

T H E S I S

OR

SKELETAL CHANGES ASSOCIATED WITH INCREASING BODY SIZE

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SKELETAL CHANGES ASSOCIATED WITH INCREASING BODY SIZE

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1. Introduction

It has long been recognized that as between such animals as a rat and a mouse, the factor of size necessitates certain anatomical and functional adjustments which cause these similarly proportioned animals to differ in important particulars. The surface area of the mouse as compared to its mass is greater than is the case with the rat and this in turn is probably responsible for the fact that the rate of metabolism is higher in the smaller animal. The mouse consequently requires more food and a more rapid circulation per unit of weight. In this connection Klatt (1919) and Parrot (1894) have shown that the heart in warm blooded animals is comparatively much smaller in the larger forms as compared with smaller ones.

Of almost equal importance is the effect of size on the relative strength of an animal. The efficiency of a muscle is measured by the area of its cross-section as was demonstrated by von Bergmann and Leuckart (1855) and this area increases as the square while the muscles and the body mass as a whole increase as the cube of the corresponding linear dimensions. It follows that if the size of the muscles of a larger animal bear the same relation to the whole weight as those of a smaller form, then the relative strength of the larger animal will be much less than that of the smaller one. If two animals of the same type such as .

the rat and the mouse were geometrically comparable in -2- every part and organ, then they would differ markedly from a physiological standpoint. In order to function in a comparable manner the relative proportions of parts must necessarily be different. It is well known that smaller animals are actually much stronger, relatively, than larger ones but whether the difference is such as would be expected from geometric comparison has never been ascertained.

In any attempt to evaluate by experimental data the actual differences present in bodily structure due to this factor of size, the skeleton should yield important data. This is especially true because the bony framework furnishes both support for the body and surface for muscle attachment.

In its role of support the skeleton will become relatively weaker with increasing body size if it grows in geometric proportion with the rest of the body. This is so because the bones enlarge in three dimensions, the same as the body as a whole, while their strength increases only as the square of the corresponding linear measurement. There is no mechanical necessity for the skeletal ratio increasing on this account since there would still be ample margin of reserve strength in even a relatively weak skeleton of quite a large animal. Small animals, such as mice have skeletons which are much stronger than necessary for their supporting functions.

As far as space for muscle attachment is concerned the increasing size of the skeleton in a strictly geometric

proportion offers no particular problem. The area of the -3- bones will increase as the square of the corresponding linear dimensions and at the same time the cross-section area of the muscles will likewise increase in the same manner. Thus under the circumstances mentioned the skeleton provides, with increasing body size, exactly the right amount of surface for muscle attachment.

2. Review of Literature

So far as could be determined Galilei Galileo in 1638 was the first to consider the problem of the transformations occurring in animals as the result of size differences. Galileo considered the possibility of animals comparable in structure and body plan to men and horses attaining monstrous sizes and came to the conclusion that such types would require either a relatively larger skeleton or bones constructed of a material much stronger than that found in the smaller prototypes. He also stated that decreasing size of such a form as that of man would not cause a corresponding decline in the relative strength of the body. He pointed out in support of these conclusions that a geometric increase in skeletal material does not give rise to a proportionate increase in the strength of the skeleton. Curiously enough, Galileo contended that the bone area of a large animal is relatively greater than that of a smaller animal of the same type. How erroneous this conclusion is will become evident from data presented in the present paper. Galileo's approach to these problems was from

a purely theoretical standpoint. He advanced no empirical -4- data, but his contentions are interesting in that certain of his conclusions are still accepted by many present day investigators.

In 1866 Plateau investigated the muscular power of insects of different sizes and found that among comparable types, the smaller ones were invariably the stronger. He tested the various forms on the basis of their ability to pull a load represented in terms of their own weights. The following list illustrates some of the results he obtained. The insects in the table are arranged in pairs and designated as number 1 and number 2. Number 1 represents the larger insect of each pair and number 2 the smaller one.

Insect	Load (in terms of own weight)
1. <i>Carabus auratus</i>	17.4
2. <i>Nebria brevicollis</i>	41.3
1. <i>Cetonia aurata</i>	15.0
2. <i>Trichius fasciata</i>	41.3
1. <i>Bombus terrestris</i>	16.1
2. <i>Apis mellifica</i>	20.2
1. <i>Necrophorus respillo</i>	15.1
2. <i>Silpha livida</i>	24.4

A.A.Packard (1898) vividly illustrated the effect of increasing size on muscular power in the following words:

" The power possessed by insects of transporting loads much heavier than themselves is easily accounted for, when we consider that the muscles of the legs of an insect the size of a housefly (a quarter of an inch long) and supporting a load 399 times its own weight, would be subjected to the same stress per square inch of cross-section as they would be in a fly 100 inches long of precisely similar shape, that carried only its own weight; from the mechanical law that while the weight of similar bodies varies as the cube of the corresponding dimensions, the area of the cross-section

of any part (such as the muscles of the leg) varies only as the square of the corresponding dimensions. In short, the muscles of a fly carrying this great proportional weight undergo no greater tension than would be exerted by a colossal insect in walking."

