THE REPRODUCTIVE CYCLES OF THE BRITISH AND CONTINENTAL RACES OF THE STARLING (*STURNUS VULGARIS* L.)

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CONTENTS

Accounts are given of the detailed structure of the reproductive systems of male and female starlings (*Sturnus vulgaris* L.). It is shown that there are differences between the sedentary British starling and the migratory Continental bird in the seasonal variations of these systems. The gonads of the first-year British and Continental starlings begin to grow in February. but the rate of growth in the British bird is greater than that in the Continental. The gonads of the adult British starlings do not regress so far in summer as those of the Continental birds, and they start to grow precociously in early autumn. The gonads of the adult Continental starlings do not begin to grow until January or February, the time when the gonad growth of the British birds is accelerated. In February and March the gonads of the adult British birds grow much more rapidly than those of the Continental birds.

These differences in the degrees of regression and in the times and rates of growth of the gonads of the British and Continental starlings are reflected in the accessory sexual organs. In the adult British males the rete testis and vas deferens show signs of growth in autumn, and although the other accessory sexual organs, apparently requiring a higher rate of sex-hormone secretion, do not begin to grow until January or February, their growth is earlier and faster than that of the accessory sexual organs of the Continental birds. In the adult British female the oviduct enlarges in autumn, and in some individuals the various organs of the Wolffian system also show signs of growth. It is apparent

that the ovary of the adult British female in autumn secretes both male and female sex hormones, but the amount of male sex hormone secreted by different individuals is very variable.

The secondary sexual characters of the starling are either permanent or vary according to the state of the reproductive cycle. The browner colour of the iris of the male and the yellowish colour of that of the female are permanent distinguishing characters, and, in addition, the throat and breast feathers of the first-year or adult male are narrower and more pointed than those of a female of the same age. The colour of the beak is a varying secondary sexual character. Owing to the secretion of male sex hormone by the testes and ovaries of the adult British starlings in autumn, the beak turns from dark grey to yellow during this season. No similar change in the beaks of the Continental birds is noted until January or February. When the beak is yellow, a grey base to both mandibles is a distinguishing feature of the male.

The behaviour of both races of birds was studied, and it was found that, coincident with the growth of the gonads in autumn, the adult British starlings showed sexual behaviour and close attachment to their nesting sites. The habit of roosting in nest-holes is seen all the year round in some birds of this race, and it becomes almost universal in early January. No similar behaviour was seen in the Continental birds in this country, and none is described in the case of those birds which remain on the Continent. At the end of February, when the gonads of the Continental starlings are actively growing, the males begin to sing, the northward migration commences, and on the Continent interest in nesting sites is first reported. The question of the relation of several aspects of bird behaviour to the activity of the gonads and the secretion of sex hormones is discussed.

It is evident that, as these two distinct races of starlings live together in the British Isles in autumn and winter, the differences in their reproductive cycles must be inherent and not dictated by environmental variations. The question of physiological species and subspecies is discussed, and on the basis of the differences described in this paper, it is proposed to rename the British race of starlings as *Sturnus vulgaris britannicus*.

I. INTRODUCTION

Marked differences in the degrees of development of the reproductive systems of starlings (*Sturnus vulgaris* L.) present in the British Isles in autumn and winter were first noticed by Rowan (1937, 1938). He found that the gonads of London birds in February were considerably larger than those of similar birds taken in the country at the same time, and he interpreted this fact as indicating that the disturbance due to the lights and traffic of the town caused a precocious development of the gonads of those birds which were nightly subjected to it. This conclusion was immediately criticized by reviewers (*Ibis*, ser. 14, **2**, 787) on the grounds that other interpretations could also be made to fit the facts, and indeed Bissonnette (1931) had already shown experimentally that it is impossible to induce precocious sexual development in the starling by means of nightly disturbance alone.

Investigations preliminary to those recorded here were made (Bullough & Carrick 1939, 1940), and these suggested that the starlings taken by Rowan in London were of a British race whereas, by chance, those taken in the country were winter immigrants from the continent of Europe. Although it is not possible to distinguish the British from the Continental bird by any constant external morphological feature, it was suggested that it would be necessary, if the results were substantiated, to consider these two types of birds as subspecifically distinct. Apart from Rowan's researches and some observations by Morley (1939, 1941) on the sexual behaviour of the starling, no work bearing on the problem appears to have been done in this country. In the United States of America, Bissonnette (1930*a*, *b*, *c*), Bissonnette & Zujko (1936), and Hart (unpublished) have given some account of the reproductive cycle of the European starling which has been introduced into that country, and an interesting description of the development of the secondary sexual characters has

been given by Witschi & Miller (1938). Even collectively, however, these studies are not in any way exhaustive, and the accounts of the starling in the United States do not necessarily apply to the bird as it is in this country.

An attempt has been made therefore to produce as complete a study as possible of the reproductive cycles of the starlings found in the West Riding of Yorkshire, and this study has included some consideration of the secondary sexual characters and of behaviour. Extensive field observations on the general biology of the starling have been made concurrently with this study of the reproductive cycle, and such matters as the migration, roosting, and nesting habits of the bird have been worked out in detail. In the present paper, however, reference is only made to such of these habits as directly affect the arguments put forward. The war has finally put an end to this work, and it is, in many particulars, not as comprehensive as had been hoped. However, the descriptions are fairly complete, and it has been possible to form a final conclusion on the question of whether the British starling is a subspecies of the European bird.

II. MATERIAL AND METHODS

(1) Material and its source

The results here recorded are based on the examination of 786 starlings taken at all times of the year between March 1939 and February 1941. Especially large numbers (585 birds) were obtained during the autumn and winter,* when the starling population of the British Isles is partly of British and partly of Continental origin. The remaining birds were taken in spring and summer when only British starlings are present in this country. All the birds, which were shot either with a 0·22 in. rifle or a 12-bore shot gun using number 7 shot, came from the West Riding of Yorkshire. They were mainly taken in Leeds, at Beamsley in Wharfedale, at North Deighton near Wetherby, at Askham Bryan and Rawcliffe near York, and at Dunsop Bridge near Slaidburn, but smaller numbers were also obtained from various other localities. The birds were mainly shot in the large communal roosts which are established in woods and plantations, but many were also shot either singly or from flocks feeding in the fields. They were obtained at various hours of the night as well as of the day. Nestlings were not examined.

(2) Histological methods

All the birds were dissected as soon as possible after death, but the length of time which elapsed before the gonads were fixed varied somewhat according to the distance which the birds had to be carried to the laboratory. At some of the shoots most distant from Leeds a few gonads were fixed immediately as a check on the condition of the others which were fixed perhaps as much as 2 hr. later. In practice it was found that a lapse of time of up to 2 hr. between death and fixation did not seriously affect the microscopic condition of the gonads, and in the majority of cases where fixation was not immediate it was carried out within this time limit. The method of dissection was to remove the alimentary canal, and to cut out a piece of the back of the bird on which were situated the cloaca, the kidneys

* Throughout this paper these terms are used in a strict sense. Spring is from 21 March to 20 June, summer from 21 June to 20 September, autumn from 21 September to 20 December, and winter from 21 December to 20 March (see Baker 1937).

and kidney ducts, and the gonads and gonoducts. The dissection in this way of a whole piece of body wall made possible the preservation of the finest ducts in an undistorted condition. The feathers were plucked from the back of the piece so dissected, and it was then fixed whole in Bouin's fluid for 2 days. After this it was washed and stored in 70% alcohol, and any parts required for sectioning were cut off and embedded in paraffin wax. Sections of the gonads and their ducts were cut to a thickness of 7μ and stained as follows. The testes with the epididymes were cut transversely, stained in Heidenhain's iron haematoxylin, and counterstained with van Gieson's stain. The ovaries with the epoöphoron were cut longitudinally and stained in a similar manner. Serial transverse sections were also cut of the gonoducts and cloacae, and these, also stained in Heidenhain's iron haematoxylin, were counterstained in Masson's triple stain.

(3) Gross measurements of the gonads

The simplest method of comparing the testes of the British male starlings with those of the Continental birds was by measuring their volumes. As many of the testes were extremely small it was not practical to do this by any method of displacement, and the volumes were therefore calculated from the measurements of the lengths and breadths. In the case of very small testes these measurements were made by means of a micrometer scale and a low-power microscope, but in the case of the larger testes the measurements were made with callipers. On the assumption that the testis is an oblate spheroid, the volume was then calculated according to the formula

$$V = \tfrac{4}{3}\pi ab^2,$$

where V = the volume, a = half the length, b = half the breadth. This assumption certainly introduced an error as did also the fact that the measurements were all made after fixation, but it was considered that the calculated volumes were sufficiently accurate for the purposes of comparison. The volumes of the two testes of each individual were calculated separately and the results added together. The figures given later therefore refer to the total testis volume per bird.

In the case of the females, comparisons of the gross proportions of the ovaries were not so easy. The ovary has a very irregular shape, and it is not easily dissected from the underlying kidneys and adrenals. An entirely different method had therefore to be adopted, and it was found that a useful factor for comparison was the diameter of the largest oocyte in each ovary measured after the ovary had been sectioned. In this case, as in the male, measurements were made after fixation, but the error so introduced, being of the same order in all cases, should not seriously affect the comparisons between the individuals.

The differences observed between the gonads of the British and Continental starlings were submitted to statistical analysis in order to discover whether they were mathematically significant. The methods used were those advised by Simpson & Roe (1939) for the comparison of small samples.

(4) External morphology

As the starling is a very well-known bird, and as more or less precise descriptions of its external morphology are given in standard ornithological text-books (Witherby, Jourdain,

Ticehurst & Tucker, 1938), a general account of the external structure is omitted here. Certain external features, however, were found by experience to be of value in distinguishing male from female, young from old, and British from Continental, and as these features are not emphasized in the text-books, they are dealt with here in some detail. The points especially noted were the colour of the iris, the colour of the beak, and the shape, size, and colour of the feathers of the lower throat and upper breast. A bunch of lower throat feathers was taken from every bird and preserved dry, and in many cases the entire head was stored in 70% alcohol. A system of numbering enabled these preserved parts to be related to the preserved reproductive system of each individual.

(5) Observations on behaviour

A special study was made of the habits and seasonal behaviour of all types of starlings, and the detailed results of this are to be recorded elsewhere. Continual observation for a period of 2 years was made in certain localities in both town and country. In order that the information obtained should be as exact as possible, many birds were trapped and marked with different combinations of coloured celluloid rings, and in this way the habits of individual birds were worked out. The sex was judged at the time of ringing, and in the breeding season these judgements were found to be correct. In autumn and winter the ringed birds were also separated into the British and Continental types, and the results so obtained are recorded in the next section. Watching was done either with the naked eye or through Leitz 8×30 Binuxit field glasses. Song, breeding, and roosting behaviour were closely studied, and it was discovered how inaccurate and inadequate are many descriptions of these habits given in ornithological text-books.

III. RECOGNITION OF THE BRITISH AND CONTINENTAL RACES

In previous publications (Bullough & Carrick 1939, 1940), and in the preceding sections, mention has been made of differences between the reproductive cycles of the British starlings resident in this country and of the Continental starlings which visit the British Isles in autumn and winter. As these two races of birds have not previously been distinguished and are at the moment grouped together under the one name *Sturnus vulgaris vulgaris* L., it is necessary to deal immediately with the evidence on which the separation is based. It will be described in detail that, after making full allowance for the differences between the sexes and the age groups, two distinct types of birds, each with a very different degree of development of the reproductive system and in consequence with different external features and different behaviour, are to be found in the British Isles between late October and mid-March. On the evidence given below it has been concluded that one of these starling types is British and resident, and that the other is an immigrant from the continent of Europe.

Many British resident birds never visit the big communal roosts, the founding of which is such a common feature of the starling's life, and for almost the whole year they roost each night, often in pairs, in the nesting holes in which they rear their young season after season. Throughout summer and into autumn it is therefore possible to distinguish many undoubted British birds. In January the habit of nest-hole roosting becomes almost universal among

those birds which will breed in this country in the coming spring, a fact which was first reported by Morley (1939). Without exception all of the very many birds which were observed to occupy nesting holes in this way were of the type described as British.

As a further check on the identification of British birds, fifteen starlings were trapped in the winter 1939–40 and separated into the two types. The birds were ringed on one leg with an aluminium ring bearing a serial number and the inscription 'British Museum Nat. Hist. London', and on the other with different coloured celluloid rings so that the individuals could easily be recognized through field glasses. At the time of ringing six birds were considered to be British,* and of these four were located in the following breeding season occupying nests within about 200 yd. of the place where they were ringed. Of the remaining nine birds which were considered to be Continental* none was seen again. During December 1940 the four British birds were traced again. They were still found within 200 yd. of the place of ringing, and again all were of the type known as British. More adults were marked during the breeding season of 1940 when fifteen starlings† were ringed at or near their nests in Leeds, near Beamsley in Wharfedale, and at Askham Bryan near York. In December 1940 and January 1941 an attempt was made to trace these birds near the old nesting places where they had been ringed. In Leeds six of the eight birds ringed were found again, near Beamsley all the four birds were by their nests, and at Askham Bryan one of the three ringed birds was rediscovered. All these undoubted British birds were of the type known as British. One further ringing record may be mentioned here. A starling‡ of peculiar colouring, whose beak description indicated that it belonged to the British type, was ringed at Oxford in November 1933. It was seen often in the following years, and there are records that it probably nested in Oxford in 1938 and 1939 (Mr W. B. Alexander, personal communication). In May 1939 it was shot a few miles from the place of ringing.

The final evidence that this type of bird is British is given by the fact that it is the only type left when the Continental starlings leave about the middle of March. The Continental birds are known to leave at this time from the results of ringing, from observations at light-houses, and from the times of the bird's reappearance in the Baltic countries recorded by Szmirnov (1929–30).

The type of starling which has been distinguished as of Continental origin appears suddenly in great numbers in Yorkshire during October and early November. This type of bird has never been seen to roost singly or in pairs in nesting holes, and it would appear that it always roosts communally in such places as reed beds or plantations. Unfortunately, only one of this type of adult was found to be ringed,§ and this, obtained near Leeds in late November 1939, had been marked as an adult at Lijasciema in Latvia on 2 April 1935. Another bird, ringed as a nestling in Sweden, was also obtained in January 1940, but this was in its first year and, as will be seen later, it is not possible to distinguish British from

* The ring numbers of these birds, most of which are probably still alive, are as follows: British, TD354, TD355, TD360, TD361, TD368, and TD371; Continental, TD357, TD358, TD359, TD364, TD366, TD367, TD369, TD370, and TD373.

† Ring numbers: at Hyde Park, Leeds, TD378, TD379, TD380, TD381, TD382, TD386; at Weetwood, Leeds, TD397, SB106; at Beamsley, TD384, TD385, TD399, SB112; at Askham Bryan, TD387, SB105, SB107.

‡ Ring number: XF624.

§ Ring number: Riga 70162.

Continental first-year birds until February. Finally, the birds of the Continental type disappear suddenly and completely in the middle of March, the time when the Continental birds are known to leave for their nesting places. Attempts were made to confirm that the first birds to arrive in Scandinavia are of the type which disappears from Britain, but unfortunately, owing to the spread of hostilities, no replies reached this country.

The external morphological features by which young and old, male and female, and British and Continental starlings may be recognized are described in detail here and by Bullough (1942*a*), and it is hoped that these descriptions may be of value in the future to the members of the British Museum of Natural History's bird-ringing scheme. It is only by means of intensive but careful ringing that the final proof of the existence of distinct races of British and Continental starlings can be obtained.

IV. OBSERVATIONS ON THE REPRODUCTIVE CYCLE

(1) General

The breeding cycle of the great majority of British and Continental starlings is very simple. Normally, one brood only is reared during the later part of April, May, and the early part of June. Before the young have flown many of the adults have lost the power to produce spermatozoa and ova, and it is therefore impossible for them to have a second brood. A proportion of individuals, which is probably small, still do, however, possess spermatozoa and ova, and these may produce a second and slightly smaller brood during June and July (Whitherby *et al.* 1938; Hagerup 1895; Niethammer 1937). In the British Isles, although there are perhaps differences in the times of nesting between the extreme south and the extreme north, over such a large area as the West Riding of Yorkshire the processes of egg laying, hatching, etc. were found to be closely synchronized throughout the whole population. In a normal season, such as that of 1939, the difference between the times, for instance, of the hatching of the various clutches of eggs was little more than a week, and no differences in time were found between birds nesting at the tops of the Dales and those nesting on the plain of York. Individual pairs which were markedly out of synchronization with the rest of the population appeared to have had their nests or first clutches destroyed. Owing probably to the extraordinarily hard winter the synchronization of nesting in the spring of 1940 was not nearly so precise, and many birds, although they paired and built nests, failed to produce any eggs at all.

As will be described in detail, it was found that the male starlings do not breed until their second year of life, whereas the female starlings breed in their first year. In Holland, Kluijver (1935) has noted that the majority of males breed for the first time in their second year and the majority of females in their first year, and in Latvia, Vilks & Transehe (1933) have also recorded a female breeding in its first year. These facts are interesting in view of the great preponderance of males over females in the starling population, a preponderance which not infrequently leads to polyandry (Grabham 1895; Newstead 1908). Of the 786 birds shot in the course of this enquiry, 559, or 71·1 %, were males. This proportion agrees closely with that given for the starling in the United States of America by Hicks (1934), who found that out of a total of 3161 birds, 2148, or 67·9 %, were males. In Holland, Kluijver (1935) has stated that there are more males than females, but although such large numbers of

birds have not been examined, the preponderance of males over females in that country does not appear to be so extreme. Brouwer (1929) found a proportion of 159 males to 146 females, and van Dobben (see Kluijver 1935) a proportion of 166 males to 124 females. An excess of males over females appears therefore to be a feature of starling populations, and the fact that the first-year males do not normally breed whereas the first-year females do, helps to restore the balance between the sexes. Perhaps also one sex has a greater expectation of breeding life than the other, although this would be difficult to prove. Hicks (1934), again referring to the starling in the United States of America where a great amount of ringing of the species has been done, states that few of the 5- and 6-year-old birds which he has handled had yellow beaks. As will be seen later, this means that they were not in breeding condition, and perhaps therefore the bird is only able to breed four or five times.

The reasons for the unbalanced sex ratio are not easily apparent. There appears to be no differential mortality of eggs or young birds in the nest, as most eggs hatch and are successfully fledged. Young birds just off the nest were obtained, and of 101 of these juveniles, 64, or 63·4%, were males. This somewhat lower ratio of males may be significant or it may be simply an error due to the smaller number of birds taken.

In the British Isles starlings have lived as long as 9 or 10 years, as evidenced by the results of the British Museum of Natural History's bird-ringing scheme. An instance of a starling which lived for 16 years is given by Loos (1932), Flower (1925) mentions two starlings which lived in captivity in Germany for between 9 and 10 years, and Kluijver (1935) also records the case of a Dutch bird which lived for 9 years. These are, however, extreme cases, and the average length of life of the starling is certainly much less. Kluijver (1935) concludes that there is a great mortality, amounting to about 83%, among young starlings in their first year, and that even if this is omitted from the calculations the expectation of life of the starling is only about 3 years.

(2) The male starling

(*a*) *British*

(i) *Male genital system*

The testes, ellipsoidal in shape, are held by the mesorchium on either side of the mid-dorsal line of the body cavity. They are situated near the anterior end of the kidneys close to the adrenal glands. The left testis is usually larger, both in length and diameter, than the right, but often they are about the same size and rarely the right testis is larger than the left. The point of attachment of the left testis is usually slightly posterior to that of the right, but individuals in which the reverse is true are frequently found. In two of the males examined only the left testis was present, although on the right side the normal Wolffian duct system ran forward from the cloaca to end in the epididymis at the point at which the testis should have been attached. Another otherwise normal male had two rudimentary Müllerian ducts attached to the cloaca, and these ran forwards and outwards for a distance of about 3 cm.

The testis is composed of a tangled mass of seminiferous tubules separated from each other by thin strands of connective tissue. Through the connective tissue strands run blood

vessels, and between the strands are interstitial cells and large pigment cells. In autumn, when the proportion of pigment cells is high, the testis appears dark grey in colour, and in spring, when the proportion is low, the testis is almost white. The whole organ is contained in a strong fibrous connective tissue sheath, the tunica albuginea. The seminiferous tubules converge on to the postero-dorsal region of the testis where they enter the rete testis. This irregular cavity is situated immediately inside the tunica albuginea, and it is lined with a simple epithelium of cells which are either cuboidal or squamous according to the time of year. From the rete testis run several small ducts, the vas efferentia, and these pass backwards through the tunica albuginea. Outside the testis these ducts join together and form a single duct, the epididymis, which follows a very coiled and tortuous course and may give off several blind side branches. The ducts of the epididymis are lined by a ciliated epithelium. The group of cilia attached to each cell are held together in a cytoplasmic sheath, the whole being called a stereocilium. The whole epididymis is embedded in connective tissue. The duct issuing from the posterior end of the epididymis is known as the vas deferens, and it may be either straight or convoluted. The lumen is lined with a columnar epithelium, and the thick wall is composed of connective tissue and a thin band of smooth muscle. Near the posterior end of the body cavity the Wolffian duct is wound into a tight mass of coils which form the seminal vesicle. Many of these convoluted tubules give off branches which end blindly, and all of them, being surrounded by connective tissue and a band of smooth muscle, are similar in structure to the vas deferens. During the breeding season the cells lining the tubules of the seminal vesicle are ciliated and glandular. The duct emerging at the posterior end of the seminal vesicle and leading to the cloaca is also similar in structure to the vas deferens, but in the last part of its course through the cloaca wall it has very thick muscular walls at all times of the year.

The size and activity of all these structures varies greatly at different times of the year.

(ii) *Testis volumes*

As already explained, the most convenient and rapid way of distinguishing the young males from the adults and the British males from the Continental is by an estimation of the volumes of their testes. Table 1 is a list of the average volumes of the testes of British birds taken month by month. In the table and throughout this paper a starling which has not yet completed its first summer moult is considered to be a juvenile, a starling which is between its first and its second summer moult is considered to be a first-year bird, and a starling which has completed its second summer moult is termed an adult. The figures given in the table represent the average total testis volume per individual. The number of individuals examined and the standard deviation from the mean volume are also given. The standard deviations of all sets of figures were calculated according to the special formula, adapted to small samples, which is given by Simpson & Roe (1939). This formula is as follows:

$$\sigma = \sqrt{\frac{\Sigma(fd^2)}{n-1}},$$

where σ is the standard deviation, f is the frequency, d is the deviation from the mean, and n is the number in the sample.

TABLE 1

type of bird	month	number in sample	mean volume (in cu. mm.) and S.D.
juvenile	June	11	3·6 ± 0·26
	July	19	2·3 ± 0·30
	Aug.	4	1·6 ± 0·22
first year	Sept.	3	1·3 ± 0·17
	Oct.	4	1·2 ± 0·11
	Nov.	5	1·2 ± 0·13
	Dec.	3	1·3 ± 0·10
	Jan.	4	1·4 ± 0·13
	Feb.	3	4·0 ± 0·42
	Mar.	7	48·3 ± 11·28
	Apr.	5	80·1 ± 7·80
	May	4	19·3 ± 6·27
	June	4	10·2 ± 1·19
	July	2	8·9 ± 0·28
adult	Aug.	10	8·6 ± 0·24
	Sept.	3	9·3 ± 0·64
	Oct.	2	11·6 ± 1·13
	Nov.	6	16·4 ± 1·90
	Dec.	10	17·6 ± 1·91
	Jan.	4	19·2 ± 1·65
	Feb.	10	62·0 ± 14·20
	Mar.	28	1670·1 ± 383·60
	Apr.	14	3988·2 ± 739·20
	May	9	1413·5 ± 621·50
	June	10	55·6 ± 31·25
	July	9	12·6 ± 1·24

(iii) *Microscopic structure of the testis*

The great seasonal variation in the volume of the testis is correlated with changes both in the rate of multiplication of the germ cells and of the other types of cells which are also present in the organ. Close examination of sections of testes taken in all months of the year has made possible the recognition of the following cell types. It will be noticed that Sertoli cells are not included in the list as none was found.

Connective tissue cell. Cells of this type are found in great numbers surrounding the seminiferous tubules when they are known as connective tissue cells of the tubule wall (figures 1, 2), lying between the tubules when they are known as common connective tissue cells (figures 1, 2), and also in the tunica albuginea when they are known as connective tissue cells of the tunica albuginea. They are very variable in shape and size, and this variability is apparently due to the differences in tension within the testis at different times of the year. In summer and autumn, when the tension is at its lowest, the cells of the tubule walls and the common connective tissue cells are oval or round, and have an average nuclear diameter of about 4·5μ. Their nuclei, containing usually one and occasionally two large nucleoli, either form a densely packed layer close to the basement membrane of the tubule or lie crowded together in the intertubular space. In spring, when the seminiferous tubules are distended, and also throughout the year in the tunica albuginea, the cells are more elongated and have an average nuclear size of about 8μ long by 2μ broad. At this time of year the cells of the tubule walls are widely separated from each other. In all types of connective tissue cells the limits of the cytoplasm are not very clear, but in favourable sections they may be seen usually attached to the strands of connective tissue. In no instances have connective tissue cells been seen in division.

Pigment cell. In some cases these cells appear almost spherical, in others they are long and threadlike, and occasionally they may be seen with a central body and many arms. This extreme variability is probably mainly due to the differences in tension in the intertubular spaces. In the small testes found in summer and autumn the pigment cells lie crowded together and take on a compact form (figure 1). In the breeding season they become rela-

tively rare and appear as long-drawn-out cells pressed flat between distended tubules. At all times pigment cells are large, and when they are approximately spherical in shape they have an average diameter of about 13μ. They are entirely filled with small spherical pigment granules of a dark grey-brown colour. These granules have a diameter of about 0·9μ, and they completely obscure the nucleus and any other internal cell structures.

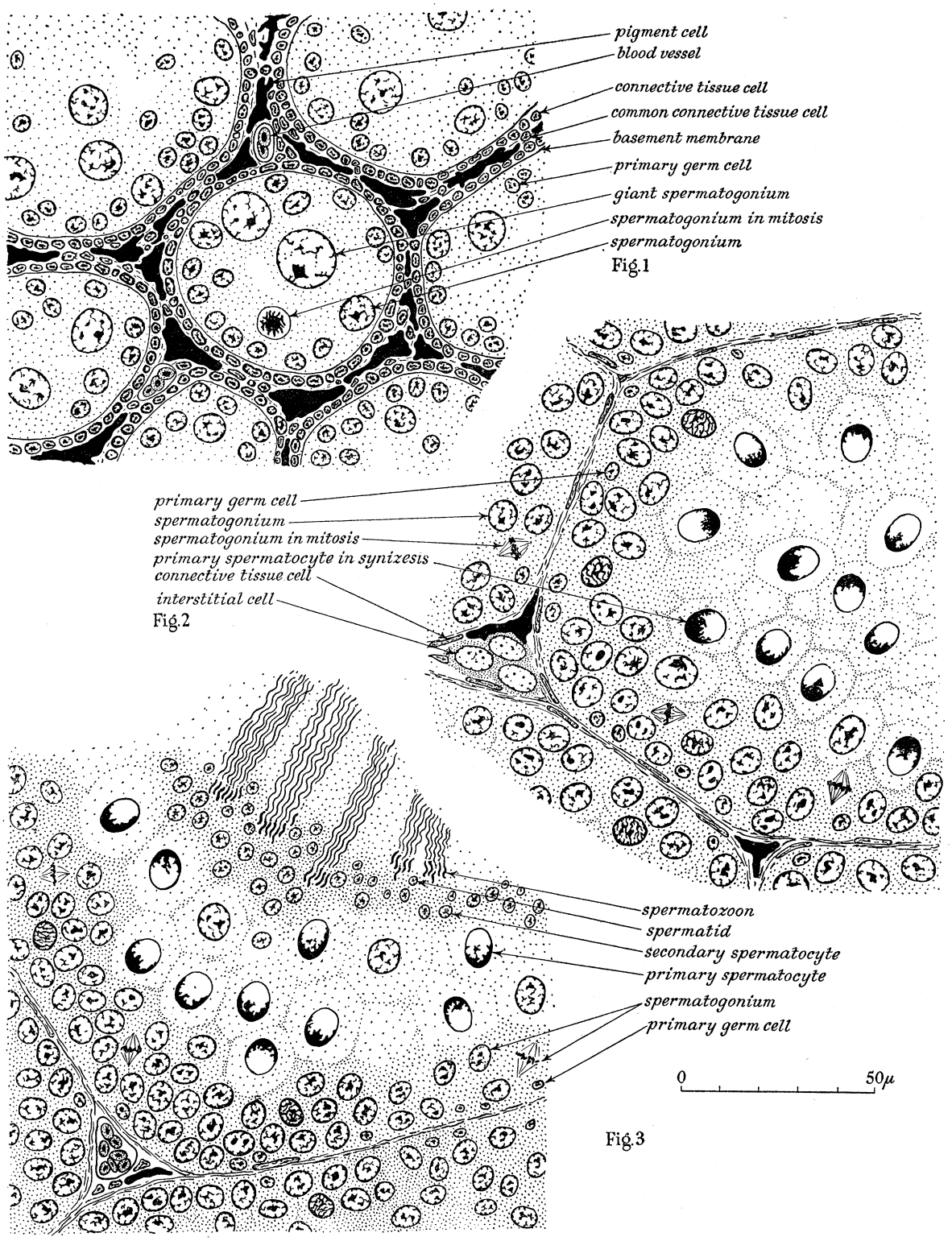
Interstitial cell. This is a large clear cell with a lightly staining nucleus (figure 2). The nucleus, which is usually slightly oval and has an approximate size of 10 by 7·5μ, sometimes contains an apparent nucleolus, but more often it is made up of a few large and many small granules of chromatin material joined by slender chromatin threads. In favourable sections the cell limits are clearly seen, and the cytoplasm appears to be slightly granular. The whole cell measures about 22 by 10μ, and it has not been seen in division. Interstitial cells may occur singly in the intertubular spaces, but usually they are found in small groups in the irregular spaces where several seminiferous tubules meet.

Primary germ cell. At all times of the year primary germ cells are to be seen as small resting nuclei close to the basement membrane of the seminiferous tubules (figures 1–3). These nuclei, which are rarely seen dividing, are either round or oval, and have an approximate diameter of between 5·5 and 6·5μ. The cytoplasmic limits of the cells are not well defined, and in autumn, when this cell type is especially common, the nuclei have the appearance of being set in a syncytium.

Spermatogonium. In autumn the nuclei of the spermatogonia are common in the centre of the seminiferous tubules. They usually have a single nucleolus, and as in the case of the primary germ cells, the limits of the cell cytoplasm are not clear. At this time of year there is a great variation in the size of the nuclei. Their diameter varies from 7·5 to about 15μ (figure 1), and in extreme cases diameters of as much as 20μ have been recorded. The cytoplasmic limits of the largest spermatogonia are usually well defined (figure 54, plate 12). Growth of the spermatogonia to this large size appears to take place without any division, and immediately division becomes frequent in the middle of winter, the large-size spermatogonia entirely disappear owing to rapid successive divisions (figure 2). Throughout the breeding season, when mitotic division continues to take the place of growth, the nuclei of the spermatogonia have only a small range of variation in size between diameters of about 7·5 and 9μ (figure 3).

Primary spermatocyte. The resting nucleus of the primary spermatocyte is very similar to that of a spermatogonium, but it is not seen until midwinter when active division of the spermatogonia has set in. The primary spermatocyte nucleus is larger than that of a small-size spermatogonium (figure 3), and it only varies in diameter between the narrow limits of about 9·5 and 10μ. The limits of the cell cytoplasm are often not clear. After a short rest the nucleus begins the reduction division, and the synizesis stage, in which the chromatin material is clumped to one end of the nuclear space, is then seen (figures 2, 3). The synizesis stage of meiosis is of very long duration. It appears to last for several weeks before the first secondary spermatocytes are formed, and synizesis stages are seen crowding the centres of the seminiferous tubules of adult British starlings throughout most of February.

Secondary spermatocyte. A zone of these cells is found inside the zone of primary spermatocytes, and the nuclei are usually seen in a resting condition (figure 3). The limits of the cytoplasm are clear, and the total cell diameter is about 11–14μ. The nucleus usually



Types of cells present in the testis of the starling.

FIGURE 1. Testis of an adult Continental starling in late February.

FIGURE 2. Testis of an adult British starling in late February.

FIGURE 3. Testis of an adult British starling in late March.

contains either a lobed nucleolus or a number of closely packed chromatin granules, and its average diameter is about 5·7μ.

Spermatid. The mitotic division of the secondary spermatocyte gives rise to still smaller cells, the spermatids (figure 3). When first formed these cells have well-defined walls, and the total diameter is about 7·5μ. Later the cell walls appear to break down leaving the nuclei embedded in a mass of residual cytoplasm. The nucleus has a diameter of about 4μ, and by an alteration in shape it gives rise to the head of the spermatozoon.

Spermatozoon. As soon as they are formed the spermatozoa come together in groups in the centre of the seminiferous tubules with their heads pointing out towards the tubule walls (figure 3; figure 59, plate 13). Like the spermatid nuclei from which they are formed these groups are embedded in the residual cytoplasm. Each spermatozoon has a solid head about 5·8μ long and 1μ broad, and a tail about 35μ long. The whole length of the spermatozoon is closely and characteristically waved. There are about nine or ten of these waves, all of exactly the same amplitude, and they affect the head of the spermatozoon as well as the tail. Later the spermatozoa break free into the cavity of the seminiferous tubules, and while they are moving towards the rete testis and the epididymis, the groups break up and the individual spermatozoa may lie at any angle.

(iv) *Seasonal variations in the testis*

The youngest testes examined were those of juvenile males obtained from a communal roost in the second part of June. At this time the testes were relatively large (figure 5), although they were covered by only a thin tunica albuginea which was, on the average, about 20μ thick. The seminiferous tubules were relatively well developed, and they were clearly outlined by the connective tissue cells of the tubule walls. Between the tubules were many common connective tissue cells, and pigment cells were also common and closely packed. Many blood capillaries were present, and interstitial cells were seen in occasional groups in the larger intertubular spaces. Within the seminiferous tubules early spermatogenesis was proceeding. This activity did not affect the primary germ cells which were mainly packed against the tubule walls, but the spermatogonia, which were more centrally placed, were frequently seen in some stage of mitosis (figure 53, plate 12). The nuclei of the spermatogonia were very variable in size, and diameters of between 8 and 18μ were normal. Spermatogonia of all these varied sizes were seen in division, but it appeared that this burst of growth did not go beyond the spermatogonium stage. It is possible that a few resting primary spermatocyte nuclei were formed, but if so, these nuclei were unrecognizable and never divided to show the typical synizesis stage of meiosis. Some darkly staining necrotic nuclei were present in the centres of the seminiferous tubules. In July the testes decreased in volume, and by August they were minute and very dark in colour. The tunica albuginea remained thin. The diameters of the seminiferous tubules became very small, and the connective tissue cells lining the walls were closely packed together. The intertubular spaces were almost entirely filled by masses of pigment cells which almost obscured the common connective tissue cells and the interstitial cells. Both of these latter cell types were, however, present. The numbers of germ cells in the seminiferous tubules were at their lowest by mid-August, and after the early part of July no mitotic activity was apparent. The basal membranes were clearly visible. The excess numbers of spermatogonia present

in June disappeared, apparently by necrosis, during the second part of July. By mid-August no necrotic cells were left, and only primary germ cells and small-size spermatogonia lined the tubules. The centres of the tubules were hollow.

From September to January little change took place in the testes of what were then known as first-year males (figure 6). During the autumn the nuclei of some of the small-size spermatogonia increased in volume, and by November very large spermatogonia with nuclear diameters of up to 20μ were recorded (figure 54, plate 12). This increase in size took place without any cell division, and it resulted in the almost complete obliteration of the cavities which had been commonly present in the centres of the seminiferous tubules in August. At the beginning of February the testis size began to increase due to a sudden burst of mitotic division of the nuclei, large and small, of the spermatogonia. Throughout February this process was continued with increasing speed, and by the end of the month the large-size spermatogonia had entirely disappeared. By early March the testis volume had increased considerably (figure 7), and the tunica albuginea was about 24μ thick. The seminiferous tubules were swollen, and both the connective tissue cells of the tubule wall and the common connective tissue cells were drawn out under tension. The pigment cells were pulled well apart and flattened, and in consequence the testis colour became light grey. The few interstitial cells were restricted to the small spaces where three or more seminiferous tubules met. The germ cells inside the tubules began to form zones. The primary germ cells were on the outside, the small-size spermatogonia were next, and the primary spermatocytes were in the centre. The spermatogonia were often seen in mitotic division, and the primary spermatocytes, whose cell limits were fairly clear, were mostly seen in the synizesis stage of meiosis. Necrotic cells were occasionally seen in the centres of the tubules. Throughout March the same structure was evident (figure 55, plate 12), but as more and more spermatogonia and primary spermatocytes were formed, the seminiferous tubules became larger and the testis volume increased. Interstitial cells were not common.

In April the testis reached its maximum size, and the tunica albuginea was about 22μ thick. The intertubular spaces and the cells within them were compressed, and the testis became very light grey in colour. Not many interstitial cells were visible even in the corners between the seminiferous tubules. Inside the tubules mitotic divisions of the spermatogonia were seen less frequently, and no primary spermatocytes had developed beyond the synizesis stage of meiosis. The centres of the seminiferous tubules were full of nuclei in the synizesis stage, but no secondary spermatocytes were seen in any of the individuals examined. Towards the end of the month necrotic nuclei appeared in increasing numbers in the centres of the tubules, and mitosis of the spermatogonia was seen less and less frequently. The testis volume decreased rapidly during May, and the tunica albuginea thickened to about 65μ. The intertubular elements were once more clearly visible. Connective tissue cells lined the walls of the seminiferous tubules and packed the spaces between them. The pigment cells contracted and moved closer together, and in some places small groups of interstitial cells were seen. In the course of the month most of the primary spermatocytes disappeared due to necrosis, but even at the end of the month a very few synizesis stages were still to be seen. Some mitotic activity was also evident among the spermatogonia, and a few of these nuclei had once more grown to a giant size. The last synizesis stages and the last signs of mitosis among the spermatogonia disappeared early in June. In June, July,

and August the testes once more reached their minimum size, and the tunica albuginea was about 68μ in thickness. The seminiferous tubules were very small and their limits were clearly outlined by the connective tissue cells of the tubule walls. In the intertubular spaces common connective tissue cells and pigment cells were closely packed so that the testes appeared very dark grey in colour. Interstitial cells were present but rare. Primary germ cells and spermatogonia were seen inside the tubules, and in many individuals the primary germ cells were situated inside the ring of spermatogonia. The nuclei of all the germ cells were completely quiescent except where an occasional cell was undergoing necrosis. The spermatogonia were all of the small size with a diameter of about 8μ, and in places vague cell limits could be distinguished. This description also applies to the condition in August of the testes of male starlings which were more than one year old.

The second complete moult was finished about this time, and the birds, then in their second year, were called adult males. The testes of these birds remained quiescent during the early part of September, but after the middle of the month they once more began to grow. The nuclei of the spermatogonia, which were mainly centrally placed in the tubules, started both to enlarge and to divide. In October and November the testis growth continued (figure 9; figure 57, plate 13), but there was little change in the thickness of the tunica albuginea. The basement membrane of the tubules was very clearly defined, and between the tubules were the usual large numbers of connective tissue and pigment cells. Interstitial cells were very rare. The nuclei of the primary germ cells were all quiescent, but those of the spermatogonia were frequently seen in mitotic division. There was a wide range of sizes of spermatogonia, some nuclei being as small as 7·5μ in diameter and others being as large as 16μ in diameter. The cytoplasmic cell limits of the largest spermatogonia were usually clearly visible. At this time of the year it was apparently normal for the spermatogonia to increase greatly in size before dividing, although smaller nuclei in division were also seen. Necrotic cells were entirely absent. These same general conditions continued throughout the months of December and January. Slow growth took place in the size of the seminiferous tubules and therefore of the whole testis. In January necrotic nuclei were not uncommon. This period of continued slow growth culminated in the great burst of rapid growth which started at the beginning of February. As the testis enlarged the tunica albuginea became strained, and was reduced in thickness to about 12μ. The connective tissue cells of the tubule walls, the common connective tissue cells, and the pigment cells were pulled farther and farther apart, and as it appeared that these cells divided seldom if at all, their relative numbers fell rapidly. Interstitial cells, on the other hand, became much more common, and were usually found in small groups in the spaces where three or more seminiferous tubules met. In spite of the considerable increase which must have taken place in their numbers, none of them was seen in division. In the seminiferous tubules there was great activity. Primary germ cells, although still present, were far outnumbered by the other cell types. All spermatogonia were of the small size, and many were seen in mitosis. Primary spermatocytes were very common and were mostly in the synizesis stage of meiosis. It appeared that the synizesis stage normally took a long time to complete, and it was not until after the middle of the month that the first secondary spermatocytes appeared in the centres of the tubules. The production of primary and secondary spermatocytes then proceeded very rapidly, and by the end of the month the

tubules were very distended and the first spermatids and spermatozoa had appeared. The spermatid stage appeared to be short, and the spermatozoa when formed came together in groups. The heads of the spermatozoa all pointed outwards towards the tubule walls, and the tails hung into the tubule centres which were filled with masses of residual cytoplasm. There was then a complete zonation of cell types. The few primary germ cells rested against the basement membrane, the spermatogonia were inside and were often dividing, next came the primary spermatocytes usually in synizesis, then the secondary spermatocytes and spermatids, and finally in the centre were the spermatozoa (figure 3).

The same general appearance with the zonation of the cell types was seen throughout the month of March (figure 59, plate 13), but the seminiferous tubules, and therefore the whole testis, became more and more distended (figure 11). The connective tissue cells of the tubule walls and the common connective tissue cells were stretched widely apart, and due to the relative scarcity of the pigment cells, the testis appeared white. Interstitial cells were commonly seen in the corners between the seminiferous tubules. Active spermatogenesis continued through the early part of April, and the testis reached its full size (figure 4). In mid-April the spermatozoa were released into the centres of the tubules, and they passed away to the seminal vesicles via the rete testis, the epididymis, and the vas deferens. With the release of these spermatozoa, the seminiferous tubules diminished in size, although spermatogenesis still continued actively. Cell division and maturation were seen throughout May, but the tubules became smaller and fewer spermatozoa were present in the lumina. After the middle of May spermatogenesis appeared to slow down. In June a great reduction took place in the testis volume, and on the average, spermatogenesis ceased about the middle of the month. There was, however, great individual variation in this respect, and some signs of spermatogenesis were still to be seen in a few individuals towards the end of the month. When cell division stopped, all necrotic nuclei and cell debris were cleared from the centres of the seminiferous tubules which then collapsed. The testis volume became rapidly less, and the tunica albuginea thickened to about 60μ. The tubules were again sheathed by closely packed rows of connective tissue cells, and the pigment cells were so tightly massed that the testis was again very dark grey in colour. Some interstitial cells were still to be seen, but the majority had disappeared. Inside the seminiferous tubules, primary germ cells and small-size spermatogonia were the only cell types remaining. No mitotic figures were seen, but occasional necrotic nuclei still remained. After the middle of the month only a few of the individuals examined

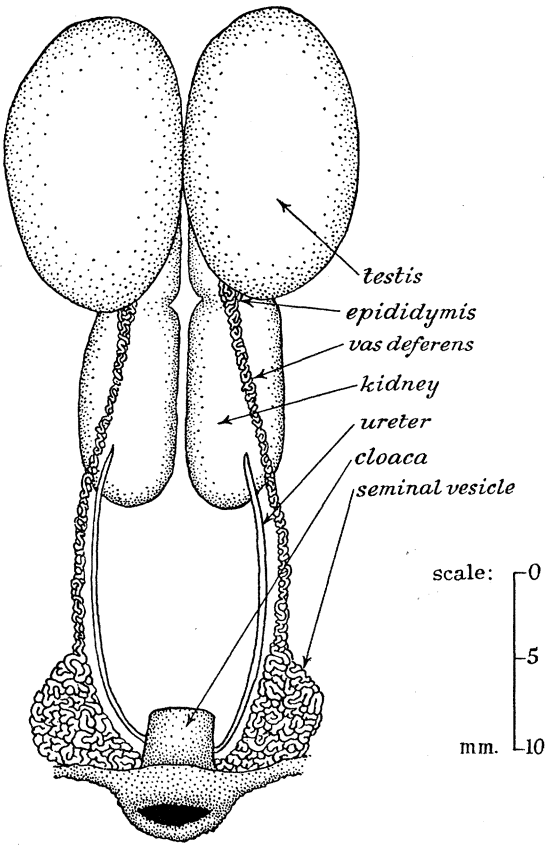


FIGURE 4. Reproductive system of an adult British starling in April.

retained any spermatozoa in their seminal vesicles. By the middle of July the testis size was at a minimum in all individuals, and the histological structure was identical with that already described for the adult males in August.

(v) *Accessory sexual organs*

Unlike the female, the male starling only possesses the accessory sexual organs typical of its sex. As already described, however, one male had two rudimentary oviducts, each of which was about 3 cm. long, and a similar abnormal male has been described by Kummerlöwe & Froböse (1930). The following account is given of the structure and seasonal variations of the normal male accessory sexual organs.

Rete testis. This was already well developed in the juvenile males in June, when it was seen as an irregular space at the postero-dorsal side of the testis immediately inside the tunica albuginea. The space was empty, and the walls lining it were covered by a cuboidal epithelium, the nuclei of which were crowded closely together. The cytoplasm of these epithelial cells appeared light grey after staining with Heidenhain's iron haematoxylin. Exactly the same structure was present in July and August except that the size of the cavity had slightly diminished. No change took place in the structure of the rete testis of the first-year male from September to early February, but in the second half of February the rete testis expanded very rapidly so that its cavity extended down both sides of the testis. The cells of the epithelium lining the cavity were pulled farther apart, and it was seen that each cell, which was cuboidal in form, was composed of a nucleus with only a thin covering of cytoplasm. The cavity remained empty. The rete testis continued to grow throughout March keeping pace with the expansion of the testis volume. As the space got larger and larger the cells lining its walls were pulled more widely apart until, after mid-March, they flattened to form a squamous epithelium. The cavity reached its largest size in mid-April when it contained necrotic nuclei and cytoplasmic cell debris from the cavities of the seminiferous tubules. In May there was a rapid collapse in the extent and size of the rete testis which still, however, received some necrotic nuclei from the adjacent parts of the seminiferous tubules. The cells of the lining epithelium were once more drawn together, and the nuclei were closely crowded. By July and August the rete testis was again small, and its cavity was almost empty. In the adult males in September the same collapsed structure was seen, but in October, November, and December growth was again taking place in the extent of the cavity. This growth drew the lining nuclei apart once more, and the epithelium became clearly cubical. In February the growth of the testis caught up with the growth of the rete testis, and from that time onwards, although the rete testis continued to grow, its cavity became proportionately smaller and smaller. At the end of March and the beginning of April the rete testis was again at its greatest development. The epithelium lining the space was tightly drawn out, and the very flat cells bulged out in the region of the nucleus. The epithelium was once more squamous. From the middle of April to the first half of June the rete testis was full of spermatozoa, of the nuclei of all types of germ cells in the first stages of necrosis, and of cytoplasmic debris. In the second half of June it was filled only with cell debris, and as this debris disorganized the space contracted. In July the cavity was empty, and the lining epithelium was made up of closely packed cuboidal cells.

Vasa efferentia. In the juvenile male in June, July, and August, several vasa efferentia led out from the rete testis through the connective tissue of the tunica albuginea. Outside the tunica the ducts appeared to join together to form one continuous tube, the epididymis. In June each vas deferens had a well-developed lumen which was often as large as 12μ in diameter. As in the rete testis, the ducts were lined with a closely packed mass of cuboidal epithelial cells whose cytoplasm stained grey with Heidenhain's iron haematoxylin. The lumina of the ducts often contained strands of what appeared to be secretory products. Exactly the same structure was seen in the first-year male throughout autumn and early winter, but by the end of February the diameter of the lumina of the tubules had increased to an average of about 15μ. The nuclei of the cells of the lining epithelium were pulled apart, and it was then clearly seen that each of the lining cells was cuboidal. The greater part of the cell body was made up by the nucleus round which the grey staining cytoplasm formed a very thin sheath. The tubules contained small amounts of apparent secretory products. During March the vasa efferentia increased still further in size, and they reached a maximum about mid-April when the diameter of the lumina was about 25μ. At this time the cells lining the vasa formed a cuboidal epithelium, and the lumina contained small traces of what appeared to be secretory products. The lumina also contained some cell debris and necrotic nuclei from the testis. In May the ends of the vasa efferentia close to the rete testis remained open and contained necrotic cells, but at a short distance from the rete most of the vasa had collapsed. In some cases the collapsed tubules had no lumina remaining and were merely represented by strands of closely packed nuclei. Possibly these strands of nuclei broke down and disappeared entirely, so that by July and August fewer vasa efferentia remained. Those remaining at that time had, however, well-marked lumina of about 8μ diameter, and they usually contained some debris. Little visible change took place in the vasa efferentia of the adult males throughout autumn and the early part of winter, but during February their cavities enlarged slightly. In early March the average lumen diameter had increased to about 25μ, and the tubules contained small quantities of apparent secretory products. By the end of March the lumen diameter had increased to over 30μ, and the cells of the walls were pulled apart so that they formed a clear cuboidal epithelium. When the first spermatozoa and cell debris passed through the tubules in mid-April, the diameter of the lumina was about 50μ and the cells of the walls were slightly flattened. It is not certain whether they were secretory or not. This structure persisted up to the first half of June when, although still retaining cell debris in their lumina, the vasa efferentia collapsed considerably. By mid-July the debris had disappeared, and the ducts were in the summer condition with lumina of a diameter of about 8μ.

Epididymis. This structure was well developed in the juvenile male in June. It was embedded in a mass of connective tissue, and closely pressed to the adrenal gland. The epithelial cells lining the tubules were closely packed, and in the sections the nuclei overlapped. The tubule lumina were extremely small and were only about 2·5μ in diameter. The parts of the tubules farthest from the vasa efferentia were completely closed, and appeared as solid rods of cells the nuclei of which were grouped closely together. No cell limits were visible, and there were no signs that the cells were ciliated. The same structure was seen in August when, although many of the tubules were still entirely closed, in others the lumina were as large as 9·5μ diameter. In these latter tubules the structure of the wall

was visible, and although in many places the cell limits were obscure, the lining epithelium was seen to be composed of cuboidal cells. Outside the ducts were sheaths of connective tissue in which were embedded many connective tissue cells. In the first-year birds the epididymis became more extensive and convoluted during the autumn, but in December and January the same general structure remained. Some tubules were still closed, but in a few places the cell limits were visible between the nuclei in the duct walls. During February there was little increase in the complexity of the ducts, but the lumina became more prominent and small quantities of secretion appeared. Very few ducts remained closed, and the cells of the walls were stretched farther apart. By the end of the month all the ducts were open, and the largest lumina were about 24μ in diameter. There were signs that the cells of the tubule walls were ciliated, and some secretion was present in the tubule lumina. By mid-March most of the lumina were between 10 and 20μ in diameter, the lining epithelium had become tall and columnar, and the cell walls were usually clearly visible. The inner margins of the cells were ciliated, and the group of cilia on each cell was held together in a sheath of cytoplasm. Cilia of this type are known as stereocilia. In April the ducts were wide open, the lumina often being as large as 25μ in diameter. The cells lining the tubules had clearly defined cell walls, and from the free surfaces of the cells hung stereocilia. In the lumina were small masses of secretion. In the second half of May the tubules collapsed, and most of the lumina disappeared entirely so that only rods of darkly staining nuclei remained embedded in a thick mass of connective tissue. This condition lasted through the summer. From September onwards the epididymis of the adult birds was simple. The lumina of the tubules were usually obscure, and only in exceptional cases could they be distinguished clearly. In some there appeared to be signs of a slight secretion in the centre, but this could not be proved with certainty. The tubules were embedded in a thick mass of connective tissue. In February the first signs of development were apparent. The lumina became clearly visible and had a diameter of about 12μ. As the tubules swelled up the cell walls appeared between the lining nuclei, and the stereocilia became visible. A few very small patches of secretion were present in the lumina. By the end of February the lumina were over 30μ in diameter, and the nuclei of the tubule walls were often seen in mitosis. The lining cells increased greatly in numbers as the tubules became larger, and they developed into a tall columnar epithelium. Their cell limits were very clear, but secretion as yet was only slight. The cells of the connective tissue were pulled farther and farther apart. By the middle of March the lumina of the tubules of the epididymis had increased in diameter to about 50μ, and secretion of the lining cells was active. The tubules continued to increase in size until just before the middle of April when the first spermatozoa came from the testis. The lumina then had a diameter of nearly 150μ, and they were crowded with spermatozoa, with necrotic nuclei and cytoplasmic debris from the testis, and with secretion from the lining cells of the epididymis tubule. During the time of this extreme distension the cells of the tubule walls were stretched so that, instead of being tall columnar as before, they became short columnar or in some cases even cubical. The stereocilia showed clearly, and the cells were actively secreting. The connective tissue surrounding the tubules had been pulled out into very thin strands, but that side of the epididymis not in contact with the kidney, adrenal, or testis was covered by a thick layer of connective tissue. The same general structure was seen throughout May, but towards the end of the

month the tubules of the epididymis became reduced in diameter. During June they collapsed rapidly, and by the second part of the month they were nearly all solid again. The few tubules containing necrotic cells from the testis retained their lumina until the necrotic cells broke down. The connective tissue formed a very solid mass all round the collapsed tubules, and the normal summer condition was reached.

