THE GROWTH OF THE EPIPHYSES OF THE LONG BONES IN THE MADDER-FED PIG

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While there is general agreement that growth in length of long bones is mainly due to diaphysial activity, the subject of epiphysial growth has not been carefully investigated, and is well-nigh absent in the literature (1–6). With few exceptions the observations available are inadequately supported.

Testut (7), Poirier (8) and Franceries (9) state that the epiphyses grow in length by additions to their diaphysial surfaces.

Jamieson (10) states that the epiphyses grow by additions to both the diaphysial and articular surfaces.

Macewan (11) states that the epiphysial discs have nothing to do with epiphyses and suggests that they should be called diaphysial discs. Keith (12) confirms Macewan's statement. Goodsir (13) states that in a physiological sense an epiphysis should be regarded as a separate bone. Bergmann (14) states that the epiphyses grow on the side nearest the joint.

These various statements have been made from the direct study of the growing bones except the last (Bergmann), where radiographs of the long bones of a girl 5½ years old have been used.

The present contribution attempts to solve the problem whether the epiphyses grow by additions to their diaphysial surfaces, to their articular surfaces, or both.

MATERIALS AND METHODS

The observations and measurements are made from the epiphyses of the limb bones of madder-fed pigs used in my recent published investigation on diaphysial growth (15).

The epiphyses were derived from the limb bones of a dozen madder-fed pigs varying in age between 80 and 587 days.

In the case of an older animal whose rate of growth was diminishing in rapidity, the madder was withheld for a longer period before killing than in the case of the younger animals. They were thus treated by the "indirect madder method," whereby the new bone of the non-madder period shows up white against the background of the thoroughly maddered skeleton. Table I gives particulars of age, madder period, and growth period without madder.

The skeletons were macerated in a weak solution of KOH (0·1 per cent.).

Table I. *Duration in days with and without madder-feeding*

Pig No.	Age at death days	Madder period days	Non-madder period
14	80	72	8
15	91	77	14
16	108	84	24
17	126	105	21
12	140	61	28
1	169	68	29
2	197	97	28
3	225	125	28
4	279	153	54
6	362	207	84
9	475	271	126
8	587	394	116

PRELIMINARY OBSERVATIONS

All the epiphyses of the limb bones separated readily except in the case of the oldest animals, in which bony union of the distal humeral and proximal radial epiphyses was seen in No. 6 (362 days). No additional epiphyses had united in No. 9 (475 days). In the oldest pig, No. 8 (587 days), in addition to the above two the distal tibial epiphysis had also united. It has been possible to ascertain from the bones of older pigs, treated in the same way as this series, that at 647 days in addition to the foregoing, the proximal ulnar, femoral and distal fibular epiphyses have united. The remaining epiphyses—distal radial, ulnar, femoral; proximal humeral, tibial and fibular—have united in a pig aged 729 days.

Both Stevenson (16) and Dawson (17), the former working on human bones, the latter on those of the albino rat, agree that in general there is an age sequence of union of epiphyses. The sequence given by these workers is noted below and contrasted with the sequence of union of the epiphyses under present consideration (Table II).

Table II. *Sequence of union of epiphyses from the first to the last*

Present investigation in pig		Stevenson's results in Man	Dawson's results in albino rat
Distal humeral, Proximal radial	362 days	Distal humeral	Distal humeral
		Proximal radial	Proximal radial
Distal tibial	587 ,,	Proximal ulnar	Distal tibial
		Proximal fibular	Distal fibular
Proximal ulnar, Proximal fibular, Distal fibular	647 ,,	Distal tibial	Proximal ulnar
		Distal fibular	Proximal fibular
		Proximal tibial	Distal fibular
		Proximal fibular	Proximal tibial
Distal radial, Distal ulnar, Distal fibular, Proximal humeral, Proximal tibial, Proximal fibular	729 ,,	Distal fibular	Proximal fibular
		Distal radial	Distal radial
		Distal ulnar	Distal ulnar
		Proximal humeral	Proximal humeral

This latter sequence is necessarily very inadequate, as only a few individual pigs are considered as contrasted with the large number of skeletons examined

by Stevenson and Dawson. These workers point out that in the limb bones the distal humeral epiphysis is the first to unite and the proximal humeral epiphysis the last. In this series of pig bones the distal humeral epiphysis is one of the first to unite and the proximal humeral epiphysis is one of the last to unite.

Humphry (18) states that "the end of the shaft at which the epiphysis is last united is the end at which growth takes place most quickly." The following table (III) confirms this for the present series of pig bones. The ends of the diaphyses with greater and lesser increments have been described in my previous paper (15), and the results therein detailed are utilised in Table III.

