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THE GROWTH AND SHEDDING OF THE ANTLER OF THE DEER

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THE GROWTH AND SHEDDING

OF THE

ANTLER OF THE DEER

THE HISTOLOGICAL PHENOMENA AND THEIR
RELATION TO THE GROWTH OF BONE

BY

WILLIAM MACEWEN, F.R.S.

GLASGOW
MACLEHOSE, JACKSON & CO.
PUBLISHERS TO THE UNIVERSITY
1920

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PREFACE

Material for this investigation has been obtained from various sources. One of the earliest contributions was from the Duke of Montrose in the shape of a fine head of the Fallow Deer which was shot by his Grace and forwarded immediately, so that it was received in excellent condition.

The vessels of the head and neck of this specimen were immediately injected so that the relations of the blood vessels of the skull to those of the antler and the velvet could be traced. Through the medium of my friend, Mr. O. E. Philippi, several fine heads were obtained, presenting the sprouting antler in various stages of growth. These comprised specimens of the Red Deer from Gaick Forest sent by Mr. Hargreaves and specimens of Fallow Dear sent by Lord Devon. The Duke of Richmond and Gordon gave permission to examine the great and beautiful collection of deer skulls and antlers at Gordon Castle and also to photograph any specimens of service. Several of these showing the result of injury to the pedicle and its effect upon the antler were photographed and appear in this volume.

My friend, Mr. Henry Evans of Jura, was good enough to give me numerous examples of the Cromie antlers, two of which are here illustrated.

To all these gentlemen the thanks of the author is due for the contributions so generously given.

He has also to thank Dr. Shaw for contributing specimens illustrative of the histological phenomena of the growing epiphysis of the human foetus and those of children at birth which were prepared in the Surgical Laboratory of the University. Dr. J. A. C. Macewen for aid in the collateral investigation of growth of bone in fractures and valuable work in the general investigation, Dr. MacMurray for making several histological drawings from slides illustrative of nuclear budding as seen in the antler of the deer and in the growing bones of other animals, and Miss Macewen for much aid in preparing these pages for the press and for work connected with the investigation generally.

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INTRODUCTION

The inquiry into the phenomena connected with the growth and shedding of the deciduous antler of the deer was undertaken to determine the data of a very interesting phase of nature which had not been already investigated, was imperfectly understood and which, on its own merits, was of intrinsic value. From the data thus obtained any differences which might be found between the development of bone in the antler and that of the ordinary production of osseous tissue would be noted and it was hoped that light might thereby be thrown on osseous development, in other parts of the animal economy. It has proved to be of service in both these respects.

The growth of the velvet is very interesting in itself, as it is an instance of the complete reproduction of the whole of the cuticular elements of the skin,—stratum lucidum, stratum Malpighi, hairs, hair follicles and glands,—which all grow with remarkable rapidity, keeping pace with the growth of bone and covering, it may be, an enormous palmate antler within three months. Apart from embryonal evolution, such an extensive growth of all the elements of the skin does not occur in the reproduction of any other part of the animal kingdom. Although the analogy may not be strictly correct, it is nearer to what occurs in the reproduction of the digits of the newt or the tail of certain lizards after their removal, than to any phenomena seen in mammalian repair of tissue after surface wounds. In the latter, in man the cuticular elements are imperfectly reproduced, the stratum lucidum and stratum Malpighi alone appearing, glands and hair follicles being absent.

In many parts of the antler, especially toward the terminal point of the tine, the cutis (stratum Malpighi) grows directly on bone without the interposition of any membrane. In this respect it resembles the manner in which the cuticular covering is seen to adhere directly to human bones (where the bone is superficial), after the healing of some compound fractures, such as in the tibia, and as has been many times seen—during the late war—on stumps after amputation where the cutis has become directly adherent to the bone.

The vessels of the velvet grow with equal rapidity, supplying abundant pabulum for the growth of the velvet and maintaining at the same time the temperature of the growing bone within the hairy covering. Whatever may be the case in the early stages of the sprouting antler, these cuticular vessels do not inosculate to any appreciable extent with those of the underlying bone.

The osseous growth in the antler is derived from pre-existing bone in the skull, a pedicle projecting from the frontal bone from which the antler springs. The nearest analogy to this is epiphyseal growth of the diaphysis of the long bones, the distal epiphysis ever being borne further away from the proximal, as it deposits its osseous framework. Ample opportunity is afforded of studying the development of the osteoblasts and the deposition of ossein among the millions of cells that spring originally from that base. The rapidity of growth is so great that all phases of bone development may be found occurring simultaneously, in one part or other, of a half grown antler. The phenomena elicited at the earlier stages of development are in the main analogous to those of the growth of bone in other parts of the mammalian skeleton. From the very inception of the antler growth, however, arrangements have been made for the rapid shedding of the antler, after it has performed its evanescent purpose. This is effected by excessive osteoblastic formation and the deposition of ossein, constricting the calibre of the internal vessels, resulting in eburnation and ultimate ischemic necrosis, the shedding of the antler ultimately occurring from the action of the living tissue on the proximal side in the pedicle.

Provision for the ultimate shedding of the velvet is similarly arranged for at the inception of the new antler. The abundant ossific pabulum issuing from the pedicle overflows and overlaps the pedicle circumferentially forming the corona. This may be seen in the sprouting antler illustrated in Figs. 4 and 5, which photographs are taken from a specimen two weeks after shedding. From that period the corona continues to grow, and it may be seen in much more pronounced form in Fig. 8 representing the corona at eight weeks. The large blood-vessels of the velvet which supply both pabulum and heat are at first protected by lying in grooves in the antler and in the ossific matter of the corona, but ultimately the ossification occurs at the corona so quickly that it encroaches on the lumen of the vessels and subsequently obliterates them.

It is to be noted that the facts adduced here are contrary to the prevalent belief that the corona appears only toward the terminal portion of the growth of the antler. It is interesting to see that nature has at the very inception of the growth provided for the fall of this deciduous structure.

The energizing entity and determining factor acting under hereditary law, is the osteoblast which is evolved from pre-existing bone cells or osteoblasts in the pedicle. Its evolution may be traced from its syncitium through its various stages until it assumes its mature form which is typical.

This typical cell, when first seen in the antler, was supposed to be peculiar to the antler of the deer, but it has been found on further search to be identical in shape with the mature osteoblast seen in other forms of osseous development, though in the latter the typical forms are not seen in such abundance as in the antler, and often in order to be observed must be looked for carefully, as synchronously with the assumption of the mature form, the deposit of ossein occurs so quickly that the outline of the cells becomes obscured. The recognition of a typical form of osteoblast enables one to trace this energizing agency through direct and indirect transformation, and the view of ossification is thereby more easily understood and simplified.

The rapidity of production of the mass of ossification in the antler requires some explanation other than could be accounted for by normal cell division, and the phenomena of nuclear budding which is seen in the antler may be interpreted as an adjunct to the ordinary methods of cellular multiplication. That such a view is heterodox does not necessarily exclude its consideration, and the fact that a somewhat similar process to nuclear budding in the antler is seen in rapidly growing tumours, such as the sarcomata, lends colour to the view.

The antler is the most characteristic feature of the deer tribe (cervidae). It is a word derived from the

French *antoillier*, a derivative from the corrupt Latin *anteocularem*—which originally was applied to the brow tine. This word antler distinguishes these cranial formations from the sheath covered horns of the Bovidae.[1]

Some species of existing deer are antlerless—Chinese water deer and the musks—and others possess permanent antlers which are not deciduous, the velvet remaining in the latter throughout the life of the animal. Some extinct ruminants, probably allied to the giraffes, have branching bony appendages springing from the skull much like that of the present day deer, except that the antlers are permanent. The males of all the other existing cervidae are adorned with antlers, the females being antlerless. In the Reindeer species, however, both sexes have antlers.

The amount of bony matter annually secreted to form antlers of the larger deer is enormous, antlers of the Red Deer having been obtained which weigh upwards of 74 lbs. while those of the extinct Irish deer must have probably scaled 100 lbs. during life.[1] "In weight the Elk will scale from 900 to 1400 pounds and the antler may weigh as much as 60 pounds. The largest span of an Elk antler on record is in possession of the Duke of Westminster. It measures six feet one and one quarter inch."[1]

It has been the custom to regard antlers as dead structures incapable of repair after injury and to look upon the pedicles as consisting generally of such solid ivory like bone that they could not transmit blood to the "core" of the antler, and therefore that they could not play a part in the reconstruction of a new antler. Such views, stated in that broad way, are not borne

[1] *The Royal Natural History*, vol. ii., Lydekker, F.R.S. London, Fred. Warne & Co. 1894.

out by the facts recorded in this volume. There is a period doubtless in which the antler is dead, and its shedding is due to its having become a necrosed structure. Prior to that, however, the antler is full of life and capable of repair after injury. The antler is capable of reconstruction during the growing period and the pedicle is then full of blood, which it transmits to the interior of the antler. The pedicle participates actively in the shedding of the necrosed antler and therefore at all times it must be in active life and nutritional condition.

In making deductions from the Genus Cervus it may be as well to remember that none of this family have a gall bladder (which all Bovidae have).

The histological data given in these pages were obtained from the heads of various varieties of deer, the red deer (*cervus elaphus*) and the fallow deer (*cervus dama*) chiefly. The roe deer (*capreolus*) though frequently examined,—and some of the sections of the antlers are included—did not present any advantage over the larger varieties.

The antler of the roe deer owing probably to its smaller size did not show the exuberance of growth of the larger varieties. The heads of deer were obtained from many sources and include specimens of the sprouting antlers, two, four, five and eight weeks after the shedding of the old antlers. Macroscopic illustrations of a few typical specimens are given, and sections of several of these are also included from which the naked eye appearance of the rapidly growing bone and cartilage may be seen.

The statement is made in the beginning of this volume that the weight of the antler in " the larger species (such as the Irish Elk) is more than that of all the bones of the skeleton put together," and this has been quoted from the *Study of Mammals*, 1891, on the authority of a careful observer, Sir William Flower. This is a very graphic statement, and brings forcibly before the mind of the reader the enormous osseous development of the antler. Sir William Flower has not, however, given any data as to whether he has arrived at that conclusion by actual weighing of the specimens.

THE GROWTH OF ANTLERS

CHAPTER I

Deer's antler a deciduous structure.
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Deer's antler a deciduous structure.

When it is remembered that the deer's antler is deciduous, a new one being formed every year, that the enormous growth of bone forming the antler is produced in three or four months, and that the weight of the antler in the larger species is said to be more [1] than that of all the bones of the skeleton put together,

[1] Sir Wm. Flower, *Study of Mammals*, 1891.

it is all the more striking that this growth of the antler proceeds from a single comparatively small centre of ossification situated in the frontal bone. The regeneration of the myriads of cells and the rapidity of cellular proliferation necessary for the growth of the antler is much greater than that which obtains in any other normal process of single bone formation within the deer or other animal. When the osteoblasts have reached maturity they extract from the blood the bone-making salts and deposit them so that the cells become imbedded and immured. In this way the fabric of the antler is built. No colony of coral insects is more replete with active life. Pathological conditions such as fractures of bones exposed to great continuous movement may show rapid and excessive osseous development, but never to the same extent or produced with the same rapidity as that of the antlers. The rapidity of growth in the antler is comparable with, but in excess of, that of the most rapidly produced tumours.

In the first year of a buck an outgrowth or exostosis rises from the frontal bone which, when the outgrowth is completed, forms the pedicle. The pedicle not only springs from the frontal bone of the skull, but it is identical with it in structure, showing Haversian canals and having the same blood supply. The pedicle at the beginning of the growing period is highly vascular and pulpy, and is covered with cartilage which ossifies from the base upwards, and as ossification proceeds the cartilage continues to grow in advance until its full size is reached, when its ossification becomes completed. The pedicle once formed is a permanent structure growing in circumference during subsequent years.

It is from the distal extremity of the pedicle that the antler springs, and when the antler is shed its shedding takes place at the same point. The antler appears during the second year of the animal's life, when it presents only a single stem. Each succeeding year the new antler shows a new tine or branch until maturity is reached, after which the growth becomes irregular.

These two specimens (Figs. 1 and 2) are presented as illustrative of the great development of bone in the antlers of the larger deer. The one is the head and antlers of the Moose or Elk, the *Alces machlis*, which was shot in the north of Canada. The other is the head and antlers of the Wapiti—*Cervus Canadensis*—from the same region. In both, the development of bone, which takes place in three months, is enormous, and as the antlers are deciduous, it occurs yearly.[1]

[1] Sir William Flower, in the introduction to the *Study of Mammals*, 1891, observed the growth of the antler of the red deer as follows:

"On March 12th, the antler was shed.

On March 25th (thirteen days after), a growth about the size of the red deer specimen figured in this volume (Fig. 3). Sprouting antlers, p. 7.

On April 9th (29 days after), the growth was about the size of the fallow deer specimen figured in this volume (Fig. 6). Sprouting antlers, p. 12.

On May 18th (39 days after), the growth was about the size of first fallow deer specimen in author's collection (Fig. 7, p. 13).

On June 27th (79 days after), antler complete but with velvet still intact.

On July 20th (102 days after), shedding of velvet advanced.

On October 1st (175 days after), hard bone.

The growth may be said to be completed on June 27th, that is, 79 days after shedding of the antler.

In red deer (*Cervus elaphus*) the antler is shed between the end of February and early part of April. The older animals shed their antlers earlier than the young. The number of points on the antler increases with the age of the animal. When there are twelve points present it is known as a Royal Stag."

"Even the great horn of the Wapiti (Fig. 1) and judging from analogy those of the Irish Elk—a pair of horns which weigh 70 lbs.,—more than all the bones of the skeleton put together ?—are produced in course of 3 or 4 months." Sir William Flower.

The mark of interrogation does not appear in the original.

HEAD AND ANTLERS OF WAPITI—CERVUS CANADENSIS.

Fig. 1.

Antlers showing great development of bone.

Author's Collection.

HEAD AND ANTLERS OF MOOSE (ELK)—ALCES MACHLIS.

FIG. 2.

Antlers showing great development of bone.

AUTHOR'S COLLECTION.

Preparation in skull and pedicle for growth of new antler.

When a new antler is about to form, the whole thickness of the skull from the brain cavity outwards, through the pedicle, exhibits greatly increased vascularity compared with the same parts when the growth of the antler has been completed. The blood supply of the pedicle comes from the vessels of the skull and frontal bone. The pedicle is highly vascular, especially toward the centre from which active osseous proliferation is proceeding—from the centre outwards toward the circumference. The new growth pours out from the whole interior of the pedicle and overlaps it circumferentially, laying thereby the foundation of the future corona (Figs. 3, 4 and 5).

New growth springs from whole surface of pedicle.

Whenever the antler is shed, the pent up forces which had been accumulating preparatory to the new growth find vent and from the whole upper surface of the pedicle a mass of new formation springs and overflows its edges—in form like a young mushroom projecting from its stalk.

It is to be noted that the distal surface of the pedicle where it abuts on the antler, before the shedding of the latter, presents a concavity, and immediately after the antler is shed a convex shape is assumed, from which the new tissue forms in the same place (Figs. 9 and 10).

In respect of this overlapping of the pedicle, it resembles the form of growth which sometimes covers the end of the human femur and humerus after amputation, through their shafts—instead of remaining a plain sawn surface, the cut shaft often becomes covered with a cone-shaped cap of new bone, which overlaps the periphery of the shaft.

Fig. 3.

HEAD OF RED DEER (CERVUS ELAPHUS)—SPROUTING ANTLERS

Head of Red Deer (*Cervus elaphus*) sent from Gaick Forest by Mr. Hargreaves through Mr. Philippi, May 1913.

Antlers have been shed about two weeks previously, and three inches partly pedicle partly new antler is seen projecting from the skull. (Description on pp, 28 and 29.)

Analogy to conical stump in children.

The growth of the antler is in some respects like the growth of bone which follows amputation through the arm or thigh of a child, forming ultimately a conical stump. The reason for this is that the humerus and femur continue to grow in length from the proximal epiphysis while the soft tissues recede, pressure being exerted on them from within by the constantly growing bone which finally protrudes through them, it being then covered only by a single layer of epithelium which is thinned toward the extremity, so that finally a pellicle of stratum lucidum alone remains, which proliferates quickly in an attempt to keep pace with the growing bone, which it covers. In the antler, however, the whole of the epithelial layers grow with great rapidity, keeping pace with the osseous growth, clothing the whole structure.

New pabulum quickly becomes cartilaginous and ossifies centrifugally.

Thus it is seen that the new antler springs from the pre-existing bone in the pedicle and skull, both of which become highly vascular preparatory to fresh ossific effort. The pabulum thus produced is thrown out from the pedicle and quickly assumes a cartilaginous form, which speedily ossifies from the centre outwards (Figs. 4 and 5).

Cap of rejuvenating cartilage.

As the antler grows it is preceded by a mass of rejuvenating cartilage which forms a cap over the extremity of the advancing bone (Fig. 4). This cartilage is in a state of active proliferation, at the same time

FIG. 4.

RED DEER (CERVUS ELAPHUS)—SPROUTING ANTLER IN SECTION

Appearance of pedicle and new antler about two weeks after shedding.

Red Deer skull, pedicle and sprouting antler all in section, showing cartilaginous new formation ossifying in centre from junction with pedicle.

reproducing itself distally while proximally it is being converted into the bone formation of the antler.

Analogy to diaphyseal cartilaginous plate.

It somewhat resembles a distal "diaphyseal" cartilaginous plate, inasmuch as, the more it contributes to the growth of bone, the farther it is borne away from the centre by the osseous deposit which it has so freely furnished.

There is an analogy also to certain forms of exostosis which grow in ossifying cartilage—the cartilage always preceding the bone until the full growth has been attained.

The cutis covering the antler (*velvet*).

The thick cutis covering the skull stops at the extremity of the pedicle, from which point a thin layer of cutis spreads with great rapidity over the bone and cartilage of the antler and keeps pace with the subsequent growth of the latter. Similarly, the dense coarse hair covering the forehead of the deer is not continued further than the distal aspect of the pedicle and from that point forward there is a growth of fine hair—at first very fine and soft but afterwards stronger, though always much more delicate in structure than the hair on the proximal side of the corona (Figs. 4, 5 and 6). During the process of shedding of the antler, the cutis may be seen spreading over the granulation tissue which constitutes the new formation, and in the early days after shedding, a thin pellicle consisting principally of the stratum lucidum covers the mass, except toward the centre where there is a bare patch of granulation tissue which is gradually cicatrised, leaving a cicatricial mark which can be distinguished for weeks afterwards. This cuticular pellicle is at first destitute of hair, being quite bald, but very soon a soft downy hair covers it.

Fig. 5.

RED DEER (CERVUS ELAPHUS)—SPROUTING ANTLER IN SECTION

About two weeks after shedding.

Red Deer skull, pedicle and sprouting antler in section, showing vascularity of skull and pedicle, mass of cartilage in antler. Ossification commencing from centre near pedicle, represented by the darker shaded portion and spreading upwards and outwards to corona.

The blood vessels of the velvet—their growth and obliteration.

The cuticular covering (the velvet) is nourished by very numerous big vessels, mostly branches of the temporal artery, which run vertically on the antler and

Fig. 6.

HEAD OF FALLOW DEER (CERVUS DAMA)—SPROUTING ANTLERS

About four weeks after shedding.

FALLOW DEER (CERVUS DAMA) SPROUTING ANTLERS.

Shot by Lord Devon. Sent through Mr. Philippi, June 1913.

Fig. 7.

HEAD OF FALLOW DEER (CERVUS DAMA)—SPROUTING ANTLERS

About five weeks after shedding.

HEAD OF FALLOW DEER (CERVUS DAMA) SPROUTING ANTLER.

Sent through Mr. Philippi, June 18, 1913.

FIG. 8.

FALLOW DEER (CERVUS DAMA)—PEDICLE, PORTION OF BASE OF ANTLER, AND SKULL IN SECTION

SECTION OF FALLOW DEER ANTLER, PEDICLE, AND SKULL. ANTLER 2/3RD GROWN. About eight weeks after shedding.

Corona well developed, cutis thinned over it. Compare thickness of cutis on pedicle with that on antler and at corona. The bone in line with corona is dense compared with that above and below in pedicle.

which supplies both pabulum and heat. Osseous growths are formed by the bone from within, growing outward between these vessels so as to leave them partially embedded in grooves. These grooves or gutters leave permanent markings on the outside of the solid antler. If this osseous encroachment on the blood vessels were continued it would ultimately encircle and obliterate these vessels in their whole length, but before this can occur, the vessels by a somewhat similar process, become strangled by osseous encroachment at the corona and shrivel off, while the intensive bone production in the interior of the antler is lessened by osseous encroachment upon the lumen of the internal vessels throughout the antler as well as at its base—an osseous sclerosis forming.

From the superficial vessels comparatively few very fine branches penetrate the deeper layers of the skin, and these either do not anastomose or they do so very sparsely with the network of thin-walled vessels in the interior of the bone.

The histological development of the velvet.

The great rapidity with which the cutis grows covering the antler and keeping pace *pari passu* with the osseous tissue is remarkable. It is interesting to see how complete the cutaneous development is. It covers the whole antler from the base to the tip not only with the epithelium of the true skin, but also with its glands, hair follicles and appendages.

The complete reproduction of all those cutaneous structures springs by cell proliferation from the pre-existing structures covering the pedicle, and differs thus from epithelial reproduction covering cicatricial tissue

FIG. 9.

RED DEER (CERVUS ELAPHUS)—SECTION OF ANTLER ABOUT TO SHED

AUTHOR'S COLLECTION.

SECTION RED DEER ANTLER AND PORTION OF SKULL, PEDICLE, AND CEREBRAL CAVITY.

Preparatory to shedding of antler. Great vascularity of skull and pedicle, "line of demarcation" beginning to form between dead bone and living at convexity of antler near corona.

The skull and pedicle are hypervascular preparatory to new growth. The antler presents its white convexity towards the pedicle. After the shedding the pedicle assumes a convexity upwards.

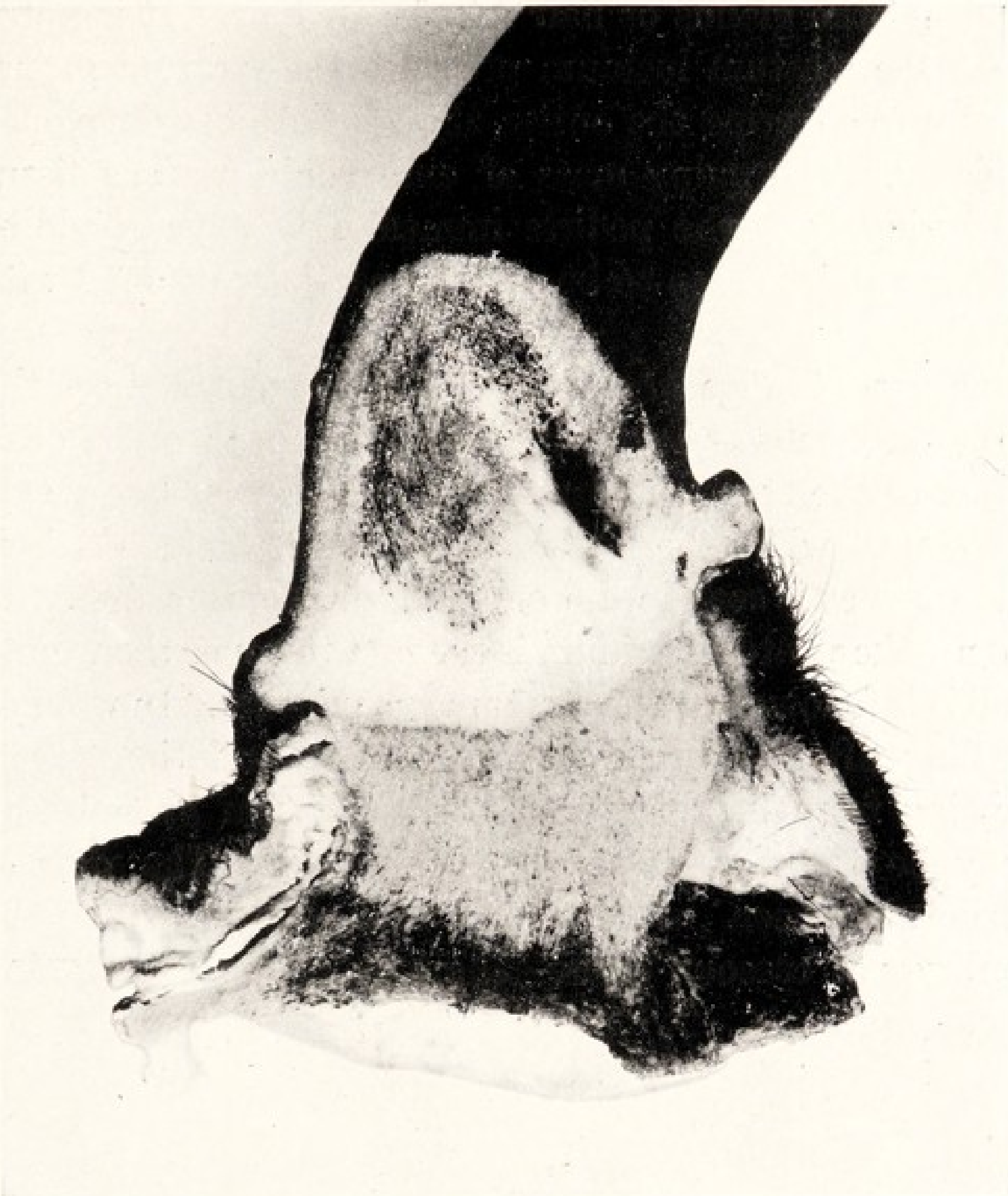

Fig. 10.

RED DEER (CERVUS ELAPHUS)—SECTION OF ANTLER ABOUT TO SHED

Author's Collection.

A stage toward the shedding of antler. Section through skull, pedicle, and base of antler. Antler is now dead bone with coagulated disintegrating blood in it. The skull and pedicle are very vascular in preparation for shedding and regeneration of new bone. The portion of the antler abutting on the pedicle consists of dense white bone, presenting a convexity toward the pedicle.

of a wound where the epithelium, stratum lucidum and stratum granulosum are the only elements reproduced and not the glands or hair follicles or hair. It is noted that the stratum lucidum precedes the stratum granulosum in covering the antler, though both are developed quickly. The pulpy mass of embryonic osseous tissue springing from the pedicle immediately after shedding of the antler is seen to be already partially covered with stratum lucidum.

One sees in Figs. 11 and 12 that the development of the superficial cells—the stratum lucidum—is in advance of those of the stratum granulosum, the former being well developed while the latter are still embryonic. This is the same as is seen in the covering of aseptic wounds in man—the stratum lucidum is the first to cover the wound and it is followed by the stratum granulosum. In wounds healing after a broad covering of granulation tissue healing from below upwards, the stratum granulosum may be the first to cover the wound. The dermal structures seen in Fig. 11, one resting upon the embryonal osseous tissue—there being no intervening membrane.

The nerves of the antler.

Branches of the trigeminal nerve ascend in the cuticular covering in line with the blood vessels and supply the acute sensitivity of the velvet—which thus protects the growing antler during its softened state when it otherwise would be liable to injury from contact with external objects. This would be more especially necessary with adult animals which had been in the habit of using the hardened antlers freely. The nerve supply in the interior of the antler in the midst of the

CUTANEOUS STRUCTURES COVERING THE ANTLER (VELVET)

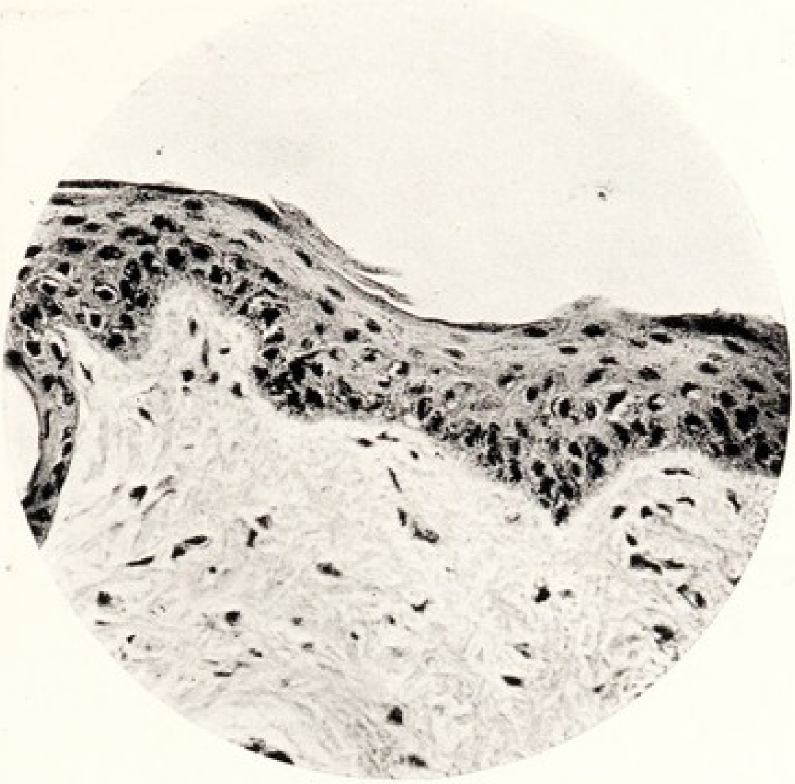

Fig. 11.

SECTION 281.—FALLOW DEER ANTLER, 2/3RD GROWTH, SECTION NEAR TIP.
4 mm. 4 eye-piece.

Cutaneous structure—stratum Malpighi and stratum lucidum superimposed on embryonal osteoblastic tissue.

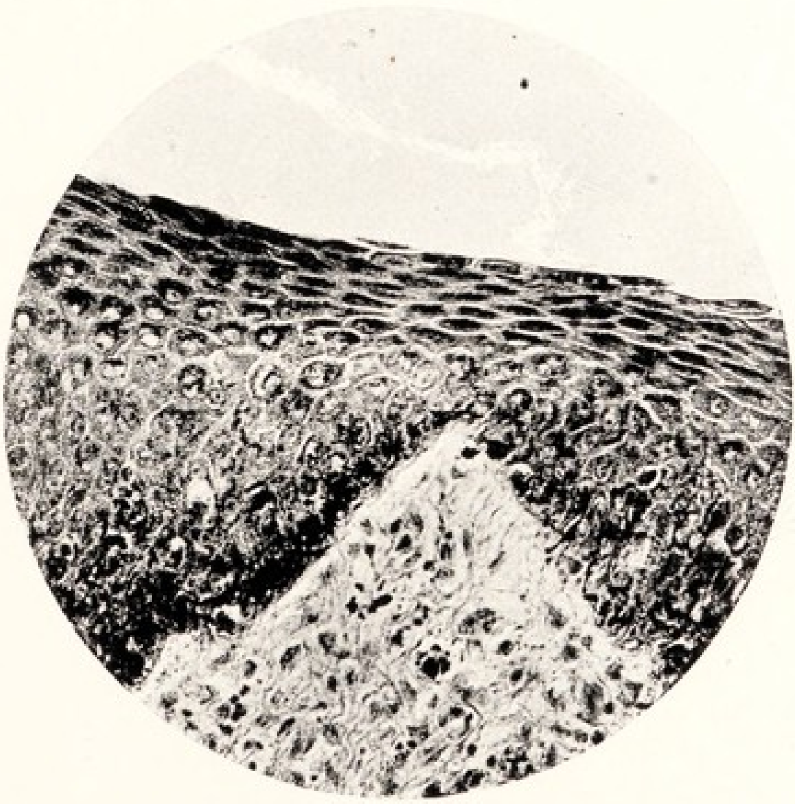

Fig. 12.

SECTION 424.—FALLOW DEER.
4 mm. 2 eye-piece.

Stratum lucidum well developed; stratum Malpighi still in embryonic state.