Vas deferens. Passing from the epididymis the Wolffian duct develops a larger lumen and a thicker wall. This wall has an inner epithelial lining of tall columnar cells which are based on a loosely constructed layer of connective tissue. Immediately outside the connective tissue is a thin layer of circular smooth muscle fibres, and the whole is set in a thick outer mass of dense connective tissue. In the juvenile male in June this duct had a lumen with a diameter of about 45μ, an inner connective tissue wall with a thickness of about 20μ, and a muscle layer with a thickness of about 5μ. At the end of July and the beginning of August the duct became thinner. The lumen contracted to a diameter of about 28μ, the inner connective tissue layer to a thickness of about 11μ, while the muscle layer remained unchanged. The same general structure persisted in the first-year males throughout the autumn and winter, the diameter of the lumen shrinking even farther to about 20μ and the thickness of the inner connective tissue layer to about 8μ. In the second half of March the size of the lumen increased to about 33μ, but the thickness of the inner connective tissue and circular muscle layers remained the same. The increase in size of the lumen was accompanied by an increase in the number of the tall columnar cells in the lining epithelium. In April growth was rapid, and a maximum was reached in the second half of the month when the whole duct became twisted and convoluted. The diameter of the lumen was then about 56μ, and the cells of the lining epithelium had multiplied and were crowded together. These epithelial cells were tall and columnar, and they had elongated nuclei. The inner connective tissue layer was about 46μ thick, and the circular muscle layer was about 23μ thick. In May this large size was maintained until the middle of the month when shrinkage began. By the middle of June the small summer size had been reached, and the whole duct became straighter. The lumen had a diameter of about 9μ, the inner connective tissue layer was about 28μ thick, and the circular muscle layer was reduced to a thickness of about 6μ. The adult male in August had a vas deferens very similar to that of the first-year male in June, and except that during the autumn the duct became slightly more convoluted (figure 9), this structure was retained without change until the end of the following January. In February the lumen, irregular in shape, reached an approximate diameter of 70μ, and the columnar epithelial cells were more numerous. The inner connective tissue layer became denser, but it remained about the same thickness of 28μ. The circular muscle layer was more prominent and increased to a thickness of about 14μ. During March the growth continued (figure 11), and by the end of the month the diameter of the lumen had increased to approximately 125μ. The thickness of the inner connective tissue layer remained about 30μ, and that of the circular muscle layer was reduced to 5μ. The duct at that time had become very twisted and convoluted (figure 4). When the first spermatozoa descended just after the middle of April, the duct was enormous and had an approximate lumen diameter of 200μ. The wall was distended and thin, the inner connective tissue layer having a thickness of only about 11μ, and the circular muscle layer a thickness of only about 8μ. This structure persisted through May, but there was a slight diminution in size towards the end

of the month. In June there was a rapid collapse, and by the beginning of July the vas deferens was much straighter. The lumen was reduced to about 11μ in diameter, the inner connective tissue layer was about 32μ thick, and the circular muscle layer was about 7·5μ thick.

Seminal vesicle. At the posterior end of the body cavity the Wolffian duct is closely coiled, and it gives off numerous blind branches. This compact body, the seminal vesicle, is encased, like the vas deferens, in a dense sheath of connective tissue. The tubules of which it is composed all have a very similar structure to that of the vas deferens. There is an inner lining epithelium of cells which are either cubical or columnar and have elongated nuclei, and this is sheathed round by a loosely built tube of connective tissue. Outside this is a narrow band of circular muscle fibres, and then the thin but dense outer sheath of connective tissue (figure 61, plate 14). In the juvenile male in June the seminal vesicle was very simple, and was composed of only a few tubules which rarely appeared to branch (figure 5). The diameter of the lumen was about 27μ. By August the lumen diameter had increased to about 31μ, the number of tubules was more than doubled, and there were signs of secretion in the lumina. During the autumn, however, the tubules of the seminal vesicles of most of the first-year males collapsed, and the outer connective tissue sheath became very dense. The tubule walls were thick, and the lumina were reduced to an average diameter of only 4μ. There were no signs of any secretion. This condition lasted throughout the autumn and until the end of February, although very occasionally individuals were found with larger lumina of up to 17·5μ in diameter. In these larger lumina there were some signs of secretion. At the end of February the tubules of the seminal vesicles greatly increased in number, and the lumina, which contained some secretion, became enlarged to an average diameter of 28μ. The growth in size of the tubules continued slowly throughout March (figure 7), but there was little change in the structure of the walls and the layer of circular muscles remained very thin. In April the growth was completed, and the lumina had an average diameter of about 45μ. The cells of the lining epithelium were tall columnar in form, and they had increased greatly in numbers. They produced a small amount of secretion. The thickness of the tubule walls remained unchanged. During May the seminal vesicles started to regress. The cells of the lining epithelium were crowded together, the inner connective tissue sheath doubled in thickness and became very dense in structure, and the circular muscle layer also became thicker. By the beginning of June the reduction in size was complete, and the lumina had an average diameter of about 8·5μ. The cells of the lining epithelium were reduced in numbers, the inner connective tissue sheath was thick and dense, and the circular muscle layer was prominent. In the adult male a similar condition of the seminal vesicle was reached in July and August (figure 61, plate 14), but the seminal vesicles of these older birds were much more complicated organs composed of very small tubules with blind side branches. No change took place in this structure until the following February. At the beginning of that month the tubules swelled up, and the lumen, which contained some secretion, increased to over 45μ in diameter. The cells of the lining epithelium increased in numbers and were frequently seen in mitosis, but very little change in the thickness of the connective tissue and muscular layers was noted. By the beginning of March the lumen had increased to over 75μ in diameter, and throughout the month the growth continued (figure 11; figure 63, plate 14). The peak of this growth was

reached about the middle of April (figure 4; figure 62, plate 14) when the tubules became distended with spermatozoa which, although they retained their characteristic twisted heads, had straight tails. The lumina then had an average diameter of over 300μ. The lining epithelial cells were pulled out into a cuboidal form, and they were seen to be ciliated and very actively secreting. The inner connective tissue and circular muscle layers were stretched and thin, and they contained many blood vessels. The same structure was seen in May, but the tubules became smaller as the month passed. In the second half of June and during July the normal summer size was again reached.

(vi) *Secondary sexual characters*

It was found that certain external characters were of great value in distinguishing the male starlings from the females of any particular age group. The points especially noted were the colour of the iris, the colour of the beak, and the size, shape, and colour of the lower throat feathers. The iris formed an almost constant feature, but the beak and the feathers of the lower throat varied greatly in appearance according to the phases of the reproductive cycle.

*Colour of the iris.** In the juvenile male the iris was usually a dark grey-brown[(a)]. There was, however, more variation in iris colour in the juvenile than in the first-year and adult birds, and of twenty-one juvenile males examined in the middle of June, fourteen had dark grey-brown irises[(a)], four had medium grey-brown irises[(b)], and three had irises of a light liver colour[(c)]. During August and September the greyness faded, and throughout the rest of their lives most male starlings had dark brown irises[(d)]. There was a slight variation in this respect as about 5% of these older males had irises with an inner or outer ring of white or yellow.

Colour of the beak. When the young starling left the nest, the beak was dark grey in colour except for the light grey cutting edge to both the upper and the lower mandibles. No change took place after the summer moult, when the bird was known as a first-year male, but in the following February the base of the lower mandible turned a dirty yellow. This colour spread to the base of the upper mandible, and then down the entire beak to the tip. By about the middle of April the beak was full yellow, but this colour was never so bright and clean as that of the adult male. In June the colour again began to change, and the beak turned dark grey at the base. By the end of the month the entire beak was again dark except for the light grey cutting edge. This appearance was retained throughout the second summer moult and until the end of September, when the bird had become an adult (figure 13). In October and November the beak again began to turn yellow (figure 14). The lightening in colour was at first especially marked at the base of the lower mandible, but by December only the distal half of the beak remained dark (figure 15). There was some variation in the extent of the yellow colour in different individuals. In mid-November the extremes were from a touch of yellow on the lower mandible to a half-yellow beak, and in mid-December they were from a quarter-yellow beak to one with only a touch of black at the tip. By mid-January (figure 16) the variation in beaks was from three-quarters to almost full yellow, the last bit of dark pigment to go being situated just above the tip of the

* The iris colours described above approximate to the following reference numbers in the list of Ostwald Colour Standards:

[(a)] 2:2:pn. [(b)] 2:2:nl. [(c)] 2:1:li. [(d)] 4:6:pl.

upper mandible. In February and throughout the breeding season, the adult male British starling normally had a full yellow beak with a blue-grey base (figures 17, 18). Three adult males were, however, found in which the beak was yellow to the base. In late June and July the beak again turned dark, the change first affecting the base of the upper mandible and that area just above the tip of the upper mandible which was the last part to turn yellow (figure 19). As the change proceeded these two dark areas joined, and the basal half of the lower mandible also became dark. At the beginning of July some individuals already had a completely dark beak, but in others the beak was still half-yellow. By the middle of July all the birds had dark beaks.

Lower throat feather. The throat feathers of the juvenile male were very broad and blunt, loosely built, and light brown in colour (figure 85, no. 1, plate 20). The juvenile plumage was only retained until the end of June when the summer moult began. This moult, which was complete, followed a definite sequence (Bullough 1942 *a*). The feathers of the upper breast were shed in July, and those of the throat in September when the moult was completed. At the beginning of October the first-year male had throat feathers which, except for the white tips, were dark brown (figure 85, no. 2, plate 20). They showed only a little of the purple and green metallic gloss which was present so markedly in the feathers of the adult male. The tips of the throat feathers were narrower than those of the juvenile bird, but not so narrow as those of the adult. It was easy to confuse this bird with the adult female, but the colour of the iris served as a distinguishing feature. As the autumn and winter passed, the tips of the feathers were worn away (figure 85, nos. 3, 4, plate 20), and by mid-February the bird did not appear so speckled. At this time a partial moult of the body feathers commenced and continued until late March. The extent of this moult varied in different individuals, but only rarely did it affect the throat feathers. All the new feathers possessed the normal white tips. In some individuals the white tips of both old and new throat feathers were never entirely worn away, and the birds remained speckled until the summer moult began in late June. This moult followed a similar course to that of the juvenile, but it was completed more rapidly and was over by the end of August. In September the bird became an adult male, and possessed very dark throat feathers shot with metallic reflexions of purple and green. The feathers were very pointed, and were tipped with white (figure 85, no. 6, plate 20). During autumn the white tips became very worn, and by December or January those of the head, throat, and breast had usually completely worn away (figure 85, no. 7, plate 20). In late February and early March a partial moult took place, and as in the first-year male, this varied greatly in extent in different individuals. The throat was again an unusual place to find new feathers, all of which when present had the normal white tips. During the breeding season in April and May, the throat feathers of the adult males were long and pointed, dark, and very glossy (figure 85, no. 9, plate 20). The summer moult commenced at the end of June, and following the same sequence, it took the same time to complete as that of the first-year male.

(*b*) *Continental*

(i) *Male genital system*

The description already given of the structure of the male genital system of the British starling applies equally to that of the Continental starling.

(ii) *Testis volumes*

Except in the case of first-year birds between November and January, the testes of the male Continental starlings were very much smaller at any one time than those of the corresponding British birds. Table 2 shows the volumes of the testes of the Continental starlings. The figures for the first-year and adult starlings in March are the totals for the birds shot both in 1939 and 1940. The birds were obtained just before the time when they would have left the country, and a comparison between the results for the two years may be of interest (table 3). It is seen that in each year the mean volumes and standard deviations approximate very closely to each other, and it appears possible that the birds migrate when their reproductive systems reach a certain stage of development. In this connexion it is interesting to note that, probably owing to the very severe winter, the gonad growth of both British and Continental birds was slower in the early months of 1940, and that apparently as a result of this, the migration of the Continental birds was delayed for nearly a fortnight. In 1939 the birds left the neighbourhood of Leeds on 15 March, and in 1940 they left on 27 March.

TABLE 2

type of bird	month	number in sample	mean volume (in cu. mm.) and s.D.
first year	Feb.	2	1·6 ± 0·14
	Mar.	9	4·6 ± 0·35
adult	Nov.	5	4·3 ± 0·42
	Dec.	7	4·6 ± 0·36
	Jan.	6	6·0 ± 0·57
	Feb.	10	11·7 ± 2·06
	Mar.	21	60·4 ± 22·20

TABLE 3

type of bird	month and year	number in sample	mean volume (in cu. mm.) and s.D.
first year	Mar. 1939	3	4·8 ± 0·26
	Mar. 1940	6	4·6 ± 0·37
adult	Mar. 1939	10	59·4 ± 17·89
	Mar. 1940	11	61·3 ± 17·05

(iii) *Microscopic structure of the testis*

A description of the cell types found within the testes of British starlings has already been given. Not all of these cell types were found in the Continental starlings because the birds left for their nesting places abroad before reaching full sexual maturity. All the cell stages which were found in the testes of the Continental birds were exactly similar to those found in the British birds, and a separate description is therefore unnecessary.

(iv) *Seasonal variations in the testis*

It was not possible to distinguish between the British and the Continental first-year males between the time in October when the Continental birds arrived in this country and the following February, and descriptions of the structure of the testes of first-year birds during this period have already been given. In the second part of February differences between

the two races became apparent. The Continental birds were distinguished by their much smaller testes, a difference which was further accentuated in March (figure 8). From early February until the second half of March, when the birds left for the Continent, division of the spermatogonia proceeded very slowly. Even at the time of leaving the testes were still very small, and the tunica albuginea was about 20μ thick. The seminiferous tubules were thin, and the intertubular spaces remained in the winter condition with closely packed connective tissue and pigment cells. The primary germ cells were usually pressed close to the basement membrane, and the spermatogonia, some of which were in division, filled most of the rest of the tubule space. About a week before the birds migrated the first primary spermatocytes in synizesis appeared in the centre of the seminiferous tubules (figure 56, plate 12), and just before this, the last of the large spermatogonia disappeared. This sequence of development from mid-February onwards was exactly the same as that of the British first-year birds, the only difference being that it was very much slower in pace.

The first adult male Continental starlings were taken in November, and these included the bird which was ringed as an adult in Latvia. The description of the structure of its testes, which also applies to the testes of the other Continental males, is as follows. The testis volume was very small (figure 10), only about half that of the smallest adult British testis recorded in any month, and the tunica albuginea was about 150μ thick. The seminiferous tubules were very thin, and compared closely with those of British birds in August. The intertubular spaces were crowded with pigment cells and common connective tissue cells. No interstitial cells were to be seen, perhaps because they were obscured by the pigment cells. The seminiferous tubules, sheathed in close masses of connective tissue cells, contained only primary germ cells and spermatogonia. The nuclei of the spermatogonia were of all sizes from 8 to over 20μ. One of the nuclei of the spermatogonia was the largest seen in any testis, and had a diameter of 21·5μ. Perhaps because of the growth of these cells there were no cavities in the centres of the tubules. In none of the testes from the birds of this group was there any sign of mitotic division in any cell, and the only activity appeared to be the growth of the nuclei of the spermatogonia. A few nuclei were seen in necrosis, and the general appearance of a testis of this group is shown in figure 58, plate 13. Birds taken during December had exactly the same testis structure as those taken in November, the slight increase in testis size during the month being explained by the slow increase in volume of many of the spermatogonia. Necrotic nuclei were still present in small numbers in the centres of the seminiferous tubules. In one or two individuals a few interstitial cells were seen in the intertubular spaces, and because of the crowded condition of the pigment cells the testis remained very dark grey in colour. In one bird taken on the last day of December, and in birds taken at the beginning of January, the first signs of mitotic division of the spermatogonia were evident. These cell divisions were, however, not frequent. They were not nearly so common as they were in the testes of adult British males in October and November, and up to the end of January individuals were frequently found in which no spermatogonia in division were evident. The wide range of sizes of the nuclei of the spermatogonia also remained.

At the beginning of February active division of the spermatogonia commenced. The testis increased in volume, and the tunica albuginea was reduced to a thickness of about

90μ. The seminiferous tubules began to swell, but still they did not seriously compress the intertubular spaces. The cells of the intertubular spaces separated slightly, and for the first time they could be clearly distinguished. Interstitial cells were not uncommon. Inside the seminiferous tubules most of the resting primary germ cells were pressed against the basement membrane, and the spermatogonia were centrally placed. The largest spermatogonia were reduced in size by successive mitotic divisions, but even at the end of the month, the range of nuclear diameters of this cell type was from 7·5 to 14·5μ. Division of the spermatogonia continued more rapidly in early March, and the size of the seminiferous tubules, and therefore of the whole testis, increased rapidly (figure 12). By the second week of March the tunica albuginea was reduced to about 20μ in thickness. The connective tissue cells of the tubule walls were pulled farther apart, and the pigment cells were drawn out and separated. The testis was then paler in colour. Interstitial cells, although they were not seen in division, increased in numbers in the corners between the tubules, and they were usually seen in small groups. Inside the seminiferous tubules the first primary spermatocytes were formed in the first week of March, and the first synizesis stages of meiosis were present in the centres of the tubules at the end of the week. The divisions of the spermatogonia and the production of primary spermatocytes in the synizesis stage continued up to the time when the birds left for the Continent. The day before they left, in both 1939 and 1940, the testes were swollen with spermatogonia and primary spermatocytes (figure 60, plate 13), but as none of the latter cells had completed the meiotic division, no secondary spermatocytes had appeared.

(v) *Accessory sexual organs*

In all the first-year Continental males between November and early February the accessory organs, as well as the testes, were indistinguishable from those of the first-year British males. The descriptions already given of the accessory organs of first-year males at these times of the year will not therefore be repeated.

Rete testis. In the second half of February the cavity of the rete testis of the first-year male began to expand slowly, but it was not until mid-March, when the birds left this country, that the lining epithelial cells were pulled apart. The cells then became individually distinct, and they were seen to be cuboidal in form. The cavity remained empty. At no time was the speed of growth or the size attained equal to that of the first-year British male at the same time of the year. The adult males in November possessed a rete testis which was very small and collapsed, smaller even than that of the adult British male during the summer months. The nuclei of the lining epithelium were pressed closely together, and the cavity was empty. No change in this structure took place during December and January, but in February, when the testis began to grow actively, the rete testis became more extensive. The size of the rete testis remained in proportion to that of the testis. At the time in March when the birds left, the epithelial cells were drawn out to form a normal cubical epithelium, but the cavity still remained empty.

Vasa efferentia. The vasa efferentia of the first-year Continental males showed the first signs of growth during February. The cavities of the tubules enlarged to a diameter of about 14μ, and they contained small amounts of what was apparently secretory matter. The epithelial cells lining the walls were stretched apart, and each cell then had a cubical

form with a very large nucleus and a very small amount of cytoplasm. At the time of migration the diameter of the tubule lumina was about 17μ. In the adult males no growth was apparent in the vasa efferentia until February. By early March the average diameter of the lumina of the tubules had increased from an autumn diameter of less than 10μ to a diameter of about 16μ. At the time of migration the diameter had reached nearly 20μ and the lumina contained quantities of apparent secretion. The cells of the tubule walls then formed a cuboidal epithelium.

Epididymis. At the beginning of February the epididymites of the first-year males were still in an undeveloped condition. Many tubules were entirely closed, and the cells lining them were pressed closely together. During February the lumina became more prominent, but it was not until mid-March that the first signs of secretion appeared in them. By the second half of March, the largest tubules had lumina with a diameter of about 12μ, and the cells of the lining epithelium were clearly defined and cubical in form. No cilia were distinguished. The adult males showed no growth of the epididymis throughout the autumn and early winter, and in this respect they were indistinguishable from the adult British males. In February development started. The lumina became prominent, reaching a maximum diameter of 6·5μ, and by the middle of March they had increased in size to an average diameter of about 23μ. The cuboidal cells lining the tubule walls were then clearly visible, and stereocilia appeared on their free inner edges. Only very small amounts of secretion were present in the lumina at the time of migration.

Vas deferens. The vas deferens of the first-year Continental male was exactly the same as that of the British first-year male except that, just before migration time, the duct tended to be less convoluted than that of the British bird. In the adult male in autumn the size of lumen and the structure of the wall were very similar to those of the adult British males. On the average, however, the duct tended to be straighter and even more collapsed than that of the British bird. No change in structure took place up to the time when the birds left, but in March the duct became more convoluted.

Seminal vesicle. In the first-year Continental male this organ was similar to that of the first-year British male except that it showed no growth during February and very little in March. At the time of migration, the tubules were only slightly larger than during the autumn and early winter. In the adult male in autumn the seminal vesicle was composed of far fewer tubules, and was therefore smaller than that of the adult British male at this time of year. The detailed structure of the tubules, however, was the same in both races of birds. In the adult Continental male there was no growth in the seminal vesicle in February, but in March the number of tubules composing the organ was doubled or trebled. At the time of leaving, the diameter of the lumina had reached about 18μ.

(vi) *Secondary sexual characters*

The youngest Continental starlings seen in this country in November are first-year birds, and these were found to be identical in their external morphology with the first-year British birds. This similarity in external appearance persisted throughout the autumn and winter. In the adult males marked differences were apparent between the Continental and British types.

Colour of the iris. In the majority of both first-year and adult Continental males the iris

was dark brown.* There was the same slight variation in this respect as in the first-year and adult British males.

Colour of the beak. In autumn and early winter the beaks of the first-year male Continental starlings were dark grey with a light grey cutting edge to both mandibles. As in the first-year British males, the base of the beak began to turn a dirty yellow colour about the second half of February. The beak of the adult Continental male did not begin to turn yellow in autumn, and it had the same dark colour with the lighter cutting edges as that of the first-year bird (figures 20, 21). In the adult the change of colour of the beak began about the middle of January (figure 22), a time when all adult British males had almost full yellow beaks. By the middle of February the most advanced Continental males had beaks about half yellow (figure 23), while the least developed had beaks still entirely dark grey. Pátkai (1939) describes how in Hungary the beaks of starlings do not begin to turn yellow until January or February, and Kluijver (1935) also indicates that the same is true in Holland. In mid-March, when the starlings left Yorkshire, their beaks varied from about two-thirds to almost full yellow (figure 24).

Lower throat feather. The first summer moult was completed before the first-year Continental males arrived in this country, and their feather structure (figure 85, nos. 10–12, plate 20) was quite indistinguishable from that of the first-year British birds. The rate of wear of the throat feathers was the same in both races, and a partial moult affecting some of the body feathers took place during early March. The throat feathers of the adult Continental males in November (figure 85, no. 13, plate 20) were exactly like those of the adult British males at this time. There was some wearing of these feathers during autumn and winter (figure 85, nos. 14, 15, plate 20), but this was not very marked and the white tips were still present in March. The birds therefore remained speckled in appearance during the whole of their stay in this country. A partial moult of the body feathers took place in early March, but the extent of this moult varied greatly in different individuals. New feathers on the throat were not common.

(*c*) *Comparisons and conclusions*

(i) *Testes*

The juvenile starling, when it left the nest in June, had relatively large testes (figure 5) in which division of the spermatogonia was frequently seen (figure 53, plate 12). Necrotic nuclei were common in July, and the testes reached a minimum size in late summer and autumn (figure 6). When the Continental birds arrived in October and November, the first-year birds of the two races were indistinguishable, and they remained so until February when testis growth commenced. The testes of the British birds then enlarged rapidly (figure 7), but those of the Continental birds only grew slowly (figure 8). Statistical comparisons of the testis volumes of the two races in February and March are given in table 4, the method followed being that recommended by Simpson & Roe (1939) for the comparison of small samples. In both February and March P, the probability that the two races were identical, is seen to be less than one in a hundred, and therefore the differences observed were significant.

* The iris colours described above approximate to the following reference numbers in the list of Ostwald Colour Standards: 4:6:pl.

TABLE 4

month	race	number in sample	mean volume and S.D.	value of t	probability P
Feb.	British	3	4·0 ± 0·42	6·14	<0·01
	Continental	2	1·6 ± 0·14		
Mar.	British	7	48·3 ± 11·28	10·84	<0·01
	Continental	9	4·6 ± 0·35		

The growth of the testes of the first-year British males continued until April, but no example was found of any such male which succeeded in producing spermatozoa. The most advanced cell stages which were recognized in the testes of the first-year males in April were the synizesis stages of the meiotic division of the primary spermatocytes, and it is concluded that the male starling does not normally breed when one year old. Towards the end of April necrotic nuclei appeared, and during May the testis volume rapidly diminished. The last signs of spermatogenesis were seen in early June.

In the adult British starlings testis growth started in September when mitoses of the spermatogonia were seen. Cell division (figure 57, plate 13) and a consequent increase in testis size (figure 9) took place fairly rapidly during October and November, but in December and January the rate of increase slackened and a few necrotic nuclei appeared. Adult male Continental starlings taken in autumn had very small testes (figure 10). Their volume was only about half that of the testes of adult British males at the time of their maximum regression in August, and only about a quarter that of the British testes in autumn. The testes of the adult Continental male also showed no signs of mitosis, and the slight increase in volume recorded from month to month appeared to be entirely due to an increase in volume of many of the spermatogonia (figure 58, plate 13). Such an increase in the size of the spermatogonia was not seen in the testes of British birds because in them spermatogenesis was proceeding actively. Very large spermatogonia were, however, present in the testes of all the first-year males at this time. In January mitotic activity of the spermatogonia in the adult Continental birds began, 4 months after the time when the first signs of such activity were noted in the British males, but the rate of testis growth remained very slow. In February the testes of the adults of both races of birds showed greatly increased activity, but the rate of growth in the British birds continued to be much greater than that in the Continental birds (figures 11, 12). These differences in the times and rates of growth of the testes of the adults of the two races are shown in table 5, and it is also seen that in all months, as P is less than 0·01, the differences between the two races are statistically significant. During February primary spermatocytes were common in the testes of the British males, and early in March the first spermatozoa were formed (figure 59, plate 13). In the Continental birds the first primary spermatocytes were formed early in March, and no more advanced stage than the synizesis of meiosis was found in them at migration time (figure 60, plate 13).

In the adult male British starlings active spermatogenesis continued, but it was not until mid-April that the spermatozoa, released into the centres of the seminiferous tubules, passed down to the seminal vesicles. From this time onwards regression took place more or less rapidly, and at the time when the young of the first brood left the nest, the testes of the

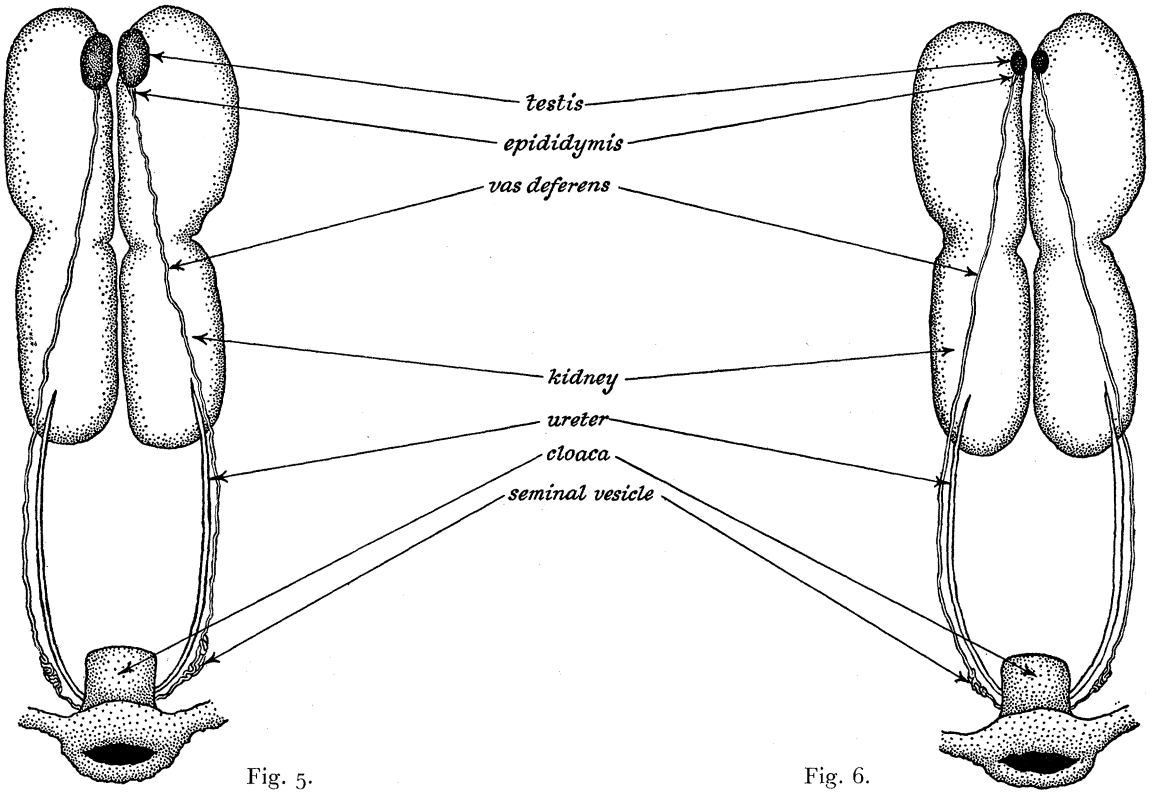


Fig. 5. Fig. 6.

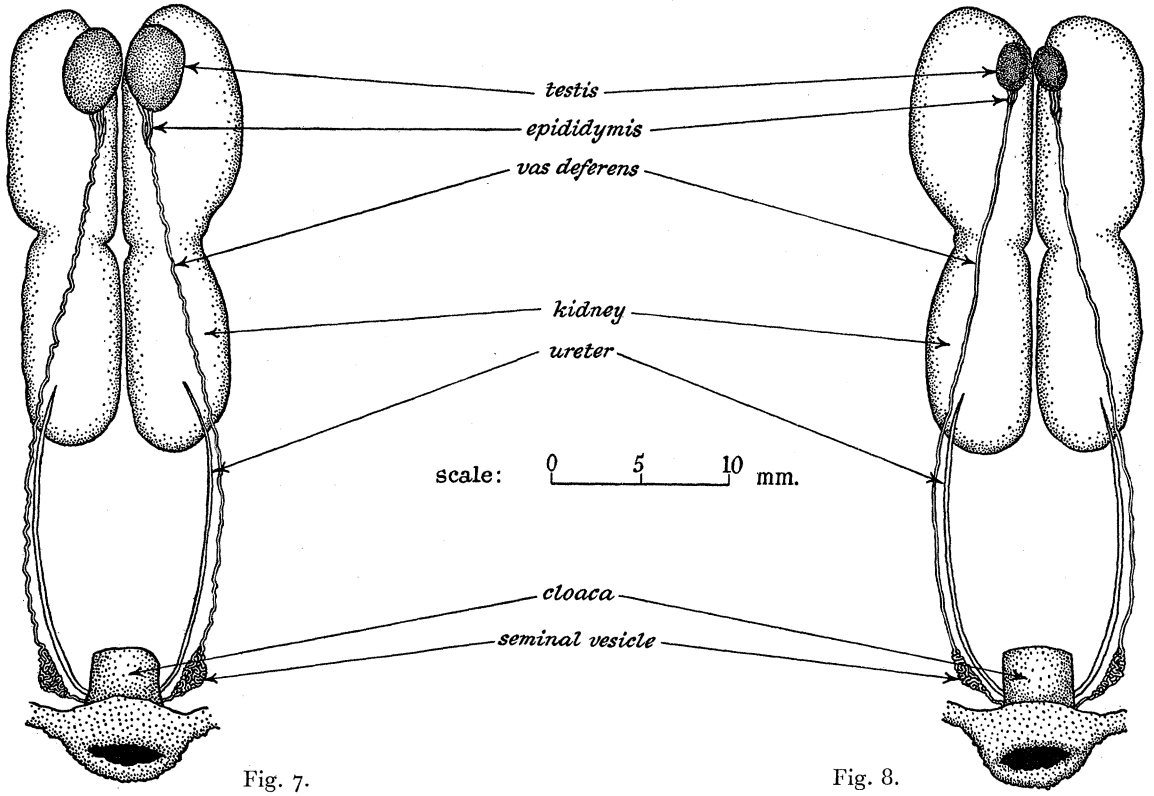


Fig. 7. Fig. 8.

Reproductive systems of male starlings

FIGURE 5. Juvenile British male in June.

FIGURE 6. First-year British male in November.

FIGURE 7. First-year British male in early March.

FIGURE 8. First-year Continental male in early March.

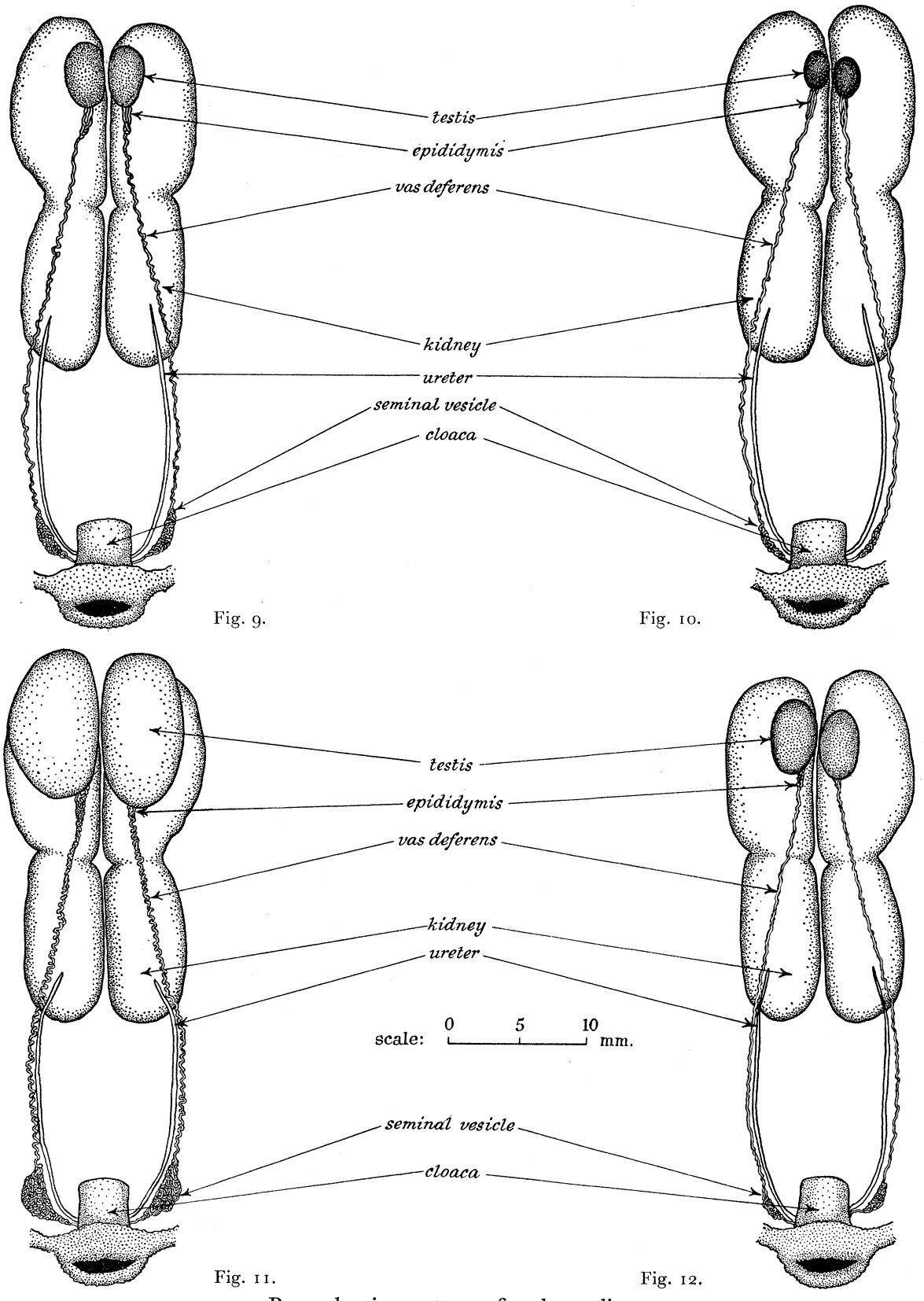


Fig. 9. Fig. 10.

Fig. 11. Fig. 12.

Reproductive systems of male starlings

FIGURE 9. Adult British male in November.

FIGURE 10. Adult Continental male in November (ringed in Latvia in 1935).

FIGURE 11. Adult British male in early March.

FIGURE 12. Adult Continental male in early March.

adults were much reduced. By this time also spermatogenesis had frequently ceased, but it sometimes happened that the parents were able to produce a second brood.

TABLE 5

month	race	number in sample	mean volume and s.D.	value of t	probability P
Nov.	British	6	16·4 ± 1·90	12·64	<0·01
	Continental	5	4·3 ± 0·42		
Dec.	British	10	17·6 ± 1·91	16·64	<0·01
	Continental	7	4·6 ± 0·36		
Jan.	British	4	19·2 ± 1·65	16·24	<0·01
	Continental	6	6·0 ± 0·57		
Feb.	British	10	62·0 ± 14·20	10·53	<0·01
	Continental	10	11·7 ± 2·06		
Mar.	British	28	1670·1 ± 383·60	18·79	<0·01
	Continental	21	60·4 ± 22·20		

(ii) *Accessory sexual organs*

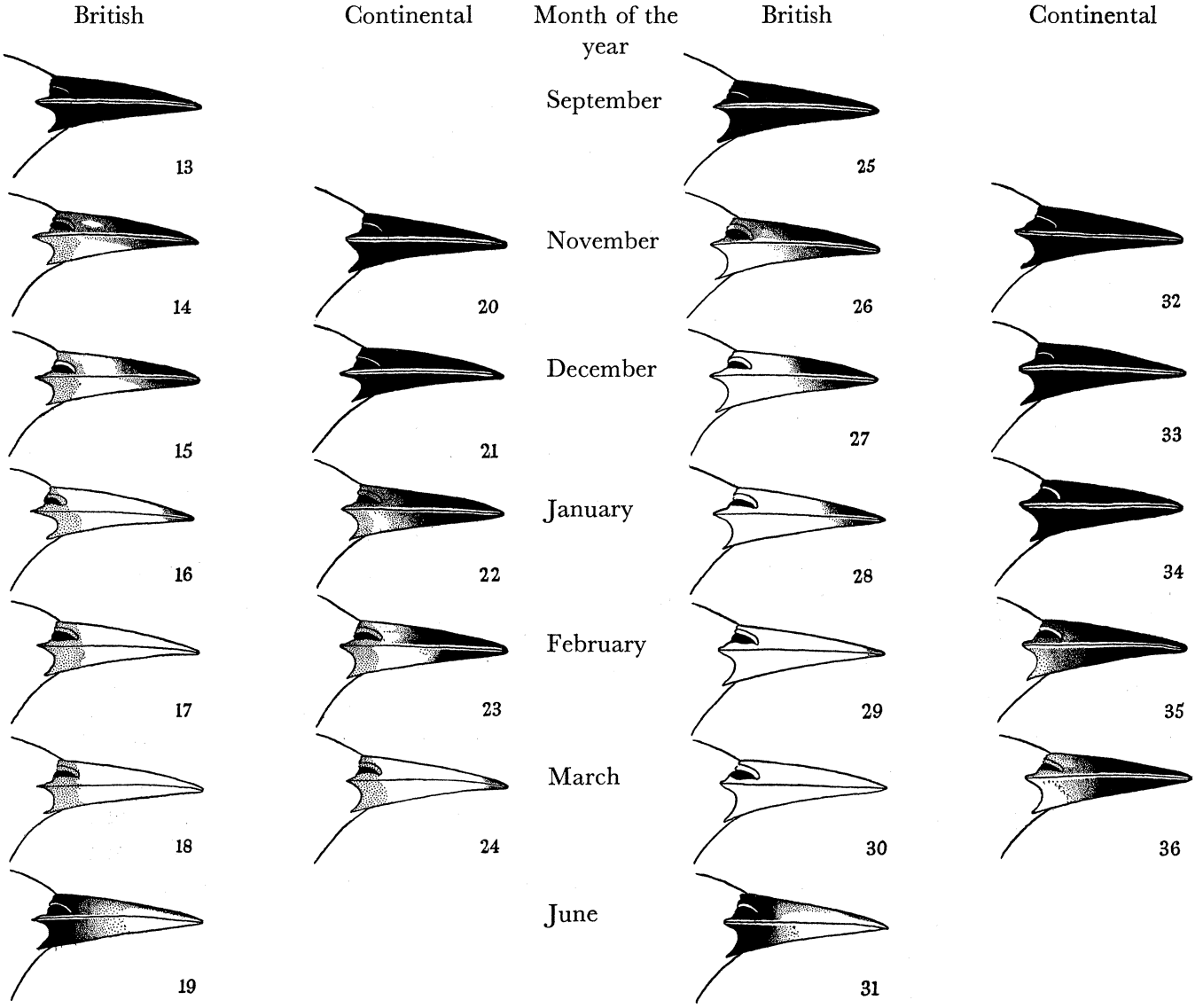
All the accessory organs appeared to depend for their degree of development on the activity or otherwise of the testes, and in many of the organs differences between the British and Continental races were as apparent as they were in the testes themselves. These differences, seen most clearly in the adults, were more evident in some structures than in others. This may perhaps be explained by a theory that some of them respond only to a higher threshold of reproductive activity. Probably a relatively high rate of male hormone secretion is required to stimulate such an organ as the epididymis, but in general the growth of all the accessory sexual organs kept pace with that of the testes.

Little change in the structure of the accessory sexual organs of the first-year males took place in autumn and early winter. Growth started in late February and March when the organs of the British birds enlarged more rapidly than those of the Continental birds. In the adult male British starling in autumn the rete testis and the vas deferens were the only two structures which showed any clear change. The cavity of the rete testis enlarged during October, November, and December, and the cells of its walls were pulled out into a cubical epithelium. No change took place at this time in the histological structure of the vas deferens, but owing to an increase in length, the duct became more convoluted. Neither of these autumn changes was evident in the adult male Continental starling, and in that bird the accessory sexual organs remained in a state of extreme regression. As in the case of the testis this regression was often much more extreme than that of the organs of the British birds in August, the time of their minimum development. This was especially true of the seminal vesicle. Growth of all the accessory sexual organs took place in the adults of both British and Continental males in late January, February, and March. In the case of the British birds this growth often started more than a month earlier, and it was more rapid and of greater extent than in the Continental birds (figures 63, 64, plate 14).

(iii) *Secondary sexual characters*

The colour of the iris was the one secondary sexual character which did not vary with the seasons. In most male birds the colour was dark brown, and only a very small proportion, about 5%, had pale brown or yellow irises.

The male starling in summer had a very dark grey beak, but in the breeding season the beak was bright yellow. Witschi & Miller (1938) have shown that the yellow colour is a secondary sexual character whose development is dependent on the secretion of male sex hormone by the gonads. The change in colour from dark grey to yellow is therefore a clear indication of testis activity resulting in the production of male hormone. As the beak of



FIGURES 13–36

Beaks of adult male starlings

Beaks of adult female starlings

the starling grows from the base and is worn away at the tip by continued use, the base of the beak is usually the first part to show a colour change, and the tip is the last part at which the change is complete. When the beak was yellow, a blue-grey base, which was especially marked on the lower mandible, formed a very clear male character. Only rarely was a male bird found with an entirely yellow beak. The juvenile and first-year birds had entirely dark beaks throughout their first summer, autumn, and early winter. In the first-year males of both races the change to a yellow beak commenced in February when the

gonads showed their first signs of growth, and in the British birds the change was complete in the second half of April. In the adult males very marked differences in colour between the beaks of the British and Continental birds were apparent during autumn and winter. The autumn testis growth of the British birds resulted in the development of the yellow beak, and the change in colour started in October and November (figure 14). An almost completely yellow beak was usually present by the beginning of January (figure 16), the time when, because of the start of testis growth, the beaks of the adult Continental males also began to turn yellow at the base (figure 22). The change in the beak colour of these Continental birds was not usually complete by the time the birds left the country in March (figure 24), so that throughout the entire autumn and winter this feature alone was sufficient to distinguish the two races. The beaks of the British males turned dark again during late June and July (figure 19), and as in all the changes in colour which affected the beaks of the male birds, there was relatively little variation between the individuals of the same age group in the time at which the change commenced.

The third secondary sexual character studied was the structure of the feathers of the lower throat. These feathers were very blunt in the juvenile male (figure 85, no. 1, plate 20), fairly blunt in the first-year male (figure 85, no. 2, plate 20), and pointed in the adult (figure 85, no. 6, plate 20). There was one complete moult each year, and this took place in summer. There was also a partial moult in March, but this varied greatly in extent in different individuals and only affected the body feathers. Except in the juvenile, all the feathers when first formed had white tips. These were large in the first-year males and small in the adults. The white tips to the feathers of all the first-year males wore slowly (figure 85, nos. 2–5, plate 20), and often even after 12 months they had not entirely disappeared. In the adult British males, however, the rate of wear of the feathers was rapid (figure 85, nos. 6–9, plate 20). Due to the growth of the testes these birds took a great interest in their nesting holes throughout the autumn and winter, and were constantly visiting them. This caused so much wear that by January or February the white tips of the head, throat, and breast feathers had usually entirely disappeared. Feather wear did not take place to the same extent in the Continental adult males (figure 85, nos. 13–15, plate 20) because these birds, having smaller testes, showed no interest in nesting holes. It was the similar lack of interest of the first-year birds which prevented any extreme wear of their throat feathers, and all the Continental birds at the time when they left this country still retained the white tips to their feathers.

(iv) *General conclusion*

The reproductive cycle of the male British starling and part of that of the male Continental starling have been described. It is shown that significant differences exist between the times and the rates of growth of the testes of the birds of these two races, both of which are present in the British Isles in autumn and winter. The testis development of the adult British males starts earlier and proceeds more rapidly, and as a result of this, the structure of the accessory sexual organs, the colour of the beak, and the structure of the feathers undergo changes which are not seen until much later in either the adult male Continental birds or any of the first-year birds.

(3) The female starling

(*a*) *British*

(i) *Female genital system*

In the very early development of the female starling the right ovary rudiment disorganizes together with the right Müllerian duct. Only the left ovary and the left Müllerian duct are to be seen in the juvenile, first-year, and adult female starlings, although in all these birds both right and left Wolffian ducts remain. During the greater part of the year the ovary is a small flattened organ, pale pink or white in colour. The dorsal side of the ovary, the hilus, is attached by the mesovarium to the dorsal wall of the body cavity near the anterior end of the left kidney. The free ventral surface of the ovary is covered by a single layer of cells which, being the source of the new ova, is called the germinal epithelium, and immediately inside this epithelium is a thin connective tissue sheath, the tunica albuginea. Beneath these two layers is a zone of very young primary oocytes, and nearer the hilus are older and larger oocytes. At the dorsal side, the base of the ovary, the largest oocytes are found, but in the first-year and adult birds, these are usually so large that they force their way back to the surface. They then bulge out from the ovary, and are covered only by the follicle cells, which invest every oocyte, the tunica albuginea, and the germinal epithelium. The Müllerian duct, which forms the oviduct, opens into the body cavity at a point just lateral to the ovary. From this point it passes back on a more or less tortuous course until it joins the left side of the cloaca. The oviduct has thick walls especially in the breeding season, and it is formed of an outer layer of connective tissue, middle layers of smooth muscle, an inner connective tissue layer, and an inner lining epithelium. In the breeding season an additional thick layer of secretory cells is developed between the muscle layers and the inner connective tissue layer.

The Wolffian system is also well developed, and undergoes seasonal variations. In the hilus of the ovary is a terminal mass of tubules which end blindly. This is equivalent to the epididymis of the male, and it is known as the epoöphoron. At the posterior end of the hilus these ducts join to give rise to the vas deferens which, after crossing the surface of the kidney, keeps close to the ureter on the right side and to both the ureter and the oviduct on the left side. At the posterior end of the body cavity the Wolffian duct is coiled to form a seminal vesicle which, although longer and more loosely constructed, is similar to that of the male. Finally, by a short duct, each seminal vesicle opens into the cloaca. The detailed structures of all the organs of the Wolffian system of the female are exactly similar to those of the male.

(ii) *Maximum diameters of oocytes*

For ease of comparison of the reproductive systems of young and old and of British and Continental male starlings, the testis volumes were measured. In the case of the females it did not prove feasible to measure the volumes of the ovaries as these have an irregular shape and are very difficult to separate from the underlying kidneys and adrenals. An alternative method was therefore adopted which, in the majority of cases, involved measuring with a micrometer scale the diameter of the largest oocyte in the ovary after sectioning. In the case of the very large eggs present in the ovaries in the breeding season, the measure-

ments were made with callipers. The figure given in each monthly group represents the average maximum oocyte diameter, and the number of individuals examined and the standard deviation from the mean are also recorded. The standard deviation was calculated according to the formula already given in the case of the testis volumes of the British males. The results are given in table 6.