Table III. *The relation of last uniting epiphysis to diaphysial end showing greatest increment*

In the case of the		Humerus	The last epiphysis to join the diaphysis is the			Proximal	The increment of this end of the diaphysis is the greater			
,,	,,	Radius	,,	,,	,,	Distal	,,	,,	,,	,,
,,	,,	Ulna	,,	,,	,,	Distal	,,	,,	,,	,,
,,	,,	Femur	,,	,,	,,	Distal	,,	,,	,,	,,
,,	,,	Tibia	,,	,,	,,	Proximal	,,	,,	,,	,,
,,	,,	Fibula	,,	,,	,,	Proximal	,,	,,	,,	,,

The general distribution of new bone of the epiphysial surfaces has already been observed (15). The articular surfaces of the epiphyses are covered by new bone. The contiguous surfaces of the diaphyses and epiphyses present a marked contrast—the ends of the diaphyses being entirely composed of new white bone, and the diaphysial surfaces of the epiphyses being red with no addition of new white bone even for the longest non-madder period.

The contiguous surfaces of epiphysis and diaphysis have reciprocal elevations and depressions which Thomson (19) has shown to be more pronounced in those animals which maintain the knee in a flexed position. In addition to being irregular the diaphysial surfaces of the epiphysis are everywhere covered by small pits which give an eroded appearance to the surface (Fig. 1). These erosions are familiar on the diaphyses and are referred to by Kölliker (20) and Sharpey-Schäfer (21) as the Foveolae of Howship, and are stated to appear wherever absorption is proceeding. It will be shown by measurement that, unless these erosions on the diaphysial surfaces of the epiphyses represent absorption, the increments of new white bone on the articular surfaces give an increase in length to the epiphyses in excess of the actual.

GROWTH IN LENGTH OF EPIPHYSES

Methods of measurement. The epiphyses of the humerus, radius and ulna were sectioned in the sagittal and those of the femur, tibia and fibula in the coronal planes (the same planes as used for the respective diaphyses).

A prominent ridge or depression on the diaphysial or articular surface of

each set of epiphyses was selected and the length (Table IV) was measured from this ridge or depression to the other surface in the long axis of the particular bone, as shown in Figs. 2–7.

Table IV. *Measurements of epiphyses in mm.*

Pig No.		14	15	16	17	12	1	2	3	4	6	9	8
Humerus:	Proximal	11·5	11·5	11·8	12·0	13·0	12·0	14·5	15·0	14·0	13·5	15·0	16·5
	Distal	12·5	13·0	13·0	13·5	14·0	13·5	14·5	16·0	16·0	14·5	15·0	17·0
Radius:	Proximal	7·0	7·5	6·0	7·0	9·0	8·5	9·0	9·0	9·5	9·0	8·5	9·0
	Distal	11·5	11·5	11·5	12·0	13·0	12·0	14·5	15·5	14·0	14·0	15·0	17·0
Ulna:	Proximal	14·0	13·0	13·5	15·0	17·0	16·0	18·0	19·5	18·5	19·0	17·5	18·0
	Distal	18·5	18·0	17·0	20·0	20·0	19·0	23·5	25·0	22·0	22·0	23·0	25·0
Femur:	Proximal	13·0	13·0	13·2	13·0	16·0	14·5	17·0	18·0	17·0	16·5	17·0	17·8
	Distal	18·5	18·5	17·0	19·0	21·5	19·5	23·8	26·5	25·5	26·0	28·3	31·7
Tibia:	Proximal	14·0	15·0	13·5	15·8	14·5	15·0	16·0	15·5	15·3	15·5	16·0	17·0
	Distal	8·4	8·0	8·0	8·0	8·5	8·0	8·8	9·0	8·0	7·8	8·5	10·0
Fibula:	Proximal	7·0	6·5	7·5	7·5	8·5	9·8	10·0	10·0	11·0	12·0	12·0	13·7
	Distal	12·0	12·0	12·0	12·8	13·5	13·5	14·5	14·5	13·0	13·0	13·5	16·4

This method of measurement was selected in preference to using an osteometric board, since the increment of new bone on the articular surface could be easily measured in the same line as the length (Figs. 2–7).

The proximal and distal epiphyses are unequal in length throughout the series; but, contrary to what one might expect, there appears to be no relation between the difference in epiphysial length and the ends of the diaphyses with the greater and lesser increments, e.g. the distal epiphyses of the humerus and fibula being longer than the proximal are adjacent to the ends of their respective diaphyses with the lesser increments.

The difference in length between the younger and the older epiphyses shows that, for each long bone, the epiphysis increases more at one end than the other. The epiphysis that increases most is situated adjacent to the diaphysial end with the larger growth (Table V).

