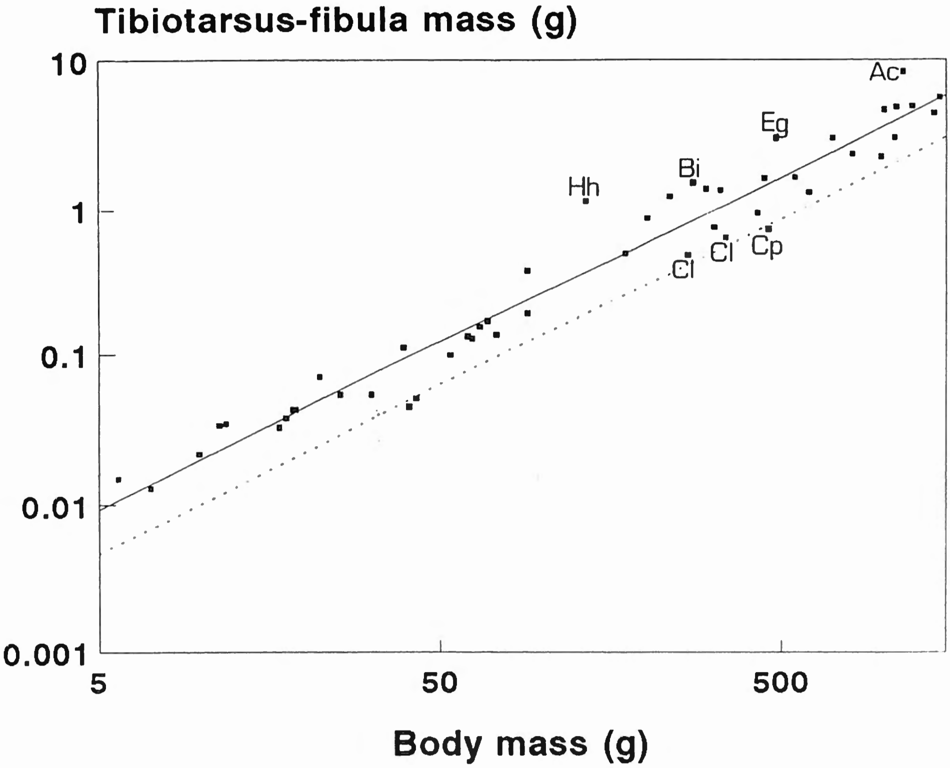

Fig. 3. — Graph on logarithmic coordinates of tibiotarsus-fibula mass to body mass, both in grammes. Abbreviations : Hh, *Himantopus himantopus*. For the other abbreviations and symbols, see figures 1 and 2.

can be seen that in the case of a bird of 100 g, the humerus and ulna-radius are heavier than any hindlimb bone (femur, tibiotarsus and fibula, tarsometatarsus). For a body mass of 1,000 g only the tibiotarsus and fibula reach a value comparable to those of the fore limb long bones. Only in the extreme case of 10,000 g are the tibiotarsus and fibula together the heaviest skeletal structures and is the femur a little heavier than the ulna-radius, but still lighter than the humerus. In fact, 10 kg is not a normal body mass for a flying bird. As far as we know, only bustards arrive at this range of body mass (CRAMP, 1980).

In Fig. 1 skull mass values are plotted against body masses. Psittaciformes display particularly heavy skulls (Aa, *Amazona aestiva* ; Ps, *Poicephalus senegalus* ; Mm, *Myopsitta monachus*) and the Corvidae studied are also placed above the regression line (Cc, *Corvus corone* ; Cca, *Cyanocorax caeruleus*). Clearly below the regression line are found the Columbiformes (Cp, *Columba palumbus* ; Cl, *Columba livia*) and one species of Charadriiformes (Cm, *Calidris minuta*) and one species of Passeriformes (Sa, *Sylvia atricapilla*).