TABLE 6

type of bird	month	number in sample	mean of maximum oocyte diameters (in mm.) and S.D.
juvenile	June	10	$0{\cdot}12 \pm 0{\cdot}024$
	July	11	$0{\cdot}17 \pm 0{\cdot}017$
	Aug.	6	$0{\cdot}28 \pm 0{\cdot}019$
first year	Sept.	6	$0{\cdot}33 \pm 0{\cdot}023$
	Oct.	3	$0{\cdot}38 \pm 0{\cdot}031$
	Nov.	3	$0{\cdot}42 \pm 0{\cdot}025$
	Dec.	6	$0{\cdot}56 \pm 0{\cdot}045$
	Jan.	3	$0{\cdot}55 \pm 0{\cdot}040$
	Feb.	4	$0{\cdot}71 \pm 0{\cdot}047$
	Mar.	11	$1{\cdot}05 \pm 0{\cdot}089$
	Apr.	3	$12{\cdot}17 \pm 2{\cdot}030$
	May	4	$10{\cdot}52 \pm 3{\cdot}130$
	June	4	$1{\cdot}37 \pm 0{\cdot}550$
	July	4	$0{\cdot}59 \pm 0{\cdot}053$
adult	Aug.	5	$0{\cdot}42 \pm 0{\cdot}030$
	Sept.	7	$0{\cdot}51 \pm 0{\cdot}037$
	Oct.	3	$0{\cdot}63 \pm 0{\cdot}026$
	Nov.	4	$1{\cdot}04 \pm 0{\cdot}128$
	Dec.	5	$1{\cdot}15 \pm 0{\cdot}082$
	Jan.	3	$1{\cdot}20 \pm 0{\cdot}046$
	Feb.	3	$1{\cdot}36 \pm 0{\cdot}061$
	Mar.	14	$1{\cdot}54 \pm 0{\cdot}130$
	Apr.	8	$12{\cdot}12 \pm 1{\cdot}410$
	May	6	$11{\cdot}58 \pm 1{\cdot}582$
	June	9	$8{\cdot}13 \pm 2{\cdot}520$
	July	4	$1{\cdot}61 \pm 0{\cdot}499$

(iii) *Microscopic structure of the ovary*

Unlike the testis, very little proliferation of the germ cells takes place in the ovary, and the main seasonal changes are due to variations in the size of the largest primary oocytes. All the cell stages up to the full-grown primary oocyte have been recognized, and they are described below. The nuclear divisions which result in the formation of the polar bodies, the secondary oocyte, and the ovum have not been seen. It appears that they take place either just before or just after the release of the egg from the ovary as they are known to do, for instance, in the case of the swallows *Hirundo r. rustica* L. and *Delichon u. urbica* L. (Durme 1914). A close examination of many of the largest eggs would be necessary before these nuclear divisions could be found, and owing to the enforced curtailment of this work, such an examination was impossible. The following are the descriptions of those cell types which have been found in the ovary of the starling:

Connective tissue cell. Cells of this type are found embedded in, or closely associated with, the thin tunica albuginea which sheaths the ovary (figure 37). These are known as the connective tissue cells of the tunica albuginea, and they have long thin nuclei of about 7·5 by 2μ. The cytoplasmic cell limits are rarely distinguishable. Between the developing oogonia and oocytes there is also a reticulum of connective tissue strands, and the cells associated with these are termed the common connective tissue cells (figure 37). These also have long thin nuclei, but they tend on the average to be larger than the nuclei of the cells of the tunica albuginea. They vary in length between 7 and 10μ, and in breadth between about 2 and 3μ. In favourable sections their cell limits can be seen, and these measure about 14 by 3·5μ. The third type of connective tissue cell is found in the thecae interna and externa of the thick follicle walls of the largest primary oocytes. These are known as the connective tissue cells of the follicle wall, and they vary considerably in shape. Most of the

nuclei are long and narrow and very similar in size to those of the cells of the tunica albuginea, but some, where there is little tension, are nearly oval and others, under extreme tension, are threadlike. Occasionally in early spring the more oval nuclei may be seen in mitosis, but apart from this, no signs of cell division have been seen in any connective tissue cell.

Interstitial cell. In the spaces between the developing oogonia and oocytes there are large numbers of interstitial cells (figure 37). In section the nuclei of these cells appear round or oval, and they have an average diameter of about 7μ. One or two nucleoli and several small chromatin granules are present in the clear nuclear space. The cytoplasmic cell limits can frequently be distinguished, and the whole cell has an average size of 11 by 8μ. Very occasionally the nuclei may be seen in mitosis, but normally they are in a resting condition.

Follicle cell. These cells are always present as a sheath round each developing egg (figure 37). Three or four of them become associated with the very small oogonium, and as the egg grows their number greatly increases. Round the younger eggs they form a layer one cell in thickness. The nuclei, which appear either oval or round, have an approximate diameter of 6μ, and the dimensions of the whole cell, which is roughly cubical, are about 9μ. The nuclei are normally in a resting state with one, two, or three nucleoli, but occasionally they are seen in mitosis. At the beginning of the secondary growth phase of the primary oocyte, when the yolk vacuoles begin to appear, the follicle cells become closely crowded and columnar in form. Then some are pushed inwards to form a second layer (figure 41), and as the growth of the oocyte continues and the darkly staining yolk droplets are laid down, the layer of follicle cells may be as much as four cells in thickness (figure 43). At this time the nuclei are closely packed, and the cell limits are obscure. Throughout the secondary growth phase of the primary oocyte, mitoses of the nuclei of the follicle cells are common.

Germinal epithelial cell. The layer of cells outside the tunica albuginea is known as the germinal epithelium (figure 37; figure 75, plate 17). It is made up of large numbers of small cells which may be regarded as primary germ cells although the great majority of them develop no further. As the ovary grows and the germinal epithelium expands, these cells, after enlarging slightly, may be seen in mitosis, the long axis of the spindle being nearly parallel with the surface of the ovary. The nuclei of the resting cells are usually either spherical or ovoid, and they have an approximate diameter of 4μ. They form a single layer of cubical epithelium which in exceptional circumstances of extreme tension may become squamous, or with lack of tension may be closely crowded and columnar. It is only rarely that the cells are seen in anything other than a resting condition when one or two large and several small chromatin masses are present in the nuclear space. When an oogonium is about to be formed, however, the nucleus of the primary germ cell swells slightly to a diameter of about 5μ, and at the same time it becomes clearer (figure 37; figure 75, plate 17). Stages of mitosis may then be seen in which the long axis of the spindle is nearly vertical to the tunica albuginea. One of the daughter nuclei formed by this division passes through the tunica albuginea into the ovary.

Oogonium. The cell which is derived from the division of the primary germ cell in the manner just described is termed an oogonium. It has not been seen to divide, and it grows rapidly into a small primary oocyte. When first formed and lodged just inside the tunica

albuginea, the nucleus of the oogonium is roughly spherical, and has a diameter of about 7μ (figure 76, plate 17). It is surrounded by a few follicle cells which increase in numbers as the oogonium rapidly increases in size. It is considered that the developing egg ceases to be an oogonium and becomes a primary oocyte when the first darkly staining granules, which later form the nucleus of Balbiani, appear in the cytoplasm (figures 37, 38). The nuclear diameter of the oogonium just before this transition stage is about 20μ, and the total cell diameter is about 35μ. The cell limits of all except the smallest oogonia are well marked, and the cytoplasm contains no granules. In all cases the nucleus is resting, and the nuclear space contains threads of chromatin joining small chromatin masses.

Primary oocyte of the primary growth phase. In the clear cytoplasm of an oogonium of between 32 and 36μ total diameter, there are suddenly laid down numbers of small granules and threads of a substance which stains darkly with iron haematoxylin (figure 38). These darkly staining inclusions are at first thinly distributed throughout the cytoplasm, but they quickly tend to become thicker and more abundant. When the primary oocyte reaches a diameter of about 38μ, they collect together in a compact mass which has been called the yolk nucleus or the nucleus of Balbiani (figure 37). This nucleus of Balbiani has strands extending into the surrounding cytoplasm which is otherwise almost free of these inclusions. As the growth of the primary oocyte proceeds, the dense nucleus of Balbiani rapidly becomes larger and larger until it spreads almost to the edges of the cell. A relatively clear peripheral zone, which is very narrow, usually remains. Bissonnette & Zujko (1936) have suggested the possibility that the clearer peripheral zone is formed by a secondary clearing after the nucleus of Balbiani has spread right to the periphery, and this theory may be correct. The nucleus of the primary oocyte becomes very simple in structure, and is made up of densely packed but lightly staining material containing two or three very black chromatin globules. In a primary oocyte with a diameter of between 135 and 150μ, a clearing of the cytoplasm appears either centrally or towards one side (figure 38). A single clearing may appear in this way, or several small ones may be found at various places in the dense nucleus of Balbiani. In either case they expand until the dark staining inclusions have entirely disappeared.

Primary oocyte of the secondary growth phase. The primary oocyte then has a diameter of about 185μ, and the nucleus a diameter of about 65μ. The nucleus remains very simple in structure with dense masses of pale material containing two or three very dark spheres of chromatin. The wall of the nucleus usually appears to be double due to the fact that it is surrounded by a narrow but well-defined loose and very pale zone. The cytoplasm has a narrow outer zone which, under high magnifications, appears to be less coarse in structure than the larger central region. None of the dark cell inclusions which mark the primary growth phase remain. The primary oocyte grows and still retains the clear cytoplasm of the central zone with the denser peripheral zone. No change takes place in the appearance of the nucleus which, while becoming larger and larger, remains clear. When a cell diameter of about 475μ is reached, small vacuoles appear along the outer edge of the central zone (figure 39), and it seems probable that these contained some lipoid material which dissolved out during fixation and subsequent treatment. As the primary oocyte increases in size, the vacuoles spread inwards, and finally they extend throughout the whole central zone.

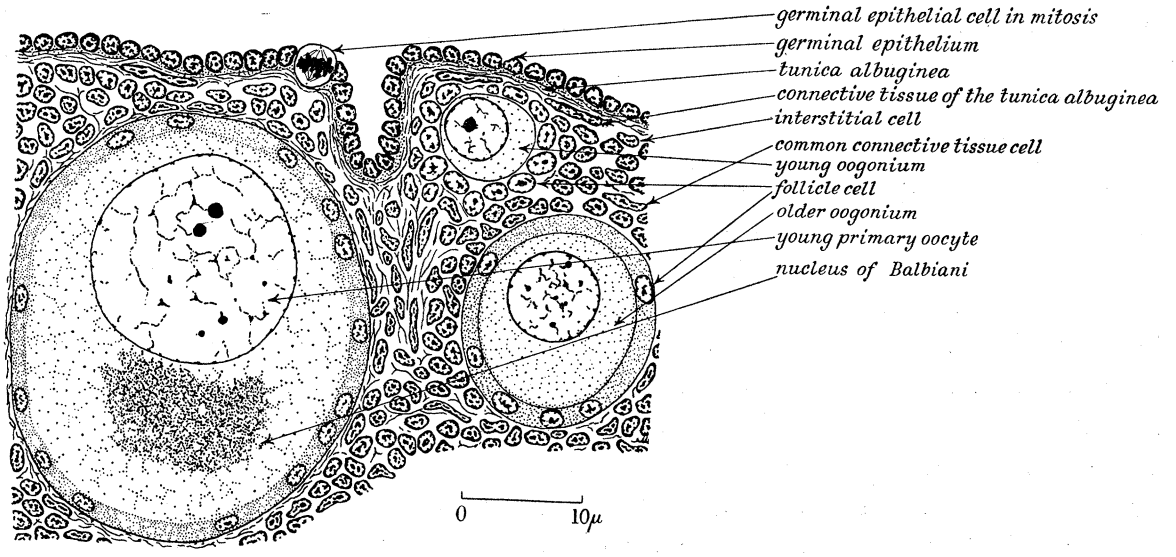


FIGURE 37. Early stages of oogenesis (from an adult British female in June).

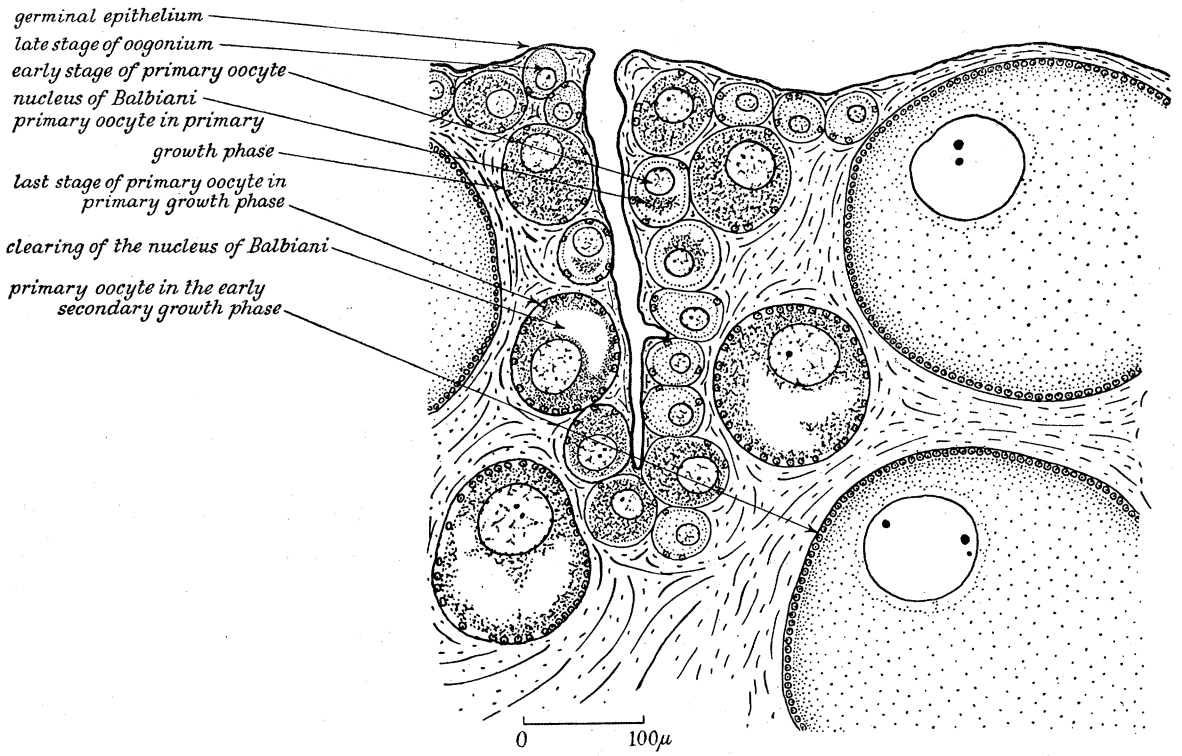


FIGURE 38. Early stages of the primary oocyte (from an adult British female in June).

Types of cells present in the ovary of the starling.

During the process of spreading, the innermost rings of vacuoles are small, but they quickly grow to the normal size of about 12μ diameter. Then new small vacuoles appear in zones in the centre, and in concentric rings among the older larger vacuoles. At first these growing zones may be restricted to the centre of the egg and to a region about half-way to the periphery (figure 40), but as the size of the oocyte increases, there may be as many as three concentric growing zones between the centre and the periphery. In some oocytes such clear zonation is not evident, but in all cases the centrally placed vacuoles are the smallest. During all this time the peripheral zone of cytoplasm remains clear. It is not affected by the process of vacuolation, and it increases in width as the whole oocyte grows. Thus it retains its relative width. When the primary oocyte of the secondary growth phase reaches an approximate diameter of 850μ, small yolk droplets appear round the edge of the central vacuolated zone (figure 41). When first formed, these droplets, which are spherical and stain jet black with Heidenhain's iron haematoxylin, have a diameter of less than 1μ, but they rapidly increase in size. They often appear to be situated inside the clear vacuoles, but frequently they are either in the walls of the vacuoles or outside them altogether. They also appear in the peripheral zone of the cytoplasm where there are no vacuoles. As the yolk droplets first laid down increase in size, small new droplets appear towards the centre of the oocyte and outside in the clear peripheral zone. Finally, the droplets make their appearance from the centre almost to the periphery (figure 42), the largest droplets then being those on the outside of the vacuolated central zone and the smallest those in the centre of the egg and in its periphery. As the yolk droplets spread into the peripheral zone, vacuoles appear after them until finally this zone is almost eliminated. At the beginning of this last process the peripheral zone is about 60μ in width, and at the end it is less than 5μ in width. The dark yolk droplets increase to a maximum diameter of about 12μ, and then start to break down into many small droplets. Each mass of small droplets grows and becomes irregular in shape, and the great majority of these masses are now situated inside the vacuoles which they entirely fill (figure 43). As in all other changes in the yolk during the secondary growth phase, this transformation is first seen in the peripheral zone whence it spreads inwards towards the centre. Throughout the entire secondary growth phase no change, other than an increase in size, is evident in the nucleus.

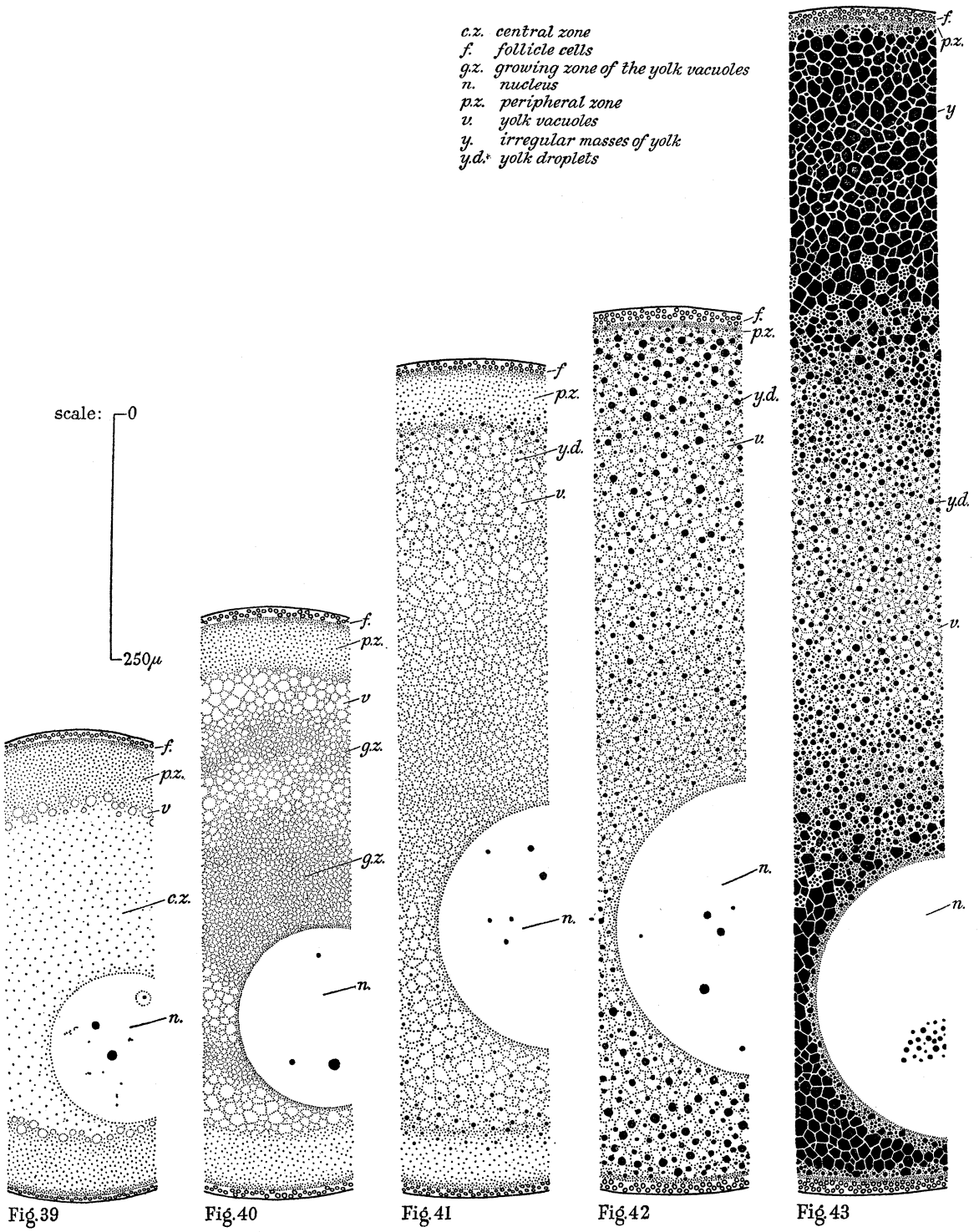
Secondary oocyte and ovum. No further change in the structure of the developing oocyte has been traced, and it appears that the final maturation divisions take place either just before or just after the egg is shed from the ovary.

'*Luteal*' *cell.* After the egg has been shed from the follicle, a structure very similar to the corpus luteum of the mammal is formed (figure 74, plate 17). The cells composing this are termed 'luteal' cells, and in the hen (*Gallus gallus* L.) it has been confirmed that the yellow pigment associated with these cells has a similar chemical constitution to that in the corpus luteum of the cow (*Bos bos* L.) (Pearl & Boring 1918). The 'luteal' cells of the starling are derived from the follicle cells, and possibly also from some of the connective tissue cells of the theca interna. They are relatively large cells with a diameter of about 13μ. The cytoplasm is clear and has a reticulate appearance. The cell walls are well defined, and the nuclei, which have an approximate diameter of 6μ, may be situated either centrally or asymmetrically. It is not known whether these 'luteal' cells have any secretory function.

(iv) *Seasonal variations in the ovary*

Juvenile starlings, shortly after leaving the nest, contained the smallest ovaries examined (figure 45). The germinal epithelia were relatively active, many mitoses being found, and there were many newly formed and very small oogonia just beneath the tunica albuginea. This tunica was very thin in both juvenile and adult ovaries, and nowhere did it exceed a thickness of 7μ. The ovary of the juvenile bird in June was almost entirely made up of oogonia of various sizes, and a very clear zonation of these sizes was evident (figure 65, plate 15). The smallest oogonia were just beneath the tunica albuginea, and the largest were situated deep within the ovary, near the hilus. Among the largest oogonia occasional eggs were found which had passed into the earliest stages of the primary growth phase of the primary oocyte. These primary oocytes usually contained evenly distributed darkly staining cytoplasmic inclusions, but occasionally an oocyte was discovered with a fully developed nucleus of Balbiani. The spaces between the oogonia and oocytes were packed with interstitial and connective tissue cells. Considerable growth took place in the ovary during the summer, and by August the organ was relatively large. Mitoses in the germinal epithelium, although not common, were still occasionally found, and just below the tunica albuginea there were numbers of young oogonia. The zonation of the various sizes of oogonia and oocytes was still evident, and all stages were found between a very young oogonium (adjacent to the tunica albuginea) and a primary oocyte with a disorganizing nucleus of Balbiani (near the hilus). The largest eggs remained deep down in the ovary, and it was between these that the masses of interstitial and connective tissue cells were largest.

In the first-year starling in autumn the growth of the largest oocytes continued (figure 46; figure 66, plate 15). The activity of the germinal epithelium had, however, ceased entirely, and, as a consequence, fewer small oogonia were present near the surface of the ovary. As autumn passed, the zonation of the various cell sizes was partially destroyed when the largest growing oocytes pushed their way up towards the surface. All the largest eggs were primary oocytes, and the majority of them contained either a fully developed nucleus of Balbiani or one which was in the process of breakdown. In no case, however, had the breakdown of this nucleus been completed, and therefore no primary oocyte had yet entered on the secondary growth phase. In December and January little, if any, change took place. In early February the inactivity of the germinal epithelium continued, and there were relatively few small oogonia. The majority of the primary oocytes showed some trace of the nucleus of Balbiani, but after the middle of the month, the largest primary oocytes had the clear cytoplasm typical of the earliest stage of the secondary growth phase. Most of the largest oocytes had pushed their way to the surface of the ovary so that almost all signs of zonation were finally eliminated. With the growth of the primary oocytes, the follicle cells also started to multiply rapidly, and they were frequently seen in mitosis. In March the germinal epithelium remained quiescent, and the increase in the size of the ovary was entirely due to the growth of the largest oocytes (figure 47) which still, however, showed no signs of vacuolation of the cytoplasm (figure 67, plate 15). The follicle cells continued to divide actively, and those associated with the largest oocytes formed a layer two cells in thickness. At the same time, two layers of connective tissue, the thecae interna and externa, thickened round the follicle. The steady growth of the largest eggs continued into April, and then a very rapid increase in size of several of these large eggs took place.



FIGURES 39–43. Yolk formation in the secondary growth phase of the primary oocyte.

They protruded from the surface of the ovary, flattening and extending the cells of the germinal epithelium which covered them. Both the germinal epithelium and the tunica albuginea were thrown into deep folds which often extended nearly to the base of the ovary. Only a few oogonia and primary oocytes of the primary growth phase then remained. The majority of the eggs were in the secondary growth phase of the primary oocyte, their cytoplasm had become vacuolated (figures 39, 40), and in many the first black-staining yolk droplets had appeared (figures 41, 42). These droplets multiplied throughout the cytoplasm, broke up, and reformed as the final yolk (figure 43). The oocytes were then growing with extreme speed, and the final growth phase, from the first appearance of the black-staining yolk droplets to the full-grown ovum, was completed within 10 days. The first eggs were shed before the end of April, and it is probable that the final reduction divisions took place at this time.

After the shedding of the eggs, the empty follicles collapsed. The follicle cells spread inwards and formed a solid core surrounded by the connective tissue cells of the much-thickened thecae interna and externa (figure 73, plate 17). Many of the follicle cells and connective tissue cells became necrotic, broke down, and finally disappeared. Those follicle cells which remained enlarged to form a clear central mass of 'luteal' cells. Some 'luteal' cells were also present in the theca interna, but the majority of the cells in this layer remained small. In the theca externa no 'luteal' cells were seen (figure 74, plate 17). The structure formed in this way closely resembled the corpus luteum of the mammal, and besides these true 'corpora lutea', the ovaries of birds which had completed one breeding season also contained atretic 'corpora lutea' in various stages of formation at all seasons of the year. An atretic 'corpus luteum' was formed after the collapse of an egg which, in all of the many instances which were noted, had developed as far as the secondary growth phase of the primary oocyte. Sometimes the cytoplasm of the oocyte burst through the follicle wall, and so escaped either to the outside of the ovary or into the spaces between the connective tissue strands within the ovary. In other cases, the first signs of atresia were given by the collapse of the follicle as the oocyte was absorbed, a small absorption vacuole appearing in the yolky cytoplasm opposite each follicle cell. Whether the egg burst outwards or was simply absorbed, the follicle cells spread in among the remnants of the oocyte, and when the absorption of these remnants was complete, they formed a solid core of cells indistinguishable from that of the true 'corpus luteum'. During the process of absorption many of the follicle cells and connective tissue cells underwent necrosis, and the thecae interna and externa became thickened. Both true and atretic 'corpora lutea' appeared to persist for about two months, but during this period, they became smaller and smaller until, just before their final disappearance, they were represented only by small groups each of about a dozen 'luteal' cells.

About the time of the shedding of the eggs, the germinal epithelium again became active (Bullough & Gibbs 1941). Considerable numbers of these epithelial cells were stretched so flat by the growth of the primary oocytes that they were apparently incapable of division. In those regions, however, where the germinal epithelium was tucked right down into the ovary between the developing oocytes, the epithelial cells were clearly defined and cubical in form, and it was there that the mitoses were especially common. A cell, when about to divide, enlarged to three or four times its original volume, and the cytoplasm became very

clear and transparent (figure 75, plate 17). Sometimes the plane of division was approximately at right angles to the surface of the ovary, and sometimes it was approximately parallel to the surface. In the former case it is probable that, as in the mouse (*Mus musculus* L.) (Allen 1923), the daughter cells would both remain in the germinal epithelium, but in the latter case, the lower cell passed through the tunica albuginea and formed a very small oogonium just below the surface of the ovary (figure 76, plate 17). In May these very young oogonia, each surrounded by two or three follicle cells, were common all along the inner side of the tunica albuginea. The wave of mitoses in the germinal epithelium quickly died down, but in those birds which produced a second brood in June, a second wave of mitoses occurred. Probably, however, such second broods, and consequent second waves of mitoses, are only found in birds of two or more years of age.

The ovaries of first-year birds in May contained many stages of true and atretic 'corpora lutea', and by June the ovary was very small. The activity of the germinal epithelium ceased entirely, and there were large numbers of young oogonia and of primary oocytes in the earliest stage of the primary growth phase. A few larger primary oocytes containing nuclei of Balbiani were also present, and there were some primary oocytes in the early secondary growth phase which were apparently left over from the previous cycle of development. By the end of June, many of the 'corpora lutea' formed when the eggs were laid had entirely disappeared, and the breakdown of those which remained was almost complete. A few of the largest primary oocytes of the secondary growth phase were still breaking down to form atretic corpora lutea, and the ovary contained masses of interstitial cells, of connective tissue, and of connective tissue cells. The same structure was typical of July, August, and September when the bird, having concluded its second summer moult, was termed an adult.

In October the growth of the largest primary oocytes of the secondary growth phase commenced, but many of the largest eggs did not appear normal. Some of them contained, opposite each follicle cell, a small vacuole in the cytoplasm, and atretic 'corpora lutea' were common. Throughout autumn the germinal epithelium remained quiescent, and inside the ovary all cell stages from the oogonium to the primary oocyte in the early secondary growth phase were common. There was little sign of any zonation of the egg sizes. The youngest eggs were, of course, nearest to the germinal epithelium, but as this epithelium was thrown into deep folds and frequently extended almost to the base of the ovary, the eggs appeared to be situated haphazardly (figure 69, plate 16). In November and December all the oogonia and primary oocytes were growing (figure 49; figure 69, plate 16), and unhealthy vacuolated oocytes were not common. The largest primary oocytes of the secondary growth phase reached the stage when the first yolk vacuoles appear (figure 39), and by January these vacuoles had spread towards the centres of the eggs. The spread of the vacuoles was, however, very slow. Occasionally one of the largest oocytes broke down to form an atretic 'corpus luteum'. Many follicle cells were seen in mitosis, and masses of interstitial cells and connective tissue cells were present. After the middle of February, the growth became more rapid, and at the end of the month the largest oocytes were vacuolated from periphery to centre (figure 40). They were enveloped by thickening layers of follicle cells, the membrana granulosa, and of connective tissue, the thecae interna and externa. In early March the steady growth of the oocytes continued (figure 51; figure 71, plate 16), and over a large area of the ovary surface the germinal epithelium became stretched and

squamous. The final growth phase was similar to that described in the case of the first-year female. In mid-April the first darkly staining yolk droplets appeared in the cytoplasm of the largest primary oocytes, and from that time the growth of these eggs took place with extreme rapidity (figure 44). They were shed before the end of the month, and in the torn ovaries, true 'corpora lutea' were fully formed at the beginning of May. At the same time the germinal epithelium became active, and new oogonia passed in to replenish the ovary. The rate of regression of the ovary of the adult starling was not so rapid as in the case of the first-year bird, and in some individuals a second clutch of eggs was developed and laid in June. This was accompanied by a further burst of activity of the germinal epithelium. By the second half of June, regression of the ovaries took place rapidly, and the activity of the germinal epithelium ceased. The large eggs which had not been shed were transformed into the atretic 'corpora lutea', and the ovary structure was indistinguishable from that already described in the case of the first-year female in June.

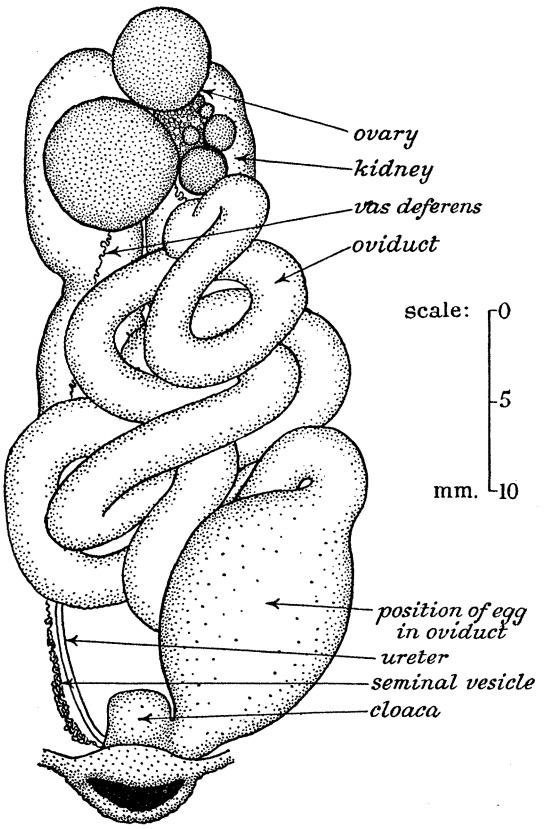


FIGURE 44. Reproductive system of an adult British female in late April.

(v) *Accessory sexual organs*

The female starling possesses a complete set of male (Wolffian) ducts as well as a partial one of female (Müllerian) ducts. The male ducts serve no apparent useful function, but like the female ducts they undergo seasonal variations in size. The structure and seasonal variations of all these ducts are described below.

Oviduct. In the juvenile female, just after leaving the nest in June, this duct was very thin and relatively straight (figure 45). The lumen was clearly defined throughout the greater part of its length, but in the region nearest the cloaca the duct was entirely closed. The cells of the opposite lining epithelia had grown together. The oviduct walls were fairly thick, and where the lumen was apparent the inner surface was thrown into deep folds. The lining epithelium consisted of a single layer of small cuboidal cells, of which each cell body was almost entirely taken up by a nucleus of about 3μ diameter. Where the oviduct was closed, these lining epithelial cells were pressed closely together forming a double, and in some places a triple, layer. Beneath the lining epithelium was a thin inner layer of connective tissue, and wherever a fold of the oviduct wall projected into the lumen, this inner connective tissue layer was much thickened and extended right into the fold. Next to the connective tissue was a layer of circular smooth muscle about 10μ in thickness, and then a layer of longitudinal smooth muscle of equal thickness. Outside was a thick binding layer of connective tissue. By August the oviduct of the juvenile female had increased in thickness, but it still remained relatively straight. The inner connective tissue layer had thickened

to about 10μ, the circular muscle layer had increased to a thickness of about 30μ, and the longitudinal muscle layer was about 50μ in thickness. The outer connective tissue layer had become thinner. No further increase in size of the oviduct of the first-year female occurred in autumn (figure 46) and early winter, but there was, on the contrary, considerable shrinkage in the thickness of all the various layers of the wall. The duct remained closed in that portion of its length nearest the cloaca. In early February the cells of the inner lining epithelium were closely crowded, and the inner connective tissue layer had a minimum thickness of about 8μ, although, where it extended into the folds of the inner wall of the oviduct it was very much thicker. The thickness of the combined circular and longitudinal muscle layers was only about 10μ, but the outer connective tissue layer was thick. Growth started again in the second part of February, but it was very slow. By the middle of March the duct had increased in length (figure 47). The cells of the inner lining epithelium were still very crowded, and they only formed a single layer. The inner connective tissue layer was about 13μ thick, the circular muscle layer about 20μ thick, and the longitudinal muscle layer about 18μ thick. The outer connective tissue layer was much thinner in all the individuals examined, but there appeared to be a considerable variation in the thickness of this layer which was unconnected with the seasons. In April the oviduct grew rapidly. In the first half of the month there was a great increase in the size of the lumen and the thickness of the wall. For the first time a lumen appeared in the lower end of the duct, and the cells of the inner lining epithelium became columnar in form. The inner connective tissue layer reached a minimum thickness of 18μ, the circular muscle layer was about 40μ thick, and the outer longitudinal muscle layer was about 45μ thick. The binding connective tissue sheath became very thin. In the second half of the month, enormous growth took place, and the thickened duct became very much convoluted and twisted. The cells of the inner lining epithelium, which were columnar in form, multiplied rapidly so that the layer was five or six cells thick. The inner connective tissue layer became stretched to extreme thinness, and the connective tissue within the folds of the inner wall was also stretched and thin. Throughout the greater part of the oviduct a new layer was interpolated between the inner connective tissue layer and the circular muscle layer. Its origin was uncertain. Possibly it developed from cells which throughout the rest of the year were obscured in the inner connective tissue layer, or perhaps it grew as a new structure formed by the conversion of cells from the neighbouring layers. The new layer was composed of masses of large secretory cells, each with clear cytoplasm and a small nucleus asymmetrically placed. The diameter of each secretory cell was about 6·5μ, and that of the nucleus about 3·3μ. These cells were grouped together to form branching tubules, and each tubule was separated from its neighbours by thin strands of connective tissue. A single layer of secretory cells formed the wall of the tubule, and in the centre there was a small lumen about 2μ in diameter. The nuclei of the secretory cells were situated basally, adjacent to the connective tissue. A large mass of cytoplasm was adjacent to the lumen. The thin sheath of the inner connective tissue layer separated the zone of secretory tubules from the lining epithelium. Owing mainly to the extreme growth of the zone of secretory cells, the inner wall of the oviduct was thrown into deep folds, and up the centre of each fold ran a thin strand of smooth muscle fibres, and outgrowth from the inner circular muscle layer. This muscle layer reached a thickness of about 90μ. The longitudinal muscle band was even thicker, averaging about 200μ, but

the outer connective tissue sheath was very thin. This description applied to the greater length of the oviduct, but in a short region of the duct, just before the junction with the cloaca, the thick secretory layer was absent. This non-secretory region was that which had remained closed until the beginning of April. The oviduct was not maintained at this enormous size for very long, and in early May there was a rapid collapse. By the middle of that month the duct was still considerably coiled, but the secretory layer had almost entirely disappeared. A few shrunken nests of cells still, however, remained, especially in the folds of the inner wall, and the inner connective tissue layer, which had thickened considerably, ramified between these small groups of cells. The cells of the inner lining epithelium were once again extremely crowded, and they formed a layer two or three cells in thickness. The inner connective tissue layer, except where it swelled into the folds of the oviduct wall, was about 13 μ thick, while the thickness of the inner circular muscle band had shrunk to about 45μ, and that of the outer longitudinal muscle band to about 40μ. The outer connective tissue layer was very variable, but it was usually very thin. By early June the duct was in the fully regressed condition typical of the adult bird in summer, and the part nearest the cloaca was again entirely closed. In August the adult female had a thin, flattened, and relatively straight oviduct. Except for the region nearest the cloaca, the lumen was clear throughout its length, and the inner wall was thrown into deep folds (figure 77, plate 18). The lining epithelium was composed of a single layer of cuboidal cells. The folds of the inner wall were mainly filled with a mass of connective tissue, outgrowths of the inner connective tissue layer, but up the centres of the folds there were a few smooth muscle fibres, outgrowths of the inner circular muscle layer. The inner connective tissue layer was about 16μ in thickness, and the thicknesses of the inner circular muscle layer and the outer longitudinal muscle layer were respectively about 43 and 35μ. In some individuals the outer connective tissue sheath was as thick as 30μ. These general conditions persisted throughout the summer and early autumn. In October and November, at the same time as the growth of the ovary, the oviduct enlarged both in width and length (figure 49). The inner lining epithelium was formed of one, and sometimes two, layers of cuboidal cells. The inner connective tissue layer increased to about 27μ in thickness, and the inner circular muscle layer and the outer longitudinal muscle layer increased respectively to thicknesses of 65 and 50μ. The outer connective tissue layer was usually well marked and about 7μ thick. The part of the oviduct nearest the cloaca still remained closed, but the lumen was large and prominent in the rest of the duct. During December and January, although the oviduct remained large, the wall became much thinner, and the inner folds were flattened to a considerable degree. The inner lining epithelium was composed of one or two layers of closely packed cuboidal cells, the inner connective tissue layer was reduced to a thickness of about 10μ, the circular muscle layer to about 12μ, and the longitudinal muscle layer to about 25μ. No great change in this structure was detected until about mid-March. Then the wall of the oviduct was found to have thickened to a condition similar to that found in autumn (figure 79, plate 18), and the whole duct had become longer and therefore more twisted (figure 51). Growth proceeded slowly until the early part of April when, as in the first-year female, it became extremely rapid. The oviduct reached its full size at the end of the month when the eggs were laid (figure 44; figure 78, plate 18). By the middle of May regression was proceeding, and although it was not so marked as in

the first-year female, it was nevertheless extensive, involving the closure of the duct at its posterior end. By the beginning of June, the oviducts of some adult females had undergone a similar degree of regression to that of the first-year female in mid-May, but in many adult birds there was a second enlargement of the duct to its full size, the birds then laying a second clutch of eggs. Thereafter regression was rapid, and the summer condition, already described, was reached by all birds about the middle of July.

Epoöphoron. The group of tubules composing the epoöphoron are embedded in a mass of connective tissue between the ovary and the anterior end of the left kidney, and the organ is directly comparable in structure with the epididymis of the male. In the juvenile female in June, the tubules of the epoöphoron were fewer than in the corresponding male bird. The lumina were usually entirely closed, and the lining epithelial cells were not so closely packed as in the male. Each tubule was contained in a thin sheath of connective tissue. During summer the epoöphoron slowly became larger due to an increase in the number of tubules. The tubules themselves did not increase in size, and in individuals taken in November the lumina remained closed. The connective tissue sheaths round each tubule and the larger sheath containing the whole organ were well developed. In autumn and early winter little change took place, but in mid-February the tubules began to enlarge and lumina appeared. In early March the average lumen diameter was about 13μ, and only rarely was a tubule found still in the closed condition. At the end of March an increase was apparent in the number of ducts composing the epoöphoron, and the largest lumina had a diameter of about 20μ. Due to the proliferation of the ducts, the whole organ increased greatly in complexity during April. There was, however, little further increase in the size of the tubules, and many of those which were newly formed remained closed even at the end of April when the bird was in full breeding condition. At that time there were slight signs of secretory products in some of the lumina. A reduction in size of the epoöphoron proceeded during May as the tubules collapsed and became reduced in numbers. In June the tubules were very small, usually without lumina, and only a few of them remained. This was also the condition seen in the adult females in August, when the lumina of the few tubules which remained open had a maximum diameter of about 5μ. The cubical cells of the lining epithelium were closely crowded together, and the connective tissue between the tubules and around the whole organ was dense. In autumn there was no change in the number of tubules, but in some of the individuals examined it appeared that there had been some slight enlargement of the lumina. This only appeared to affect a proportion of the birds, and the effect was transitory. During late autumn and early winter the whole organ was small, and active growth did not begin until the second part of February. In early March the number of tubules increased, and the lumina became swollen. The largest lumen diameter recorded in early March was 22μ, but at that time many tubules were still closed. More and more tubules continued to be formed, and the organ reached its largest size when the eggs were laid at the end of April. Then the largest tubules had a lumen diameter of over 30μ, while the smallest of the new tubules remained closed. Regression started in May, but in those birds which produced a second clutch of eggs in June, the epoöphoron again attained full size early in that month. In all birds the minimum summer size was reached early in July following a great reduction in the number of the tubules and the collapse of those which persisted.

Vas deferens. Leading from the epoöphoron was the vas deferens, a duct exactly similar in structure to that already described in the male. This duct, although very thin and uncoiled (figure 45), was well developed in the juvenile female starling just after leaving the nest, and the lumen had an average diameter of about 23μ. The inner lining epithelium of tall columnar cells was based on a ring of loose connective tissue, and in all these epithelial cells the nucleus was retracted to the base of the cell adjacent to the connective tissue. That part of each cell next to the lumen was clear cytoplasm. The connective tissue layer had a thickness of about 10μ, and outside was a circular band of smooth muscle fibres with a thickness of about 6μ. The whole structure was bound in an outer sheath of connective tissue which varied in thickness in different individuals. During summer the vas deferens was reduced in size, and in the first-year female in autumn the lumina of the tubules had an average diameter of about 10μ. The inner connective tissue layer was then about 3μ thick, while the thickness of the muscle layer had not changed. In autumn and winter the duct remained simple and uncoiled (figure 46), and in February the lumen diameter averaged 13μ, the thickness of the inner connective tissue layer was about 3μ, and that of the muscle layer was about 7μ. In March the duct still remained uncoiled (figure 47), and there was no change in the structure of the wall. During April, however, when the oviduct was actively growing, the vas deferens increased rapidly both in width and length, and as a result it became twisted and coiled. By the end of the month the diameter of the lumen had reached a maximum of about 45μ, the inner wall of the duct being thrown into folds. The inner connective tissue layer was about 13μ in thickness, and the muscle layer was about 12μ in thickness. This large size was only maintained until early May, and by the middle of that month, although the duct was still moderately coiled, the lumen had shrunk to a diameter of about 18μ, the thickness of the inner connective tissue layer to about 12μ, and that of the muscle band to about 8μ. By June the condition typical of the adult female in summer was reached. The adult female in August had a vas deferens thin and almost straight with a lumen diameter of about 10μ, an inner connective tissue layer with a thickness of about 18μ, and a circular muscle layer with a thickness of about 8μ. As in the male, there was no change in this structure during the autumn except that, as the duct increased slightly in length, it became slightly more twisted (figure 49). Active growth of the vas deferens started in late February, and early in March the diameter of the lumen reached 25μ. The layers of connective tissue and smooth muscle, however, remained thin. By the end of March the lumen diameter was about 35μ, and the cells of the lining epithelium were tall columnar in form. The thickness of the connective tissue layer was then about 16μ, and that of the muscle layer about 23μ. The growth in April was similar to that seen in the first-year female, and about the same maximum size was attained at the end of that month (figure 44). The subsequent regression was slower, and a second maximum size was reached in early June in those birds which had a second clutch of eggs. The summer condition was reached by the end of June in all the birds examined.

Seminal vesicle. At the posterior end of the body cavity the Wolffian duct was coiled into a more or less compact body, the seminal vesicle. The position of the organ was similar to that in the male, but the structure in the female was less compact. It was always thinner and usually very much longer than that of the male. In the juvenile female in June, the seminal vesicle was only composed of a few tubules which rarely branched. The diameter

of their lumina was about 17μ, and as in the vas deferens, the wall was composed of an inner lining epithelium surrounded by successive sheaths of inner connective tissue, circular smooth muscle, and outer connective tissue. The inner connective tissue layer was about 6μ in thickness, and the circular muscle layer was about 17μ in thickness. By August the lumen diameter was enlarged to over 20μ, and the number of tubules had also increased. In the first-year bird in late summer and autumn the whole organ collapsed, and was encased in a very thick connective tissue capsule. Many of the tubules closed entirely, and in those which remained open the maximum lumen diameter was about 6μ. The thickness of the inner connective tissue layer was about 2μ, and that of the circular muscle layer was about 15μ. No change in this structure took place until about the middle of February when the tubules of many individuals began to swell. By the end of the month the diameter of the lumina of the most advanced birds was about 10μ, but there was considerable variation in the degree of growth so that, even at the end of March, individuals were discovered with a maximum lumen diameter of only 5μ. In April growth was very rapid, but as this involved a great lengthening of the seminal vesicle in a manner not observed in the male, the organ appeared less and less complicated in cross-section, only three or four tubules being commonly seen. The large seminal vesicle so produced was not compact like that of the male, but straggled along the side of the oviduct or the ureter for a considerable distance. The diameter of the lumen increased to nearly 50μ, the thickness of the connective tissue layer to 16μ, and that of the circular muscle layer to 27μ. The cells of the lining epithelium produced a slight amount of secretion which lodged in the lumina. In May the seminal vesicle remained long and thin. About the middle of the month the diameter of the lumina, although very variable, was, on the average, about 20μ. The connective tissue layer changed very little, and the thickness of the muscle layer varied greatly in different individuals. The summer condition was reached in early June when, as in the adult female in August, the seminal vesicle was only short and simple (figure 81, plate 19). Many of the tubules had completely closed, and many more must have been absorbed. Those which remained open had an average diameter of about 4μ. The thickness of the connective tissue layer was about 18μ, and that of the circular muscle layer was about 14μ. In many of the adult females in autumn the tubules became swollen, the increase in size taking place at the same time as the autumn burst of gonad growth. The largest seminal vesicle found at this time of the year was from an adult female with a half-yellow beak taken in November. In this bird the lumen diameter had reached over 25μ, the connective tissue layer was about 14μ thick, and the muscle layer was about 24μ thick. In December and January all seminal vesicles were of the smallest size once more, and it was not until the middle of February that they enlarged again. In early March the lumen diameter was about 25μ, and in late March it reached 28μ (figure 83, plate 19). Some slight traces of secretory products were then produced, apparently by the cells of the lining epithelium. The growth in April was identical with that of the first-year female (figure 82, plate 19), but no cilia developed on the free edges of the cells of the inner lining epithelium as they did in the male. The whole organ underwent regression in May, but the extent of this varied in different individuals. In those birds which produced a second clutch of eggs in early June, the seminal vesicle enlarged once more. During June regression was rapid, and by the beginning of July the small summer size was reached.

(vi) *Secondary sexual characters*

The female starling, like the male, possessed one obvious secondary sexual character, the colour of the iris, which did not vary with the seasons, and two, the colour of the beak and the appearance of the lower throat feathers, which did vary according to the phases of the reproductive cycle.

*Colour of the iris.** In the juvenile females the colour of the irises was usually a light greyish yellow[a]. Of twelve juvenile females taken in June, seven answered to this description, one had a light grey iris[b], three had light yellow irises[c], and one had a lemon yellow iris[d]. Throughout the late spring and early summer, none of the juvenile females examined had irises of the dark grey or liver colour typical of the juvenile male. After the first summer moult, the first-year, and subsequently the adult, females almost all had lightly coloured irises. Sometimes they were uniformly sandy yellow[e] in colour, but usually they were brown[f] with either a narrow inner or outer ring of some lighter colour, brown, yellow, or even white. Only rarely was a female found with the entirely dark iris typical of the male.

Colour of the beak. In the juvenile female, and in the first-year female in autumn and early winter, the beak was dark grey with lighter grey cutting edges to both mandibles. In late February and early March, the beak began to turn yellow from the base, but even as late as the middle of March, some first-year British females still had completely dark beaks. By the second half of April the beak was entirely yellow except for the lighter yellow or white base typical of the female starling in the breeding season. The darkening of the beak started in early June, the dark colour being first apparent at the base and at a point just above the tip of the upper mandible. By the end of the month the whole beak was again dark grey except for the lighter grey cutting edges (figure 25). As in the adult male, the beak of the adult female began to turn yellow in October and November (figure 26), and it was the lower mandible which first showed the colour change. There was, however, a much greater variation in this respect between the different individuals than there was in the male, and adult British females with completely dark beaks were still to be found as late as the end of December. In mid-February the beak colour varied from a third to full yellow (figure 29), and in mid-March from three-quarters to full yellow (figure 30). As in the male, the last bit of dark pigment to go was just above the tip of the upper mandible. By April all adult females had a bright yellow beak, usually with a light yellow or white base. Some females were, however, found with an entirely yellow beak. The beak turned dark once more during late June (figure 31) and early July, the process of the colour change being the same as in the adult male.

Lower throat feather. The lower throat feathers of the juvenile female had exactly the same broad, loosely built, and light brown appearance (figure 85, no. 16, plate 20) as those of the juvenile male. After the first summer moult, however, the feathers of the first-year female were very distinctive. They were medium or light brown in colour, broadly tipped with white, and usually they showed no gloss (figure 85, no. 17, plate 20). The breadth at the tip was as great as that of the juvenile, and much greater than that of the first-year male.

* The iris colours described above approximate to the following reference numbers in the list of Ostwald Colour Standards:

[a] 4:1:ie. [b] 0:e. [c] 4:1:ea. [d] 8:1:ia. [e] 8:2:lc. [f] 4:6:ni.

Throughout autumn, winter, and spring the white tips of these feathers became worn (figure 85, nos. 17–20, plate 20), but they were so large and broad that they never entirely disappeared. The partial moult in late February and March did not usually affect the throat region. The second summer moult began in late June, and it was completed by the end of August. The new feathers of the adult bird in September were similar to those of the adult male, but the purple and green gloss was not so bright and the white tips to the feathers were broader (figure 85, no. 21, plate 20). The colour of the iris was necessary to afford a certain distinction between the adult female and the first-year male, as the feathers of these two types were very similar during early autumn. The white tips of the throat feathers of the adult British females wore away during autumn and winter (figure 85, nos. 21–23, plate 20), but being larger they did not wear away so rapidly as those of the male. In many individuals the white tips had disappeared by January, but in many others they were just visible in March. By the beginning of the breeding season in April they had completely disappeared from all the feathers of the throat and upper breast, except perhaps in the case of one or two of the new feathers which were developed in a few individuals during the partial moult in March. The summer moult took the same course as that of the first-year female.

(*b*) *Continental*

(i) *Female genital system*

The description already given of the genital system of the female British starling applies equally to that of the Continental bird.

