STUDIES ON THE GLANDULA UROPYGIALIS OF BIRDS

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PART I.

GENERAL STATEMENT.

Birds differ from mammals in having only one gland of a sebaceous nature. This is the glandula uropygialis, commonly known as the oil gland or preen gland. It is present in most birds and is always situated at the base of the tail. It secretes an oily substance which by means of the beak is smeared all over the feathers. It is generally thought that in this way birds oil their feathers in order to prevent wetting. Does this account for the existence of the gland? Can birds continue to live without the gland? Has it any other function than merely to oil the plumage? In other words, is it necessary for the maintenance of life or for the preservation of the feathers?

Previous workers concluded from their experiments that the oil gland is not necessary for the maintenance of life. Birds deprived of the gland lived on indefinitely. Comparative anatomical studies on the size of the gland, which varies considerably in different species, and on the presence or absence of the organ did not throw any light on its function. As to the wetting of the plumage, some believed the oil necessary to effect an efficient coating against wetting, while others did not, since the feathers remain "impermeable to water" without oil. On the whole the anatomy of the organ was very thoroughly /

thoroughly studied but the physiological experiments and data were far from convincing.

My interest in this study is further accentuated by the possible relationship between the organ and the formation of vitamin D. The body of the bird is entirely covered by a thick layer of plumage except a small portion of the legs and the claws where there is a very scanty blood flow and the skin is devoid of any gland. The theory is that the gland elaborates some sterols such as ergosterol or cholesterol or both. These, it is suggested, when spread over the feathers, become irradiated by the ultra-violet rays of the sun and converted into vitamin D, which is then taken in by the beak in the process commonly known as "preening the feathers."

I have also attempted to elucidate the question of the wetting of birds by rain, in swimming or in bathing, and the bodily temperature changes associated with it in normal and operated birds.

The results obtained lead me to believe that the gland secretion is partly responsible for the maintenance of a smooth contour of the plumage, making it an effective protection against wetting of the body. I have also obtained sufficient evidence to substantiate the theory that the oil gland is a source of vitamin D. Absence of the oil gland may result in the development of the disease rickets if extra vitamin D is not added to the diet.

PREVIOUS /

PREVIOUS WORK.

General. - The first recorded observation on the oil gland was credited to Emperor Frederick II, who in 1598 noted the presence in birds of a bilobular gland, the secretion of which served to oil the plumage. He believed that the oily product possessed a toxic action which in the case of birds of prey poisoned the victims through the claws. Willoughby in 1676 attempted to confirm the statement regarding the toxic action but found no evidence.

Ray (1691), Schneider (1784) and Bechstein (1791) described the external appearance of the gland. Bechstein stated that it was believed that a disease called "darre" developed in birds when the opening of the oil gland became stopped, and could be cured by opening the duct with a needle. This assertion again cannot be confirmed.

Cuvier (1799-1805) was the first to describe the internal structure of the gland. His view, namely that the gland originated from a closed secreting vesicle, proved however to be erroneous.

Tiedemann (1810), Bleinville (1822) and Müller (1830) discovered the presence of a number of non-branched tubules converging toward the hollow cavity.

Nitsch (1840) studied specially the number of excretory openings, and the distribution and presence or absence of plumules about the openings. To these he attached a taxonomic significance in regard to the groups of birds studied.

Hussey (1860) described the manner in which ducks used the bill to get the secretion and spread it over the feathers.

A /

A careful description of the process of preening was given by Mathews (1861) as follows:- "The bird first raises the feathers over the oil-gland. With beak sideways he presses a considerable quantity of the oil to the surface. Then having rubbed the feathers of the throat immediately below the beak on the gland so as to ensure their wiping the oil off, he proceeds to rub his thus annointed throat on his back and other parts of his plumage, at the same time constantly passing the feathers through the beak."

Owen (1866) described the general anatomy of the oil gland and believed that the "unctuous" fluid served to lubricate the feathers of the bird, the gland being largest in aquatic birds.

Work of real scientific value was not done until Kossmann (1871), who studied the histology and embryology of the oil gland in the hen, pigeon and duck, and described in detail the innervation and vascularization of the organ. He believed the function of the oil gland was to oil the feathers and discussed at length its similarity to the sebaceous gland of mammals.

Bert, Goubaux and Philippeaux (1872) performed ablation experiments on the gland of the duck. Their results are contradictory and inconclusive.

De Jonge (1878-79) made a chemical analysis of the secretion of the gland in ducks and geese.

Pillet(1889) and Orlandi (1902) continued the experiments of Kossmann. They confirmed the results of his histological and embryological studies and noted further similarity in the structure of /

of the oil gland and that of the sebaceous gland in mammals.

Röhmann(1904) published a long article on the chemical composition of the secretion of the oil gland of the goose.

Margarete Stern (1906) studied the oil gland of ducks and attempted to explain the mechanism of secretion by the histo-chemical reaction of the cells and granules.

Lunghetti (1903-1906) studied the anatomy and embryology of twenty species of birds, making careful drawings of the structure. He confirmed in general the work of Kossmann.

Trouessart (1906) described the use of the oil gland for oiling the plumage and the skin and aiding the moult.

Paris (1910-1914) made a study of 350 species of birds with reference to the structure, comparative anatomy and functions of the oil gland, and believed that the oil is not necessary to render the plumage impermeable to water. He stressed the close analogy in origin, development, situation, form, structure and nature of the secretion with the odoriferous gland of the amniotic mammals and particularly of reptiles. His final conclusion was that the uropygial gland must be considered as an odoriferous gland.

H. Granvik (1913) made a study of the structure of eleven different species of birds and confirmed the results of the previous workers.

F. /

F. Schmidt (1924) gave a long account of the comparative anatomy and histology of the oil gland of seven different species of birds. His results are essentially the same as those obtained before.

Ablation of the Gland. - This was first performed by Kossmann (1891). He found no change in the condition of the bird after the removal of the gland from a pigeon. Paul Bert, Goubaux and Philippeaux (1872) worked on ducks and found in some that the plumage became dull, soiled and remained for a long time wet, while in others the plumage showed neither any difference in the appearance of the feathers nor any tendency to become more wet. They thought in the latter case some small glands had developed to take up the function of the oiling of the feathers when the usual oil gland had been removed. This however cannot be substantiated. Paris had studied two glands from a bird which looked like oil glands but were revealed under the microscope to be lymph glands. Lunghetti (1906) removed the glands from three months old chicks and found no abnormal changes.

Paris (1913)extirpated the oil gland of a number of birds of different species and always obtained a negative result. The birds used were a young pigeon, an adult pigeon, a hen, a starling, a parrot, two wild ducks and four young ducklings.

Some /

Some of them lived on for several years and still showed no difference in habit, appearance, permeability to water or moulting of the plumage. It should be pointed out here that Paris kept the operated birds in the same cage with the normal controls, and undoubtedly the birds which lacked the gland obtained their supply of oil by stealing it from the controls. This is further substantiated by the fact, noted by Paris, that the birds without glands were not welcome to their comrades who possessed glands. "Il est à noter cependant qu'ils furent toujours mal vus de leurs compagnons de captivité qui ne voulurent jamais les admettre dans leur société pendant l'année qu'ils passèrent ensemble."

Occlusion of the opening of the gland. - This was at one time thought to have caused certain illness in birds. Paris failed to confirm it. The results I obtained with birds whose gland had been occluded were similar to those obtained by removal of the gland. Paris found in one hen whose gland had been occluded for two months that the lobes became much swollen and the interior filled with a waxy mass, which pressed upon the glandular tissue and the septa causing much atrophy. No alteration in the health of the birds was noted. Again the operated birds were kept together with the control.

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The Physiological Action of the Secretion. - This was first thought to be of toxic origin, as noted in the travel account of the Emperor Frederick II, who described how a dog suffered nervous disorder for one month after devouring the hind part of a bird.

Paris tried the effect of the gland excretion of a number of birds and found it had no physiological action whatsoever. Filtered product from the gland aseptically ground when injected subcutaneously into frogs always gave a negative result. When injected into the vein of a rabbit or a dog it exerted no influence on the blood pressure or the nervous system.

Nervous Control of the Glandular Secretion and its Relation to Blood Supply. - By means of electrical stimulation of the nerves, ligation of the vessels and section of the nerves, Kossmann (1871) made the first study on the nerves and blood supply of the oil gland. The results obtained were recently confirmed by Paris, as follows: Stimulation of the nerve supplying a lobe of the gland by induction current results in an outflow of the secretion from one lobe. The flow took place some time after the excitation and then continued without any visible contraction of the gland.

Stimulation of the nerve was accompanied by a marked vasodilation of the arteries which supply the lobe. Kossmann considered this to be due to the sympathetic fibers contained in /

in the nerves of the gland, though he gave no evidence to prove it. Ligation of the artery of the stimulated lobe causes the stoppage of the flow of the secretion.

Kossmann obtained atrophy of a lobe of the gland when the nerve supplying it was cut. Paris repeated the experiment and found no difference in the operated lobe as compared with its normal homologue. The latter believed however that the nerve must play an important part in regulating the sphincter muscles of the nipple of the gland. Ordinarily the opening is closed down by the contraction of the sphincter, which must be relaxed to allow the secretion to flow out.

Relation of nutrient fat to secretion fat. - Plato (1901) fed three geese with fat-free uncooked barley in amounts of 100 to 150 gm. a day each. To this amount he added 20 gms. of the oil of sesame. From time to time some secretion was carefully pressed out of the gland and tested with hydrochloric acid and furfurol. On the fifth day the reaction became positive and it did not disappear until 11 to 19 days after the cessation of feeding with oil. When the geese were given the oil a second time, the reaction was again positive from the 10th to the 18th day. He concluded that 10 to 18 days are necessary for the transference of oil from the cells of the exterior zone to those in the center. Experiments of this nature however do not exclude the possibility that, when the bird is overloaded with sesame /

sesame oil, part of this may be transuded into the interior of the gland, and that the secretion is a genuine secretion process. Röhmann (1904) repeated the same experiment and confirmed the results. Paris (1913) performed a similar experiment but he added a mixture of Sudan III and olive oil to the diet of several ducks for some months. At autopsy he found that the peritoneal fats were stained deep orange red, while the intramuscular and subcutaneous fats, also fats present elsewhere in the body, were stained lighter orange red. On the other hand, the oil secretion of the gland was not at all stained. Paris concluded from this result that the Sudan III may be either retained or converted when oil is elaborated in the gland.