In more recent times, R. du Bois-Reymond (1928) has investigated the effect of increasing body size on the thickness and strength of the limb bones in vertebrates of similar build. His results were obtained from dry skeletons, the weights of the animals being calculated in the case of mammals by adding together the following measurements: length of the backbone from the skull to the pelvic girdle, lengths of the two femora and tibiae, and lengths of the two humeri and ulnas. He used the measure of the circumference of the femur as an index of bone thickness for each animal investigated and then calculated the bone strength from the weight the femur was able to bear at its center when it was supported at its extremities. Du Bois-Reymond reported that there was no consistent relative increase in bone thickness with increasing body size but that the relative strength of the bones was markedly less in larger vertebrates when compared with smaller ones. His findings show, for example, that the femur of the mouse will support 62.5 times the weight of the body, that of the rat 34.5 times, that of the cat 7.5 times, and man's femur will support only 5 times the body weight. Du Bois-Reymond's results and conclusions will be considered again in a later portion of this paper.

It is evident from the above survey of the literature on the subject that the effect of increasing body size as it pertains to the bony skeleton has received very little attention. As far as could be determined, no one has ever attempted to discover whether or not the cartilaginous skeleton of mammals of comparable structure but greater size actually increases its ratio to the weight of the body. There have been, it is true, numerous papers published giving the results of investigations of the skeletal ratios of individual forms but in view of the various techniques employed it is impossible, in most instances, to use these data in a comparative study.

The present paper undertakes to answer two specific questions. First, what changes occur, if any, in the relative weight of the bony skeleton in adult mammals of comparable form in association with varying body sizes? Secondly, what changes occur, if any, in the relative areas of the main limb bones in adult mammals of comparable form in association with varying body sizes?

In an attempt to answer these questions, an investigation was undertaken to determine the relative and absolute weights of freshly prepared total bony skeletal material and the relative and absolute areas of the main limb bones for a series of mammals varying sharply in body weights but representing comparable types. The results obtained

as well as a critical analysis of the data and their impli-⁻⁷⁻
cations are presented for consideration.

At this point, I wish to express my gratitude and appreciation to Dr. Nathan Fasten and Dr. Ralph Huestis for their many helpful criticisms and suggestions.

4. Materials and Methods

(a) Comparative Weights of Skeletons

In this investigation, three species of mammals differing widely in weight but not manifesting any fundamental differences in body plan or skeletal proportions were utilized. These were, (1) the gray digger squirrel, Otospermophilus grammurus douglasii Richardson, weighing about 600 grams, (2) the domestic cat, Felis domestica Linnaeus, averaging in weight about 3500 grams, and (3) a series of dogs, Canis familiaris Linnaeus, whose weights varied from slightly over 7000 grams to nearly 20,000 grams. In addition data are included on the skeletal ratio of the albino rat, as reported by Donaldson (1919) as well as that for man which has been reported by a number of workers.

The procedure utilized was as follows: the animals were killed with ether and the total body weight recorded immediately. The bony skeleton was then dissected out, as much of the muscle tissue being removed as came away without too much difficulty. Following this, the treatment was similar to that described by Donaldson (1919) in connection with his work on the growth of the skeleton of the albino rat.

The bones were immersed in a 2% solution of soap powder -8-
(commercial " Gold Dust") which was heated almost to the
boiling point and kept there until the connective tissue
had loosened enough to permit the scraping of the bones
clean.

After the entire skeleton had been dissected out, sur-
face moisture was carefully removed with absorbent paper
and then the weight was recorded. After drying at room
temperature for two months or more, the skeletons were
again weighed. It was noted that the bones when allowed
to dry for a few weeks reach a condition of equilibrium
with the amount of moisture in the atmosphere and thereafter
weigh slightly more or less in accordance with whether
the relative humidity is high or low.

In order to check the effect of the method of preparing
the skeletons on the weights of the bones, specific
gravities were recorded and compared of femora cleaned by
scraping off the raw muscle and connective tissue and of
femora prepared by the method outlined above. These
specific gravity determinations were obtained by dividing
the weight of the bone in air with that of the fluid dis-
placed when the femur was submerged in water. It was found
that the use of the soap solution caused a slight loss in
weight but since all the bones were prepared similarly this
source of error applies equally to all of them and therefore
tends to minimize itself.

9.

The question of the density of bone in relation to -9- body size was considered to have a bearing on the investigation. Consequently the specific gravities were obtained for a series of mammals ranging in size from a mole to a large dog. The main limb bones were selected for these determinations and in every instance the untreated bone from which every particle of raw muscle and connective tissue had been carefully removed was utilized. The figure obtained in each case was for the specific gravity of the bone as a whole.

(b) Comparative Bone Areas

For this aspect of the investigation, femora and humeri that had been dried at room temperature were used. The areas of these bones were computed for a series of animals including the albino rat, guinea pig, domestic cat, dog, man, and cow. The figures obtained were added together giving a number which expressed the combined area of the four bones for each animal.

The irregularities in the shape of the limb bones are such as to make accurate determination of the areas difficult. The method finally selected, however, gave very satisfactory results. Each bone was covered with adhesive tape, care being taken to have the various strips coincide exactly. For the irregular uncovered spaces of bone, pieces of tape were cut to match these with the result that when the covering process was finished, the bone presented a

homogeneous appearance looking at first glance like a -10- plaster cast of a bone rather than the actual structure covered with tape. Conservatively, it required between three and four hours to prepare a humerus or a femur in this manner.

By this procedure the area could be computed in two ways, first, from the weight of the tape used, (the number of square centimeters per gram of tape was found to be constant for each roll) and second from the actual dimensions of the tape used in covering the bone as computed through taking the tape from the bone and laying it out on square millimeter paper.

From a number of determinations worked out according to the above method, a modification of Du Bois' formula (1916) for calculating the area of the human body was found to give the combined area for femur and humerus with fair accuracy in the case of such forms as the rat, cat, dog, and man.

