Severe undernutrition in growing and adult animals

7. Development of the skull, jaws and teeth in pigs

By R. A. McCANCE AND E. H. R. FORD

Medical Research Council Department of Experimental Medicine, and Department of Anatomy, University of Cambridge

AND W. A. B. BROWN *Department of Dentistry, Queen's University, Belfast*

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The plane of nutrition has a profound effect on the development of the skeleton, but skeletal growth has been shown to continue slowly even when the supply of food is very small (Aron, 1911; Morgulis, 1923; Jackson, 1932). The rate of growth affects the shape and form of the whole carcass and this is particularly important in preparing farm animals for the market (Waters, 1908, 1909; Moulton, Trowbridge & Haigh, 1921, 1922; Hammond, 1932). The literature was reviewed by Smith (1931). The general principles as they apply to the pig were defined by a masterly investigation of McMeekan (*1940a-c; 1941);* 1941). The inspiration for it came from the personal influence and published work of Dr John Hammond, to which full references were given. McMeekan (19406) made an 'age' comparison at 16 weeks and established that a low plane of nutrition had produced skulls and lower jaws about half the weight of, and a different shape from, those of animals reared on a high plane. Growth in length was penalized less than growth in width, but the thickness of the cranium was affected more than either and was only 3 mm in the animals on a low plane as against i8mm in the others. McMeekan (1940c) made a 'weight' comparison at 200 Ib, which the animals on the high plane of nutrition reached in 180 days and those on the low plane in 300 days. He found that at this weight the skulls and lower jaws of the animals on the low plane were heavier and longer, but relatively narrower, than those of the animals on the high plane. Other measurements of the skull were made, particularly of its weight, but the teeth were not investigated.

The present investigation concerns animals much more severely undernourished than those of McMeekan, and observations have been included on the teeth, which have not hitherto been systematically investigated in undernourished animals or in man. Hellman (1923) (see also Boas, 1933) reported that, although the poorer children in a population were less well developed physically than the rich, their dentition was not delayed, and in fact accelerated. Trowell, Davies & Dean (1954) made a note that even the severe protein deficiencies and stunting of growth met with in kwashiorkor did not seem to hold up dental development. They pointed out how incongruous it was to see the mouths of these tiny children crowded with teeth. The observation is in agreement with the experimental work on protein deficiencies in rats outlined by Baume (1959). The converse was demonstrated by Widdowson & McCance (1960), who showed that accelerating the growth of rats by an unusual amount of food in the first 10 days of their lives made very little difference to the times at which the teeth erupted. Broadly speaking, these generalizations about the effects of varying the protein and calorie intakes on skeletal and dental development have not been shown to apply so certainly to minerals. Deficiencies of magnesium (Watchorn & McCance, 1937) and of calcium and phosphorus have usually beeen found to affect the bones as much as or more than the teeth (Coleman, Becks, Kohl & Copp, 1950; Franklin, 1950; Coleman, Becks, Copp & Fransden, 1953; Baume, 1959).

METHODS

The pigs were reared as described by McCance (1960) and came from the same stock. The diets used for the well-nourished and undernourished animals were similar in all respects except that the animals to be undernourished were given very much less food, and some of the results in this and the previous papers in this series were provided by studying the same pigs. In the earlier experiments the animals were not weaned and undernourished quite so young as in the later ones. Once the food intake was reduced the pigs gained scarcely any weight and their growth curves were like those given by Widdowson, Dickerson & McCance (1960).

For this investigation sixteen normal pigs have been killed at various ages from birth to 15 months; eighteen undernourished pigs have been available which died or were killed when they were 3-15 months old, also five pigs undernourished for 12-24 months and then allowed to grow by returning them to a full diet until they were slaughtered.

After the death of the animals the heads were removed and cut in half in the mid-sagittal plane. Lateral and occlusal radiographs were then taken of the half-heads. Measurements and observations were made on the specimens themselves; the development of the teeth was studied from the radiographs and the fresh material.

The measurements (see Fig. 1) made on the skull were:

Total skull length: greatest antero-posterior length of the skull in a plane parallel to the cranial base.

Cranial base length: prosthion-basion length of skull (P-B).

Endocranial length and height: horizontal and vertical measurements of the part of the endocranial cavity related to the cerebral hemispheres.