Margarete Stern, using histo-chemical evidence, claimed to have proved that some fatty substance is first brought to the outermost layer of gland cells. There it undergoes chemical changes as the cells go from the outside toward the lumen of the tubes. She showed that in the process of the transformation of the fat into secretion the secretion granules are stained differently at the different stages of formation. The difference in color reaction appears distinctly in the three zones defined. She believed that in the changes of nutrient fat into secretion there were involved various chemical reactions in the cells. Thus she said: "Die Ölsäure wird nach der an nahme Röhmanns zum octadecylalkohol reduziert. Die Bildung der Ester ist im synthetischer/

synthetischer Prozess, durch Oxydation entstehen aus höheren Fettsäuren solche mit geringem Kohlenstoffgehalt." She concluded that the process must result from the action of the protoplasm. At the periphery of the tubes the cells contain the fat in an extraordinarily finely divided condition before it is converted into secretion. Next they are changed into lipoid granules and finally into secretion droplets which show chemical behavior toward certain solvents and stains as octadecyl ester, i.e. palmitic acid- and stearic acid- ester of octadecyl alcohol. Stern concluded from her studies that the secretion formation is a true secretion process and not a cellular degeneration. The oil gland forms a characteristic secretion from fat, which is imported from outside. The breaking up of the cells follows only after they have fulfilled their purpose in elaborating the oil which accumulated and finally burst them. Schmidt (1924) studied the oil gland of seven common species of birds and concluded that this glandula uropygialis is a necrobiotic secretory gland.

Chemical composition of the secretion. - The first analysis of the excretory product was made by Chevreul in 1833. He concluded that the sebaceous substance was developed by the setting free of a volatile acid in the presence of water. But a complete chemical investigation was not made until 1879, when de Jonge in about two grams of the oil from a goose found the following /

following substances present: Casein, albumin, nuclein, lecithin, low and high fatty acid, and a non-saponifiable portion, which he believed to be cethyl-alcohol. There were also found inorganic substances such as potassium, sodium, calcium, magnesium and chloride, and free sebaceous acid, as well as traces of sodium and potassium soaps.

Röhmann (1904) repeated the chemical analysis in a very careful way and concluded that the secretion had only a small portion of fat (triglyceride of fatty acids) but a larger portion of fatty acid, ester of octadecylalcohol, and a chloroform-soluble body. He divided the gland extract into three portions:-

(a) Portion soluble in dilute alcohol but insoluble in absolute alcohol.

(b) Portion soluble in ether and chloroform.

(c) Portion insoluble in ether and soluble in chloroform.

De Jonge found that in 100 parts of the solid secretion 47.7 to 59.5 parts are soluble in ether, while Röhmann obtained 60 parts for the ether soluble portion and 14 parts for the chloroform-soluble and ether-insoluble portion.

The ether extract is a clear oil of varying yellow colour. When allowed to stand, a solid substance separates out. Its reaction is almost neutral. The index of acidity is 0.75 - 3.4.

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The saponification index and iodine number is much less than for ordinary fat. This small saponification index indicates that if the ether extract contains fat it in all probability possesses an alcohol which is heavier than glycerine in molecular weight, i.e. cethyl-alcohol (according to Jonge) or octadecyl-alcohol (according to Röhmann).

The cholesterol and ester of cholesterol were not found in the secretion of geese.

Oil and the plumage. - Early investigators of the oil gland generally agreed that it secretes an oily substance, serving to make the plumage lustrous and waterproof. The indispensableness of this for the welfare of the plumage however is questionable, since a number of birds do not possess it and yet maintain a well kept plumage. It has been found (Lunghetti, 1906) in some birds that in the embryo there is a rudimentary oil gland which disappears in the adult. Kossmann associated the disappearance of the gland with a marked development of the plumage in this region. Paris (1906) found that atrophy or engorgement of the gland did not in any way affect the plumage. He found that, although the oil gland is larger in most aquatic birds than in land birds, yet there are birds of aquatic habit possessing no oil gland at all. He (1913) stated that even at its largest the gland of aquatic birds had not sufficient oil to cover the entire plumage. He admitted however that, when a large amount of the oil gland

secretion did pour out, the bird by the process of preening kept the air between the feathers and rendered the plumage impermeable to water.

Embryological study. - Kossmann (1871) undertook this study, which was continued by Pillet (1889) and Orlandi (1902). Their view was confirmed by Lunghetti(1906) who described how in the hen the gland arises from two recesses which become visible between the ninth and tenth day of incubation at one side of the midline. Its further development may be differentiated into three phases:-

(a) The formation of two indentations at which the glandular cavity originates.

(b) From the wall of these indentations subsequently arise some comb-shaped epithelial buds (primary buds) which soon become hollow and give rise to the spongy portion.

(c) From the primary buds originate thin long epithelial pivots (secondary buds), from which the tubes are formed.

PART II.

STRUCTURE OF THE GLAND.

This has been fairly thoroughly studied and described by previous workers. My studies on pigeons, fowls, ducks, geese, and a great horned owl led me to confirm their results, except that in these birds I have not found the "numerous elastic fibers"described by Lunghetti, Schmidt and others. These "elastic fibers" appear to be identical with the reticular tissue fibers when stained by the gold chloride method for reticular tissue (Fig. 1). They do not stain with Unna's Orcein stain for elastic fibers.

Gross Anatomy. - The oil gland, the only cutaneous gland in birds except some small organs in the external ear passages, consists of two symmetrical lobes, more or less united posteriorly in the shape of a heart. Each lobe is broad and rounded in front and pointed behind (Fig. 2). They are conjoined at the apices, which are directed backwards.

The gland is situated dorsally immediately above the levator muscle at the root of the tail, being embedded below the skin in a mass of fat tissue with a nipple-like process projecting to the exterior. Here are the openings of the gland, one for each lobe. Round about each opening is a row of hair-like downy feathers, evenly arranged in an oval and well developed in ducks and geese but less so in pigeons and /

and hens and entirely absent in the owl. Nitsch (1840) made a careful study of the distribution of these feathers, their presence or absence, and the number of excretory openings which may number three to five in many aquatic birds. The whole organ is surrounded by a fibrous capsule. It is innervated by the first caudo-spinal nerves and supplied by a branch from the caudal artery and vein.

Capsule. - The capsular sheath encloses each lobe of the oil gland. In the interior of the gland it forms partitions between the glandular tubes, remaining parallel to them as they coalesce. So the septa become wider as they approach the central collecting cavity (Fig. 3). The capsule consists of fibrous connective tissue but no elastic fibers or muscle fibers. Kossmann (1871) and Orlandi (1902) noted the presence of smooth muscle fibers, but this is contradicted by others. Paris (1906) and Schmidt (1924) indicated the presence of elastic fibers, while Lunghetti found that the capsule consisted exclusively of connective tissue.

Inner structure. - Each lobe of the gland possesses a longitudinal central cavity where the secerning tubules end with angular openings. The tubules are straight, closely set and parallel to each other as they extend to the periphery of the gland with ramifications (Figs. 1 and 3) but without intercommunication. The diameter of the tubes remains about the /

the same throughout. The peripheral ends of the tubes are blind. The nipple-like portion consists of two ducts one from each lobe and a continuation of its cavity, each surrounded by smooth muscle fibers and connective tissues, penetrated by blood vessels and nerves and their end organs, the corpuscles of Herbst.

The glandular epithelium of the tubes. - This consists of several rows of cells, of which the outermost or nearest to the lumen of the tube are flattened out and are distended with numerous fat globules, many of them in process of disintegration or degeneration. Lunghetti termed these cells of the superficial solution layer. In the middle transitional layer the cells are columnar in type and filled with smaller fat globules. The outermost or germ layer consists of cells of columnar type, some containing fine fat granules mostly in process of active division showing numerous mitotic figures.

Taking as a whole the tubules as they approach the lumen of the lobe become less active in mitosis and more loaded with fat globules. One can discern three definite zones on which Margarete Stern laid much stress in her interpretation of the histological evidence in its relation to the mechanism of secretion. She stained the section of the gland with Osmic acid and scarlet red. She noted that in the outer two zones the secretion droplets stained dark brown. As the tubules approach /

approach the center, the stains become lighter. The color thus varies from black brown, red brown to red, and show in the last part of the tubules a uniformly intensive red. Similar coloring differences are noticeable with Bielchowsky treated preparation. Even grossly or stained with ordinary hematoxylin-eosin one can easily differentiate the three zones.