This formula may be written:

$$A = 12 \left(\frac{W}{4} \right)^{.415} \left(\frac{L}{4} \right)^{.725}$$

where A denotes the combined area of femora and humeri in square centimeters; L refers to the total of lengths of femora and humeri in centimeters and W the total weight of femora and humeri in grams.

When applied to such divergent animals as the rat and man, this equation predicted the area of the bones measured

with a deviation of about 1% from the experimentally determined areas. However, the areas given in this paper were experimentally obtained in each case; the formula being used as a check and as an indicator of the comparability of form in the material used.

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5. Comparative Skeletal Ratios

(a) Total Skeletal Weight to body weight

Table 1 gives the relation between the weight of the skeleton and the body weight for the animals studied. An examination of these data discloses a definite trend towards a proportionately heavier skeleton in the larger forms. This is noted especially in the rat, the dog, and man. Even between the cat and the smallest dog the difference is greater than can be accounted for on the grounds of experimental error. Such errors as were likely to arise would tend to increase the skeletal percentage of the smaller animal as compared with the larger one. The surface area of the bones, as will be shown later, is proportionately greater in the smaller skeletons so that any surface moisture that may have been present at the time of weighing would favor these at the expense of the larger skeletons. Also the larger bones were easier to clean so that any difference due to this factor would again tend to increase the skeletal ratio of the smaller animals in comparison with the larger ones. Figures for the squirrel represent the average of seven animals and for the cat the average

TABLE 1

Weight of fresh skeleton on body weight

animal	body weight grams	skeletal weight (fresh) grams	skeleton to body weight percent
Albino rat Donalson (1919)	485	24	4.95
Gray digger squirrel	6601	331.2	5.2
Domestic cat	3750	263	7.02
Dog #1	7272	607	8.35
DOG #2	9250	821.45	8.9
Dog #3	9550	846.5	8.86
Dog #4	13181.8	1111.5	8.45
Dog #5	19772.7	1868	9.44
Man *			16.0

* Reported by Bischoff (1863), Liebig (1874), Thiele (1884), and Walters (1909).

of six. In the case of the dog there was such difference in size as to indicate listing them separately.

Of special interest is the distinct increase in skeletal ratio as between dog #1 and dog #5. Table 1 shows that dog #5 is about 2.7 times heavier than dog #1, a greater difference than exists between dog #1 and the cat. This would seem to show that the differences noted are not due to the diversity of the species compared. Further it may be mentioned that all the dogs and cats used in these determinations were males and all were in about the same physical condition, though some deviation in this respect was inevitable. Animals with excess fat were rejected.

(b) Combined Weights of Femora and Humeri to Body Weights

The main limb bones in animals of similar build and habits constitute a fairly definite proportion of the whole skeleton. The data contained in Table 2 reveal that the ratio of the combined femora and humeri weights to body weights increases with increasing body size. Here, as would be expected, there is more irregularity than is true for the ratios given in Table 1 but the general trend for the skeletal material to become relatively greater with increasing body size is the same. The weights of the limb bones used were taken from bones that were dissected out and cleaned without the use of the soap solution. Dog #6 was a large German police dog with comparatively longer legs than those possessed by other dogs studied. This may account, in part,

TABLE 2

Femora and humeri weights to body weight

animal	body weight grams	femora and humeri weights grams	ratio to body weight percent
Rat *	229.0	2.12	.93
Albino rat Donaldson (1919)	485.0	3.17	.65
Domestic cat	3073.0	45.72	1.49
Dog #1	7272.0	120.0	1.65
Dog #2	9250.0	145.0	1.57
Dog #3	9550.0	151.0	1.58
Dog #4	13181.8	206.2	1.57
Dog #5	19772.7	361.0	1.83
Dog #6	29600.0	555.0	1.87

* Rattus norvegicus (Erxleben)

for the higher index in this case. However, it will be -15- noted also that this animal was unusually heavy in comparison with the others.

6. Comparative Bone Densities

Whether or not a gram of bone from a large animal occupies the same volume as a gram of bone from a small animal is a matter of importance in such problems as are dealt with here. Table 3 records the specific gravities of the femora and humeri of a brief series of mammals. It reveals a general tendency for the bone density to be lower in the large animal, thus increasing the available area per unit of weight. It is possible that the differences recorded may be due to the factor of age. It is well known that in older animals the limb bones become more porous with advancing age. The animals used in the present investigation appeared to be in the full vigor of maturity but the exact ages were not definitely known. Also it will be seen that the densities of the main limb bones for the smallest animal in the series, namely the mole, do not follow the tendency common to the bones of the other animals in the table. Further data on this question would be necessary before accurate generalizations could be advanced.

7. Analysis of Data on Comparative Skeletal Ratios

The results which have been obtained seem to indicate that among mammals of comparable form there is considerable

TABLE 3
bone densities

animal	bone	specific gravity
Mole *	femur	1.45
	humerus	1.50
Norwegian rat	femur	1.54
	humerus	1.61
Guinea pig	femur	1.55
	humerus	1.56
Cat	femur	1.47
	humerus	1.49
Dog	femur	1.38
	humerus	1.39

* *Scapanus townsendi* (Bachman)

deviation, as far as the skeleton is concerned, from a strictly geometric growth of all parts with increasing body size. That the bone and muscle systems do not increase in accordance with physiological requirements has been strikingly shown by du Bois-Reymond's (1928) investigation, but apparently the other extreme of proportional increase in the size of parts and organs does not obtain either.