Bizygomatic width: greatest width between the outer surfaces of the two zygomatic arches.

Cranial vault thickness: thickness of cranial vault just to one side of mid-line at junction of frontal and parietal bones.

Basi-sphenoid thickness: thickness of basi-sphenoid bone at floor of pituitary fossa.

Upper jaw length: prosthion to back of pterygoid plates.

Mandible, length: greatest antero-posterior length of mandible parallel to mandibular plane (plane of lower border of mandible).

Mandible, height of condyle: distance from upper surface of mandibular condyle to most posterior point on mandible of a line drawn along the mandibular plane.

Mandible, height of body: vertical height of mandibular body at mandibular diastema (just in front of second premolar). Chronological records were made for the deciduous and permanent dentition; four stages were recognized.

(i) Tooth formation begins: the first appearance of calcification on a radiograph.

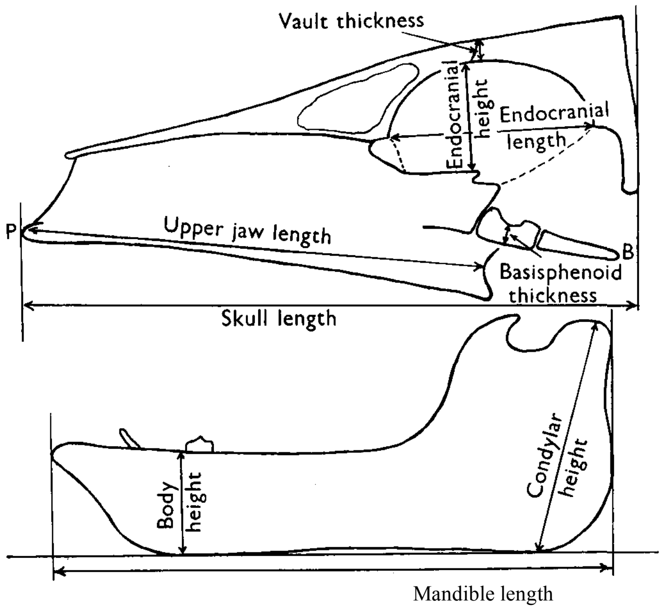


Fig. i. Diagram of the skull of a pig, to show the measurements made in this investigation.

(2) Crown formation complete: the time at which the crown first appeared fully formed on a radiograph (only measurable in premolars and molars, since in canines and incisors the point of junction of crown and root could not easily be distinguished).

(3) Eruption: the emergence of the crown through the oral epithelium.

(4) Root formation complete: the time at which the root reached its maximum length.

RESULTS

Skull

Table i sets out the age, sex, weight and skull measurements of eleven of the normal pigs. The measurements can be divided into three groups.

(1) Body-weight and cranial thickness. These were relatively small at birth and about 0.5-3% of their value at 65 weeks (age of oldest control pig completely measured).

(2) Skull and jaw lengths. These were at birth 20-30% of the value at 65 weeks.

(3) Endocranial dimensions. These were at birth already about 70% of the value at 65 weeks.

The figures reflect the early development of the head and skull, and particularly the brain, in comparison with the rest of the body, and entirely support the general principles which have been laid down by previous investigators such as McMeekan (1940*a*–*c*, 1941).

Table 2 gives the ages, sex, weights and skull measurements of the undernourished animals. The pigs have been grouped according to their age at death and the results averaged. Some of those in group 5 and one of the animals aged 65 weeks had had longer periods of full growth in early life and were not therefore quite comparable with the others (Widdowson *et al.* 1960).

Table 1. *Dimensions (mm) of the skulls of normal pigs*

Age (weeks/days)	Newborn	2/6	3/2	3/4	9/2	13/5	14/3	20	31	47	65
Sex	—	♂	♂	♂	♂	♂	♂	♀	♂	♀	♀
Body-weight (kg)	1·2	3·72	5·14	8·00	20·9	38·7	36·8	50·9	150	190	205
Skull length	87·0	103·5	115	121	157	186	189	203	261	279	331
Cranial base length (basion–prosthion)	79	96·5	104	110	150	180·5	179	202	260	274	332
Endocranial length	51·5	55	61·5	58	63	67	65·5	62·5	77	75	82
Endocranial height	29·5	32·5	31	34	35	36	37	35	34	40	39
Bizygomatic width	50	64	69	82	94	104	113	115	172	176	180
Cranial vault thickness	1·1	1·7	2·5	2·8	4·7	7·8	6·5	9·0	27·5	32	38
Basi-sphenoid thickness	3·4	3·5	4·8	5·1	7·5	8·0	7·2	5·1	11·0	11·0	17
Upper jaw length	54	67	74	78	108	134	129	150	194	209	264
Mandible: length	57	—	80	88	120	150	136	165	242	260	297
height of condyle	26·5	—	38	41	52	76	77	89	120	124	145
height of body	9	17	17·5	21	26	31·5	30·5	33·5	57	56	65