(ii) *Maximum diameters of oocytes*

By following the same procedure as in the case of the British females and measuring the maximum diameters of the largest oocytes, it was possible to compare the ovaries of the female Continental birds with those of the corresponding British birds. Differences between the ovaries of the birds of the two races were obvious in all except the first-year females

TABLE 7

type of bird	month	number in sample	mean of maximum oocyte diameters (in mm.) and S.D.
first year	Feb.	3	0·57 ± 0·038
	Mar.	12	0·74 ± 0·043
adult	Nov.	5	0·55 ± 0·024
	Dec.	4	0·60 ± 0·032
	Jan.	5	0·58 ± 0·025
	Feb.	4	0·75 ± 0·032
	Mar.	20	0·91 ± 0·062

TABLE 8

type of bird	month and year	number in sample	mean of maximum oocyte diameters (in mm.) and S.D.
first year	Mar. 1939	7	0·74 ± 0·048
	Mar. 1940	5	0·73 ± 0·040
adult	Mar. 1939	10	0·92 ± 0·067
	Mar. 1940	10	0·89 ± 0·058

from November to January (table 7). As in the case of the testis volumes of the male Continental starlings, it was found that the mean of the maximum oocyte diameters and the standard deviations were very similar in the two groups of birds taken in March 1939 and in March 1940. A comparison of the separate results of the two years is given in table 8.

(iii) *Microscopic structure of the ovary*

The structure of the ovary of the Continental starling resembles that of the British bird, except, of course, that not so many egg stages can be observed in the birds found in this country. For instance, at no period was any activity noted in the germinal epithelium, and therefore no very young stages of oogonia were seen. Similarly, no egg was observed in a later stage of development than that of the primary oocyte in the early secondary growth phase, when the ring of clear yolk vacuoles appears near the periphery.

(iv) *Seasonal variations in the ovary*

The first-year Continental starling in autumn had ovaries which could not be distinguished from those of first-year British birds. The germinal epithelium was quiescent, and all stages of egg development were evident as far as the primary oocyte with a nucleus of Balbiani in the early stages of breakdown. In late February slow growth of the largest eggs was taking place, and as a consequence these eggs were pushing up towards the surface of the ovary. This growth continued until the birds left the British Isles in March (figure 48), but even at this time, no primary oocyte had entered the secondary growth phase (figure 68, plate 15). In none of the ovaries of the first-year females were any atretic 'corpora lutea' to be found, and it appeared that, as in the British birds, these structures did not develop until after the first clutch of eggs was laid.

In the adult Continental starlings in November, the ovaries were very similar in appearance (figure 50; figure 70, plate 16) to those of the British birds in summer. The germinal epithelium showed no activity, but many oogonia and very young primary oocytes were present. Some of the primary oocytes in the early secondary growth phase appeared to be unhealthy, and in their cytoplasm they contained rows of absorption vacuoles adjacent to the follicle cells. All stages of atretic 'corpora lutea' were also present. The most advanced primary oocytes had developed a ring of clear yolk vacuoles near the periphery, but in most cases this ring was only composed of a single or double row of vacuoles. Very little change in this general structure took place in December and January, but in these months there was very slight growth of the largest primary oocytes in the secondary growth phase. Some atretic 'corpora lutea' continued to be formed. The growth of the largest oocytes was accelerated after the middle of February, but there was still little change in the general appearance. Many follicle cells were to be seen in division. In March the growth of the large oocytes proceeded (figure 52; figure 72, plate 16), but even at the time when the birds left this country the clear yolk vacuoles had not spread throughout the cytoplasm and no marked change in structure was apparent.

(v) *Accessory sexual organs*

The accessory sexual organs of the female Continental starling were identical in position and structure with those of the British birds. They differed, however, in their seasonal development, and in so far as it was possible to obtain information in the British Isles, these

seasonal variations are described below. In the case of the first-year females no differences could be detected between the two races from November to early February, and the descriptions already given of the accessory sexual organs of the first-year British birds in this period applies equally to those of the Continental race.

Oviduct. At the beginning of February the oviduct of the first-year Continental female was thin, flattened, and almost straight. It was closed posteriorly. The cells of the inner lining epithelium were closely crowded and cubical in form, and the inner wall was thrown into shallow folds. The inner connective tissue layer had a minimum thickness of about 8μ, and the thicknesses of the inner circular muscle layer and the outer longitudinal muscle layer were respectively about 5 and 4μ. Slight growth took place at the end of February and in early March, but even at migration time the duct remained thin and straight (figure 48). In mid-March there was no change in the inner lining epithelium, the inner connective tissue layer was at least 10μ in thickness, and the circular muscle layer and the longitudinal muscle layer were respectively 6 and 7μ in thickness. The duct remained closed in its posterior region. The oviduct of the adult Continental female in autumn was similar to that of the adult British bird in summer, and it showed no signs of any growth. In November the duct was thin, flattened, and almost straight (figure 50). The inner lining epithelium was composed of a single layer of small cuboidal cells. The inner connective tissue layer was about 12–15μ thick, the circular muscle layer was about 36μ thick, and the longitudinal muscle layer was about 28μ thick. The outer connective tissue sheath was often well developed. As in the British birds there was a considerable reduction in the thickness of the oviduct wall during late autumn and early winter. By early February the thickness of the inner connective tissue layer had shrunk to about 8μ, that of the circular muscle layer to about 12μ, and that of the longitudinal muscle layer to about 15μ. Just before the birds left this country the oviduct became thicker and longer (figure 52). In mid-March there was no change in the appearance of the lining epithelium, but the thickness of the inner connective tissue layer increased to 14μ, and those of the circular and longitudinal muscle layers to 31 and 25μ respectively (figure 80, plate 18). The posterior region of the oviduct remained closed.

Epoöphoron. In early February the tubules of the epoöphoron of the first-year Continental female were entirely closed. At the end of that month the lumina first appeared, and by mid-March they had an average diameter of about 10μ. In the adult Continental female in autumn, the tubules of the epoöphoron were also entirely closed, and the organ was very small. In these birds the lumina first appeared at the end of February, and by mid-March they had an average diameter of about 15μ.

Vas deferens. Throughout autumn and winter the vasa deferentia of the first-year birds remained thin and comparatively straight. In early February the lumen diameter was about 10μ, the thickness of the inner connective tissue layer was about 3μ, and that of the circular muscle layer was about 6μ. Growth started slowly at the end of the month, but in mid-March, when the birds migrated, the duct was still relatively straight (figure 48) with a lumen diameter of about 12μ. The thickness of the inner connective tissue layer and that of the circular muscle layer remained unchanged. In the adult Continental starling in November the vas deferens was almost straight (figure 50), with a lumen diameter of about 10μ. The inner connective tissue layer had a thickness of about 15μ, and the circular

muscle layer a thickness of about 9μ. No change in this structure was apparent until February. At the end of this month the first signs of growth were evident, and when the birds left in mid-March the duct had increased in length (figure 52) and the lumen diameter was about 17μ. The inner connective tissue layer and the circular muscle layer remained unchanged in thickness.

Seminal vesicle. In the first-year Continental female in February the tubules of the seminal vesicle began to enlarge, and by the end of the month the lumen diameter in many individuals had increased to nearly 10μ. The inner connective tissue layer had a thickness of about 2μ, and the circular muscle layer was about 12μ thick. Slow growth continued during the first part of March, but when the birds left the British Isles the seminal vesicles were still very small (figure 48). In the adult female in autumn the seminal vesicle was small and simple (figure 50). It was similar to, and in many individuals smaller than, that of the British bird in summer. The lumina of the tubules were usually obscured, and those which remained open were extremely small. The thickness of the inner connective tissue layer was about 12μ, and that of the circular muscle layer had an average of about 10μ. No change in this structure took place until the end of February when the lumina swelled up. In mid-March the organ was larger (figure 52), and the average lumen diameter was about 13μ (figure 84, plate 19). The thickness of the tubule wall altered very little.

(vi) *Secondary sexual characters*

It was impossible to distinguish the first-year Continental female from the corresponding British bird by external appearance alone, but marked differences in the external appearances of the adult Continental and British females were usually apparent.

*Colour of the iris.** As in the British birds, the irises of the first-year and adult Continental females were often a light sandy colour[a]. Usually, however, they were brown[b] with an inner or outer ring of light brown, yellow, or white.

Colour of the beak. The first-year female had a dark grey beak with light grey cutting edges, and in some individuals the base of the beak began to turn yellow about the end of February. At migration time, however, many birds still had entirely dark beaks. In the adult female the beak also remained dark until early February (figures 32–35). In mid-March the most advanced females had only about a quarter of the beak yellow (figure 36), while the least advanced birds still retained the completely dark beak.

Lower throat feather. Throughout their stay in the British Isles, the first-year Continental females possessed plumage exactly similar to that of the first-year British birds (figure 85, nos. 25–27, plate 20). The lower throat feathers of the adult Continental female in November (figure 85, no. 28, plate 20) also resembled those of the corresponding British bird. Throughout autumn and winter, however, these feathers showed less wear at the tips than did those of the adult British females, and when, in March, the normal partial moult took place, the white tips still remained on the throat feathers (figure 85, no. 30, plate 20).

* The iris colours described above approximate to the following reference numbers in the list of Ostwald Colour Standards:

[a] 8:2:lc. [b] 4:6:ni.

(c) *Comparisons and conclusions*

(i) *Ovaries*

Female British starlings, when they left the nests in June, had extremely small ovaries, and in this they differed markedly from the juvenile males which had relatively large testes. However, the size of the ovary is determined mainly by the growth of the eggs, and not, as in the case of the testis, by cell division. The only process definitely known to take place within the ovary of the starling which is strictly comparable to the cell divisions of the testis is the mitotic activity of the germinal epithelium which results in the production of the oogonia. The germ cells of the testis of the male juvenile starling just off the nest were actively dividing. The cells of the germinal epithelium of the ovary of the female juvenile starling were also actively undergoing mitosis. In the male this activity resulted in an increase in testis size. In the female it made very little difference to the size of the ovary. The testes of the juvenile male regressed during summer, and the mitoses of the germinal epithelium also slackened and finally ceased. Growth of the oogonia, and later of the young primary oocytes, continued however, and the ovary increased in size during the summer and autumn. This growth did not appear to be accompanied by any secretion of sex hormones, and the germinal epithelium remained quiescent.

When the first-year Continental starlings arrived in the British Isles in autumn, they could not be distinguished from the first-year British birds, as the ovaries of both races were in the same stage of development. About the middle of February there was a burst of ovarian activity in both races, but in the Continental birds it was less intense. This activity showed itself especially as an increase in size of the largest primary oocytes. The germinal epithelium remained inactive. The growth of the primary oocytes became more rapid in all birds in March, but the speed of growth in the British females was always faster than that in the Continental females (figures 47, 48; figures 67, 68, plate 15). The statistical comparisons of the ovaries of the birds of the two races in February and March are given in table 9. The same method of comparison is followed as in the case of the males. From this it is seen that in February P, the probability that the two races are in fact identical, is less than two in a hundred, and therefore the observed differences are probably significant. In March, as P is less than 0·01, the differences observed must be considered significant.

TABLE 9

month	race	number in sample	mean maximum diameter of oocytes and s.D.	value of t	probability P
Feb.	British	4	$0{\cdot}71 \pm 0{\cdot}047$	3·59	$<0{\cdot}02$
	Continental	3	$0{\cdot}57 \pm 0{\cdot}038$		
Mar.	British	11	$1{\cdot}05 \pm 0{\cdot}089$	10·29	$<0{\cdot}01$
	Continental	12	$0{\cdot}74 \pm 0{\cdot}043$		

In the first-year British female the ovary developed further during late March and April, and at the end of April the eggs were laid. There is also some evidence that it is common for the female Continental starling to lay eggs when only one year old (Niethammer 1937). Egg laying resulted in the formation of 'corpora lutea' which were remarkably similar to those of mammals, and many large primary oocytes in the secondary growth phase also

broke down to form atretic 'corpora lutea'. After the bird's first breeding season, atretic 'corpora lutea' were found in the ovaries in all months of the year. Beginning about the time of ovulation and continuing for a week or two, there was a burst of activity of the germinal epithelium resulting in the replenishment of the ovary with the oogonia destined to form the new crop of eggs. This activity rapidly ceased, and at the same time the regression of the ovary, due to atresia of the larger oocytes, proceeded rapidly. A minimum size was reached by the end of June.

Growth of the oogonia and primary oocytes of the adult British females started again in early autumn, and when the Continental birds arrived the ovaries of these British birds were enlarging rapidly (figure 49; figure 69, plate 16). There were also signs, for instance in the colour of the beak, that active secretion of sex hormones was taking place. In the ovaries of the Continental birds the growth of the largest primary oocytes, if it occurred at all, was extremely slow (figure 50; figure 70, plate 16), and it was not until the first half of February that their growth became active. The ovaries of the British birds enlarged rapidly in February, and until the time when the Continental birds left this country the ovaries of the British birds remained very much larger (figures 51, 52; figures 71, 72, plate 16). The averages of the maximum diameters of the oocytes in the ovaries of the British and Continental adults is given in table 10, and a statistical comparison is made. In all months it is shown that, as P is less than 0·01, the differences observed between the two races of birds are statistically significant.

TABLE 10

month	race	number in sample	mean maximum diameter of oocytes and S.D.	value of t	probability P
Nov.	British	4	$1{\cdot}04 \pm 0{\cdot}128$	7·37	$<0{\cdot}01$
	Continental	5	$0{\cdot}55 \pm 0{\cdot}024$		
Dec.	British	5	$1{\cdot}15 \pm 0{\cdot}082$	11·26	$<0{\cdot}01$
	Continental	4	$0{\cdot}60 \pm 0{\cdot}032$		
Jan.	British	3	$1{\cdot}20 \pm 0{\cdot}046$	21·33	$<0{\cdot}01$
	Continental	5	$0{\cdot}58 \pm 0{\cdot}025$		
Feb.	British	3	$1{\cdot}36 \pm 0{\cdot}061$	14·45	$<0{\cdot}01$
	Continental	4	$0{\cdot}75 \pm 0{\cdot}032$		
Mar.	British	14	$1{\cdot}54 \pm 0{\cdot}130$	18·26	$<0{\cdot}01$
	Continental	20	$0{\cdot}91 \pm 0{\cdot}062$		

In the British birds the growth of the oocytes continued until, in the second half of April, they were shed from the ovaries. True and atretic 'corpora lutea' were then formed, and the germinal epithelium was active once more. If, as frequently happened in the adults, a bird produced a second clutch of eggs in early June, the germinal epithelium had a second short period of activity. Regression was rapid in June, and the ovary reached a minimum size in early July.

(ii) *Accessory sexual organs*

The accessory sexual organs of both the Wolffian and Müllerian systems varied in their seasonal development according to the degrees of activity of the ovary. As in the case of the male, some organs appeared to react to a lower threshold of sex hormone secretion than others, and therefore they showed earlier signs of development. The fact that all the

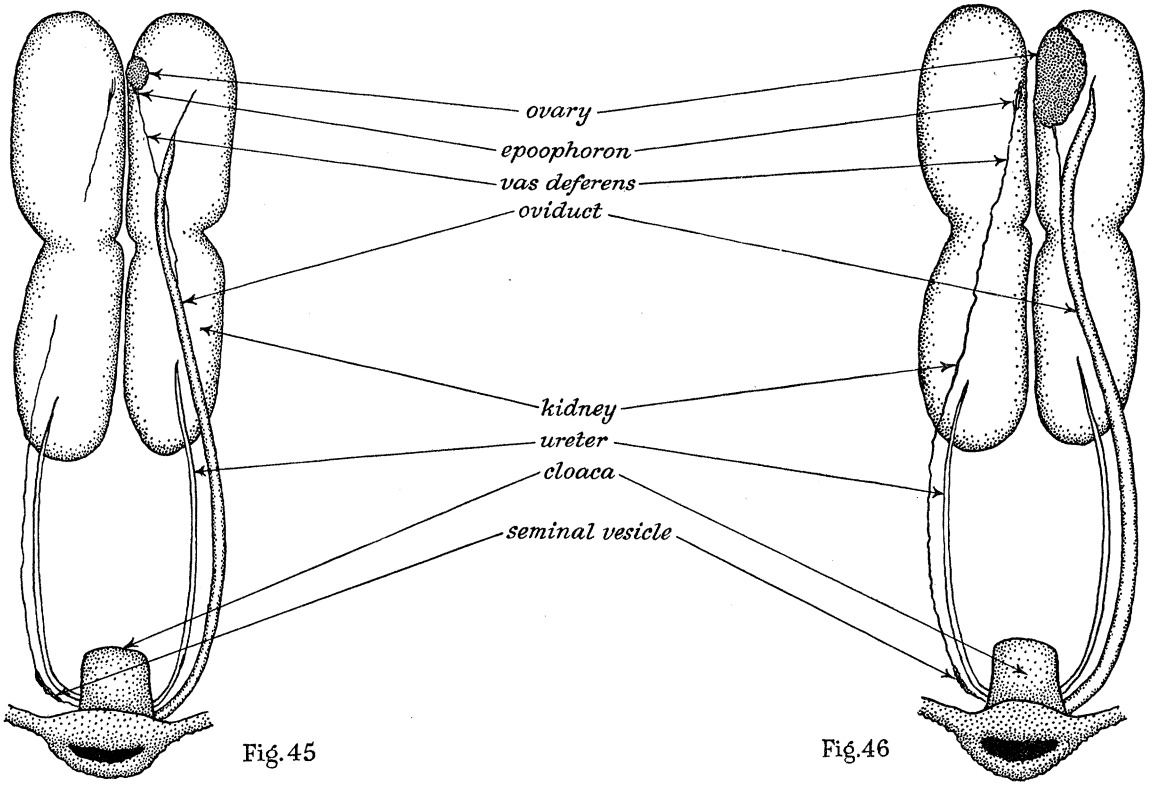


FIGURE 45. Juvenile British female in June.

FIGURE 46. First-year British female in November.

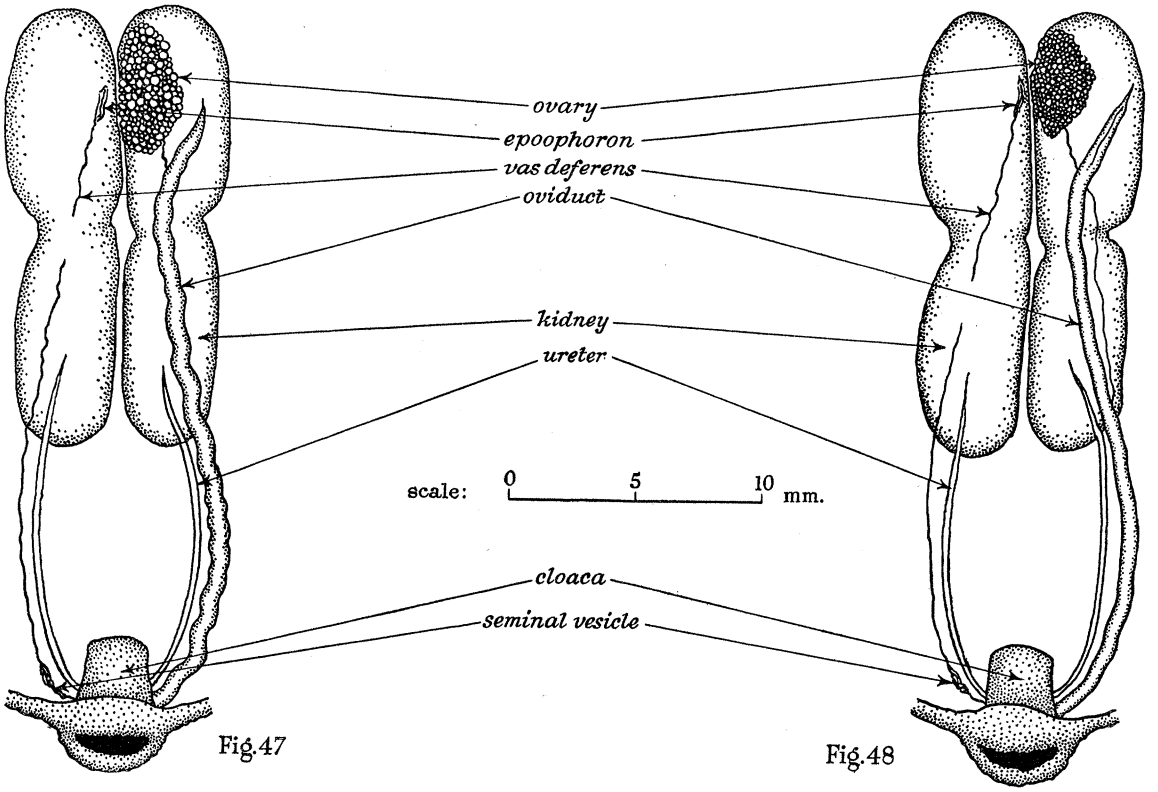


FIGURE 47. First-year British female in March.

FIGURE 48. First-year Continental female in March.

Reproductive systems of female starlings.

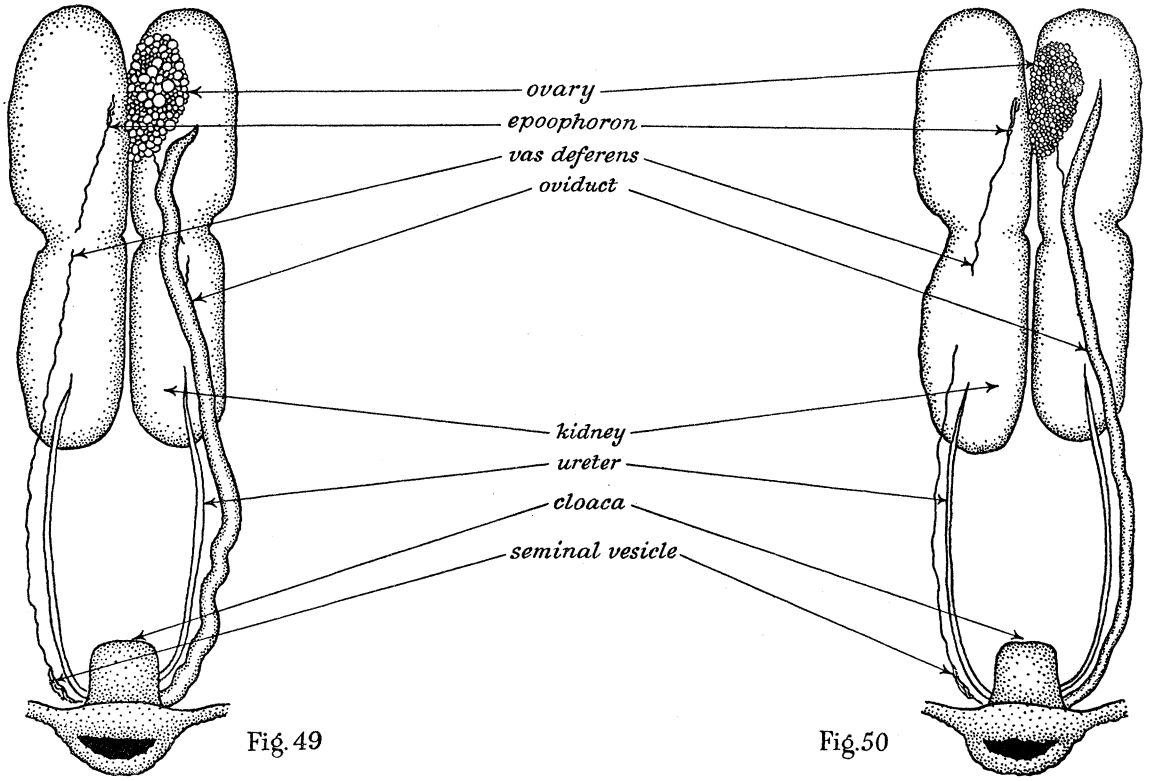


FIGURE 49. Adult British female in November.

FIGURE 50. Adult Continental female in November.

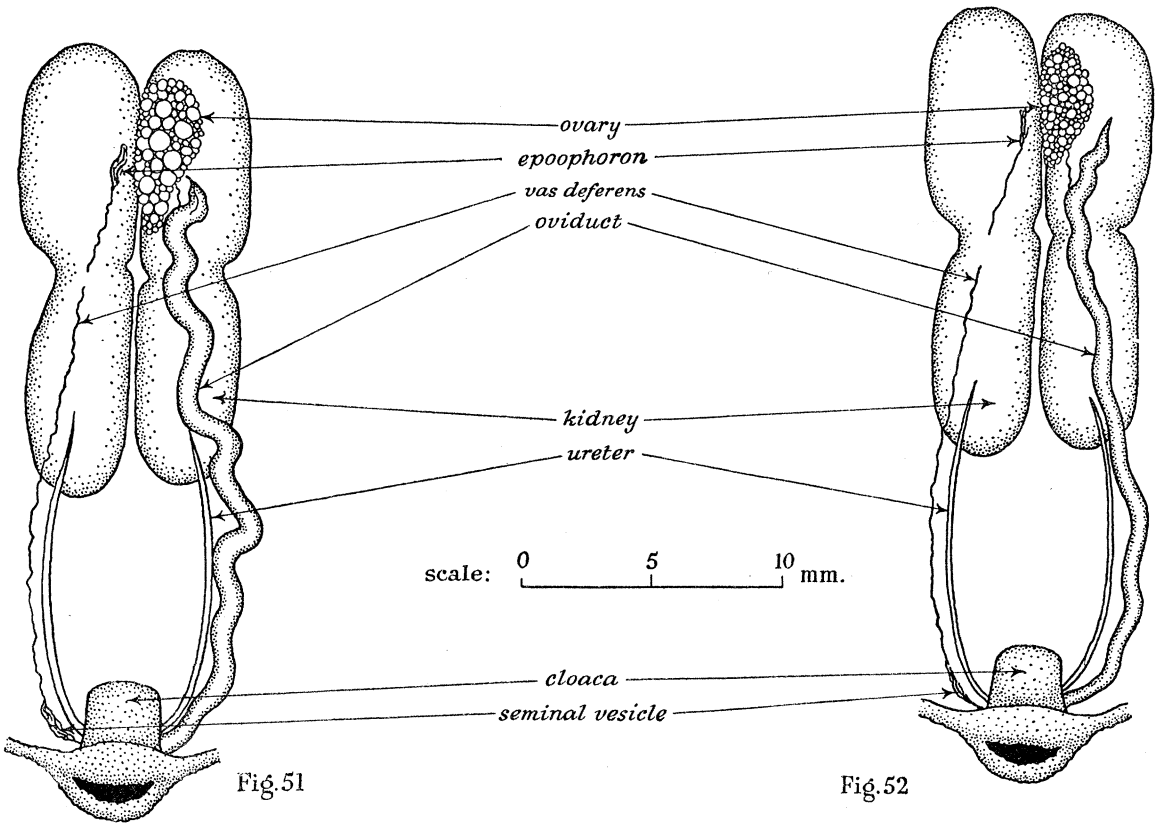


FIGURE 51. Adult British female in early March.

FIGURE 52. Adult Continental female in early March.

Reproductive systems of female starlings.

male accessory sexual organs also enlarge when the ovary is active provides further evidence in favour of the theory put forward by Witschi & Miller (1938) that the ovary of the starling secretes both male and female sex hormones. The same marked differences which were apparent between the ovaries of the British and Continental races were also evident between the accessory sexual organs.

After the regression of the accessory sexual organs of the juvenile starlings in late summer, there was no apparent change in structure in either the first-year British or first-year Continental birds during autumn and early winter. When growth started again in the second part of February, the accessory sexual organs of the British birds grew more rapidly than those of the Continental birds, and when the Continental females left the British Isles in mid-March, the two races were easily distinguishable by means of the accessory sexual structures alone. This distinction between the races was as clear in the organs of the Wolffian system as in those of the Müllerian system, the epoöphoron, vas deferens, and seminal vesicle being larger in the British female. In the adult British females in autumn, growth, accompanying that of the ovary, was noted in the oviducts of all birds, and in the epoöphoron, vas deferens, and seminal vesicle of many birds. There appeared to be considerable variation in the amount of male sex hormone produced by different females at this time of year. In the birds which produced a large amount of this hormone, the Wolffian duct enlarged in the same degree as the Müllerian duct, but in other females there appeared to be little secretion and no growth of the Wolffian system occurred. No activity or growth of the accessory sexual organs of the adult Continental females was noted in autumn, and all the sexual organs of these birds remained in a state of extreme regression similar to, if not more pronounced than, that seen in the adult British females in summer. In late autumn all the accessory sexual organs of the adult British females underwent some regression, and in February active growth started in both British and Continental birds. As in the case of the males the growth of the accessory sexual organs of the adult British females usually started some weeks before, and always proceeded more rapidly than that of the Continental birds (figures 79, 80, plate 18; figures 83, 84, plate 19). In both races and in all individuals, this winter growth affected both the Wolffian and Müllerian systems. At the height of the breeding season the ducts of the Wolffian system were never so highly developed as in the male, and only rarely were any signs of secretory products seen in their lumina.

(iii) *Secondary sexual characters*

The one secondary sexual character of the female starling which did not vary seasonally was the colour of the iris. When the juvenile stage was passed, first-year and adult starlings of both British and Continental race had irises sometimes light brown or yellow in colour, but often dark brown with a thin inner or outer ring of light brown, yellow, or in exceptional cases white. Only rarely was a female discovered with entirely dark brown irises similar to those of the male.

The beak of the female starling was dark grey in the season of ovary regression (figure 25), and bright yellow in the season of ovary activity (figure 30). In the breeding season the yellow beak of the female usually had a lighter yellow or white base, but occasionally individuals were found with a fully yellow beak. Witschi & Miller (1938) have shown that the yellow beak of the sexually active female is really a male secondary sexual character,

and is due to the secretion by the ovary of male sex hormone. The juvenile and first-year females possessed a dark grey beak during their first summer, autumn, and early winter. The beaks of the first-year British females usually began to turn yellow after mid-February, but in the Continental birds only a few individuals showed a similar colour change before mid-March. By April the beaks of the first-year British females were fully yellow. In the adult British females in autumn the first sign of the yellowing of the beak (figures 26–29) was noticed in early October, but unlike the male, there was considerable variation in this respect between the different individuals so that a few adult females with completely dark beaks were still to be found at the end of December. As already noted, some females appeared to produce much more male sex hormone in autumn than others, and it was found that the females with yellowing beaks also possessed stimulated Wolffian systems. The adult Continental females also showed much individual variation in the times when the yellow colour first appeared at the base of the beak. The earliest Continental birds showed this change in the first half of February (figure 35), and the latest birds still retained an entirely dark beak in mid-March. The beaks of the British females turned dark once more in June and early July (figure 31).

The varying structure of the lower throat feathers also formed a useful feature for distinguishing age, sex, and race. In the juvenile and first-year females these feathers were broad and blunt (figure 85, nos. 16, 17, plate 20), but after the second summer moult the tips of the throat feathers of the adult females were much narrower (figure 85, no. 21, plate 20). There was a partial moult in March which did not usually affect the throat feathers. In all females, except the juveniles, the throat feathers when newly formed had white tips, very large in the first-year birds but narrower in the adults. So large were they in the first-year females that they never entirely disappeared before the second summer moult (figure 85, nos. 17–20, plate 20). During autumn and winter no difference between the structure of these feathers in the first-year British and Continental birds was noticed. Owing to the constant visits of the adult British females to their nesting holes, the narrower white tips to their throat feathers were rapidly worn away (figure 85, nos. 21–23, plate 20). In many individuals they had disappeared by January, and they were lost by all birds before the end of March. As the Continental birds did not visit nesting holes, there was relatively little wearing of their throat feathers (figure 85, nos. 28–30, plate 20), and when the birds migrated in March the white tips to the throat feathers still remained.

(iv) *General conclusion*

Significant differences are shown to exist between the reproductive cycles of the female British and Continental starlings. The growth of the ovaries of the British birds starts earlier and proceeds more rapidly than that of the Continental birds, and because of this, differences are also apparent between the accessory sexual organs and the secondary sexual characters.

V. OBSERVATIONS ON HABITS AND SEXUAL BEHAVIOUR

(1) General

In the previous sections it has been shown that because of differences in the times and rates of growth of the gonads of the British and Continental starlings, differences between the two races also exist in the accessory sexual organs, the colour of the beaks, and the rate

of wear of the plumage. It is well known that the state of the gonads influences or determines not only the structure of the accessory and secondary sexual organs, but also the type of behaviour in which the animal indulges. The effect on behaviour of the growth of the gonads is especially clear in those animals which, like the starling, have only one short breeding season in the course of the year. A study was therefore made, especially in autumn and winter, of the behaviour of the British and Continental starlings. The accounts given below of the behaviour of the birds in this country are mainly original, but acknowledgements to several authors are also made in the text. The accounts given of the behaviour of the Continental starlings in other European countries have been compiled from the descriptions given in various Continental journals.

There is one preliminary difference between the habits of the British and the Continental starlings which is obvious, but which, owing to a certain confusion in the various text-books (for instance, Witherby *et al.* 1938), requires stating clearly. This concerns the migratory habits of the two races of birds. So many results of the ringing of starlings have been recorded by the British ringing scheme and by similar schemes of the various other European countries,* that it is possible to describe the seasonal movements of these birds with some precision. In the case of the British starling it has been necessary to work out the problem of migration entirely afresh. All the British ringing returns, which are now stored in the British Museum of Natural History, have been examined, and the detailed results of this examination are to be recorded in a separate paper. Many more results are yet needed in the case of the British starling before a clear picture of the normal movements can be obtained, but it is possible at the moment to make the following generalizations. When the young leave the nests in June, a certain percentage (perhaps 25% or more) desert the district and wander haphazardly in any direction. This wandering continues through the summer and, perhaps to a lesser extent, through the autumn as well. The remaining young starlings are very static in their habits, and continue to be found in the close vicinity of the nest in which they were hatched. In the following spring, all the young birds appear to settle wherever they find themselves, and from that time they are all sedentary. It is very rare to find any bird of undoubted British origin ringed as an adult being found more than about 20 miles from the place of ringing, and as the daily flights to the roosts are often 20 miles or more, this slight discrepancy is easily accounted for. In has been necessary to give these details because most ornithological text-books state that the British starling is a migratory species which moves south in late summer and autumn. They even go so far, on the evidence of a single young starling which in its first summer wandered from Kent to Boulogne, as to consider that some British starlings winter abroad. Many hundreds of ringing returns show that most juvenile and all adult British starlings are entirely sedentary in their habits. In this the British starling contrasts strongly with the Continental bird which appears almost always to leave its nesting area in autumn and to move south or south-west (Niethammer 1937). The Continental starlings which arrive in this country between late September and early November come from Norway, Denmark, Germany, and Holland, and from the Baltic countries as far north as Russia. The return journey to these nesting areas is made in late February or March.

* Almost all the ringing returns to date for starlings ringed in the British Isles and recaptured abroad, or ringed abroad and recaptured in the British Isles, are to be found recorded in past volumes of *British Birds*.

(2) British starlings

It has already been shown that male starlings do not breed in their first year, and although it is probable that they exhibit some sexual behaviour in spring in consequence of the growth of their testes, it has not been possible to make a sufficient number of observations on the first-year male at this time of the year to justify any final statement on the subject. The adult birds and the first-year females show many diverse trends of sexual behaviour which appear and which reach a pitch of maximum intensity at definite times of the year. These behaviour traits are clearly connected with the times and rates of growth of the gonads, and they are summarized below.

(*a*) *Attachment to nesting sites*

The starling is in the habit of nesting in holes in trees or buildings, and such nest-holes often endure for many years. It appears that the same bird, and perhaps the same pair of birds, will nest year after year in the same hole. Starlings not only visit the holes for breeding purposes in the spring, but they also visit them in every month of the year. These visits were found to be least frequent in July and August, but even at these times they were by no means uncommon. In September and October nest-hole visiting became universally common. The birds, often in pairs, spent long periods just outside the holes, and they frequently passed in and out. The males staked out small territories which were often merely part of a roof-top with the chimney as a song-post. Adult females all appeared to be paired at this time of year, and the surplus of unpaired males also occupied holes and staked out territories (see Morley 1941). From September to the following nesting season, interest in and attachment to the nesting holes became more and more intense.

(*b*) *Roosting habits*

The degree of attachment of the British starlings to their holes is also shown in their roosting habits. When the attachment is weakest it is the nightly habit of most starlings to come together in enormous gatherings to roost. This well-known habit has been described, for instance, by Marples (1932, 1934), Wynne-Edwards (1929, 1930), and Fitter (unpublished). The communal roosts at night may contain any number of birds from about a hundred to a hundred thousand, and they are found in a variety of situations. In the country the birds occupy such places as woods, plantations, and reed beds, and in the towns they roost on the ledges of buildings or inside empty towers. The same situation is used night after night for months on end, and it usually serves as the roosting place of most of the starlings within about a 20 mile radius. It was found that the communal roosts continued to exist in a very depleted form during the early part of the breeding season, the birds using them at this time being mainly first-year and unpaired males. Once the eggs hatched, only the female remained to brood the young at night, and most males returned to roost communally. About 12 days after hatching, when the young birds were fairly well feathered and often filled the nest-hole, both parents left at night and roosted communally. This return to communal roosting coincided with the beginning of the rapid reduction in gonad volume. When the juveniles flew they also joined in, and the gatherings of roosting birds each night became enormous. These habits were not, however, those of all the British

starlings. Some, except perhaps for a short period when the feathered young filled the nest-hole, remained every night in their nests, and this type of bird, which never visited a communal roost at all, appeared to be commoner in the towns than in the country. All other starlings, however, and these were greatly in the majority, roosted communally every night from about the middle of May throughout the summer and autumn. In January, when the gonads reached a certain stage in their growth and the attachment to the nesting sites became even stronger, the great majority of British birds forsook the communal roosts and once more spent the nights, often in pairs, in their old nests. This fact was first noticed by Morley (1939). As the birds retired into the dark holes in the evening when it was still broad daylight and did not emerge again until, in the morning, it was once more broad daylight, they were exposed to as much as an hour and a half less light per day than the birds which continued to roost communally. They also had far less exercise as the flights to and from the roosting place, which together were often as much as 40 or 50 miles a day, were eliminated. The very few British starlings which continued to use the communal roosts throughout February and March appeared to be mainly unpaired adult males and first-year birds, but occasionally an adult female was also found to be continuing this habit. By the end of March few adult birds and few first-year females remained to roost communally, but it was found that many pairs of birds living in the immediate neighbourhood of the roosting place continued to do so (figure 87, plate 21).

(*c*) *Sexual behaviour*

In this section there could be included a large mass of descriptive material of the various sequences of starling behaviour. Much of this has, however, already been published (for instance by Morley 1939, 1941), and only the main points will be mentioned here.

The most marked behaviour trait of the sexually stimulated starling is song, which, however, must be clearly distinguished from the chattering notes common to all starlings, young and old, at all times of the year. The true song of the starling has been well defined by Tucker (Witherby *et al.* 1938) as 'a lively rambling medley of throaty warbling, chirruping, clicking and gurgling notes interspersed with musical whistles and pervaded by a peculiar creaky quality'. Such song was heard, usually from the male bird, at all times of the year, but like the attachment to the nesting sites it varied greatly in intensity. During July and August song appeared almost to cease, but when the adult males were watched carefully it was found that they did produce a large amount of very quiet song. In autumn, when the gonads were growing, song became very loud, and it was accompanied by the most energetic waving of the wings and by elevation of the throat feathers. As already described by Bullough & Carrick (1940), this autumn song is produced not only by the adult male but also by the adult female, although the latter sings less lustily. Subsequent observations have made it appear probable that not all females sing, and that great variation in this respect exists within the sex. There was some diminution in the volume of song during December and January, but this may have been merely due to the cessation of the female song which took place at this time. The male birds continued to sing hard throughout both these months. In February, March, and April the volume of the male song rose to a maximum.

Of the many other behaviour traits which may be connected with the growth of the gonads, the following, extracted from Morley's paper (1941), may be mentioned. The ceremony of 'branch running', which is often a preliminary to copulation, was first seen on 24 November, and thereafter it became more common. Copulatory behaviour was first seen on 2 January when nest-hole roosting was beginning, but at this time no spermatozoa could yet have appeared in the testes. The first collecting and carrying of nesting material was noted on 14 February, although this material, after being put into the nest-hole, was pulled out again by the female. Nest building became more common in late February and March. It is evident from the description that new behaviour trains, which are connected with sexual display and with reproduction, make their appearance in September, October, and November, and that, after a short interval, more and more are seen in January, February, and March.

(*d*) *Abnormal nesting times*

There are several records of isolated pairs of starlings nesting and rearing their young at abnormal times of the year. The precision and shortness of the breeding season of the starling have already been noted, and these make the occurrence of such abnormal cases all the more remarkable. The instances recorded below have been reported in the British Isles in autumn and winter, and they probably refer to British starlings. The possibility, however, must not be overlooked that the birds were actually immigrant Continental starlings. Pairs of birds have been found nesting successfully in September (Nelson 1907; Lewis 1933), October (Allen 1933), November (Wade 1910), December (Livens 1931; Forrest 1940), January (Fortune 1921; Robinson 1923), and March (Astley 1925). It would appear that in most of these birds the autumn burst of gonad growth had progressed so far that breeding became possible, and as it is mentioned by some authors that the season was mild, it may be that this fact in some way helped the abnormal development. In the case of the birds found nesting in March it is probable that the late winter development had been unusually precocious. Such autumn and winter breeding is, however, very rare.

(3) Continental starlings

The study of the breeding behaviour of the Continental starlings present in this country in autumn and winter produced results, mainly negative, which are described below. In order that their significance may be better understood accounts are also given of the behaviour of the Continental starling on the Continent at these times of the year.

(*a*) *Attachment to nesting sites*

During the whole of the time the Continental starlings were present in this country no instance was noted of any interest shown by any bird of this race in a nesting hole or in any hole at all. The birds spent their days ranging the countryside in flocks, and the time not used for feeding was spent merely in flying or in sitting about. Occasionally they were attracted on to some roof-top by the presence of the British starlings whose territory it was, but even at these times they showed no interest in the nearby nesting hole. It was also interesting to note that the British starlings, apparently realizing the non-sexual state of

the visitors, usually took no notice of them, although they furiously drove away any trespassing British bird.

In Holland, where some local starlings remain throughout the winter, Kluijver (1933, 1935) has shown that the birds rarely visit their nesting holes in July, November, December, January, and early February. He also states, however, that, as in Germany (Schneider 1927; Niethammer 1937), Hungary (Vasvári 1931–4; Pátkai 1939), and Transylvania (Tolvaly 1931–4), the birds show a temporary recrudescence of interest in the nesting holes in September. They then visit their nests, often in pairs, especially in the mornings and evenings. Such activity was not seen in the Continental birds at the time when they arrived in the British Isles, and probably this phase of behaviour is over in October. Kluijver notes that the onset of the cold weather entirely breaks the attachment to the nesting sites in Holland, and that the birds show no more interest in them until the end of February. Throughout a large part of autumn and winter the Continental starlings live entirely in flocks. Kluijver describes how in late February and March the males leave the flocks for short periods, especially in the mornings, and return to the nest-holes. These visits become longer as the days go by, but the flock life does not finally break down until April when most of the females have also visited the nest sites and pairing has taken place. This description of the bird in Holland is substantially the same as those given for Germany by Schneider (1927) and for Hungary by Pátkai (1939), although in the latter country in autumn and winter the bird is entirely absent except when, in very mild weather, the birds coming from the more northerly countries remain. On the average the starling returns to Hungary in early March (Pátkai 1939), and to Czechoslovakia about the middle of March (Jirsík 1933). In France, Quépat (1874) records the return of the starlings to their nesting places on 10 March, but in Switzerland, as in Holland, Fatio (1899) states that the birds often return in February. No observations appear to be available for the Mediterranean countries, but in northern Europe the return of the starling, and therefore the occupation of the nest-holes, is later. Szmirnov (1929–30) has worked out the times of the return of the starling to most of the northern countries between the years 1872 and 1926. He shows that, with a rate of migration of about 32 miles per day, the birds do not reach Finland and south Russia until about 31 March, and north Finland and north Russia until about 15 April. The starling also reaches the north of Norway about the second week of April (Collett 1921), so that the sexual activity of these northern birds must be greatly delayed. There is, however, some indication that when possible they visit holes during the spring migration. In Savoy, where the birds rarely remain to nest, Bailly (1853) has noted that migratory starlings often roost in holes in trees.

(*b*) *Roosting habits*

The Continental starlings visiting the British Isles in autumn and winter were never seen to spend the night anywhere except in the large communal roosts in plantations or reed beds. In March, when the gonads were actively growing, they were not seen even to visit possible nesting holes. The great flights of starlings to the roosting places in winter (figure 86, plate 21) appear to be composed largely of these Continental immigrant birds.

The starlings on the Continent also have the same habits. The communal roosting of the birds in Holland has been well described by Kluijver (1933). The feeding flocks come

together in the evenings, and large and small parties leave for the roosting places which, in that country, are usually in the reed beds. It has been proved by ringing (Bouma, Klein & Koch 1932) that some of the birds roosting communally near the Hague were Dutch, some German, and some Finnish. An account is given by Koch (1930) of little groups of starlings in Holland which, not joining in the life of the large flocks, roosted together in small numbers under the tiles of a roof. This would appear to have been a small roost of local birds, such as were found in Britain (for instance, in an empty tower in Bradford), and not a true case of nest-hole roosting. No mention of the habit of nest-hole roosting in autumn and winter, which is so universal in the case of the British starlings, has been discovered in the literature. The Continental communal roosts often do not break up for the breeding season until the second half of April (Kluijver 1933), and even then, as in Britain, small numbers of birds, mostly males, continue to roost communally each night (Tischler 1905, 1908; Tschusi zu Schmidhoffen 1906).

In view of the theory put forward by Rowan (1937, 1938) that the growth of the gonads of starlings roosting in towns is precocious and rapid, owing perhaps partly to extra light but mainly to extra disturbance and exercise, an attempt was made to find out the relative amounts of light, exercise, and disturbance to which the Continental starlings are exposed in the British Isles. It was found that in winter the Continental birds left the suburbs of Leeds for a roosting place about 15 miles distant either just before or about the same time as the British birds retired into their nesting holes for the night. For instance, on 6 January the whole movement of Continental birds, fourteen separate flocks, crossed the University of Leeds between 3.36 and 3.48 p.m. (winter time), whereas the various British birds roosting in the University buildings went into the holes between 3.20 and 3.45 p.m. The same thing was seen in the mornings, the Continental birds passing over Leeds in flocks shortly after the British birds had emerged from their nest-holes. The day length of the Continental starlings was therefore relatively long. They had about half an hour's flight after the British birds retired for the night and again before they came out in the morning. These flights represented a total distance of about 30 miles each day. Also on arrival in the neighbourhood of the roosting places the Continental starlings usually spent some time gathering into larger flocks before they finally entered the wood or plantation, and even when inside they were still exposed to all the remaining daylight. Rowan (1938) suggested that starlings frequenting the big country roosts spent much quieter and less disturbed nights than did the birds roosting by main thoroughfares in the big cities. During the winter therefore three entire nights and part of another night were spent at a very large starling roost of about a hundred thousand birds at Rawcliffe near York in order to test the statement made by Rowan that in such a country roost all the birds spent the night quietly asleep. It was found that only during half an hour just before dawn on one of the nights was the roost entirely quiet. The conclusion was reached that as a normal thing, although large numbers of birds are always asleep, there are thousands of starlings which, owing to their own inherent restlessness or to such disturbing factors as hunting owls or sudden rainstorms, are wide awake, continually chattering, and frequently flying about even in extreme darkness. The roost was rarely entered during the observations in case added disturbance should be caused, and indeed on one occasion when the roost was approached for the first time at 3.40 a.m., the great noise made by the birds could be heard a quarter of a mile away.

(c) *Sexual behaviour*

Throughout all the autumn and winter no sexual behaviour, such as that described in the case of the British starlings, was seen in the Continental birds, except that in early March, just before migration time, the adult Continental males, in addition to making the normal chattering noises, started to sing. The first undoubted instance of this was noted on 16 March, but it is probable that the habit became common a week or two earlier.

On the Continent there is some sexual behaviour in early autumn, but this phase quickly passes and it is entirely over by the time the birds arrive in this country in October. In Holland (Kluijver 1933), Germany (Schneider 1927), Hungary (Pátkai 1939; Vasvári 1931–4), and Transylvania (Tolvaly 1931–4) the male starlings sing in September, and in extreme cases some nesting material is carried. Copulatory behaviour is very rare, but a case of this is described by Sopp (1932). Such behaviour is quickly subdued, and Kluijver states that, throughout the greater part of the autumn and winter periods, the birds live entirely in flocks. There is no sign of pairing or indeed of any other behaviour than that of searching for food. The next signs of sexual behaviour are seen at the end of February when the males return to the neighbourhood of the nesting sites, fight for the possession of some hole, and sing. When a hole has been acquired it is cleaned out and new nesting material is taken in. Kluijver (1933) found new nesting material for the first time in one of his nesting boxes on 18 March. Even at this time, however, the flock life is predominant, and the females do not visit the nesting places until some time after the males. The establishment of the pairs takes place in March or early April, but copulatory behaviour was not noted by Kluijver until 25 April.

(d) *Abnormal nesting times*

Records of the unseasonal nesting of starlings on the Continent do not appear to be common, and only the following cases have been discovered. Two pairs of birds were found nesting in Germany in January (Menzel 1927), and two pairs in Denmark in March (Moesgaard 1931). Apparently such abnormal nesting is rarer on the Continent than it is in Britain, and as all these instances occurred in the early months of the year it would seem that they were due to unusually rapid winter growth of the gonads. As the gonads of the Continental starlings do not normally start to grow until midwinter, the extreme rarity of such abnormal breeding and the entire lack of any cases of autumn nesting is not surprising. It must, however, be noted that Arrigoni degli Oddi (1929) mentions that in Italy starlings sometimes nest in autumn and winter. It is, however, not entirely clear to which species of starling he refers, and no details of time or place are given.

(4) Comparisons and conclusions

(a) *Migrations*

The most obvious difference between the behaviour of the British and the Continental starlings lies in the migratory habits. The British starling is entirely sedentary, while the Continental starling usually moves south or south-west in the early autumn. This difference cannot at the moment be definitely linked with the difference in the reproductive cycles,

but it seems possible that the growth of the gonads of the adult British starlings in autumn and the consequent production of sex hormones may prevent a southward migration at this time. Schildmacher (1933) has shown that injections of female sex hormone at this time of the year stop the migration urge in redstarts (*Phoenicurus p. phoenicurus* L.). In the Continental starlings the gonads reach their smallest size in autumn, and the complete lack of reproductive activity may allow or even cause the southward migration. It has been shown by Putzig (1937) that castration, which is equivalent to very acute gonad regression, allows the autumn migrations of the lesser black-backed gull (*Larus f. fuscus* L.) and the black-headed gull (*Larus r. ridibundus* L.) to take place normally. It appears probable that the northerly spring migration of the Continental starling is due to the growth of the gonads, and in the case of the adult birds in the British Isles, the movement starts when the total testis volume of each male reaches about 60 cu. mm. or when the maximum oocyte diameter of each female is about 0·9 mm. If, because of a hard winter, gonad growth is slow, the spring migration takes place later than usual. In the British starling, there being no autumn migration, a northward spring migration is also absent. It appears that the only time in the life of the British starling when the gonads regress sufficiently to allow the bird to desert its own locality is in the first summer and autumn of its life.

(*b*) *Attachment to nesting sites and roosting habits*

Some adult British starlings, which are especially common in towns, remain attached to their nesting sites and roost in them throughout the whole year. In the great majority of British birds, however, the attachment to the nests is weakest and the communal roosting habit is therefore strongest in July and August. The autumn gonad growth induces a new interest in the nest-holes, and during January the attachment becomes so strong that most birds leave the communal roosts and remain to sleep in their nests at night. The Continental starlings show no interest in nesting sites throughout their stay in the British Isles, and they continue to roost communally up to the middle of March when they leave for their nesting places. The same is true of the Continental starlings on the Continent.