It is of interest to calculate what the skeletal percentages would be in Table 1 if the skeleton increased in such a manner with increasing body size as to have the same relative supporting strength in the larger as in the smaller animals. As stated before, the strength of the skeleton increases as the square of the linear measure while the body weight increases as the cube of the same measure with increasing body size in comparable forms. Hence in comparing a larger mammal with a smaller one, the skeletal percentage which would obtain in the former, when the same relative skeletal strength had been maintained can be calculated from the following formula:

$$P = \frac{pb \left(\frac{B}{b} \right)^{\frac{2}{3}}}{B}$$

In the above equation P is the percentage of skeletal material necessary in the larger of two mammals in order for the skeleton to have the same relative supporting strength, p the percentage of skeletal material for the smaller animal, B the body weight of the larger animal, and

TABLE 4

Experimental and theoretical skeletal ratios

animal	actual percentage	physiological percentage
Albino rat	4.95	4.95
Gray digger squirrel	5.2	5.50
Domestic cat	7.02	13.76
Dog #1	8.35	19.20
Dog #2	8.90	21.6
Dog #3	8.86	22.0
Dog #4	8.45	25.5
Dog #5	9.44	31.5
Man	16.0	58.50

b the body weight of the smaller animal.

By use of the above formula and taking the albino rat as a standard for comparison, these theoretical skeletal ratios have been calculated. The skeletal ratios obtained in this manner are shown in Table 4 together with a repetition of the experimentally determined percentages given in Table 1.

It becomes apparent that the requirements of physiological comparability are not so striking until the body size has increased to many times that of the smaller animal. Hence it becomes understandable that in larger animals there would be a tendency for the skeletal ratio to be greater than is the case with smaller types. Undoubtedly there is much deviation in this respect in accordance with the needs of the individual species. It is not likely that relatively inactive animals would show as much proportional increase in skeletal material as is true for the more vigorous and active types. But within each series, this tendency probably holds good.

8. Comparative Bone Areas

(a) Ratio of Femur and Humerus Areas to Bone and Body Weights

Data on the areas of such parts of the skeleton as the main limb bones serve to indicate the degree of uniformity of shape in the bones studied and at the same time act as a check for the results on skeletal ratios.

Table 5 records the absolute area of femora and humeri for each species in a series of mammals. In addition it shows the area in square centimeters per gram of bone. A glance at this table reveals that the available bone area becomes relatively less with increasing size of the bones. Thus we see a change from 10.6 square centimeters per gram of bone for the rat to .69 square centimeters per gram of bone for the cow. Even as between the smallest and largest dog there is a drop from 3.35 to 1.73. Chart 1 illustrates in graphic form the data given in Table 5.

In order to relate bone area to body weight, the square centimeter area per gram of bone for each species as given in Table 5 was multiplied by the total weight of the dry skeleton and then divided by the body weight in kilograms. This calculation gives the comparative bone area per kilogram of body weight for each animal in the series. Table 6 contains these comparative bone areas and it will be noted that here again the relative available bone area drops considerably with increasing body size.

(b) Theoretical and Empirical Bone Areas

It was important to know whether the areas obtained were such as would be expected in geometric comparability between larger and smaller animals. If they were, it would cast suspicion on the results obtained with respect to skeletal ratios. On the other hand, if they proved to be significantly higher, it would lend added support to the conclusion

TABLE 5

Absolute and relative areas of femora and humeri

animal	femora & humeri weights grams	femora & humeri areas sq. cm.	area per gram of bone sq. cm.
Albino rat	2.26	24.0	10.6
Guinea pig	4.37	35.92	8.2
Domestic cat	32.4	138.0	4.26
Dog #1	74.0	248.0	3.35
Dog #2	89.3	277.6	3.11
Dog #3	92.8	288.0	3.10
Dog #4	129.48	360.4	2.78
Dog #5	225.48	558.0	2.47
Dog #6	450.4	776.0	1.72
Man	950.0	1484.0	1.56
Cow	4344.0	2988.0	.69