Table 2. *Dimensions (mm) of the skulls of undernourished pigs*

Group no. ...	1	2	3	4	5	6
Mean age (weeks) and age range	13	22	32 (30–34)	42 (41–43)	52 (43–60)	65
No. of pigs	3	2	3	3	3	2
Sex	♀, ♀, ♀	♀, ♀	♀, ♂, ♂	♀, ♀, ♀	♀, ♂, ♂	♀, ♀
Body-weight (kg)	3·99	4·26	4·43	4·47	6·80	10·2
Skull length	128·8	122·5	129·0	132·7	150·7	166·7
Cranial base length (basion–prosthion)	118·7	111·0	118·0	120·0	140·0	154·5
Endocranial length	58·8	58·0	62·1	64·3	66·3	63·8
Endocranial height	29·3	32·0	34·5	35·2	38·8	35·9
Bizygomatic width	74·0	75·0	80·0	73·7	89·0	98·2
Cranial vault thickness	2·9	2·3	2·4	2·6	2·7	2·7
Basi-sphenoid thickness	4·2	3·8	4·3	4·5	4·4	5·5
Upper jaw length	84·2	79·3	86·3	88·3	110·3	121·7
Mandible: length	95·7	96·0	101·7	109·7	136·0	135·0
height of condyle	45·1	47·0	46·5	53·7	65·3	72·9
height of body	20·7	18·3	20·3	20·7	21·7	21·3

The principle used in all the present experiments has been to compare the severely undernourished animals with normal litter-mates or brood-mates of the same weight and with others of the same age. These comparisons are set out in Tables 3 and 4, which were constructed in the following way. Each of the measurements made of the skulls of the normal animals was plotted against age and also against body-weight. Through these points curves were drawn freehand and, from these curves and the measurements of the skulls of the undernourished animals given in Table 2, the figures for the undernourished groups were related to those for well-nourished animals of the same age and of the same size. These figures, shown in Tables 3 and 4, are expressed on the assumption that the normal value in each instance was 100. Similar tables were made for the effect of undernutrition on the increments of growth after birth, but they have not been submitted for publication. As was to be expected they showed larger, often much larger, differences between the undernourished animals and normal animals of the same age and weight.

Table 3. *Effect of undernutrition on the development of the skull and jaw of pigs. Values for undernourished animals expressed as a percentage of those for normal animals of the same weight*

Body-weight (kg)	3.99	4.26	4.43	4.47	6.80	10.2
Skull length	120	113	118	121	126	128.5
Cranial base length	123	114	120	121	128	132
Endocranial length	107	105	112	116	116	108
Endocranial height	94-5	100	108	110	118	108
Bizygomatic width	114	114	120	110	117	118
Cranial vault thickness	145	109	114	121	100	87
Basi-sphenoid thickness	104	93	103	107	90	100
Upper jaw length	126	117	125	126	143	147
Mandible: length	132	132	136	147	161	144
height of condyle	128	132	129	147	159	169
body height	134	117	i27	127	111	99.1

The comparisons of the undenourished animals with normal animals of the same weight (Table 3) show that undernutrition did not prevent some development, at any rate in the first few weeks, for almost all the measurements were larger than they would have been in a well-nourished weight control. These results, therefore, support the general conclusions reached by Aron (1911), Jackson (1932) and Hammond (1952), and supply a great deal more detail about the skull, particularly of the pig. They show that some of the dimensions were affected more than others. The condylar height of the mandible, for instance, increased relatively more than the length of the skull, and the thickness of the cranial vault decreased absolutely. The height of the body of the mandible decreased with the progress of undernutrition in comparison with that of the weight controls, and extensive remodelling may have gone on in this bone. The ratio of the length of the mandible to the height of the body changed from 4.6 to 5.3 between 3 and 9 months without any great change in the body-weight, and it was almost 6.5 in the somewhat larger animals at 15 months. In normal animals there was little if any change in the ratio, which remained about 4.5 between the age of 3 months and 9 months and was 4.6 at 15 months.

