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Histological Changes Associated with Enlargement and Regression of the Thymus Glands of the Red-Billed Quelea Quelea quelea L. (Ploceidae: Weaver-Birds)

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Phil. Trans. R. Soc. Lond. B 1975 **273**, 65-78
doi: 10.1098/rstb.1975.0104

Phil. Trans. R. Soc. Lond. B. 273, 65–78 (1975) [65]
Printed in Great Britain

HISTOLOGICAL CHANGES ASSOCIATED WITH ENLARGEMENT AND REGRESSION OF THE THYMUS GLANDS OF THE RED-BILLED QUELEA *QUELEA QUELEA* L. (PLOCEIDAE: WEAVER-BIRDS)

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(*Communicated by E. C. Amoroso, F.R.S. – Received 24 February 1975*)

[Plates 1–5]

CONTENTS

Thymic lobes from over 200 red-billed queleas, *Quelea quelea* L., were examined histologically. Samples were taken from embryos about to hatch, juveniles and adults. The lobes varied in size from very small to very enlarged (1–> 5 mm long).

The constituent cell types are described in detail and the occurrence of these cells in different sized lobes is discussed.

A cycle of events is proposed which accounts for the observations presented here. It is suggested that the large numbers of erythroid cells found in the cortex of some individuals were developing *in situ*. The significance of erythropoiesis within the thymus is discussed.

Introduction

The red-billed quelea, *Quelea quelea* L., a weaver-bird inhabiting tropical Africa, is an important pest species over much of its range owing to its grain eating habits. The distribution and breeding biology of this species has been studied extensively for a number of years. As

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part of one such study in East Africa,† seasonal changes in size, form and colour of the thymus glands were observed in these birds. Specimens were taken for histological examination from over 5000 birds sampled in all months from 1969 to 1971.

The changes in size of the glands throughout the life cycle have been described elsewhere (Ward & Kendall 1975) but it may be useful to include here a résumé of the life cycle and the observed changes in queleas. Breeding birds form highly synchronized colonies lasting 6–8 weeks. The females usually lay three eggs that hatch after 10 days. The chicks start to acquire their juvenile plumage while in the nest and are called juveniles when this is attained. There is then a period of approximately 3 months during which time each bird undergoes a postjuvenile moult; after that the birds are regarded as first-year adults. The prenuptial moult that follows is a light moult that precedes breeding. In this way first-year adults, and adults which have bred in previous years, obtain full breeding plumage. The males acquire conspicuous face masks and rosy breasts, and the colour of the female bill changes from red to yellow. Most breeding colonies last a minimum of 6 weeks and it is thought that the adults may breed several times in East Africa (Ward 1971) before entering the postnuptial moult. The birds in East Africa probably start the prenuptial moult immediately after finishing the postnuptial moult.

At hatching most of the 14–16 lobes of the thymus in the bird were small (about 2 mm long). By the time the young had grown their juvenile plumage, over 90% of the birds had enlarged thymic lobes (over 4–5 mm long). The percentage of birds with lobes as large as this decreased, with minor fluctuations, during the postjuvenile moult, until at the end of the moult about 40% of the birds had these large thymi. Thereafter through the adult life of the birds there was often a minimum of about 10% of individuals in the population with enlarged thymi. During moulting this percentage rose to around 60–80% and in the breeding colonies it dropped to zero and then rose to 60–70% over 7 days.

Associated with these size changes were alterations in structure in the thymic lobes which have been briefly summarized (Kendall & Ward 1974). Macroscopically there was a change in colour from white to blood-red occurring particularly in the first-year birds during moult, and during the breeding season. This was associated with the development of erythrocytes within the thymus. This paper describes the structure of the thymus glands in this bird as seen with a light microscope. It forms the basis for further studies on erythropoiesis with the electron microscope (Kendall & Frazier, in preparation) and for a consideration of cell numbers and relations in young queleas (Kendall, in press).