CHART I

Comparative areas per gram of bone

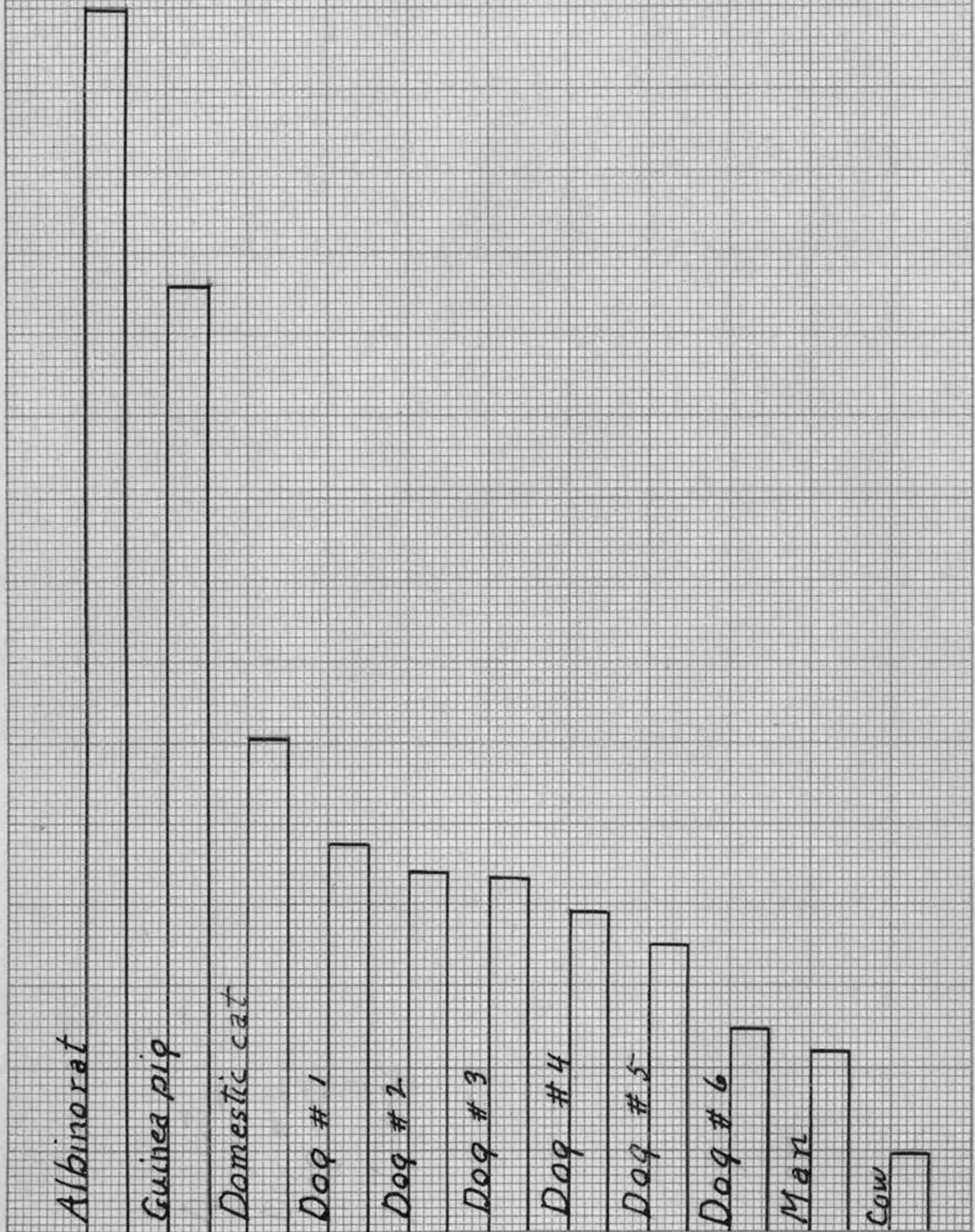


TABLE 6

Comparative bone areas per kilogram of body weight

animal	body wt. grams	skeletal wt.(dry) grams	area per gm. bone sq. cm.	area per gm. bone times wt. skeleton sq. cm.	bone area per kilo. body wt. sq. cm.
Rat (albino)	485	18.5	10.6	196	405
Cat	3750	198.5	4.26	845	226
Dog #1	7272	478	3.35	1600	220
Dog #2	9250	624	3.11	1940	210
Dog #3	9550	667	3.10	2070	217
Dog #4	13181.8	850	2.78	2363	180
Dog #5	19772.7	1400	2.47	3460	175

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that the skeleton becomes relatively heavier with increasing body size. The bone area of a larger animal as compared with a smaller one will vary as the square of the corresponding linear dimensions. The size of the smaller animal being taken as one, the size of the larger is equal to the cube root of the number of times the larger form is heavier than the smaller one. The square of the number so obtained times the bone area per gram of bone, times the weight of the skeleton of the smaller form and divided by the body weight of the larger animal, gives the comparative bone area per unit of body weight which would be true for the larger animal if increase in size had been accompanied by a proportional increase in skeletal material.

These relations are expressed in the equation,

$$A = \frac{\left(\frac{B}{b}\right)^{\frac{2}{3}}}{B}$$

where A is the comparative bone area per kilogram of body weight which would be true for the larger form if geometric comparability obtained, a, the bone area per gram of bone times the skeletal weight of the smaller form, B, the body weight of the larger animal, and b, the body weight of the smaller animal.

Table 7 contains the results of applying this formula to the animal series indicated in Table 6. Chart 2 illustrates these same results graphically. The albino rat serves as the standard for comparison in the calculations. It will be observed in the various forms considered that the bone area per kilogram of body weight is decidedly not in accord with

TABLE 7

Comparative bone areas as they are and as they would be if geometric comparability prevailed.

animal	area per kilo. of body wt. (experimental) sq. cm.	area per kilo. of body wt. (theoretical) sq. cm.
Albino rat	405	405
Domestic cat	226	202.5
Dog #1	220	164
Dog #2	210	152
Dog #3	217	150
Dog #4	180	135
Dog #5	175	117

CHART II

Left hand column = experimental bone areas.

Right hand column = Theoretical bone areas as per geometric comparability

Albino rat

Domestic cat

Dog #1

Dog #2

Dog #3

Dog #4

Dog #5

the requirements of geometric comparability. When measured ⁻²⁵⁻ by this standard the bone area is found to be much higher in the larger animals than it should be, if the relationship mentioned holds good.

Moreover it will be noted that the divergence in this respect is greatest in the largest animals of the group. For the cat, the figure is 226 square centimeter per kilogram of body weight from the experimental data and it is 202.5 square centimeters per kilogram of body weight from the theoretical calculations. On the other hand, for dog #5 the figures are 175 to 116.5. The ratio of the experimental figures to the theoretical in these two animals is for the cat 107 and for the dog 150.