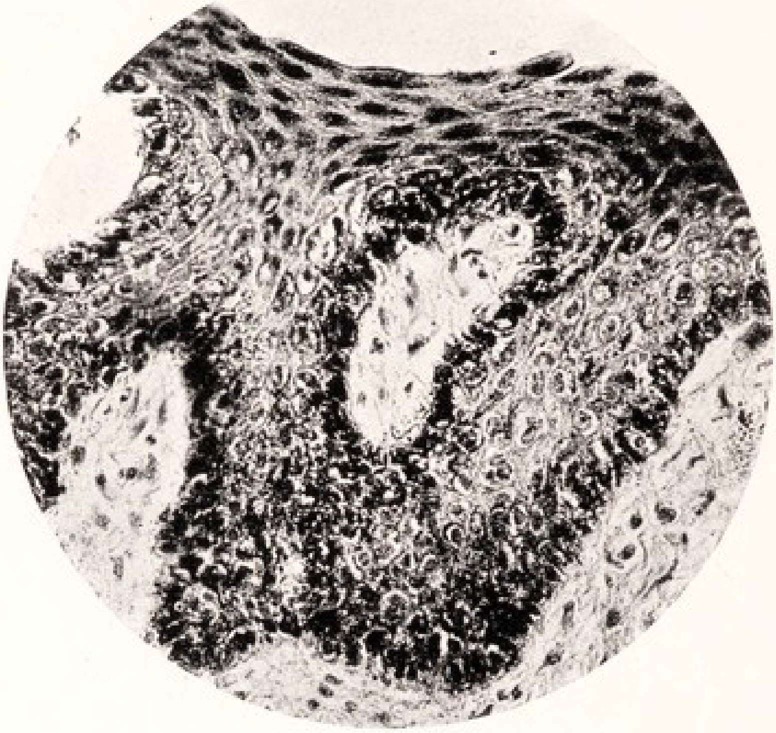

FIG. 13.

SECTION 425.—FALLOW DEER.

4 mm. 2 eye-piece.

Stratum lucidum well developed: stratum Malpighi still embryonic and ill defined.

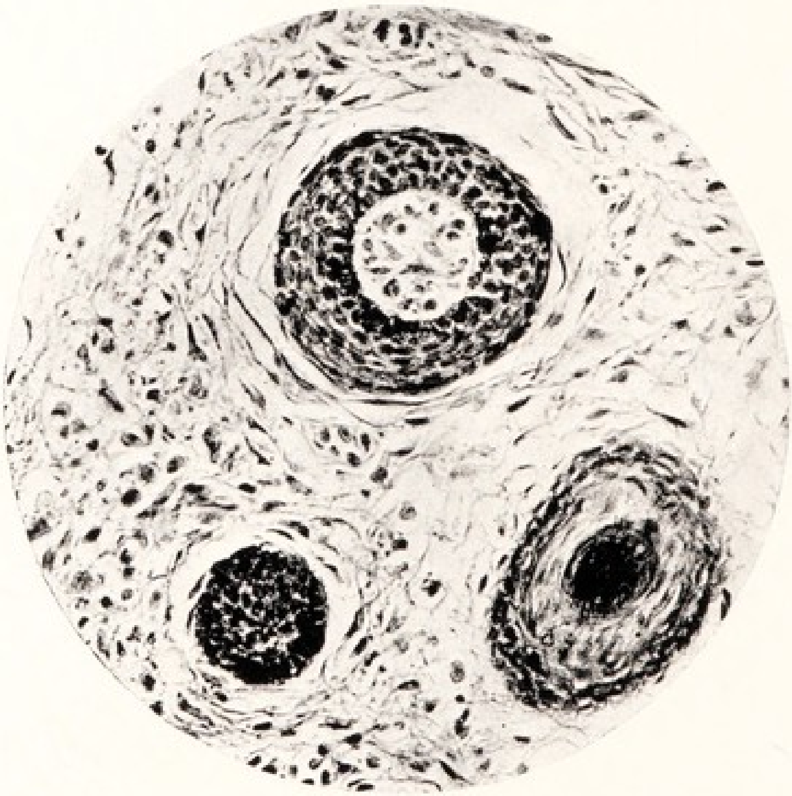

FIG. 14.

SECTION 479.—FALLOW DEER, 2/3RD GROWN, $1\frac{1}{2}''$ FROM TIP.

Three hair bulbs in section.

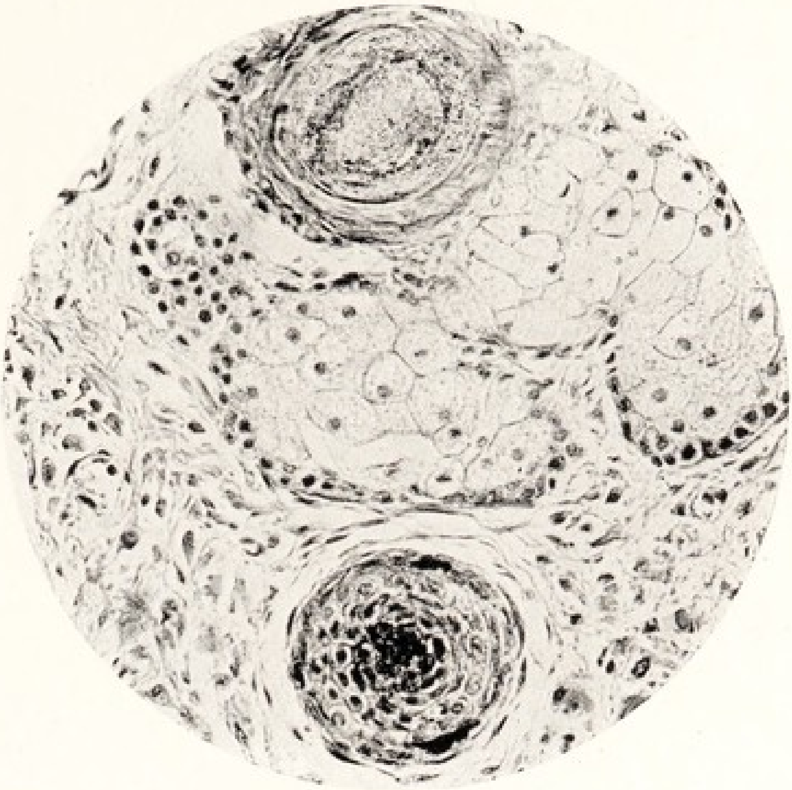

Fig. 15.

SECTION 281.—FALLOW DEER, 2/3RD GROWTH, NEAR TIP.
4 mm. 4 eye-piece.
Hair bulbs and cutaneous glands in section.

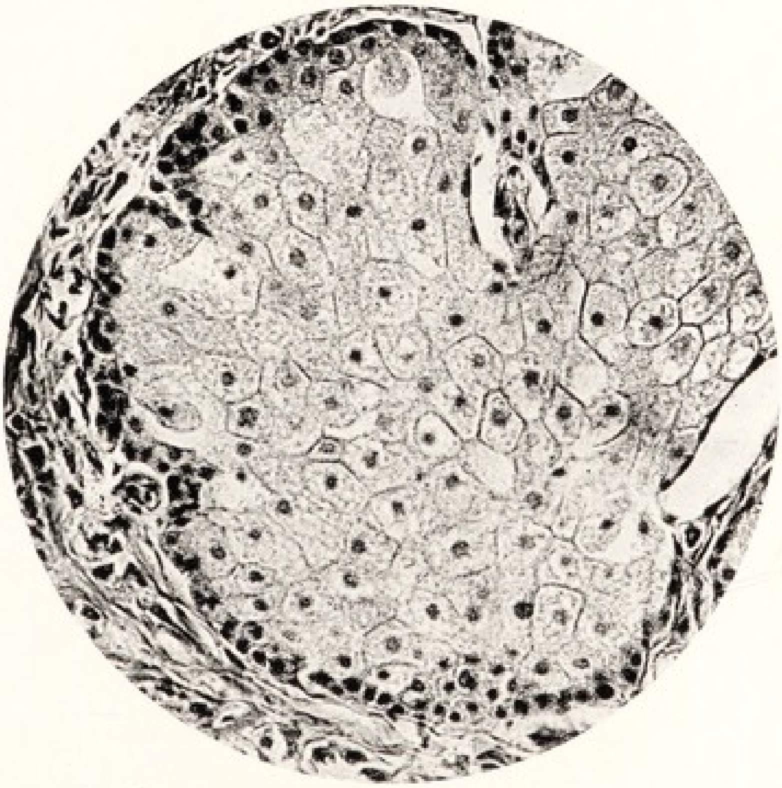

Fig. 16.

SECTION 479.—FALLOW DEER ANTLER, 2/3RD GROWTH, $1\frac{1}{2}''$ FROM TIP.
4 mm. 4 eye-piece.
Cutaneous gland in section.

Fig. 17.

SECTION OF SKIN (VELVET) AND HAIR BULB WITH GLANDS. LOW POWER.

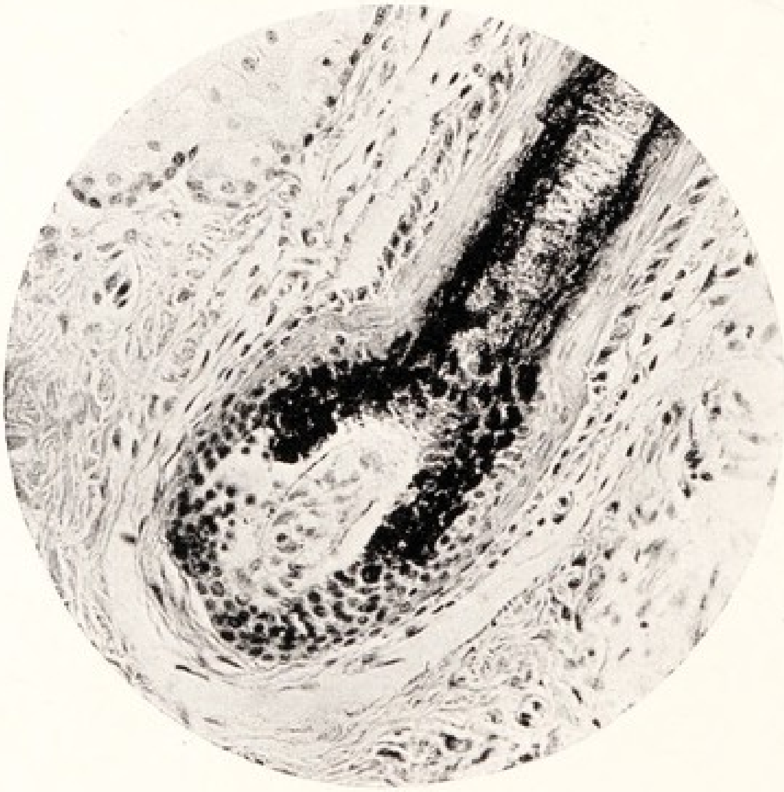

Fig. 18.

SECTION 424.—FALLOW DEER.
4 mm. 2 eye-piece.

Hair bulb in longitudinal section.

osseous matter is very difficult to trace during the period of rapid osseous deposition.

Effect of injury or disease to pedicle or skull (ossifying centres) on growth of antlers.

When the pedicle or skull from which it springs is injured or altered by pathological processes, the antler is directly affected thereby. Thus a bullet passed through the right pedicle of an antler of the Red Deer at its junction with the skull, a groove being formed in the latter while the pedicle was thrown outwards and downwards, in which position it still adhered by an osseous attachment to the skull. The growth from the injured pedicle resulted in a deformed left antler dwarfed to a fourth of the size of its neighbour.

In another instance a bullet struck the left pedicle, penetrating its outer aspect near the corona, without damaging the base of the pedicle. This disturbed the relation of the component parts in the growing centre and deflected the growth of the subsequent antlers springing from that point. Though the antler on that side was irregular in form, being divided into two, one part having a very long basal line in front, and though it was shorter than its neighbour, yet the whole amount of the ossific matter produced was not lessened by more than a third of that of the normal (Fig. 19).

On the other hand, when a pyogenic process has affected the base of the pedicle and adjacent skull, the growth may be entirely destroyed and the portion of the antler which existed at the time of the pyogenic invasion may be entirely shed or retained by skin only—falling flail-like over the eye on the same side. In such a case no fresh antler can grow as the ossifying

Fig. 19.

SKULL AND ANTLERS OF RED DEER—CERVUS ELAPHUS.

DEFORMED AND DWARFED RIGHT ANTLER. RESULT OF INJURY TO PEDICLE.

From Collection of Duke of Richmond and Gordon.

Deformed and dwarfed right antler from bullet penetrating outer side of pedicle near corona.

centre has been destroyed. The pedicle of the neighbouring antler being unaffected, the antler grows to its normal dimensions. See Fig. 20.

Fig. 20.

SKULL AND ANTLER OF RED DEER—CERVUS ELAPHUS—PATHOLOGICAL.

The right side showing osteomyelitis affecting skull and pedicle with consequent stunted antler. The pedicle and antler are in one piece, the pedicle having separated from the skull. It was attached by skin only and swayed to and fro with the movements of the animal.

From Collection of Author.

The antler itself is liable to injury especially in its early life. The abundant supply of sensory nerves to the velvet of the growing antler makes the animal careful in using the antler or bringing it into violent contact with external objects. Occasionally, however, accidents happen, as is seen in the twisted antler shown in Fig. 21, which was the result of an injury to the

RED DEER (CERVUS ELAPHUS)—GREENSTICK FRACTURE OF ANTLER.

FIG. 21.

ANTLER—RED DEER—PATHOLOGICAL.

Greenstick fracture, result of injury during growing period, and subsequent thickening of bone at point of damage.

FROM COLLECTION OF AUTHOR.

growing antler, producing a "greenstick fracture" which has firmly united in its deformed position. Not having been set when still soft, it has become consolidated in the twisted position.

Cromie antlers—views as to their causation.

The Cromie Antlers are found not infrequently in Jura Forest. All the specimens in Author's collection have come from there. Some writers favour the view that they are illustrative of atavism from an odd species of deer now extinct, the strain only showing occasionally. It cannot be due to a general malnutrition, as many of the animals with cromie antlers attain a good size and weigh heavy. In-breeding is said to be a cause, but this cannot be the whole cause, as in some isolated forests where in-breeding has occurred cromie antlers have not resulted. Whatever may be the true cause, the pedicles are, usually, smaller than normal both in length and circumference. The form assumed by the antler is somewhat similar to that assumed by antlers whose ossifying centres have been impaired;—a rickets of the antler;—or where the incentive to the production of bone in the antler has been diminished. There is no indication of malformation in any of the other bones of the skeleton. In this respect, observation on the condition of the testicles in the cromie would be of value not only as to whether they are normal in form, but whether they functionate properly.

In one instance a cromie was found to have undescended testicles, though it does not necessarily follow that they were defective in function. The arrest of growth of the bone in the antler due to castration, and the deformity and stunting which occurs in other cases where the testicles have been injured, make it desirable that inquiry should be made in that direction for the elucidation of the subject. Castrated animals fatten much more quickly than normal ones, and cromies usually are heavy and fat. Data as to their procreative power would be of value.

Macroscopic appearance of specimen of antlers commencing to grow—about two weeks growth after shedding (Figs. 3, 4 and 5).

On the head in front of the ears, a couple of dark knobs presented, bearing near the centre of the apex of each, a slightly depressed reddish-white mark doubtless cicatricial in character due to the final stage of shedding of the antler. These two knobs somewhat resembled two large ripe dark figs, from which the flower had separated.

They were still soft superficially, the right bearing an indentation from external pressure. The kernel within conveyed to the touch the impression of yielding cartilage.

The stout, vigorous hairs of the skin covering the skull and pedicle stopped at the junction of the pedicle with the new growth. Toward the base of the sprouting antler very fine hairs were seen, on the upper part they were scarcely visible and there were spaces toward the apex of the antler where there was no visible appearance of hair.

The cutis was very thin over the new growth and especially over the top. (Like a conical human stump, the cutis covering the bone being very thin—stratum lucidum.)

A longitudinal section was made through the sprouting antler, pedicle and skull of the specimen of Red Deer presenting the appearance shown in Figs. 4 and 5.

The measurements of the specimen were, in longitudinal direction :

1. From the inside of the skull—brain cavity to tip of sprouting antler	$3\frac{5}{10}$ inches.
2. From indication of corona to tip of sprouting antler	$1\frac{9}{10}$,,
3. From V shape in centre of pedicle to tip of sprouting antler	$2\frac{5}{10}$,,

So that the actual height of the rudimentary antler was nearly two inches.

The measurements of the diameter through the pedicle compared with that of the rudimentary antler were :

Diameter of pedicle	$1\frac{1}{10}$ inches.
Diameter of rudimentary antler	$1\frac{4}{10}$,,

In the reverse direction :

Diameter of pedicle	$2\frac{1}{10}$ inches.
Rudimentary antler	$2\frac{5}{10}$,,

This showed that the two diameters of the rudimentary antler was greater by three-tenths in one direction and four-tenths in the other, than the pedicle from which the new growth sprang. Thus the new growth had overflowed or overlapped the pedicle.

The whole bone from the interior of the skull through the pedicle upwards is much more vascular than the same parts when the growth has stopped. The great mass of the new growth is cartilaginous and soft. At the darker part in the centre where it joins the pedicle—the apex of the V seen in the specimen—new bone is growing from the centre, while the edges and circumference are still cartilaginous and the skin very thin over the cartilage. Fine hairs are also seen sprouting from the new skin.

The two heads (Figures 6 and 7) were those of Fallowdeer, the sprouting antlers shown being four and five weeks respectively after shedding. They were good specimens received in very fresh condition, and from which many valuable sections were obtained.

Macroscopic appearance of sprouting antlers.

The histological data were obtained from the heads of various varieties of deer, the red deer (*Cervus elaphus*) and the fallow deer (*Cervus dama*) chiefly. The roe deer

RED DEER—ABNORMAL ANTLERS

Fig. 22.

RED DEER—CROMIE ANTLERS.
Presented by the late Mr. Henry Evans, shooting tenant, Jura.
Author's Collection.

(*Capriolus*), though frequently examined,—and some of the sections of the antlers are included,—did not present any advantage over the larger varieties. The antler of the roe deer, owing probably to its smaller size, did not show the exuberance of growth of the larger varieties.

The heads of deer were obtained from many sources and include specimens of the sprouting antlers, two (Fig. 3),

RED DEER—ABNORMAL ANTLERS

Fig. 23.

RED DEER—CROMIE ANTLERS.
Presented by the late Mr. Henry Evans, shooting tenant, Jura.
Author's Collection.

four (Fig. 6), five (Fig. 7), and eight (Fig. 8) weeks after the shedding of the old antlers. Macroscopic views of a few typical specimens are given and sections of several of these are also included (Figs. 4 and 5), from which the naked-eye appearance of the rapidly growing bone and cartilage may be seen.

The section of the base of the antler eight weeks old shown in Fig. 8 presents a mass of well grown bone already presenting greater density at the coronal line than that on the proximal and distal side of that line where the bone is still very vascular. It is at this line that the separation of the antler from the pedicle will ultimately take place, and it does so by the obliteration of the blood vessels at that line within the antler and the obliteration of the cutaneous vessels by the spur of bone projecting into them from the corona without. Already the cuticular covering at the corona is thin compared with the cutis above and below that point.

In the two illustrations (Figs. 9 and 10) one sees in section the base of the old antler and pedicle and skull,—the dead antler,—showing the avascular coronal line and the avascular coronal spurs bereft of cutaneous covering—that having been long shed—still adherent to the very vascular pedicle preparing to effect the separation of the dead antler and to reproduce a fresh one. The antler presents a convexity toward the pedicle. That concavity in the pedicle will be transformed into a convexity immediately after the shedding of the antler. It is said that in castrated animals the antler presents a concavity before shedding instead of a convexity.

CHAPTER II.

HISTOLOGY

Evolution of Osteoblast.

Under the heading, the evolution of the osteoblast, the whole phenomena of bone formation might be described, as the osteoblast plays the principal role in osseous development. For convenience, however, this chapter is considered under three headings: first, the evolution of the osteoblast; secondly, direct formation of bone; thirdly, indirect bone formation or evolution of bone through cartilage.

The histological figures represented under the heading of the evolution of the osteoblast have been chosen from sections from fallow deer antlers, but identical appearances are seen in the antler of the red deer and to a modified extent in those of the roe.

The osteoblast—its evolution.

In the earlier evolutionary stages of bone development in the antler of the deer, an embryonic mesodermic tissue of indefinite structure appears (Figs. 58, 59, 60). At parts this indefinite looking tissue may bear a resemblance to the early stages of embryonic fibrous tissue or even occasionally to the very early stages of embryonic myomatous tissue without either of these two tissues being present. In the process of evolution, from this indefinite embryonic tissue ill-defined cells at first appear, gradually assuming a more distinctive form, from which the osteoblasts ultimately emerge (Fig. 27 *et seq.*). Once the osteoblast assumes its mature form it becomes distinctive and the cell may be easily recognised and traced through its further evolution into bone.

In the antler the whole of the mesodermic embryonic layer, situated peripherally, is transformed into bone directly or indirectly, and none of it into any other tissue, such as fibrous tissue. Into bone, as it is forming, thin walled blood vessels penetrate and take with them the necessary connective tissue involved in their formation. In many instances the blood spaces in the interior of the growing bone are so large, the walls so thin, and the periphery so crowded with osteoblasts that it is difficult to determine the endothelial lining of the vessels.

The syncytium from which bone and cartilage is developed is seen to be alike in the antler of the deer—in bone grown experimentally within glass tubes [1]—in dog's bone, in human growth, and in regeneration of bone—such as in repair after osteomyelitis and in the healing of fractures.

The typical form of the mature osteoblast.

The typical form of the mature osteoblast is an oval cell with its nucleus situated peripherally and occupying its narrow end (Fig. 37). When the osteoblast assumes its mature form, it is the immediate precursor of changes tending toward the formation of bone as an organised structure—such as the evolution of a matrix and the deposition of ossein. The deposit of ossein quickly obscures the osteoblast.

The recognition of a definite form assumed by the *mature* osteoblasts is advanced and is likely to be conceded by those who study the histological phenomena in the deer's antler. A favourable opportunity is afforded of observing the osteoblasts in such sections, as they occur in immense numbers and are neither obscured by too close packing—at the early stages of the development at least—nor are they burdened by obtrusive invasion of other tissues. Whilst the osteoblast is still in the early embryonic state, its cellular form, like that of all other germinal tissues, is indefinite, but as it becomes mature it takes on the typical forms by which it is identified. Once this form is assumed, it is coincident with a series of phenomena occurring in the cartilage

[1] See volume on *Growth of Bone*—James MacLehose & Sons, 1912, p. 102.

envelopes, the deposition of ossein and other changes which constitute bone as a fixed structure. The osteoblast is apt to be obscured by the resultant transformation of the tissue and especially by the deposition of ossein. There are, however, in the antler so many osteoblasts in a field that abundant opportunity is afforded for observing them in all stages of their evolution so that their form and development can be easily traced.

After recognising this mature form of osteoblast in the deer antler, sections of growing bone from other animals were re-examined and found to exhibit the same typical form of mature osteoblast. This may be seen in the growing epiphysis of the dog, Figs. 38 to 43, in the growing epiphysis and in the repair of bone in man, especially in the young adolescent. In re-examining the sections made from dog's bone grown in glass tubes recorded in a previous volume, the mature form of the osteoblast is clearly visible. So that this mature form of osteoblast is not confined to the antler of the deer, but has been found in each of the species examined—though not so markedly evident in these as in the osseous development of the deer.

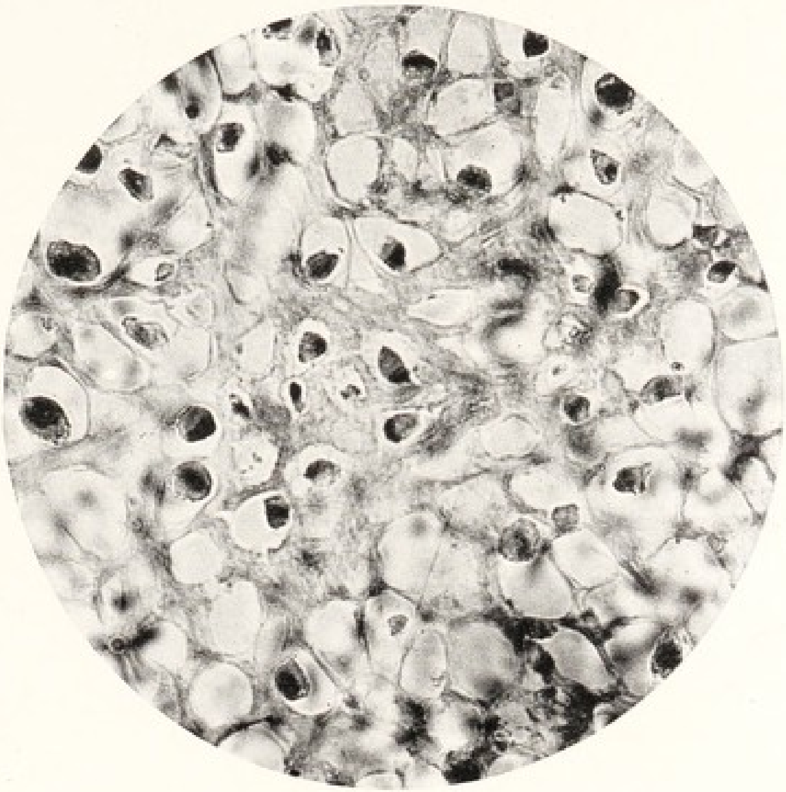

FIG. 24.

SECTION 477.—FALLOW DEER ANTLER, 2/3RD GROWTH, 2″ FROM TIP.
4 mm. 4 eye-piece.

Osteoblasts assuming their mature form in the inside of cartilage capsules preparatory to bone formation, seen best in centre.

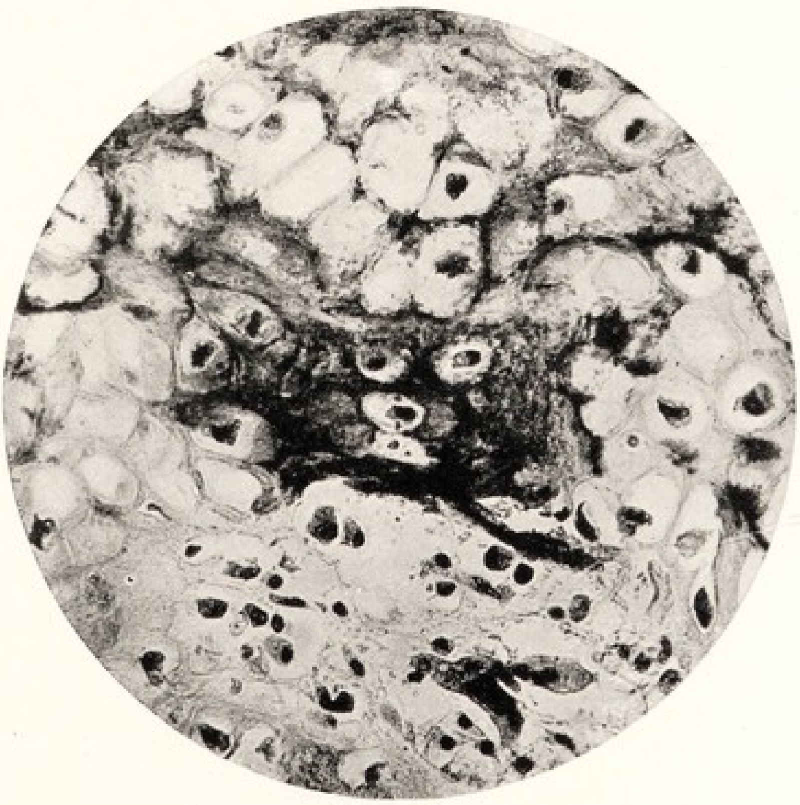

FIG. 25.

SECTION 479.—FALLOW DEER ANTLER, 2/3RD GROWTH, 2″ FROM TIP.
4 mm. 4 eye-piece.

Osteoblasts inside cartilage capsules being surrounded and periphery impregnated with ossein.

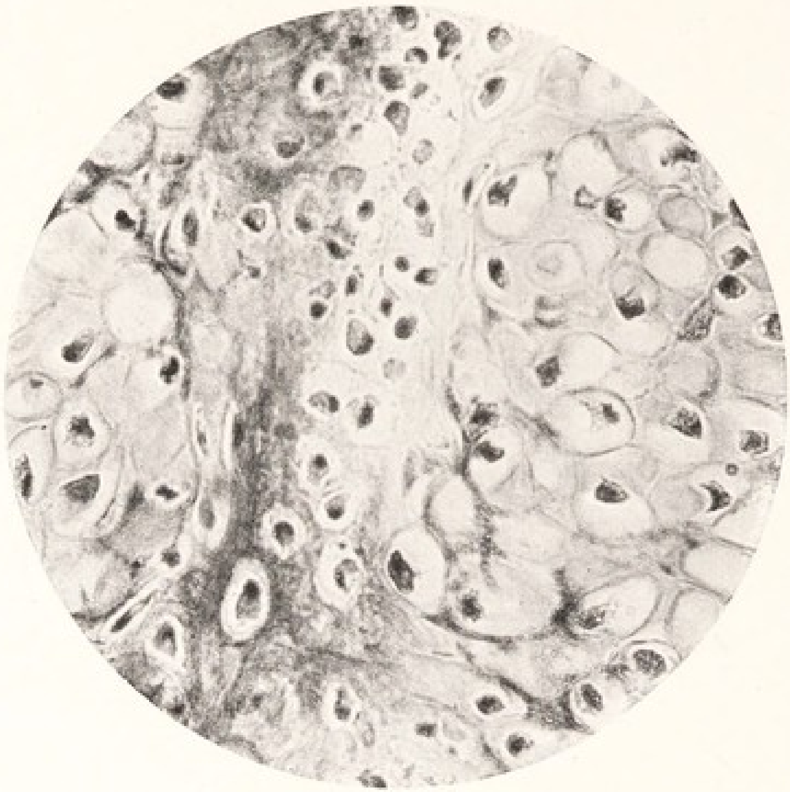

Fig. 26.

SECTION 465.—FALLOW DEER ANTLER, 2/3RD GROWTH, 2″ FROM TIP.
4 mm. 4 eye-piece.

Osteoblasts assuming mature form inside and outside cartilage envelopes; ossein depositing in periphery of cytoplasm in cartilage envelopes.

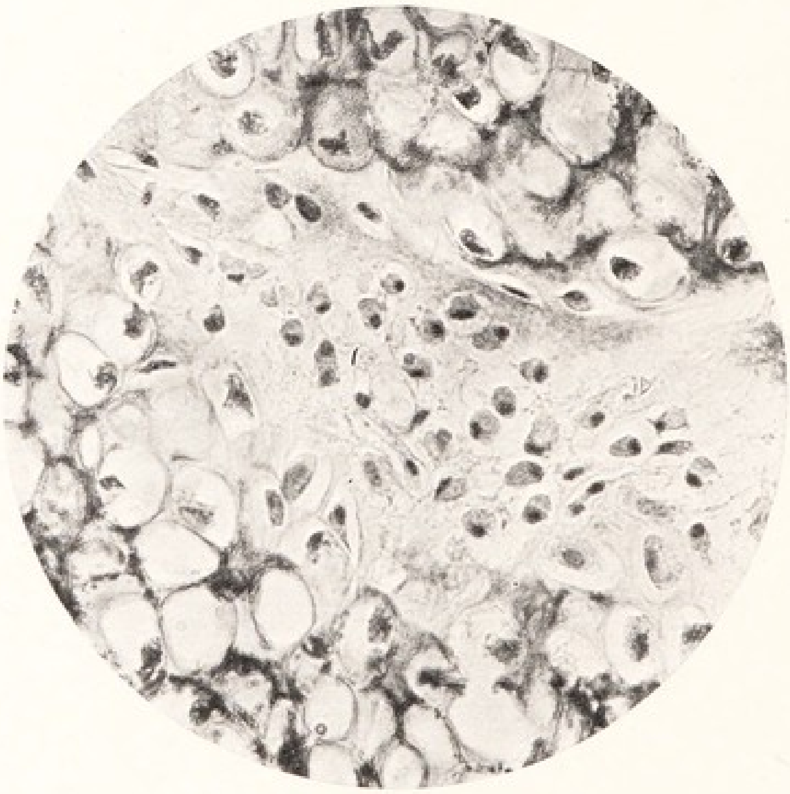

Fig. 27.