Materials and methods

Thymic lobes were taken from approximately 200 of the 5000 samples of *Quelea quelea intermedia* Van Someren collected in mist nets over a three year period in Kenya and Tanzania. The birds were killed with chloroform, the thymic lobes were dissected out, fixed in Bouin, Duboscq–Brasil or Formol-saline, dehydrated in Supercedrol, cleared, embedded in Paraplast and cut at 6 or 8 μm. Sections were stained either in Masson's trichrome, Haematoxylin and Eosin, Leishman, Maximow, a modified Azan, Schiff's reagent (PAS) or by a differential

† During the Tropical Bird Pest Research Project instituted jointly by the East African Community's Tropical Pesticides Research Institute in Arusha, Tanzania and the Centre for Overseas Pest Research in London, 1969–71.

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cell staining technique (Alvarez & Valladares 1972). Some of the Formol-saline fixed material was also stained with either Perl's Prussian Blue method for haemosiderin; the Dunn–Thompson or Pickworth's benzidine methods for haemoglobin; Krag's Kiton – red almond green method for erythrocytes (Lendrum 1949) or Barratt's method for bone marrow smears. Blood smears, and impression smears of cut lobes pressed onto slides and fixed in methanol or formalin vapour, were stained with May-Grünwald Giemsa.

Results

The thymus gland in birds consists of discrete lobes of thymic tissue situated in two long chains, one on either side of the neck (Romanoff 1960). The lobes in *Quelea quelea* were enclosed in a sheath, situated in connective tissue and fat, and served by a thymic artery and vein, and nerves. In first-year birds most of the lobes were similar in size, reaching maximum size (over 5 mm long) as the juvenile plumage developed. In adults there was more variation in size along the chains and the largest lobes were smaller than the largest lobes of young birds.

The stroma of every lobe was a network of epithelial reticular cells. Most lobes (except the smallest) could be differentiated into cortex and medulla by the differing densities of the epithelial reticular cells. The medulla typically contained many more epithelial reticular cells per given area than the cortex. Lymphocytes, lymphocyte-like cells (Yoffey & Courtice 1970), macrophages, granulocytes, plasma cells, erythroid cells, mature erythrocytes and pyknotic cells were lodged within this reticulum (figures 1–8).† The proportions of these cell types varied from lobe to lobe and even within one lobe in a bird. Other cells which may have invaded the gland, i.e. leucocytes and fibroblasts, were present in some lobes. The connective tissue sheath surrounding the gland was continued inwards as septa with arteries, veins and capillaries (figures 9 and 10). Wide channels that might have been lymphatics or channels of the air sac system were found around the periphery (figures 11–13). Myoid cells were not identified but they are known to be present from later electron microscope studies. Hassall's corpuscles and cysts were also present (figures 15–18).

Cell types

Epithelial reticular cells were quite large with thin strands of cytoplasm extending to nearby cells forming a cellular reticulum throughout the gland. The fine cytoplasmic strands were not easily seen with the light microscope. The nucleus of the reticular cell was rounded or elongated (5 μm × 7 μm on average). The chromatin was not regularly dispersed throughout the nucleus but formed a layer immediately within the nuclear membrane. The nucleus contained a prominent central nucleolus connected to the chromatin with fine strands of chromatin-like material (figure 17). A summary of the characteristics of some of the following cell types under discussion here is given in table 1. Lymphocytes in the thymus are especially small (Yoffey & Courtice 1970). In Masson stained sections of the thymic lobes of quelea chicks just before hatching, the nuclear diameter of *ca.* 71 % of the cortical small lymphocytes was 3–4 μm. Twenty-one percent of the small lymphocytes were over 4 μm in diameter and a small number (7.5 %) had diameters of less than 3 μm. Six days later the majority of small

† Figures 1–18 appear on plates 1–5.

lymphocytes (*ca.* 94 %) measured 2–4 μm. The cytoplasm was very scant in these cells, and when visible in the light microscope it stained a pale green with Masson. The nucleus was rounded, slightly pachychromatic, and contained one nucleolus (figures 2, 3, 5 and 6). Some of the small lymphocytes of the larger size range appeared to have two nucleoli. In sections examined under the light microscope the medullary small lymphocytes appeared similar.