Table V. *The association of greater epiphysial growth with the end of greater diaphysial growth*

		No. 14 mm.	No. 8 mm.	Difference mm.	Diaphysial end with greatest increment
Humerus:	Proximal	11·5	16·5	5·0	Proximal
	Distal	12·5	17·0	4·5	
Radius:	Proximal	7·0	9·0	2·0	Distal
	Distal	11·5	17·0	5·5	
Ulna:	Proximal	14·0	18·0	4·0	Distal
	Distal	18·5	25·0	6·5	
Femur:	Proximal	13·0	17·8	4·8	Distal
	Distal	18·5	31·7	13·2	
Tibia:	Proximal	14·0	17·0	3·0	Proximal
	Distal	8·4	10·0	1·6	
Fibula:	Proximal	7·0	13·7	6·7	Proximal
	Distal	12·0	16·4	4·4	

It will also be seen from Table V that the amount of growth over a period of (587 – 80) 507 days varies from 1·6 mm. in the case of the distal

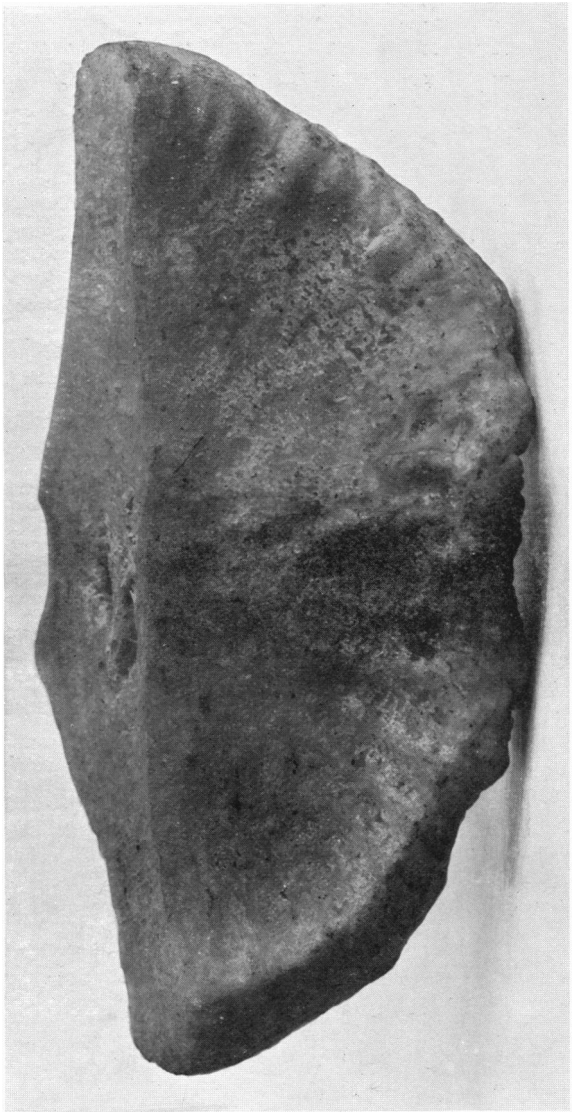

Fig. 1. Photograph of the posterior half of the diaphysial surface of the proximal tibial epiphysis (Pig No. 6). To show the eroded appearance of this surface as described in text. Mag. × 3 approx.