The comparisons with animals of the same age (Table 4) show that undernutrition of this severity may have allowed some growth to take place, but that it held up most of the normal development, and the effect became progressively more obvious the longer the weight was held steady. This is most certainly shown by a study of the first four groups of animals whose weights were all within 0.5 kg of each other. As noted before, undernutrition affected some of the measurements much more than others. The endocranial dimensions were almost normal, which is in line with findings of Widdowson *et al.* (1960) for the weights of the brains, and is in keeping also with the work of Ruden (1935) on the effect of undernutrition on the development of the brain in rats. The measurements of the thickness of the cranial vault and of the basi-sphenoid region show how the large size of the brain cavity was achieved (McMeekan, *1940b).* This endocranial expansion with thinning of the cranial bones and underdevelopment of the air sinuses produced a doming of the frontal region never seen in normal animals.

Table 4. *Effect of undernutrition on the development of the skull and jaw of pigs. Values for undernourished animals expressed as a percentage of those far normal animals of the same age*

Age at death (weeks)	*13*	*22*	*32*	*42*	*52*	*65*
Skull length	*72.3*	*55.6*	*50*	*51.3*	*51.8*	*50.4*
Cranial base length	*65.8*	*51.0*	*46.7*	*43.2*	*47.2*	*46.5*
Endocranial length	*88.5*	*82.0*	*82.5*	*83.2*	*84.8*	*77.8*
Endocranial height	*82.0*	*86-5*	*91.0*	*92.0*	*101*	*92.0*
Bizygomatic width	*70.0*	*56.3*	*49.5*	*40.8*	*4.0*	*54.6*
Cranial vault thickness	*45.5*	*i8.3*	*8.9*	*8.1*	*7.7*	*7.1*
Basi-sphenoid thickness	*55.8*	*40.5*	*39.0*	*38.8*	*36.5*	*32.4*
Upper jaw length	*66.5*	*49.5*	*44.7*	*42.0*	*49.5*	*46.1*
Mandible: length	*68.0*	*51.0*	*43.2*	*41.5*	*48.4*	*45.4*
height of condyle	*63.5*	*50.0*	*39.7*	*41.8*	*47.5*	*50.3*
body height	*6.-8*	*44.0*	*40.0*	*36.0*	*34.8*	*32.8*

Rehabilitation of the undernourished animals produced restoration of normal size and proportions, so far as could be judged from the skulls and jaws of the five animals available. An animal, for example, which had been undernourished for $12^{1/2}$ months and then restored to a normal diet for a further 9 months had a skull almost as big as that of a normal animal 11 months old. The only evidence remaining of the long period of undernutrition was to be found in the teeth, and this is described below.

Teeth

Table 5 gives the ages at which the deciduous teeth in the mandibles of the normal and undernourished animals erupted and were fully formed. The findings for the former did not vary much from those given by Sisson & Grossman (1953). Chronological records were also made for the maxillary teeth but, as the latter followed the same order of development but at a slightly slower rate, they have been omitted from the tables. The formation of all the deciduous teeth begins *in utero,* too early to have been affected by undernutrition. No undernourished animals were killed before they were 3 months old, so nothing can be said about the effect of undernutrition on the eruption of the deciduous teeth, but Table 5 shows that undernutrition had already by this time affected the age at which some of the milk teeth completed their formation. The first incisors were conspicuously delayed, the second appreciably so, but the third little if at all. The formation of the canines was completed at almost the normal age. The first molar, like the first incisor, was delayed, which was quite to be expected from the comparatively late age at which formation was normally completed and can be compared with the development of the second incisor. The second and third molars were not delayed, although, to judge by the first incisor and the age at which formation was normally completed, delay might have been expected.