TABLE 1. THE CHARACTERISTICS OF LYMPHOID AND ERYTHROID CELLS IN PARAFFIN-EMBEDDED SECTIONS OF THYMIC LOBES FROM ADULT AND JUVENILE *QUELEA QUELEA*, STAINED WITH MASSON AND ROMANOWSKY TYPE STAINS

	overall		nucleus			cytoplasm	
cell type	size μm	shape	size μm	shape	appearance	amount	staining
small lymphocyte	2–4	round	2–4	round	slightly pachychromatic	scant	slightly basophilic
lymphocyte-like	4–5	rounded	4	ovoid	fairly leptochromatic	just obvious	slightly basophilic
possible transitional	7.5	rounded	5.5	rounded	leptochromatic	clearly present	very basophilic
early erythroid	5	ovoid	3	rounded	leptochromatic	moderate amount	basophilic
erythroblasts	3	ovoid or irregular	4 × 2	ovoid	leptochromatic slightly homogeneous	moderate amount	slightly basophilic‡
late erythroblasts†	8.5 × 3.5	ovoid or slightly irregular	4.5 × 2.5	elongated	slightly pachychromatic	moderately extensive	mainly acidophilic
mature erythrocytes	8 × 3.5	fusiform	4 × 2	fusiform	pachychromatic	extensive	acidophilic
pyknotic	2–3	round	2–3	round	homogeneous	scant	acidophilic

† These probably correspond to polychromatophilic erythroblasts of man.
‡ Cytoplasm is red with Krag's stain.

The small lymphocyte was common in the cortex of most thymic lobes of *Quelea quelea* juveniles and adults but whenever mitosis was seen in the cortex there was always in addition a large number (variable amongst different individuals) of lymphocyte-like cells (figures 1, 2 and 3). The nuclei of lymphocyte-like cells were more irregular in shape and on average slightly larger (mean size 4 μm diameter) than the nuclei of small lymphocytes. Some cells showed distinct cytoplasm surrounding the nucleus and the nuclei were clearly leptochromatic.

Larger cells occurred in the cortex of some juveniles and adults (figures 3, 5 and 6). The mean nuclear size of these cells was 5.5 μm. The cytoplasm was obvious, giving an overall size for the cells of approximately 7.5 μm. The nuclei, which were rounded, had slight indentations and contained dispersed chromatin. Under phase contrast it was usually possible to identify one nucleolus to each nucleus. The cytoplasm was in some cells greater on one side of the nucleus than on any other. With Masson the cytoplasm stained green and was very basophilic with Leishman, Maximow and Barratt's method for bone marrow smears. The status of these cells is very difficult to determine. The basophilic cytoplasm and large nucleus containing dispersed chromatin suggest a blast cell or a transitional cell. They were

present in large numbers in glands when the cell population consisted of lymphocyte-like cells, small lymphocytes, early erythroid cells and pyknotic cells. They were not found when the cortex contained predominantly small lymphocytes or predominantly erythrocytes. However, the possibility that these were larger cells of the lymphocyte series cannot be ruled out from light microscope studies.

The macrophages in the lobes were very similar in size and shape to epithelial reticular cells, although the nuclei tended to be more rounded. They were more common in the cortex than the medulla. Their cytoplasm contained numerous inclusions and sometimes ingested cells (figure 5). The inclusions were usually rounded, 1–3 μm in diameter, of a homogeneous nature and resembled pyknotic cells. When the macrophages were full of these inclusions the rest of the lobe also contained large numbers of free pyknotic cells. At these times the lobes, which had a dense, darkly staining appearance with Masson due to the large numbers of lymphocytes and pyknotic cells, were studded with lightly staining regions where there were single large macrophages (figure 14). Macrophages in some lobes were positive when stained with Schiff's reagent (PAS). A few macrophages stained more evenly and more deeply than others but these were not common in the specimens examined.

Granulocytes (neutrophils) occurred in both the cortex and the medulla. Possible promyelocytes were found in impression smears stained with May–Grünwald Giesma and there were also a large number of immature granulocytes with fairly small acidophilic inclusions. Mature granulocytes occurred in many glands; some were in small patches alongside connective tissue (figure 8) and others were found in vacuoles and cysts. These stained magenta red with PAS stains. In some sections the vacuoles appeared to have coalesced and granulocytes could be found in several compartments of small cysts (figure 17).