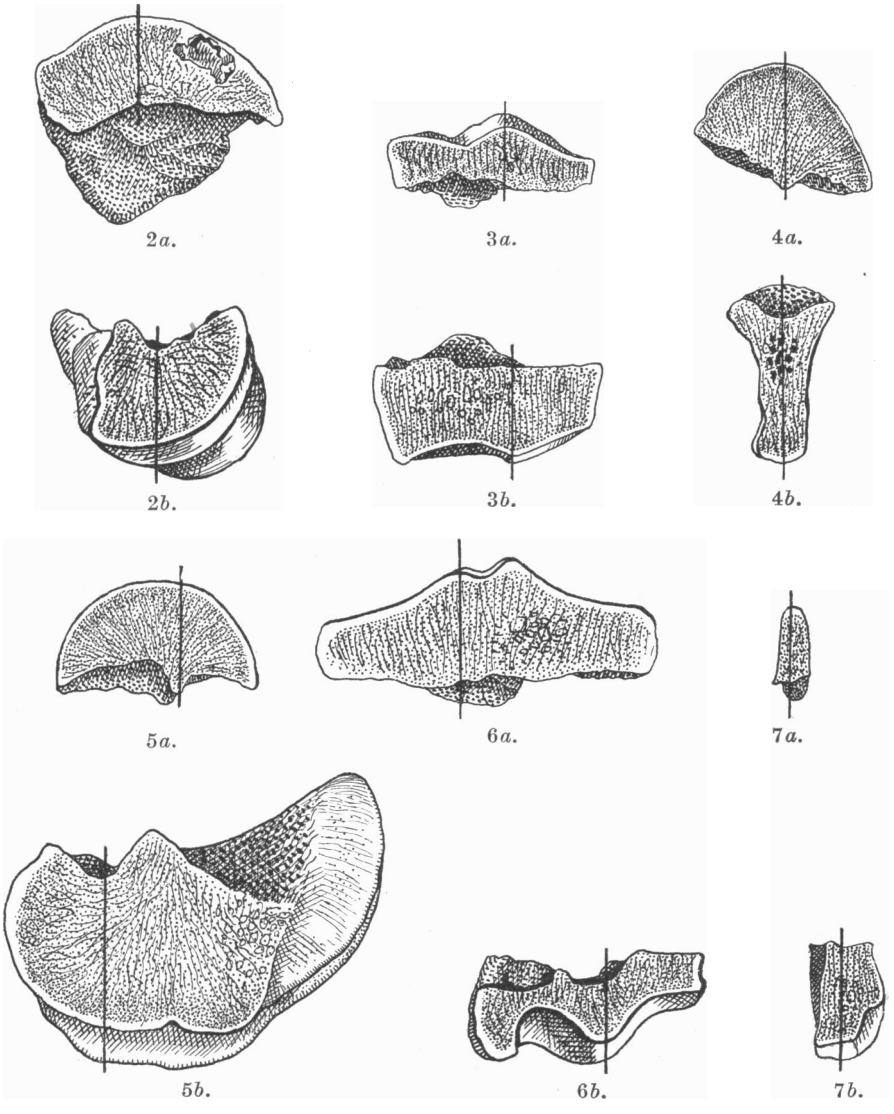

Fig. 2. Sagittal sections of (*a*) proximal and (*b*) distal epiphyses of humerus of pig 169 days old (No. 1).

In each of these figures (2–7) the areas of bone unstained by madder are represented white and indicate new bone laid down during the second non-madder period (29 days). Bone stained by madder is stippled. A vertical line indicates where the length of the epiphysis was measured as described in text.

Fig. 3. Sagittal sections of (*a*) proximal and (*b*) distal epiphyses of radius of same pig as Fig. 2.

Fig. 4. Sagittal sections of (*a*) proximal and (*b*) distal epiphyses of ulna of same pig as Fig. 2.

Fig. 5. Coronal sections of (*a*) proximal and (*b*) distal epiphyses of femur of same pig as Fig. 2.

Fig. 6. Coronal sections of (*a*) proximal and (*b*) distal epiphyses of tibia of same pig as Fig. 2.

Fig. 7. Coronal sections of (*a*) proximal and (*b*) distal epiphyses of fibula of same pig as Fig. 2.

epiphysis of the tibia to 13·2 mm. for the distal epiphysis of the femur. These amounts are arranged in order in Table VI.

Table VI. *Extent of growth in various epiphyses for period of 507 days*

	mm.
Tibia, distal	1·6
Radius, proximal	2·0
Tibia, proximal	3·0
Ulna, proximal	4·0
Fibula, distal	4·4
Humerus, distal	4·5
Femur, proximal	4·8
Humerus, proximal	5·0
Radius, distal	5·5
Ulna, distal	6·5
Fibula, proximal	6·7
Femur, distal	13·2

MEASUREMENTS OF EPIPHYSIAL GROWTH

The growth increments at the articular ends of all the epiphyses, as represented by the layer of new white bone laid down during the respective non-madder periods, have been measured in the same axes as the length and are recorded in Table VII.