During winter the adult British starlings, which roost, often in pairs, in their dark nesting holes, retire early for the night and emerge late next morning. The birds both go to roost and emerge from their nests in broad daylight. Their day length is therefore considerably shorter than that of the Continental starlings which are exposed to all the daylight, which make long flights to and from the roosting places, and which spend very restless nights in the company of thousands of their fellows.

(*c*) *Sexual behaviour*

The autumn gonad growth of the adult British starlings induces pairing, and causes the appearance of many trains of sexual behaviour including song. In January and February many more behaviour trains appear, copulatory behaviour being first seen on 2 January and nest building on 14 February. The Continental starling shows an unexplained recrudescence of sexual behaviour in September just before it leaves the district in which it nested. This behaviour quickly dies away, and during all the time the birds are present in the British Isles, no sexual behaviour is seen except that in early March the adult males

sing. On the Continent there is a similar lack of sexual behaviour until the birds return to their nesting sites between the middle of February and the middle of April according to the latitude. In Holland song begins in February when the nest-holes are claimed by the males. Nest building was first noticed on 18 March, pairing takes place during that month, and copulation was first seen on 25 April.

(*d*) *Abnormal nesting times*

In the British Isles instances of the abnormal breeding of starlings have been noted in almost every month of autumn and winter. It is probable that the birds concerned were resident and British, and that their gonads had undergone an abnormally active autumn growth phase. On the Continent, where apparently no autumn gonad growth occurs, no cases of autumn breeding were discovered, and even in winter such cases were very rare.

(*e*) *General conclusions*

A sufficient description has been given of the behaviour of the British and Continental starlings in autumn and winter for the conclusion to be drawn that, because of the autumn gonad growth, the adult British starlings are attached to their nesting sites and indulge in sexual behaviour throughout the entire period, while the Continental birds, both in the British Isles and on the Continent, remain in a non-sexual state. The sexual behaviour of the British birds becomes more intense and more complicated towards the middle of winter, and at this time also the Continental birds show their first signs of breeding activity. As the British starlings pair in autumn and as the Continental birds do not do so until after the return to the nesting places in March, there is an effective barrier preventing the inter-breeding of the two races.

VI. DISCUSSION

The observations and comparisons recorded in this paper lead to the conclusion that, whereas in spring and summer only one type of starling is present in the British Isles, two distinct types are present here in autumn and winter. The essential difference between these two types lies either in the gonads or in whatever controls them. In one type the testes and ovaries, not regressing so far in summer, grow precociously in autumn. In the other they regress considerably in summer, and the next cycle of growth does not begin until January or February. In the former type the growth in winter is rapid, and in the latter type it is slow. These differences in degrees of regression and in times and rates of growth of the gonads are reflected in the accessory sexual organs, in the secondary sexual characters, and in behaviour. The accessory sexual organs and the secondary sexual characters of the former type are enlarged or developed earlier than those of the latter type, and throughout the whole of the autumn and winter the birds may be distinguished either by internal or external features. The external morphology of the former type of bird is further modified by the considerable feather wear which is caused by repeated visits to nesting holes.

These differences are clear and unmistakable, and it remains to assess their significance. Rowan (1937, 1938) concluded that the birds with large gonads were those which roosted in the towns, and that the gonads had been stimulated to precocious growth by the extra

disturbance to which the birds were exposed each night. It was not suggested that the lights of the town had any great effect, as they were shown to be of insufficient strength. For many reasons Rowan's theory cannot now be accepted, and even at the time when it was propounded there were some difficulties in its way. These difficulties have been added to and reinforced by the evidence given in the present paper, and the main criticisms may now be summarized. According to Rowan's theory, the town birds should nest earlier than the country birds, but it is shown that this is not the case. The times of nesting, egg laying, hatching, etc., are very uniform over wide areas which include both town and country districts. Further, any immigrant Continental starlings which might spend the winter in the towns should be equally stimulated, and so induced to migrate to their nesting places where they would perish. In the mass of ringing records there is no evidence that such abnormal and unseasonal migrations actually occur. Then there is the great difficulty that both types of birds are to be found in large numbers in the supposedly quiet country roosts from which Rowan obtained his unstimulated birds. It is also shown that these country roosts are not quiet, and that the birds which roost in them spend nights which are probably quite as disturbed as those of the birds which roost communally in the towns, and far more disturbed than those of the birds which roost each night in their nesting holes both in town and country. These last birds, which *all* have large gonads, have the quietest nights, and a day length which, in winter, is as much as two hours less than that of the communally roosting birds. Further, the 'black-out' of the first autumn and winter of the war, with the consequent great reduction in the amount of traffic in the streets after dark, failed to prevent the precocious growth of the gonads of a proportion of the starlings present in the British Isles, and finally, the heavy bombardment and anti-aircraft barrage of the second autumn and winter of the war failed to accelerate the speed of development of the gonads. It is in any case unlikely that, as postulated by Rowan, disturbance alone would cause any acceleration in gonad growth. Bissonnette (1931) has shown experimentally that nightly disturbance without extra light is insufficient to induce any abnormal growth of starling gonads.

Because of these points, Rowan's theory has been rejected, and on evidence given in full earlier in this paper, it is suggested that the only theory which will fit the known facts is that the precociously developing type of starling is actually the resident British bird, and that the other type is an immigrant from the Continent of Europe. This theory would also fit Rowan's facts as, except in very bad weather, flocks of Continental starlings are not commonly seen in towns. The lack of sexually stimulated birds which he observed in the country was probably due to the fact that a sufficiently large sample was not taken. The theory of separate races is further strengthened by the results of Nicholson's 1925–6 London starling survey (see Fitter, unpublished). The town birds with large stimulated gonads, which were taken by Rowan, were starlings roosting communally in the middle of London. Nicholson carefully traced the movements of these birds during the daytime, and he concluded that they represented the resident suburban population. Contrary to popular belief, no Continental immigrants were involved. All the evidence therefore points to the conclusion that the British starling is a distinct physiological subspecies of the Continental race, and it is evident, as the two kinds of starlings are present together during the autumn and winter in exactly the same environment in the British Isles, that this physiological

difference is entirely inherent. It is known that extra light in winter is capable of stimulating the gonads of starlings to precocious growth (see review by Bissonnette 1936), and it is therefore probable that, in late winter and early spring, the increase in the length of day helps to induce the growth of the gonads in both races of starlings. The variation of the external environment, however, merely helps as a superficial control to render more precise the timing of an animal's internal rhythm, a conclusion which, supported by the evidence obtained from a study of the reproductive cycle of the minnow (*Phoxinus laevis* L.), was put forward by Bullough (1939, 1941). Both in the minnow and in the starling the inherent reproductive rhythm may be overcome by the effects of spring-like conditions in winter. It is, then, clearly the internal reproductive rhythms of the British and Continental starlings which are so different, and it appears probable that this difference will be found to be centred in the anterior pituitary gland. In the British bird there is an internal rhythm which causes gonad growth in autumn, and which induces the very pronounced and rapid reaction to the increase of light in winter. In the Continental bird there is no stimulus in autumn, and the reaction to the increase of light in winter is at first only slow.

Besides these differences in physiology and consequently in structure, the two races of starlings show correspondingly great differences in behaviour. At the same time as the autumn gonad growth there is a burst of sexual behaviour in the British birds which is not so intense and varied but nevertheless, as far as it goes, is typical of that seen in the breeding season. No such behaviour has been noted during autumn in the Continental starlings which come to the British Isles, and a comparison with the various accounts of starling behaviour on the Continent shows that a lack of sexual activity in autumn is normal in this race of bird. There is an unexplained burst of interest in the nesting sites during September which is commented on by many Continental writers (for instance, Kluijver 1933; Pátkai 1939), but after this month no behaviour which can be distinguished as sexual is noted by any author until the second part of February. Such a marked difference of behaviour between British resident birds and Continental immigrants is probably not entirely peculiar to the starling. There are many odd references in British ornithological literature to sexual behaviour in autumn and winter, and in some of them it is suggested that the birds concerned are British residents and not Continental immigrants. Although in some cases these recorded instances may have their explanation in unseasonal weather, or in some peculiarity of the particular individual involved, some of them may help to prove, when further observations are made, that sexual behaviour is common in many British species at this season and absent in the Continental representatives of the same species. Probably, where such a difference exists, it will be found that the British birds concerned are sedentary, whereas their Continental equivalents are migratory. Many of the latter may come to the British Isles. One instance of this is furnished by the rook (*Corvus f. frugilegus* L.) which is sedentary in Britain and migratory on the Continent. The autumn sexual activity of the adult British birds has been described by several authors. The rookeries and nests are visited each day, especially in the early morning (Cummings 1908), and the birds often carry nesting material and build or repair their nests. It is also reported (Brown 1924) that they may brood in the empty nests. In the accounts of the behaviour of the rook on the Continent, no sexual behaviour is noted at this season, although it is stated that the birds may take part in a flying display which is considered to have a sexual significance (Niethammer

1937). Jourdain & Tucker (Witherby *et al.* 1938) do not consider, however, that these aerial antics have any sexual significance. The robin (*Erithacus rubecula melophilus* Hart.) is another resident British bird which shows very active sexual behaviour in autumn when the birds sing and stake out territories (Lack 1939), but in this species autumn sexual behaviour is not confined to the British race. Alexander (1917) has described how Continental robins, arriving in southern Italy after their autumn migration, also sing and stake out territories. A survey of the available evidence regarding sexual behaviour by resident British birds in autumn has been prepared by Miss A. Morley (private communication). This evidence is extremely suggestive and should stimulate further observations on the problem.

A point of great interest connected with this problem of sexual behaviour in autumn is furnished by the two peculiar cases which have been described of male behaviour by the female bird at this time of the year. Such unusual behaviour was first described in the case of the robin (Lack 1939). Song and the staking out of territories, which are defended against intruders, are male characteristics in this species, but in autumn many females also behave in this manner. This abnormal behaviour breaks down about December or January when the females enter the territories of the males and pairing takes place. In the starling, song is also characteristic of the male over the greater part of the year, but in autumn some females also sing. It has been shown that this male-like behaviour is probably due to the secretion by the ovaries of male sex hormone (Bullough & Carrick 1940). This secretion also results in the change of colour of the beak to yellow, a feature which is really a male secondary sexual character (Witschi & Miller 1938). The degree of maleness, which is probably merely an expression of the amount of male sex hormone produced, varies considerably in different females, a fact which is shown in two ways. In some females the beak begins to turn yellow early (October) and the change proceeds rapidly, but in others the beak may still be entirely dark at the beginning of January. Similarly, some females, which in all cases had partly yellow beaks, sing hard while others appear not to sing at all. As in the robin, this abnormal behaviour ceases about December when it is superseded by typical female behaviour. The continued yellow colour of the beak is evidence, however, that the secretion by the ovaries of male sex hormone is actively continuing. A similar effect, the induction of song in normally quiet female birds, has been caused experimentally by Leonard (1939) and Shoemaker (1939). They injected female canaries (*Serinus c. canarius* L.) with male sex hormone, and so induced them to produce typical male song. Shoemaker also demonstrated that sex hormones are probably the physical basis of social dominance within the flock. In a group of six birds the 'peck order' was worked out, and the three birds of the lowest grades were injected with male hormone. Besides singing, these birds rose to the top of the 'peck order'.

These observations on the starling and the results of the experiments of Leonard and Shoemaker are important in that they clearly show the effect of the sex hormones on behaviour, a connexion which has also been stressed by Roberts (1940) as a result of his work on the gentoo penguin (*Pygoscelis papua* Forster). It appears that the relative concentrations of the male and female sex hormones in the blood strongly influence, if they do not actually determine, the type of sexual behaviour indulged in. In the male starling, when the level of the male sex hormone in the blood rises above the point at which the beak begins to turn yellow, loud song and the behaviour associated with it commence. In the

female it appears that if the rise in the blood content of male sex hormone exceeds that of the female sex hormone, this bird also sings and exhibits male behaviour. The development of the yellow beak colour and the appearance of loud and persistent song both require about the same rate of male sex hormone secretion, but some behaviour traits, for instance, the actions leading up to copulation or to nest building, require a much higher rate of sex hormone secretion. On the contrary, others, for instance, the attachment to nesting sites which never breaks down in adult British birds, require less. The increasing complexity and intensity of the sexual behaviour of the British starling during autumn and winter may be correlated with the increase in the size of the gonads, and therefore, in all probability, with the increase in the rate of sex hormone secretion.

It has been shown that in the adult British starlings the gonads do not regress as far in summer as do those of the Continental birds, and that, probably as a consequence, the attachment of the British birds to their nesting sites and nesting localities is never broken. The only time in the life of the British starling when the gonads regress sufficiently to allow a breaking of this attachment appears to be in the first summer and autumn. A certain amount of wandering by the young birds is then observed. It is, however, possible that, after a bird's reproductive life is over, the gonads may again regress sufficiently to allow that bird to wander away from its nesting area. The regression of the gonads of the adult Continental starlings after the breeding season appears normally to be carried so far that the attachment to the nesting sites is broken, and the birds are released for the southward migration. In late winter and spring, when the gonads grow once more, the birds are induced to return to their nesting areas. Applied to birds in general, this theory, which is certainly oversimplified, means that the basis of the autumn southward migration is negative (the absence of a stimulus), and that of the spring northward migration is positive (the renewal of the stimulus). This theory is able to explain several peculiar facts. It has frequently been reported (see reviews by Rollin 1932 and Nice 1933) that in many species of birds the adult males regularly winter to the north of the adult females which, in turn, may winter to the north of the young birds. Much more evidence is needed on these points before detailed statements can be made, but in the case of the chaffinch (*Fringilla coelebs* L.) and the song thrush (*Turdus philomelos* Brehm) in Switzerland, and in that of the Mississippi song sparrow (*Melospiza melodia beata* Bangs) and the Cabanis woodpecker (*Dryobates villosus hyloscopus* Cabanis & Heine) in North America, it seems fairly certain that the females normally travel farther south in autumn than do the males. It seems probable that testes often do not regress relatively so far as ovaries, and that they also begin to grow earlier and faster in the late winter months. There is evidence that in such a bird as the sparrow (*Passer domesticus* L.) a much greater stimulation from the anterior pituitary gland is necessary to activate the ovaries than is required to activate the testes (Kirschbaum, Pfeiffer, Heuverswyn & Gardner 1939). The lesser regression and quicker activation of the testes may mean that in autumn and winter there is a sufficient secretion of sex hormone in male birds to limit, if not actually to prevent, the southward movement from the breeding areas. In the case of first-year birds the evidence concerning the extent of the autumn migrations is not so definite, but it appears probable that the extreme regression of their gonads releases them to migrate farthest from the breeding areas. In the following spring the relative lack of gonad growth in the first-year birds of many species results in the failure of these birds

to undertake the spring migration. Birds such as the purple sandpiper (*Erolia m. maritima* Brünnich) often remain in their winter quarters until the spring of their second year of life (Bullough 1942*b*).

It is also possible on the theory of the determination of behaviour by the sex hormones to suggest an explanation for several peculiar facts about the activities of young birds in their first summer. As in juvenile starlings, it may be a common feature for these young birds just off the nests to have relatively active gonads, and the secretion of sex hormones by these gonads may account for the sexual behaviour of juvenile birds which has frequently been described. Young swallows (*Hirundo r. rustica* L.) of the first brood may help to feed the second brood (White 1941; Williamson 1941). Young noddy terns (*Anous stolidus* L.) are recorded as collecting and carrying nesting material when only 16 days old (Watson 1908), and Craig (1909) describes how a young ring dove (*Streptopelia risoria* L.), 21 days old, incubated its parents' egg. It is also stated by Hudson (1892) that young oven birds (*Furnarius rufus* Gmelin) sing when still in the nest. Similar, but more intense and varied, effects were obtained experimentally by Noble & Wurm (1938) when they injected month-old chicks of the black-crowned night heron (*Nycticorax n. hoaetli* Gmelin) with testosterone propionate. The secretion of sex hormones by the active gonads of young birds just off the nests may also account for the short northward migrations made in their first summer by the juveniles of such species as the common tern (*Sterna h. hirundo* L.) and the sandwich tern (*Sterna s. sandvicensis* Latham) (Marples & Marples 1934). The movements of the juvenile Continental starlings are perhaps comparable to this short northward movement of the young terns. Niethammer (1937) states, for instance, that in Switzerland the juvenile starlings scatter soon after flying and spread northwards in great numbers as far as the North Sea coast, and that because of this they are probably late for the normal autumn southward movement. The British starlings are not accustomed to migrate in spring, and this may explain why the juvenile birds of this race make no similar movement. The wandering in which they indulge is probably due to the later regression of their gonads. As the burst of mitotic, and presumably secretory, activity in the gonads of the juvenile starlings is short-lived, so also are all these phases of precocious sexual activity.

The separation which has been made of a physiological British race of starling, with its varying morphology and behaviour so distinct from that of the main or European species, is a separation which will probably not be popular with those systematists who prefer specific and subspecific distinctions to be based on unvarying morphological differences in hard and easily preservable parts of the body. Constant morphological distinctions are of course merely external expressions, and often relatively unimportant expressions, of inherent physiological differences. Important physiological differences often arise without the external structure being affected in any discernible way. Many instances are known of curiously distinct physiological races of animals. There are, for instance, the two races of the leaf-hopper (*Cicadulina mbila* Nande), one of which can transmit the virus of 'streak disease' to maize and the other of which cannot (Storey 1932). Then there is the case of a species of cricket (*Nemobius fasciatus* De Geer) split up into races which, although they cannot be separated morphologically with any certainty, are clearly distinguishable by their song (Fulton 1931). Although the habitats of these races overlap, interbreeding, which is possible, appears to be very rare, and therefore in this case the physiological difference,

whatever its basis, is of great importance. Among birds, it has been shown by Promptoff (1930) that chaffinches (*Fringilla coelebs* L.) in south Russia may also be divided into distinct populations on the basis of song. The species is migratory, but there is a strong disposition for an individual bird to return to the same little district year after year. Because of this, little or no mixture of the different populations takes place. The differences recorded here between the British and Continental starlings are more distinct than those recorded in any of these cases, and in addition, the external morphology is also modified by the physiological difference.

One of the best discussions of the problem of physiological species is given by Thorpe (1940) who suggests that, to avoid confusion, some modified system of nomenclature may ultimately be necessary to deal with these peculiar cases. In the meantime, he defines the modern conception of a species 'as a population of individuals prevented from interbreeding with all other populations by physiological differences (in the widest sense) whether or no structural differences are also present'. He suggests that before full specific rank is accorded to a group of animals which are physiologically distinct, these physiological differences should interfere with cross-breeding. In the case of subspecific physiological differences, interbreeding may still be possible if animals of the two races are brought together. Usually, however, the breeding places of the two races or subspecies are separated from each other, and this is true in the case of the British and Continental starlings. Although their ranges overlap in winter, the breeding areas are entirely distinct, and it is not known whether, if the two races were brought forcibly together, they could interbreed successfully. Information on this point may be obtained from a study of the starling in the United States of America, and in other countries where the bird has been introduced. Starlings, taken to the United States from Europe, were released in the Central Park, New York, in March 1890 and in April 1891 (Lewis 1927), and they are now spreading rapidly across the continent. Their place of origin in Europe appears to be unknown, but if they were caught in the British Isles in autumn or winter, it is possible that both British and Continental races would be found represented among them. Judging from the accounts (for instance, by Kalmbach 1928) of the habits of these birds in the United States in autumn and winter, the Continental race is certainly present, but there are also indications that the British race is there as well and that it has retained its identity. Hicks & Dambach (1935) state that, in addition to the enormous flocks of birds which roosted communally in autumn and winter, 'many square mile tracts of land in Muskingum County had from 2 to 10 pairs of mated starlings, which roosted, fed, and lived independently of the others through the winter near cavities where they will nest in the spring'. Hicks (1934) also states that in late autumn between 5 and 10% of the population have already developed yellow beaks, although the majority of the population, like the Continental birds in the British Isles, do not do so until after January. Professor T. H. Bissonnette (private communication) has also discovered in Connecticut some starlings which, in winter, had unusually large gonads. If both races of starlings are present in the United States, they must have retained their separate identities over a period of 50 years. This may have been due to some difference which interferes with successful copulation, or it may simply be because the birds of the British race have tended to pair in autumn and so remain separated from those of the Continental race which did not pair until late winter.

Whether interbreeding between the two races is possible or not, the distinction between them clearly amounts at least to a subspecific difference. Many European subspecies of the starling have been distinguished merely by minute differences in the gloss of some of the feathers, distinctions which have been strongly criticized on the grounds of looseness of definition by Pátkai (1939). The difference between the British and Continental starlings is much clearer than this, and it is therefore proposed that the British bird should be recognized as an insular subspecies of the Continental race which was first named by Linnaeus. The name of the Continental starling then remains as *Sturnus vulgaris vulgaris* L., and a new name of *Sturnus vulgaris britannicus* is given to the British form.

It is only possible to mention by name some of those who have been of great assistance in the various phases of this research. Professor E. A. Spaul has given much invaluable help, and he has kindly read and criticized the manuscript. Dr and Mrs R. Carrick were constant companions and helpful critics in the many field expeditions, the ringing of the British and Continental birds was carried out mainly by them, and they were also mainly responsible for the analysis of the movements of British starlings. Various landowners in the West Riding of Yorkshire readily gave permission for shooting over their lands, and special thanks are due to Mr W. Nelson for his many kindnesses when shoots were taking place near his farm. Great help with the literature on bird behaviour was received from the Rev. E. A. Armstrong and Miss A. Morley. The Continental papers on starling behaviour were obtained at the Edward Grey Institute of Field Ornithology, Oxford, and very grateful thanks are accorded to Mr W. B. Alexander for the facilities which he so readily gave. The more difficult translations of some of these papers were made by Mr C. Berczi, and the statistical calculations were checked by Mr A. Gibbs.

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Description of Plates

Plate 12

Figure 53. Section of the testis of a juvenile British starling in June a few weeks after leaving the nest. The seminiferous tubules are large, and some spermatogonia are dividing (*spg.m.*). × 700.

Figure 54. Section of the testis of a first-year starling in November. The small seminiferous tubules are separated by masses of pigment cells (*pi.c.*), and both normal (*spg.*) and giant (*spg.g.*) spermatogonia are present. × 700.

Figure 55. Section of the testis of a first-year British starling in March. Many spermatogonia are undergoing mitosis (*spg.m.*), and many primary spermatocytes are in the synizesis stage of meiosis (*spc.s.*). × 700.

Figure 56. Section of the testis of a first-year Continental starling in March. There are many resting spermatogonia (*spg.*), some spermatogonia in mitosis (*spg.m.*), and a few primary spermatocytes in the synizesis stage (*spc.s.*). × 700.

PLATE 13

FIGURE 57. Section of the testis of an adult British starling in November. Some spermatogonia are undergoing mitotic division (*spg.m.*). × 700.

FIGURE 58. Section of the testis of an adult Continental starling in November. There are many resting spermatogonia, some of them normal in size (*spg.*) and some of them giant (*spg.g.*). × 700.

FIGURE 59. Section of the testis of an adult British starling in March. Primary germ cells (*pgc.*), spermatogonia (*spg.*), primary spermatocytes (*spc.*1), secondary spermatocytes (*spc.*2), spermatids (*spd.*), and spermatozoa (*spz.*) are present, and spermatogenesis is proceeding actively. × 700.

FIGURE 60. Section of the testis of an adult Continental starling in March. Only primary germ cells (*pgc.*), spermatogonia (*spg.*), and primary spermatocytes in the synizesis stage (*spc.s.*) are present. × 700.

PLATE 14

FIGURE 61. Transverse section of the seminal vesicle of an adult British starling in August showing the maximum regression of the tubules. × 60.

FIGURE 62. Transverse section of the seminal vesicle of an adult British starling in April showing masses of spermatozoa distending the tubules. × 60.

FIGURE 63. Transverse section of the seminal vesicle of an adult British starling in March showing the partial growth of the tubules. × 60.

FIGURE 64. Transverse section of the seminal vesicle of an adult Continental starling in March showing only slight growth of the tubules. × 60.

PLATE 15

FIGURE 65. Longitudinal section of the ovary of a juvenile British starling in June. × 60.

FIGURE 66. Longitudinal section of the ovary of a first-year starling in November showing the zonation of the cell sizes. The oogonia and small primary oocytes are near the germinal epithelium while the large primary oocytes are at the base of the ovary. × 60.

FIGURE 67. Longitudinal section of the ovary of a first-year British starling in March. × 60.

FIGURE 68. Longitudinal section of the ovary of a first-year Continental starling in March. × 60.

PLATE 16

FIGURE 69. Longitudinal section of the ovary of an adult British starling in November. × 30.

FIGURE 70. Longitudinal section of the ovary of an adult Continental starling in November. × 30.

FIGURE 71. Longitudinal section of the ovary of an adult British starling in March. × 30.

FIGURE 72. Longitudinal section of the ovary of an adult Continental starling in March. × 30.

PLATE 17

FIGURE 73. Young 'corpus luteum' in the ovary of an adult British starling in early May showing the theca externa (*t.e.*), theca interna (*t.i.*), and solid core of follicle cells (*l.c.*). × 60.

FIGURE 74. Older 'corpus luteum' in the ovary of an adult British starling in the middle of May. The theca externa (*t.e.*) contains no 'luteal' cells, the theca interna (*t.i.*) contains some 'luteal' cells, and the solid core is composed entirely of 'luteal' cells (*l.c.*). × 120.

FIGURE 75. Germinal epithelium (*g.e.*) of the ovary of an adult British starling in early May showing mitotic divisions (*m.*) of the epithelial cells. × 1000.

FIGURE 76. Very young oogonium (*o.*) just below the germinal epithelium of the ovary of an adult British starling in May. × 1000.

PLATE 18

FIGURE 77. Transverse section of the oviduct of an adult British starling in August showing maximum regression. × 40.

FIGURE 78. Transverse section of the oviduct of an adult British starling in late April showing the full development typical of the breeding season. × 11.

FIGURE 79. Transverse section of the oviduct of an adult British starling in March showing considerable growth. × 40.

FIGURE 80. Transverse section of the oviduct of an adult Continental starling in March showing only slight growth. × 40.

PLATE 19

FIGURE 81. Transverse section of the seminal vesicle of an adult British starling in August showing maximum regression of the tubules. × 120.

FIGURE 82. Transverse section of the seminal vesicle of an adult British starling in late April showing the greatest development of the tubules. × 120.

FIGURE 83. Transverse section of the seminal vesicle of an adult British starling in March showing the partial growth of the tubules. × 120.

FIGURE 84. Transverse section of the seminal vesicle of an adult Continental starling in March showing the slight growth of the tubules. × 120.

PLATE 20

FIGURE 85. Feathers (natural size) taken from the lower throat or upper breast of British and Continental starlings in various months of the year. It is seen that the white tips of the feathers of the first-year birds are broader than those of the adults, and that they are also broader in the female than in the male. In the first-year birds of the British and Continental races the rate of wear of the tips is about the same. Owing however to the repeated visits of the adult British starlings to their nesting holes, the white tips of their throat feathers wear away much more rapidly than do the tips of the feathers of the adult Continental starlings.

PLATE 21

FIGURE 86. A flock of starlings, mostly Continental birds, coming in to the communal roosting place near Beamsley in Wharfedale on the evening of 14 March 1939.

FIGURE 87. A very small flock of British starlings, part of the population from the immediate neighbourhood of the roosting place near Beamsley in Wharfedale, coming in to sleep communally on the evening of 20 April 1939. The way in which the pairs of birds kept together was most marked.

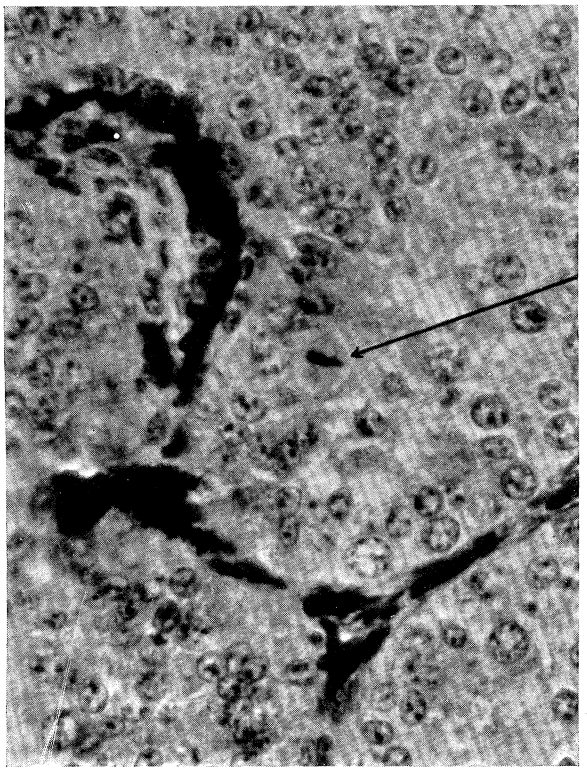


FIGURE 53

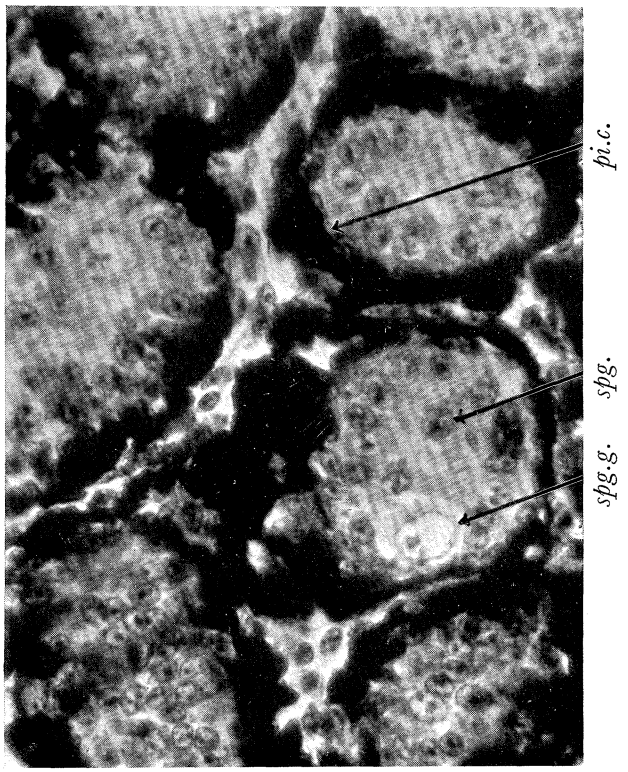


FIGURE 54

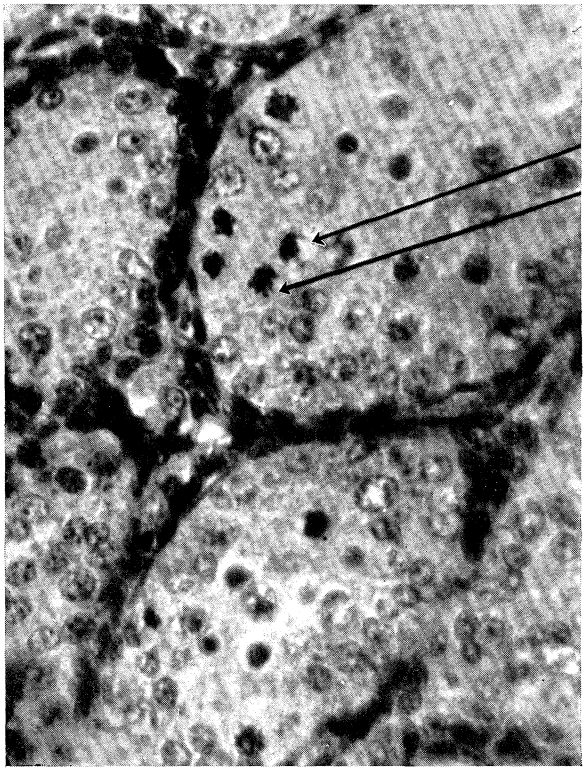


FIGURE 55

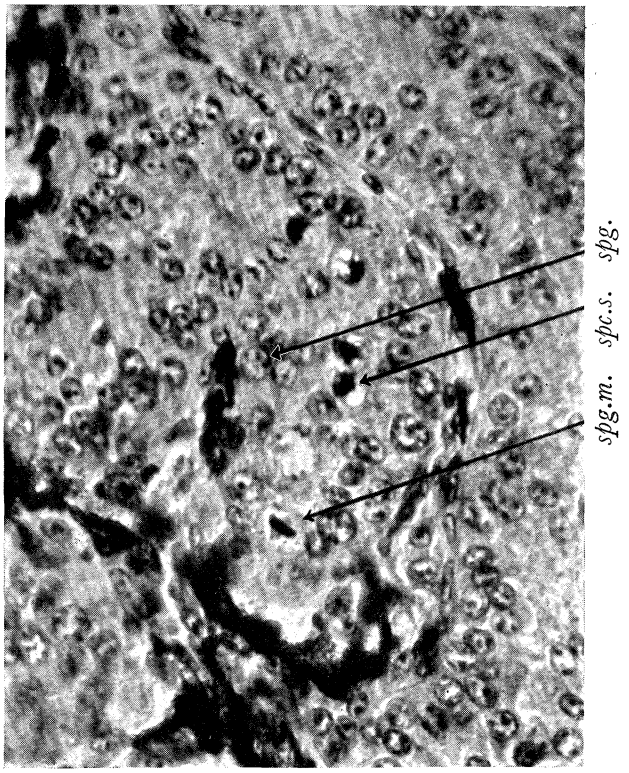
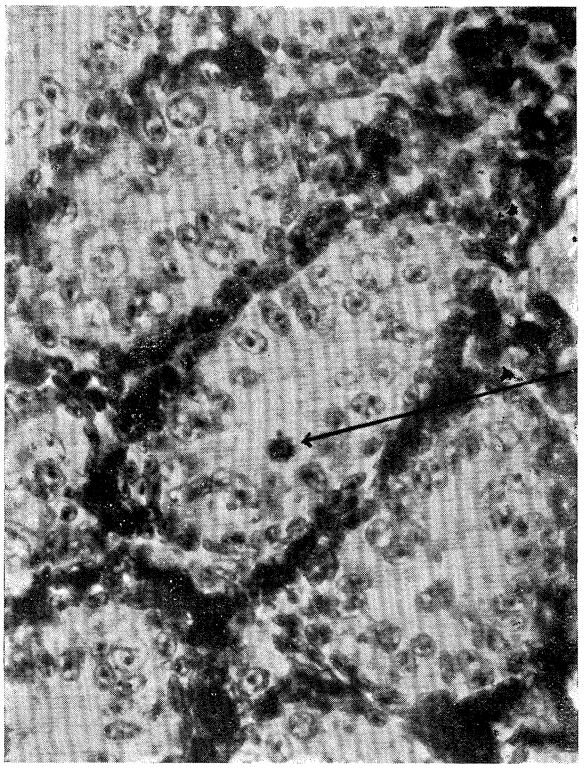


FIGURE 56



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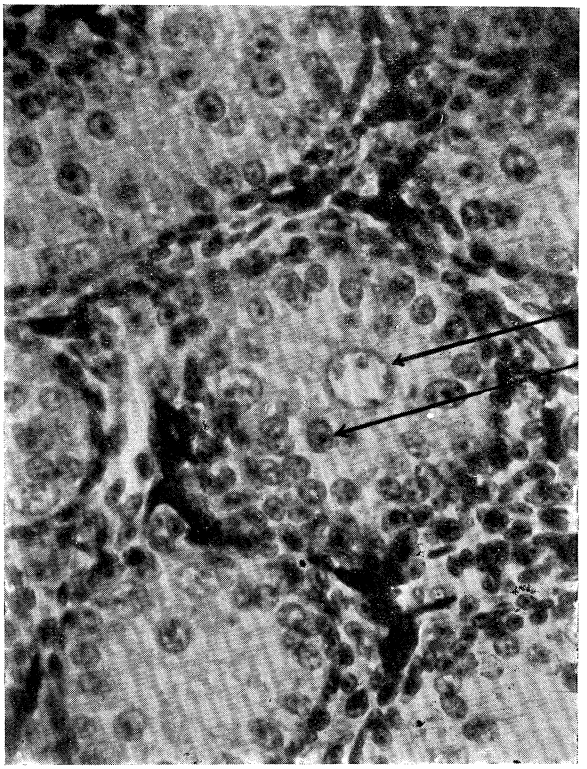

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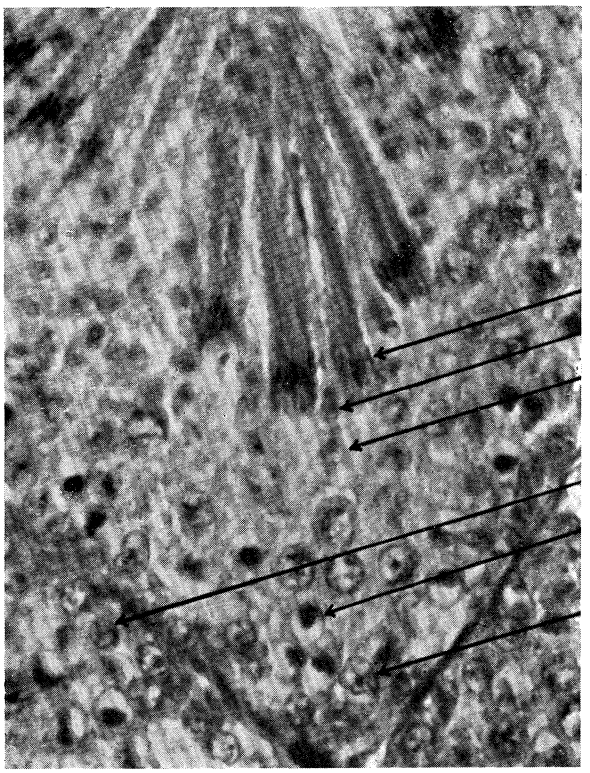

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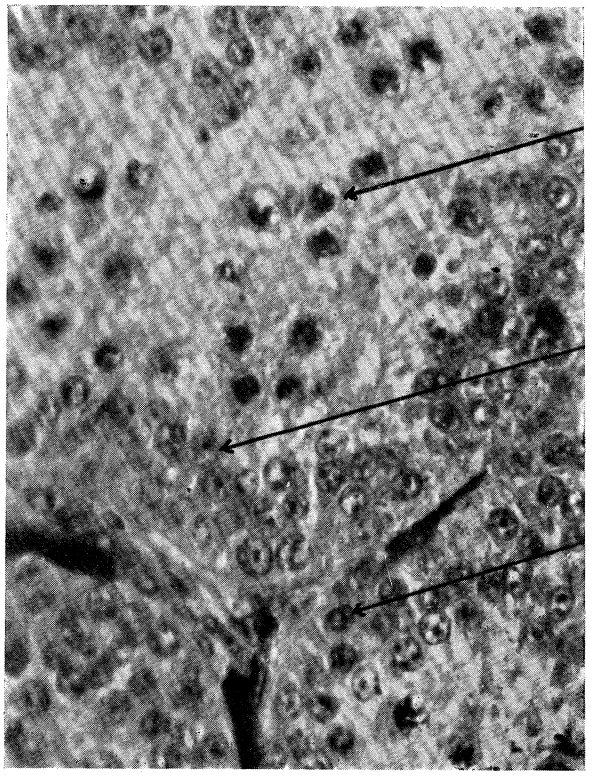

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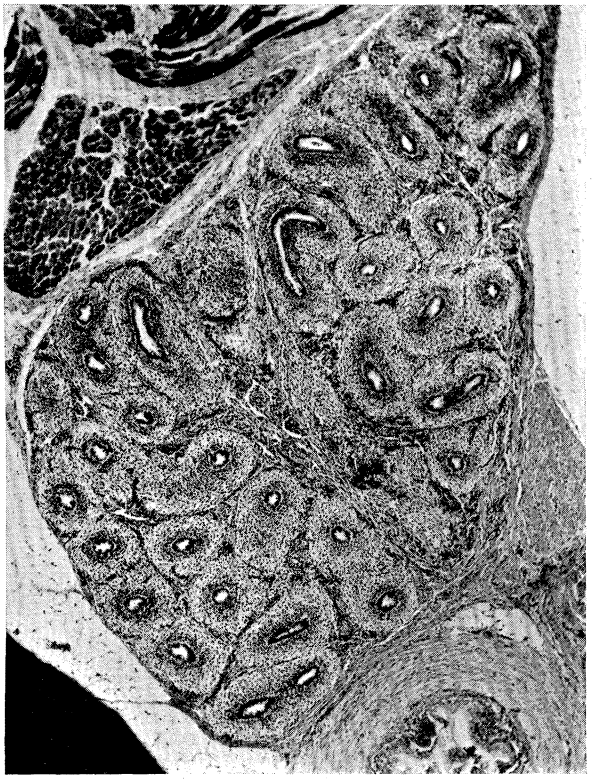

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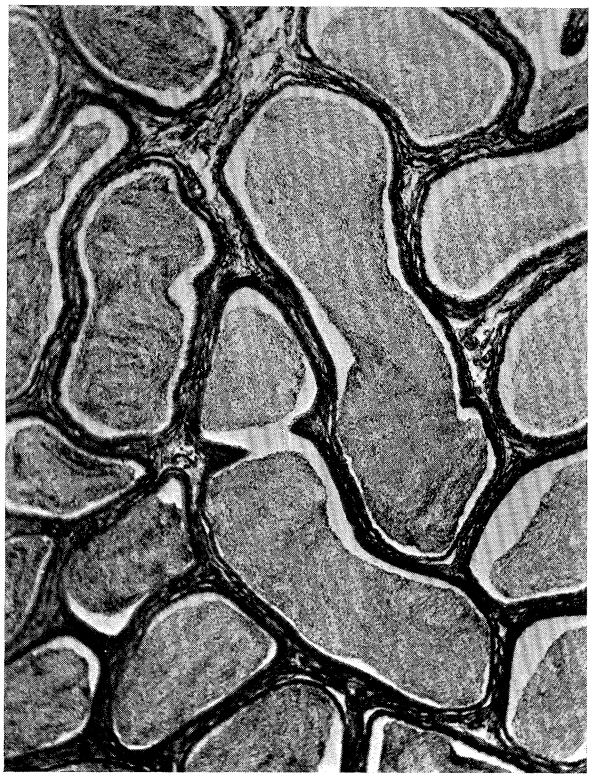

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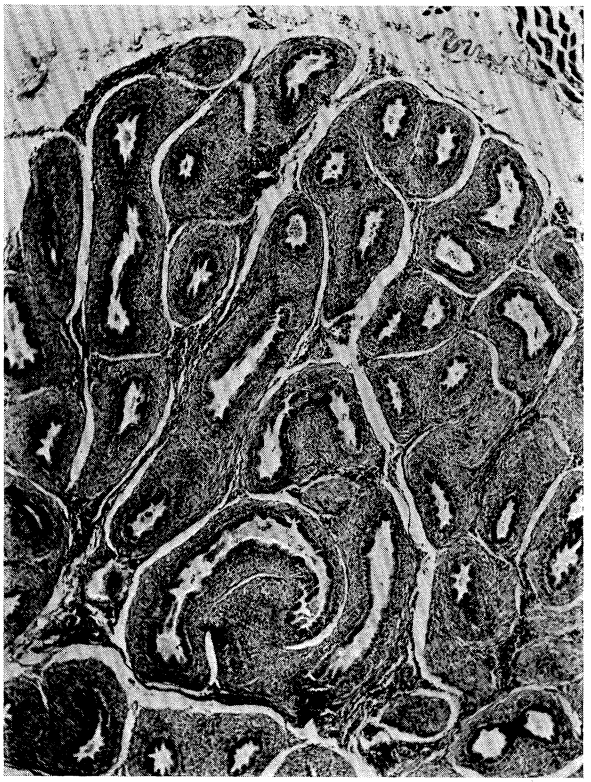

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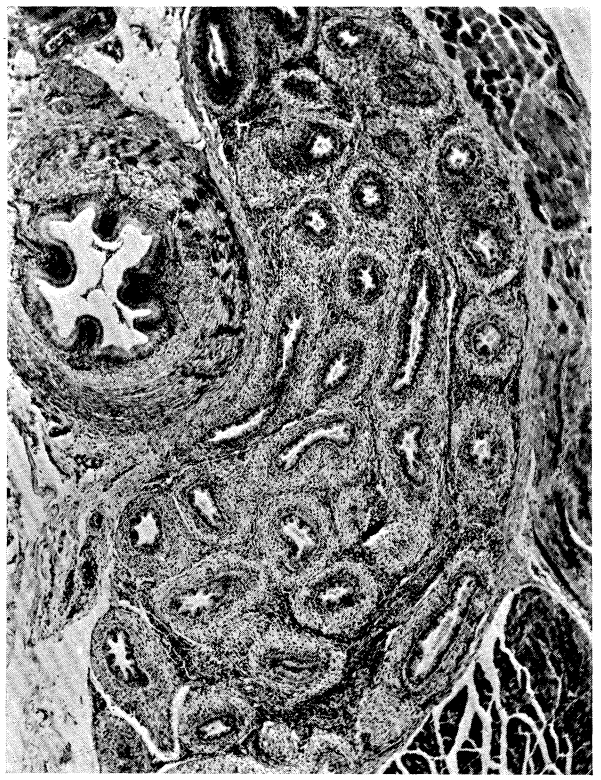

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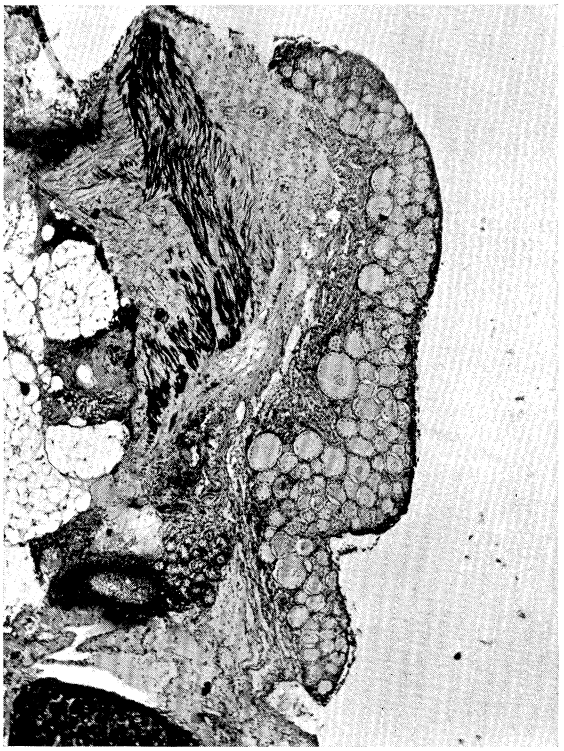

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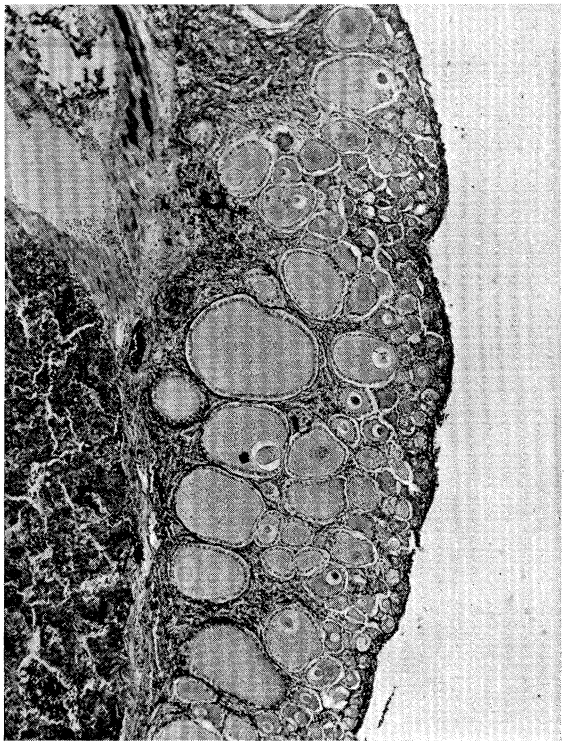

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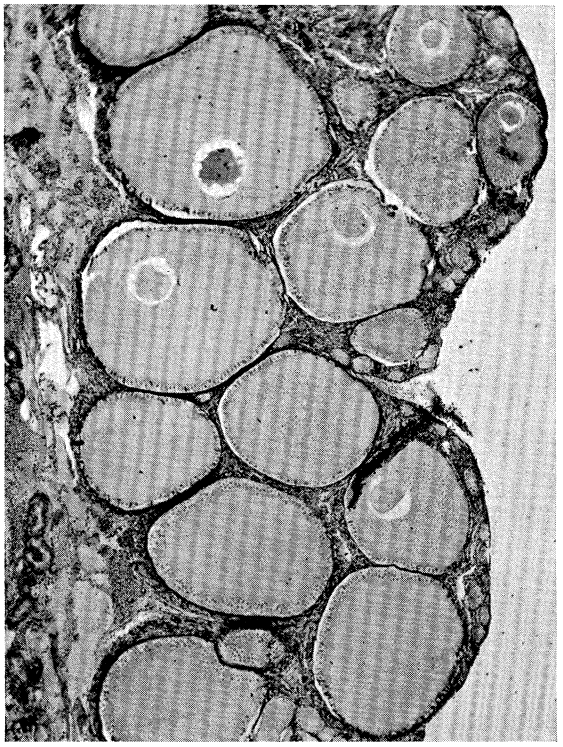

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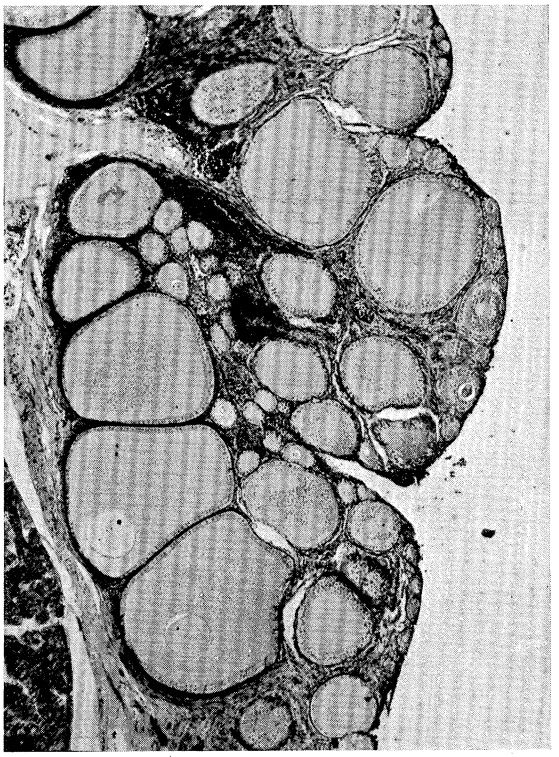

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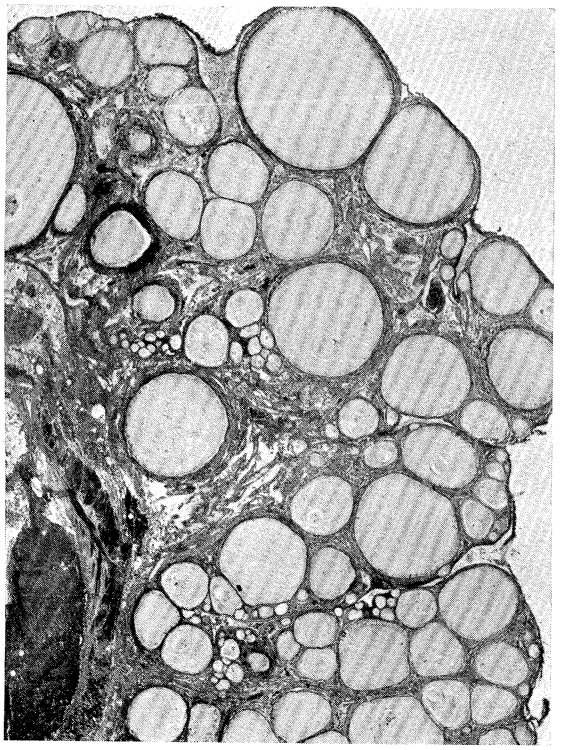