Mature avian erythrocytes are nucleated unlike most mammalian erythrocytes. The nuclei in the erythrocytes of *Quelea quelea* were elongated, very pachychromatic and surrounded by homogeneous cytoplasm. The cell shapes were typically fusiform and flattened in one plane. The cytoplasm stained evenly with acidic dyes and pale yellow with Dunn–Thompson. Krag's stain imparted a deep magenta colour to the cytoplasm, but left the condensed chromatin of the nucleus unstained. Less mature cells, probably corresponding to the polychromatophilic erythroblast of man, had larger nuclei than mature cells with chromatin less clumped. Both the cytoplasm and the nucleus stained with the Krag's stain, but the staining was uneven with acidic dyes and the Dunn–Thompson stain. Cell shape was rarely fusiform, more often very irregular as though distorted by the pressure of adjacent cells (figures 3 and 4). Where the cells were apparently developing in the cortex of the gland or in blood vessels, adjacent cell boundaries fitted together with little intercellular space.

Basophilic erythroblasts, unlike the more mature red blood cells, had rounded nuclei, often clearly leptochromatic (figures 2 and 6). They contained more cytoplasm than lymphocyte-like cells which they frequently closely resembled. The cytoplasm was clearly basophilic and did not stain with acidic dyes, nor with Dunn–Thompson's stain. The reaction to Krag's stain was more variable than the more mature forms of erythroblasts in that the cytoplasm only sometimes stained and then faintly. The nucleus, however, often stained entirely or in one or two small patches. These weakly staining cells were sometimes found in patches of lymphocyte-like cells, when they imparted a pale pink colour to the section.

Many erythroblasts and erythrocytes were refractory to staining and refractile, probably owing to the lytic action of fixatives such as Bouin.

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Immature erythrocytes frequently had refractory nuclei whereas cells which appeared more mature had refractory cytoplasm but not nuclei. Occasionally isolated erythrocytes with irregular outlines and refractory cytoplasm were found in the medulla of glands when there were no signs of immature erythrocytes in the rest of the gland.

Pyknotic cells (figures 1 and 5) were very common in some glands, but completely absent from others. Pyknotic cells had small (1–3 μm diameter) round nuclei which were homogeneous with no signs of chromatin differentiation or nucleoli. Sometimes a small rim of cytoplasm could be identified and many pyknotic cells (figure 1) contained unstained spheres (as did a few immature erythrocytes). All pyknotic cells stained with Krag's stain for erythrocytes and were refractile. Electron microscope studies (Kendall & Frazier, in preparation) show that pyknotic cells are in some cases degenerate erythroid cells. The differential stain for cells in mitosis suggests that some at least may be formed very soon after mitosis has taken place.

Hassall's corpuscles (of epithelial origin) occurred mainly in the medulla (figure 10). To facilitate later descriptions they were called early and late Hassall's corpuscles. In early Hassall's corpuscles the component cells were large (8 μm × 10 μm) with distinct cell boundaries. The cytoplasm of most cells was granular and often contained intracellular cysts 5–6 μm in diameter. The contents of the cysts and the limiting membranes stained very strongly with the green of Masson, and were strongly PAS positive. Hoshino (1962) describes similar intracellular cysts in reticular cells in mouse thymus. Larger cysts (up to 10 μm diameter) contained cells or cell debris. Late Hassall's corpuscles had a clearly delimited central mass which stained with PAS, Krag's, Perl's, Dunn–Thompson and Pickworth's stains. The intracellular cysts in the peripheral cells were often multilocular or became part of much larger cysts (30 μm × 45 μm).

Other large cysts also occurred in the gland when late Hassall's corpuscles were found. These are often called ciliated cysts although the cilia may be restricted to one region of the cyst or so dispersed that the cyst appears to be non-ciliated. These often had smaller ciliated cysts or ducts attached. These cysts contained large numbers of lymphocytes, pyknotic cells, erythroid cells and granulocytes. The contents were strongly PAS positive perhaps because of material secreted into them by the mucous cells around the periphery (figure 7).

Histology of the lobes

The main histological features of lobes of different sizes are shown in table 2. Additional information is given below.

Very small lobes

Sixteen lobes were examined. Small lobes (under 1 mm) were of four main types: small lobes containing cells in mitosis; effete lobes; fully regressed lobes; and small actively growing lobes of embryos (not examined).