Table VII. *Measurements of new bone of epiphyses in mm.*

Pig No.		14	15	16	17	12	1	2	3	4	6	9	8
Humerus:	Proximal	1·2	1·8	1·7	1·5	1·5	1·0	1·2	1·0	1·3	1·0	2·0	2·0
	Distal	1·0	1·5	1·0	1·5	2·0	1·0	1·0	0·8	1·0	1·0	1·5	1·7
Radius:	Proximal	1·0	1·0	0·8	1·0	1·0	1·0	1·0	0·8	0·8	0·8	1·0	1·2
	Distal	1·0	1·0	0·8	1·0	1·5	1·0	0·8	1·0	1·0	1·0	2·5	1·8
Ulna:	Proximal	0·5	1·0	0·5	0·5	1·0	0·5	0·5	0·5	0·5	1·0	1·0	2·0
	Distal	1·0	1·0	1·0	1·0	1·0	1·0	1·0	1·0	0·5	0·5	2·0	2·0
Femur:	Proximal	1·0	1·5	1·0	1·4	1·8	1·0	1·0	1·3	1·0	1·5	1·5	1·0
	Distal	1·0	1·3	1·5	2·0	1·8	1·0	1·5	1·5	1·5	1·4	1·9	1·7
Tibia:	Proximal	1·0	2·0	1·5	1·5	2·0	1·8	1·5	1·5	1·0	1·5	2·0	1·5
	Distal	1·0	1·2	0·8	1·0	1·5	1·0	1·0	1·0	0·5	1·0	1·0	1·0
Fibula:	Proximal	1·0	1·0	1·0	1·3	1·6	1·5	1·0	1·0	1·0	1·5	1·8	1·8
	Distal	1·0	1·4	0·8	0·8	1·0	1·0	1·0	1·0	0·8	1·0	1·5	1·5

It is obvious from Table V that the growth increment is similar in the proximal and distal epiphyses, an interesting and also remarkable contrast to the unequal growth of the two ends of the diaphyses. Generally, the amount of growth in any epiphysis is rather less than that of the lesser growing end in any diaphysis.

GROWTH PER WEEK

Since the non-madder growth periods of the individual bones vary, having been increased with the age of the animal in order to obtain about the same amounts of new bone as the general rate of growth diminished, the growth increments cannot be directly compared. The table of measurements of new bone (Table VII) shows the increments during periods varying from 8 to

126 days. In order to compare rates of growth in young and old epiphyses, the amount of new bone laid down at the proximal and distal epiphyses has been calculated to one week (Table VIII).

Table VIII. *Calculated measurements of new bone in mm. per week during non-madder periods*

Pig No.		14	15	16	17	12	1	2	3	4	6	9	8
Humerus:	Proximal	1·2	0·9	0·5	0·5	0·37	0·25	0·3	0·25	0·16	0·08	0·11	0·12
	Distal	1·0	0·75	0·29	0·5	0·5	0·25	0·25	0·2	0·12	0·08	0·08	0·10
Radius:	Proximal	1·0	0·5	0·23	0·33	0·25	0·25	0·25	0·2	0·10	0·06	0·05	0·07
	Distal	1·0	0·5	0·23	0·33	0·37	0·25	0·2	0·25	0·12	0·08	0·14	0·11
Ulna:	Proximal	0·5	0·5	0·14	0·15	0·25	0·12	0·12	0·12	0·06	0·08	0·05	0·12
	Distal	1·0	0·5	0·29	0·33	0·25	0·25	0·25	0·25	0·06	0·04	0·11	0·12
Femur:	Proximal	1·0	0·75	0·29	0·47	0·45	0·25	0·25	0·32	0·12	0·12	0·08	0·06
	Distal	1·0	0·65	0·44	0·66	0·45	0·25	0·4	0·4	0·19	0·11	0·10	0·1
Tibia:	Proximal	1·0	1·0	0·44	0·5	0·5	0·45	0·37	0·37	0·10	0·12	0·11	0·09
	Distal	1·0	0·6	0·23	0·33	0·37	0·25	0·25	0·25	0·06	0·08	0·05	0·06
Fibula:	Proximal	1·0	0·5	0·29	0·43	0·4	0·37	0·25	0·25	0·19	0·12	0·10	0·11
	Distal	1·0	0·7	0·23	0·26	0·25	0·25	0·25	0·25	0·10	0·08	0·08	0·09

From Table VIII it is clear that there is a gradual diminution in the rate of growth in every epiphysis as one passes from the younger to the older epiphyses. The diminution is greater in the epiphyses which are adjacent to the end of the diaphysis with the lesser increment and which unite with the diaphysis first (Table III).

EXPECTED INCREMENTS OF NEW BONE

The rate of the epiphysial growth of the individual epiphyses now being known between 80 and 587 days, it is possible, taking the lengths of the youngest epiphyses as a starting-point, to calculate the growth increments that might be expected to be added at the stage of each successive older epiphysis. The differences in age of the successive older epiphyses do not always correspond to the non-madder growth periods, so that it is necessary to calculate from the rates of growth, the amount of growth for these periods of differences in age. The results of these calculations are set out in Table IX.