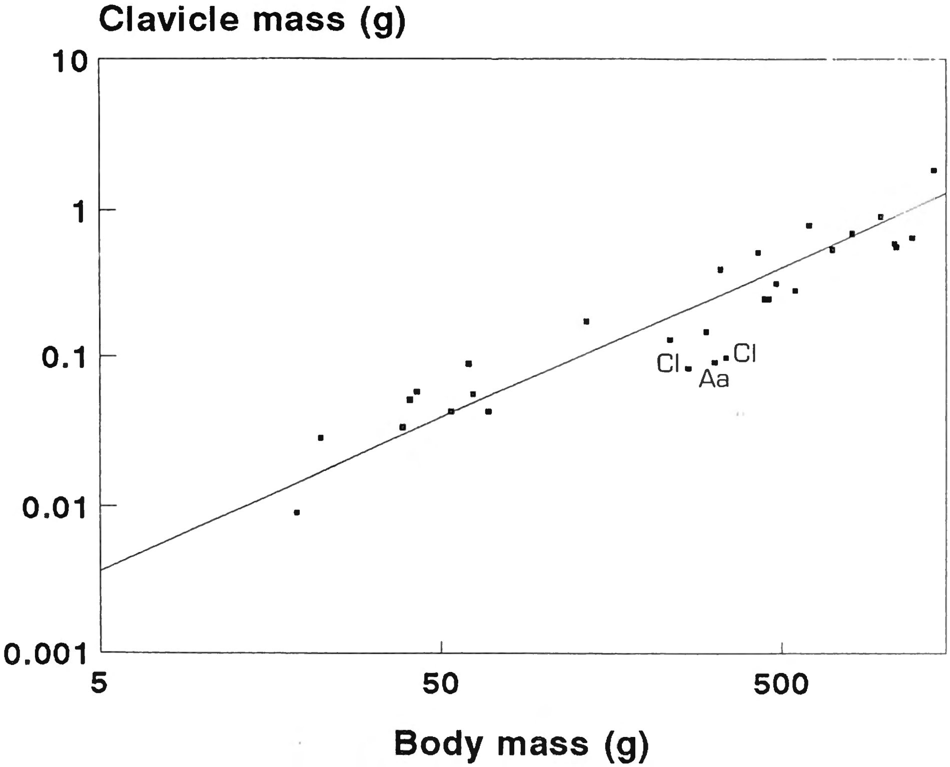

Fig. 4. — Graph on logarithmic coordinates of clavicle mass to body mass, both in grammes. For abbreviations, see figure 1.

Fig. 2 shows the plotting of the ulna-radius masses. In particular, above the regression line we can recognize the Ciconiiformes that were studied (Ac, *Ardea cinerea* ; Eg, *Egretta garzetta* ; Bi, *Bubulcus ibis*) the Laridae (La, *Larus argentatus* ; Lr, *Larus ridibundus*) and *Milvus migrans* (Mmi). Inversely, all the Galliformes studied are clearly below the regression line (Nm, *Numida mealeagris* ; Pc, *Phasianus colchicus* ; Gs, *Gallus sonnerati* ; Ar, *Alectoris rufa*). The distribution of the humerus values is very similar to that discussed for the ulna-radius.

Whilst the dispersion of femur points is very small, some of the tibiotarsus-fibula values are clearly separated from the regression line (Fig. 3). For example, the Ciconiiformes species studied (Ac, *Ardea cinerea* ; Eg, *Egretta garzetta* ; Bi, *Bubulcus ibis*) and *Himantopus himantopus* (Hh) are above the regression line. The Columbiformes studied (Cp, *Columba palumbus* ; Cl, *Columba livia*) are situated below the regression line. The tarsometatarsus points shows a distribution pattern very similar to that of the tibiotarsus.

The skeletal elements of both girdles, with the single exception of the clavicle, show practically no dipersion, as might be expected from the sample sizes and the

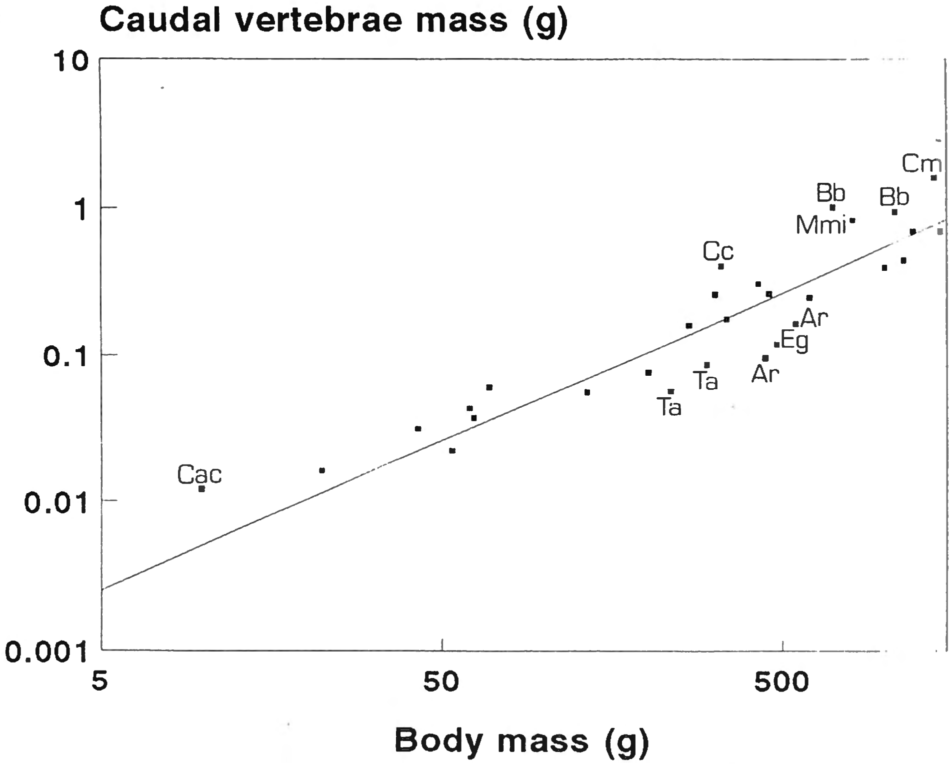

Fig. 5. — Graph on logarithmic coordinates of caudal vertebrae mass to body mass, both in grammes. Abbreviations : Bb, *Buteo buteo*; Cac, *Carduelis carduelis*; Cm, *Cairina mostacha*; Ta, *Tyto alba*. For the other abbreviations, see figures 1 and 2.

correlation coefficients. Even the dispersion of clavicle values is less marked than those found for long bones (Fig. 4).

Within the vertebral elements, the thoracic region is that with the minimum dispersion, whilst the caudal vertebrae show the maximum dispersion (Fig. 5).

In general it seems that two orders (Galliformes and Columbiformes) show a tendency to display lighter skeletal structures, at least in the cases illustrated by the figures.

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