SECTION 465.—FALLOW DEER, 2/3RD GROWTH IN ANTLER, 2″ FROM TIP.
mm. 4 eye-piece.

Osteoblasts assuming their mature form and free in pocket in midst of cartilage, their cytoplasm taking on deposition of ossein.

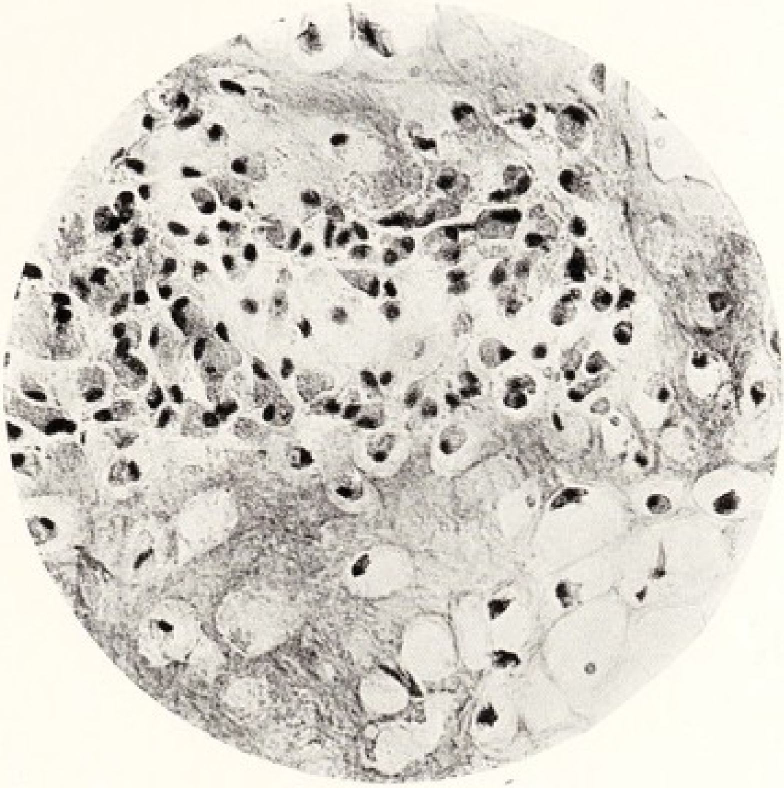

FIG. 28.

SECTION 477.—FALLOW DEER ANTLER, 2/3RD GROWTH, 2″ FROM TIP.

4 mm. 4 eye-piece.

Osteoblasts forming a pocket in the cartilage and assuming their mature form. They are to be seen within and without cartilage capsules, ossein being deposited in periphery of cytoplasm and matrix.

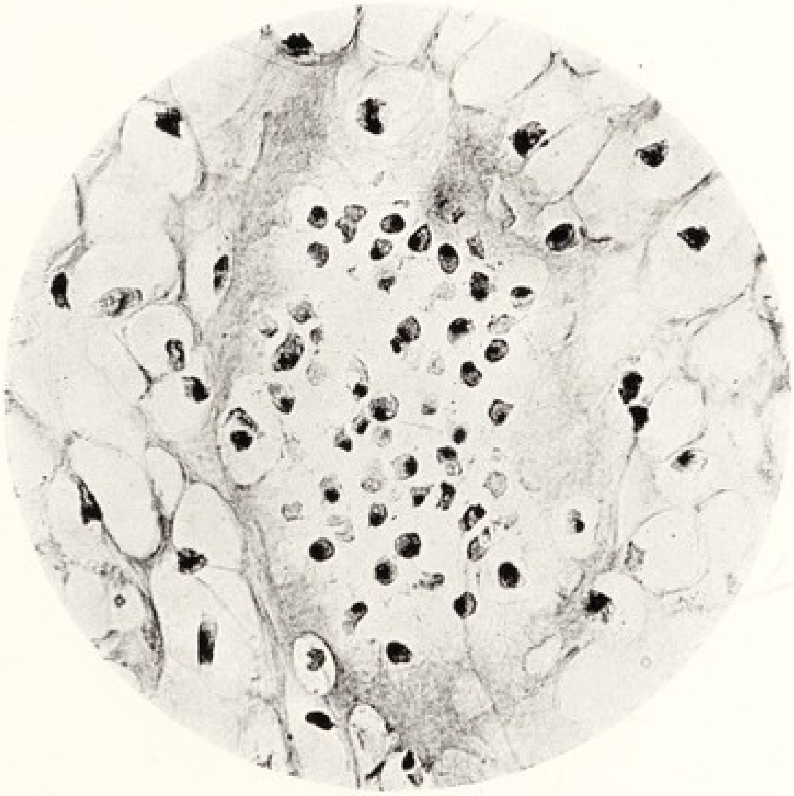

FIG. 29.

SECTION 477.—FALLOW DEER ANTLER, 2/3RD GROWTH, 2″ FROM TIP.

4 mm. 4 eye-piece.

Osteoblasts free forming a pocket in midst of the cartilage. They are assuming mature form and ossein is being deposited in their periphery.

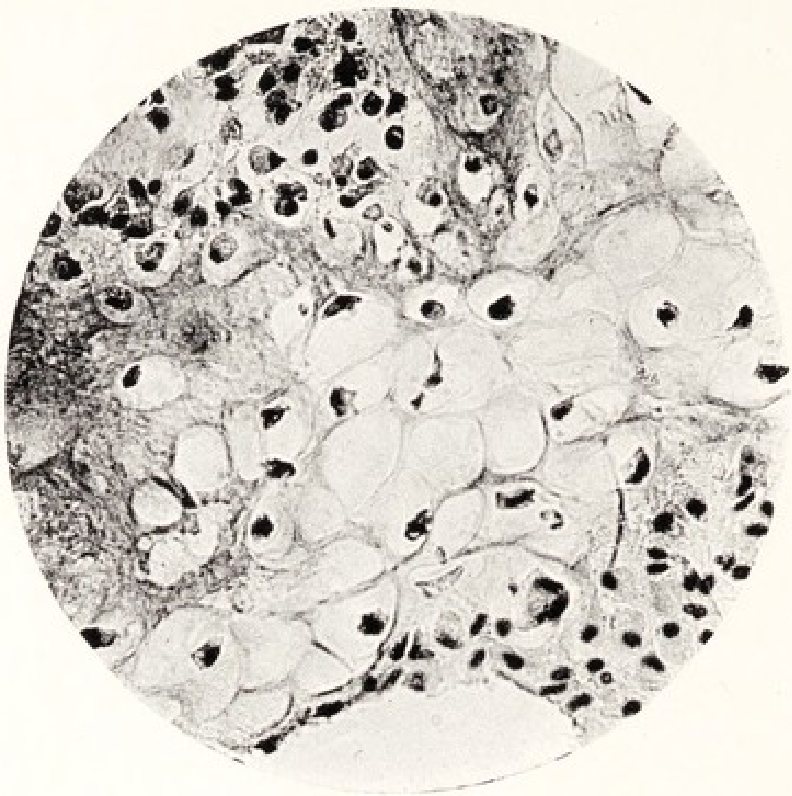

Fig. 30.

SECTION 477.—FALLOW DEER ANTLER, 2/3RD GROWTH, 2″ FROM TIP.
4 mm. 4 eye-piece.

Osteoblasts assuming their mature form within and without, ossein being deposited.

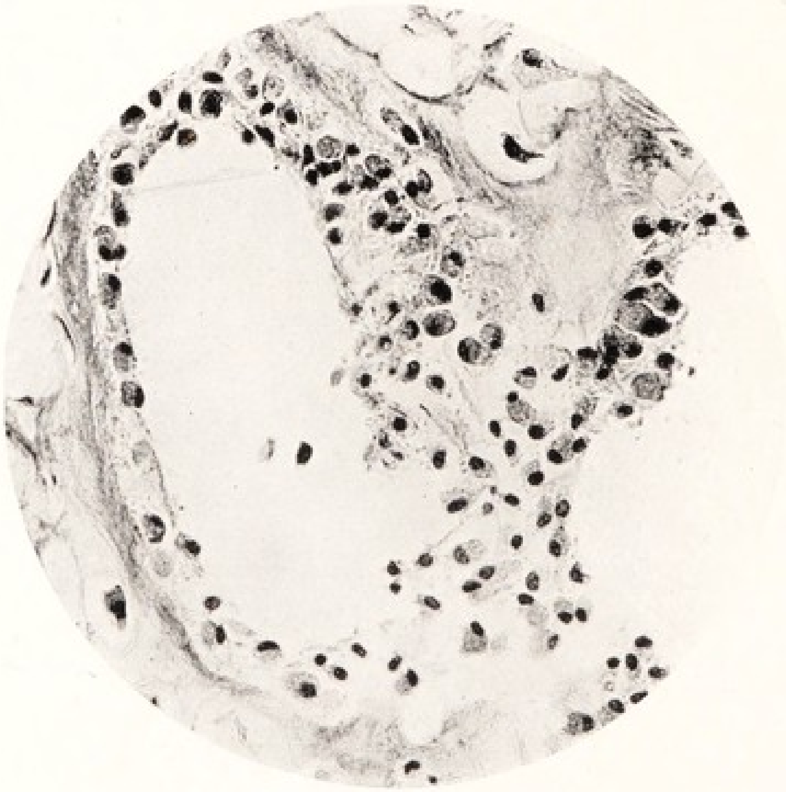

Fig. 31.

SECTION 479.—FALLOW DEER ANTLER, 2/3RD GROWTH, 2″ FROM TIP.
4 mm. 4 eye-piece.

Osteoblasts, having assumed their mature form, congregating outside the cartilage round a blood space, ossein being deposited in their periphery of the cytoplasm and in the cartilage matrix.

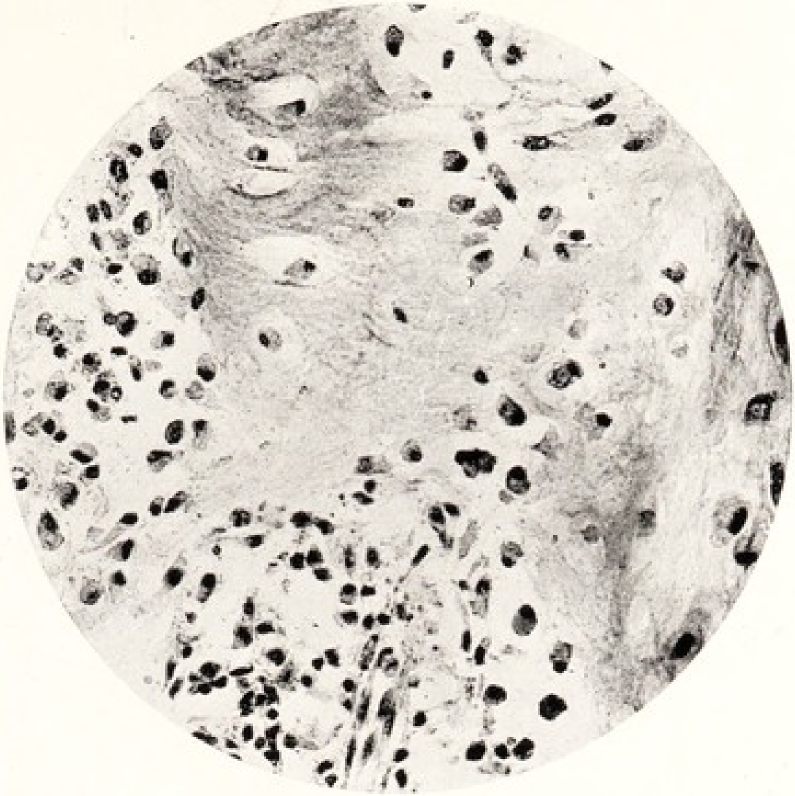

FIG. 32.

SECTION 477.—FALLOW DEER ANTLER, 2/3RD GROWTH, 2″ FROM TIP.
4 mm. 4 eye-piece.

Osteoblasts seen within and without cartilage capsules. In both the periphery of the cytoplasm is impregnated with ossein as well as the surrounding matrix.

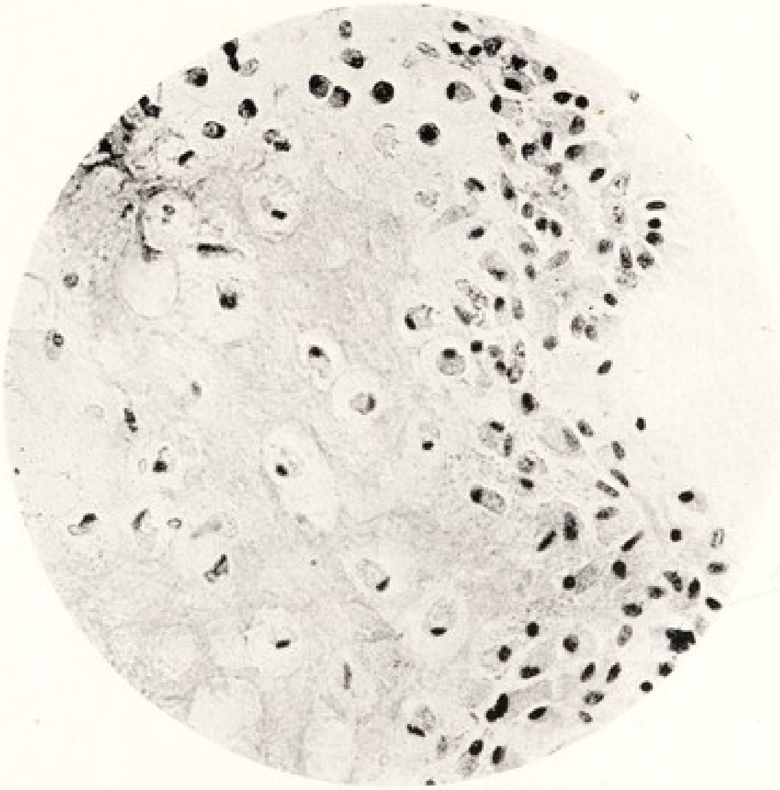

FIG. 33.

SECTION 477.—FALLOW DEER ANTLER, 2/3RD GROWTH, 2″ FROM TIP.
4 mm. 4 eye-piece.

Osteoblasts within cartilage capsules assuming their mature form and the same form may be seen free on outside of cartilage. Cartilage capsules are flattened into matrix in which ossein is deposited.

Fig. 34.

SECTION 477.—FALLOW DEER ANTLER, 2/3RD GROWTH, 2″ FROM TIP.
4 mm. 4 eye-piece.

Osteoblasts within and without cartilage capsules; ossein deposited in both and in matrix.

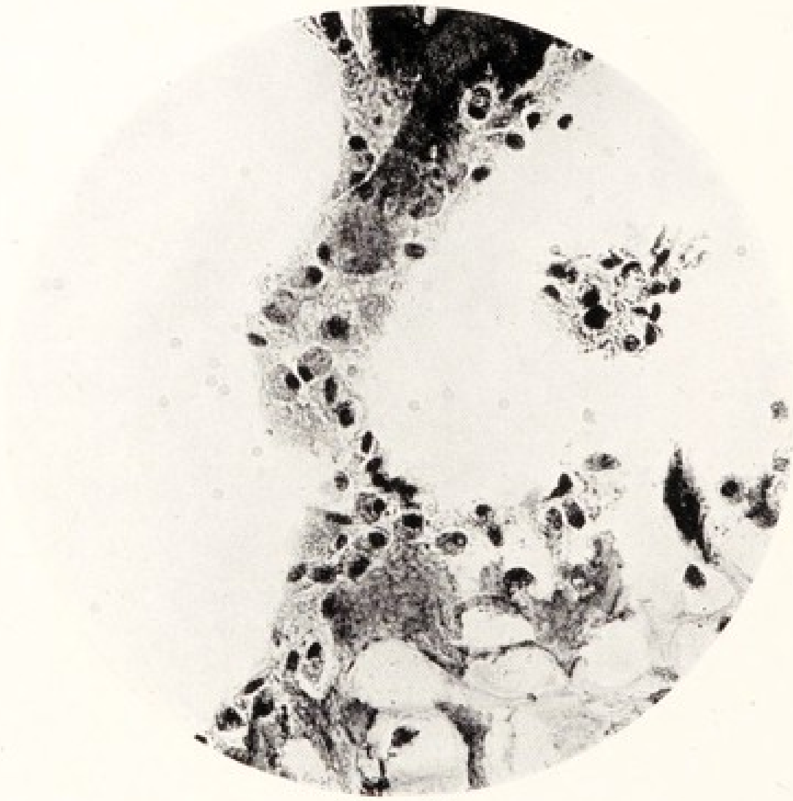

Fig. 35.

SECTION 479.—FALLOW DEER ANTLER 2/3RD GROWN, 2″ FROM TIP.
4 mm. 4 eye-piece.

Free osteoblasts assuming their mature form and forming a bridge of bone between two osseous trabeculae.

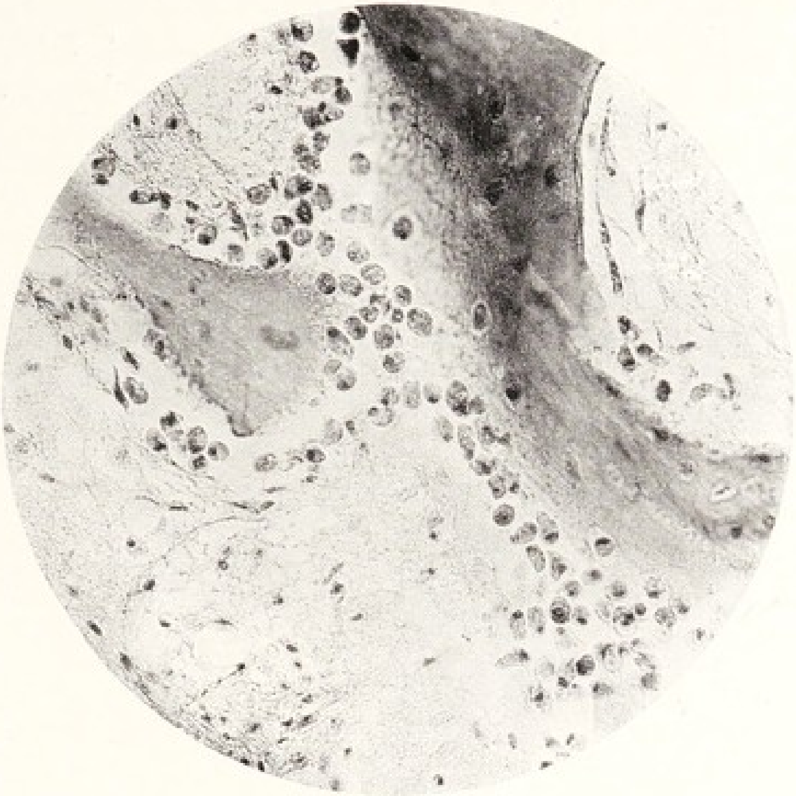

FIG. 36.

SECTION 461.—FALLOW DEER SPROUTING ANTLER, 2″ FROM TIP.

4 mm. 2 eye-piece.

Osteoblasts which have assumed their mature form, developing bone trabecula.

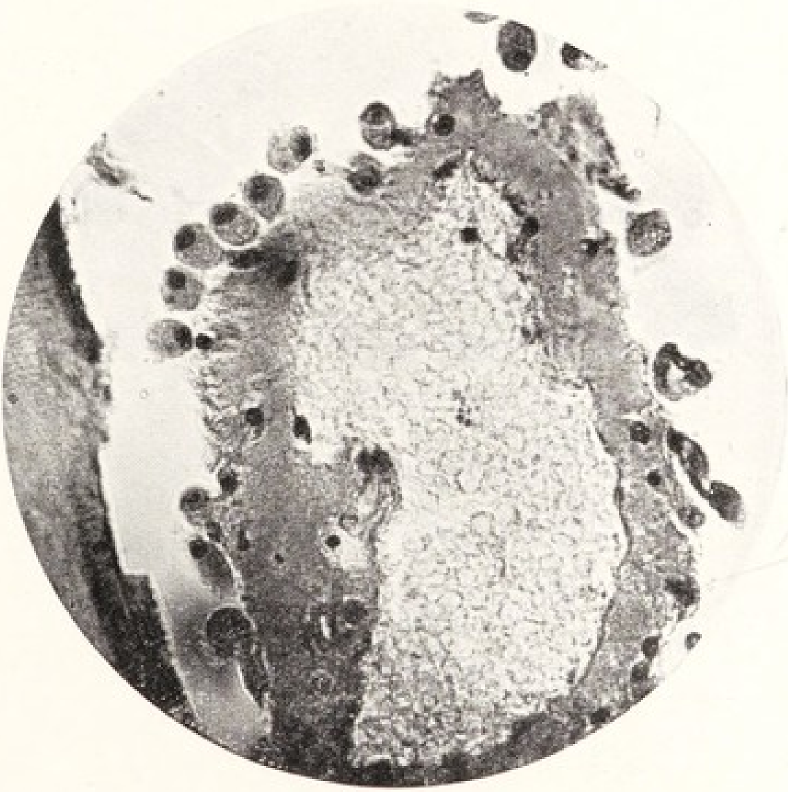

FIG. 37.

SECTION 281.—FALLOW DEER ANTLER, 2/3RD GROWTH FROM TINE.

4 mm. 8 eye-piece.

Osteoblasts, withdrawn from osseous trabecula by the shrinking of a vessel wall, are seen in their fully mature form. Blood clot is seen in interior of blood vessel.

SECTIONS FROM DOG'S EPIPHYSIS NEAR JUNCTION WITH DIAPHYSIS—FOR COMPARISON

FIG 38.

SECTION 509.—OBJECTIVE 4 mm. 4 eye-piece.

Osteoblasts on diaphyseal side of epiphyseal cartilage arranged in rows surrounding themselves with ossein—seen on right hand of figure.

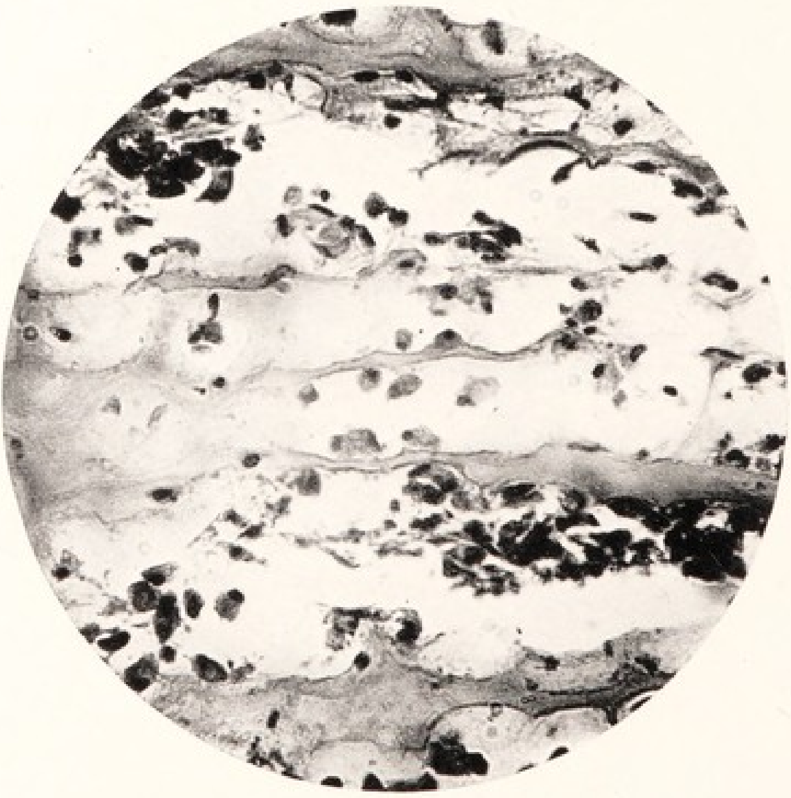

FIG. 39.

SECTION 513.—No. 3—4 mm. objective. 2 eye-piece.

Osteoblasts assuming mature form in transition of cartilage into bone. Ossein beginning to be deposited. Cartilage capsules have mostly disappeared, traces of longitudinal lines still remaining.

FIG. 40.

SECTION 505.—(4)—4 mm. objective. 2 eye-piece.

Osteoblasts beginning to assume mature form in cartilage at epiphyseal line, the cartilage envelopes having almost disappeared.

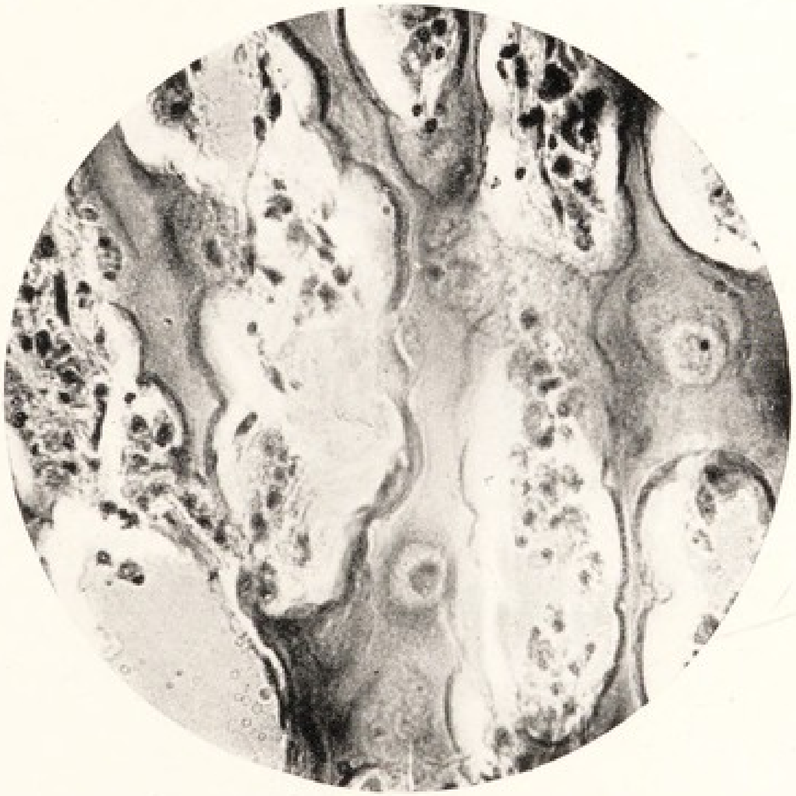

FIG. 41.

SECTION 513.—No. 6—4 mm. objective. 4 eye-piece.

Transition from cartilage into bone, mature osteoblasts being surrounded with ossein and incorporating themselves into bone. Osseous trabeculae in process of formation.

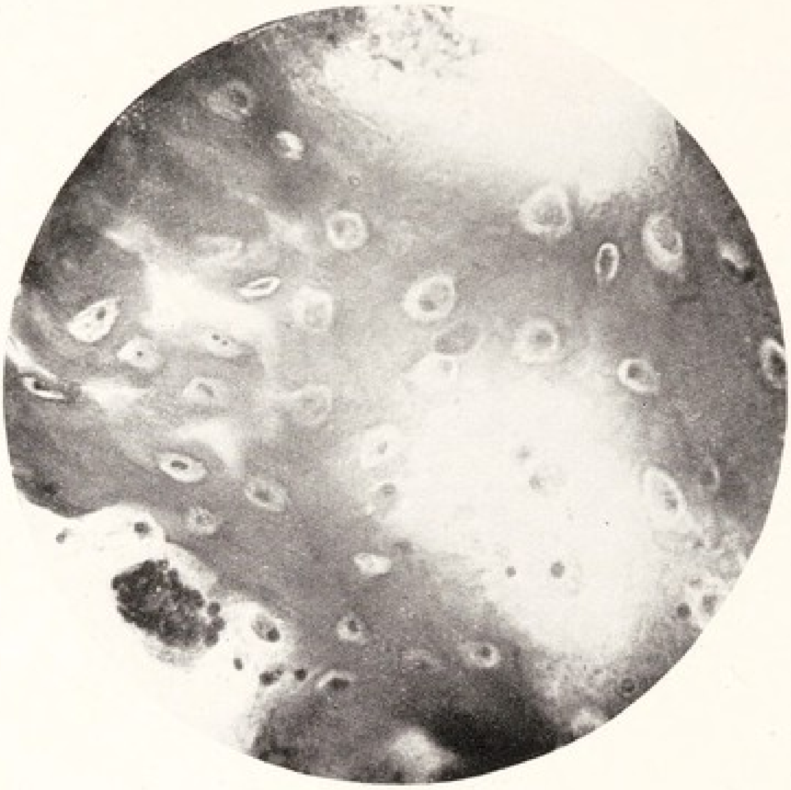

FIG. 42.

SECTION 507.—4 mm. objective. 2 eye-piece.

Mature osteoblasts are seen inside and outside spaces and are being surrounded by ossein in formation of bone from cartilage.

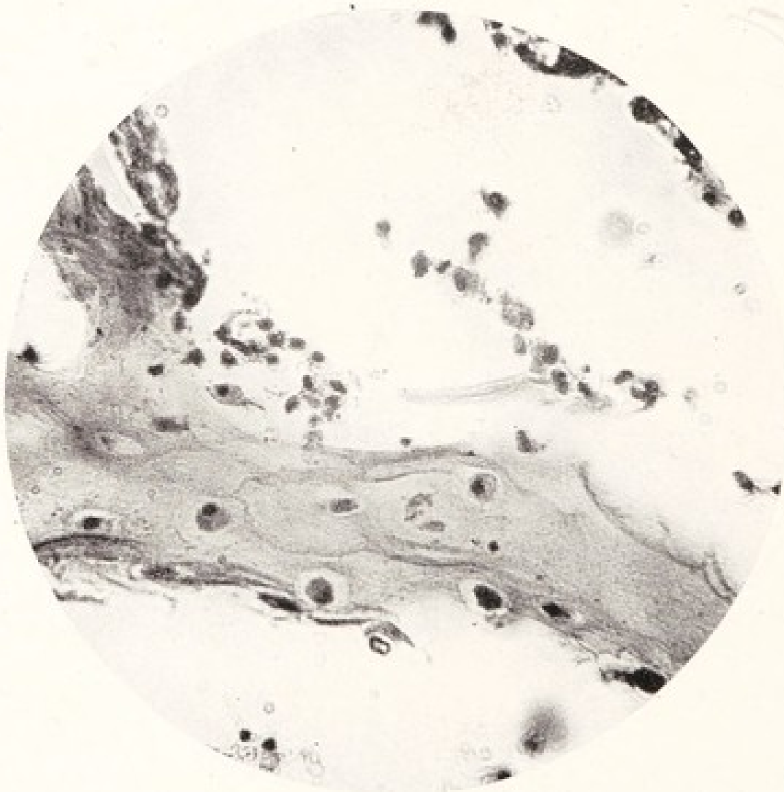

FIG. 43.

SECTION 512.—4 mm. objective. 2 eye-piece.

Osteoblasts of mature form being enveloped in bone. Osseous trabecula in process of formation from cartilage, indications of cartilage, capsules still remaining.

The osteoblast embedding itself in ossein.

When osseous trabeculae are forming, rapidly multiplying osteoblasts pavement the periphery and add to the circumference of the area by imbedding themselves in fresh osseous increments. Once they have surrounded themselves by ossein, the osteoblasts become part of the fixed osseous structure and are regarded as bone cells, each of which controls, probably under the influence of the trophic nerves, the osseous area which immediately surrounds it.

The Osteoblast may free itself from the surrounding ossein.