Table IX. *Measurements of new bone in mm. for periods of differences in age*

Pig No.		14	15	16	17	12	1	2	3	4	6	9	8
Humerus:	Proximal	—	1·35	1·20	1·25	0·74	1·0	1·2	1·0	1·23	0·96	1·77	1·92
	Distal	—	1·12	0·69	1·25	1·0	1·0	1·0	0·8	0·92	0·96	1·28	1·6
Radius:	Proximal	—	0·75	0·55	0·82	0·50	1·0	1·0	0·8	0·77	0·72	0·81	1·12
	Distal	—	0·75	0·55	0·82	0·74	1·0	0·8	1·0	0·92	0·96	0·99	1·76
Ulna:	Proximal	—	0·75	0·53	0·37	0·50	0·48	0·48	0·48	0·46	0·96	0·81	1·92
	Distal	—	0·75	0·69	0·82	0·50	1·0	1·0	1·0	0·46	0·48	1·7	1·72
Femur:	Proximal	—	1·22	0·69	1·17	0·90	1·0	1·0	1·28	0·92	1·44	1·28	0·96
	Distal	—	0·97	1·0	1·6	0·90	1·0	1·6	1·6	1·5	1·32	1·61	1·6
Tibia:	Proximal	—	1·5	1·06	1·25	1·0	1·80	1·48	1·48	0·77	1·44	1·77	1·44
	Distal	—	0·9	0·55	0·82	0·74	1·0	1·0	1·0	0·46	0·96	0·80	0·96
Fibula:	Proximal	—	0·75	0·69	1·06	0·8	1·48	1·0	1·0	1·5	1·44	1·61	1·76
	Distal	—	1·0	0·55	0·65	0·50	1·0	1·0	1·0	0·77	0·96	1·28	1·44

In Table X the differences in the actual length between the youngest and oldest epiphyses representing the actual amount of growth is compared with the expected amount of growth. This expected amount of growth is obtained from the summation of the successive increments of each successive older epiphysis shown in Table IX.

Table X. *The difference between actual and expected growth*

		Length No. 14 mm.	Length No. 8 mm.	Growth increase mm.	Expected increment mm.	Difference mm.
Humerus:	Proximal	11·5	16·5	5·0	13·62	8·62
	Distal	12·5	17·0	4·5	11·62	7·12
Radius:	Proximal	7·0	9·0	2·0	8·84	6·84
	Distal	11·5	17·0	5·5	10·29	4·79
Ulna:	Proximal	14·0	18·0	4·0	7·74	3·74
	Distal	18·5	25·0	6·5	10·12	3·62
Femur:	Proximal	13·0	17·8	4·8	11·86	7·06
	Distal	18·5	31·7	13·2	14·70	1·50
Tibia:	Proximal	14·0	17·0	3·0	14·99	11·99
	Distal	8·4	10·0	1·6	9·19	7·59
Fibula:	Proximal	7·0	13·7	6·7	13·09	6·39
	Distal	12·0	16·4	4·4	10·15	5·75

It is noted that the expected exceeds the actual increment to a varying amount of 11·99 mm. (proximal tibia) to 1·50 mm. (distal femur), the average excess being 6·25 mm.

It is remarkable that the comparison of the actual lengths of some of the youngest and oldest epiphyses shows a very small actual increase in length (distal tibia 1·6 mm., proximal radius 2·0 mm., proximal tibia 3·0 mm.) although the expected increments for these same epiphyses are 9·19, 8·84 and 14·99 mm. respectively, the last being actually the largest of the expected increments.

Now this excess of expected over actual increment presumably represents the amount of absorption which is occurring at the diaphysial surfaces of the epiphyses. Indeed the extent of absorption is almost as much as the increment.

The data provided by Table IX have been used to illustrate graphically the relative rates and amounts of growth and absorption at the articular and diaphysial ends respectively of the epiphyses (Figs. 8–9).

SUMMARY AND CONCLUSIONS

This investigation of epiphyses of the madder-fed pig offers further confirmatory evidence that:

(1) The epiphyses grow at the side nearest the joint—Bergmann (14).

Attention is drawn to a new observation relating to the appearance of the diaphysial surfaces of the epiphyses indicating absorption.

This absorption is extensive and remarkable, because the expected exceeds the actual increment by an average of 6·25 mm., and because some of the epiphyses increase very little in length (distal tibia 1·6 mm., proximal radius