The outermost zone, zone 1, has the tubular cells in the process of active multiplication with new cells in the periphery and in the center degenerating but relatively few. The lumen of the tube is small. If one stains this with alkaline scarlet red, one finds red granules in the protoplasmic network. They were first noticed by Plato in unstained section as markedly refractile granules resembling fat. He called them hipophore granules because he believed that they are the precursors of the actual fat secretion of the gland. Stern contradicted this and showed by her staining method that these granules are really fat droplets. My Sudan III stained frozen sections show findings confirming this view. Stern placed frozen sections in osmic acid and at the same time stained them with scarlet red, and she obtained a second kind of granules in the peripheral layer of cells. These granules she described as disk-shaped when looked at from above and rod-like when looked at from the side. They appear in groups and stained brown and black. Their size is the same as that of the smallest secretion droplets and they can /

can be differentiated from the latter by the characteristic shape and staining reaction. These Stern called lipoid granules. They are seen in unstained section as highly refractile gramules. They are not so sensitive to alcohol and xylol, etc., as the secretion droplets. If one places the frozen section in dilute alcohol for a day and then stains it with safframin, the protoplasm and nucleus are not stained but the lipoid granules are stained red. In zone II, the middle zone, the cells of the tubules are as much in mitosis as those in zone I. The breaking up of cells however begins sooner and so the number of intact cells is fewer. The lumen of the tube is correspondingly larger. In a hematoxylin stained section one finds that the cells contain much more protoplasm than in zone I, but instead of the regular net work the protoplasm appears irregular and spongy. In it one finds the secretion droplets which no longer show the resistance to alcohol or zylol and stain light blue with hematoxylin stain. The coloration of zone II with scarlet, according to Stern, gives no longer a bright red but rose, except for a ring of cell next to the lumen of the tube which is stained intensely red as in zone I.

In zone III the breaking up of cells appears sooner, the lumen of the tube is wider still and the secretion becomes more abundant.

In the neighbourhood of the cavity of the lobe the epithelium of the tubes consists of only two or three layers

of /

of flattened cells. On the other hand the intertubular connective tissue which has become wider in zone II has increased considerably and actually supports the weakened thin wall of the tubes which are now filled with the secretion.

Other structures. - Between the gland tubes lie numerous lymph nodes which are embedded in the intertubular connective tissue. These are mostly round, but may be oval in shape. Here are also lymphatic vessels and numerous capillary loops which wind about the tubes. Besides one often finds corpuscles of Herbst, the terminations of tactile nerve, scattered in the connective tissue septa.

Blood supply. - The blood supply of the gland is fairly rich. Kossmann was the first to study this and Lunghetti later confirmed it. The gland is supplied with branches of the arteria caudalis, a branch of the descending aorta. These branches rise along with the corresponding veins between the epiphysis of the 1st caudal vertebra up to the back and reach the gland through the canal between the muscularus spinalis caudae and the musculus levator rectricium. Thus the blood comes to the gland by a rather direct course and meets with but little resistance, and so we may assume that the blood supply is very abundant and regular. The vein also receives a branch from the nipple just before the former reaches the base of the gland, and another from the connective tissue septa /

septa between the gland tubes. Here the arterioles give rise to numerous capillaries which anastomose freely and form a network around the tubes.

Nerve supply. - The nerves supplying the oil gland take a course similar to the blood vessels, and they come out between the 1st and 2nd caudal vertebrae. According to Kossmann and subsequently Paris, they arise partly from the spinal cord and are partly of sympathetic origin. Vasomotor action comes from the sympathetic fibers. The nerve coming from the medulla is frequently seen to end in nervous end-bodies. These are the corpuscles of Herbst which are only found in birds but are present in mammals in a degenerate form and known as the corpuscles of Vater. In the oil gland of birds they are found chiefly in the teat and occasionally in the heavy intralobular connective tissue septa. They are mostly oval in shape but in cross section often appear round.

The corpuscles have in the center a continuation of the nerves, surrounded usually by a single layer of nuclei - occasionally by a double layer - and these in turn are embedded in concentric layers of hyalin material. Thus the corpuscle stands out clearly against the surrounding tissue. Schmidt (1924) believed that these corpuscles are the medium through which the gland receives pressure sensation when the bird places its beak against it.

Ablation /

ABLATION EXPERIMENT.

The birds used for the experiment were domestic fowls (Gallus bankiva), domestic duck and drakes (Anas domestica), pigeons (Columba domestica) and geese (Anser domesticus). The actual numbers under observation were as follows:-

	Pigeons	Hens	Ducks	Geese
Gland removed	16	4	4	1
Control	10	4	4	1

Operative procedure. - The birds were usually put under anesthesia. The area around the gland was denuded of feathers to the extent of about 1½ inches in diameter, and then sterilized with iodine and alcohol. Under aseptic technique I incised the skin around the base of the nipple, lifted up the skin flap and dissected close to the capsule of the gland to free it from the surrounding fat and connective tissue. After tying the arteries at the base of the gland, the latter was easily enucleated without much loss of blood. In many cases the blood lost was not more than a drop or two. The wound was sewn up tight with two or three interrupted sutures to prevent any possible oozing of blood.

Care of the birds. - No special care is needed after the operation. The wound invariably healed by primary union in about a week. I have not encountered a case of sepsis in the wound. After operation the birds without the oil gland were separated /

separated from the controls and placed in different cages or in a different section of a partitioned room. Their living conditions, diet, sunlight (of which however there was very little) and exercise were kept as nearly as possible the same for both operated and control birds. The diet consisted of corn, oats, milk and bread, with coarse sawdust and sand scattered on the floor. They were given adequate water baths once or twice weekly. Temperature and weight of the birds were taken daily during the first week after the operation and subsequently twice weekly.

Results. - No striking results were obtained in the first three weeks. There was always some loss of weight in the first two or three days, but soon the weight picked up and in fact the birds kept on increasing in weight as much as the normal controls in the first forty to one hundred days.

It should be noted here however that, if the operated birds were kept together with the controls, the former very soon began to steal oil from the latter by picking at their glands with the beak. Thus isolation became necessary.

From the fourth week on the plumage began to look dull and soiled and to lose its smooth contour. The birds became wet more easily and appeared much more draggled after a bath (Figs. 5 and 6).

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In the meantime bodily temperature records taken before and after swimming in cold water showed that there is a greater fall and slower recovery in the operated birds than in the normal controls (Figs. 20 - 23). Thus the plumage has apparently become less adequate as a means of protection against wetting of the skin and subsequent chilling. It appears then that the oil is necessary to a certain extent for the maintenance of a smooth contour of the plumage, thus forming an efficient protection against heat loss, although the behaviour of the individual feathers to water remains unchanged.

Microscopic examination of the feathers at this time also revealed some change, which was brought out clearly by staining with alcoholic solution of Sudan III overnight and washed thoroughly in running water for a few hours or longer. The number of oil droplets, normally present in great number between the barbs, barbules and barbicels as globules before staining and as irregular clumps after staining, has become much reduced. The disappearance of the oil droplets is progressive. So in most cases by the beginning of the third month they are almost all gone (Figs. 8 and 9). This may be accounted for by the fact that the bird removes the oil from the feather with his beak and cannot replace it with a new supply. Thus normally during the process of preening the bird not only puts the oil on but also takes it off.

The /

The loss of weight in the operated birds in some cases began about the fortieth to the fiftieth day after operation. Most of them however showed a decrease only after the hundredth to one hundred and twentieth day. One of the operated birds began to lose weight in the third week, and another even before the third week. In every case the loss of weight is progressive, being slow but steady. The weight of the normal controls shows either steady increase or slight fluctuation but never a progressive decrease. Examples of the weight curves are shown in figures 10, 11, 12 and 13.

Bodily temperature records of all the operated birds under observation show on the whole neither a tendency to a lower or higher temperature, nor a greater fluctuation from day to day, when kept in a room of more or less even temperature.

Regarding the question of maintenance of life, I may mention that the first series of birds, which had the oil gland removed, has been under observation for 195 days up to the time of writing. Although they showed marked derangement of the contour of the plumage, with discoloration, shedding of feathers, lack of the usual luster and cleanliness, and gradual loss of weight, with a few exceptions they continue to live and do not behave abnormally. Two died rather suddenly almost a hundred days after operation. Autopsy findings revealed enlarged liver with marked congestion of most of the abdominal organs. The liver of one, a pigeon, was three times the normal size /

size. The other bird, a hen, had impacted, old, calcified eggs and a hematoma in the egg sack. Both appeared to have died of general weakness. A third, a duck, showed marked "leg weakness" and severe ophthalmia two weeks before it died with progressive loss of weight and general weakness. Sections of the organs showed considerable cellular infiltration in the liver and pancreas. X-ray of the leg-joints however showed no definite sign of decalcification (Fig. 14). The symptoms and findings are somewhat suggestive of those of rickets in birds.

EXPERIMENTS ON YOUNG CHICKS.

The young chicks were taken to the laboratory when they were eight days to two weeks old and were put on a diet of crushed yellow corn and wheat and whole milk with coarse sawdust. Four of these had the oil gland removed after they had been in the laboratory for two weeks. Four were kept as controls, and all of them were placed in a room with double glass windows and away from direct sunlight. In the course of three weeks they all developed typical symptoms of rickets with marked "leg weakness" and roughness of plumage. They were listless, inactive, straddling and awkward in gait, squatting frequently. Their feathers also were poorly developed, and became loose. The leg and toe joints showed considerable enlargement. Two of each series died suddenly. X-rays of the joints show poor calcification but enlargement with much soft tissue. (Fig. 24) Though their feathers /

feathers contained much "oil" at the time of death they could not utilize it.

The rest were then irradiated with a mercury vapor lamp of 4 inches gap for five minutes daily at a distance of 3 feet from the quartz tube. After ten days the chicks with the oil gland began to show marked improvement in general appearance and in the growth of plumage. They had a steadier gait and greater alertness and were more active and did not squat so much. The chickens without the oil gland showed practically no improvement, and the increase in weight was less in these than in the controls.

EXPERIMENTS ON FEATHERS.

Physical phenomena. - "Grease" lowers surface tension. This is true with the "grease" on feathers. I have noted that in the case of normal feathers when placed on water the individual plumules quickly spread out and flatten down evenly on the surface of the water, while in the case of feathers previously treated with ether and chloroform or methyl alcohol for removal of "fat", or feathers taken from an operated bird after a month or two after operation, the plumules spread out very slowly and it takes a long time for such feathers to rest evenly on the surface of the water. The difference can be explained as due to the presence or absence of "oil" in the feather. Herein lies the explanation of the fact that water penetrates more easily /

easily and deeply through the feathers to the skin when the former are devoid of "oil." Then the usually smooth layer of relatively "impermeable" plumage is disturbed and crevices formed between the individual feathers allowing water to pass through. This is in accord with the "feather film" idea of Stubb (1910), who believed that a well arranged pile of cilia and barbules when spread out serve to prevent the "coarse touch of the hard feather" against the surface film of water.