(c) Skeletal Ratios Calculated from Bone Areas

To still further relate the data on relative bone areas and bone weights, the skeletal ratios were calculated for the dogs, from the bone areas given in Table 6, using the cat as a standard for comparison. This was also done for the largest dog alone using the smallest dog as a standard of comparison in the calculation.

This can be done in view of the relations existing between surface and weight in bodies of varying sizes which are comparable in form and material. The method may be illustrated as follows. If we compare two cubes, cube A and cube B of which cube A has a linear measure of 1 centimeter, a surface area of 6 square centimeters and a weight of 1 gram, and

cube B a linear measure of 2 centimeters, a surface area of ⁻²⁶⁻ 24 square centimeters, and a weight of 8 grams; then the area of A over the area of B equals weight of A reduced to the two-thirds power over the weight of B reduced to the two-thirds power. So given the areas of A and B and the weight of A the weight of B can be calculated.

In the bone calculations, the same relations obtain though it becomes necessary to express them a little differently. Here the geometrically comparable bone area of the larger animal is to its actual bone area as the skeletal ratio of the smaller animal times the body weight of the larger one, reduced to the two-thirds power, is to the real skeletal weight of the larger animal reduced to the two-thirds power.

The equation

$$\frac{A'}{A} = \frac{(pB)^{\frac{2}{3}}}{(PB)^{\frac{2}{3}}}$$

expresses these relations, where A' is the area necessary to make the larger animal geometrically comparable with the smaller animal, A is the comparative bone area of the larger form as determined experimentally, p the skeletal ratio of the smaller form, P the skeletal ratio of the larger form and B the body weight of the larger animal. A' or the comparative bone area necessary in the larger animal to give it the same proportions as the smaller one is obtained by taking the cube root of the number of times the larger animal is heavier than the smaller one, squaring this figure and multiplying by the comparative bone area of the smaller form. That is

$$A = \left(\frac{B}{b}\right)^{\frac{2}{3}} a$$

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where a, is the comparative bone area of the smaller animal, and the other symbols as in the previous formula.

By combining and simplifying the two formulas last given the following equation is obtained:

$$P = \frac{pb}{B} \left(\frac{A}{a}\right)^{\frac{3}{2}}$$

Table 8 shows a comparison of the skeletal ratios which were calculated and those determined experimentally from Table 1. It will be observed that the general rule for the skeleton to become relatively heavier with increasing body size in comparable forms holds true whether the cat or the smallest dog is used as a standard for comparison. The record also shows that, in general, the two sets of skeletal ratios are in accord with each other. In both instances a marked increase in body size is accompanied by a relatively heavier bone system.

The weight of the combined evidence from bone areas and bone weights warrants the statement that the skeleton of the larger animals, in a series of comparable mammals, is distinctly heavier than would be the case if geometric comparability in this respect were the rule. It must be added, however, that du Bois-Reymond (1928) in his paper, referred to before, on strength and thickness of bones in vertebrates of varying sizes, came to the opposite conclusion. He states in part that:

TABLE 8

Skeletal ratios as computed from the data on bone areas and as determined experimentally.

The cat used as a standard for comparison

animal	skeletal ratios from bone areas percentage	skeletal ratios from bone wts. percentage
Domestic cat	7.02	7.02
Dog #1	8.74	8.35
Dog #2	8.10	8.90
Dog #3	8.29	8.86
Dog #4	8.42	8.45
Dog #5	10.8	9.44

Dog #1 used as a standard for comparison

Dog #1	8.35	8.35
Dog #5	10.2	9.44

" Die Knochen grosser und kleiner Tiere verhalten sich in Wirklichkeit nahezu so, wie es bei geometrischer Ahnlichkeit der Tiere der Fall sein wurde. Die Knochen grosserer Tiere sind im Verhaltnis zu denen der kleinen weder wesentlich dicker noch fester, als es dem linearen Grosse-massstab entspricht."

Recalling again that du Bois-Reymond's investigation was conducted on dry skeletal material; that he deduced the weights of the animals from the skeletons themselves, and finally that he did not concern himself at all with skeletal weights or bone areas, his data seem to have a less direct bearing on the problem than that presented in this paper.

9. General Discussion

(a) Physiological Implications

Increased size in vertebrates is, as we have seen, gained at the expense of relative muscular strength, but the loss is not as great as would be the case if all parts of the body maintained the same size relations with increasing body size. Both the supporting strength of the bones and available area for muscle attachment increase faster than proportional growth would require but slower than will allow physiological comparability in strength with smaller forms.

The tendency for mammalian forms such as the cat, dog, and man to compensate in some measure for the loss in strength because of greater size by increasing the ratio of skeletal material to the rest of the body lowers the efficiency, comparatively, of the organism as a whole. It means that a relatively greater quantity of inert tissue must be

carried about, supported, and supplied with nutriment. On the other hand, the larger mammal suffers less heat loss from its relatively smaller body surface and so becomes less dependent on temperature variation and general climatic conditions. Larger size also brings a greater immunity from attack by other animals and a longer span of life. It is such advantages as these which counterbalance the handicaps inherent in an increased skeletal ratio. After all, it is the absolute strength of an animal over and above that utilized in supporting and carrying its weight which counts. The mouse is, relatively, much stronger than the cat but as du Bois-Reymond points out, the cat seizes and eats the mouse just the same.