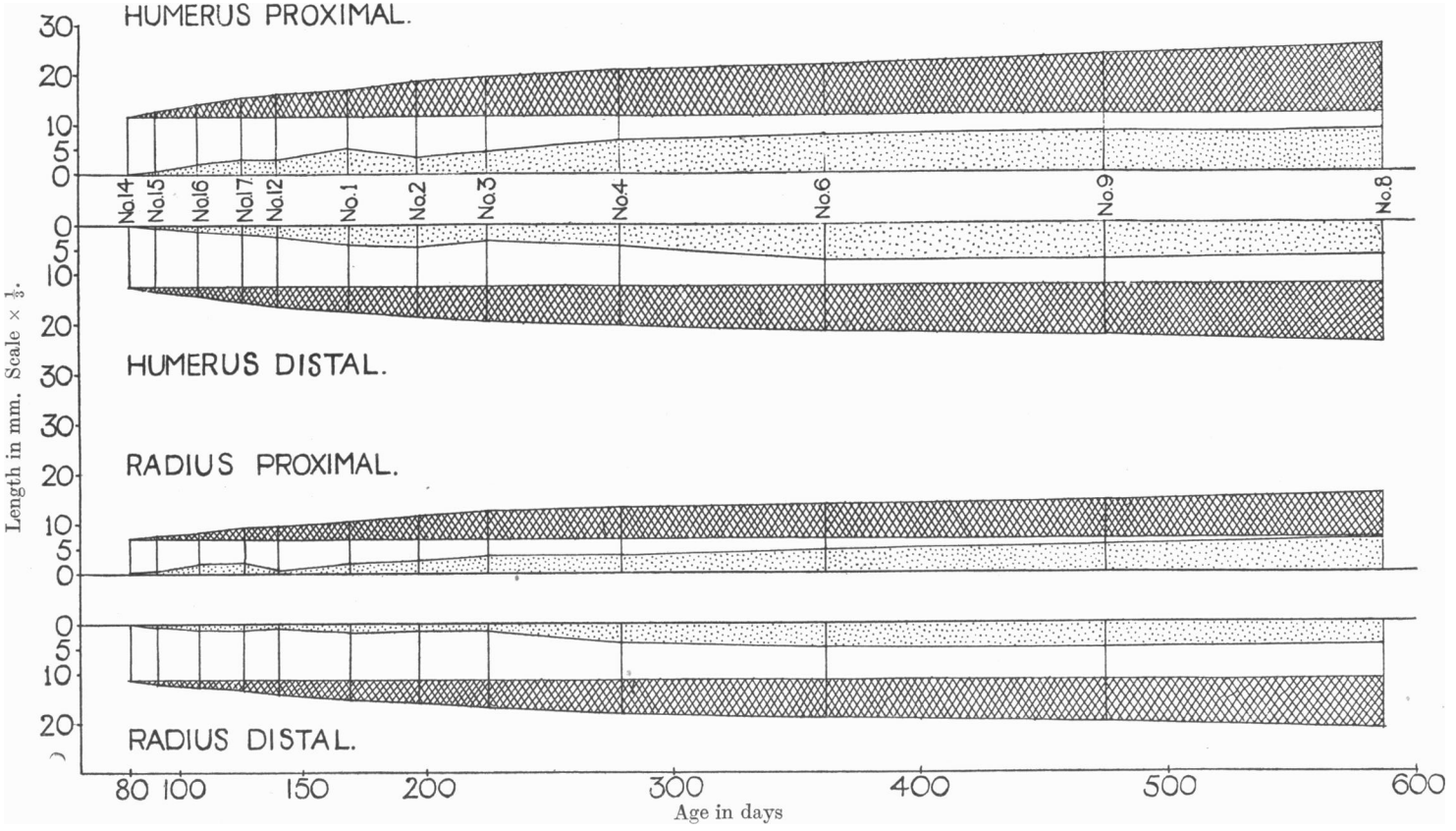

Fig. 8. Graphic representation of relative rates and amounts of growth and absorption at the articular and diaphysial ends respectively of the humeral and radial epiphyses of madder-fed pigs as explained in text. The horizontal line represents 80–600 days on a scale of one day per 0·33 mm. The vertical scale represents length (scale natural). A vertical line cuts the horizontal base line at the age of each successive bone. The cross-shaded areas represent the observed increments of new growth. The actual length has been measured on the vertical lines representing age, so as to include the new growth, and the space between the actual and expected lengths has been stippled to represent the amount presumably absorbed. The actual length of each bone therefore includes cross-shaded and plain areas.