Changes in weight when treated with chloroform and methyl alcohol. - The primary purpose was to make a "fat-free feather" for determining its behavior toward water. But some unexpected changes which took place during the extraction led me to investigate whether the operated and control feather would behave differently during the process of "extraction."

First I dried a bundle of feathers, which had been tied together, in a calcium chloride desiccator for twenty-four hours, and then weighed it. After weighing, the bundle was put in a reflux condenser and "extracted" with a mixture of $\frac{1}{3}$ methyl alcohol and $\frac{2}{3}$ chloroform, placed in a bottle which was heated in a water bath on an electric hot plate. The process of "extraction" was continued for twenty-four hours. When this was completed, the feather was removed from the condenser, dried in the air and then in the calcium chloride desiccator for twenty-four /

twenty-four hours and afterwards weighed. There was a definite increase in weight. In order to exclude the possibility of this being due to inadequate drying, a more drastic method of drying was employed.

The feather was first dried by putting it in a drying incubator with a temperature ranging between 55° and 60° C. The extraction was made with chloroform or methyl alcohol alone. After the extraction the feather was again put in the drying incubator for forty-eight hours, when a stationary weight was obtained. The results showed that in feathers taken from a normal bird there is a decrease in weight upon treatment with chloroform or methyl alcohol, while in the feathers of an operated bird there is an increase in weight.

Table I.

	With chloroform							With methyl alcohol
Source of feather	Control bird				Operated bird			Control bird
No. of exp. bird	No. *131	No. 116	No. 174	No. 110	No. *130	No. 173	No. 108	No. 116
Orig. wt. mg.	829	613	726	1315	924	800	1136	608
Wt. after treatment	774	583	694	1255	949	819	1156	579
Loss %	6.6	4.9	4.4	4.6	-	-	-	4.8
Gain %	-	-	-	-	2.7	2.4	1.8	-

* 64 hours "extraction" - others 24 hours.

The table above shows that there is always a loss of weight in the feathers from the control bird. The percentage loss is fairly constant when the time allowed for the treatment is the same. With longer time for "extraction" the percentage loss is considerably increased, while with the operated birds there is always an increase in weight. The time factor thus plays a part in the percentage weight increase. The actual significance of this I cannot go into at present, but suffice it to suggest the following possibilities:-

(1) A chemical action between the chloroform or methyl alcohol and the substance on the feather may have resulted in the formation of a compound which remains attached to the feather. The presence of oil interferes with this action.

(2) The chemical reaction may have progressed to the same degree but the loss of weight is to be explained by the fact that a large quantity of the oil had been removed and only a small quantity of the newly formed substance had resulted.

I have excluded the possibility of a mere adsorption of the extracting substance to the feather by prolonged heating in a dry incubator kept at 55° to 60°C. for two to three weeks. No change in weight took place after the first week. Further in favour of the chemical reaction is the fact that during the first three or four days there is a steady increase in weight of the feather the longer the process of extraction is continued.

Change in weight by immersion in water. - When a bundle of clean feathers is immersed in water for some time and then dried, there is always a loss in weight, no matter whether they are feathers taken from a normal bird or from a bird with the oil gland removed some months previously, or feathers that have been treated with chloroform or methyl alcohol. The percentage loss varies considerably in various conditions but apparently something has been dissolved by the water. What it is remains to be determined. It is certain however that this is not due to a loss of the "oil" globules on the feather, since no reduction in the number was seen under the microscope after the feather had been immersed in running water for twenty-four hours. Part of the loss in weight undoubtedly is due to the disappearance of some fine dust attached to the barbules of the feathers.

Permeability to water. - In order to determine whether water soaks into the interior of the barbules and cilia I submitted some normal feathers to staining with a water solution of methylene blue for an hour and then thoroughly washed them in running water for two hours, after which I examined them under the microscope. This treatment reveals the presence of a considerable amount of dye in the interior of the barbules and barbs and also the cilia, showing that the feather is quite permeable to water.

Furthermore it is generally known that if one immerses a feather in water for any length of time, it becomes soaked.

I took a bunch of feathers, weighed it and then immersed it in water for fifteen minutes. They appeared quite wet. On weighing them after they had been dried for varying intervals I obtained the following results:-

Table II.

	Feather, Control bird	Feather, Operated bird
Original weight in mg.	352	505
*Weight after drying for 15 mins.	701	899
" " " " 30 "	430	598
" " " " 60 "	361	518
" " " " 24 hrs.	351	500
" " " " 8 days	349	498

*After having been immersed in water for 15 minutes.

Intake and output of moisture. - Having determined the permeability of feathers to water I proceeded to find out the behaviour of feathers toward a moist atmosphere when they are thoroughly dried, and to a "dry" atmosphere when saturated with moisture. I took a bunch of feathers and dried it in a drying incubator heated to 55° to 60° C. for twenty-four hours. The weight was now determined and the feathers next placed in a glass jar completely saturated with water vapor. The whole was kept at a temperature of 21°C. throughout the experiment. At various intervals the feathers were taken out and weighed in a weighing bottle, tightly stoppered. Results of some of the

experiments are tabulated as follows:-

Table III.

	Control bird feathers			Operated bird feathers		
No. of bird	131a	131b	110	130a	130b	108
Original wt. in mg.	829	826	1318	899	896	1122
Wt. after exposure - 2 min.	-	856	-	-	920	-
" " " 3 "	857	-	-	941	-	-
" " " 5 "	867	870	1356	956	939	1160
" " " 10 "	887	884	1374	975	960	1179
" " " 15 "	893	903	1389	980	972	1192
" " " 20 "	896	910	-	983	983	-
" " " 25 "	899	-	-	984	-	-
" " " 50 "	-	-	1644	-	1025	1245
" " " 60 "	939	952	-	1027	-	-

After the feathers had been saturated with water vapor I exposed them to air and weighed them similarly in a weighing bottle at different intervals. The following table shows some of the results obtained:-

Table IV.

	Control bird feathers			Operated bird feathers		
No. of bird	131a	131b	110	130a	130b	108
Original wt. in mg.	939	952	1644	1027	1025	1245
Wt. after exposure - 2 min.	916	924	-	997	1004	-
" " " 5 "	903	905	1422	980	992	1222
" " " 10 "	890	891	1412	968	983	1210
" " " 15 "	883	883	1405	960	978	1204
" " " 20 "	878	879	-	955	975	-
" " " 25 "	-	-	-	-	-	-
" " " 30 "	873	-	-	949	-	-
" " " 60 "	-	868	-	-	966	-

The same phenomenon occurs with feathers after being immersed in water for twenty-four hours or having the oil extracted with chloroform or methyl alcohol for the same period of time. Longer periods of exposure to a moist or dry atmosphere showed a very slow but progressive increase or decrease in weight respectively up to a certain point, when no more moisture could be taken up or given off. This equilibrium was reached in about forty-eight hours under the above experimental conditions.

The results show that the increase or decrease of weight was at first quite considerable but very soon it became smaller. If one plots the percentage loss or gain in weight per unit time as ordinates against time as abscissae, one gets a curve of the exponential type. The exact significance cannot be discussed here but suffice it to say that the feathers with oil behave in an exactly similar way to the feathers without oil with respect to the intake and output of moisture by them.

MAINTENANCE OF THE FEATHERS.

Whether the oil is necessary for the maintenance of the integrity of feathers is rather difficult to say. It is true that lack of oil does not result in destruction of the individual feathers, although birds that have been without the oil gland for four or five months show feathers having the veins disarranged, with gaps between, and small holes in them.(Fig. 15).

Microscopically the "holes" are due to the absence of the barbules, which have disappeared in patches from the barbs (Fig. 16). In several cases the feathers became loose and were shed or often plucked out by other birds. This may be explained by the fact that when the birds cannot strip any more "oil" from the feather, they adopt the more vigorous measure of removing patches of the barbules in order to get what little oil there is in the interior of them. One cannot however exclude the possibility of an actual structural change which prepares the way for destruction. Further in support of this view there is the disappearance of the usual brilliant colors of the plumage. According to Beebe (1907) changes of color in the plumage may take place either "(1) by a moult during which the new feathers may have the same pigmentation as their predecessors or a different one, (2) by a loss of certain portions of the feather, or (3) by a physical disintegration in the cortex of the feathers as the result of exposure." The change noted here in the feathers of birds without the gland is not due to the first cause. It appears therefore that there is also a structural change in the feather.

THE OIL-GLAND IN RELATION TO VITAMIN D.

That birds spread the secretion from the oil gland on to the feathers in the process of "preening" is well known. As mentioned above, an accurate description of the act was first

given by Hussey in 1860, and later by Mathews in 1861. The microscopic appearance of the "oil" droplets in an unstained or stained specimen of feather and their actual presence is here described by the writer for the first time.

The fact that they disappear from birds whose oil gland has been removed some time previously implies in the first place that the oil gland serves as the only source of the"oil" droplets, and in the second place that they are removed in some way. This removal, I believe, is accomplished by the birds themselves in the process of "preening". By close examination one can quite often see that the birds place the two blades of the beak to either side of a feather and then move them in such a way as to scrape off anything adhering to the veins. This is then followed by further motion of the blades of the beak and an act of swallowing, indicating that something has been taken in by the beak and eaten.

Cholesterol in the oil gland and feathers. - My first object is to find out if the gland secretion contains cholesterol, and next if the feathers also contain the same thing.

The secretion of the oil gland can be obtained easily by applying pressure to the sides of the lobes of the gland. The substance that emerges may have the appearance of a brown paste or a limpid straw-colored fluid.