When conditions are normal, the cell may remain quiescent imbedded in its calcareous surroundings, but when stimulated, it can promote the dispersal of its solid walls by causing absorption of the lime salts which are removed through the blood stream ; the regenerating process is set up and the young cells assume the role of osteoblast, being ready to take part in fresh osseous deposition when normal conditions are restored.

Osteoblasts may evolve into bone in either of two ways : direct and indirect bone formation.

From the germinal layer the osteoblasts may evolve into bone directly, or pass through an intermediary cartilaginous stage, from which they become finally converted into bone.

These two methods of direct and indirect transference of the osteoblast into bone may be seen in the same antler at the same time, though usually at some distance apart. The indirect method, where the osteoblast passes through a cartilaginous phase before it is converted into bone, is the predominating one in the development of the deer's antler. It is to be noted that the antler is primarily formed in a mass of cartilage springing from the osseous fixed tissue cells of the pedicle and adjacent skull, and that any subsequent direct transference into bone, which may be seen in the same antler, is an evolution from this base. Both direct and indirect modes of ossification may be seen in processes of repair after fracture and injuries in the lower animals and in man; the process of repair of the same bone, the tibial diaphysis for instance, may assume either the direct or indirect method according to the conditions under which it is placed, though under ordinary circumstances, where considerable movement takes place between the fragments, the indirect method—healing through cartilage—is the rule. Where fixation of fragments of fractured bones is brought about immediately after the injury, and the immobilization is maintained, healing takes place principally by the direct method.

The osteoblast is the same cell which is evolved from the embryonic tissue, whether it passes directly into bone, or through a phase of transition cartilage. In either case it arrives at a definite shape and contour and becomes imbedded in a matrix surrounded by calcareous salts—when it assumes the role of a bone cell.

When the germinal layer is about to pass directly into bone, the osteoblast assumes its mature form, but when the intermediary cartilaginous type is assumed, the mature type of the osteoblast is delayed in appearing until toward the end of the process, when the bone formation is about to take the place of the transition cartilage.

Direct bone formation.

The photomicrographs of the sections illustrative of the method of direct bone formation occurring in the antler of the deer have been taken mostly from some of the tines of antlers of the Fallow deer of about eight weeks' growth. At this stage in the development of the antler some of the tines were in process of sprouting from the main stem, while others had attained about one half of their growth, though they were still in process of evolution. Some of the sections were taken in series from near the tip of the latter, while, by way of comparison and contrast, a few were taken from near its base. Those sections from near the tip of the tine showed the bone formation to be direct. Those from the base of the tine, though more mature, had the appearance of indirect formation of bone through cartilage.

Direct bone formation has not been found in the main stem (beam) of the deer's antler, its ossification being through cartilage springing from the pre-existing cartilage and bone of the pedicle. As one finds direct bone formation occurring in some of the tines, toward their tip, it is probable that one might also find it in the terminal processes of the main stem toward the completion of its evolution. Direct bone formation, as far as the present investigation goes, has chiefly been found in the tines of the fallow deer. The antlers showed vigorous formation of bone through cartilage of the main stem and the basal portions of the tines, while the terminal parts of the same tines developed through direct bone formation.[1]

One would, *a priori*, look for the direct method of bone formation, as likely to occur in the expanding palmate portions of the antlers of the reindeer and moose varieties, as the flatter formation of the palmate form would lend itself more readily to that mode of

[1] Direct formation has subsequently been found in the antler of the red deer under similar conditions depending on the stage of its development.

osseous development than the cylindrical mass of the main stem. Hitherto no opportunity of investigating the histological phenomena occurring in *growing* antlers of the moose or reindeer has been had by the author.

It is also possible that the relative amounts of bone produced by direct and indirect formation may vary according to circumstances, such as the condition of the animal.

The sections have been made in series from without inwards, the first showing the superficial layers of the cutis and the substratum of embryonic osteoblastic tissue, the latter ultimately developing into dense sclerosed bone. The cutis in this specimen is thinner than that covering the main stem of the antler. Any cuticular appendages which have dipped into the basement of the epithelial layer are extruded by the advancing osteoblastic encroachment.

There seems to be little or no interchange of blood between the blood vessels of the underlying bone of the antler and those of the epidermal layer—the velvet. Whether by differential coloured injections the vessels of the cutis and those of the interior of the antler could be shown to have some slight inosculation has yet to be determined, but there is certainly no obtrusive evidence of such inosculation in the antler at this period.[1] If it does occur at any time, it would probably be found during the earlier periods of antler growth, and not toward the completion of the process, when the osseous matter has absorbed all the pabulum for its rapid production and then shut off the supply of blood through the vessels by compressing them circumferentially and finally obliterating them by the rapid encroachment of

[1] Such injections have been tried by the author without showing inosculation between the cuticular vessels and those of the interior.

sclerosed bone. The absence of such inosculation between the vessels of the interior of the antler and those of the velvet, hastens the separation of the latter when the coronal abutment strangles the long vessels of the cutis at their base. Had there been inosculation, the velvet would have remained longer and would probably have bled when separating from the bone, unless the vessels of the bone had previously become obliterated.

In the direct formation of bone one sees in the early period a syncitium almost identical with that seen in the indirect mode of bone formation (Fig. 49). In the same section almost contiguous with the field from which Fig. 49 was taken, the distinctive cellular development peculiar to the embryonic form of direct osseous formation is observed (Figs. 50 and 51). Within both the beginning of the deposit of ossein is seen, but more distinctly in the latter. In Fig. 52 the osteoblast is beginning to assume its mature form and to deposit ossein in its periphery, so as to form a layer of bone in its early stage.

In the succeeding views, the mature form of the osteoblast is more distinct and the osseous trabeculae better formed. The pavementing of the trabeculae by the osteoblasts and the envelopment of the cells in the ossein so as to make firm bone are all represented.

Direct bone formation bears a resemblance to the ossification in the parietal bones of the skull.

Intramembranous ossification.

Here, as in the parietals, there is occasionally a slight appearance of fibro-cartilage. In the human parietals one sees this at certain stages in the foetal developments and in regeneration taking place in the parietal bones after injury, there is often seen a slight cellular zone somewhat resembling fibro-cartilage appearing in the midst of the predominant characteristics of direct bone formation.

DIRECT TRANSITION OF OSTEOBLASTS INTO BONE

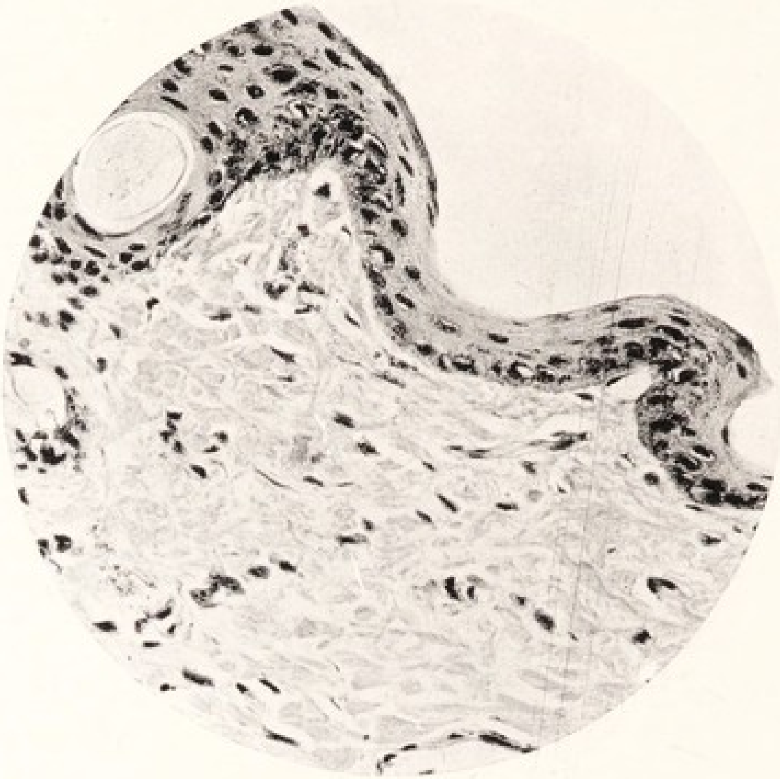

Fig. 44.

SECTION 280.—FALLOW DEER ANTLER, 2/3RD GROWTH, NEAR TIP OF TINE.
4 mm. 4 eye-piece.

Cutaneous tissue, hair bulb in section—directly covering embryonic form of osteoblastic tissue.

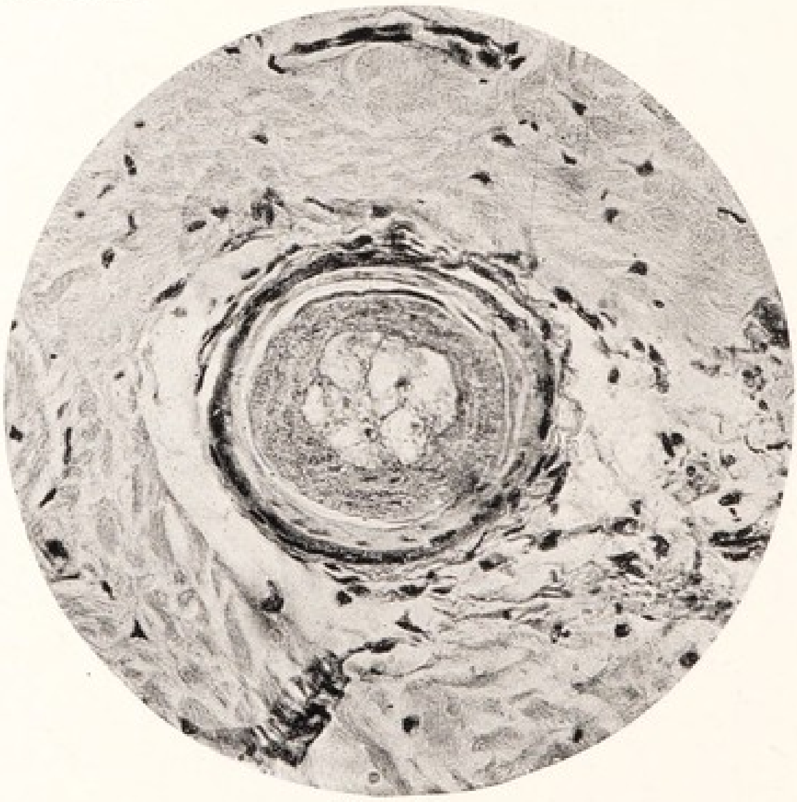

Fig. 45.

SECTION 280.—FALLOW DEER ANTLER, 2/3RD GROWTH, NEAR TIP OF TINE.
4 mm. 4 eye-piece.

Cutaneous layer, hair bulb in section, in midst of embryonic form of osteoblastic tissue.

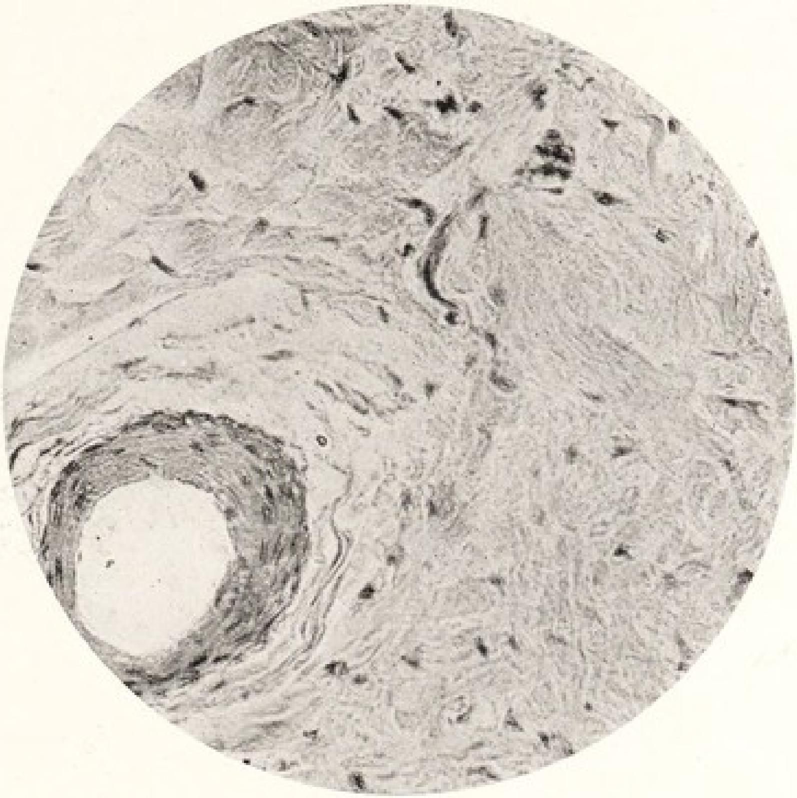

Fig. 46.

SECTION 281.—FALLOW DEER ANTLER, 2/3RD GROWTH, NEAR TIP OF TINE.
4 mm. 4 eye-piece.

Hair follicle, dipping into embryonic osteoblastic tissue.

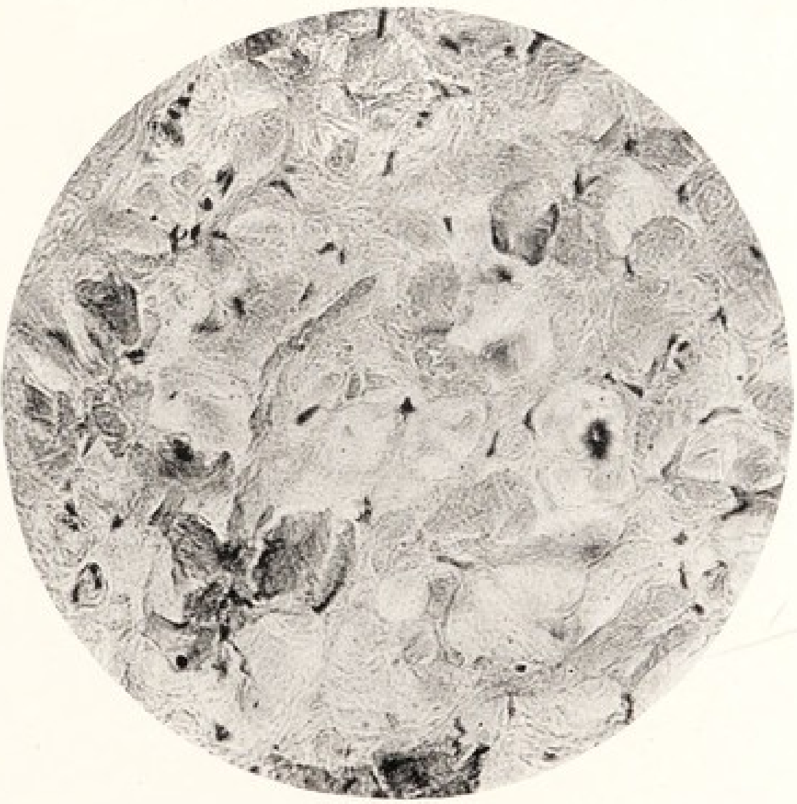

Fig. 47.

SECTION 281.—FALLOW DEER ANTLER, 2/3RD GROWTH, NEAR TIP OF TINE.
4 mm. 4 eye-piece.

Embryonic form of osteoblastic tissue (one phase).

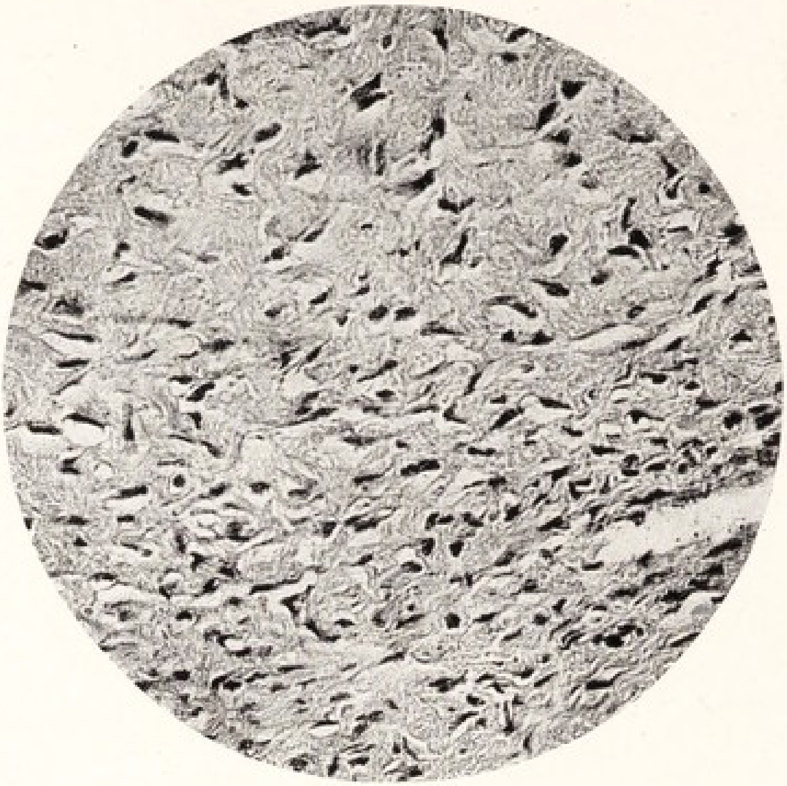

FIG. 48.

SECTION 281.—FALLOW DEER ANTLER, 2/3RD GROWTH, NEAR TIP OF TINE.
4 mm. 4 eye-piece.
Embryonic osteoblastic tissue, beginning to assume distinctive cellular growth.

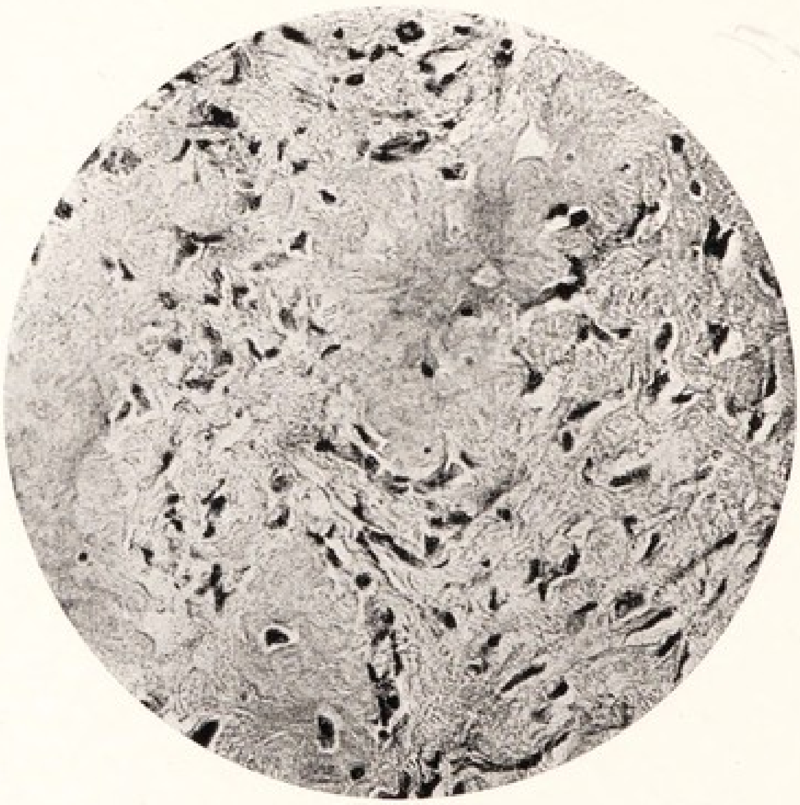

FIG. 49.

SECTION 281.—FALLOW DEER ANTLER, 2/3RD GROWTH, NEAR TIP OF TINE.
4 mm. 4 eye-piece.
Embryonic osteoblastic tissue, osteoblasts being transformed directly into bone.

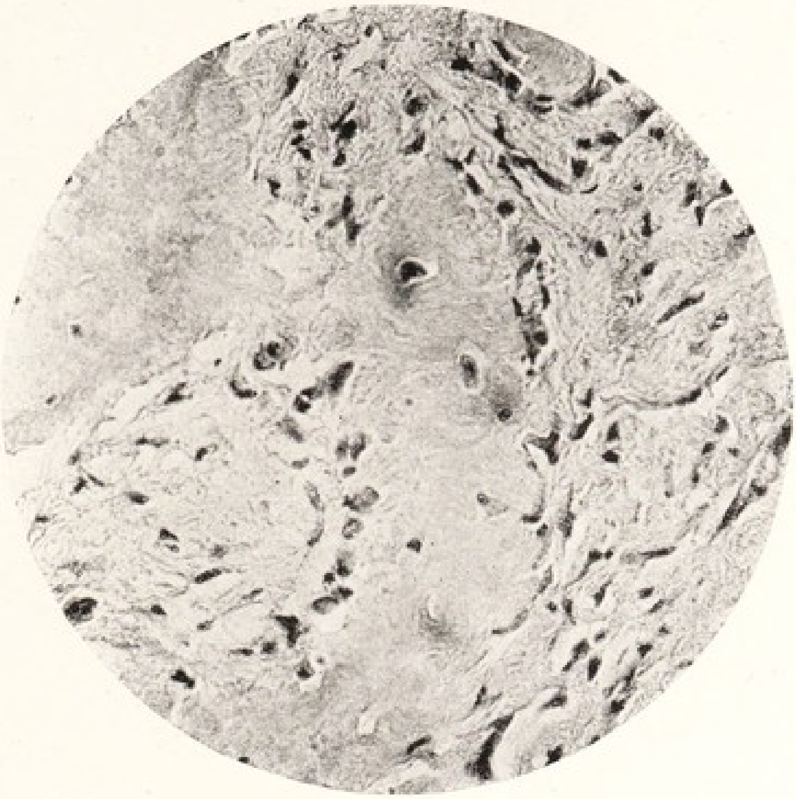

FIG. 50.

SECTION 280.—FALLOW DEER ANTLER, 2/3RD GROWTH, NEAR TIP OF TINE.
4 mm. 4 eye-piece.

Embryonic osteoblastic tissue, osteoblasts transforming directly into bone, and beginning to pavement primitive trabecula.

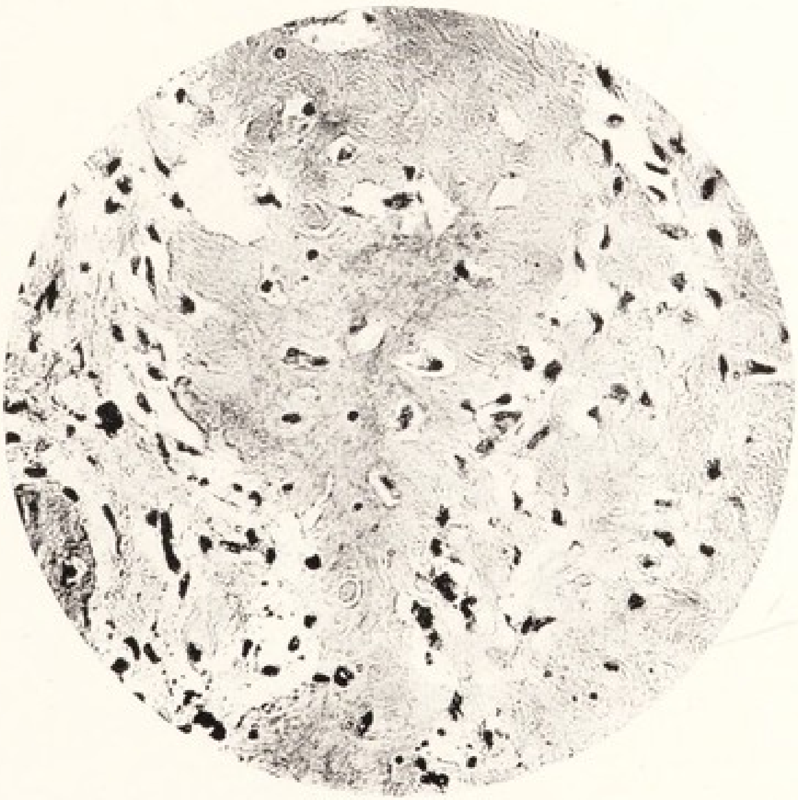

FIG. 51.

SECTION 281.—FALLOW DEER ANTLER, 2/3RD GROWTH, NEAR TIP OF TINE.
4 mm. 4 eye-piece.

Evolution of osteoblasts directly into bone. Osteoblasts beginning to approach mature form.

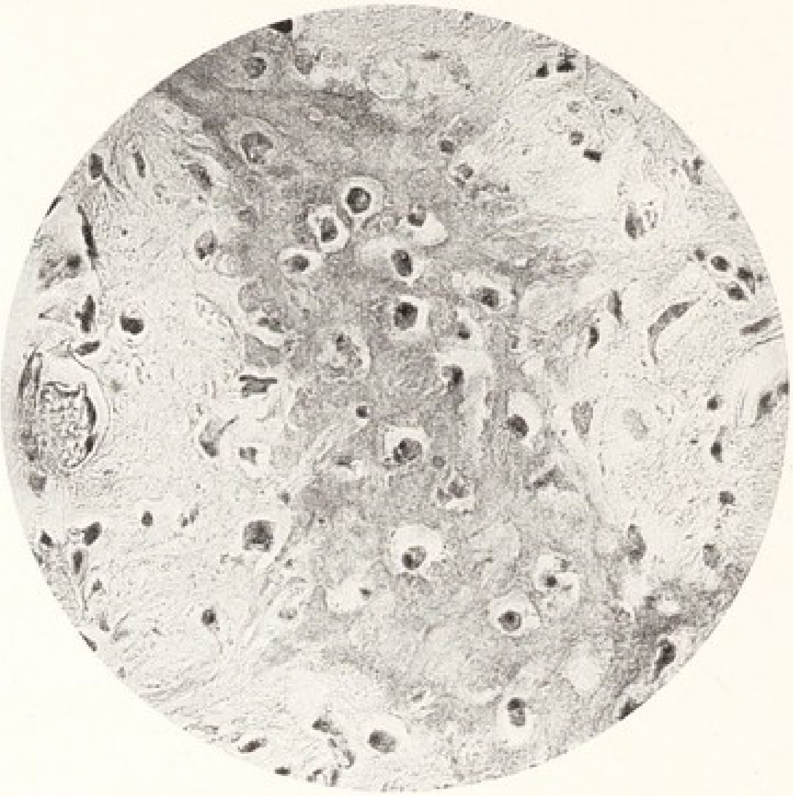

Fig. 52.

SECTION 330.—ROE DEER ANTLER, SPROUTING ANTLER, 1½″ FROM TIP OF TINE.
4 mm. 4 eye-piece.

Imperfect cartilaginous formation (fibro-cartilaginous), between direct and indirect bone formation. Osteoblasts assuming mature form inside of spaces—cart. cells.

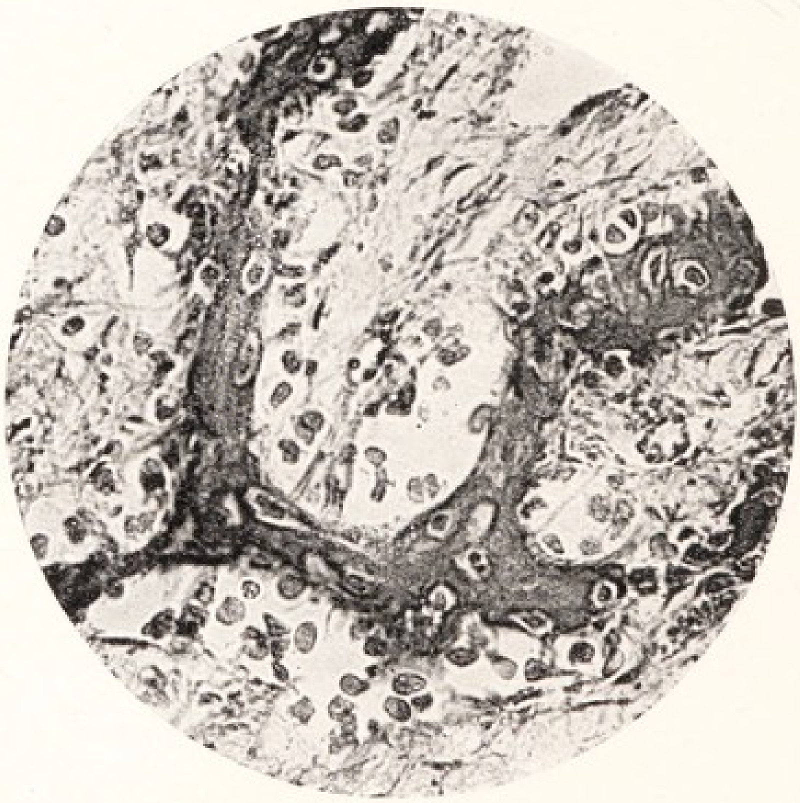

Fig. 53.

SECTION 450.—FALLOW DEER ANTLER, SPROUTING 1½″ FROM TIP OF TINE.
4 mm. 2 eye-piece.

Osteoblasts passing directly into bone—bone trabeculae forming. (Membranous bone.)

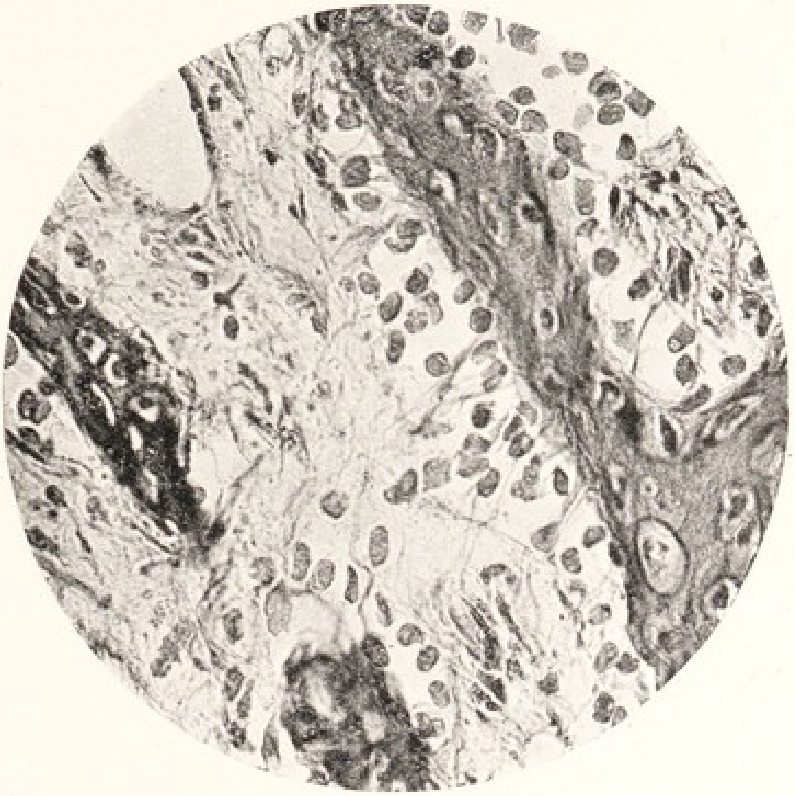

Fig. 54.

SECTION 450.—FALLOW DEER ANTLER, SPROUTING $1\frac{1}{2}''$ FROM TIP OF TINE. 4 mm. 2 eye-piece.

Osteoblasts passing directly into bone though a few spaces show in the trabeculae, giving appearance of ill-formed fibro-cartilage (and resembling membranous bone).