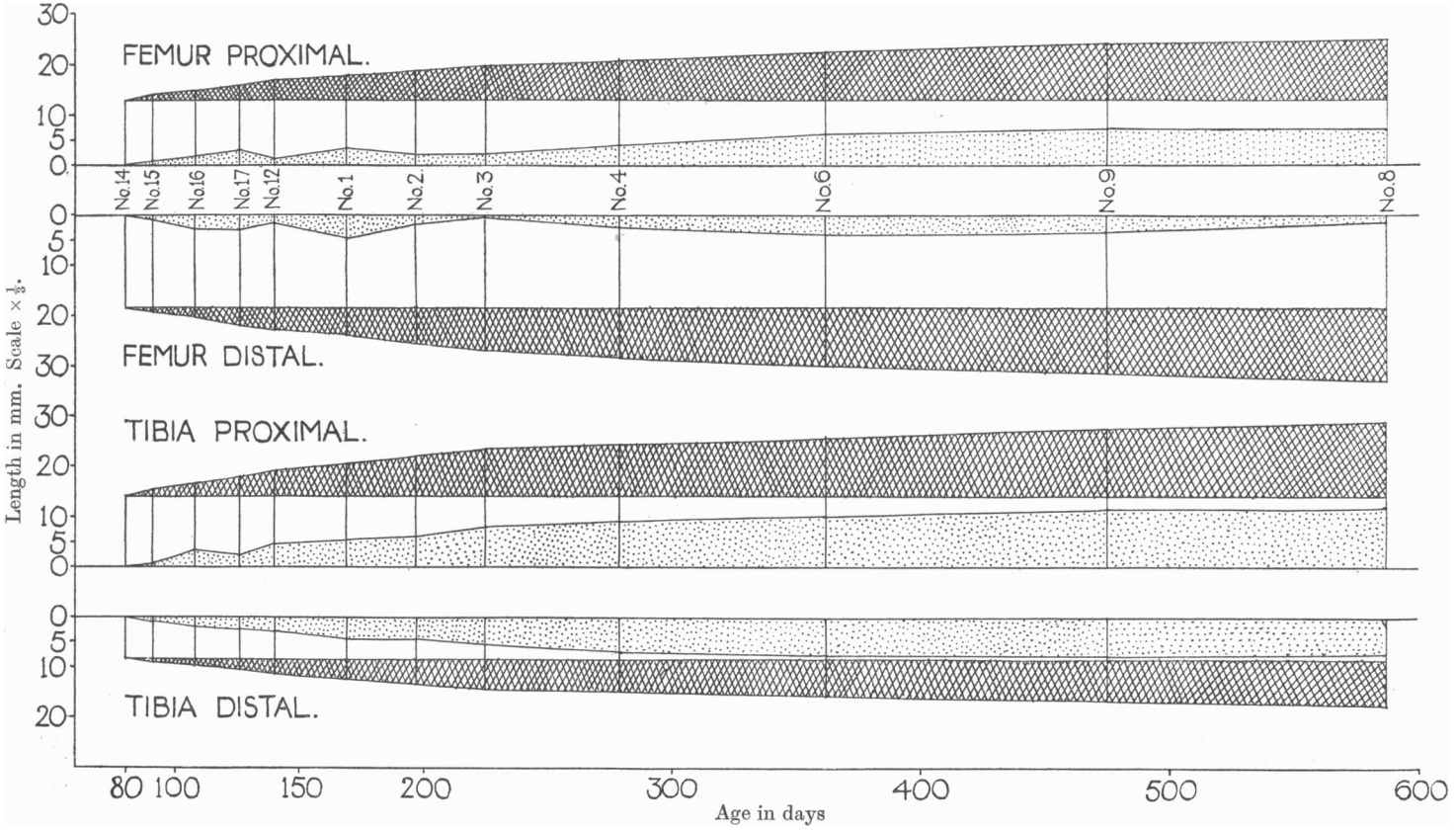

Fig. 9. Relative rates and amounts of growth and absorption at the articular and diaphysial ends respectively of the femoral and tibial epiphyses of the madder-fed pig. Scales as in Fig. 8.

2·0 mm., proximal tibia 3·0 mm. in 507 days) although their rates of growth differ little from those epiphyses increasing as much as 13·2 mm. (distal femur) in the same period.

A method of graphic representation shows the relative amounts and rates of new bone added to the articular surfaces and of absorption from the diaphysial surfaces.

The actual measurements of the epiphyses show that, although the proximal and distal epiphyses are unequal in length, there is no relation between the difference in length and the ends of the diaphyses with the greater and lesser increments. The epiphysis of one end of each long bone increases more than that of the other. The one that increases most is situated adjacent to the diaphysial end with the larger growth. The amount of actual increase in length varies considerably from 1·6 mm. (proximal epiphysis of tibia) to 13·2 mm. (distal epiphysis of femur).

The amounts and quantitative ratios of new bone added to the articular surfaces of the epiphyses are demonstrated over given periods. The growth increment is seen to be similar in the proximal and distal epiphyses in contrast to the unequal growth of the two ends of the diaphyses.

Measurements of growth per week show that there is a gradual diminution in the rate of growth in every epiphysis as one passes from the younger to the older epiphyses.

(2) There is an age sequence of union of epiphyses as described by Stevenson (16) and Dawson (17).

(3) "The end of the shaft at which the epiphysis is last united is the end at which growth takes place most quickly"—Humphry (18).

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