I took some of the secretion and dissolved it in chloroform. With the Liebermann Burchard test I found the solution was

invariably strongly positive for cholesterol. Next I immersed a bunch of feathers in chloroform for two to four days and applied the same test for cholesterol. The reaction was again strongly positive.

I then proceeded to isolate the pure substance cholesterol from a number of oil glands and also from a large bundle of feathers. This was done by extracting from them first with boiling acetone with the aid of a reflux condenser for eight to ten hours. The acetone was then distilled over. To the residue was added a 5 per cent. alcoholic solution of potassium hydroxide. The mixture was boiled for six to eight hours and then poured into distilled water. From the product I extracted with several portions of chloroform by shaking the mixture in a separating funnel. The chloroform extract was then purified with blood charcoal and filtered several times. The filtrate was evaporated to dryness. The residue was then dissolved in boiling alcohol, filtered and crystallized in cold alcohol at 0°C.

An ether solution of the crystals gave the characteristic absorption bands in a spectrum for cholesterol when the photograph was taken with the light from a carbon arc lamp or mercury vapor lamp according to the technique employed by Bills, Honey and MacNair (1928).

Biological tests. - Having found cholesterol present in both the gland and the feathers of the birds, I proceeded to

feed a pigeon from which the gland had been removed and which had developed marked weakness and loss of weight with an irradiated gland removed from another pigeon. The pigeon began to put on weight soon after the feeding (Fig.10), and subsequently became stronger and more active with great improvement in general appearance and in the plumage (Figs. 17, 18 and 19). Another pigeon without the oil gland was fed with an oil gland which had been placed in the dark immediately after its removal. No change in weight or general health was noted.

Moreover, I may add that my ablation experiments and experiments with young chicks tend to show that removal of the oil gland from birds results in the development of rickets, which never happens in the case of birds with the oil gland intact, though kept under the same conditions.

I have also carried out the usual line test experiment with young rats fed on McCollum's 4026 diet after rickets have definitely developed. I fed the rats in one set with feathers and in another set with the extract of the feather, and in a third set with extract of the gland, with adequate controls. Up to the time of writing the animals have not been fed long enough to show the specific results of the test, but already those fed with feathers and feather extract are showing improvement in general appearance and more rapid increase in weight.

Supporting this view is a recent note by William Rowan in "Nature" (March 3rd, 1928). He noted that young hawks and owls

died of rickets before attaining maturity, when given adequate meat diet and sunlight, but they grew up normally if mice and sparrows or chicken's heads complete with feathers were added to their diet. The only essential difference between the new diet and the old was the inclusion of feathers.

He stated also that merlins (Falco columbarius oesalon) in feeding their young had from time to time added feathers to the regular plucked bird meat, apparently as a kind of "medicine". Rowan suggested that there may be some relation between the oil gland and the formation of vitamin D, though he was not certain of this.

Previous observations. - Further study of the literature on the subject reveals that Hansemann in 1906 pointed out that cats do not develop rickets, whereas dogs do, and he believed that this is due to the fact that cats have a tendency to prey upon birds and rodents, thus supplementing a rather restricted diet and escaping rickets. He however did not attribute this result to eating of the feathers of birds or the skin of rodents, but believed that it is the glandular organs and soft bones which supplement the diet.

Cheadle and Poynton (1908) called attention to the fact that cubs in the London Zoo were fed with horse flesh alone and invariably died from extreme rickets.

According to McCollum and Simmonds (1925) it is now the practice in the American Zoo in rearing young carnivora to

supply them with liver, flat bones, together with fat, and at intervals of a few days to give them rabbits or small birds, such as pigeons. These are consumed entirely. Confinement then does not seriously interfere with their successful development under these conditions of feeding.

Jost and Koch (1914) state that rickets was extremely common among young carnivorous animals in zoos and circuses, but is less common since those in charge have adopted a more rational system of feeding.

From the evidence given I incline to believe that there is a definite relation between the secretion of the oil gland and the elaboration of vitamin D. I do not think for a moment however that the bird depends on this as the only source of its vitamin D supply, but that the oil gland serves as a reserve for extra cholesterol, as the chalk glands of the frog for extra calcium. The feathers in turn serve as a means for displaying of the cholesterol to secure a maximum irradiation by sunlight for its conversion into vitamin D.

CONCLUSIONS.

1. My studies on the structure of the gland confirm those of previous workers, except in one point which was not generally agreed upon, namely, the presence or absence of elastic fibers in the capsule and the septa. My observation is that there are no elastic fibers, or only very few.

2. Ablation experiments along with careful isolation and comparison with normal controls reveal that birds without the oil gland suffer a progressive impairment of general health, discoloration of the plumage, "deterioration" of the individual feathers, loss of an efficient means of heat protection, and gradual loss of weight. Some birds without the gland eventually died exhibiting symptoms and signs suggestive of rickets.

3. Chicks with the oil gland intact, after developing rickets on a rachitic diet, improved rapidly on daily irradiation with a mercury vapor lamp. Chicks with the oil gland removed, when treated in the same way, showed very little or no improvement.

4. Presence of oil droplets on the feathers is demonstrated microscopically for the first time as lying mainly between the barbs and barbules, only being present however in very small number in their interior. Removal of the gland results in a depletion of oil droplets on the feathers. This seems to account for the changes in the coloration of the plumage, in the chemical behavior toward chloroform and methyl alcohol, and in the smooth contour of the feathers.

5. The disappearance of the oil droplets from the feathers is believed to be due to the fact that birds take them off and eat them by means of the beak.

6. It is proved that feathers are definitely permeable to water, no matter whether there is oil in them or not. They take up water steadily though slowly. Graphs of the intake and output of moisture by feathers per unit quantity per unit time, when they are exposed to a moist or dry atmosphere respectively, are of the exponential type.

7. Absence of "fat" from the feather appears to be related directly or indirectly to some changes in the structure of the feather.

8. The oil gland of birds contains a fair quantity of cholesterol. A large quantity of the same substance can be recovered from the feathers, especially those of hens, ducks and geese.

9. Results obtained with biological tests on rats and "rachitic" birds indicate the possibility of the presence of vitamin D in the feather after being irradiated by sunlight or a mercury vapor lamp. Previous observations suggestive of this view are discussed.

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EXPLANATION OF PHOTOGRAPHS.

Fig. 1. Cross section of the oil gland of duck, photographed under high power magnification, showing secretion masses in lumen of tube, glandular epithelium and intertubular connective tissue septa.

Fig. 2. Gross appearance of the glandula uropygialis of a goose. Actual size.

Fig. 3. Section of the oil gland of hen showing the connective tissue septa becoming wider toward the gland cavity.

Fig. 4. Cross section through the middle of the nipple of the oil gland of a hen, photographed under lower power magnification, showing the two ducts surrounded by smooth muscle fibers and connective tissue.

Fig. 5. Duck, No. 109, before operation, showing plumage smooth and glossy.

Fig. 6. Same duck, 1½ months after operation, showing feathers ruffled and dull.

Fig. 7. Same duck, 4½ months after operation, showing feathers in worse condition than before, with a number of neck feathers lost through shedding or being plucked by other operated birds.

Fig. 8. Microphotograph under low power magnification of feather from a control bird, showing spaces in between the barbules filled with lumps of "oil" stained with Sudan III.

Fig. 9. Similar photograph of the feather from an operated duck, two months after operation. The spaces between the barbules are clear. The feather is devoid of "oil" droplets.

Fig.10. Weight curves of pigeons, plotted with weights in gm. as ordinates against time in days as abscissae.

Continuous line indicates weight curve of control pigeon, No. 171; broken line, of operated pigeon, No. 172. The first arrow along the abscissa indicates the day of operation and the second arrow the day of feeding with an irradiated oil gland removed from another pigeon.

Fig.11. Weight curves of white ducks plotted with similar particulars as Fig. 10.

Continuous line indicates weight curve of control duck, No. 112; broken line, of operated duck, No. 111. The arrow indicates when the operation was performed.

Fig.12. Weight curves of domestic hens plotted with particulars similar to Fig. 10.

Continuous line indicating weight curve of control hen, No. 152; broken line with circles, of operated hen, No. 150; broken line with crosses, of operated hen, No. 151. The arrow along each curve indicates the day of operation.

Fig. 13. Weight curves of domestic drakes.

Continuous line indicates weight curve of control drake, No. 110; upper broken line, of operated drake, No. 109; lower broken line, of operated drake, No. 108. Other particulars as Fig. 12.

Fig. 14. X-ray photograph of the knee-joint and toes of operated duck, No. 111, after death, showing normal appearance of the bones.

Fig. 15. Upper row, feathers from a control duck, No. 110. Lower row, feathers from a duck, No. 108, which had its oil gland removed four months previously.

Fig. 16. Microphotograph of feather of a duck without oil gland for 4½ months, under high power magnification, showing absence of patches of barbules.

Fig. 17. Operated pigeon, No. 172, 1½ months after operation. Note rough appearance of feathers and listless attitude.

Fig. 18. Control pigeon, No. 171.

Fig. 19. Operated pigeon, No. 172, 2½ months after operation and 10 days after feeding with an irradiated gland removed from another pigeon, showing alertness and smooth appearance of feathers again.

Figs. 20 and 21. Showing temperature changes caused by moderate swimming in cold water (10°C.) for 10 minutes.

Graphs are plotted with temperature in degrees Centigrade as ordinates, against time in minutes as abscissae. Continuous line indicates temperature of control duck; broken line, temperature of operated duck. The figures at the end of the curves indicate the numbers of the experimental ducks.

Fig. 22. Showing temperature changes caused by moderate swimming in cold water (10°C.) for 7 minutes. Graphs plotted

with particulars as in Fig. 20.

Fig. 23. Showing temperature changes caused by vigorous swimming in cold water (10°C.) for 7 minutes. Graphs plotted with particulars as in Fig. 20.