Table 5. *Comparison of development and eruption of mandibular deciduous teeth in normally fed and undernourished pigs*

Tooth	Formation begins Normal and undernourished	Eruption Normal and undernourished (weeks)	Formation completed Normal (months)	Formation completed Undernourished (months)
1st incisor	*In utero*	2–4	3	7
2nd incisor		8–9	7	10
3rd incisor		Before birth	2	By 3
Canine		Before birth	2	By 3
1st molar		4–5	4–5	6–7
2nd molar		2–4	3	By 3
3rd molar		2–4	3	By 3

Table 6 shows the effect of undernutrition on the permanent teeth. The progress of the incisors and canines is given as the total length of the tooth in mm, because it was found impossible to determine from the radiographs where crown ended and root began. Since, however, the crowns and roots of the molars and premolars were easily distinguished in the lateral radiographs, the times at which both crown and root were fully formed could be determined for these teeth, and are given in the table.

The table shows that, except for the second incisor and the third molar, calcification had begun in all the teeth by the 3rd month. Undernutrition delayed the inception of calcification of these teeth considerably and may have delayed others. Under-nutrition appeared to hold up the completion of the crown, whenever this could be timed, except that of the first molar. In some, such as the second, third and fourth premolar, the delay was as much as 6 months.

Except again for the first permanent molar the eruption of all the permanent teeth was materially delayed by undernutrition. This delayed eruption was coupled with delayed resorption and exfoliation of the deciduous teeth.

No incisors were completely formed as judged by the radiographs of any of these pigs and in the undernourished animals there was considerable delay in their development. Undernutrition also delayed the completion of all the premolars and molars, but only the delay in the first molar could be timed, for none of the other molars or premolars had completed their development in the undernourished animals by the time the oldest one, aged 15 months, was killed. Table 6 and PI. 1a, *b* demonstrates this; PI. 1 *a* shows the skull of a normal animal aged 13 months, by which time most of the molars and premolars had completed their development, and PI. 1*b,* presented on

Table 6. *Comparison of development and eruption in the mandible of permanent teeth in normal and undernourished pigs*

Tooth	Tooth formation begins: Normal (months)	Tooth formation begins: Under-nourished (months)	Crown formation complete: Normal (months)	Crown formation complete: Under-nourished (months)	Eruption: Normal (months)	Eruption: Undernourished (months)	Progress (incisors and canines) and completion (premolars and molars) of tooth formation: Normal	Progress (incisors and canines) and completion (premolars and molars) of tooth formation: Undernourished
1st incisor	2–3	By 3	—	—	12–13	After 15	60 mm at 13 months	32 mm at 15 months
2nd incisor	7	10·0	—	—	12–13	After 15	55 mm at 13 months	19 mm at 15 months
3rd incisor	2–3	By 3	—	—	7–8	11–12	32 mm at 13 months	26 mm at 15 months
Canine	1–3	By 3	—	—	10–11	After 15	50 mm at 13 months	35 mm at 14 months
1st premolar	2–4 (weeks)	By 3	4–5	7–8	4–5	8–9	10–11 months	After 15 months
2nd premolar	3–4	By 3	9–10	After 15	12–13	After 15	12–13 months	After 15 months
3rd premolar	1–2	By 3	7–8	13–14	12–13	After 15	12–13 months	After 15 months
4th premolar	1–2	By 3	7–8	13–14	12–13	After 15	12–13 months	After 15 months
1st molar	*In utero*	*In utero*	2–3	2–3	3–4	3–4	7–8 months	13–14 months
2nd molar	1–2	By 3	6–7	10–11	8–9	14–15	12–13 months	After 15 months
3rd molar	3–4	10–11	12–13	After 15	13–14	After 15	After 13 months	After 15 months

the same scale, shows the skull of an undernourished pig aged 15 months. PI. 1 also shows that undernutrition interfered with normal occlusion, for from PI. 1b it can be seen that the mandibular teeth of the undernourished animals were too far forward for their maxillary opponents. The mandibular incisors, moreover, were horizontally inclined to an abnormal degree, a usual finding in the animals undernourished for the longer periods of time, and the second and third molars were impacted (see Fig. 2). PI. 1*b* demonstrates further that the occlusal surfaces of the deciduous and permanent molars were very irregularly and extensively worn in the undernourished animals.