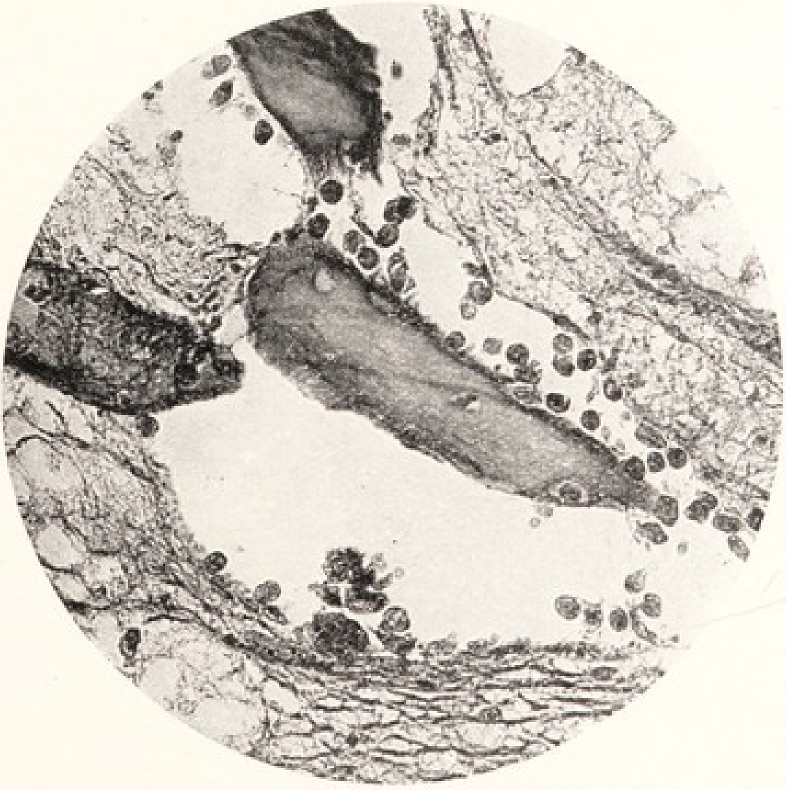

Fig. 55.

SECTION 453.—FALLOW DEER SPROUTING ANTLER, $\frac{3}{4}''$ FROM TIP OF TINE. 4 mm. 2 eye-piece.

Osteoblasts becoming incorporated into osseous trabeculae.

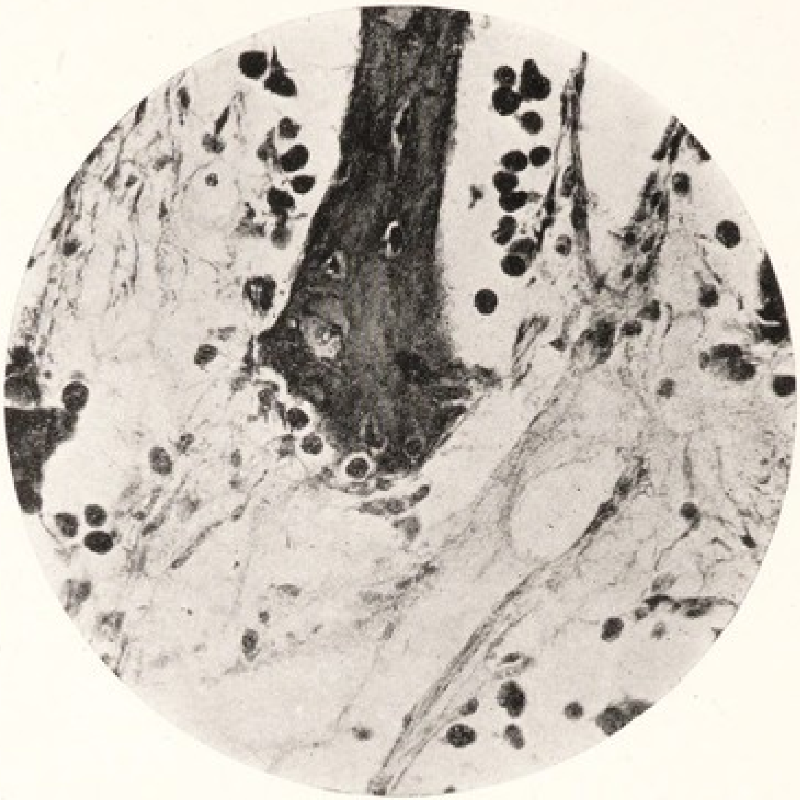

Fig. 56.

SECTION 433.—FALLOW DEER SPROUTING ANTLER, 1″ FROM TIP OF TINE.
4 mm. 2 eye-piece.
Osteoblasts at end of trabecula incorporating themselves into bone.

Fig. 57.

SECTION 450.—FALLOW DEER SPROUTING ANTLER, 1½″ FROM TIP OF TINE.
4 mm. 2 eye-piece.
Dense bone with osteoblasts on outside and incorporated into the bone as bone cells.

The evolution of bone through cartilage (*Indirect bone formation*).

Specimens from the Red Deer (cervus elaphus), the Fallow Deer (cervus dama) and the Roe Deer (capriolus) have been examined. Indirect bone formation—the evolution of bone through cartilage—is the predominant method seen in the development of the Deer's antler. The whole basal structure springs from pre-existing bone in the pedicle and passes through the cartilaginous phases before evolving bone in its final stages.

The same appearances are seen in the early embryonic tissue, from which the indirect bone is evolved, as were seen in the embryonic tissue from which the direct bone was formed. So that, at an early period the embryonic tissue from which they both severally spring is histologically relatively indistinguishable [1] (Figs. 58, 59, 60). Both forms spring from an antler which primarily is formed in cartilage.

The sections which follow have an ever increasing distinctive cartilaginous appearance (Figs. 61, 62 *et seq.*).

The better developed bone, as seen in Figs. 69, 70, 71, 72, shows the appearance of an Haversian system with its concentric rings. The spaces are still filled with osteoblasts embedding themselves in the periphery and advancing the bone formation centripetally, and so lessening the lumen of the space and finally probably effecting its closure as the bone advances towards its dense sclerosed end.

In the succeeding views, the mature form of the osteoblast is more distinct and the osseous trabeculae

[1] Even in more mature forms of bone formation such as in epiphyseal plates of cartilage there may be seen contiguous cartilaginous cells of identical form, the one destined for epiphyseal, the other for diaphyseal growth.

better formed. The pavementing of the trabeculae by the osteoblasts and the envelopment of the cells in the ossein so as to make firm bone are all represented.

When the osteoblast assumes the form of transition cartilage it weaves a capsule round itself, in which it lies imbedded as long as the cartilage exists. When the promptings of higher development stimulate the osteoblast, it assumes its mature form, which is followed immediately by a series of changes in the cartilage capsule.

EVOLUTION OF BONE THROUGH CARTILAGE (INDIRECT BONE FORMATION)

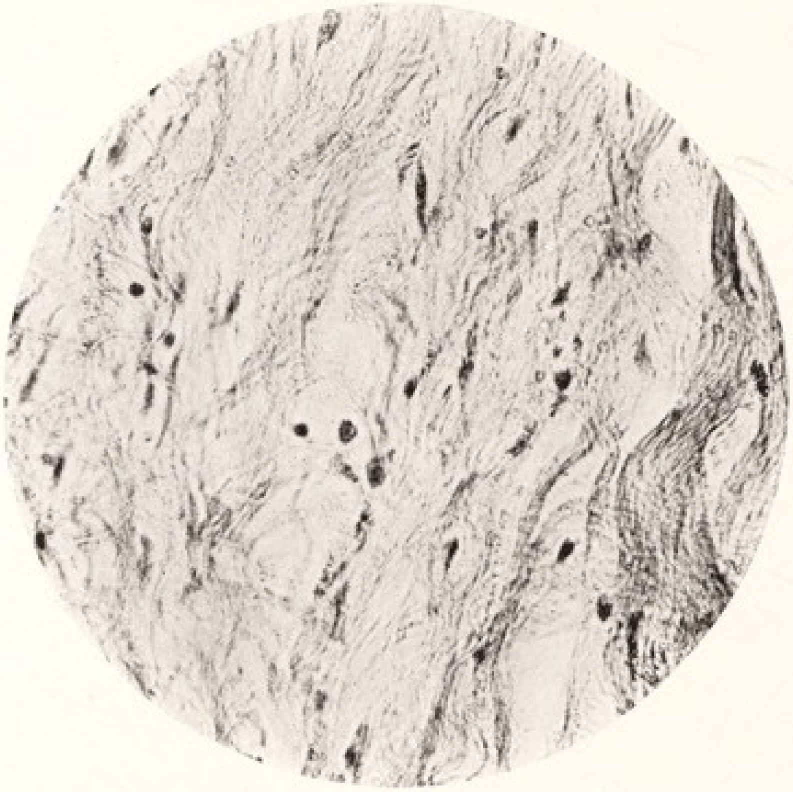

Fig. 58.

SECTION 13.—FALLOW DEER ANTLER, 3/4TH GROWTH, 8″ FROM TIP.
4 mm. 2 eye-piece.

Osteoblastic embryonic tissue from which cartilage and bone is ultimately evolved. The same phase is seen in direct transition.

FIG. 59.

SECTION 351.—RED DEER SPROUTING ANTLER, NEAR TIP.
4 mm. 2 eye-piece.
Osteoblastic embryonic tissue, a phase in evolution of cartilage and bone.

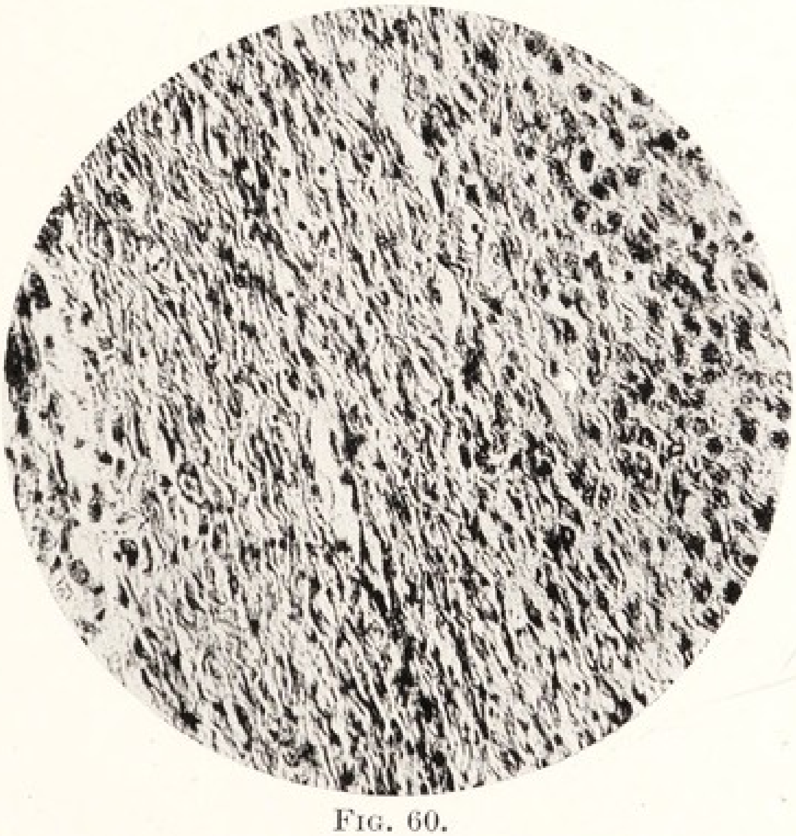

FIG. 60.

SECTION 351.—RED DEER SPROUTING ANTLER, NEAR TIP.
4 mm. No eye-piece.
Osteoblastic embryonic tissue assuming cellular formation marked on one side of field.

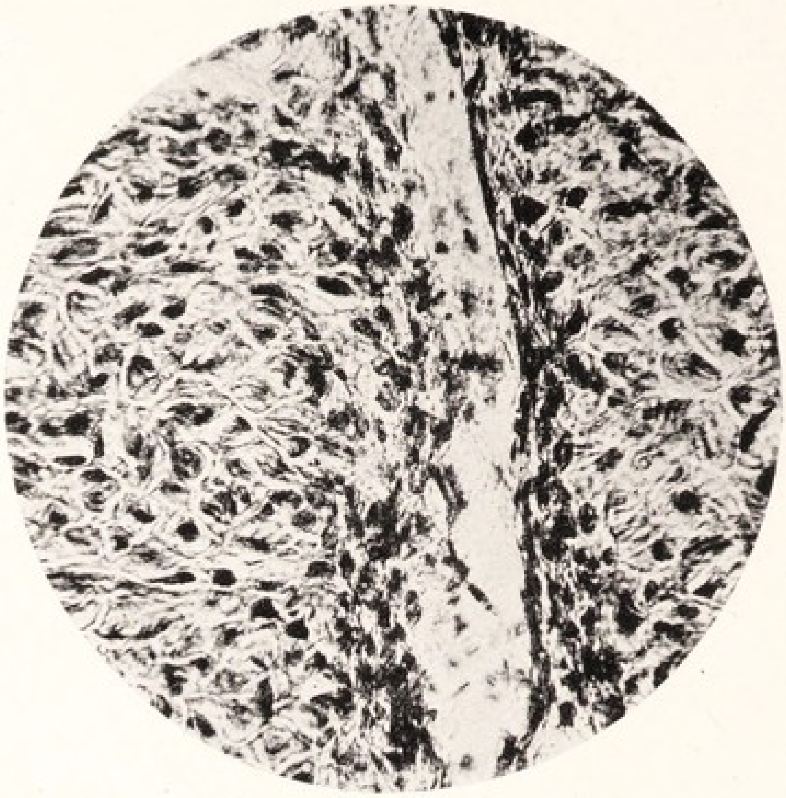

FIG. 61.

SECTION 351.—RED DEER SPROUTING ANTLER, NEAR TIP.
4 mm. 2 eye-piece.
Cellular formation more pronounced. Blood vessels beginning to penetrate.

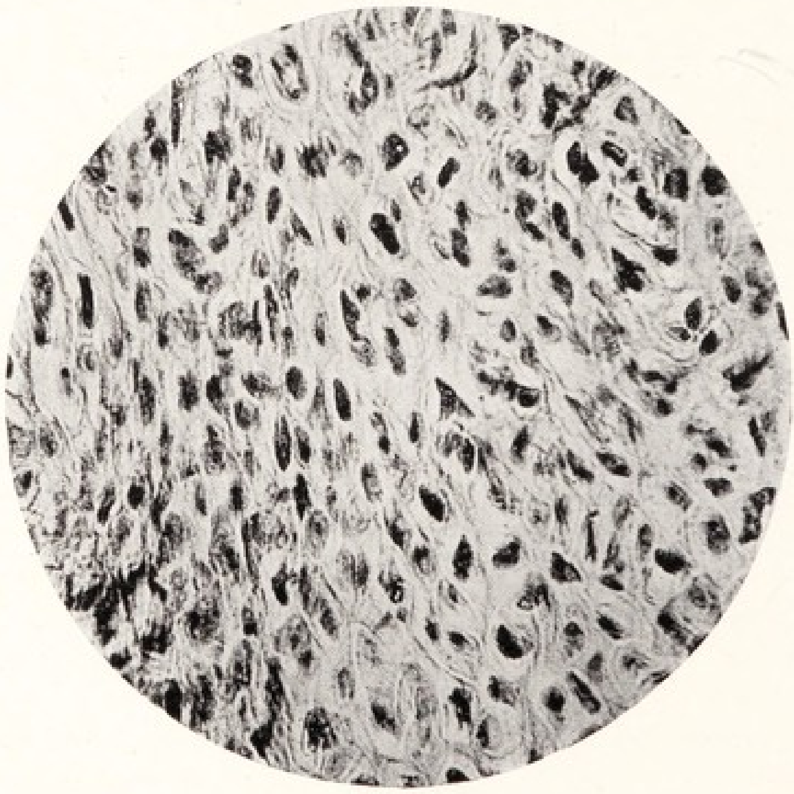

FIG. 62.

SECTION 351.—RED DEER SPROUTING ANTLER, NEAR TIP.
4 mm. 2 eye-piece.
Cartilage cells taking on more distinctive appearance. Capsules beginning to show.

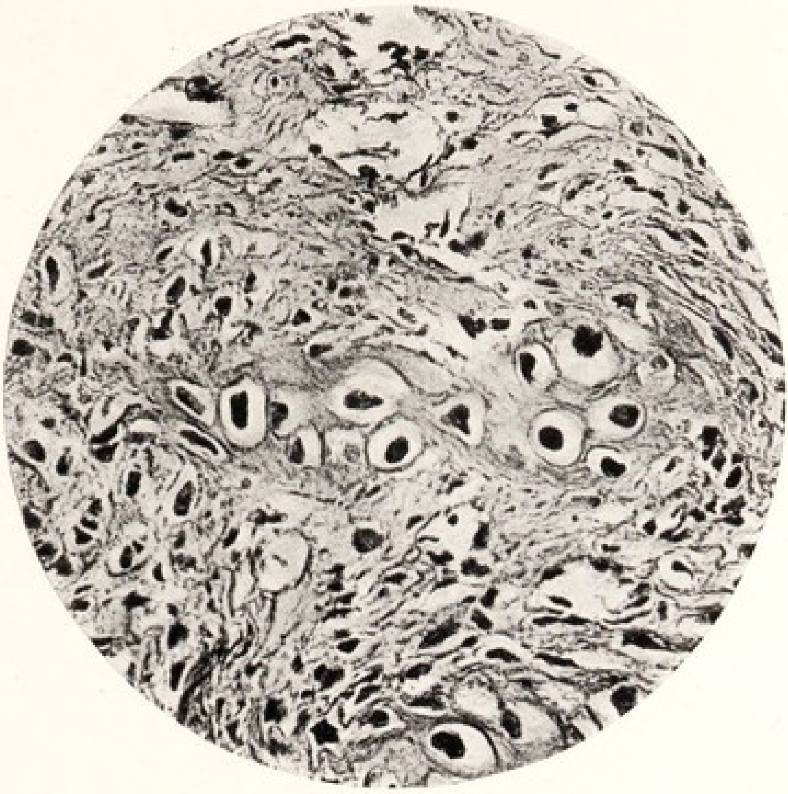

FIG. 63.

SECTION 423.—FALLOW DEER SPROUTING ANTLER, NEAR TIP.
4 mm. 4 eye-piece.
Cartilage assuming definite form.

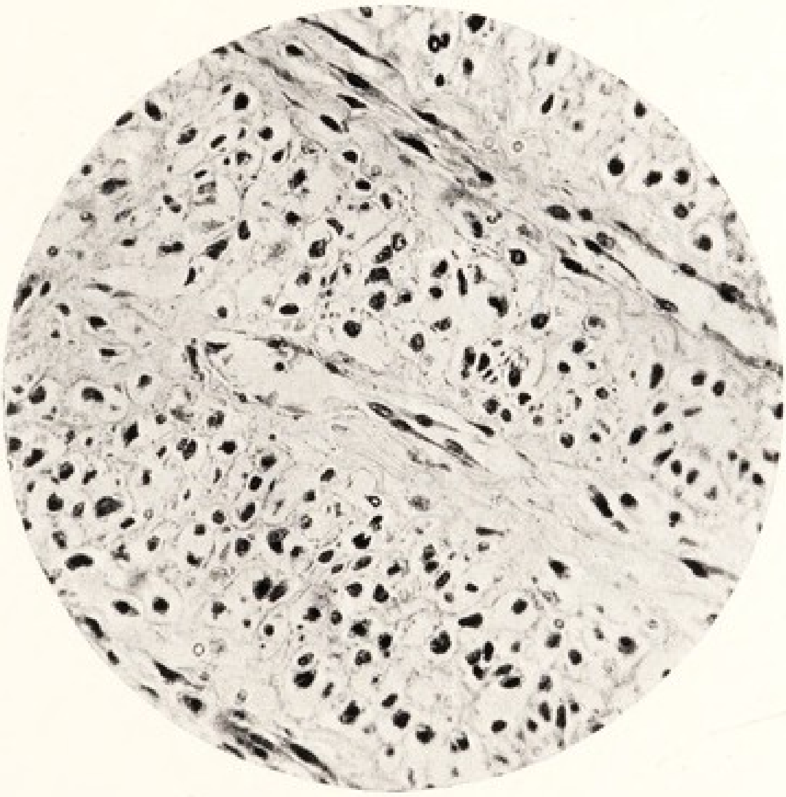

FIG. 64.

SECTION 346.—RED DEER SPROUTING ANTLER, NEAR TIP.
4 mm. 2 eye-piece.
Blood vessels beginning to penetrate the immature cartilage.

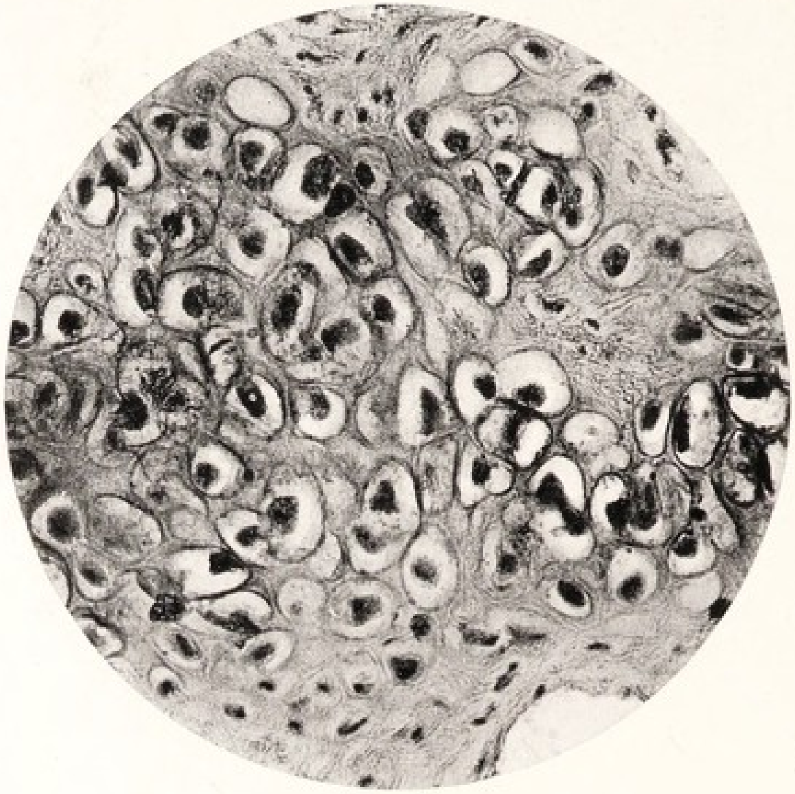

FIG. 65.

SECTION 423.—FALLOW DEER SPROUTING ANTLER, 1″ FROM TIP.
4 mm. 4 eye-piece.
Cartilage well formed, capsules distinct.

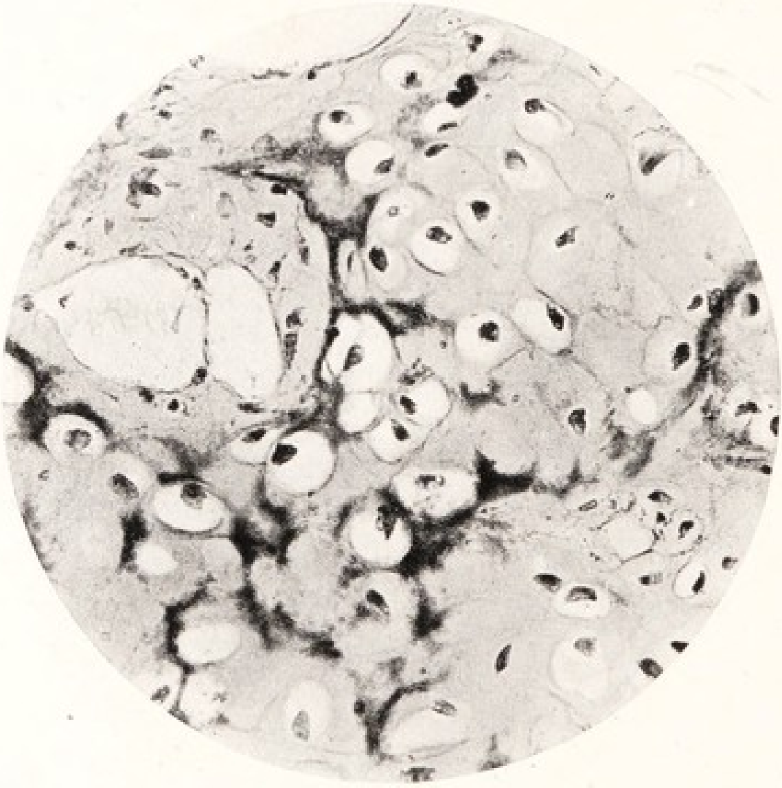

FIG. 66.

SECTION 454.—FALLOW DEER SPROUTING ANTLER, $\frac{3}{4}''$ FROM TIP.
4 mm. 4 eye-piece.
Cartilage fully developed, thin-walled blood vessels penetrating and ossein being deposited in periphery of cartilage cells. Osteoblasts beginning to assume mature form inside cartilage envelopes.

FIG. 67.

SECTION 335.—FALLOW DEER ANTLER, 2/3RD GROWTH, 8″ FROM TIP.
4 mm. 8 eye-piece.

Fully formed cartilage with multiple osteoblasts within capsules. Some osteoblasts also on outside, free. Cartilage capsules are thinning.

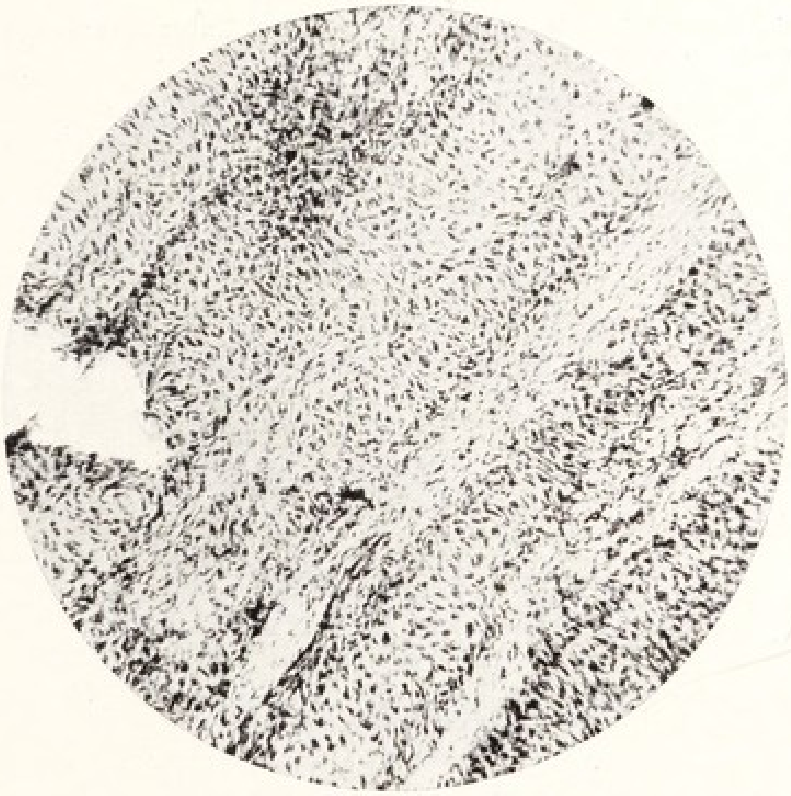

FIG. 68.

SECTION 351.—RED DEER SPROUTING ANTLER, NEAR TIP.
12 mm. No eye-piece.

Cartilage *en masse*.

EVOLUTION OF BONE THROUGH CARTILAGE (INDIRECT BONE FORMATION)

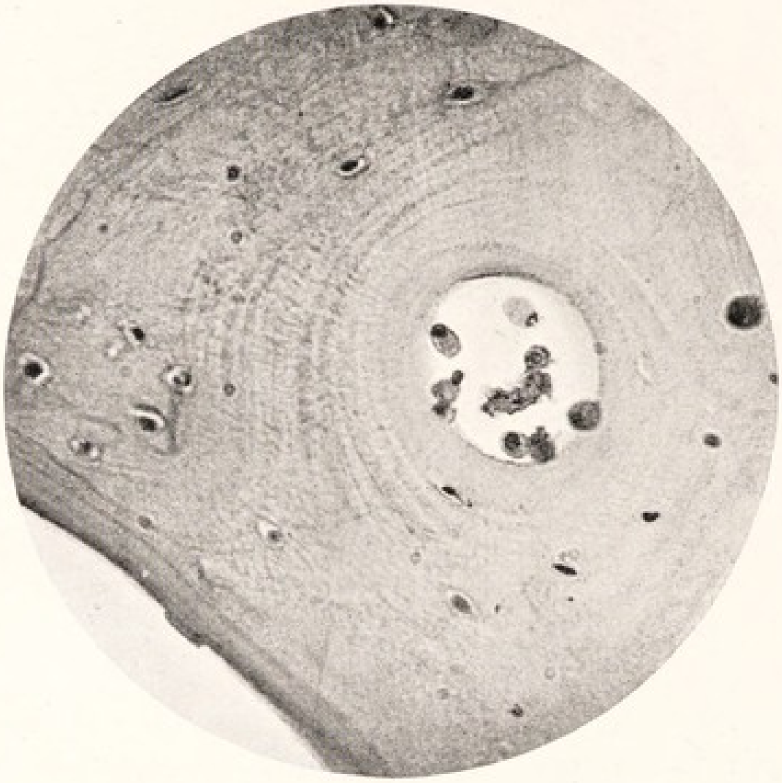

Fig. 69.

SECTION 317.—FALLOW DEER ANTLER—EIGHT WEEKS' GROWTH, NEAR BASE.
4 mm. 4 eye-piece.

Osteoblasts embedded in ossein. Appearance of Haversian system—osteoblasts still lining spaces.

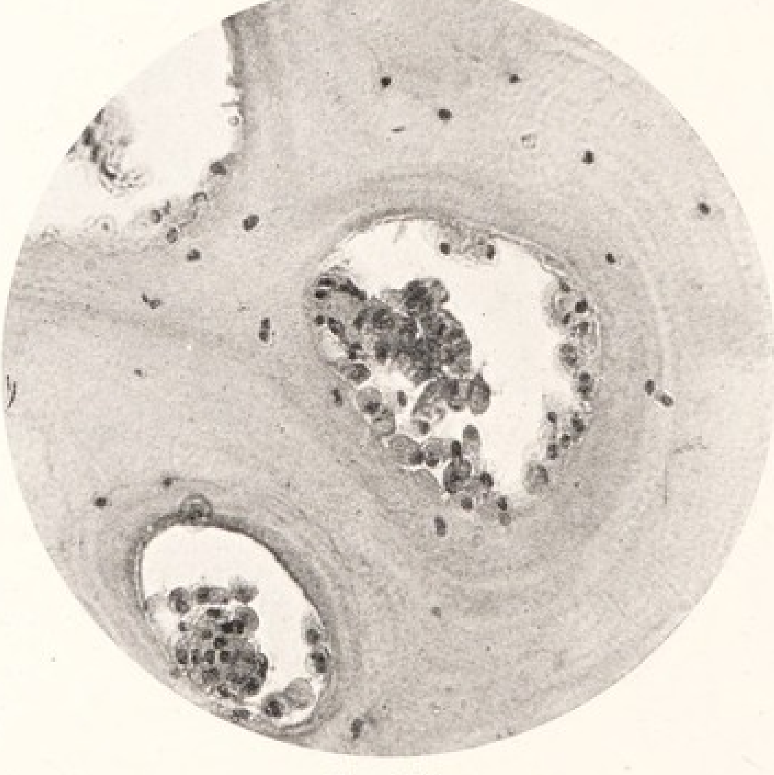

Fig. 70.

SECTION 317.—FALLOW DEER ANTLER—EIGHT WEEKS' GROWTH, NEAR BASE.
4 mm. 4 eye-piece.

Haversian system beginning to be formed—osteoblasts still lining interior of bone spaces and congregating therein, threatening occlusion.

Fig. 71.

SECTION 280.—FALLOW DEER ANTLER, 2/3RD GROWTH, NEAR BASE.
4 mm. 4 eye-piece.

Appearance of Haversian systems beginning to be formed—osteoblasts still lining interior of bone canals. This may have formed in cartilage at base of tine of antler.