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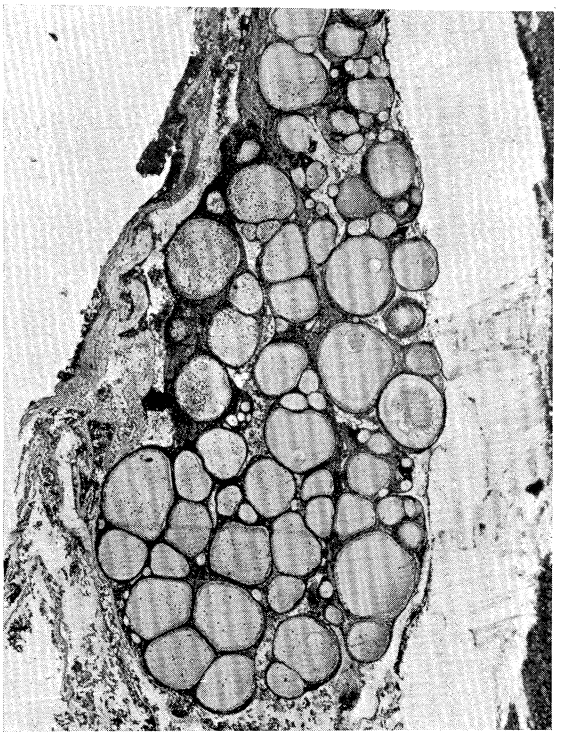

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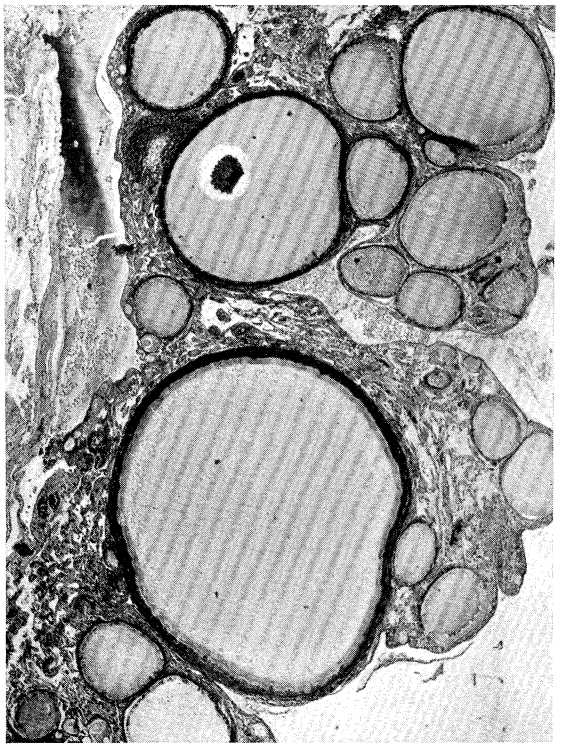
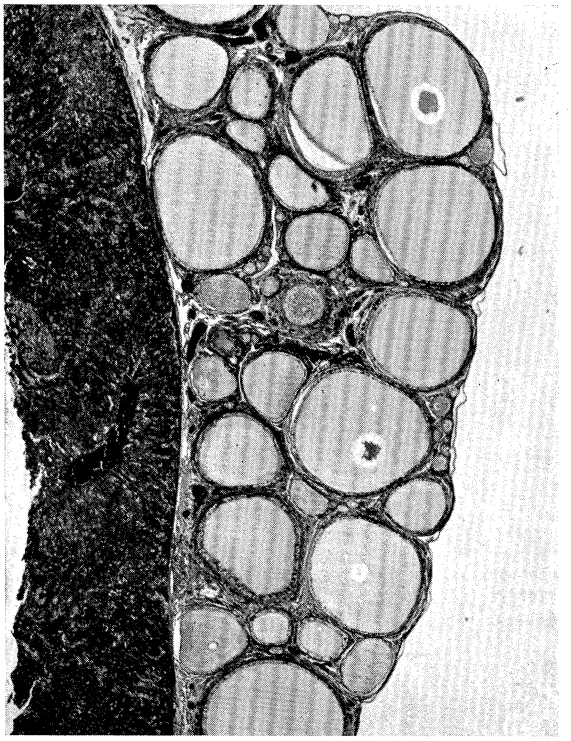


FIGURE 71



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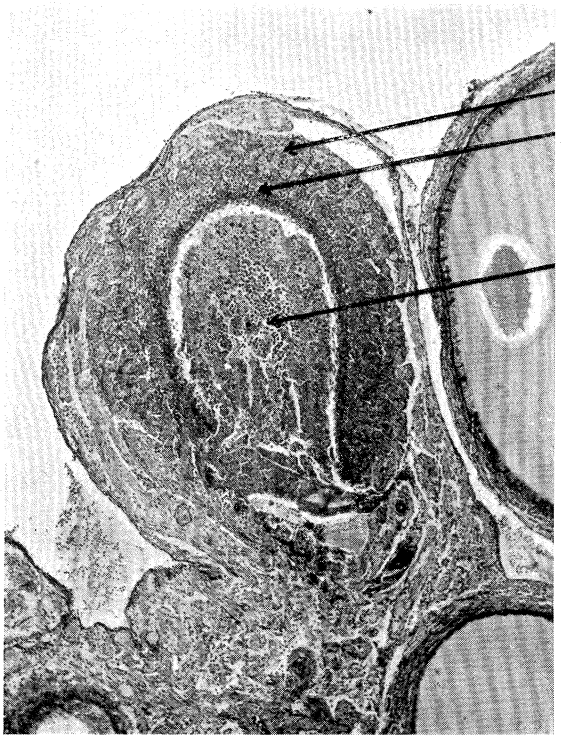

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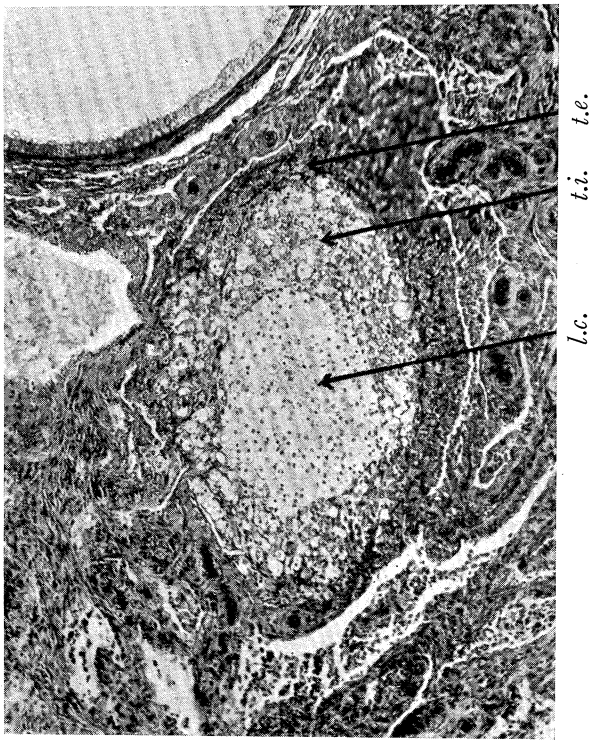

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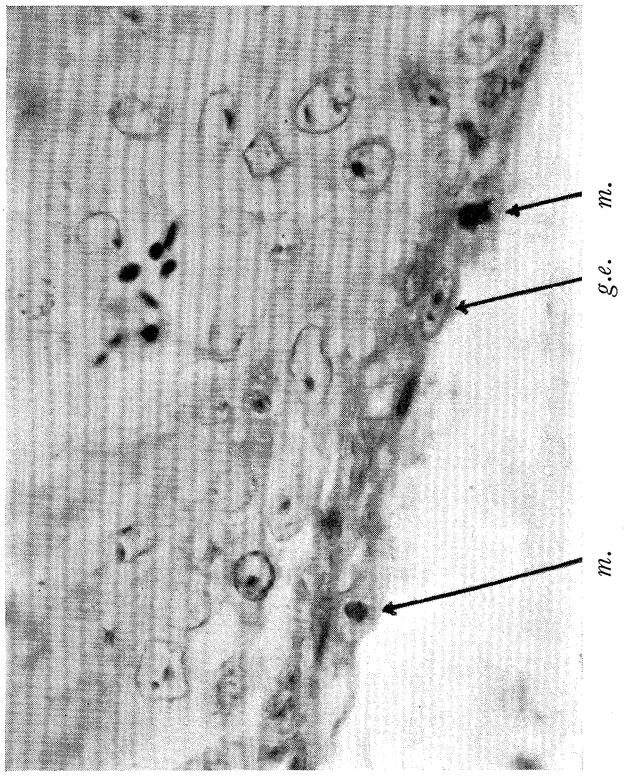

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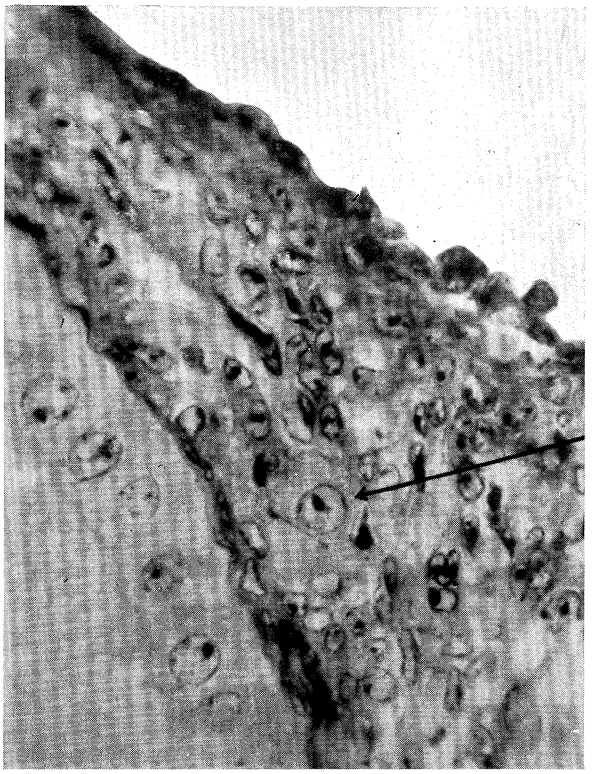

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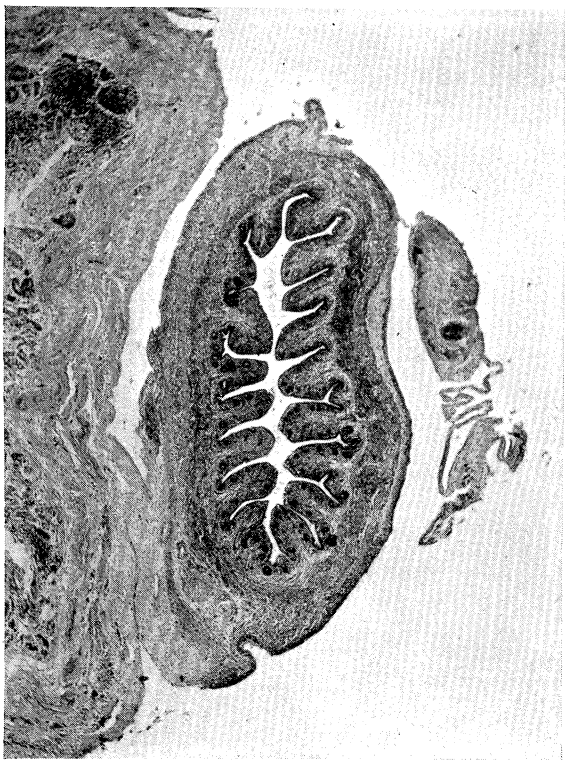

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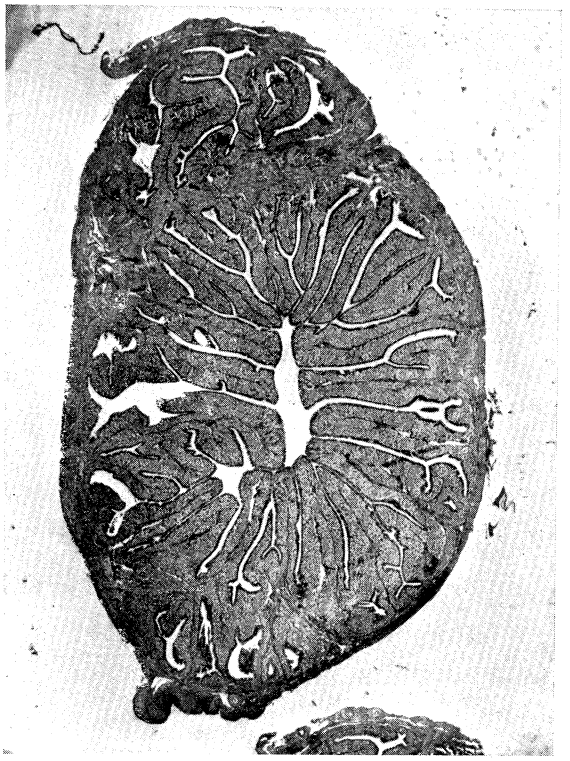

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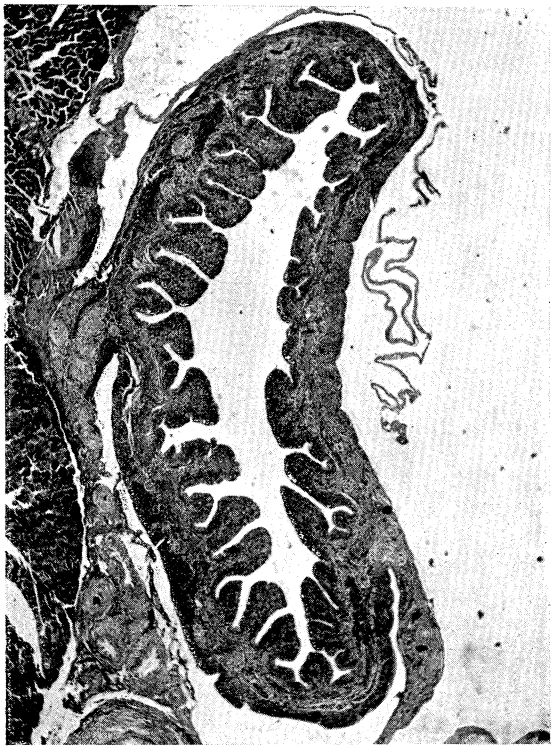

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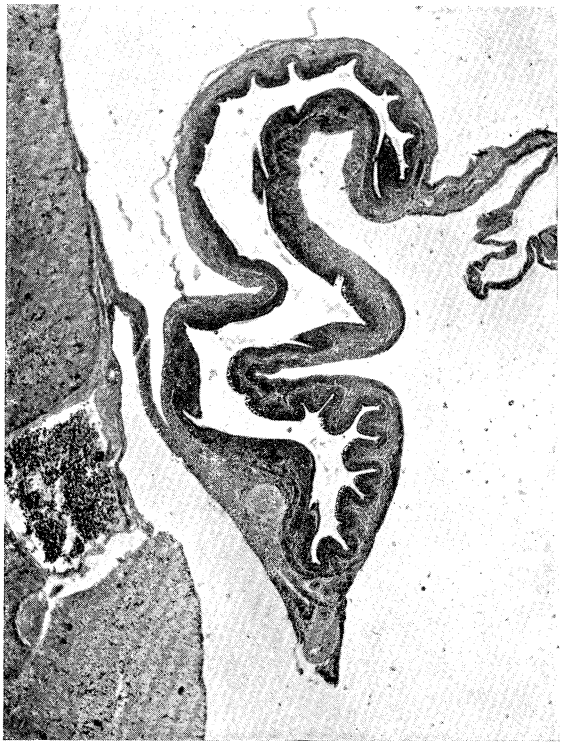

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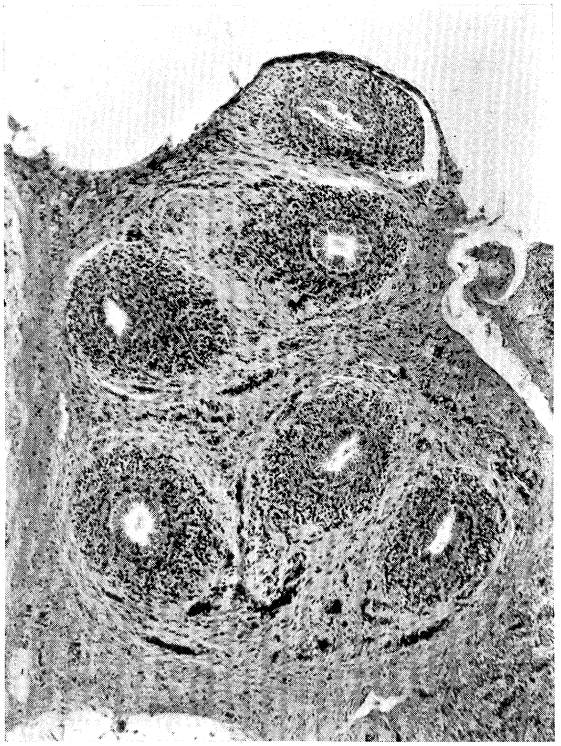
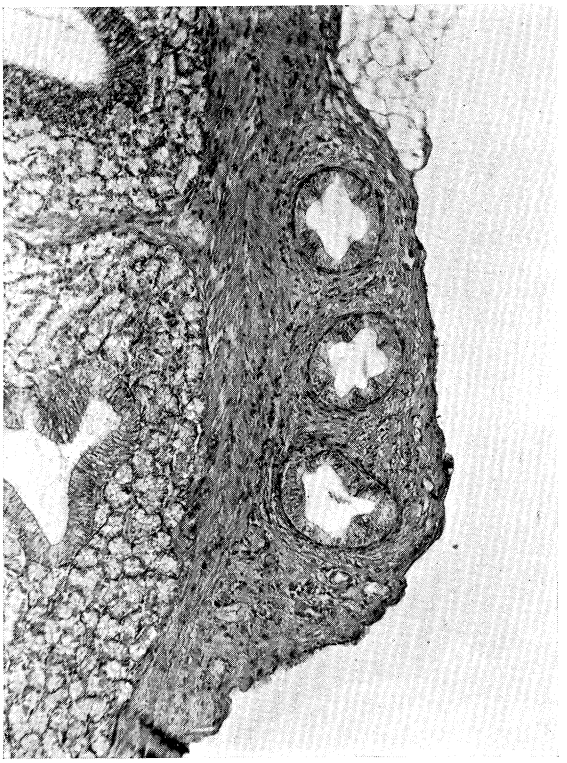


FIGURE 81



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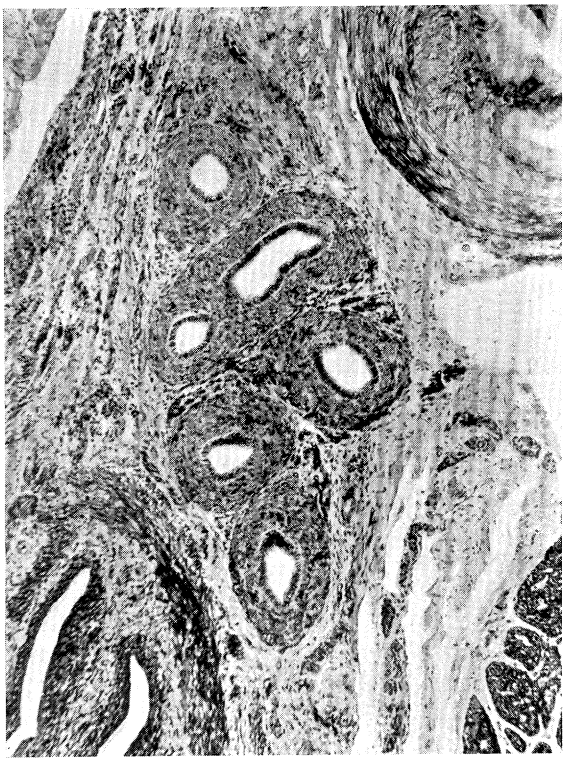

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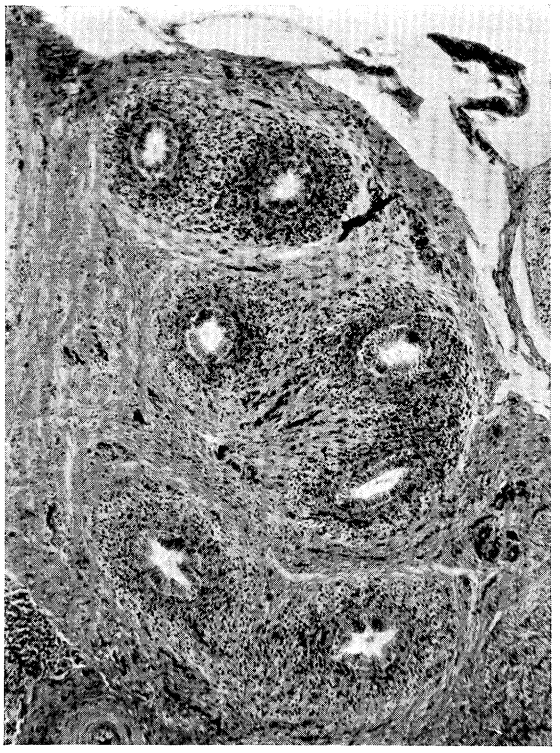

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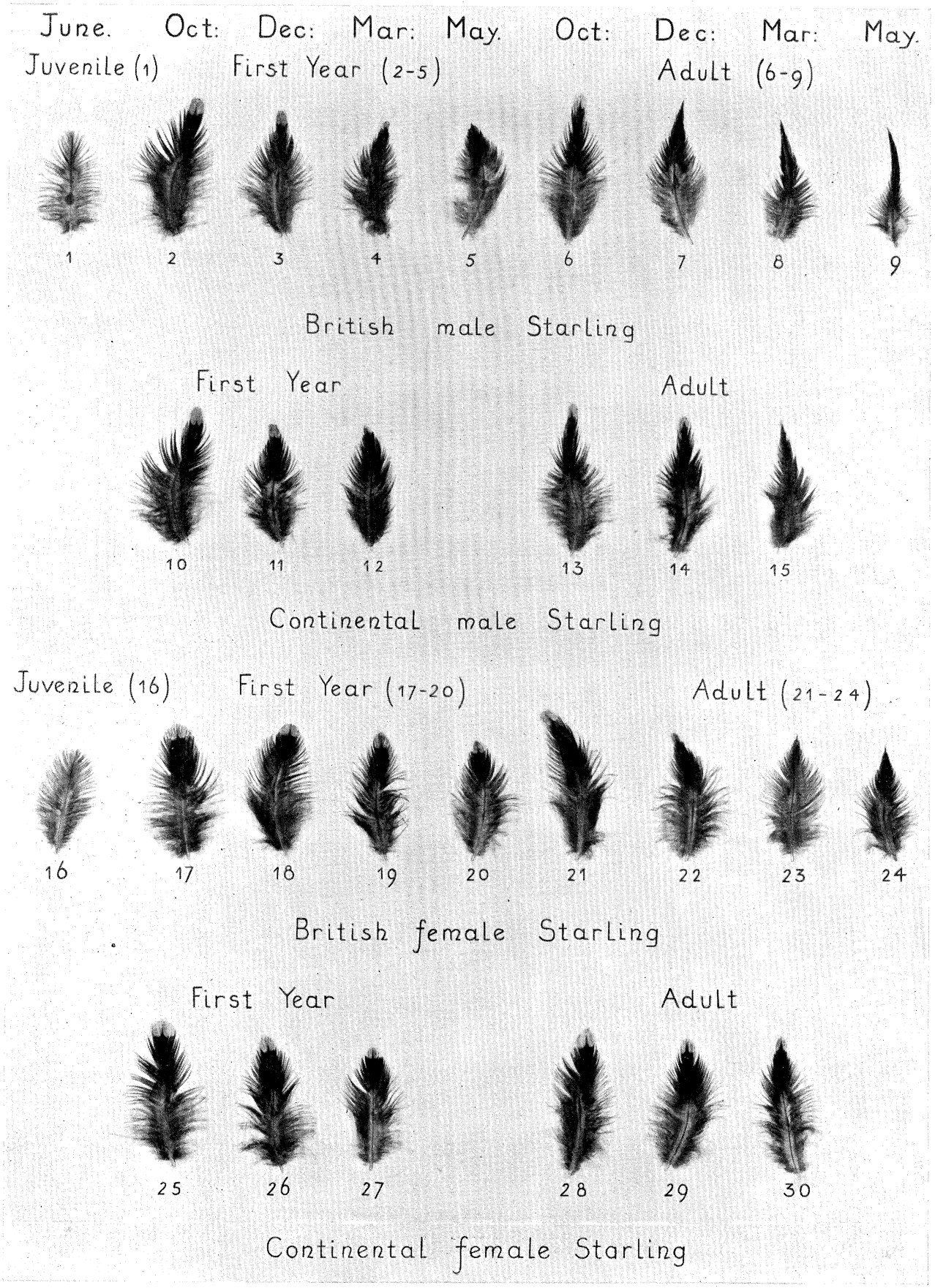
June. Oct: Dec: Mar: May. Oct: Dec: Mar: May.
Juvenile (1) First Year (2-5) Adult (6-9)
1 2 3 4 5 6 7 8 9
British male Starling
First Year Adult
10 11 12 13 14 15
Continental male Starling
Juvenile (16) First Year (17-20) Adult (21-24)
16 17 18 19 20 21 22 23 24
British female Starling
First Year Adult
25 26 27 28 29 30
Continental female Starling

FIGURE 85

FIGURE 86

FIGURE 87

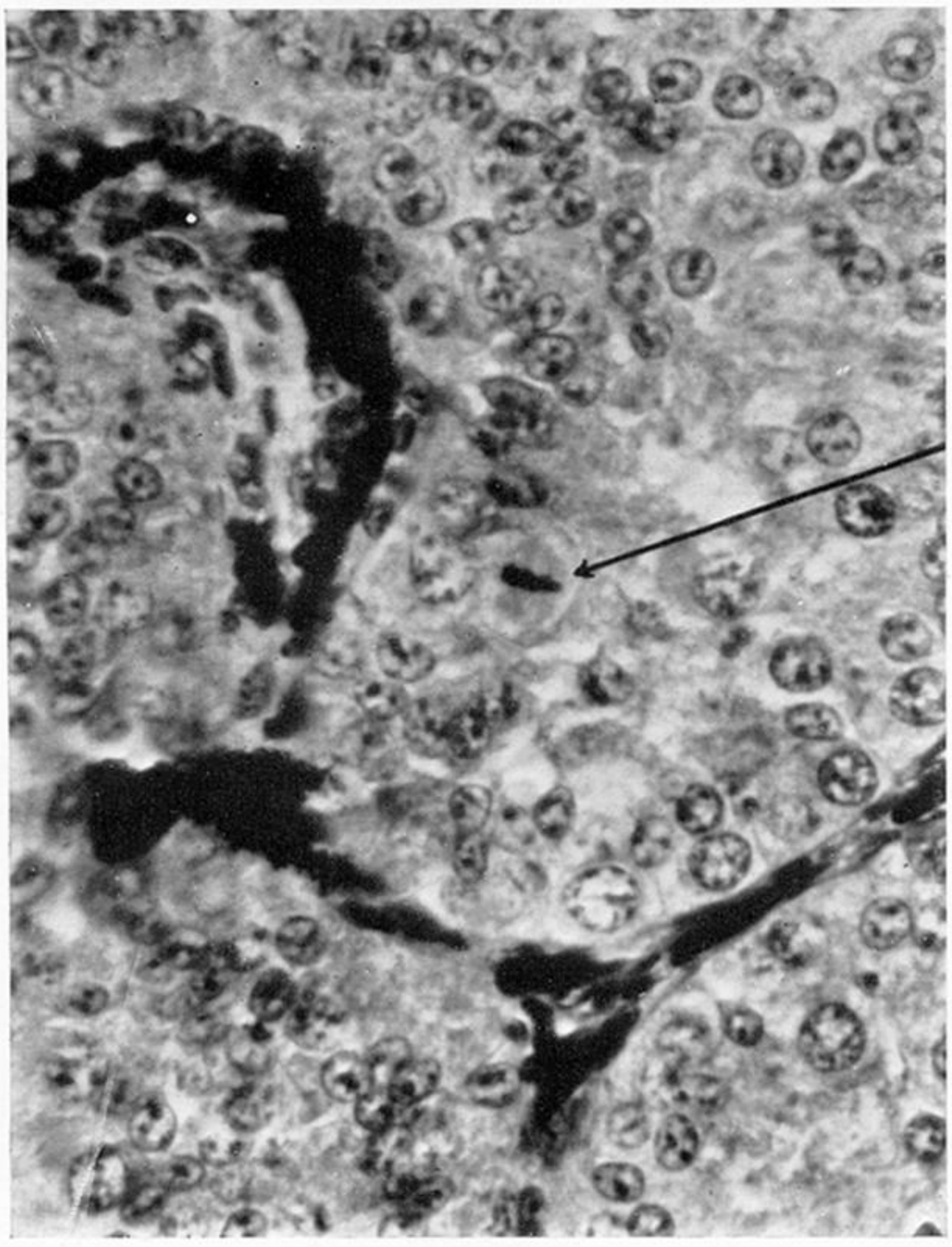

FIGURE 53

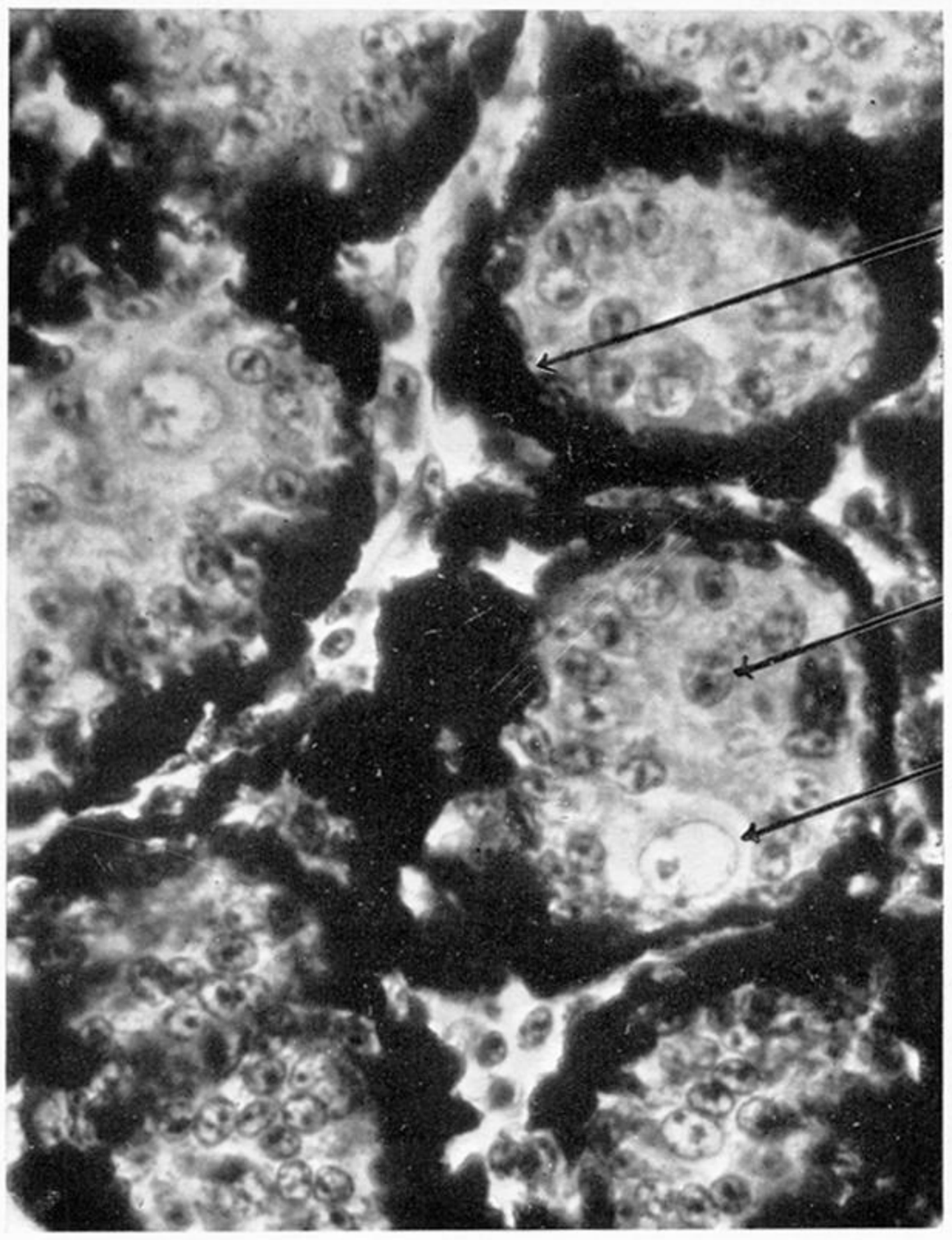

FIGURE 54

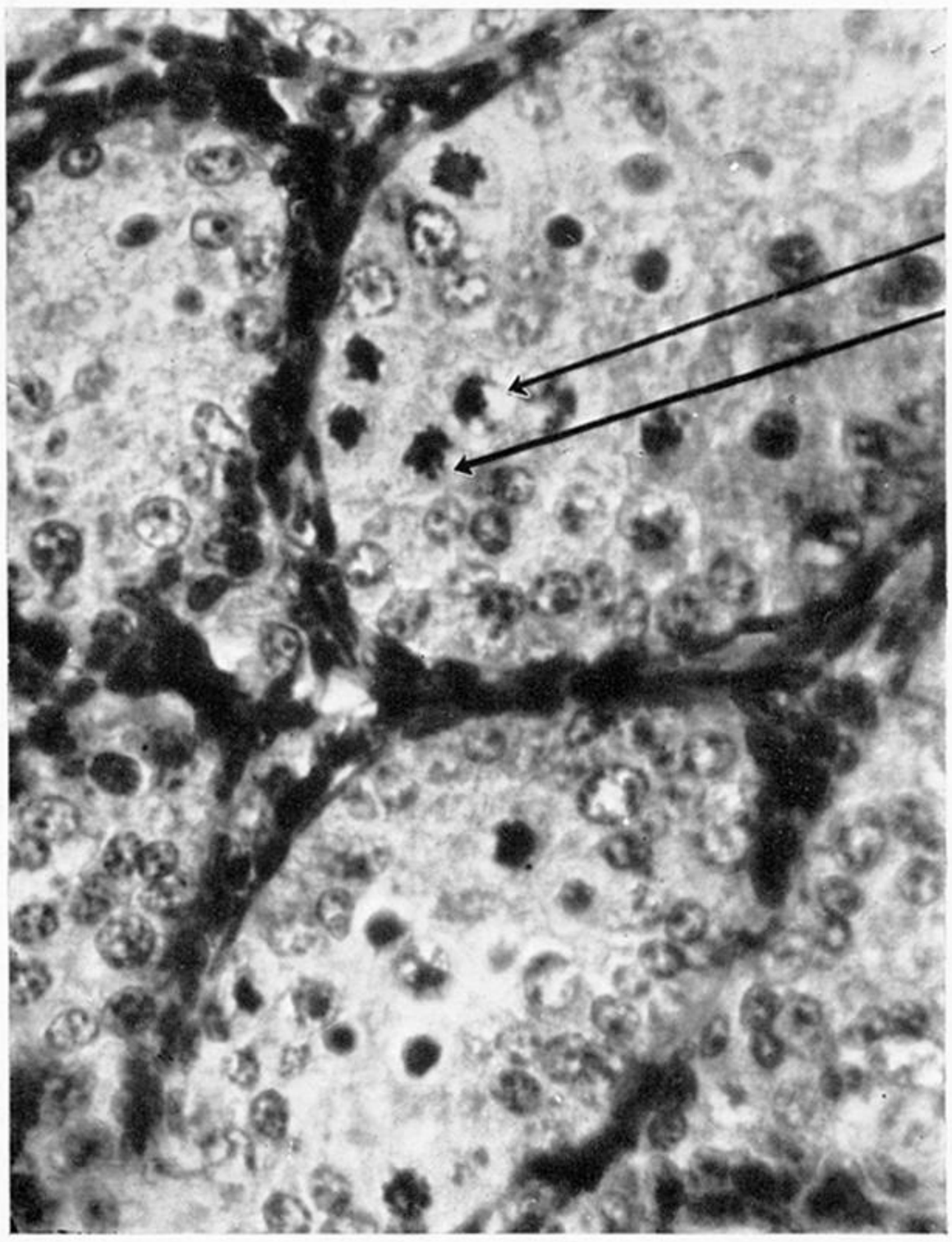

FIGURE 55

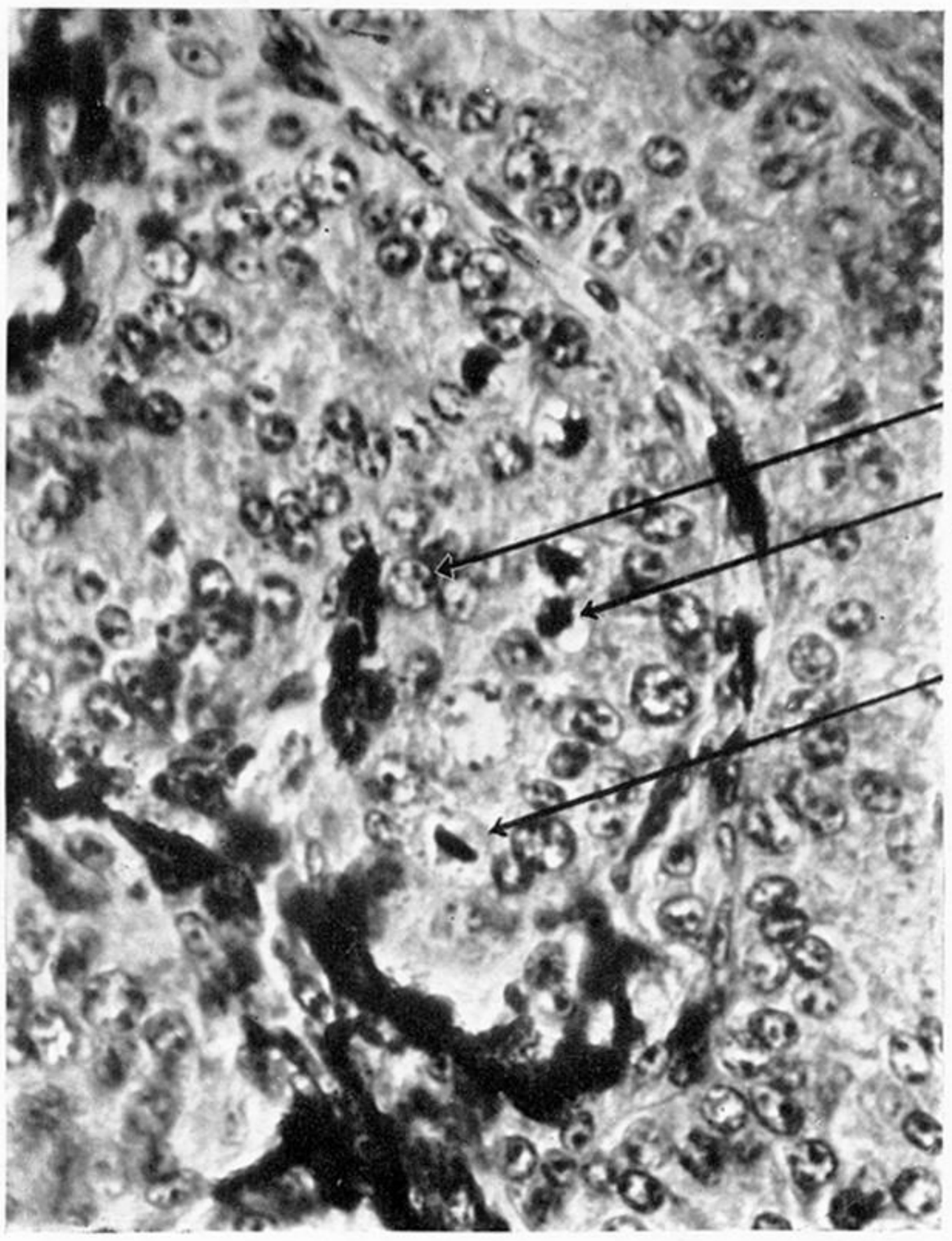

FIGURE 56

PLATE 12

FIGURE 53. Section of the testis of a juvenile British starling in June a few weeks after leaving the nest. The seminiferous tubules are large, and some spermatogonia are dividing (*spg.m.*). × 700.

FIGURE 54. Section of the testis of a first-year starling in November. The small seminiferous tubules are separated by masses of pigment cells (*pi.c.*), and both normal (*spg.*) and giant (*spg.g.*) spermatogonia are present. × 700.

FIGURE 55. Section of the testis of a first-year British starling in March. Many spermatogonia are undergoing mitosis (*spg.m.*), and many primary spermatocytes are in the synizesis stage of meiosis (*spc.s.*). × 700.

FIGURE 56. Section of the testis of a first-year Continental starling in March. There are many resting spermatogonia (*spg.*), some spermatogonia in mitosis (*spg.m.*), and a few primary spermatocytes in the synizesis stage (*spc.s.*). × 700.

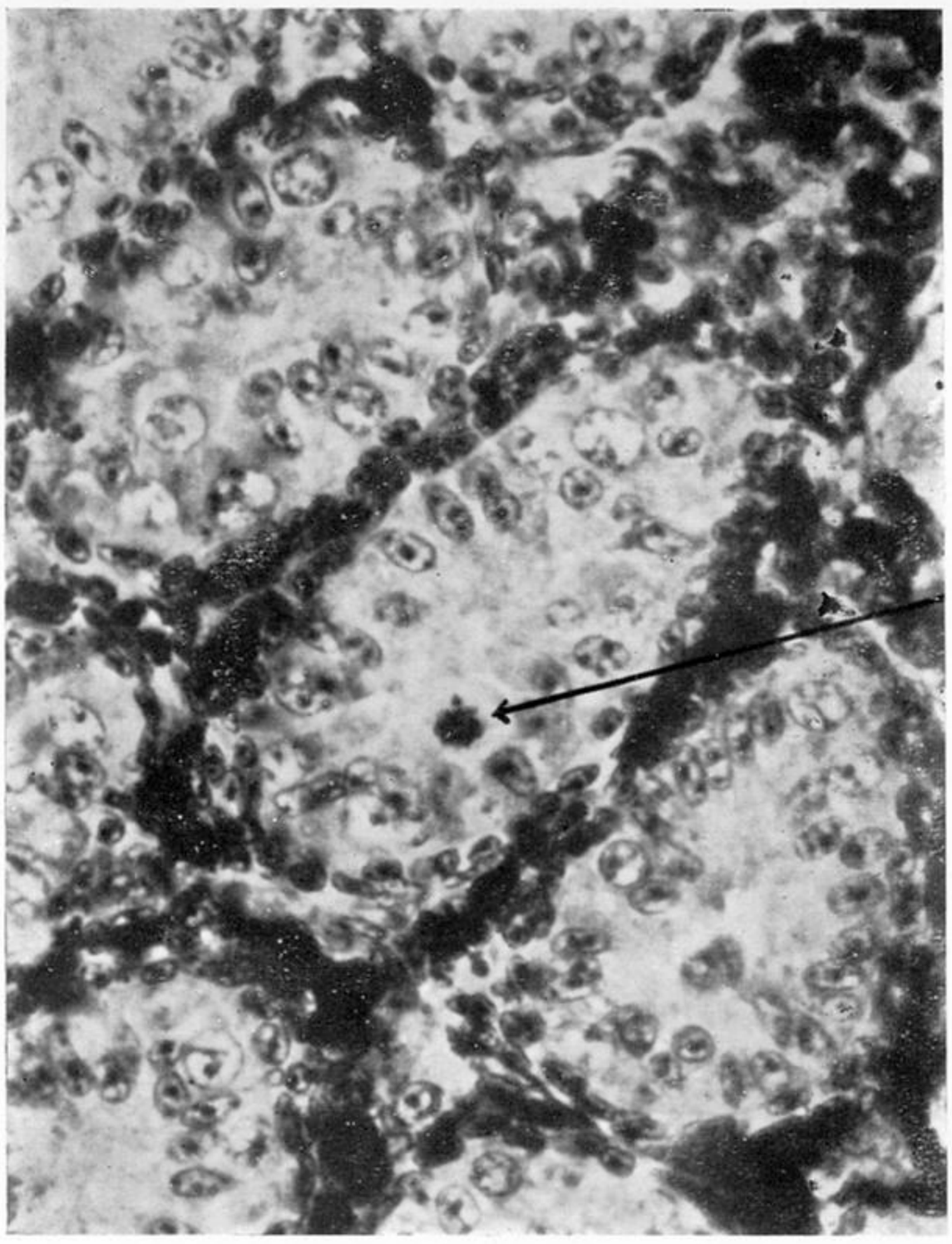

FIGURE 57

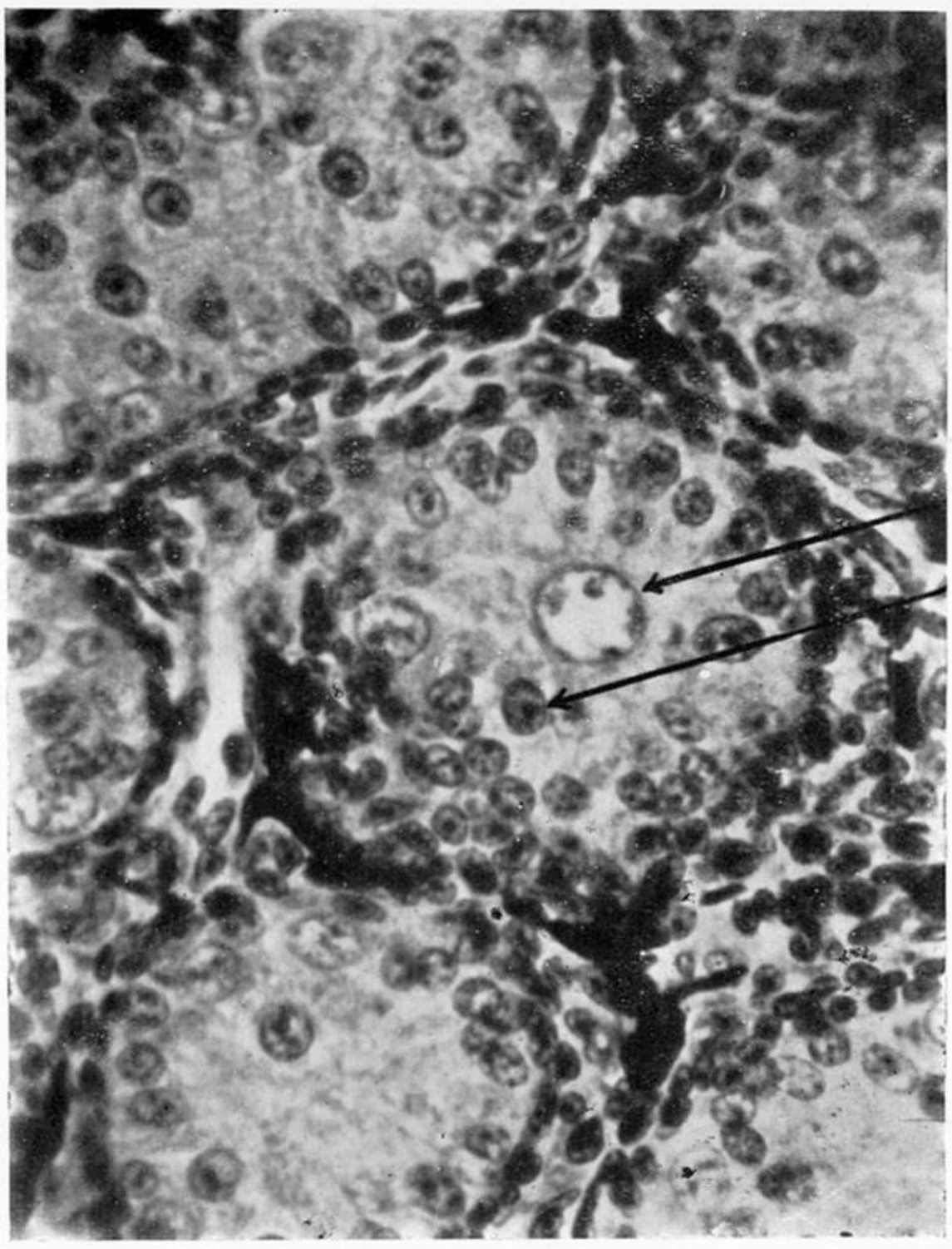

FIGURE 58

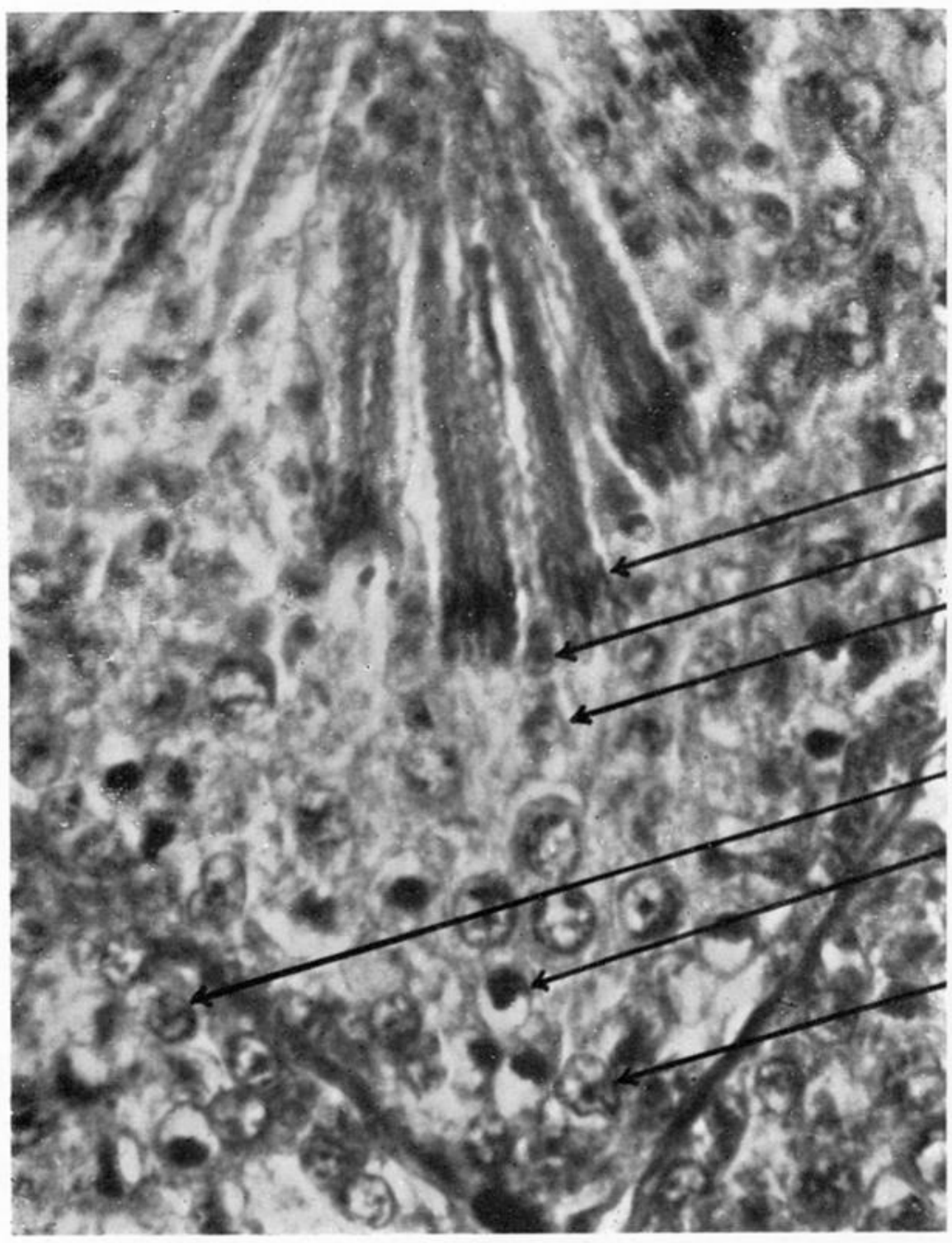

FIGURE 59

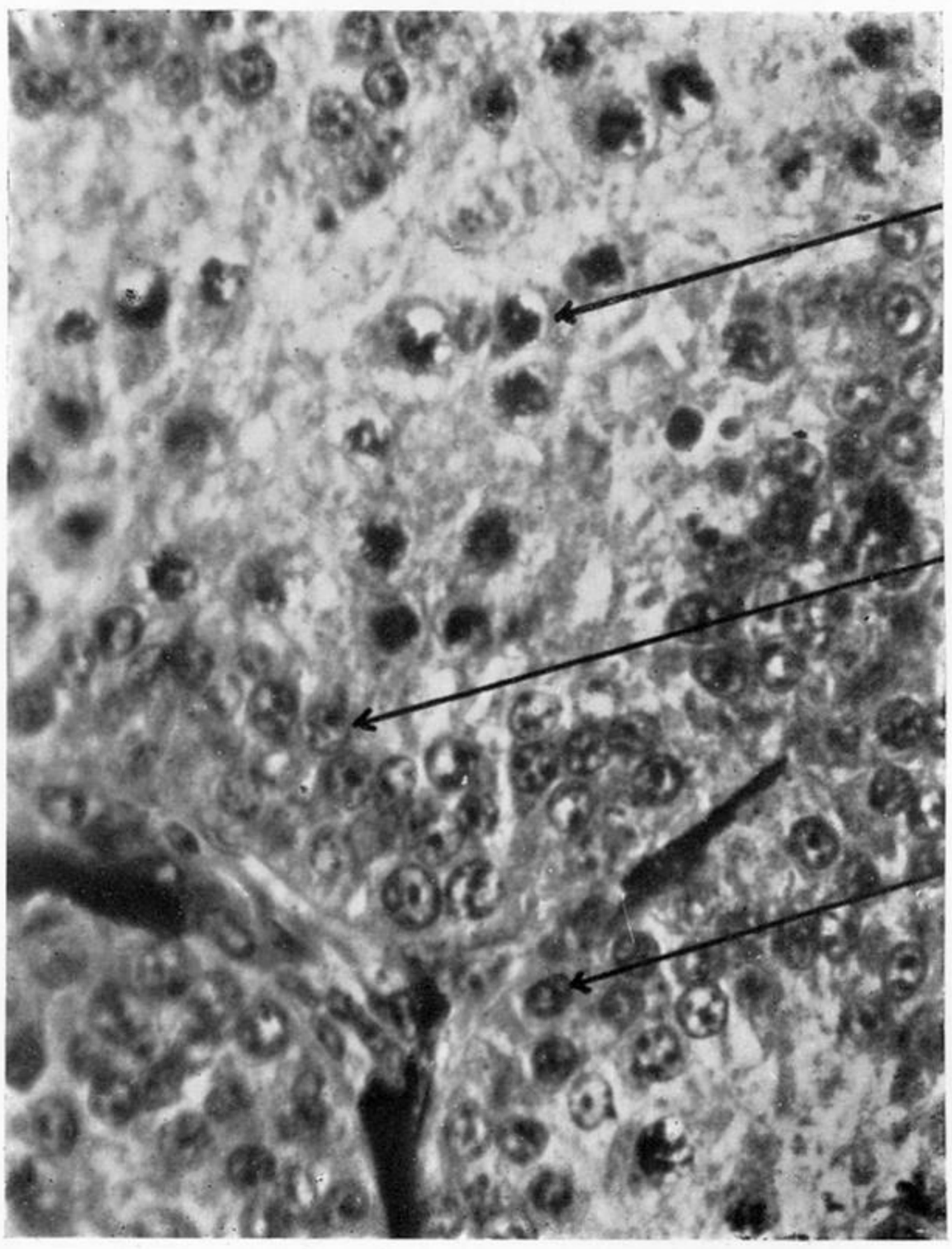

FIGURE 60

PLATE 13

FIGURE 57. Section of the testis of an adult British starling in November. Some spermatogonia are undergoing mitotic division (*spg.m.*). × 700.