When unusual body sizes are attained, it is more than likely that the purely mechanical factors involved serve to inhibit further increase in this direction. If an elephant weighing 6000 kilograms had the skeletal ratio of the cat, its bone area per kilogram of body weight would be about one-fortieth that of the cat or one twenty-fifth that of man. It is more likely that an increased skeletal ratio has compensated to some extent for the relatively great size.

In this connection, the question arises as to just what constitutes the maximum size possible for the terrestrial type of vertebrate animal. From the findings of paleontology, we know that in the Jurassic and Cretaceous periods of the Mesozoic era, reptilian forms, presumably land types many times larger than the African elephant existed.

Judging from the data presented here in regard to the re-⁻³¹⁻lations between available bone areas and body size, it would seem that either such animals were relatively very weak and sluggish or they frequented aquatic habitats where their bodies were wholly or partially submerged.

An idea of the difficulties involved in the mechanics of locomotion in terrestrial animals as large as some of the dinosaurs are said to have been may be gained by using an illustration similar to the one A.A.Packard gave with regard to muscular power in insects. If we compare two vertebrates similar in form and proportions but differing in weight, say one weighing 50 pounds and the other 25 tons, then the leg muscles of the smaller form would be under the same stress per square centimeter of cross-section area when it carried a load nine times its own weight, or 450 pounds, as would the muscles of the larger form in carrying its own weight. Some of the larger terrestrial dinosaurs are assumed to have weighed 25 tons or more and it is evident that, relatively, they must have had larger bone and muscle systems than smaller vertebrates.

(b) Evolutionary Implications - Orthogenesis

One of the most intriguing problems in the field of vertebrate evolution is that of orthogenesis. A certain character, often contrary seemingly to the principles of natural selection, becomes in the course of the evolution of a group of animals progressively more developed, finally

threatening the well-being and perpetuation of the type. One of the best illustrations of this orthogenetic trend of character development is found in the geological history of the extinct titanotheres. Henry Fairfield Osborn and his associates (1929) discovered and described a complete series of these hoofed herbivores beginning with small forms in the middle Eocene and culminating in the gigantic Brontotherium of the Oligocene. This latter genus, according to Osborn (1918), contained animals which were, aside from the Proboscidea, among the largest mammals ever to have existed upon the earth.

Among some of the earliest and smallest of these titanotheres are found specimens with the beginnings of fronto-nasal horns consisting of tubercle-like bony prominences. As these forms evolved towards greater body size these bony projections became so much enlarged that, in Brontotherium, they became huge elongated horns. The remarkable characteristic about the development of these bony projections is that in the larger forms they are relatively larger than in the smaller ones; so much so as to constitute a handicap which may have been instrumental in causing the extinction of the race.

J.S.Huxley (1924) reported the same growth relation between the horns and the body of deer. The larger deer have relatively larger horns. Huxley considered that the rate of action of the factor controlling the growth of such heterogonic organs was dependent upon body size and that

increase in size would necessitate an exponential increase -33- in the size of such appendages.

It is suggested here that the relatively greater size of such structures can be explained by reference to the data which have been presented with respect to skeletal ratios in comparable mammals of different body sizes. Such appendages as the horns of the titanotheres or of the deer are essentially parts of the skeleton and the same determiners which caused a relative increase in the size of the bone system in response to increasing body size would probably bring about a corresponding increase in them. So if the skeletal ratio of the larger titanotheres in comparison with the smaller types was greater, then such parts of the skeleton as the horns would reflect such a condition. For example, an increase in the skeletal ratio from 10 to 15 percent would cause the larger animals horns, on this basis, to be relatively one and a half times larger than the horns of the smaller animal.

It may be objected that since such appendages as the horns are not subjected to the stresses which obtain for other parts of the skeleton, and since the increased skeletal ratio is supposed to be called forth in an effort to compensate to some degree for these increased strains these parts would not necessarily be affected. However, it must be kept in mind that the stimulus towards an increased skeletal ratio with increased body size applies to the greater part of the bony structure of the body so that it

is likely the determiners for the size of the skeleton as⁻³⁴⁻ a whole would be affected. Further, as Huxley has shown, increased body size is invariably a concomitant factor and if increased body size means an increased skeletal ratio it would seem more logical to associate the growth of such heterogonic organs with the skeletal system of which they form a part.

It is not intended to imply that such a relation would hold in the case of skeletal structures highly adaptive in character. But in the instance of the horns of the titanotheres, there seems to be no reason for supposing an increase out of proportion with the rest of the body with increasing body size would have any particular adaptive value when carried to extremes. It seems more reasonable to suppose that the actual presence and characteristics of the horns are controlled by specific determiners but that the amount of evolution towards increased size is governed by the same factors which determine the amount of evolution in increased size of the skeleton as a whole.

Whether or not such a relationship exists can only be determined by empirical evidence. If the horns of the large deer though relatively larger in proportion to body weight than the horns of its smaller prototype, should be found to bear about the same relation by weight to the skeleton as a whole as the smaller form, then we could be fairly certain that this type of orthogenetic evolution was merely a product of the skeleton's adaptation to the mechanical difficulties attendant upon increasing body size. Moreover, it would be

understandable why such skeletal protuberances as the horns of the titanotheres or the antlers of the great Irish elk increased in size until they became a positive handicap to the animals bearing them. It is probable that in many instances where a character in a group of animals increases in relative amount until it threatens the survival of the types concerned, the trait in question is linked to other characters whose selective value is strong enough to cause continuous progression, inspite of the fact that at the same time some other feature is being developed unduly.