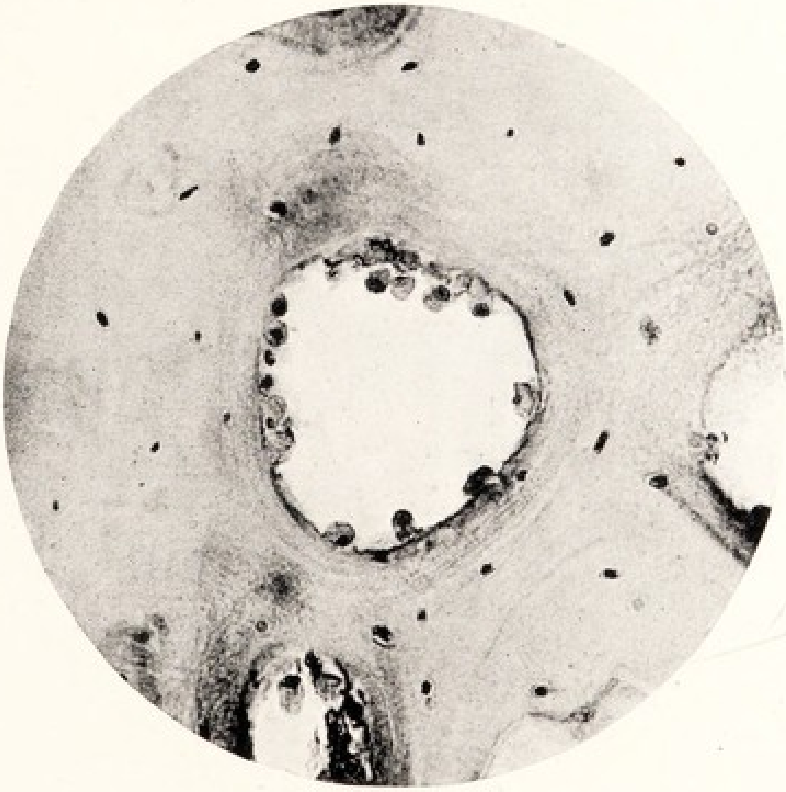

Fig. 72.

SECTION 280.—FALLOW DEER ANTLER, 2/3RD GROWTH, NEAR BASE.
4 mm. 4 eye-piece.

Early indications of Haversian systems, but as this section was from base of tine it may have been formed originally in cartilage.

Changes in the cartilage capsules during evolution of osteoblasts into bone.

After the cartilage capsules have served their purpose they may undergo one of several changes: first, the disintegration of capsules and freeing of osteoblast; second, the flattening of capsules and matrix forming from them.

(1) *Disintegration of cartilage capsule and freeing of osteoblast.*

The capsules may become attenuated and ragged, and the osteoblasts (the "cartilage corpuscles") being freed congregate together in spaces or pockets in the midst of the cartilage.

Active osteoblastic proliferation ensues both inside the disappearing capsule and especially in the spaces where the free osteoblasts congregate.

In the periphery of the osteoblasts congregated in these spaces, ossein is deposited, enclosing the osteoblasts as bone cells; trabeculae are soon formed and rapidly assume the characters of growing bone. These trabeculae are always being augmented in size by peripheral increments aided by the pavementing osteoblasts. Spaces in the interior of the trabeculae are likewise pavemented with osteoblasts which fill the space centripetally. Ossein also colours the cytoplasm of the osteoblast. Figs. 73 to 80.

Such changes are generally seen in the neighbourhood of thin-walled blood vessels which have penetrated the cartilage.

EVOLUTION OF BONE THROUGH CARTILAGE (INDIRECT BONE FORMATION)

FIG. 73.

SECTION 465.—FALLOW DEER ANTLER, 2/3RD GROWTH, 2″ FROM TIP.
4 mm. 4 eye-piece.

Cartilage capsules disappearing setting osteoblasts free. Ossein beginning to be deposited in matrix.

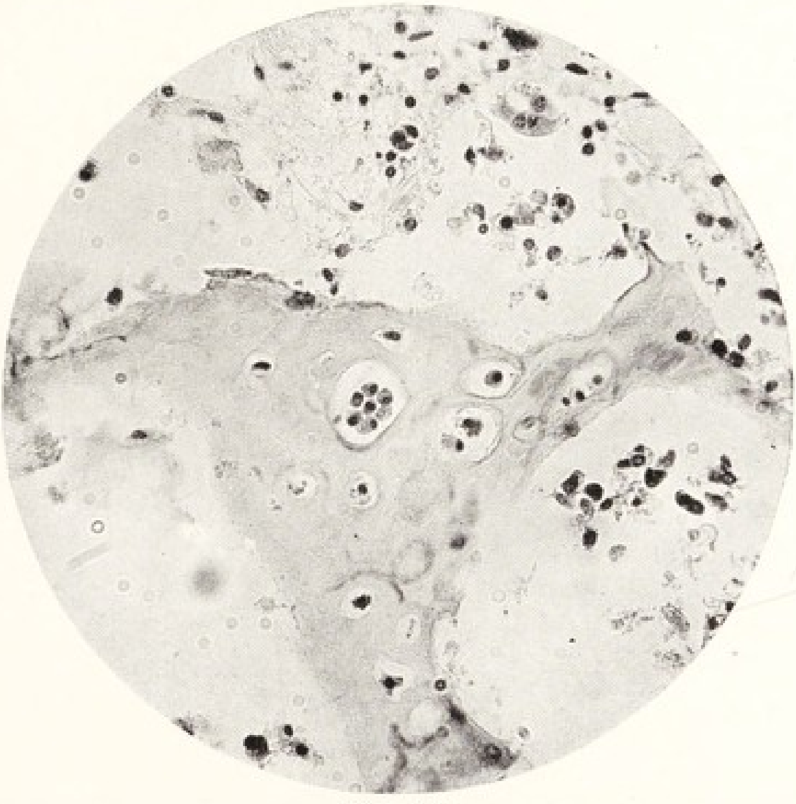

FIG. 74.

SECTION 366.—RED DEER SPROUTING ANTLER, $\frac{3}{4}$″ FROM TIP.
4 mm. 2 eye-piece.

Disappearing cartilage capsules, multiple cells inside capsule. Seven osteoblasts in one capsule. Osteoblasts assuming mature form inside cartilage envelope.

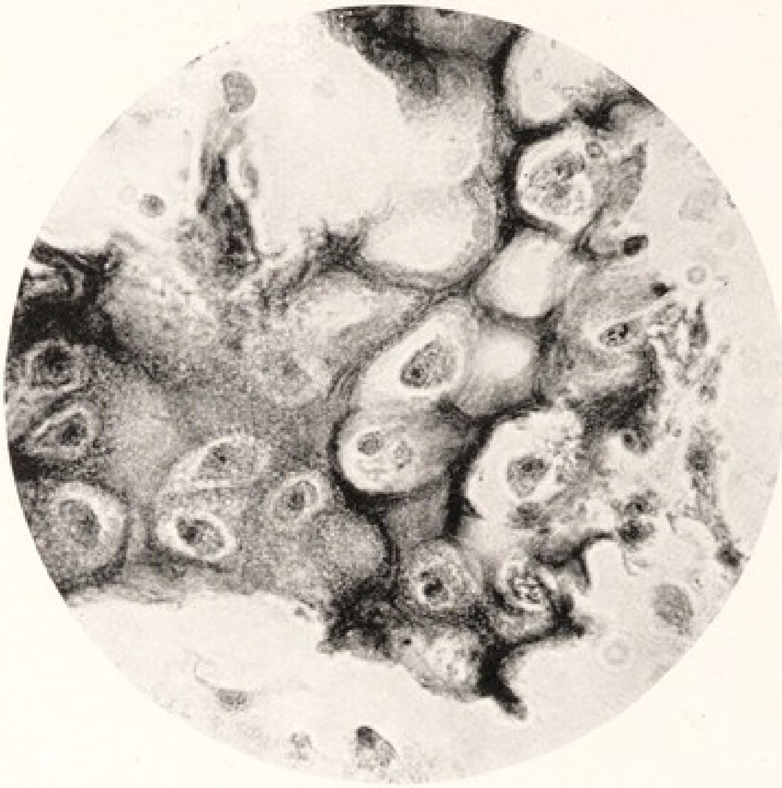

Fig. 75.

SECTION 335.—FALLOW DEER ANTLER, 2/3RD GROWTH, 8″ FROM TIP.
4 mm. 8 eye-piece.
Cartilage capsules disappearing, osteoblasts becoming free.

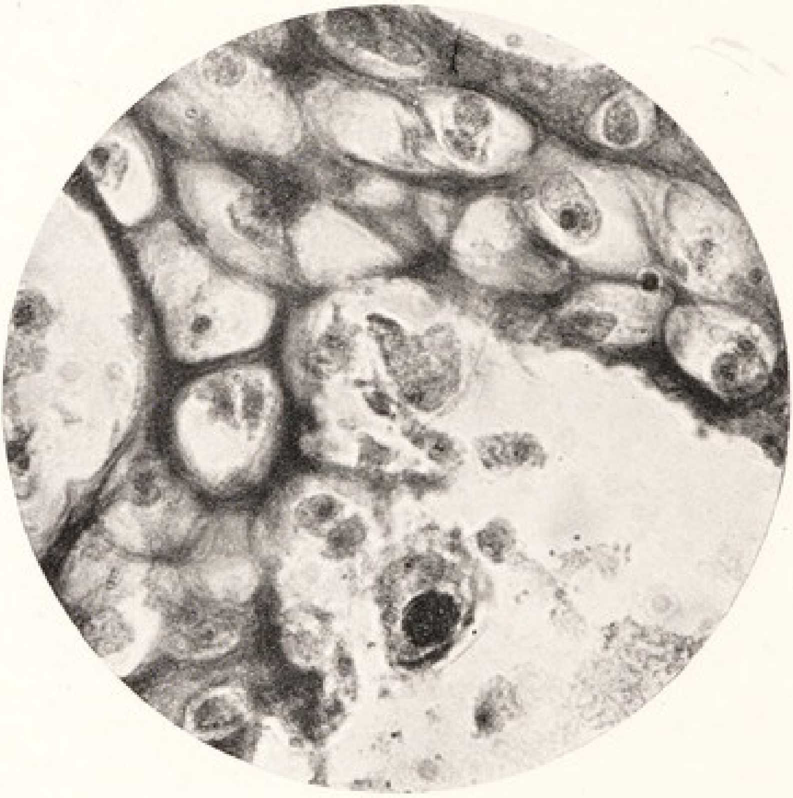

Fig. 76.

SECTION 335.—FALLOW DEER ANTLER, 2/3RD GROWTH, 8″ FROM TIP.
4 mm. 8 eye-piece.
Osteoblasts freeing themselves from cartilage capsules and beginning to assume mature form.

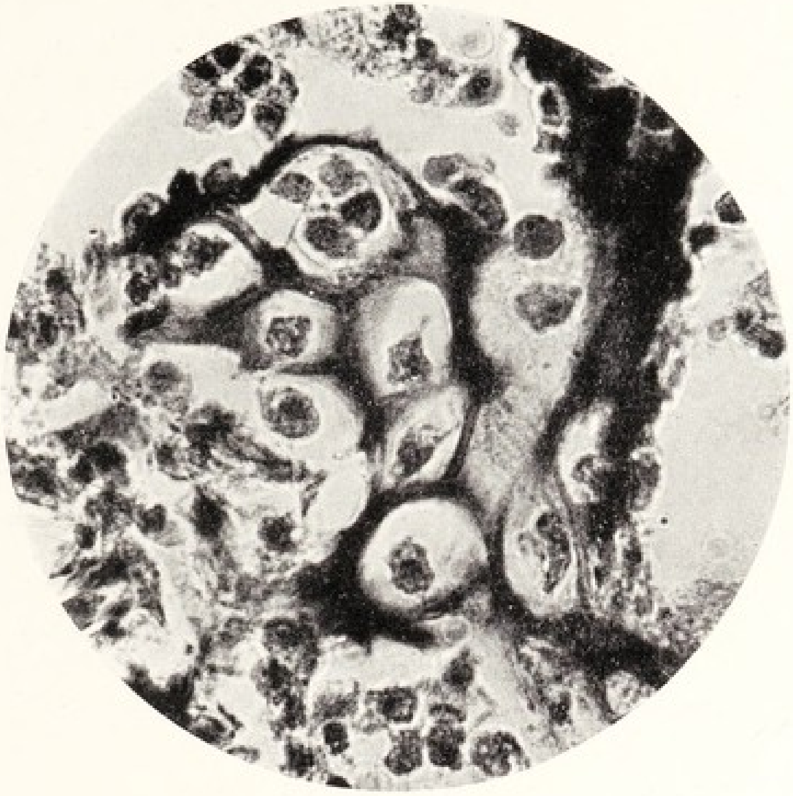

Fig. 77.

SECTION 335.—FALLOW DEER ANTLER, 2/3RD GROWTH, 8″ FROM TIP.
4 mm. 8 eye-piece.

Cartilage capsules disappearing, osteoblasts being set free, and beginning to assume mature form. Osteoblasts escaping in groups.

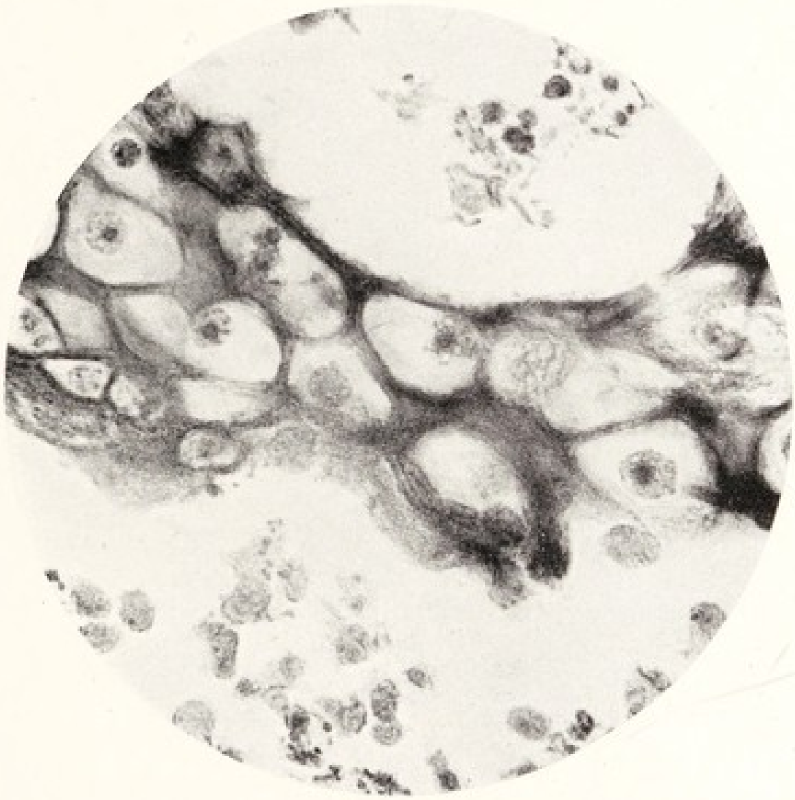

Fig. 78.

SECTION 335.—FALLOW DEER ANTLER, 2/3RD GROWTH, 8″ FROM TIP.
4 mm. 8 eye-piece.

Cartilage capsules disappearing. Osteoblasts being set free.

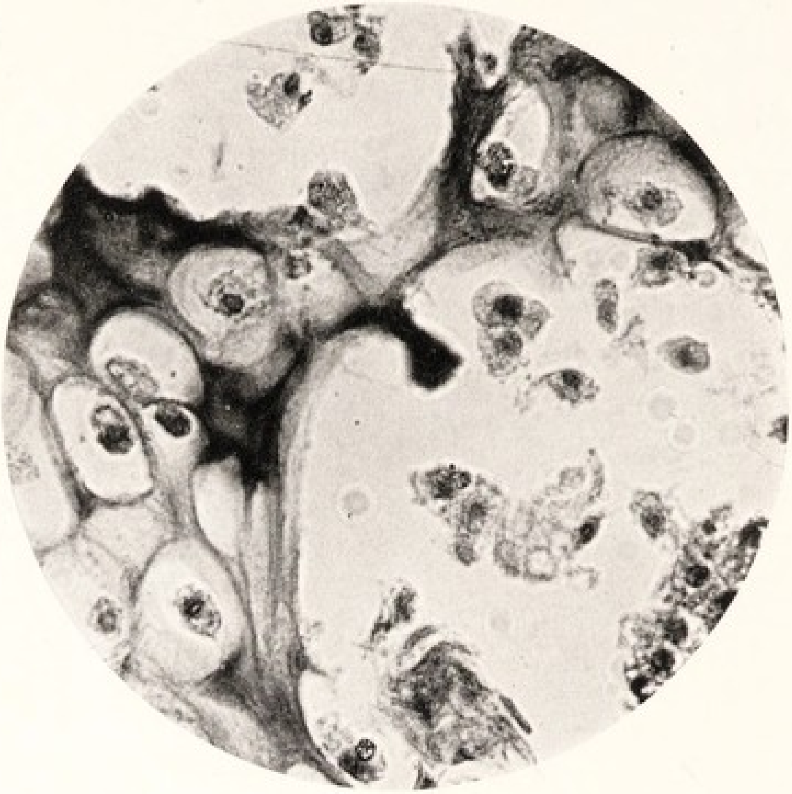

Fig. 79.

SECTION 336.—FALLOW DEER ANTLER, 2/3RD GROWTH, 8″ FROM TIP.
4 mm. 8 eye-piece.

Cartilage capsules disappearing, osteoblasts beginning to assume mature form inside capsules.

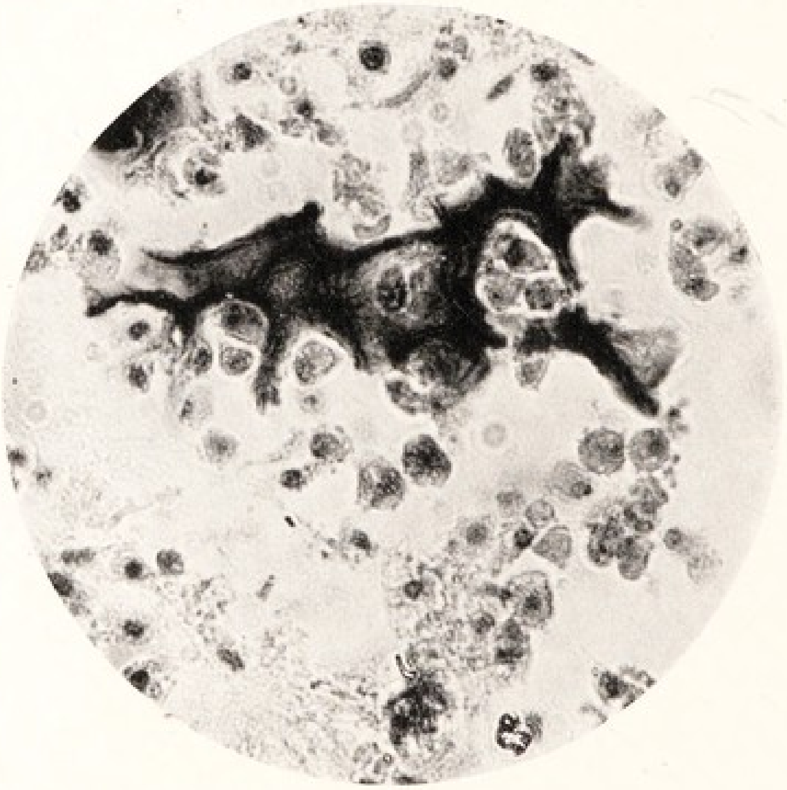

Fig. 80.

SECTION 335.—FALLOW DEER ANTLER, 2/3RD GROWTH, 8″ FROM TIP.
4 mm. 8 eye-piece.

Osteoblasts being set free from disintegrating cartilaginous matrix.

(2) *The cartilage capsule becomes thicker and flattened and participates in the formation of matrix.*

(2) The cartilage capsule, instead of attenuating, becomes thicker by encroachments inward toward the contained osteoblast (or corpuscle), which meanwhile becomes smaller and approaches its mature type. Then there appears to be an increasing distance between the corpuscles giving an increased matrix. The capsular substance has fused into a matrix. Figs. 81 to 85.

EVOLUTION OF BONE THROUGH CARTILAGE (INDIRECT BONE FORMATION)

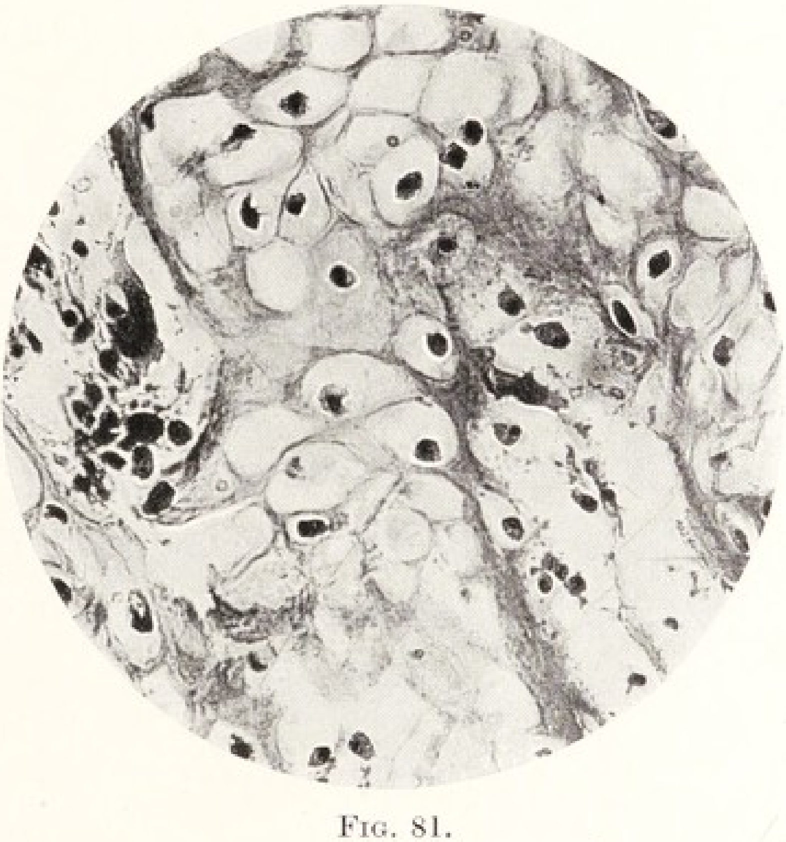

Fig. 81.

SECTION 475.—FALLOW DEER ANTLER, 2/3RD GROWTH, 2″ FROM TIP. 4 mm. 4 eye-piece.

Cartilage capsules broadening into matrix. Ossein beginning to be deposited.

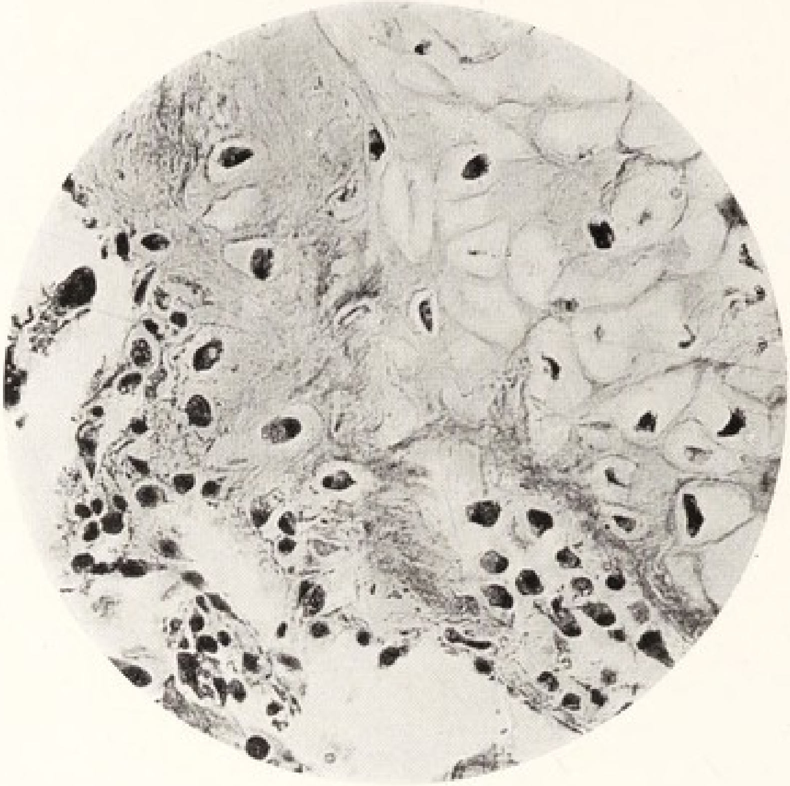

Fig. 82.

SECTION 475.—FALLOW DEER ANTLER, 2/3RD GROWTH, 2″ FROM TIP.
4 mm. 4 eye-piece.

Cartilage capsules broadening into matrix, shaded with ossein. Osteoblasts assuming mature form inside of capsules and outside in pockets. Thin-walled blood vessels in periphery.

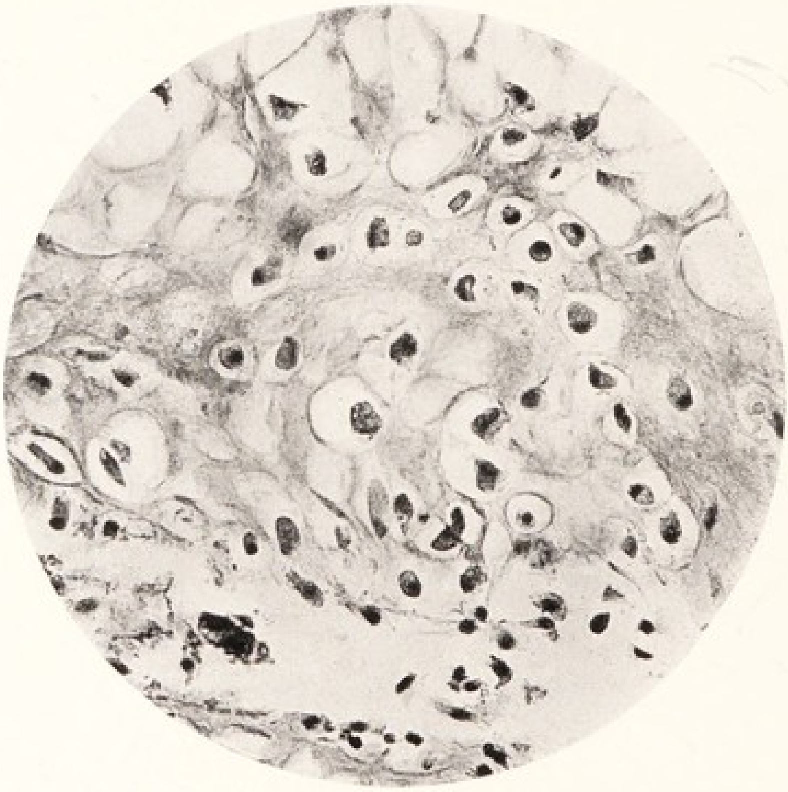

Fig. 83.

SECTION 477.—FALLOW DEER ANTLER, 2/3RD GROWTH, 2″ FROM TIP.
4 mm. 4 eye-piece.

Cartilage capsules becoming flattened into matrix and shaded with ossein deposit. Osteoblasts assuming mature form inside of capsules.

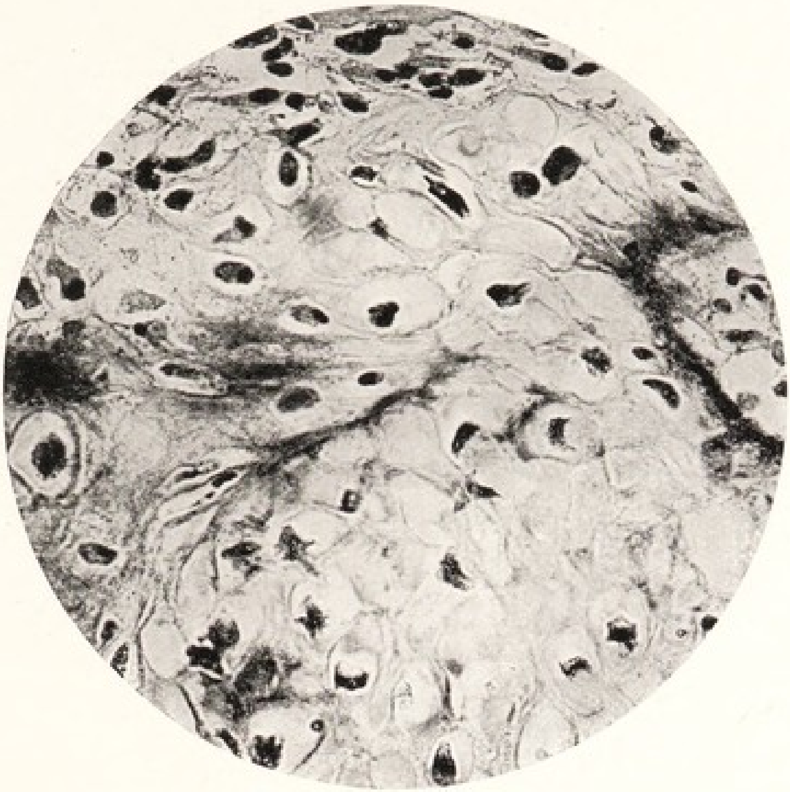

FIG. 84.

SECTION 465.—FALLOW DEER ANTLER, 2/3RD GROWTH, 2″ FROM TIP.
4 mm. object glass. 4 eye-piece.
Broadening of cartilage capsules into matrix in which ossein is being deposited.

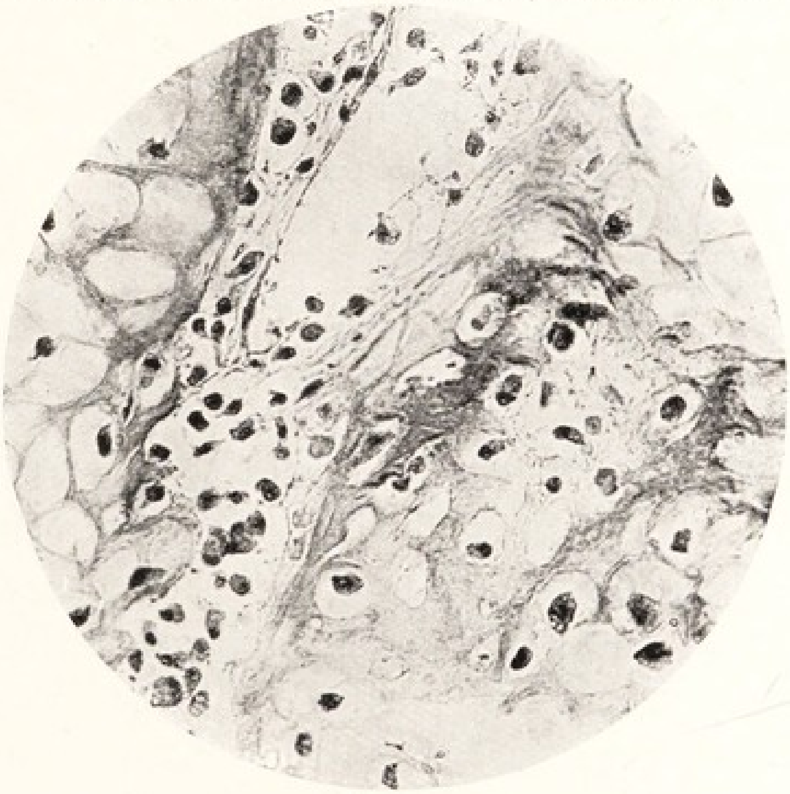

FIG. 85.

SECTION 475.—FALLOW DEER ANTLER, 2/3RD GROWN, 2″ FROM TIP.
4 mm. object glass. 4 eye-piece.
Cartilage capsules broadening into matrix, in which ossein is deposited. Free osteoblasts forming in pockets.

Deposits of ossein round osteoblasts and in matrix.