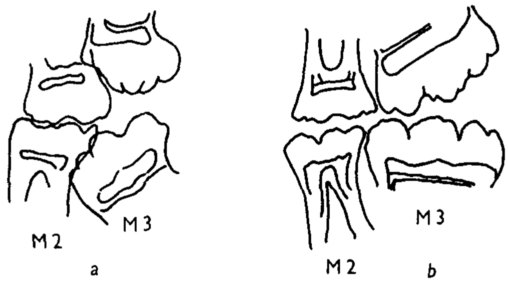


Fig. 2. Diagram comparing the size and position of the third molar teeth of a pig which had been undernourished for 2 years and then rehabilitated for 9 months *(a)* with one aged 13 months which had never been undernourished *(b)*. Tracing from radiograph x ^.

The crowns of all the teeth that had begun to form before the period of under-nutrition began were of normal size. The third molar, however, and the second incisor began to be formed much later, and in the two pigs undernourished for the longest times and then rehabilitated, the crowns of the third molars never developed beyond 60-70% of their normal size (Fig. 2). The size and position of these teeth before rehabilitation began can be appreciated from a comparison of PI. i *a* and i *b*.

DISCUSSION

It has already been pointed out that the present work on the skull confirms and considerably extends the findings of Hammond (1950), McMeekan (19400-0) and others who showed that varying the plane of nutrition might affect some parts of the bony framework much more than others. The size of the endocranial cavity was less affected by undernutrition than the skull as a whole, and it continued to enlarge in the undernourished pigs to a greater extent than the rest of the skull. Even so, it was always smaller than that of a normal pig of the same age, suggesting that even the brain, which was accorded the highest priority of growth by Ruden (1935) and Hammond (1950), was affected by a degree of undernutrition as severe as this experimental one.

Undernutrition did not retard the growth of the two jaws to the same extent. The lower jaw was less affected and became relatively larger than the upper jaw and projected in front of it. The height of the condyle of the mandible also increased more than the length of skull, and growth of the condylar part of the mandible was probably responsible for the forward movement of the mandible. Some protrusion of the lower jaw is normal in pigs with increasing age but in the undernourished pigs the protrusion of the lower jaw was abnormal for their size and led in some instances to serious malocclusion, all the lower teeth being relatively too far forward.

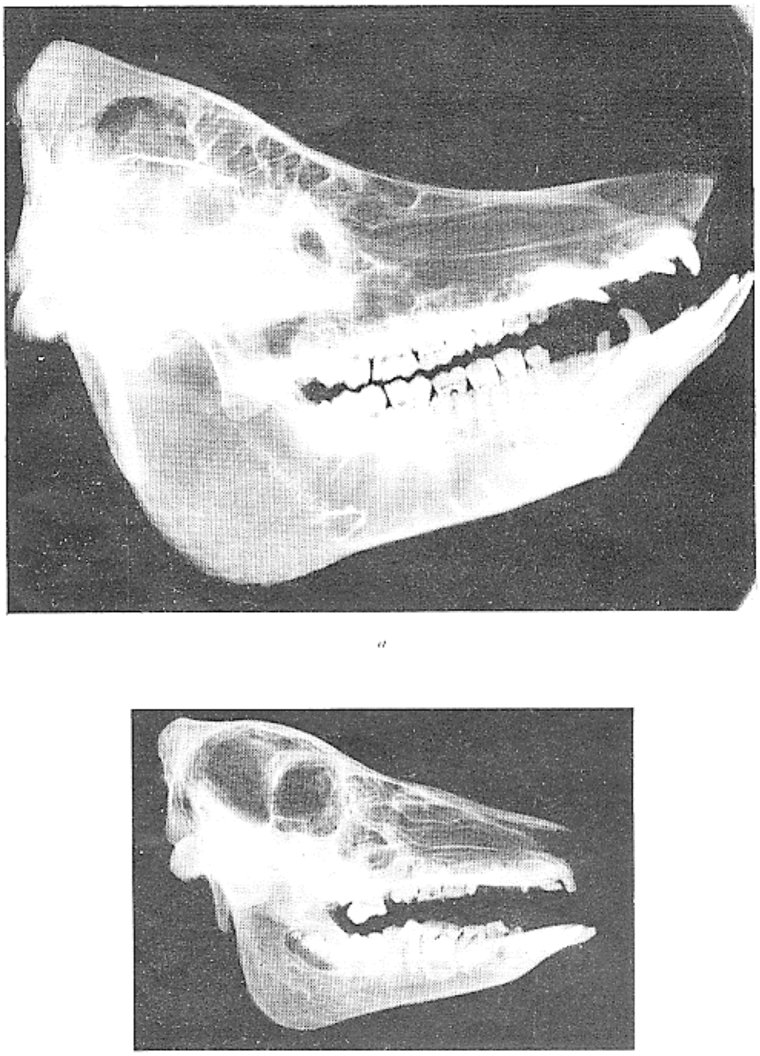
On several of the radiographs of the undernourished animals, hypercalcified lines parallel to the posterior border were seen in the rami of the mandibles. Harris has previously described these lines in the pig's mandible (Harris, 1939) and in other bones (Harris, 1933) and has called them lines of arrested growth. So far as the mandible is concerned they would appear to indicate the direction of incremental growth, and probably the phasic nature of the developmental process.