In the case of the titanotheres, for example, size probably early attained high selective value. And the fact that secondarily and concomitant with increase in size such structures as the horns were becoming disproportionately large would not inhibit the main tendency until such time as the assets of size equaled the liability of further increase in size of the horns.

10. Concluding Remarks

Weiske (1895) and Burnett (1908) have shown that the kind of food utilized by an animal may affect the composition, weight, and strength of its bones. Such findings would seem to weaken the conclusions reached from the data presented in the present paper. It is well to recall again the fact that the bones of the various forms used were checked with regard to bone densities. The variations in the specific gravities of the bones within any one of the species studied

were found to be so slight as to be negligible. The lack of³⁶⁻ any significant degree of variation in this respect was the criterion of importance. When old members of a species are compared with younger ones there is found to exist a definite variation in bone density. Invariably the bones of the older animals have a lower specific gravity than those belonging to the more youthful ones.

Finally it must be emphasized that the results of the present investigation apply only to comparable forms and the term comparable includes such items as age, physical condition, and diet of the forms compared. It is only when the animals compared differ widely in body size, such as those utilized in the present studies that the term comparable can be applied in a broader sense since the tendency seems to be strong enough to show in such cases even when all the conditions of comparability are not present. It is not likely that such domestic animals as cattle or hogs bred for generations with a view to their utility as meat producers would show as high a skeletal ratio as otherwise comparable forms still in the wild state, and it is not expected that animals relatively inactive through adaptation would realize the full potentiality of their bone systems. It does seem that both the evidence on bone areas and bone weights points towards the probability of a general tendency for the skeleton to become relatively heavier as the body in comparable terrestrial vertebrates attain through evolution to increased body size.

1. Data presented on the ratio of fresh skeletal weight to body weight in a series of mammals of varying body sizes indicate that the percentage of total skeletal material becomes progressively and proportionately higher in comparable mammals with increasing body size.

2. Data presented on the comparative and absolute areas of femora and humeri in a series of mammals of varying body sizes disclose a distinct proportionate decrease in bone area with increasing body size. The relative bone area is, however, higher than would be expected if geometric comparability between smaller and larger mammals prevailed.

3. A mathematical calculation of the skeletal ratios from the data on bone areas confirms the tendency observed in the data on comparative skeletal weights.

4. The relatively larger size of the horns of larger deer as compared with the horns of smaller deer, and the similar condition prevailing with respect to the horns of the large titanotheres as compared with the horns of the earlier, smaller titanotheres, can be explained on the basis of this tendency for the percentage of skeletal material to be higher in the larger of two comparable mammals. It is unnecessary to assume, therefore, that these phenomena are due to a mysterious orthogenetic trend.

- Bergmann and Leuchart (1855) 'Vergleichende Anatomie und Physiologie', Stuttgart.
- Bischoff, E. (1863) 'Einige Gewichts und Trocken Bestimmungen der Organe des menschlichen Körpers', Zeitschr. f. Rationelle Medicin. 20:75-118.
- Burnett, E.A. (1908) 'The effect of food on breaking strength of bones'. Bull. 107 of the Agric. Exp. Station of Nebraska, Vol. 21, article 1.
- (1911) 'The effect of food on the strength, size, and composition of the bones of hogs'. 24th Ann. Report Agric. Exp. Station, Nebraska pp 178-208.
- Donaldson, H.E. (1919) 'Quantitative studies on the growth of the skeleton of the albino rat'. Am. Jour. of Anatomy, 26:237-314.
- Du Bois-Reymond, R. (1928) 'über Dicke und Festigkeit der Knochen bei grossen und kleinen Tieren'. Zetschr. f. Wissensch. Zool. 132:1-36.
- Du Bois, D. and E.F. (1916) 'A formula to estimate the approximate surface area if height and weight are known'. Arch. Internal Med. 17.
- Galilei, Galileo. (1638) 'Discorsi e Dimostrazioni matematiche interno a due nuovo science'. Leida Elsevirii. Dial. 2 P. 128.
- Huxley, J.S. (1924) 'Constant differential growth rates and their significance.' Nature, 111 p. 865.
- Liebig, G.V. (1874) 'Gewichtsbestimmungen der Organe des menschlichen Körpers.' Archiv f. Anat. Physiol. und Wissensch. Med. pp. 96-117.
- Osborn, H.F. (1929) 'The titanotheres of ancient Wyoming, Dakota, and Nebraska.' Vol. 1 and 2 Monograph 55, U.S. Govt. Printing Office, Washington.
- Packard, A.A. (1898) 'A text-book of entomology of insects.' p. 219. The MacMillan Co. N.Y.
- Plateau (1866) 'Sur la force musculaire des insects.' Bull. de L'Acad. R. Belge, T. 20, p. 132.

- Theile, F.W. (1884) ' Gewichtsbestimmungen zur Entwicklung des Muskel-systems und des Skelettes beim Menschen.' Durch eine biographische Notiz eingeleitet von W. His. 4 Hefen, E. Blochmann u. Sohn, in Dresden.
- Walter, H.E. (1918) ' The human skeleton, an interpretation.' MacMillan and CO. New York.
- Walters, F.M. (1909) ' Physiology and hygiene.' D.C. Heath and Co. N.Y.
- Weiske, H. (1895) ' Weitere Beitrage zur Frage uber die Wirkung eines Futters mit sauren Eigenschaften auf den Organismus insbesondere auf das Skelett. Zeitschr. f. Physiol. Chem. Bd. 20.