Coincidentally with this increase of matrix between the corpuscles, the remaining capsules and the matrix formed from them becomes filled with deposits of ossein, sometimes appearing as a fine haze or shade over the flattened framework ; at others the deposit is particulate and often spherical in shape, the spheres being very variable in size as if they had been sprayed on. This deposit of ossein is sometimes seen in the capsular framework early, before it has become flattened out, at other times it is only after the flattening that this granular deposition of ossein appears. In either case, as the matrix increases, the deposition of ossein increases.

The osteoblast assumes the role of bone cell.

The osteoblast (the *Cartilage corpuscle*) which, during these changes, has assumed its mature form, remains *in situ*, becoming imbedded in the tissues which it gradually forms round it into bone, the osteoblast then assuming the role of bone cell.

Osteoblasts pavement the trabeculae.

These two methods of the evolution of cartilage into bone may be seen not only in the same specimen but sometimes in the same field. In all these cases it is the osteoblast which is the energizing agent, the capsule playing a mere passive part. Whatever form is first assumed, free osteoblasts from the same source line the trabeculae and may be seen incorporating themselves into bone, generally augmenting that already formed.

Ossification advancing both centripetally and centrifugally in cartilage.

Bone formation is frequently seen commencing in the periphery of cartilaginous masses and surrounding these and enclosing well formed cartilage toward the centre. In such cases bone formation advances centripetally, until the whole island becomes converted into bone.

The osteoblasts in this case remain inside their capsules, which gradually form into a matrix enclosing the osteoblasts as bone cells.

While ossification proceeds centripetally, enclosing the cartilaginous mass, and converting it into bone, there is at the same time centrifugal augmentation from the periphery of the bone first formed, osteoblasts pavementing its circumference, each adding its quota to the increase.

Blood vessels in relation to osteoblastic bone formation. Part played by blood in the evolution of bone.

While the osteoblast in the early stage develops quite independently of blood vessels in its immediate vicinity, and appears in a form of tissue in which few blood vessels exist, yet the osteoblast seldom assumes its mature form until thin-walled blood vessels penetrate into its vicinity, after which the osteoblasts become very active, proliferation ensues and ossein is deposited in the tissue. The blood brings pabulum for the increased nutrition of the osteoblast and ossein is conveyed to the tissue at the same time. The osteoblast exerts a selective influence over pabulum carried by the blood, extracting the ossein from the blood and fixing it in the matrix round itself. Figs. 86 to 89.

EVOLUTION OF BONE THROUGH CARTILAGE (INDIRECT BONE FORMATION)

VASCULARISATION OF CARTILAGE

Fig. 86.

SECTION 173.—FALLOW DEER SPROUTING ANTLER.
4 mm. 2 eye-piece.

General view of vascularisation of cartilage and deposition of ossein. Thin-walled blood vessels.

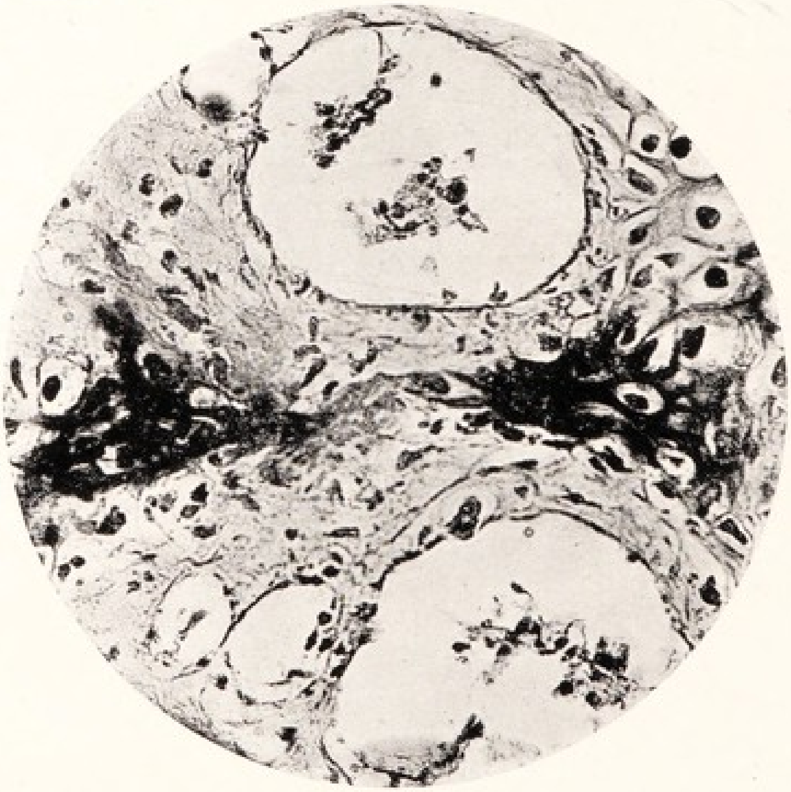

Fig. 87.

SECTION 454.—FALLOW DEER SPROUTING ANTLER, $\frac{3}{4}''$ FROM TIP.
4 mm. 4 eye-piece.

Penetration of cartilage by thin-walled blood vessels and blood spaces. Ossein beginning to be deposited round and in osteoblasts.

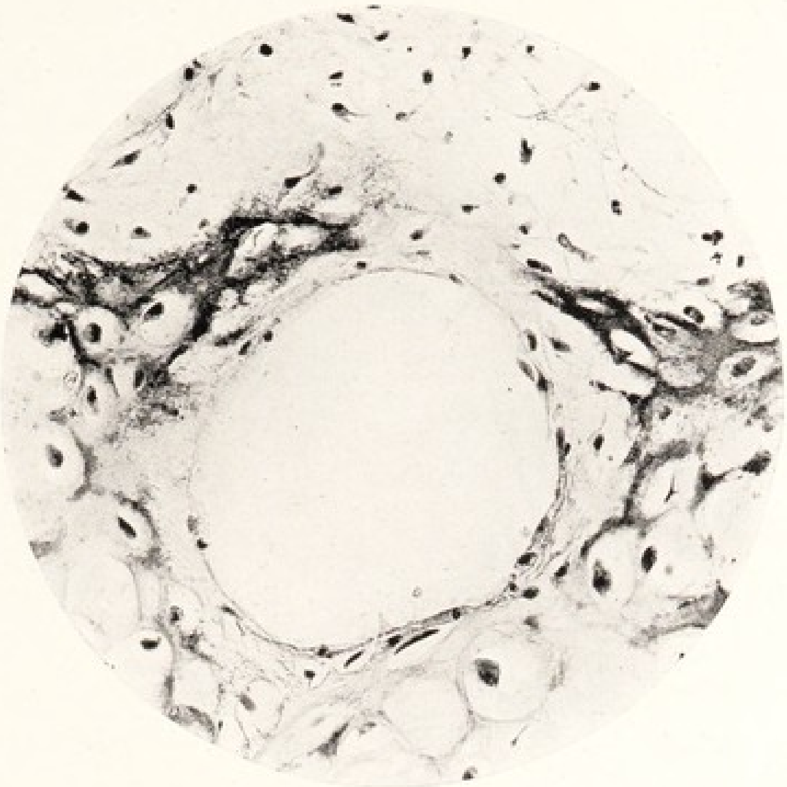

Fig. 88.

SECTION 454.—FALLOW DEER SPROUTING ANTLER, $\frac{3}{4}''$ FROM TIP.
4 mm. 4 eye-piece.

Osteoblasts and cartilage capsules becoming impregnated with ossein in neighbourhood of thin-walled vessel.

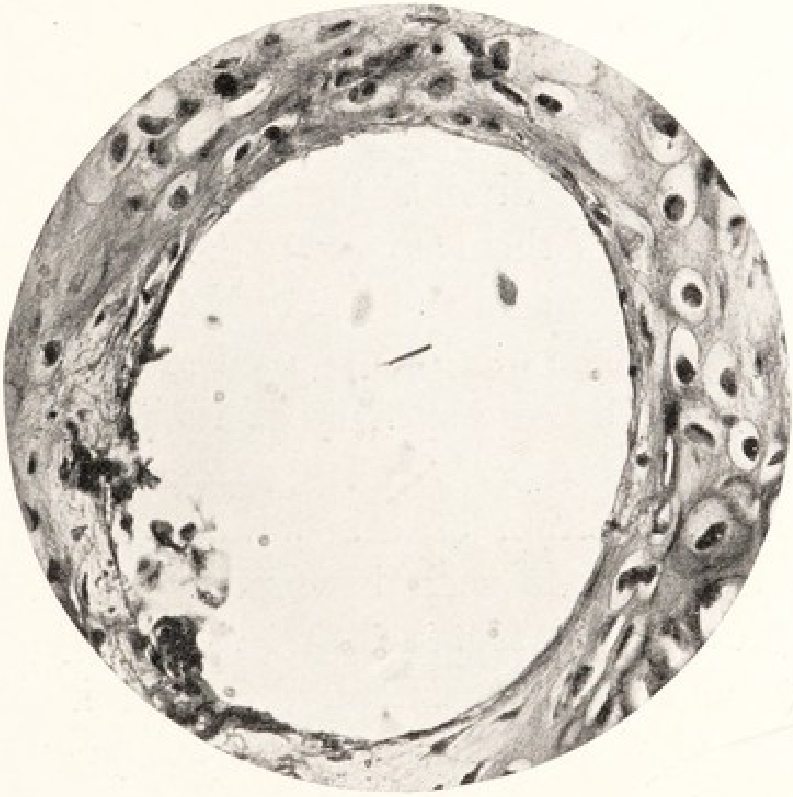

Fig. 89.

SECTION 453.—FALLOW DEER SPROUTING ANTLER, $\frac{3}{4}''$ FROM TIP.
4 mm. 4 eye-piece.

Bone formation encroaching on lumen of a blood vessel which has penetrated the cartilage. Obliteration of blood spaces thus occurs by the deposition of cartilage centripetally.

The vascularization of the antler.

The deer's antler in its sprouting stage is full of blood, thin-walled blood vessels appearing everywhere round which osteoblasts grow and which penetrate into the embryonic layers and cartilage. There is at the highest point of the stem of the antler an ever advancing rapidly proliferating zone of cartilage which is followed by blood vessels which penetrate the advanced tissues.

Obliteration of vessels in antler by centripetal osseous deposit. Solidification.

The blood vessels appear in great abundance whenever the osseous growth is rapid, and in the antler the thin-walled blood vessels are very large; often only a single layer of endothelium separates the blood current from the neighbouring structures.

After the bone is well formed, it is interesting to note that the calibre of these vessels becomes less and less, by osseous encroachments upon their periphery, spreading centripetally, which diminishes their lumen and finally obliterates many of them (Fig. 89). The tissue which at an early period was soft and full of blood becomes solid and avascular. The more perfectly the vessels perform their function the more speedily is their own obliteration secured.

A similar deposition of thin-walled vessels prior to bone development is seen in experiment when dog's bone is grown in glass tubes and also in growth and repair of human bone generally, though in the later the calibre of the vessels do not assume the same dimensions.

The osteoblasts do not grow from the blood vessels.

The osteoblasts are not seen in the blood vessels normally and do not grow from them, though it is possible were they introduced they might be carried by the blood stream. The osteoblasts may be seen lying on the surface of the bone on the outside of the blood vessels in the same way as they may be observed pavementing the growing bone where blood vessels are not immediately adjacent.

In histological examination, osteoblasts in certain specimens may be seen adherent to the outside of blood vessels where, owing to the action of reagents used in preparation the vessel has shrank from the osseous trabeculae, drawing the osteoblasts with it (Fig. 37).

CHAPTER III

THE SEPARATION OF THE ANTLER

The blood supplies of the antler and the effect of their arrest.

The process of separation of the antler.

- Preparation for shedding appears at the birth of the new antler and increases during its vigorous growth.
- Process commences at level of corona.
- Obliteration of superficial vessels at corona.
- Corona presses through cutis and superficial vascular supply is cut off.
- Osseous tissue in antler becomes avascular and dies—the changes in the vessels.
- The separation of the dead antler by means of intensified action of the living tissue in pedicle.
- The production of granulation tissue in pedicle.
- The shedding of the antler is an aseptic process occurring in the open air.

The separation of the antler is dependent primarily on the withdrawal of its blood supply. In this relation it must be borne in mind that the vascular supply of the antler is from two sources, the main one being internal, giving pabulum to the proliferating osteoblasts and conveying the salts which the osteoblasts deposit as ossein ; the other is superficial, the vessels supplying the cuticular covering (the velvet), few if any capillaries from these vessels penetrating deeper than the cutis ; but the cuticular vessels aid materially in the maintenance of the temperature of the soft growing antler, while the active osteoblastic proliferation proceeds within. These two sources of blood supply require to be cut off before the antler and its velvet dies. The arrest of blood flow from the superficial vessels causes the drying up and shrivelling of the velvet, but does not cause necrosis of the antler, which at this stage still continues to be supplied with blood from the interior of the pedicle, and the osteoblasts are still proliferating and depositing ossein though both are now somewhat toned compared with the exuberant previous growth. The centripital deposition of the osteoblasts round the blood vessels reduces their lumen and finally obliterates them. The blood supply to the interior of the antler must likewise be arrested before the antler dies or becomes necrosed. Ample provision has been made to effect both these purposes at the proper time.

The process of separation of the antler.

At the birth of the new antler, provision for its ultimate separation is already foreshadowed and preparation for its shedding may be seen during the period of its most vigorous growth. At the very outset, the pent-up ossific pabulum emanating from the pedicle of the sprouting antler overflows and forms a circumferential projection, afterwards known as the corona, at about the level of which the principal changes leading to ultimate shedding of the antler occurs.[1]

Ossification in the growing antler commences in line with the corona, proceeding from the centre outwards, and as it becomes completed, the vascularity at that part visibly lessens, in contrast to the vascularity of the adjacent base of the antler on the distal side and of the pedicle on the other.

The obliteration of the superficial vessels in the cutis-velvet—at the corona.

While these changes occur in the interior of the shaft, important ones are simultaneously taking place in the periphery of the base, in the corona itself. At the

[1] Much in the same way as osteoblastic granulation tissue sometimes overflows the circumference of the femur after section of the shaft of that bone for amputation—forming a mushroom-shaped covering.

outset the corona projects beyond the circumference of the pedicle, continues to increase circumferentially and

Fig. 89a.

RED DEER (CERVUS ELAPHUS)—SECTION OF ANTLER ABOUT TO SHED

Author's Collection.

A stage toward the shedding of antler. Section through skull, pedicle, and base of antler. Antler is now dead bone with coagulated disintegrating blood in it. The skull and pedicle are very vascular in preparation for shedding and regeneration of new bone. The portion of the antler abutting on the pedicle consists of dense white bone, presenting a convexity toward the pedicle.

to send osseous projections between the subcuticular blood vessels. At first these coronal osseous irregularities form a protection for the blood vessels, as they lie embedded in the grooves, but gradually by the advancing ossific invasion these vessels are not only embraced but their lumen is encroached on by osseous increments until they have been finally compressed and strangled.

The edge of the corona pressing through the cutis of the antler.

At the same time the edge of the corona still growing outwards, puts the cutis over it, and its contained vessels, upon the stretch, which consequently becomes thinner and ultimately gives way in front of the pressure, exposing the underlying bone.

Thus the superficial vascular supply to the antler—the long vessels extending from the pedicle to the tip—is cut off, and there being no inosculation with the vessels of the interior, the whole cutis becomes avascular, dries, shrivels and peels off in shreds. This is known as the shedding of the velvet. The growth of the interior of the antler is however still active—bone being laid down making for consolidation—though sclerotic changes have already supervened.

The manner in which the velvet parts in front of the pressure of the corona somewhat resembles the yielding and sloughing of the human cutis, in front of the anterior superior spines of the ilium, for instance, in cases of emaciation—without external pressure ; but in the latter case there is no increase of osseous growth, only the shrinkage of the cutis over the bony prominence, due to the want of nutrition, and the stretching of the skin over the underlying bony prominence.

The separation of the antler from the pedicle.

The osseous tissue within the antler at the level of the corona becomes very dense and gradually avascular

—the lumen of the internal vessels being encroached on by the rapid proliferation of the osseous tissue round them until obliteration of the vessel ensues. Thus an avascular barrier is formed on the side of the antler cutting off the blood supply, passing through the pedicle to the antler. The antler bereft of its pabulum ultimately becomes dead tissue.

The avascularity of the whole thickness of the base of the antler at the coronal junction is thus apparent, a dense white bone presenting (Fig. 89a).

When this has taken place, the living bone requires to part with the dead antler and preparations are made on the side of the pedicle and adjacent skull toward this end.

These are analogous to the shedding of dead tissue—necrosis or sloughs—which occur in other animal tissue as a result of injury or disease.

Preparatory to the shedding great vascularity occurs in the pedicle and underlying skull, the bone near the level of the dead antler becomes softened, ossein is absorbed and a granulation tissue, derived from the pre-existing osseous tissue cells of the pedicle, forms and gradually loosens the organic connections between the pedicle and the dead antler, which is finally floated off, falling by its own weight or by accidental contact with external objects. While those changes are occurring, the free bone cells within the skull and pedicle proliferate with remarkable rapidity and the proliferated cells, assuming the role of osteoblasts, are ready for fresh effort in producing a new antler.

The proliferation of the pre-existing bone cells, in the highly vascularized adjacent skull and pedicle, form the granulation tissue which aids in the separation of the old antler and furnish material for the growth of new bone.

Prior to those processes immediately concerned in the separation of the antler, the osseous tissue of the pedicle, and even the skull tissue from which it springs, present marked preparatory changes.

Normally the bone cell is closely surrounded with ossein, but during these preparatory changes the ossein is absorbed from the immediate vicinity of the bone cell, which then shows itself distinctly isolated, as if it were in a cavity opened in the bone. Later, these spaces round the bone cells become larger and proliferation of osteoblasts occurs within them. The Haversian canals become wider and osteoblasts congregate within them in ever increasing numbers.

Blood vessels also increase in number and in size within the skull and pedicle, all denoting renewed potentiality for further osseous reproduction.

It is interesting to note that the whole of the process of shedding of the antler takes place in the open air, and does so aseptically, and consequently without suppuration. The animal cannot lick the part, as most animals do wounds in other parts of their body; it has no hands to convey germs to the raw surface, and the part is too tender to permit the animal to rub the surface against external germ-laden bodies. The free growth of pre-formed granulation tissue forming over the raw surface at the pedicle prior to the shedding and the rapidity of the formation of the superficial layer—the stratum lucidum—of the cuticular covering contributes to this end.

Doubtless suppuration may occur, as a possibility, in the pedicle at this period—a specimen of this kind having been sent me, showing a partly necrotic pedicle from a pyogenic osteitis and a consequent mal-formed aborted antler (Fig. 20).

Fig. 90.

1. SHED (DEAD) ANTLER

SECTION 281.—RED DEER—ANTLER SHED—SECTION NEAR CORONA.
4 mm. No eye-piece.
Dead bone—no bone cells—empty spaces mostly.

Fig. 91.

2. PREPARATION IN PEDICLE FOR SPROUTING ANTLER

SECTION 387.—RED DEER SPROUTING ANTLER, $2\frac{1}{2}''$ HIGH.

Taken from near coronal line—showing old bone of pedicle from which fresh cartilage is springing.

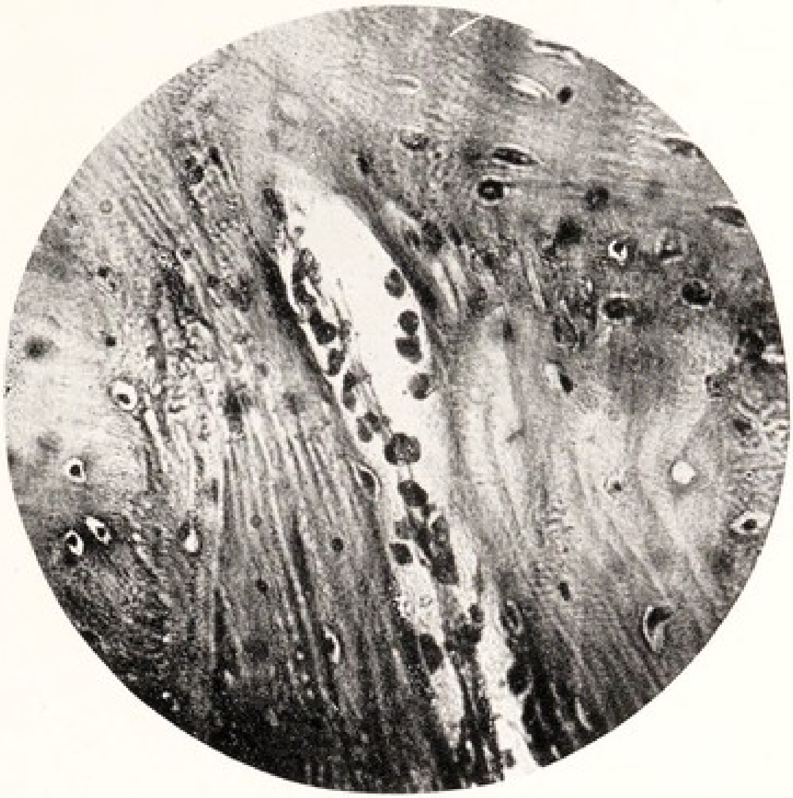

Fig. 92.

3. PREPARATION IN PEDICLE FOR SPROUTING ANTLER

SECTION 386.—RED DEER SPROUTING ANTLER, $2\frac{1}{2}''$ HIGH.
4 mm. 2 eye-piece.

Bone in pedicle preparatory to issuing fresh osteoblasts to form new antler. Osteoblasts accumulating in Haversian canals.

Fig. 93.

4. PREPARATION IN PEDICLE FOR SPROUTING ANTLER

SECTION 386.—RED DEER SPROUTING ANTLER, $2\frac{1}{2}''$ HIGH
4 mm. 2 eye-piece.

Bone in pedicle preparatory to sprouting—wide spaces seen round bone cells—first step toward regeneration.

CHAPTER IV

NUCLEAR BUDDING

Nuclear budding occurring in osteoblasts in developing antlers.
- As seen occasionally inside of cartilage envelope.
- Much more frequently in free osteoblasts.
- Many cells in all stages of growth seen near the cells exhibiting nuclear budding.
- Daughter cells
- Giant and multiple cells—their formation.
- Castration, its effect upon nuclear budding.
- Nuclear budding of same kind may be seen in epiphyses of dog and in human epiphyses and in pathological products.

Notes on chromidiosis from Howard and Hertwig.

Nuclear budding.

While examining sections of the deer's antler, nuclear budding was observed and was at first regarded as an anomalous and accidental production, such as might arise possibly from antifracts.

Inquiry showed, however, that nuclear budding occurred so frequently and was seen in many sections taken from the antlers of deer of different species, especially appearing at parts of the antlers where proliferation was most active, that it seemed to be other than a fortuitous production and rather that of cells preparing to participate in a general design. The data here are not complete. It presents a field for further investigation.

The following are the facts as far as observed :

The phenomena of nuclear budding occurs in the osteoblasts in the deer's antler during its developmental stages. Occasionally it may be seen in a cartilage corpuscle, while inside of its cartilage envelope (Fig. 103); much more frequently it arises from the osteoblast when freed from cartilage and when it has assumed its mature form and is actively proliferating before it is about to transform itself into bone. In the latter, cells showing nuclear budding may be found in groups of twos and threes and as many as a dozen have been seen in a single field under a 4 mm. lens with 4 eye piece[1] (Figs. 94 to 102).

Nuclear budding met with in the antler is confined to the osteoblasts and in them shows itself in cells which have reached or are approaching their mature form.

The osteoblast at that stage is oval, with the nucleus (containing several spheres of nuclear material) situated peripherally at the narrow end of the oval, and from that peripheral nucleus buds are extruded, some of them at least carrying a halo of cytoplasm along with them. In the vicinity of cells exhibiting nuclear budding, numerous small cells are seen in all stages of growth, from that of the immature, free nuclear buds, to small cells with their proportional nucleus and cytoplasm, and from these upwards to those of mature form and size. In one specimen (photographed) the nucleus and cytoplasm issuing from the cell form a distinct bud-like and complete daughter cell issuing from the osteoblast.

[1] It is difficult to photograph these cells in groups owing to the different levels in which the cells are situated, but with the alteration of the focus the eye perceives them directly through the lens or as transmitted to the screen.

The fixing fluids used for the various antlers have been varied—strong spirit, formalin, Flemming's fluid, etc. It was endeavoured to avoid artefacts.

From some cells two nuclear buds extrude, though in the great majority there is only one seen extruding at the same time. A trailing thread of cytoplasm or nuclear substance is sometimes left attached between the nuclear bud and the cell.

Nuclear buds have occasionally been seen within the cytoplasm apart from the nucleus. In one such instance, where the nuclear bud was found within the cytoplasm at a distance from the nucleus, an indentation was left on the periphery of the cytoplasm, as if the bud had penetrated the cell from without. Search was made for evidence of a similar occurrence in other cells with negative results, though there were many instances of nuclear bud-like bodies lying contiguous with or attached to the outer wall of the cytoplasm.

In giant or multiple cells which are seen frequently, the multiple nuclei may have been formed by nuclear budding into the cytoplasm. Though these multinucleated cells may also be produced by splitting off multinucleated masses and by fusion, some compound cells appear to be undergoing division into single cells.

Nuclear budding has been seen in the antlers of the Fallow Deer, Red Deer, and lees frequently in that of the Roebuck (the amount of bone produced in Roebuck is relatively small), occurring where growth of bone is quickest and where osteoblasts were most abundantly reproduced.

FIG. 94.

1. NUCLEAR BUDDING

SECTION 11.—FALLOW DEER ANTLER, 2/3RD GROWN, 8″ FROM TIP.
4 mm. 8 eye-piece.

Nuclear bud being separated from mature form of osteoblast.

FIG. 95.

2. NUCLEAR BUDDING

SECTION 11.—FALLOW DEER ANTLER, 2/3RD GROWN, 8″ FROM TIP.
4 mm. 8 eye-piece.

Three maturely formed osteoblasts showing nuclear budding.

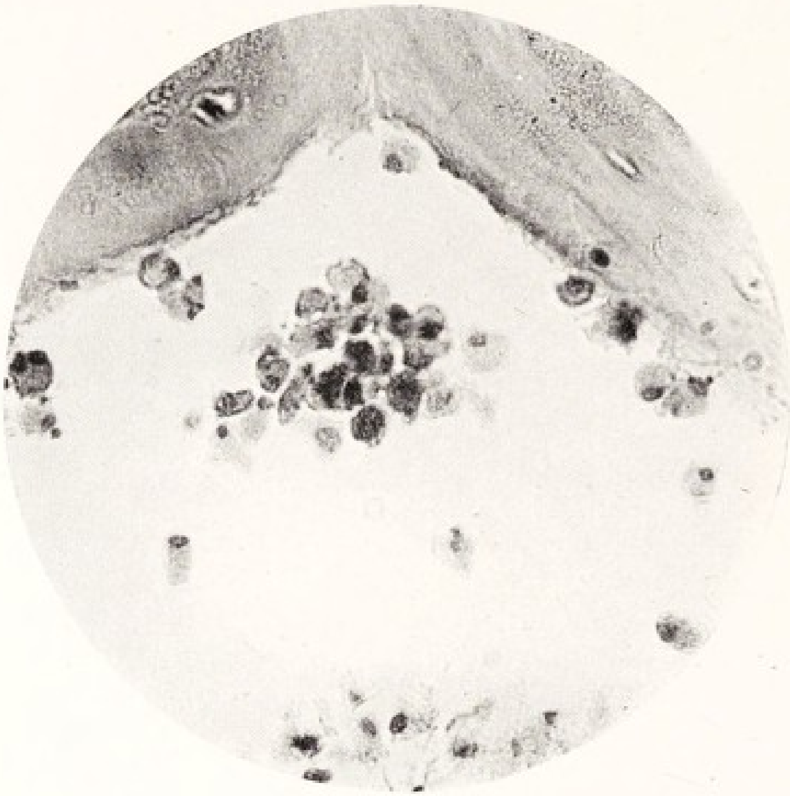

Fig. 96.

3. NUCLEAR BUDDING

SECTION 12.—FALLOW DEER ANTLER, 2/3RD GROWN, 8″ FROM THE TIP.
4 mm. 8 eye-piece.

Mature form of osteoblasts in vicinity of bone, showing nuclear buds—some in act of separating.

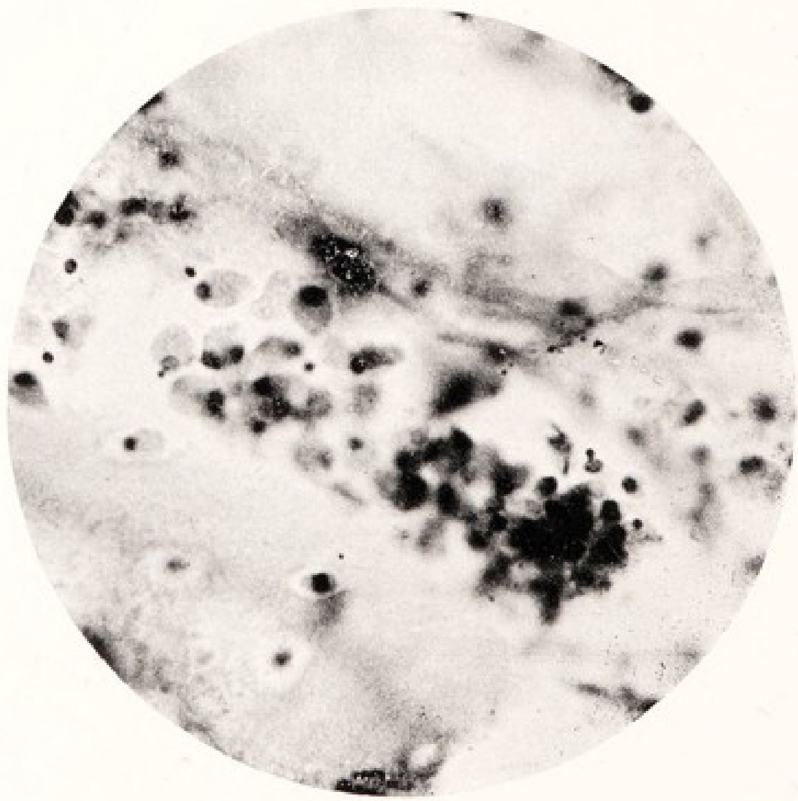

Fig. 97.

4. NUCLEAR BUDDING

SECTION 13.—FALLOW DEER ANTLER, 2/3RD GROWN, 8″ FROM TIP.
4 mm. 8 eye-piece.

Group of free mature osteoblasts near bone trabecula, exhibiting nuclear budding.

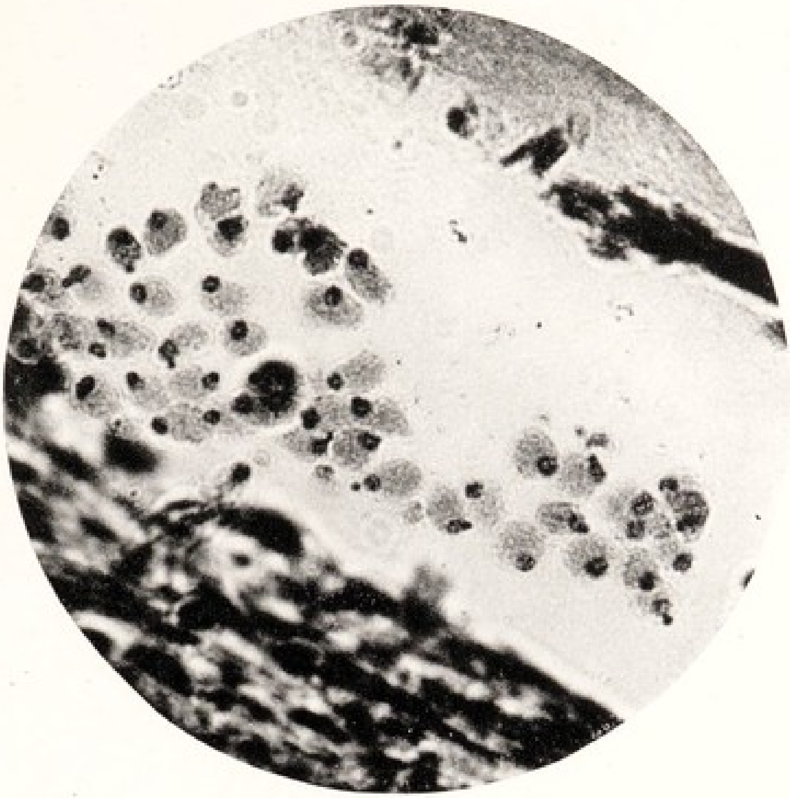

Fig. 98.