Small lobes containing cells in mitosis occurred in adults in breeding colonies (particularly in the early stages of the colony when egg laying and incubation was in progress), and in birds undergoing a postnuptial moult. None of these lobes showed a clear distinction between cortex and medulla and groups of cells in mitosis occurred throughout the lobe.

Effete lobes were found in adult birds towards the latter stages of colony formation (nestlings present and becoming independent), in adults in late prenuptial moult, and in adults in the middle and end of postnuptial moult. The medulla was always distinct from the cortex and

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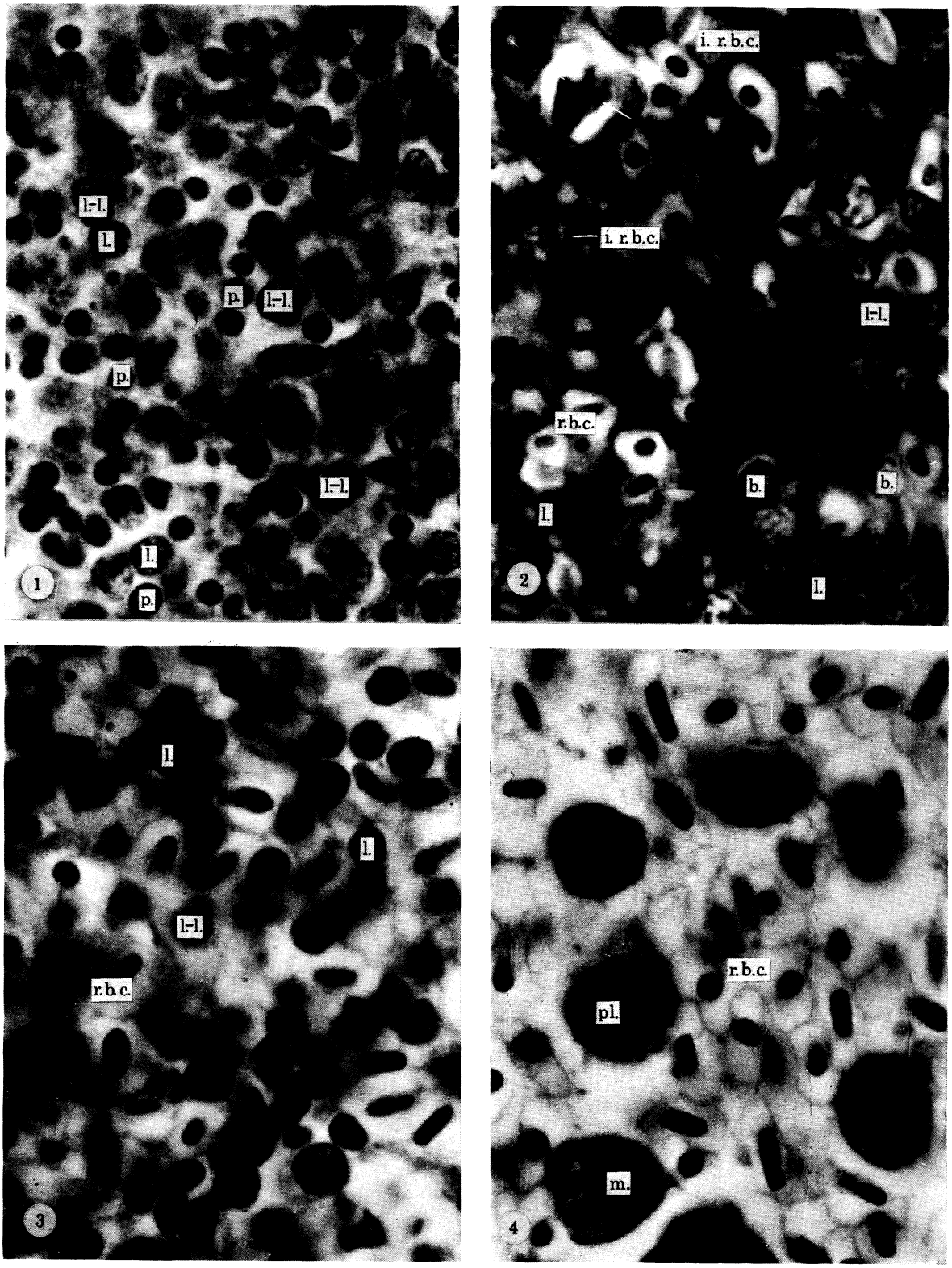

FIGURES 1–4. Thymic cortex of queleas. Masson stained 8 μm thick sections (all × 1600).