The deciduous teeth may have been worn down by their continued retention and use, but the state of the first permanent molars suggests that undernutrition had caused some gross disturbance in the structure and chemistry of the teeth as it had done in the bones (Pratt & McCance, 1960; Dickerson & McCance, to be published).

Although the length of the mandible was always considerably greater in the undernourished animals than in normal animals of the same weight (Table 3), the growth of this bone was interfered with more than the development of the teeth. At 13 weeks, for example, the mandible was only 68 % of its proper length (Table 4), but the formation of all the teeth which should have appeared at this age had begun. Growth of the mandible was also held up more persistently than that of the teeth, for at 15 months the mandible was only 48 % of its correct length, but by that time all the permanent teeth had begun to form. It was this failure in the forward growth of the mandible and maxilla which led to so much dental impaction in the undernourished animals and prevented the usual vertical eruption of the second and third molars.

Franklin (1950) described developmental disturbances of the teeth in sheep very similar to our findings, and showed that on a diet deficient in calcium the teeth were often crowded and impacted. There is, however, no evidence that our animals were suffering from a calcium rather than a general deficiency. The calcium: collagen ratio in their bones was in fact abnormally high (Dickerson & McCance, to be published).

If the observations of Trowell *et al.* (1954), referred to earlier, are extended and confirmed, these experiments on the development of the teeth have clinical interest. It remains to be seen what effect the abnormal tooth structure suggested by the attrition may have on resistance to caries in later life. One way of looking at these experiments is to fall into line with Hammond (1950) and all the others who have investigated the effect of nutrition on development and to accord teeth a very high growth priority even when the plane of nutrition is very low. Another, possibly more instructive, way of looking at these and all previous experiments of the same kind is to view them in the light of the work of Widdowson & McCance (1960), who pointed out that the development of some structures and bodily functions were much more closely linked with chronological age than others. The eruption of rat's teeth, for example, and the opening of their eyes, were not materially accelerated by a nutritional device which produced intensely rapid growth and unusually large adults.



a

b

SUMMARY

1. A study was made of the differential effects of severe and prolonged under-nutrition on the growth and development of the pig's skull and teeth.

2. The endocranial dimensions were a little smaller than in animals of the same age but they were much nearer their correct chronological size than the other skull measurements. The bones were very thin and the air sinuses poorly developed.

3. The growth of the jaw was more severely retarded than the development of the teeth; the mandible was less affected than the maxilla. Lines of arrested growth were seen at the posterior border of the angle of the mandible suggesting the incremental pattern of its growth.

4. Tooth development and eruption, and the resorption of the deciduous dentition, were all delayed. The angle of eruption of the incisors was abnormal.

5. The size of the crowns of the teeth was unaffected, except that of the third molars, which were only 60-70 % of their normal dimensions.

6. The reduced growth of the jaw and the normal size of the crowns led to crowding of all the teeth and impaction of the molars.

7. Forward movement of the mandible, probably due to growth of the condyle, often produced severe malocclusion.

8. There was extensive attrition of both the temporary and permanent teeth.

9. Rehabilitation of the undernourished pigs restored the proportions of their skull and jaws to normal, but left many of the abnormalities in the teeth as they were.

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EXPLANATION OF PLATE: *a*. Skull of a normal pig aged 13 months. *b*. Skull of an undernourished animal aged 15 months (same scale as *a*) to show how undemutrition interfered with the position, growth and normal occlusion of the teeth. It also shows that the surfaces of the deciduous and permanent teeth in the undernourished animal were being rapidly worn away.

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