5. NUCLEAR BUDDING

SECTION 13.—FALLOW DEER ANTLER, 2/3RD GROWN, 8″ FROM TIP.
4 mm. 8 eye-piece.

Many osteoblasts in this group, exhibiting nuclear budding—some in process of separation.

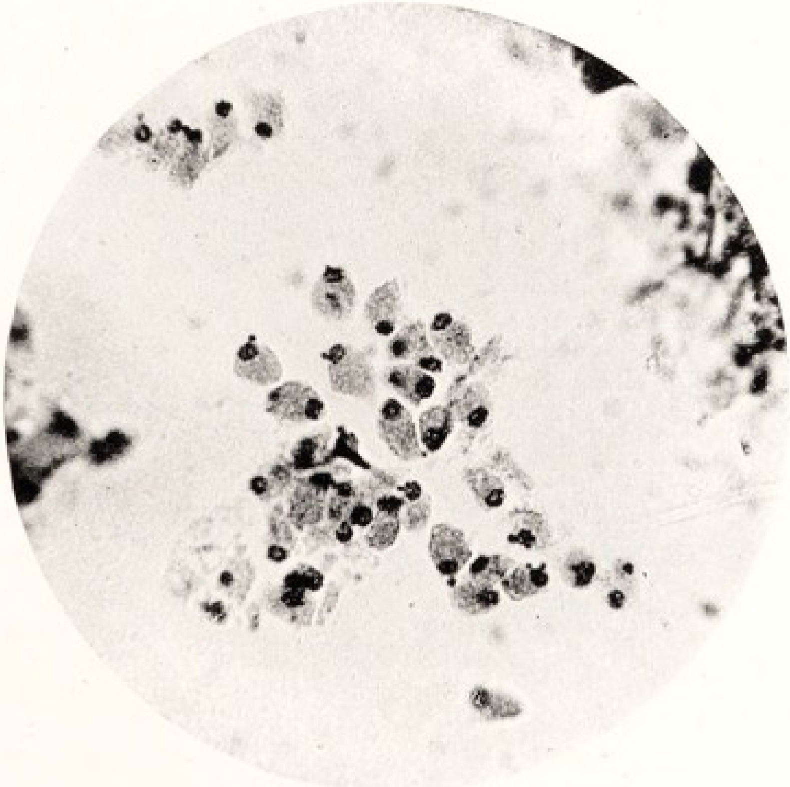

Fig. 99.

6. NUCLEAR BUDDING

SECTION 13.—FALLOW DEER ANTLER, 2/3RD GROWN, 8″ FROM TIP.
4 mm.

Groups of free mature osteoblasts—showing nuclear buds, several exhibiting two buds.

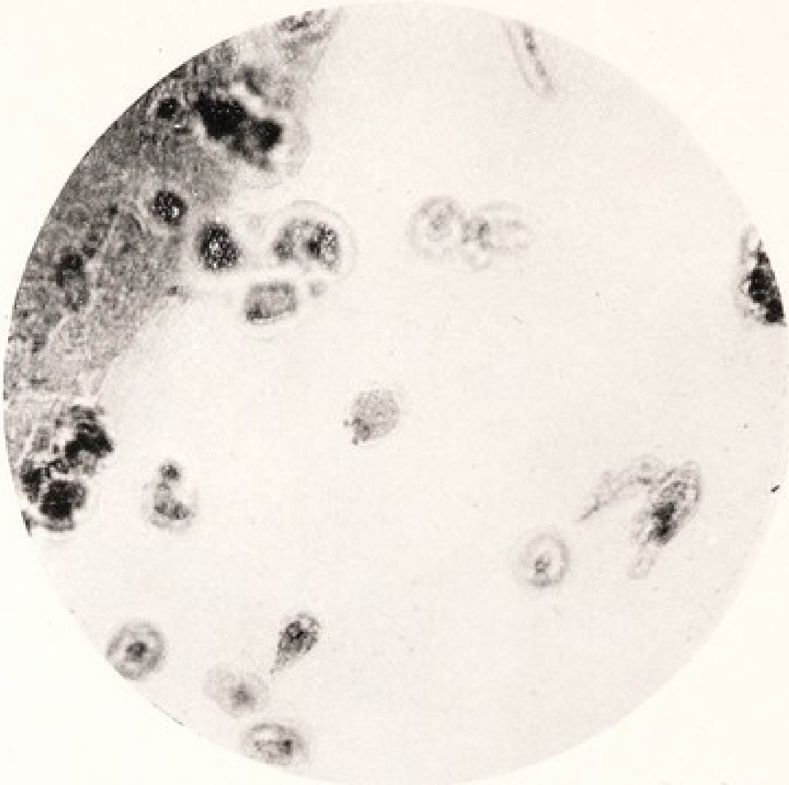

Fig. 100.

7. NUCLEAR BUDDING

SECTION 11.—FALLOW DEER ANTLER, 2/3RD GROWN, 8″ FROM TIP.

Mature form of osteoblast near centre of section, showing two distinct buds and one other projecting from side of nucleus. Inside the nucleus two more may be seen.

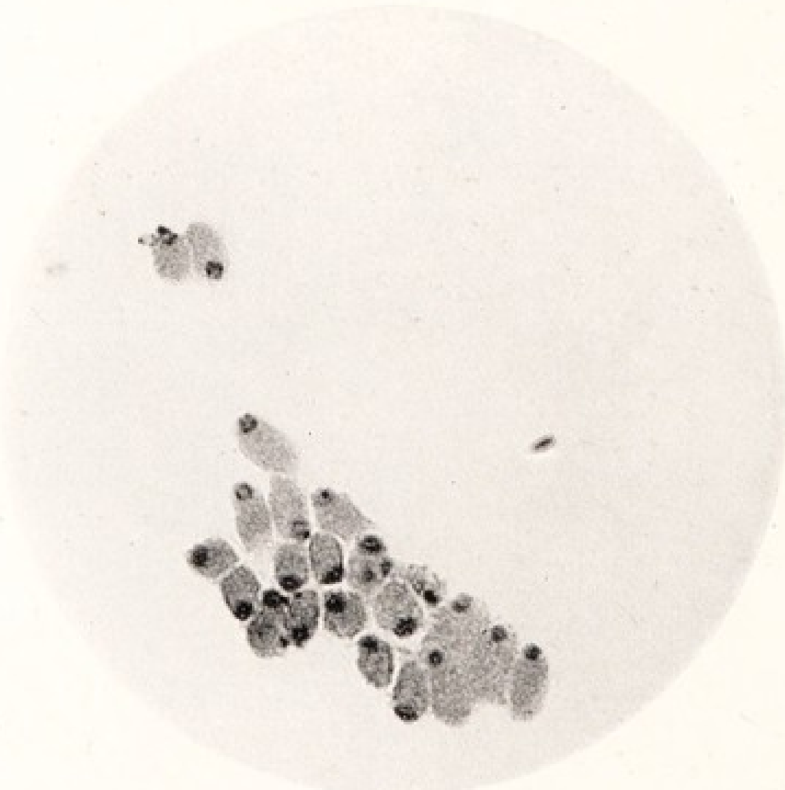

Fig. 101.

8. NUCLEAR BUDDING

SECTION 11.—FALLOW DEER ANTLER, 2/3RD GROWN, 8″ FROM TIP.
4 mm. 8 eye-piece.

Appearance of daughter cell being thrown off from one of the group of two, where nuclear budding is taking place.

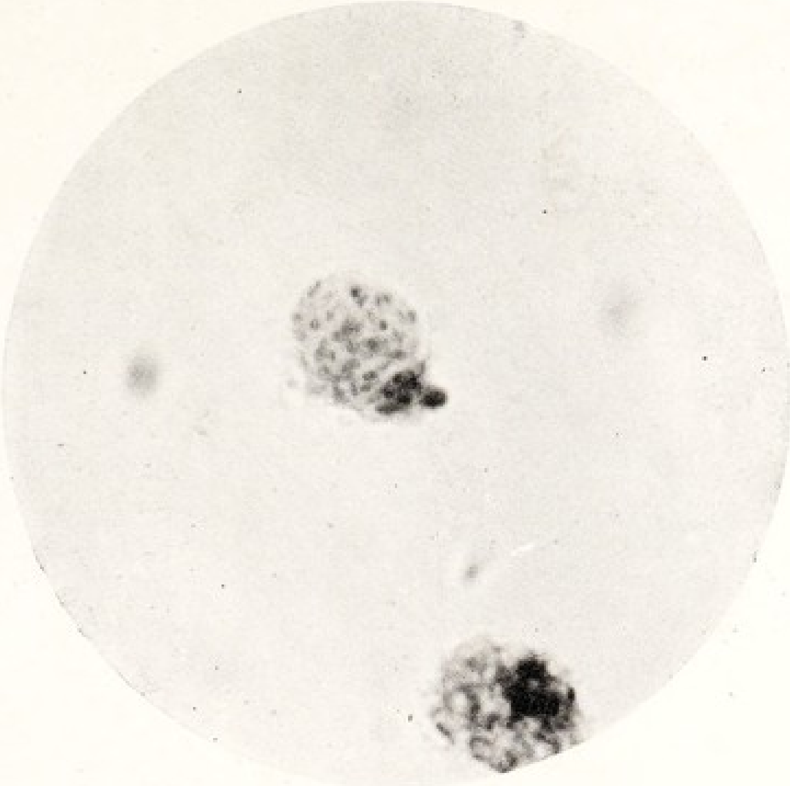

FIG. 102.

9. NUCLEAR BUDDING

SECTION 12.—FALLOW DEER ANTLER, 2/3RD GROWN, 8″ FROM TIP.
4 mm. 12 eye-piece.

The separated bud shows cytoplasm and darker portion like nucleus at one end. Several bud-like masses are seen in the nucleus.

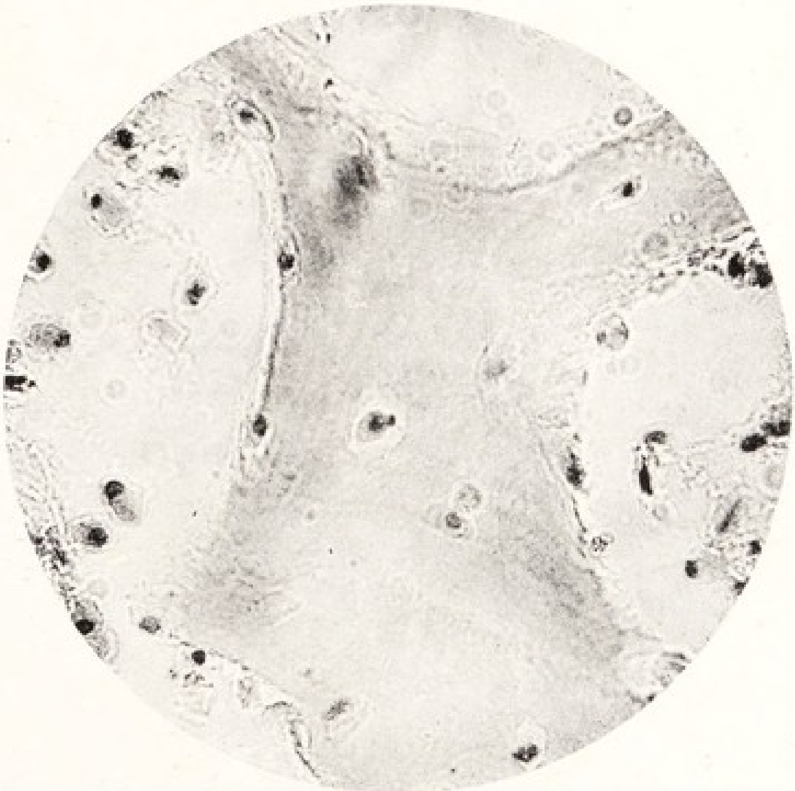

FIG. 103.

10. NUCLEAR BUDDING

SECTION 12.—FALLOW DEER ANTLER, 2/3RD GROWN, 8″ FROM TIP.
4 mm. 4 eye-piece.

An osteoblast inside of new bone, showing bud from nucleus.

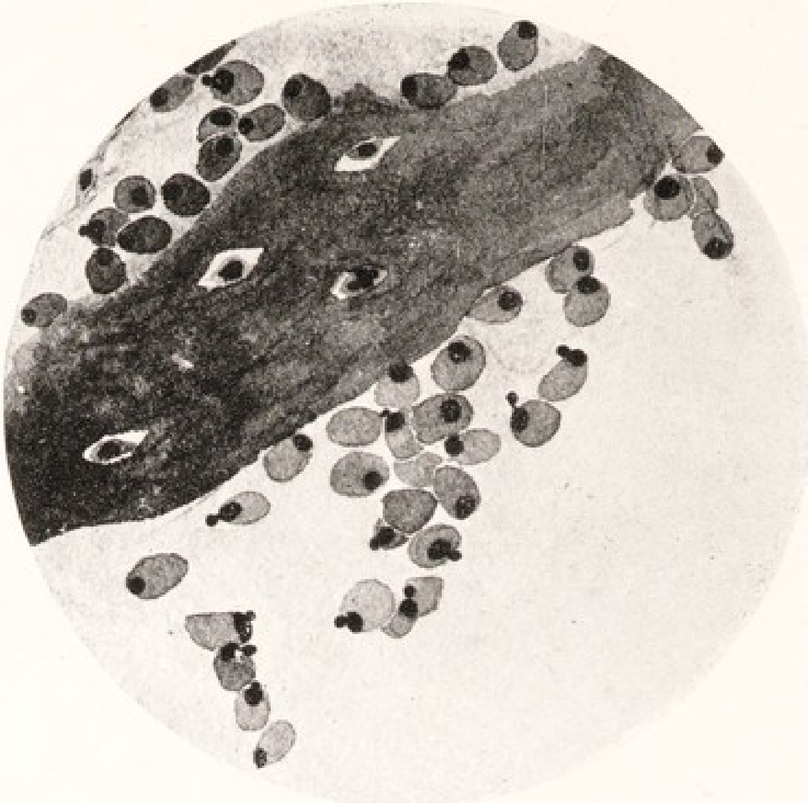

Fig. 104.

11. NUCLEAR BUDDING

Photograph of a drawing by Dr. Macmurray of osteoblasts showing nuclear budding, the cells being taken from different fields and sections.

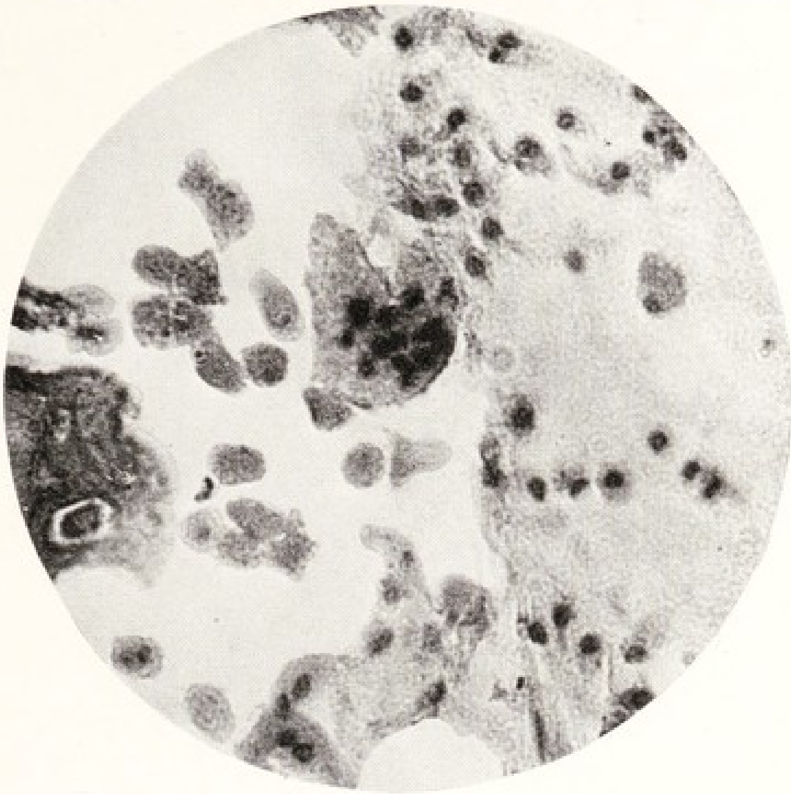

Fig. 105.

1. GIANT CELLS

SECTION 335.—FALLOW DEER ANTLER, 2/3RD GROWN, 8″ FROM TIP.
4 mm. 8 eye-piece.

Early stages of bone formation. Giant (multiple) cells seen throughout the section. Many not in contact with trabeculae.

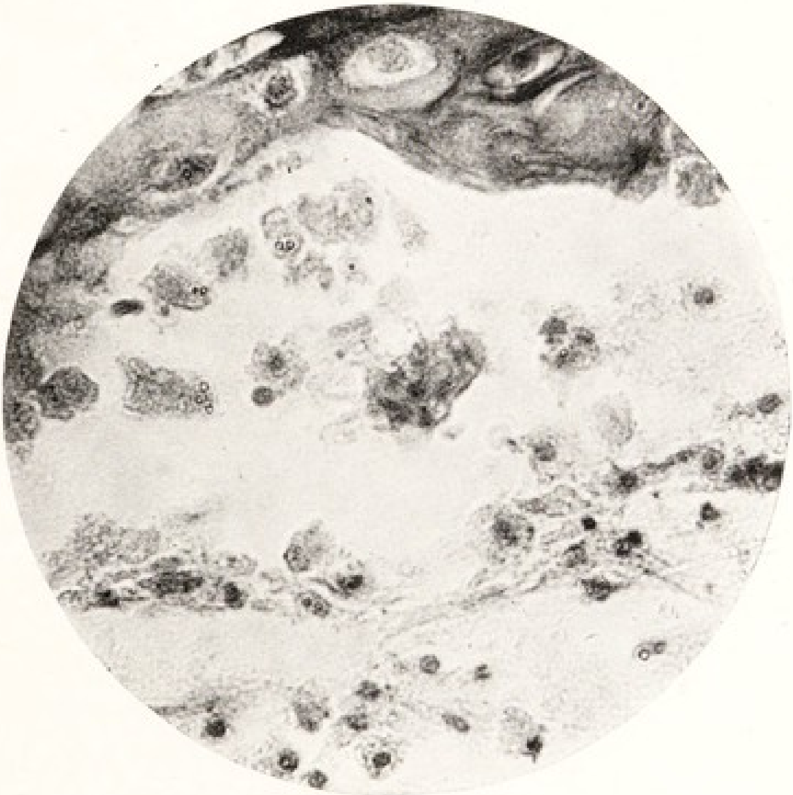

Fig. 106.

2. GIANT CELLS

SECTION 335.—FALLOW DEER ANTLER, 2/3RD GROWN, 8″ FROM TIP.
4 mm. 8 eye-piece.

Giant cell (mother cell ?) with long process extending from its protoplasm and containing many nuclei (or separate cells).

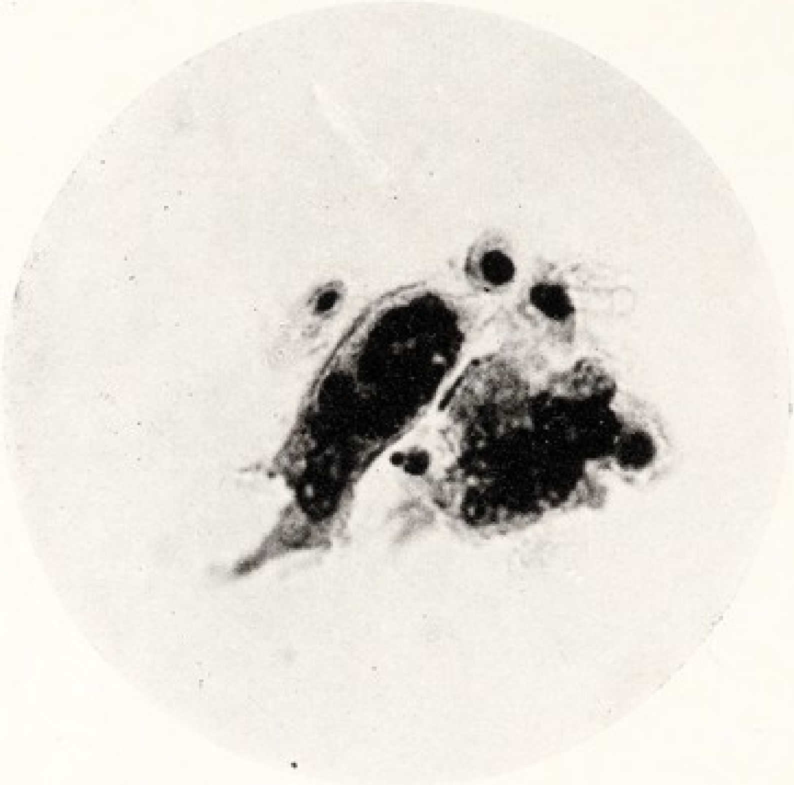

Fig. 107.

3. GIANT CELLS

SECTION 13.—FALLOW DEER, 2/3RD GROWN, 8″ FROM TIP.
4 mm. 8 eye-piece.

Smaller cells escaping from compound cell (mother cell ?). Budding seen in one of the escaped cells.

PROCESS OF REPAIR IN HUMAN TIBIA AFTER ACUTE OSTEOMYELITIS (FOR COMPARISON)

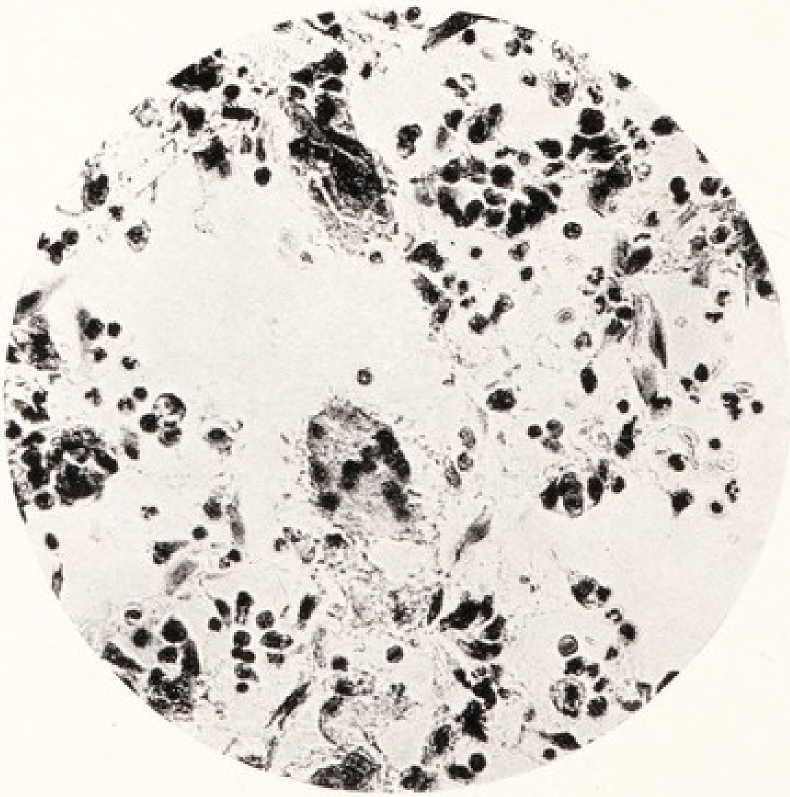

Fig. 108.

4. GIANT CELLS

SECTION 482

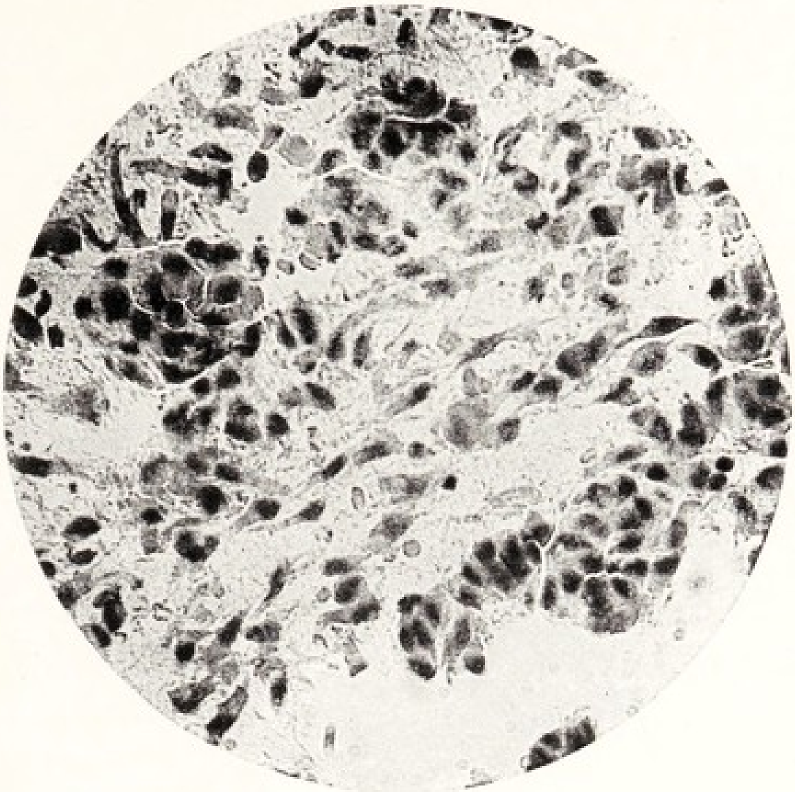

Fig. 109.

5. GIANT CELLS

SECTION 483.

Compound cells dividing into single cells. The rest of the tissue is the embryonic form of osteoblastic tissue, like what is seen in deer's antlers.

The check to the growth of the antler produced by castration probably involves among other changes that of the cessation of nuclear budding, and undoubtedly restriction of regeneration of osteoblasts follows castration. The author has had no opportunity of examining the head of a castrated animal—except as a preserved specimen in a museum and once in a living animal in captivity.

Now that nuclear budding has been recognized in the osteoblasts of the deer's antlers, nuclear budding of a similar description has been found, much more limited in extent, in the rapidly growing bone near the epiphyses of the young dog, and it has been occasionally seen in the transition of the human epiphyses into bone. In pathological processes, where tissue growth is rapid, nuclear budding may also be found, sometimes in considerable quantity.

The regenerative force seen in the development of the antler is out of all proportion in excess of that exhibited in any other part of the animal's body, and this excessive reproduction of cells requires explanation. This is the more striking when the fact is recalled that the whole osseous pabulum originally springs from the narrow pedicle and neighbouring skull. The phenomena of nuclear budding as seen in many of these rapidly growing antlers seems to contribute to the reproduction of cells and may be at least one of the contributory factors to the extraordinary rapidity of growth.

In rapidly growing malignant tumours, such as Sarcomata, a somewhat similar form of nuclear budding is exhibited—which probably contributes to the rapid production of cells. Though instigated by micro-organisms the rapidity of growth must in these tumours be evolved by different biological phenomena from those obtaining in the normal tissue.

In the antler the osteoblastic cells are an ordered, purposeful entity, playing their part in definite design, and ceasing when they have fulfilled the behests of hereditary law. In the quick growing malignant tumours the constituent cells, stimulated by an extraneous alien force, proliferate with great rapidity, producing an inchoate mass, unlimited in extent, except by the destruction of the animal economy of their host. But in both, the vitality exhibited by these cells, their enormous proligerousness and rapidity of production, is such that some other force than that seen in the ordinary methods of cell division, has to be evoked to account for their evolution.

A somewhat similar phenomena to nuclear budding as seen in the deer's antler—though differing from it—is chromidiosis, where the nuclear buds usually pass into the cytoplasm. Hertwig, in 1904, from observations on the actino-sphaerium, drew attention to the phenomena of chromidiosis—" the throwing out from the nucleus into the cytoplasm—there to be broken down or extruded—of excessive chromatin staining nuclear material." Since then he and his pupils—Howard, Popoff and others—have shown it to be a widely adopted method in various protozoa, in sex cells and in thymus cells, " of getting rid of excessive nuclear material and of restoring the nucleus plasma relation." [1]

" In certain of the malignant and rapidly growing types of tumours, chromidiosis is seen and seems to play an effective role in the regeneration of cells, somewhat as is seen in protozoan, sex and thymus cells in production of mitotic division. It is evident that cells of such tumours must employ biological processes differing from those usually utilized in the normal tissue from which they spring. If the cells from which a tumour arises could only exhibit in their regeneration the same phenomena as characterized their normal matricial type, they would then run the same life cycle as these and would have the same destiny—there would be no tumour.

" The relationship of amitosis to nuclear budding has long been recognized. In protozoan cells it is a true reproductive process.

" Chromidiosis occurs previous to division in sex cells. The removal of the energy used up in growth may require phenomena other than the usual asexual division of the cells."

Hertwig holds that conjugation is essentially a phenomena of cell regulation without which the cell must finally perish, and he says that so far as is known protozoa and sex cells are the only cells which have been able to preserve this most important regulatory process (" from the avoidance of and the recovery from depression "). " Whatever its nature, the division energy

[1] W. T. Howard, *On the role of Nuclear Budding in the Regulation of Tumour Cells.* Papers from the Lakeside Hospital, Cleveland, 1910.

R. Hertwig, *Über physiologische Degeneratiom bei Actinosphærium.* Eichhorni, 1904.

controlling and determining nuclear budding seems to reside within the nucleus."

"Nuclear buds tend to wander to the periphery of the cell. They may degenerate and become disintegrated or be extruded from the cytoplasm. They may divide by mitosis or amitosis —or they may separate with portions of the cytoplasm or mother cell, thus forming well regulated daughter cells capable of growth and of divisions by either mitosis or amitosis."

THE EFFECT OF CASTRATION ON THE GROWTH OF THE ANTLERS

The data regarding the effect of castration on the growth of the antler has probably not been thoroughly wrought out, but sufficient evidence has been adduced to show that castration produces a profound effect upon their growth, and though this may be expressed in a variety of ways, all of them indicate retardation or arrest of growth. This is especially marked in the main factor, the growth of bone of the antler. The effects vary according to the period at which the castration takes place, relatively to the growth of the antler. If the animal be castrated when the antler is fully grown, the shedding is retarded, and when it does shed, the base of the antler is seen to be concave instead of convex as it is normally.[1]

[1] There are 11 specimens in the Royal College of Surgeons Museum from fallow deer (*Cervus dama*) which had been kept at Oulton Park, Cheshire, illustrative of castration in male deer. Some had one testicle removed. Some had one half of each testicle removed and some had both testicles taken away.

In specimen 1557—half of each testicle was removed and both antlers were shed but never afterwards attained full size; bases of antlers were concave instead of being convex as in normal specimens.

Specimen 1567—left testicle removed and left antler shows a corresponding arrest of growth.

Specimen 1569—castration, antlers not shed at proper time and malformation by exostosis.

The new antler, springing after castration, is dwarfed and malformed and the shedding of the velvet is retarded —sometimes it does not shed. According to Flower the horns are imperfectly formed and spongy, there being no true bone in their composition.[1]

[1] "When castration is performed in an adult stag, it often dies; but when the animal survives during horn-growing time and the velvet is peeled off, the horns are seen to be imperfectly formed and spongy, there being no true bone in their composition. They do not solidify and are consequently of small benefit. The horns are never cast and the animal rarely lives to any age."—Sir William Flower.

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