Fig. 24. X-ray photograph of the legs of a chick with symptoms of rickets, showing poor calcification at the ends of bones.

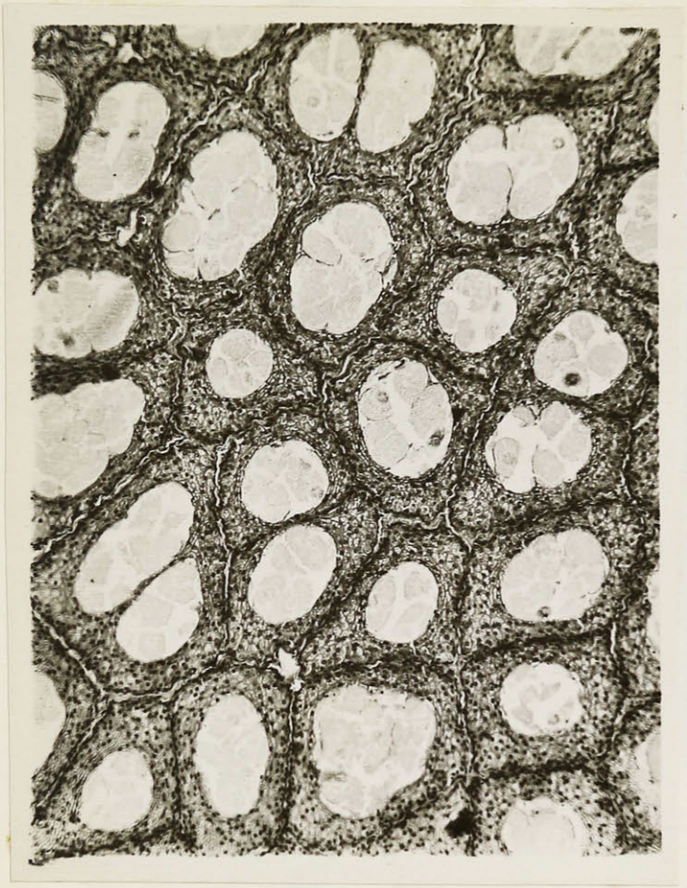


Fig. 1.

Fig. 3.

Fig. 2.

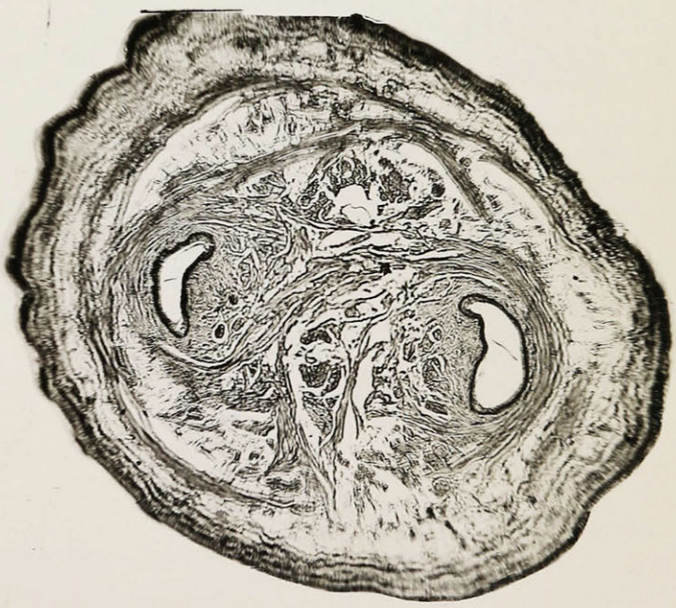


Fig. 4.

Fig. 5.

Fig. 6.

Fig. 7.

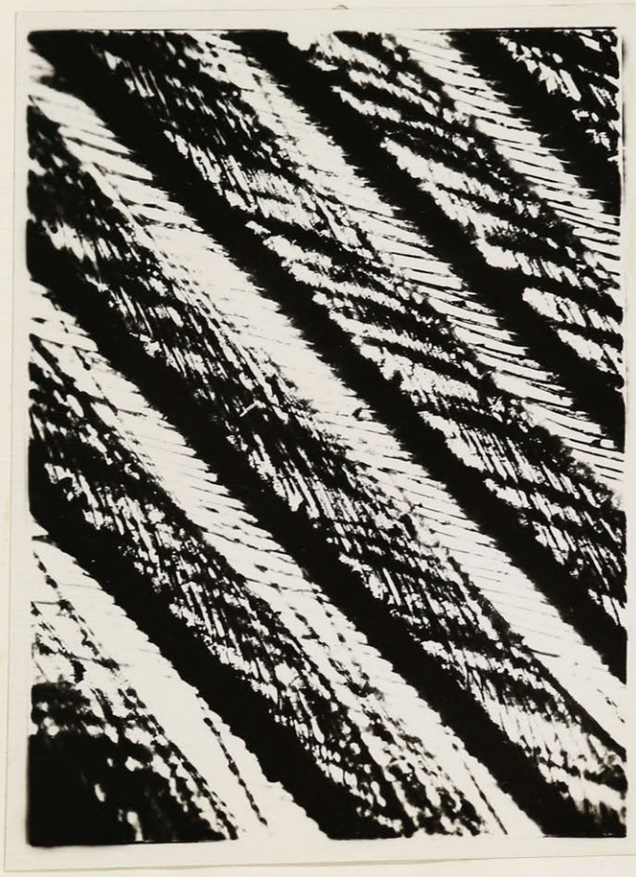


Fig. 8.

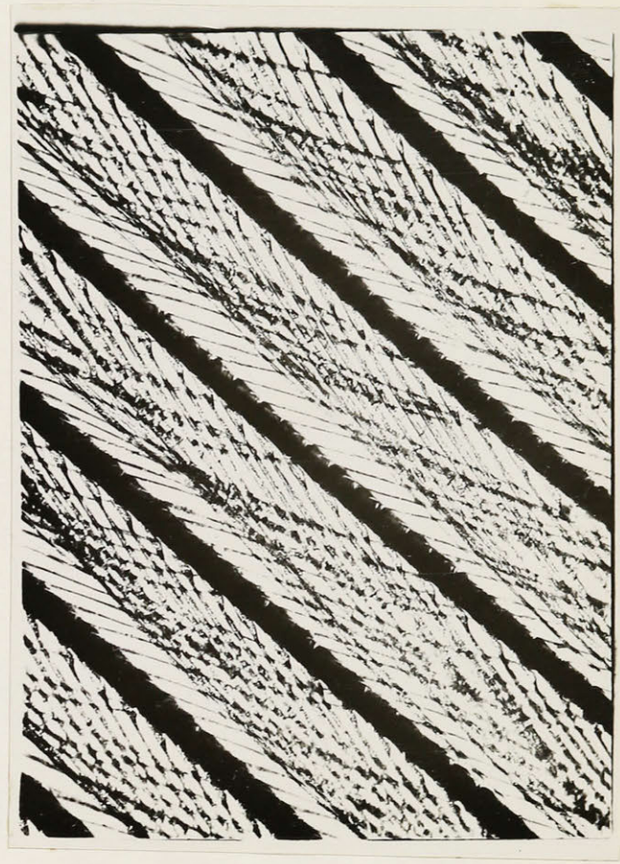


Fig. 9.