FIGURE 58. Section of the testis of an adult Continental starling in November. There are many resting spermatogonia, some of them normal in size (*spg.*) and some of them giant (*spg.g.*). × 700.

FIGURE 59. Section of the testis of an adult British starling in March. Primary germ cells (*pgc.*), spermatogonia (*spg.*), primary spermatocytes (*spc.*1), secondary spermatocytes (*spc.*2), spermatids (*spd.*), and spermatozoa (*spz.*) are present, and spermatogenesis is proceeding actively. × 700.

FIGURE 60. Section of the testis of an adult Continental starling in March. Only primary germ cells (*pgc.*), spermatogonia (*spg.*), and primary spermatocytes in the synizesis stage (*spc.s.*) are present. × 700.

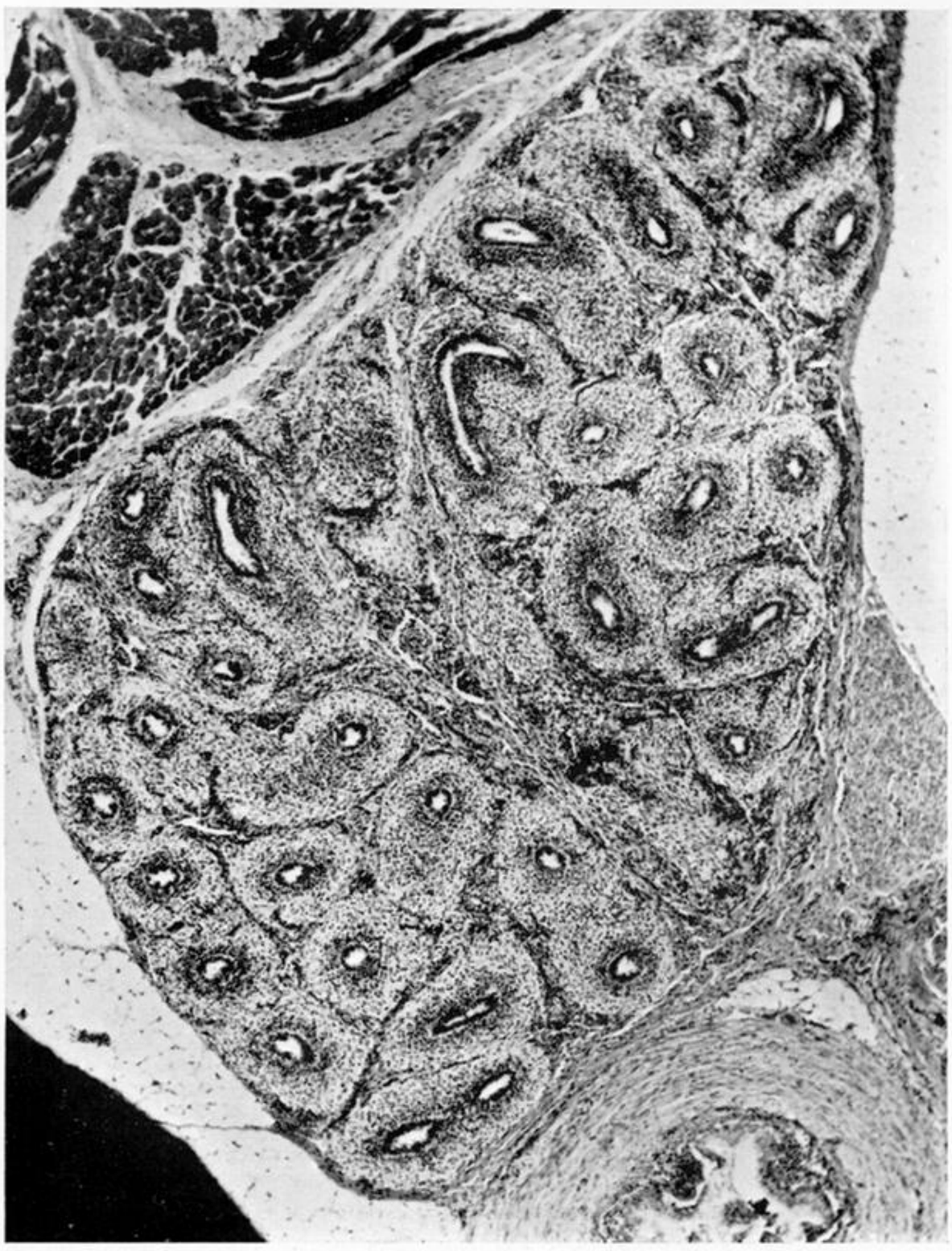

FIGURE 61

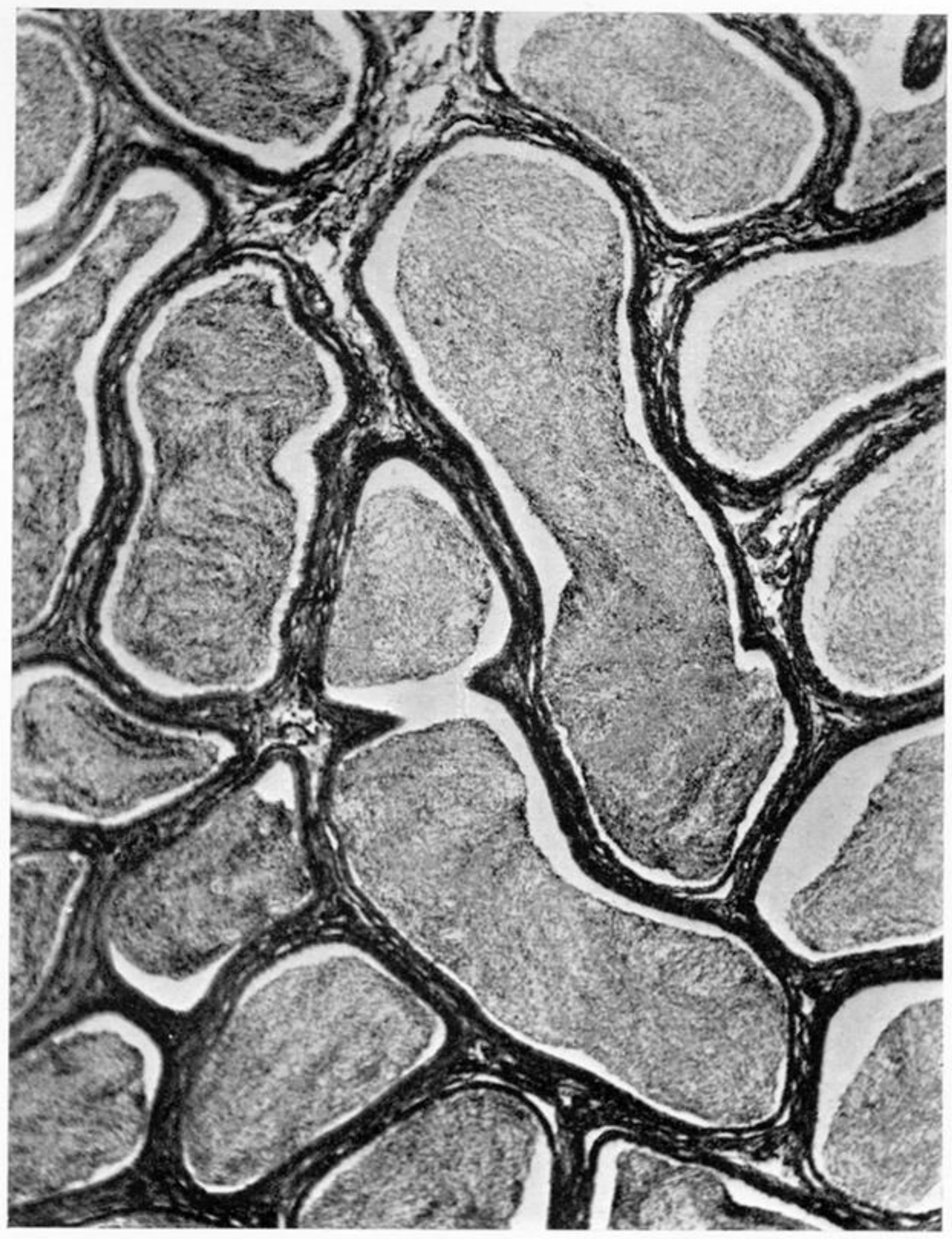

FIGURE 62

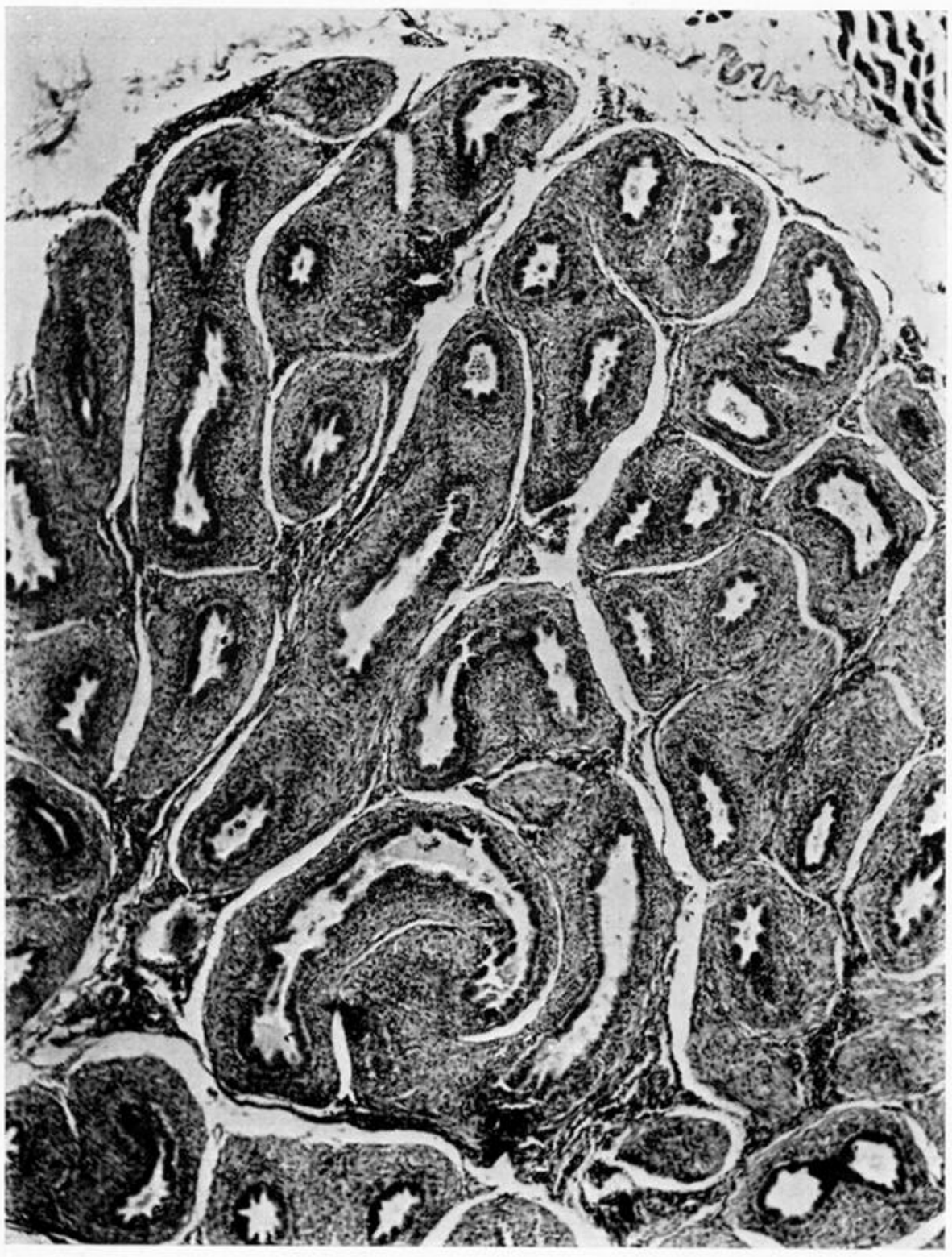

FIGURE 63

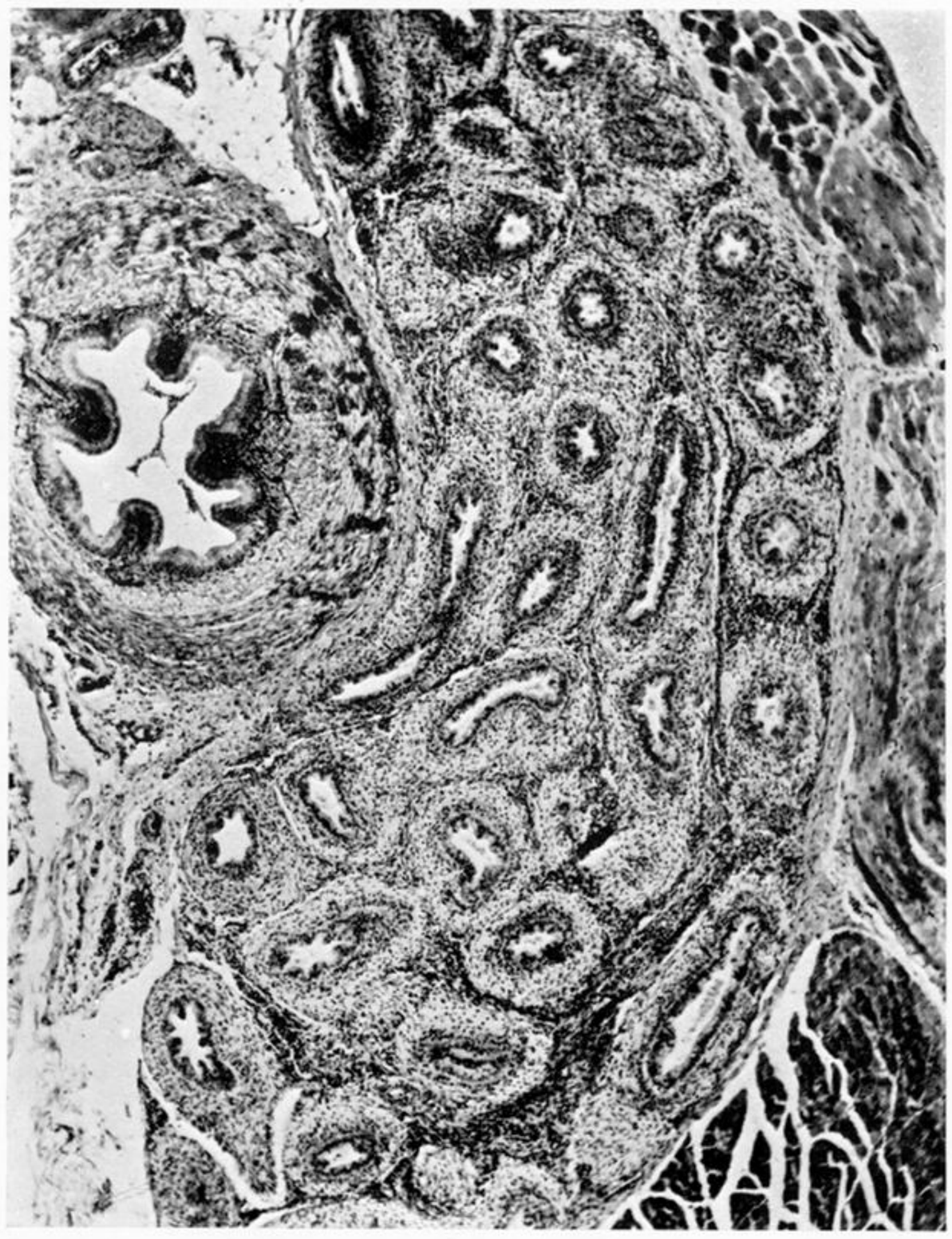

FIGURE 64

PLATE 14

FIGURE 61. Transverse section of the seminal vesicle of an adult British starling in August showing the maximum regression of the tubules. × 60.

FIGURE 62. Transverse section of the seminal vesicle of an adult British starling in April showing masses of spermatozoa distending the tubules. × 60.

FIGURE 63. Transverse section of the seminal vesicle of an adult British starling in March showing the partial growth of the tubules. × 60.

FIGURE 64. Transverse section of the seminal vesicle of an adult Continental starling in March showing only slight growth of the tubules. × 60.

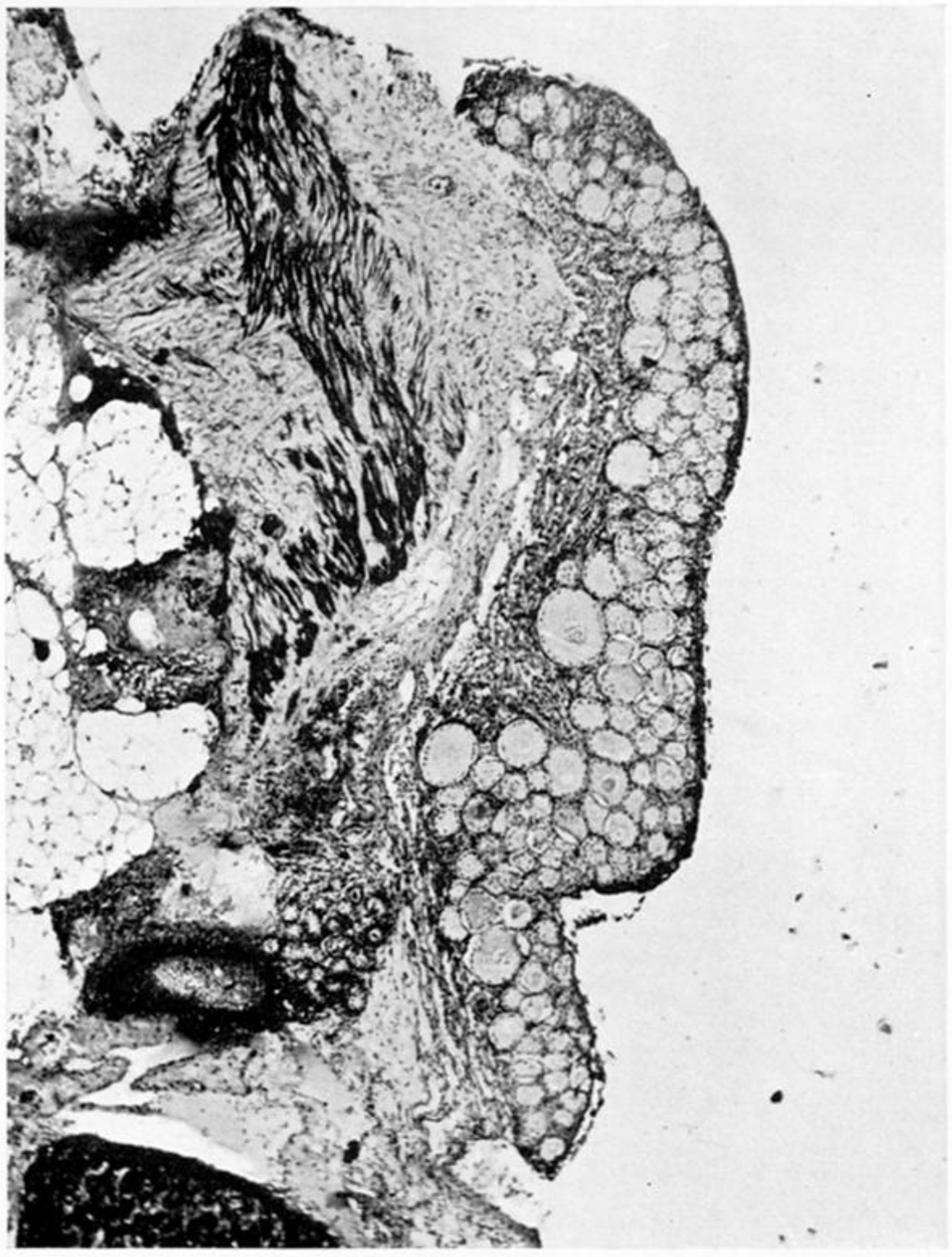

FIGURE 65

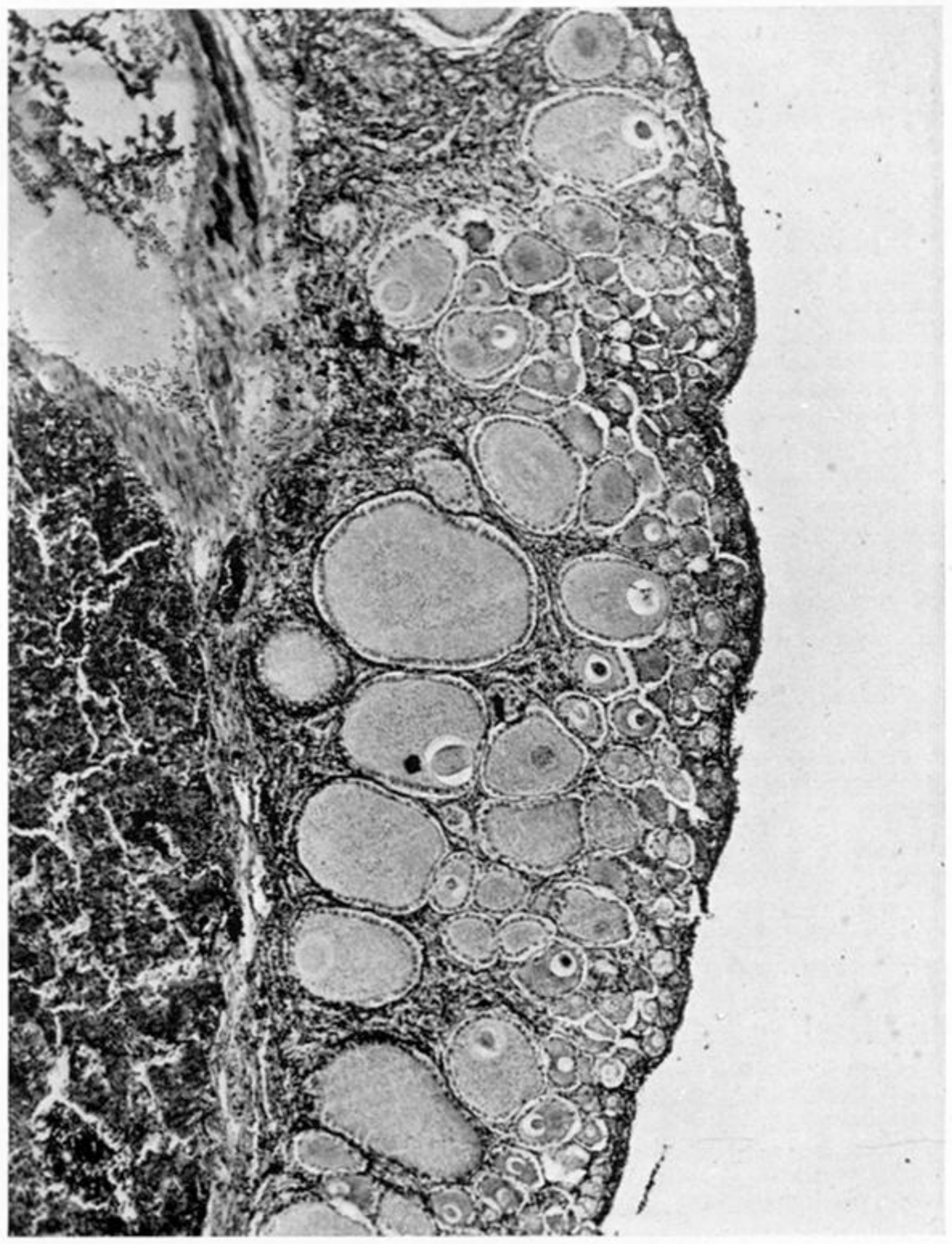

FIGURE 66

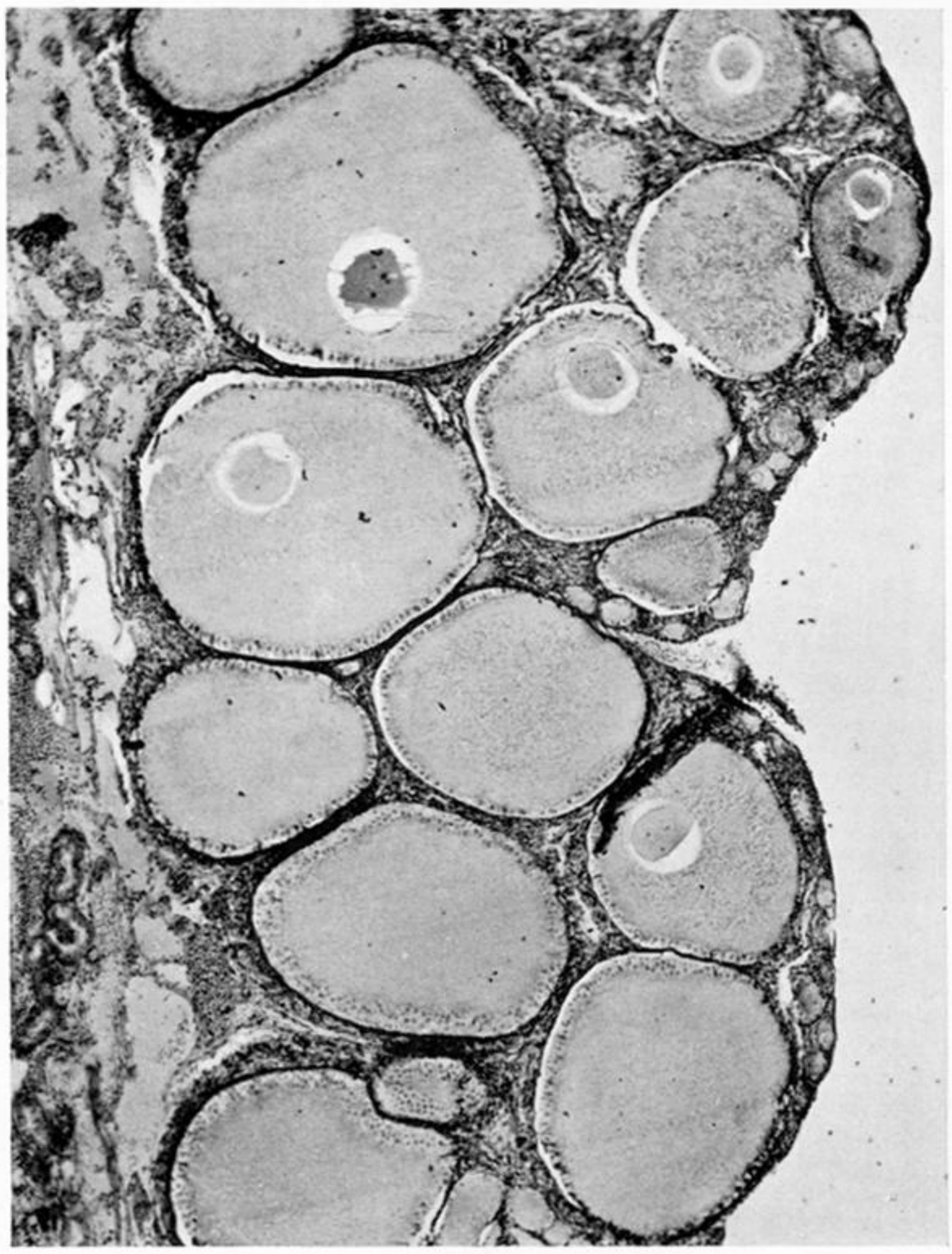

FIGURE 67

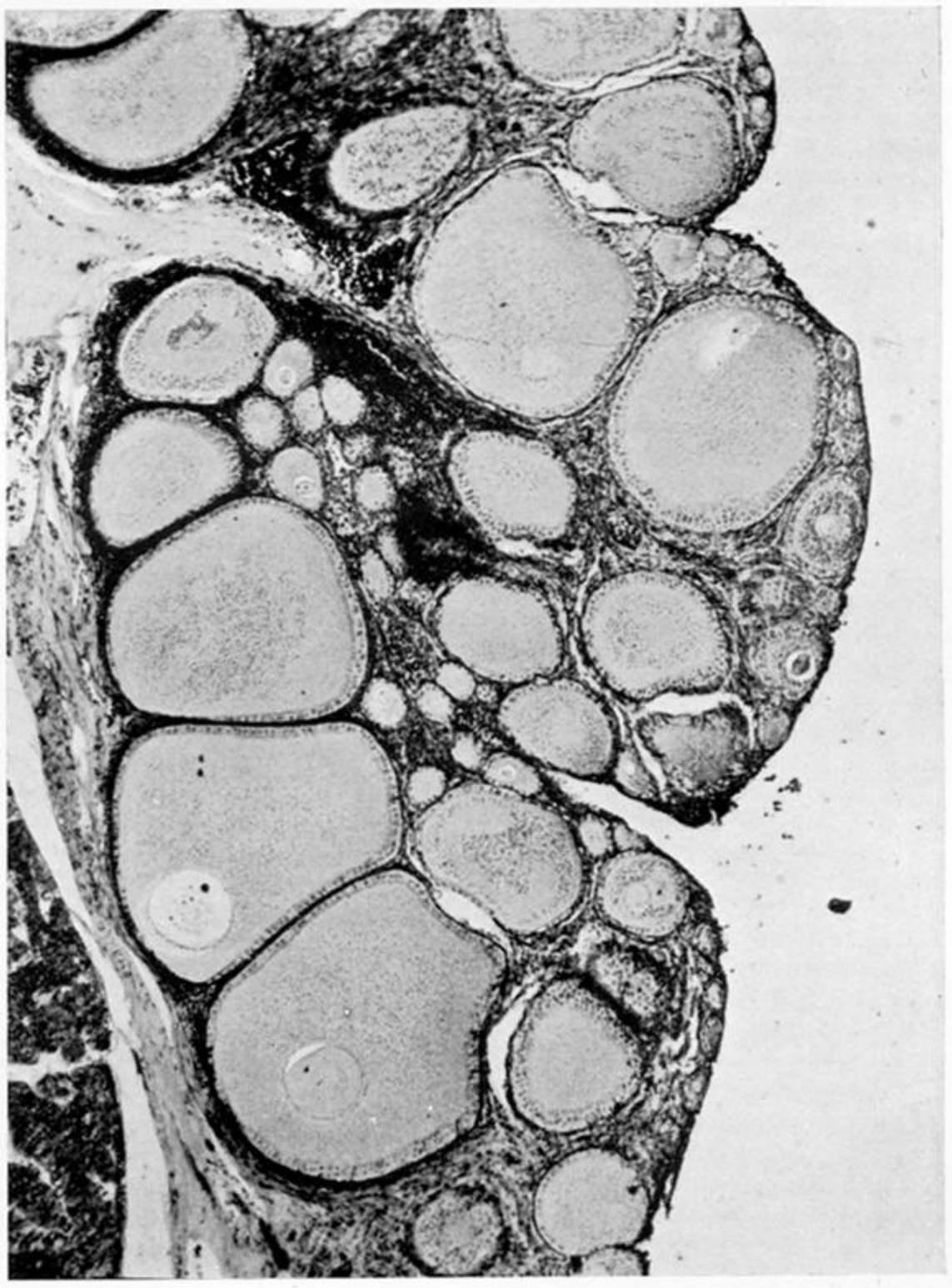

FIGURE 68

PLATE 15

FIGURE 65. Longitudinal section of the ovary of a juvenile British starling in June. × 60.

FIGURE 66. Longitudinal section of the ovary of a first-year starling in November showing the zonation of the cell sizes. The oogonia and small primary oocytes are near the germinal epithelium while the large primary oocytes are at the base of the ovary. × 60.

FIGURE 67. Longitudinal section of the ovary of a first-year British starling in March. × 60.

FIGURE 68. Longitudinal section of the ovary of a first-year Continental starling in March. × 60.

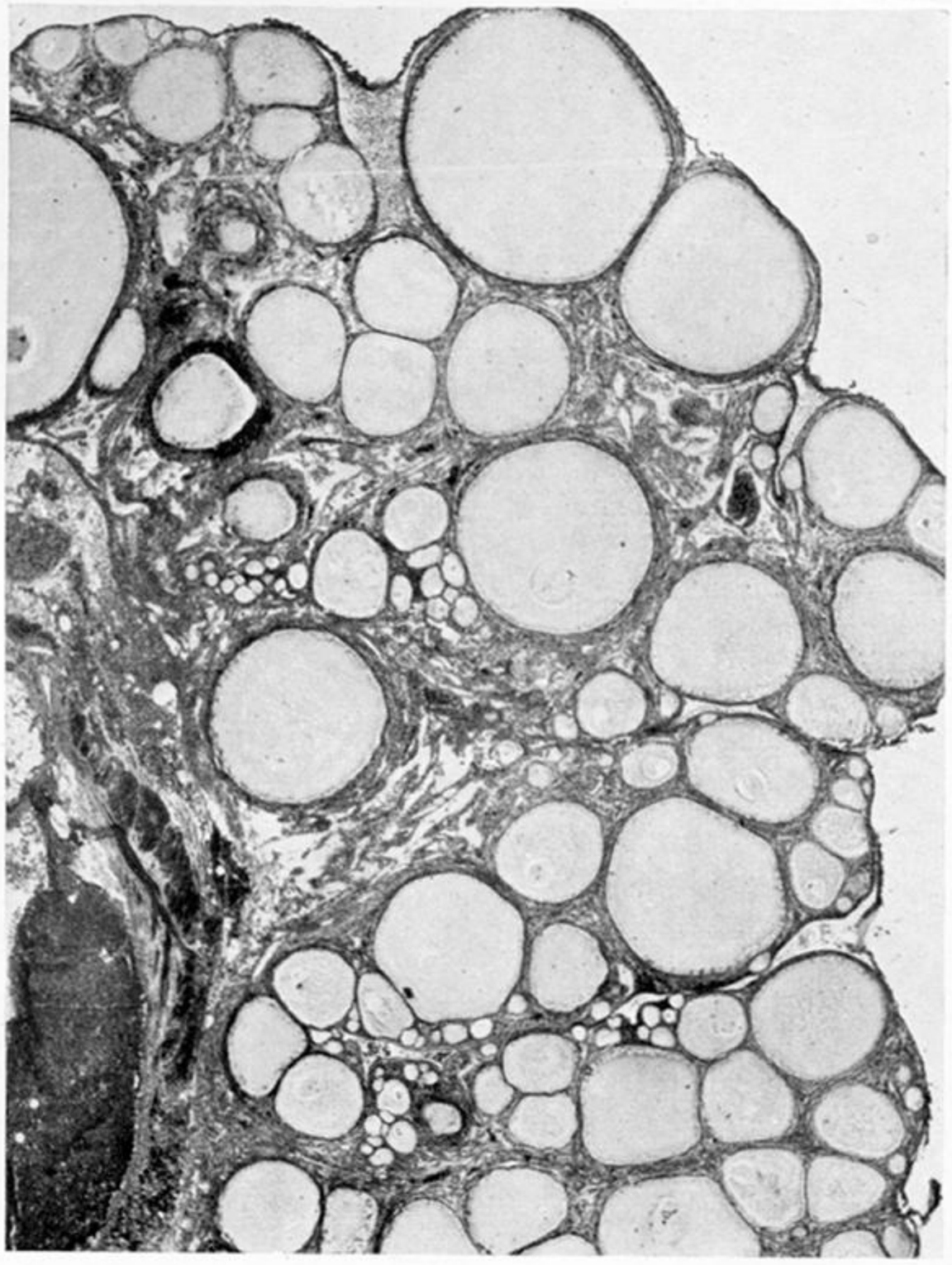

FIGURE 69

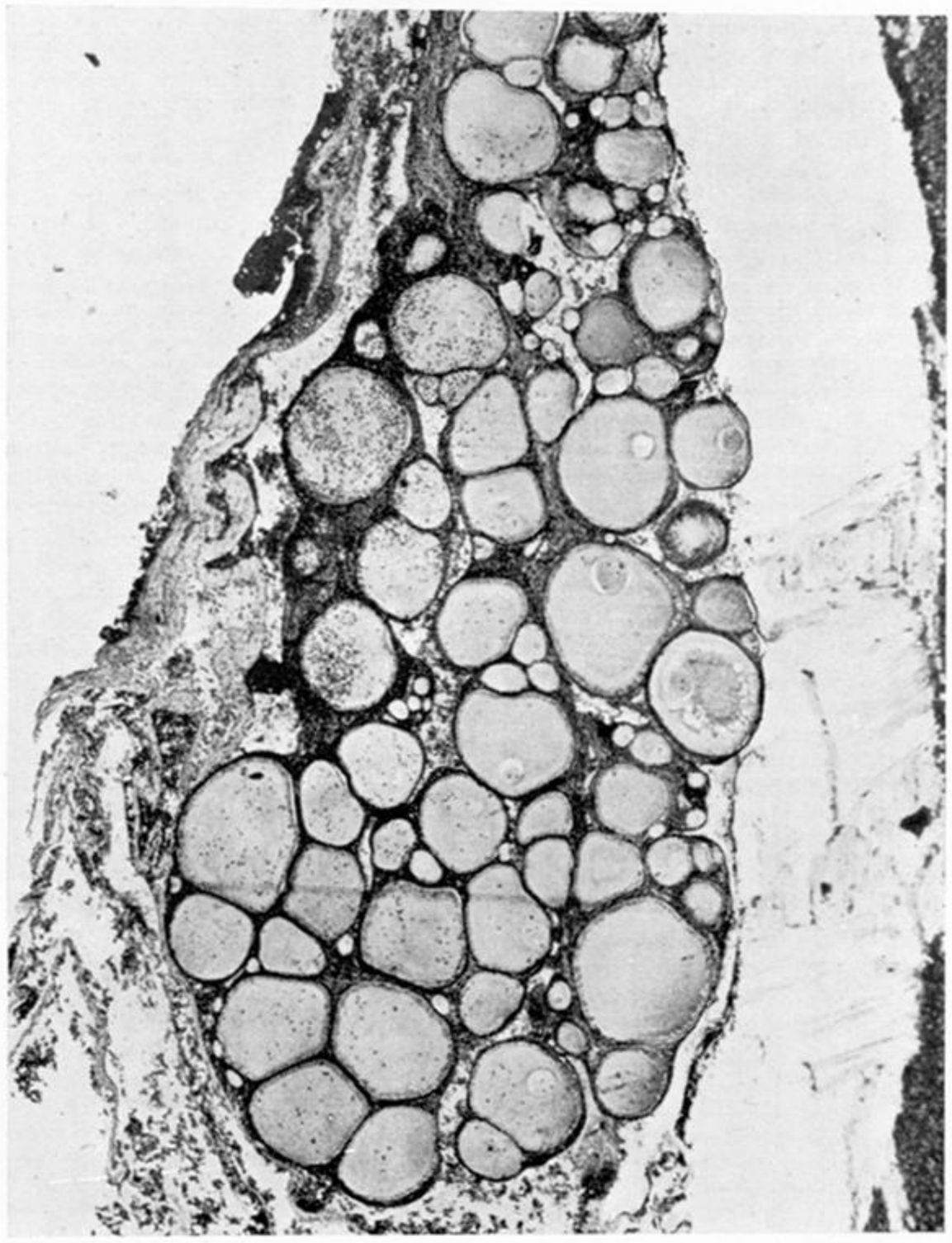

FIGURE 70

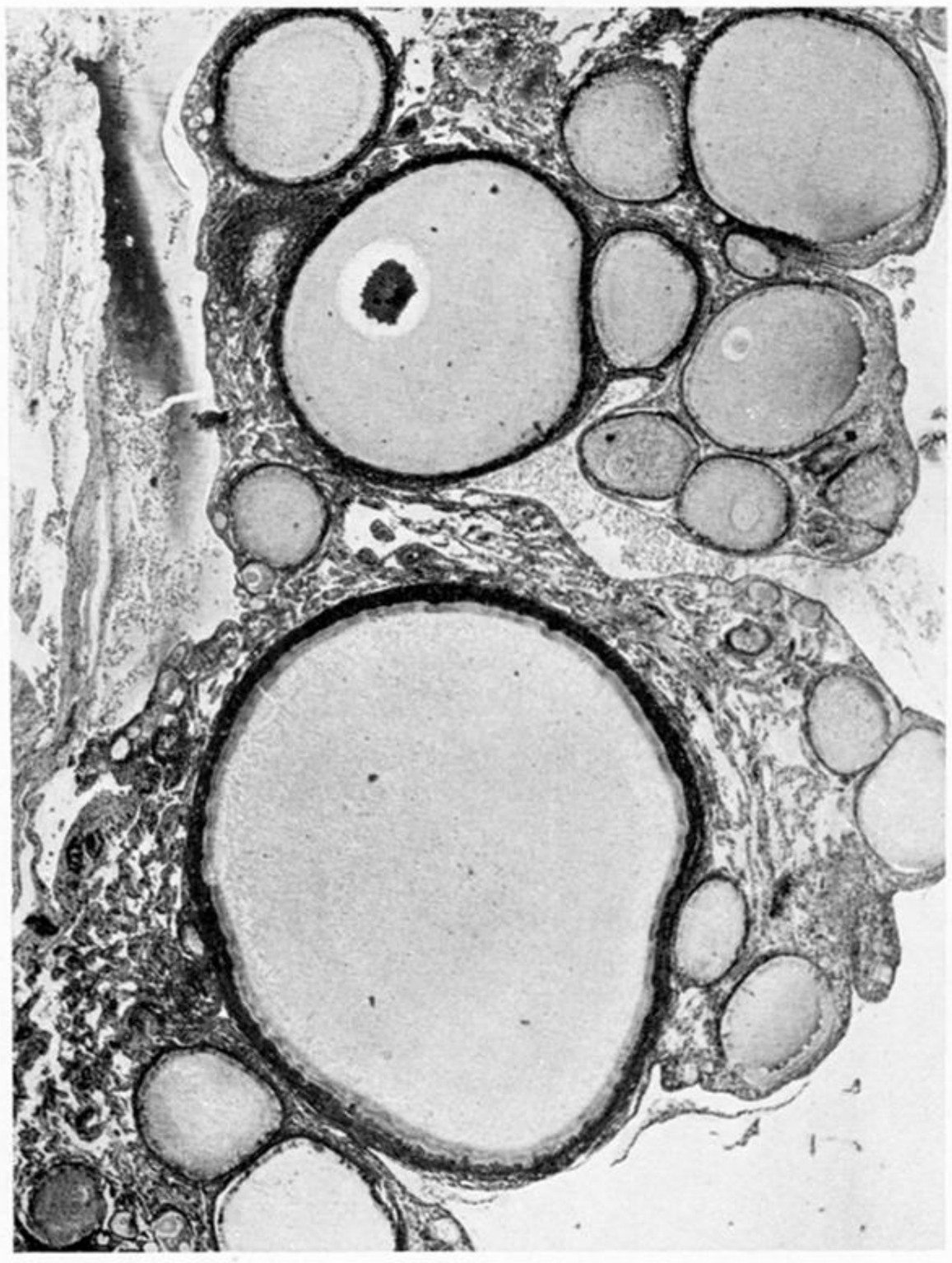

FIGURE 71

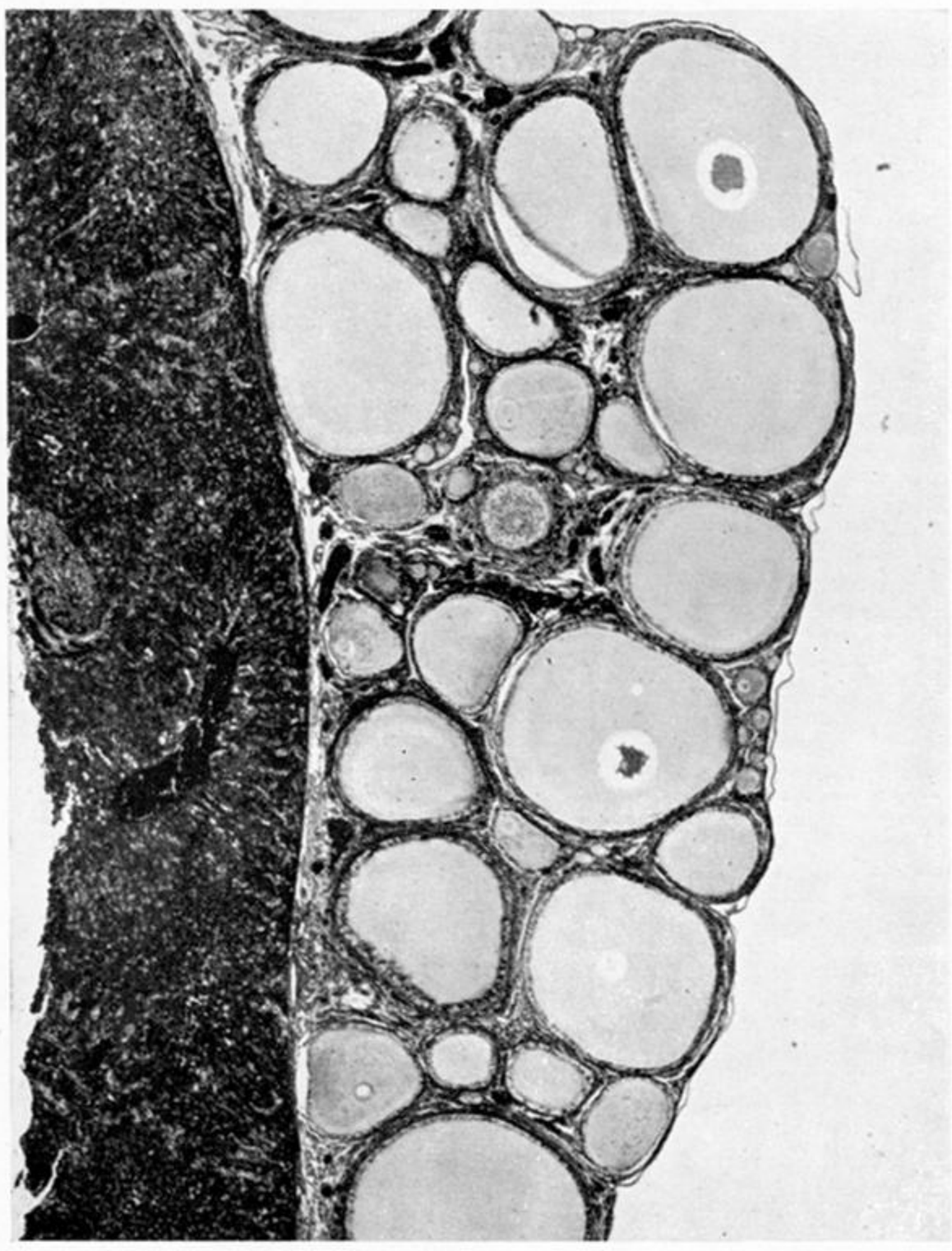

FIGURE 72

PLATE 16

FIGURE 69. Longitudinal section of the ovary of an adult British starling in November. × 30.

FIGURE 70. Longitudinal section of the ovary of an adult Continental starling in November. × 30.

FIGURE 71. Longitudinal section of the ovary of an adult British starling in March. × 30.