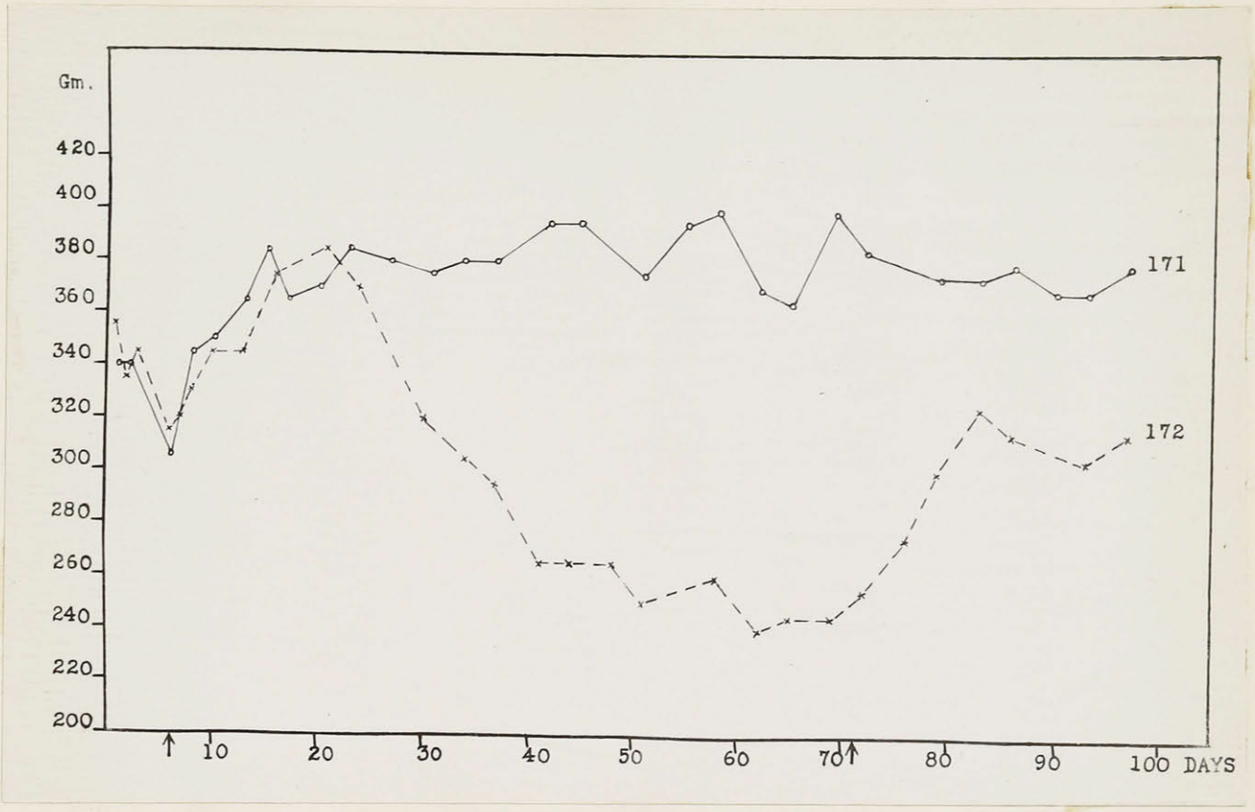
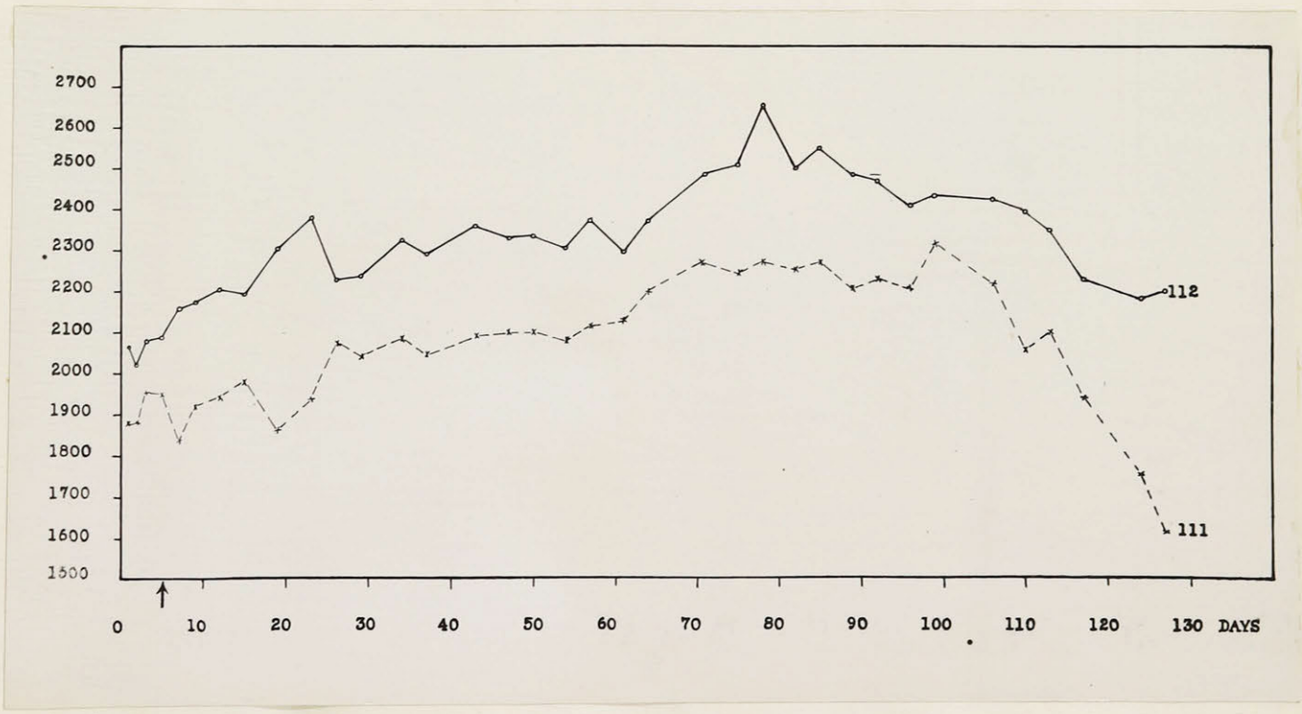

Gm.
420
400
380
360
340
320
300
280
260
240
220
200
10
20
30
40
50
60
70
80
90
100 DAYS
171
172

Fig. 10.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1900
1800
1700
1600
1500
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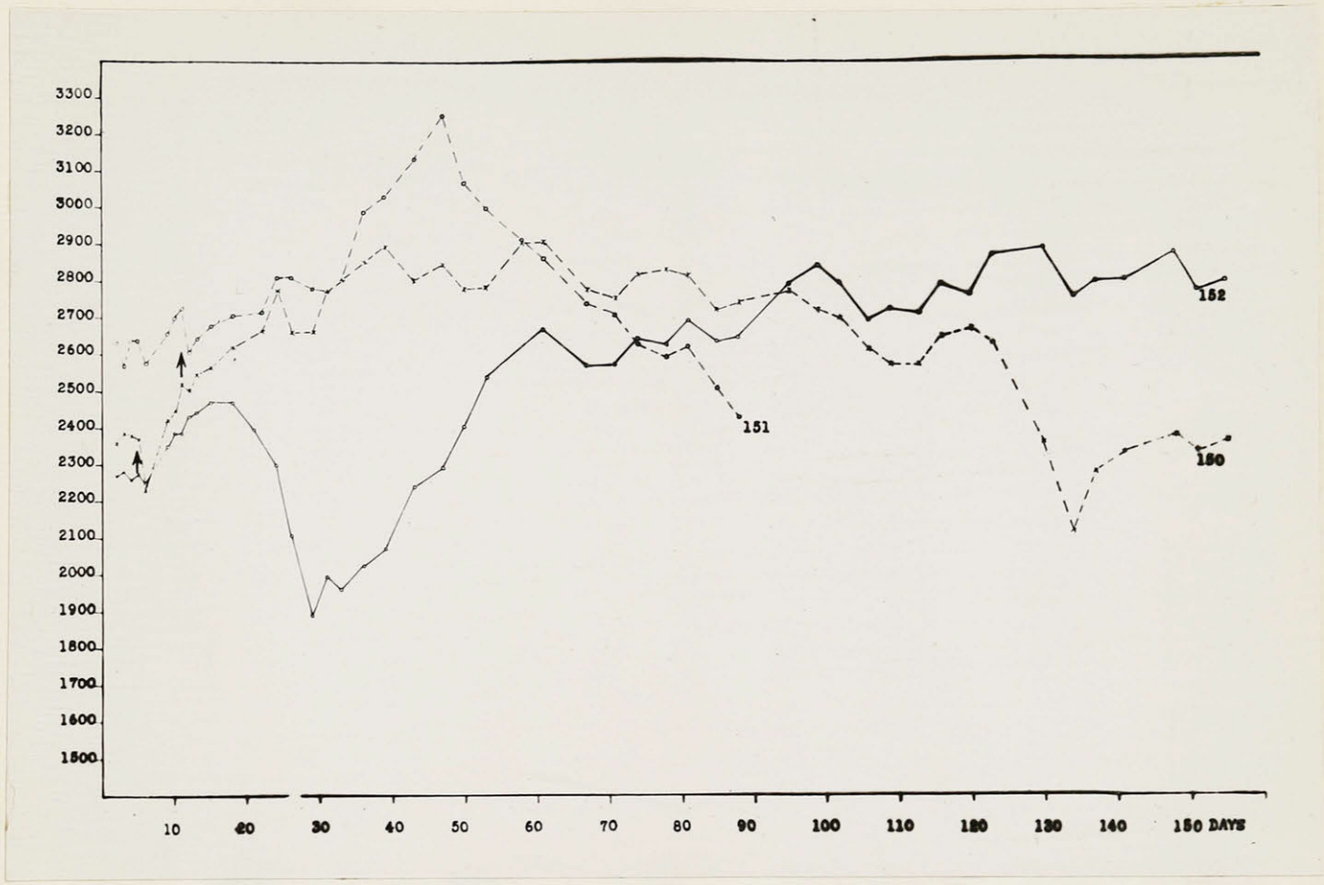
20
30
40
50
60
70
80
90
100
110
120
130 DAYS
112
111

Fig. 11.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1900
1800
1700
1600
1500
10
20
30
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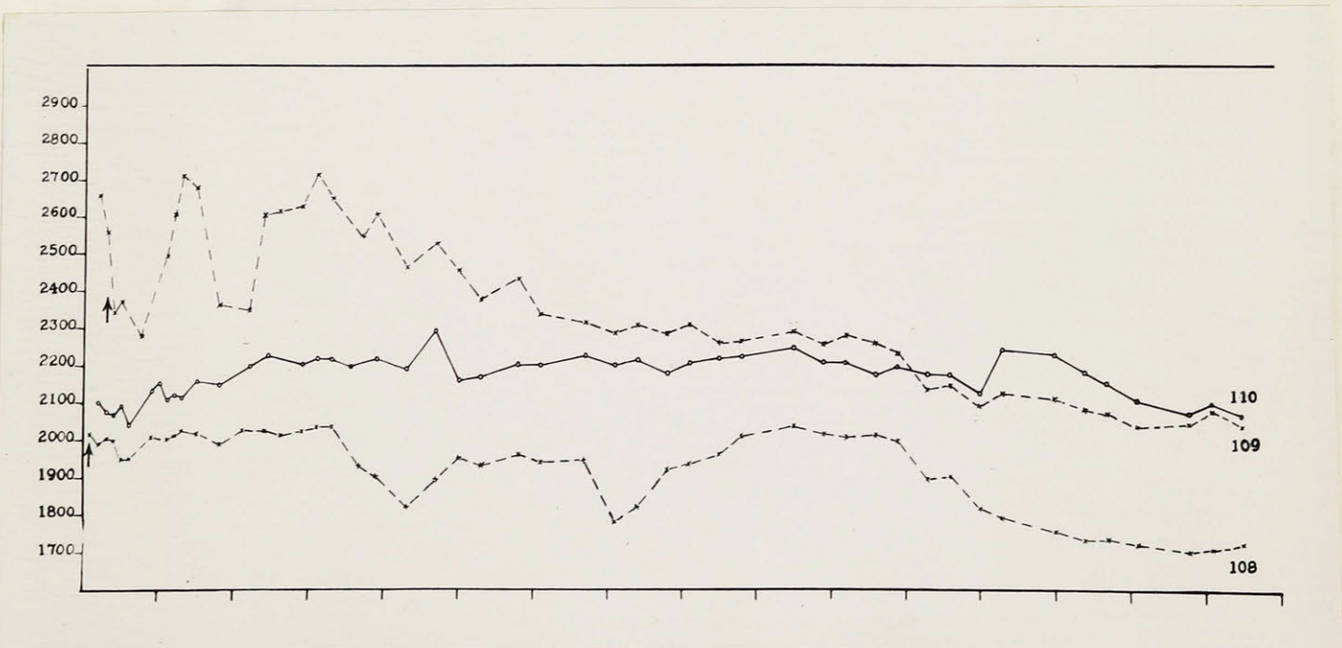
50
60
70
80
90
100
110
120
130
140
150 DAYS
152
151
150

Fig. 12.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2200
2100
2000
1900
1800
1700
110
109
108

Fig. 13.

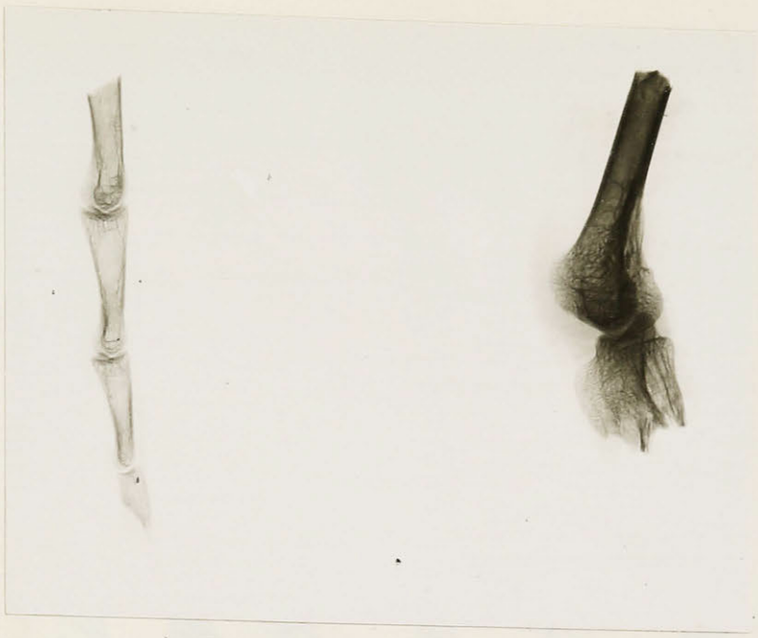

Fig. 14.

Fig. 15.

Fig. 16.

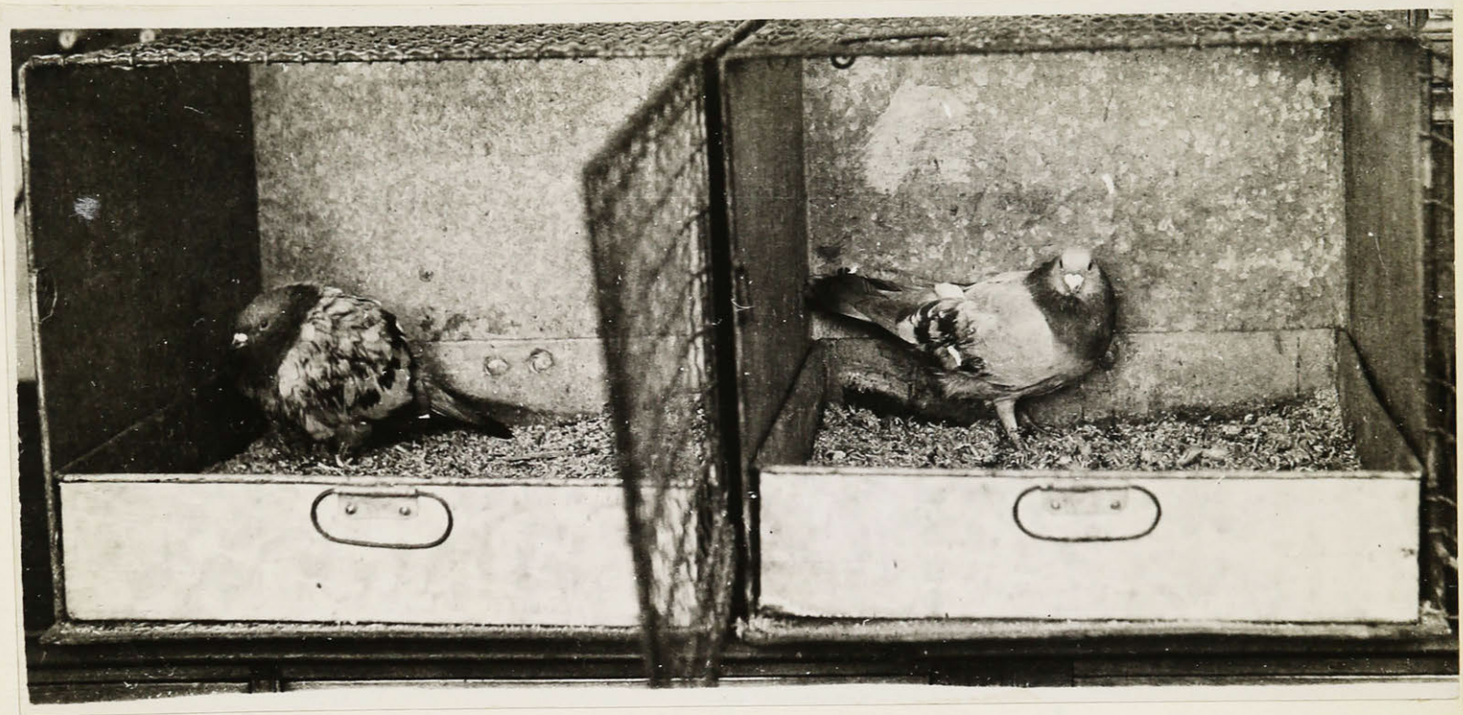

Fig. 17.

Fig. 18.

Fig. 19.

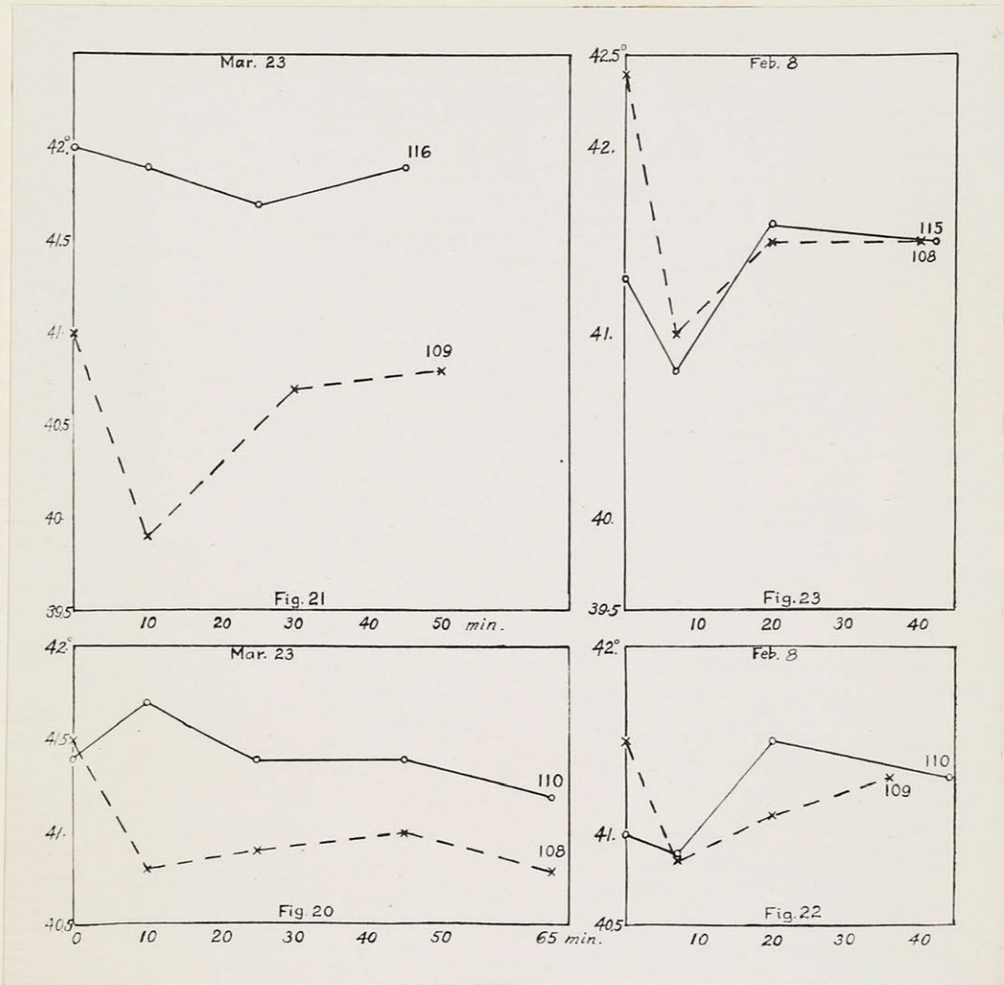
Mar. 23
42°
41.5
41
40.5
40
39.5
116
109
Fig. 21
10 20 30 40 50 min.
Feb. 8
42.5°
42.
41.
40.
39.5
115
108
Fig. 23
10 20 30 40
Mar. 23
42°
41.5
41.
40.5
110
108
Fig 20
0 10 20 30 40 50 65 min.
Feb. 8
42°
41.
40.5
110
109
Fig. 22
10 20 30 40

Fig. 20-23.

Fig. 24.