FIGURE 72. Longitudinal section of the ovary of an adult Continental starling in March. × 30.

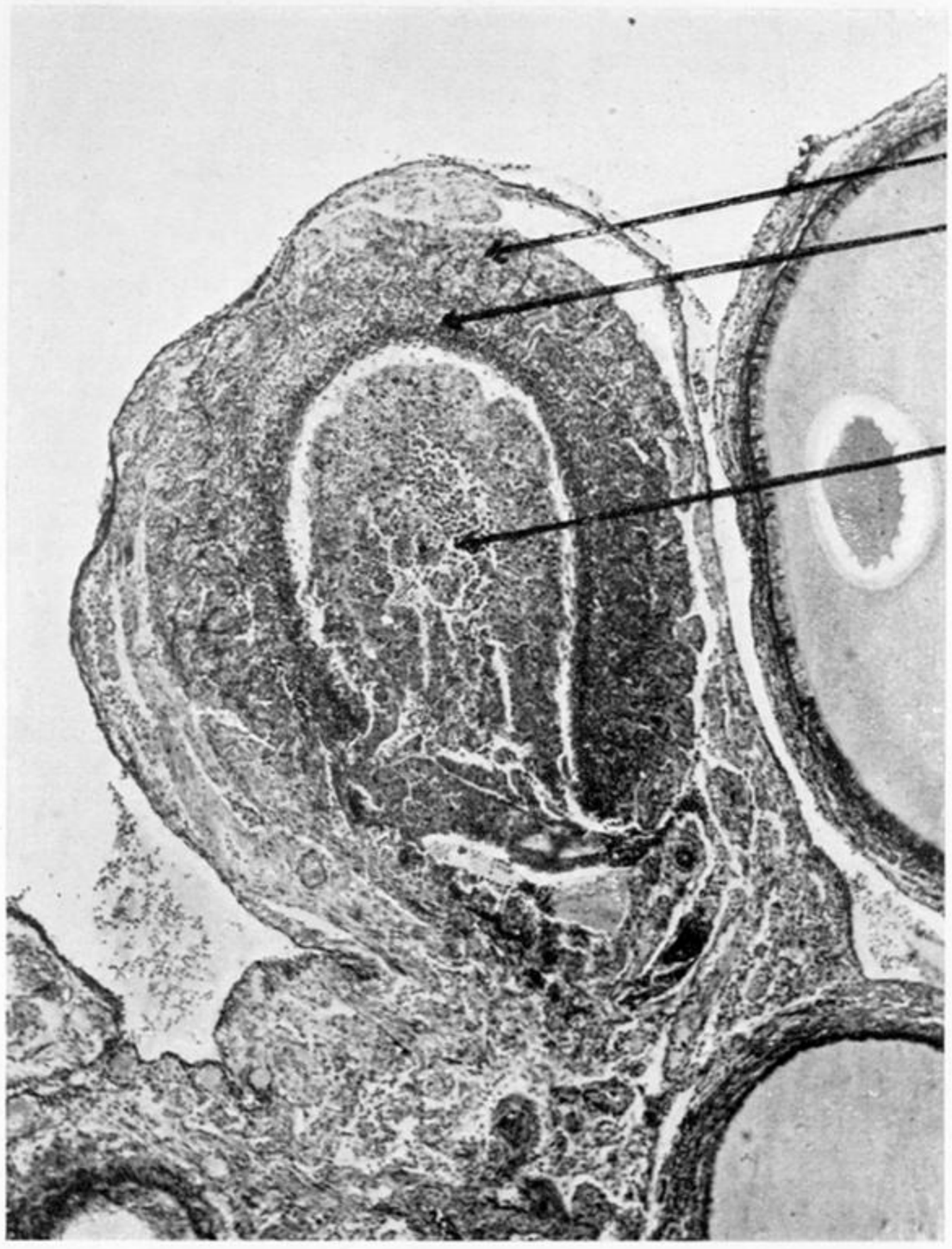

FIGURE 73

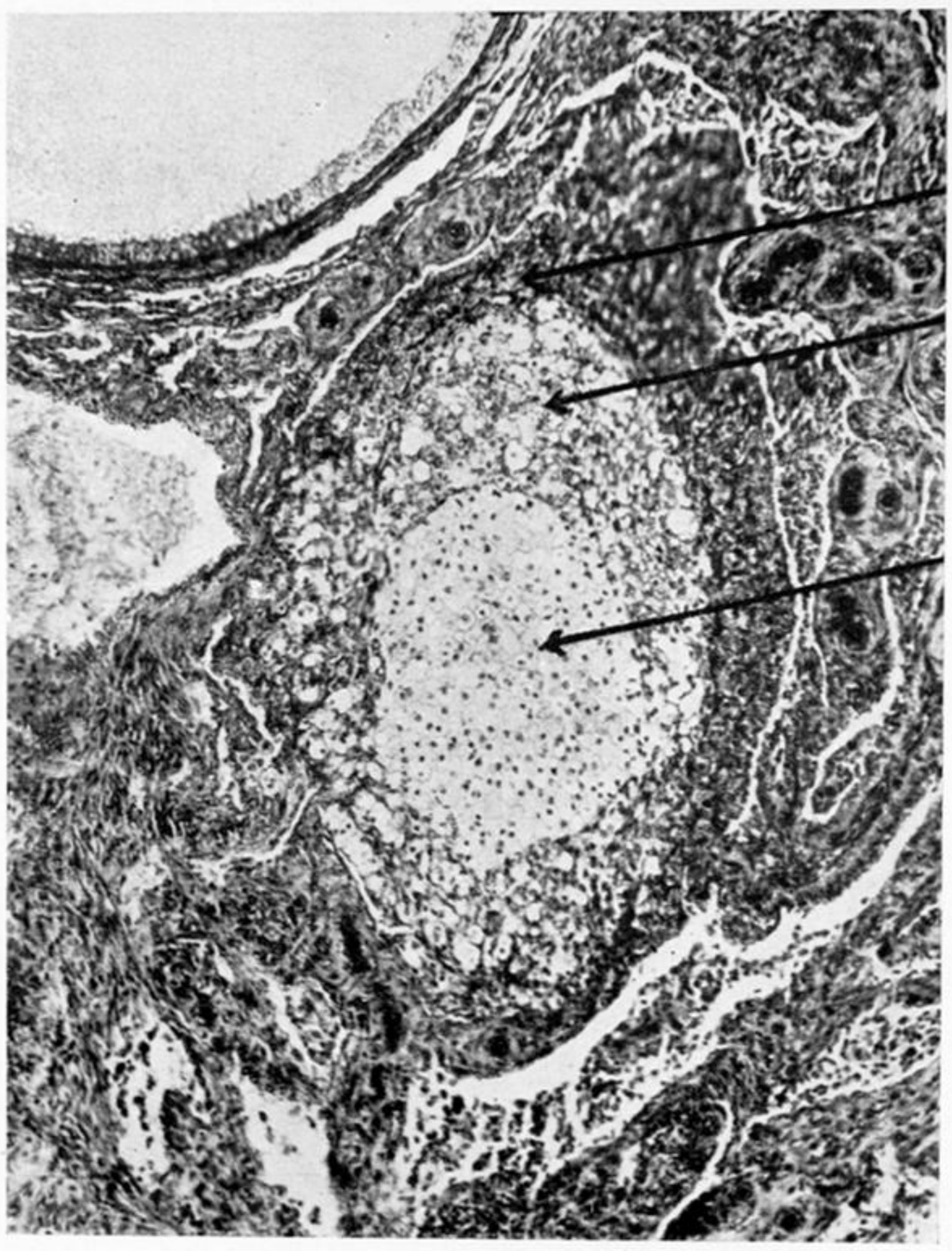

FIGURE 74

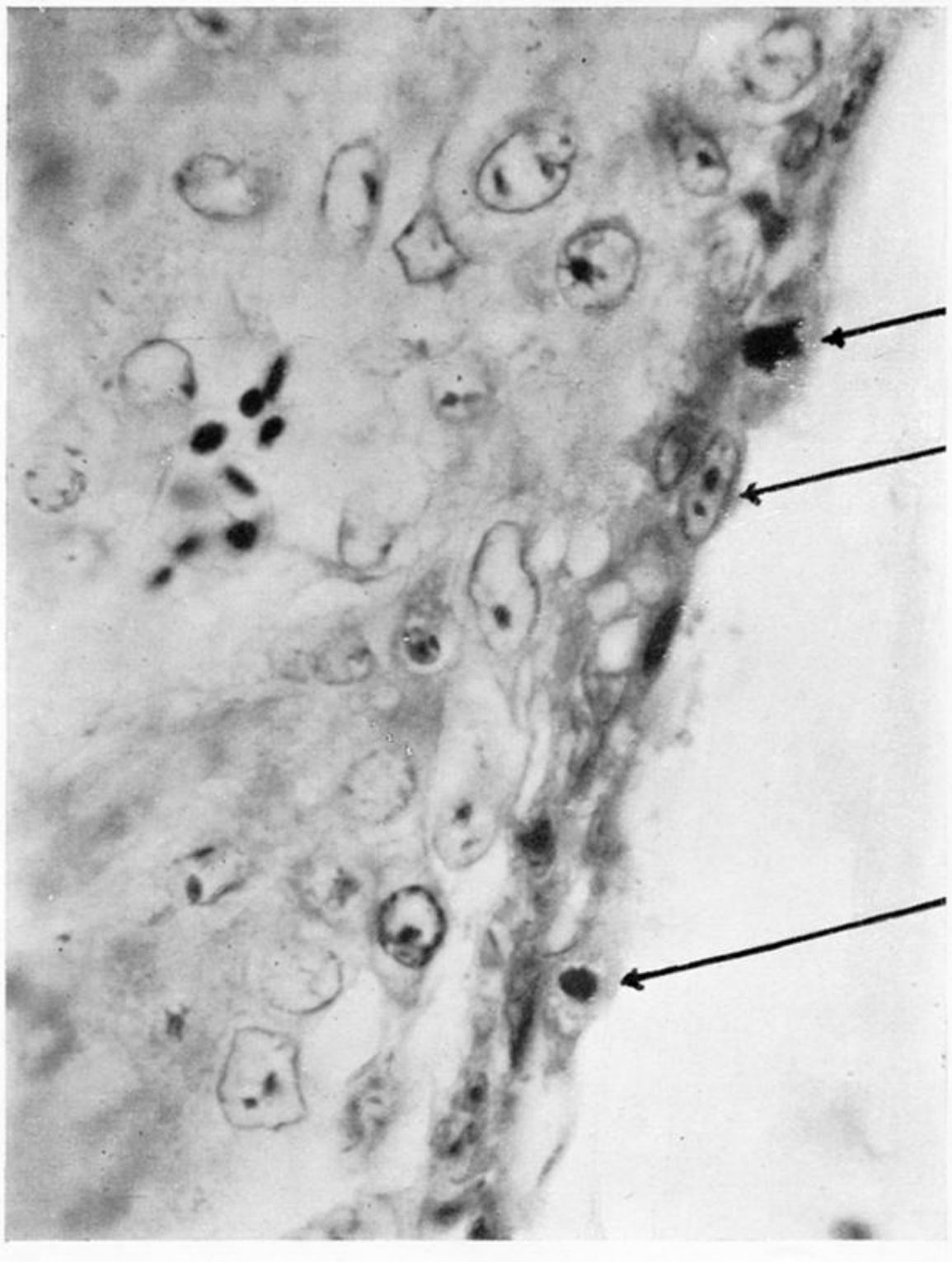

FIGURE 75

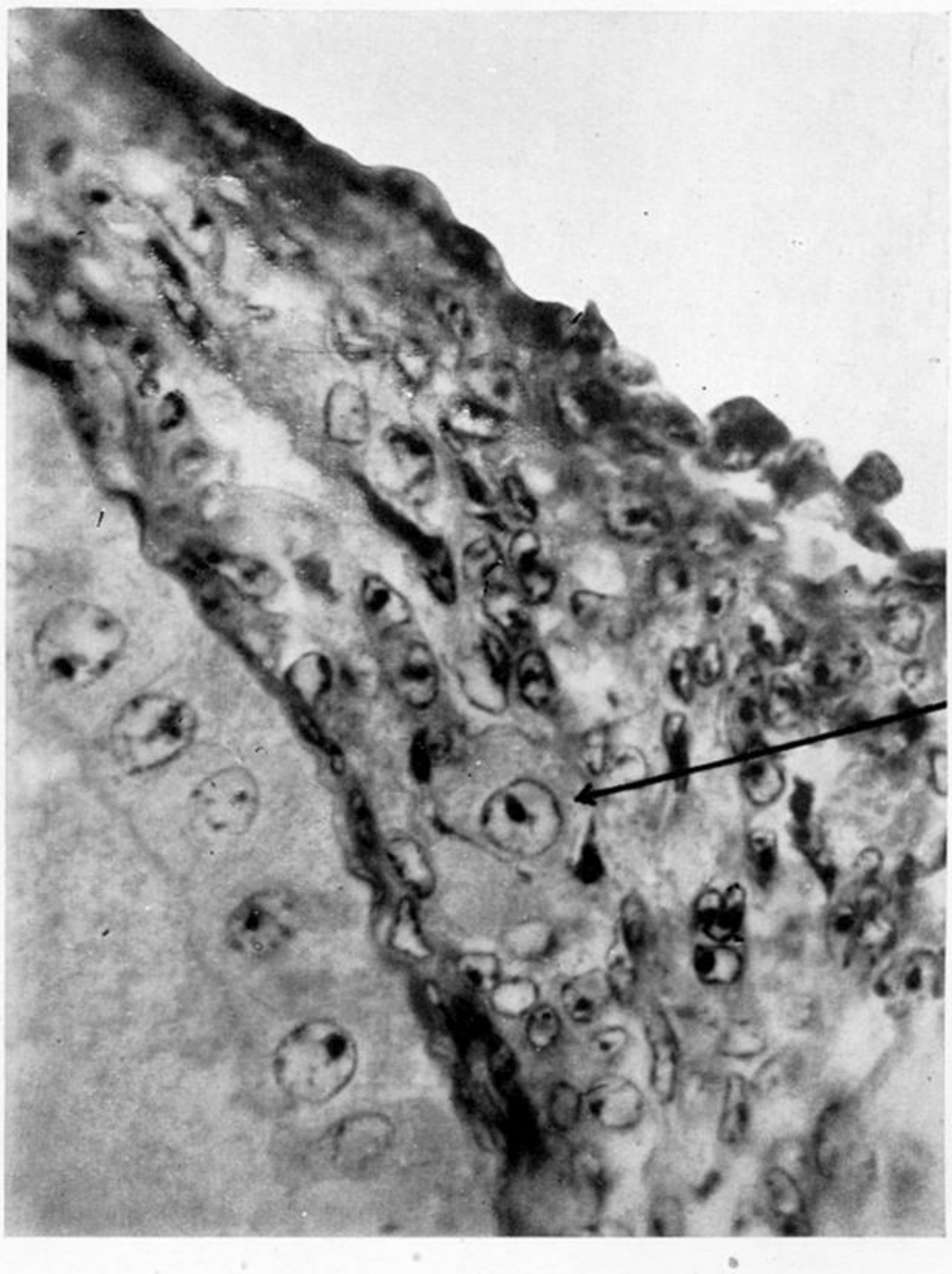

FIGURE 76

PLATE 17

FIGURE 73. Young 'corpus luteum' in the ovary of an adult British starling in early May showing the theca externa (*t.e.*), theca interna (*t.i.*), and solid core of follicle cells (*l.c.*). × 60.

FIGURE 74. Older 'corpus luteum' in the ovary of an adult British starling in the middle of May. The theca externa (*t.e.*) contains no 'luteal' cells, the theca interna (*t.i.*) contains some 'luteal' cells, and the solid core is composed entirely of 'luteal' cells (*l.c.*). × 120.

FIGURE 75. Germinal epithelium (*g.e.*) of the ovary of an adult British starling in early May showing mitotic divisions (*m.*) of the epithelial cells. × 1000.

FIGURE 76. Very young oogonium (*o.*) just below the germinal epithelium of the ovary of an adult British starling in May. × 1000.

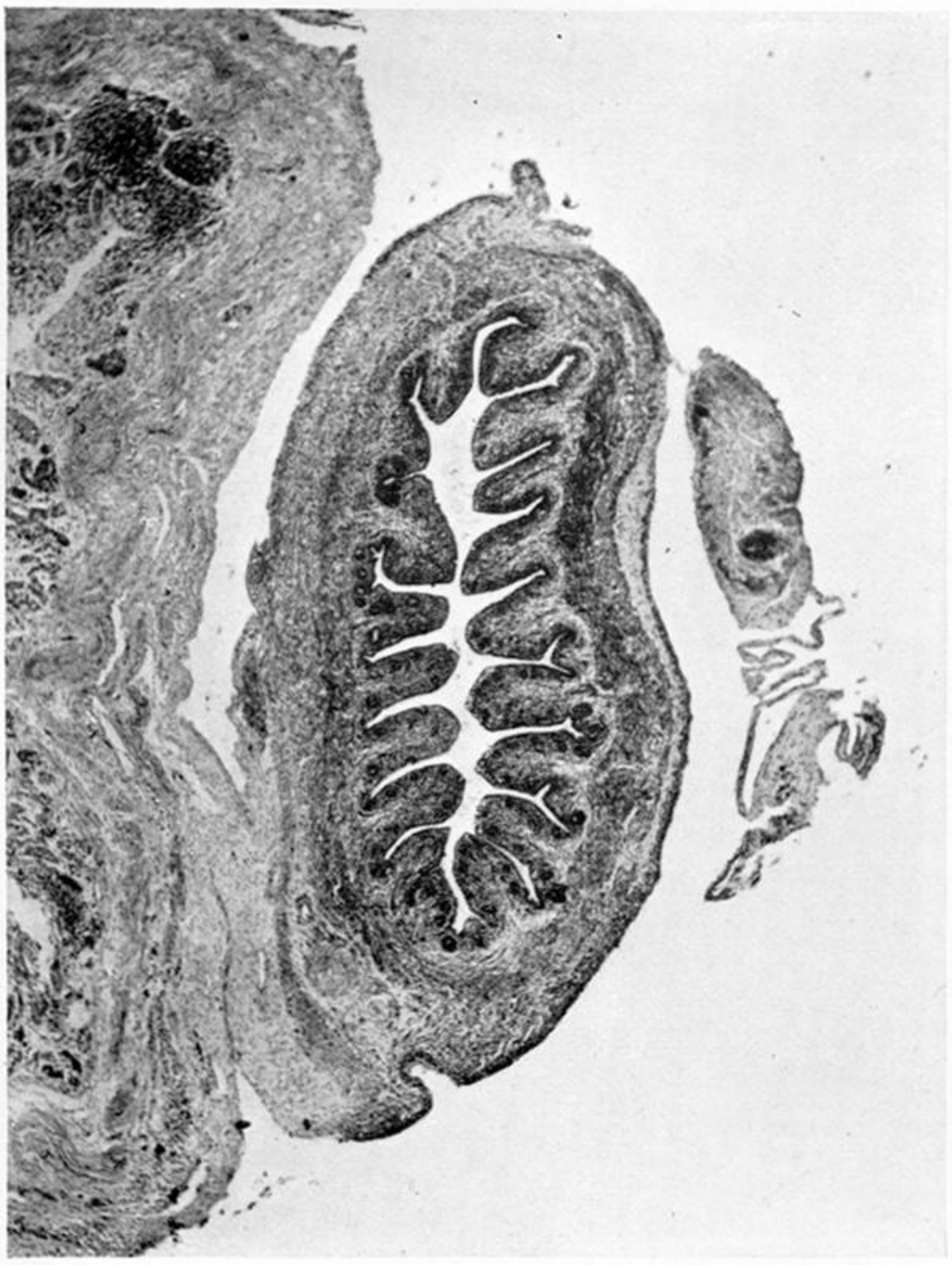

FIGURE 77

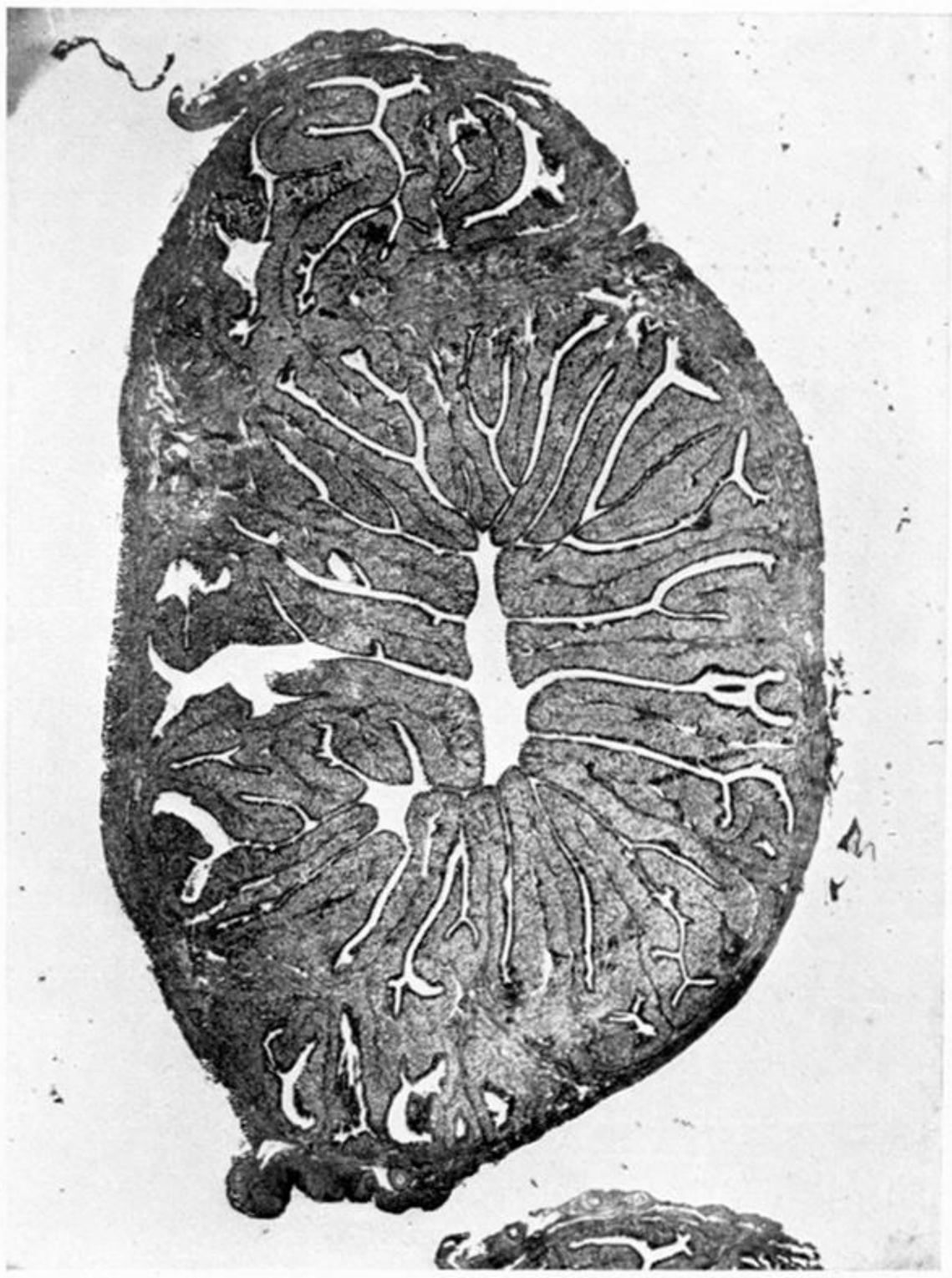

FIGURE 78

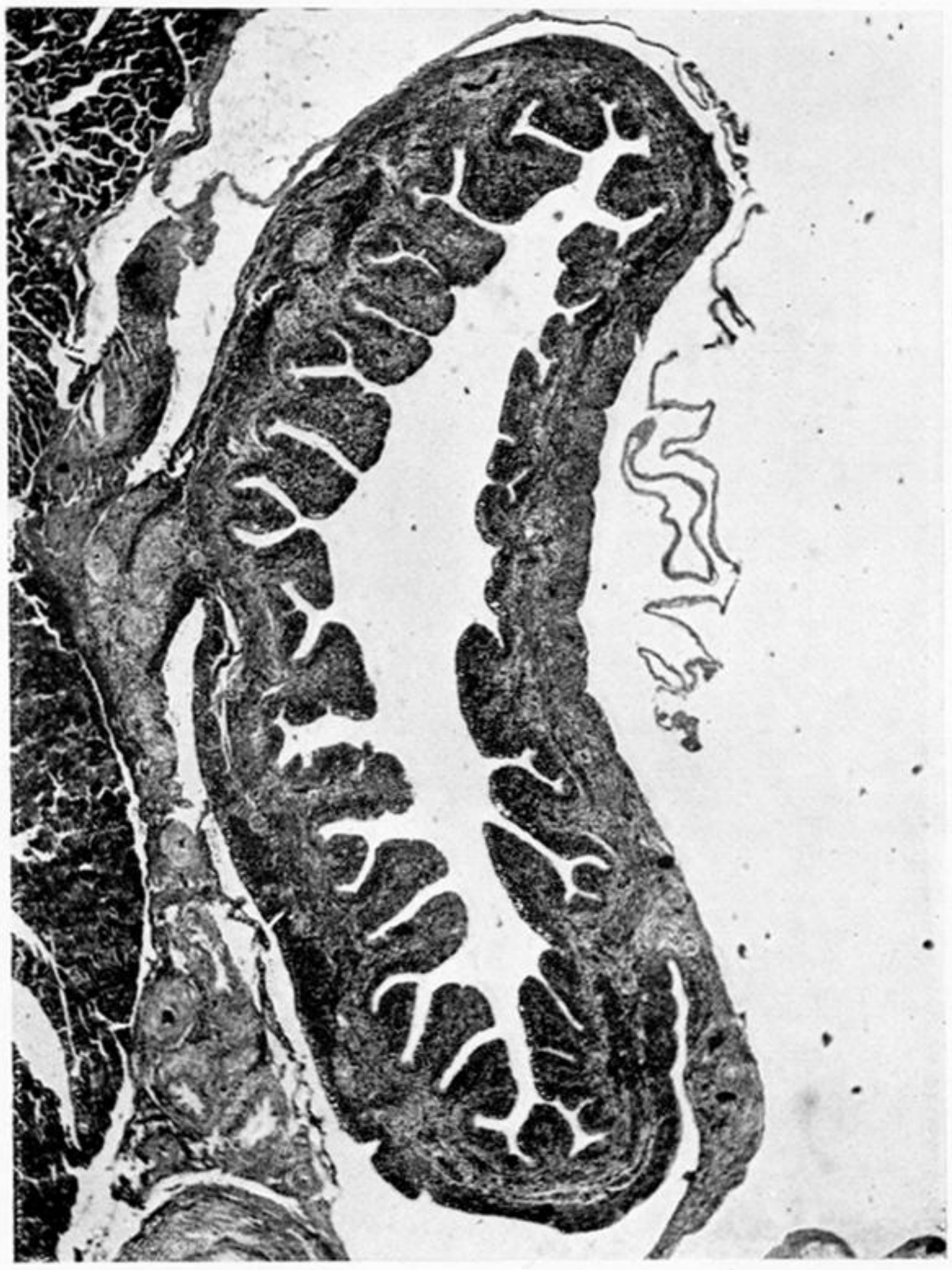

FIGURE 79

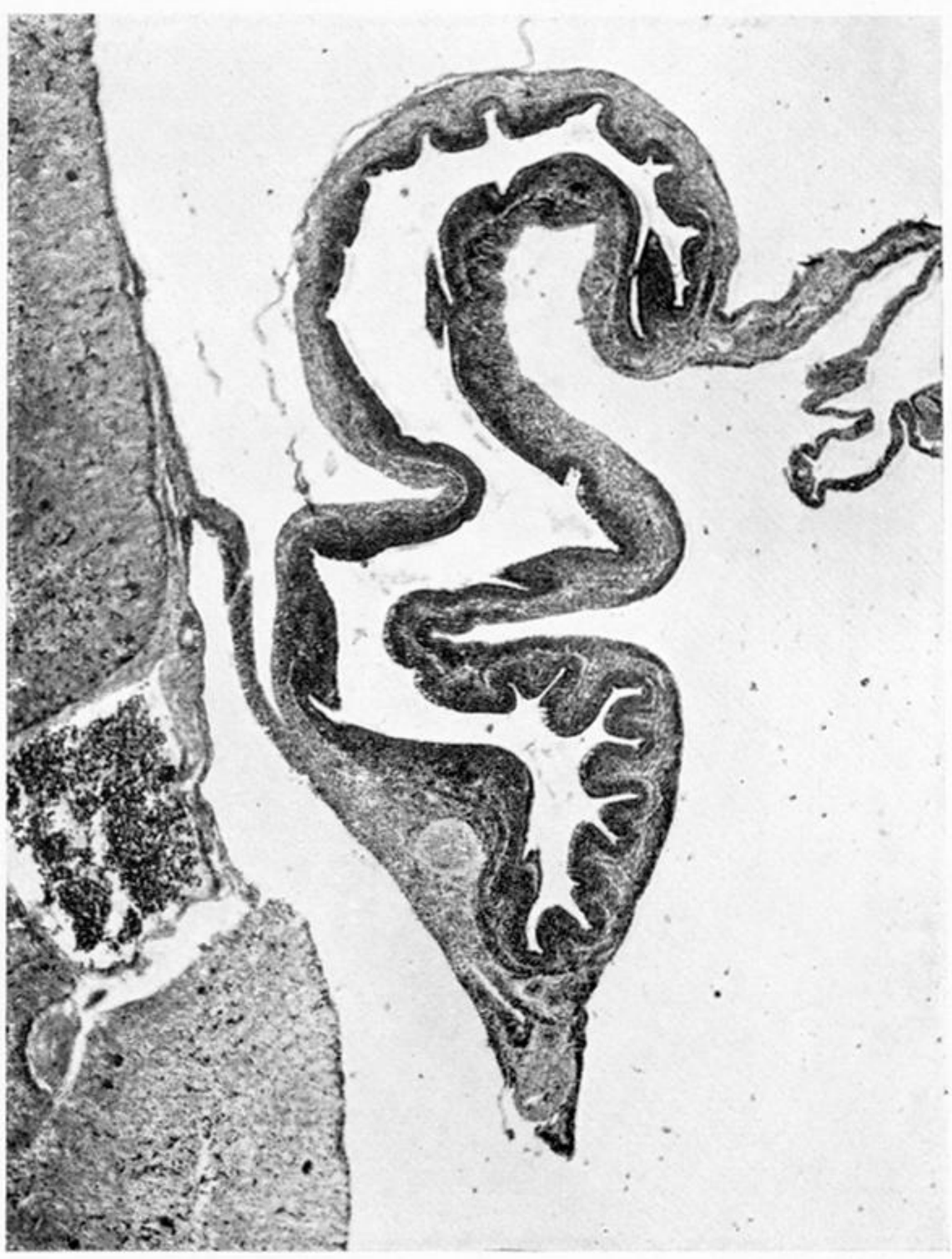

FIGURE 80

PLATE 18

FIGURE 77. Transverse section of the oviduct of an adult British starling in August showing maximum regression. × 40.

FIGURE 78. Transverse section of the oviduct of an adult British starling in late April showing the full development typical of the breeding season. × 11.

FIGURE 79. Transverse section of the oviduct of an adult British starling in March showing considerable growth. × 40.

FIGURE 80. Transverse section of the oviduct of an adult Continental starling in March showing only slight growth. × 40.

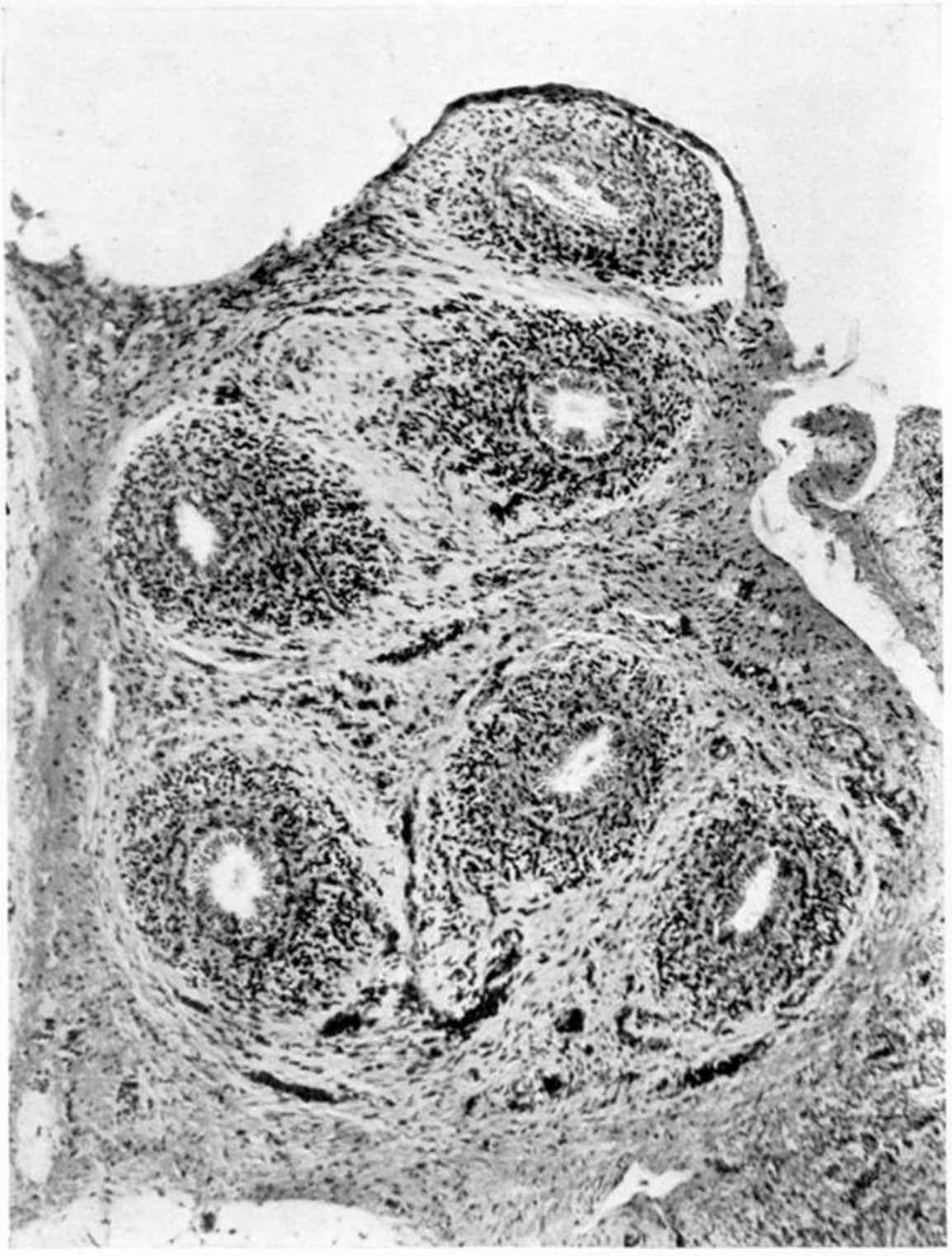

FIGURE 81

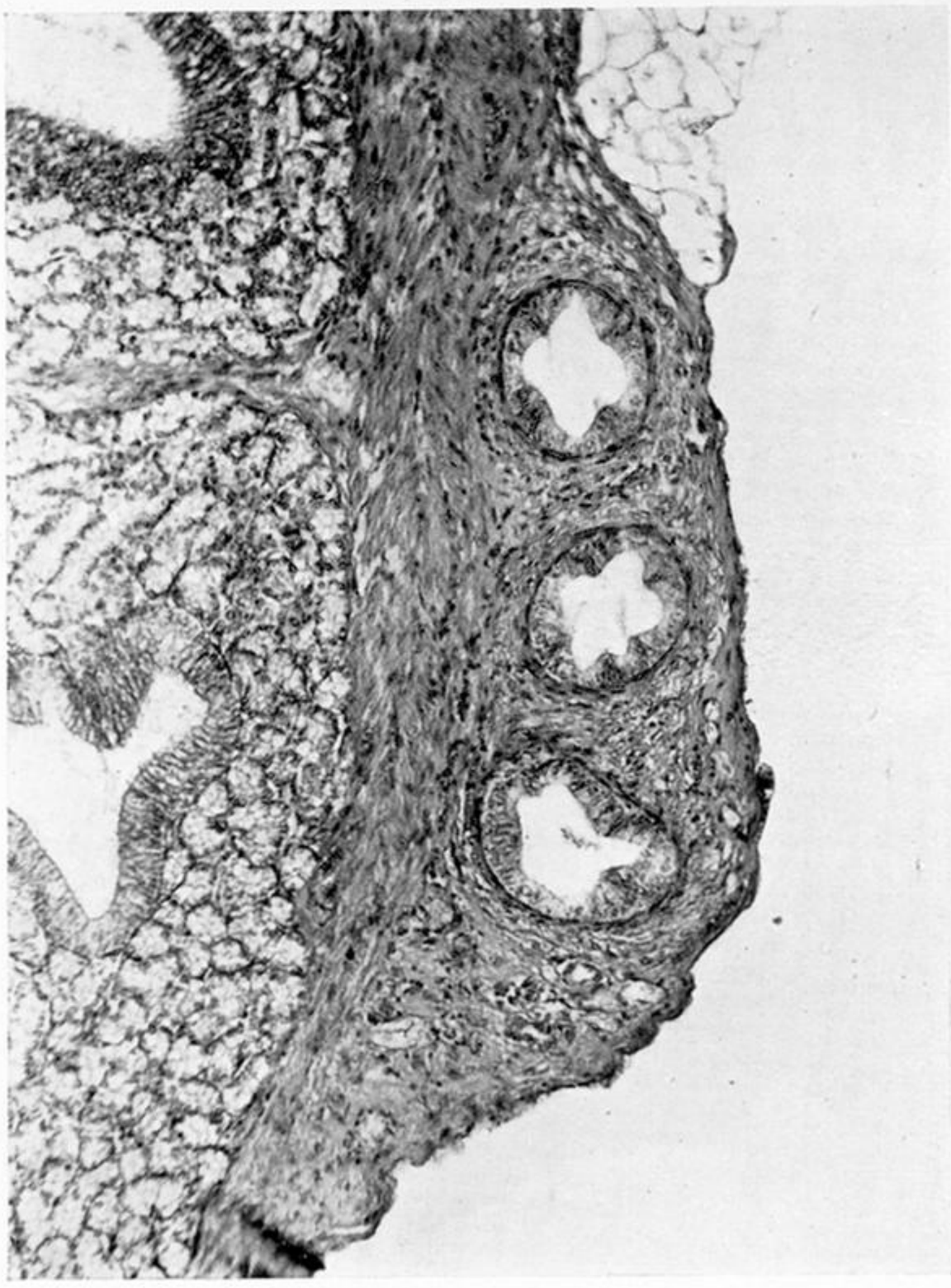

FIGURE 82

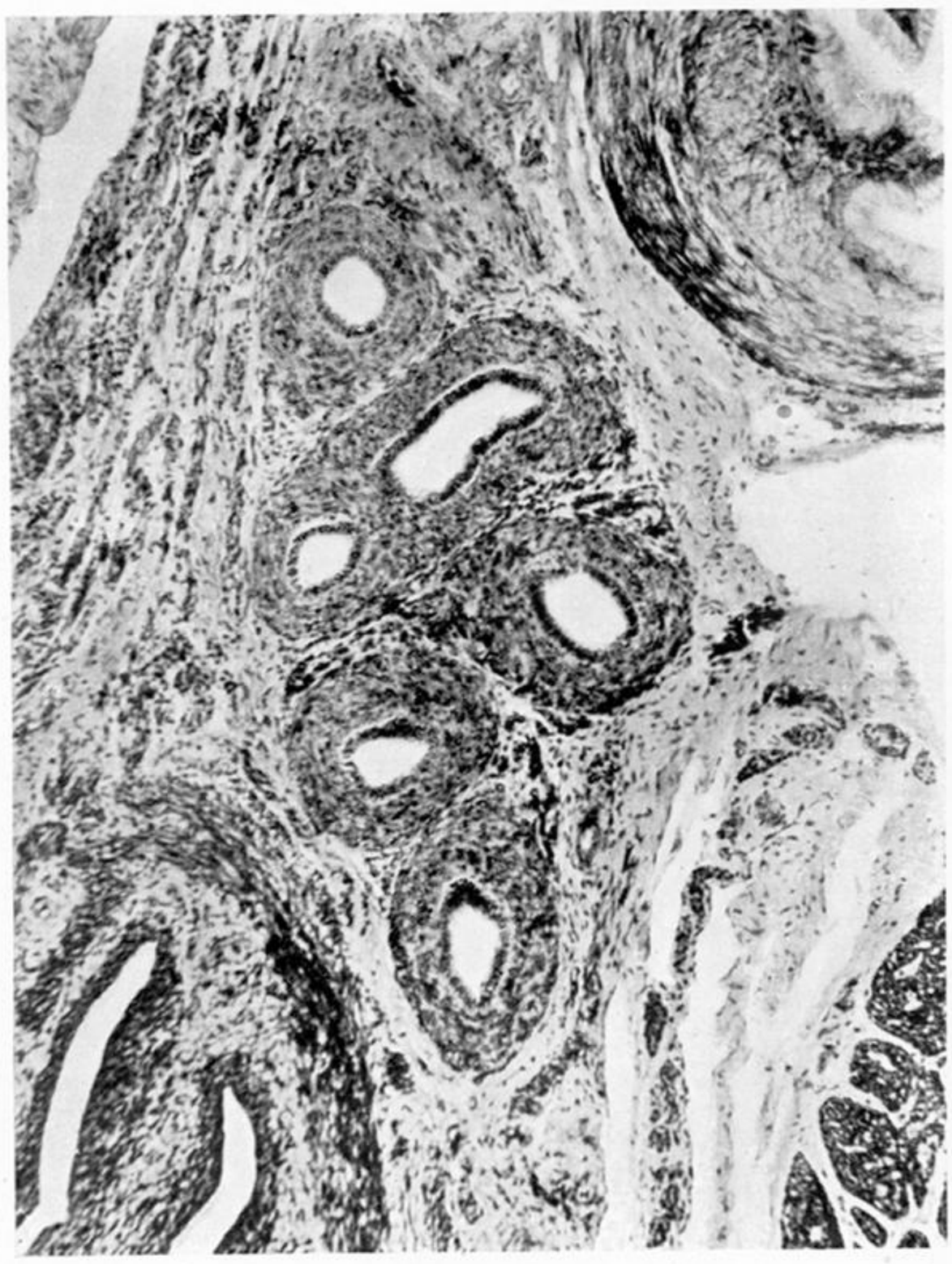

FIGURE 83

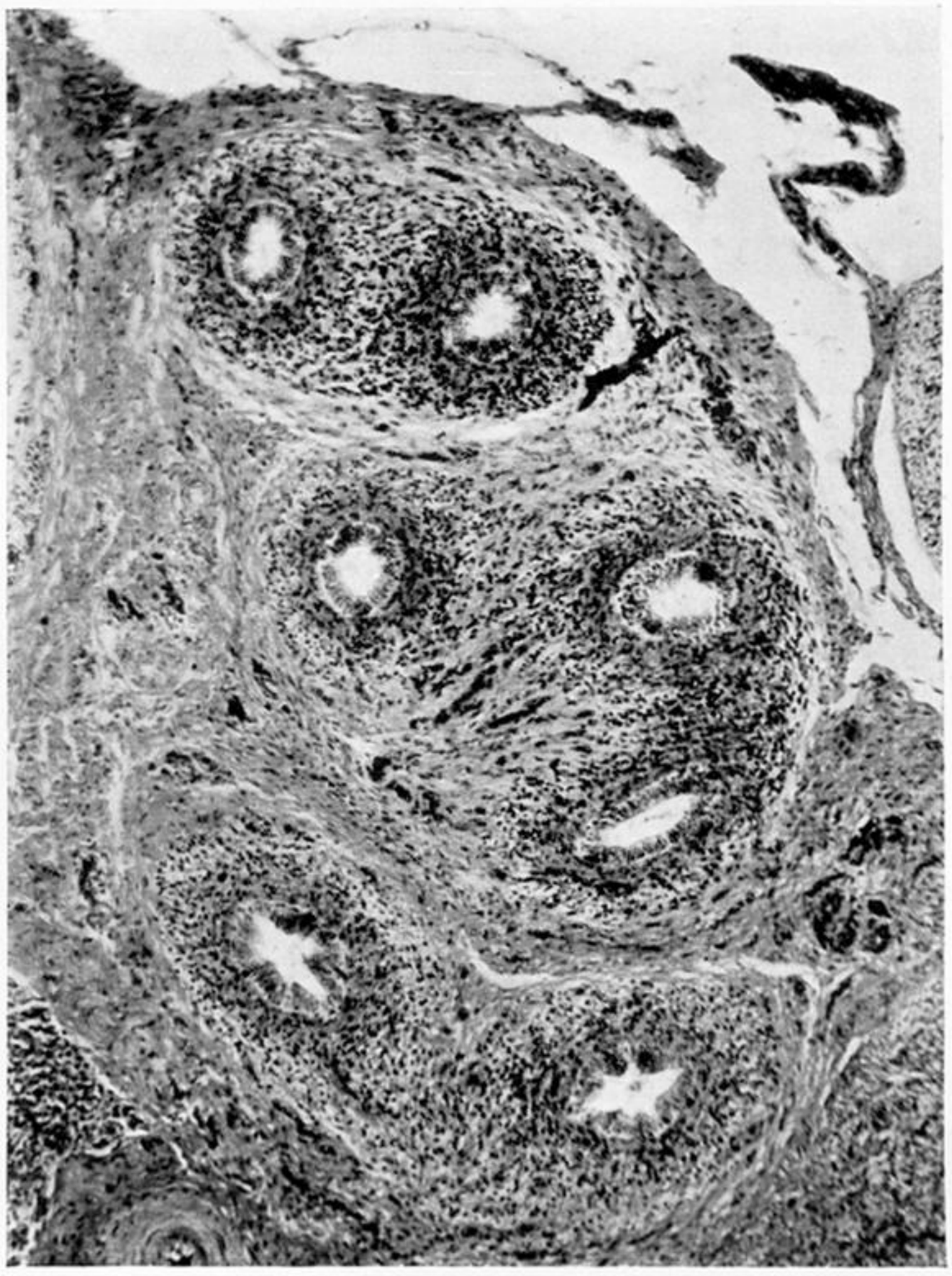

FIGURE 84

PLATE 19

FIGURE 81. Transverse section of the seminal vesicle of an adult British starling in August showing maximum regression of the tubules. × 120.

FIGURE 82. Transverse section of the seminal vesicle of an adult British starling in late April showing the greatest development of the tubules. × 120.

FIGURE 83. Transverse section of the seminal vesicle of an adult British starling in March showing the partial growth of the tubules. × 120.

FIGURE 84. Transverse section of the seminal vesicle of an adult Continental starling in March showing the slight growth of the tubules. × 120.

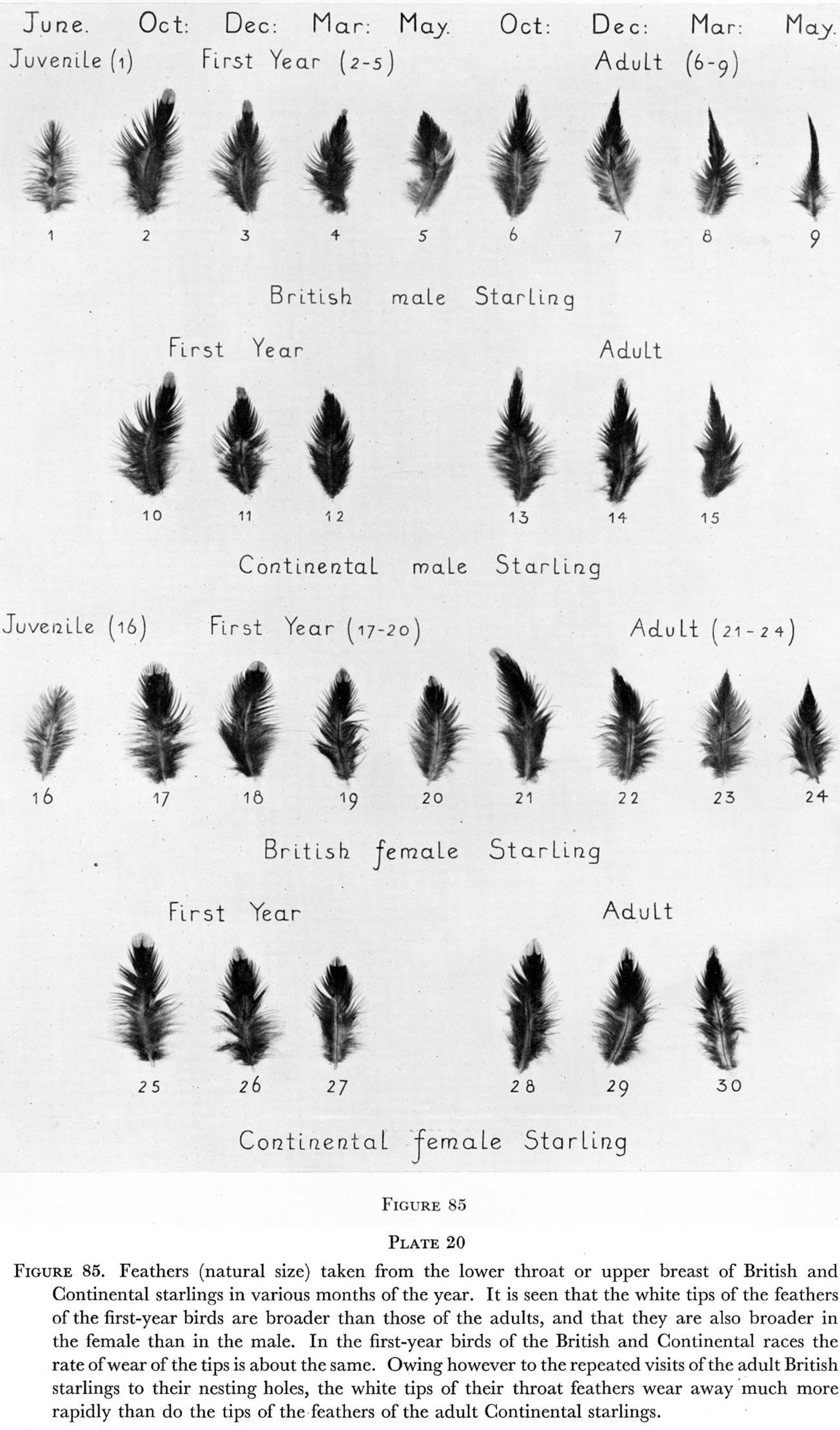

FIGURE 85

PLATE 20

FIGURE 85. Feathers (natural size) taken from the lower throat or upper breast of British and Continental starlings in various months of the year. It is seen that the white tips of the feathers of the first-year birds are broader than those of the adults, and that they are also broader in the female than in the male. In the first-year birds of the British and Continental races the rate of wear of the tips is about the same. Owing however to the repeated visits of the adult British starlings to their nesting holes, the white tips of their throat feathers wear away much more rapidly than do the tips of the feathers of the adult Continental starlings.

FIGURE 86

FIGURE 87

PLATE 21

FIGURE 86. A flock of starlings, mostly Continental birds, coming in to the communal roosting place near Beamsley in Wharfedale on the evening of 14 March 1939.

FIGURE 87. A very small flock of British starlings, part of the population from the immediate neighbourhood of the roosting place near Beamsley in Wharfedale, coming in to sleep communally on the evening of 20 April 1939. The way in which the pairs of birds kept together was most marked.