FIGURE 1. Six day old chick. Most of the cells are lymphocytes (l.), lymphocyte-like (l.-l.) or pyknotic (p.). Several pyknotic cells have small unstained spheres attached.

FIGURE 2. Adult female from breeding colony with eggs. The thymic lobe was enlarged and appeared red in colour. Lymphocytes (l.), lymphocyte-like cells (l.-l.), fairly mature erythrocytes (r.b.c.), immature erythrocytes (i.r.b.c.) and basophilic erythroblasts (*b*) are present.

FIGURE 3. Adult female captured from a feeding flock, caged overnight during which time she laid an egg, and killed next morning. Most of the cortex consists of erythrocytes (r.b.c.) with some lymphocytes (l.) and lymphocyte-like cells (l.-l.) and one larger cell (*) which might be a transitional cell.

FIGURE 4. Adult female from breeding colony with young chicks. The cortex is almost entirely composed of erythrocytes (r.b.c.). The other cells are difficult to identify but may be plasma cells (pl.) or macrophages (m.).

(*Facing p.* 70)

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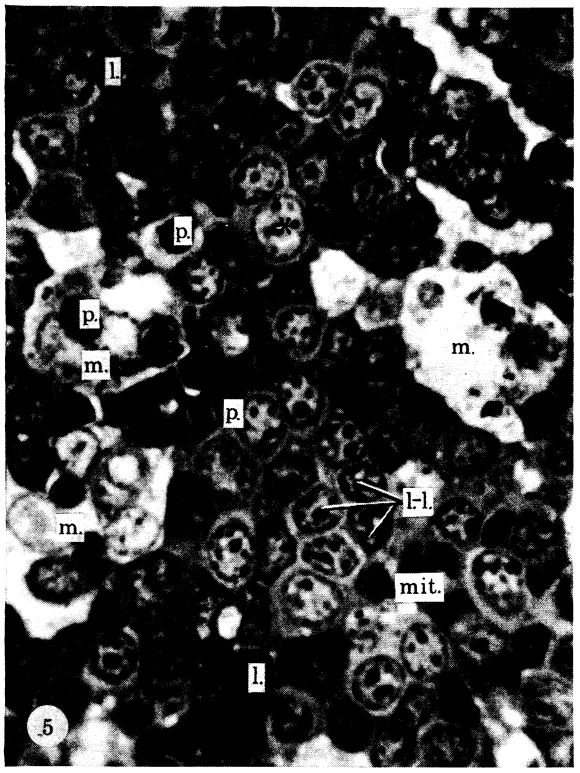

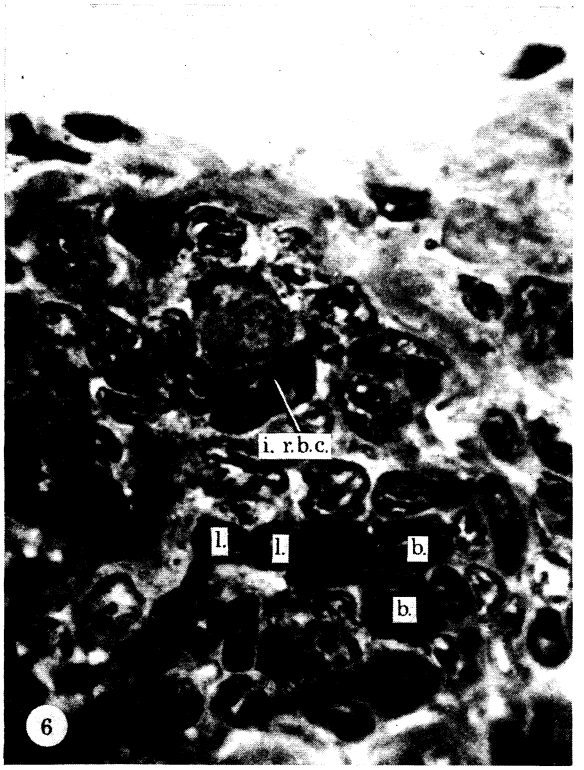

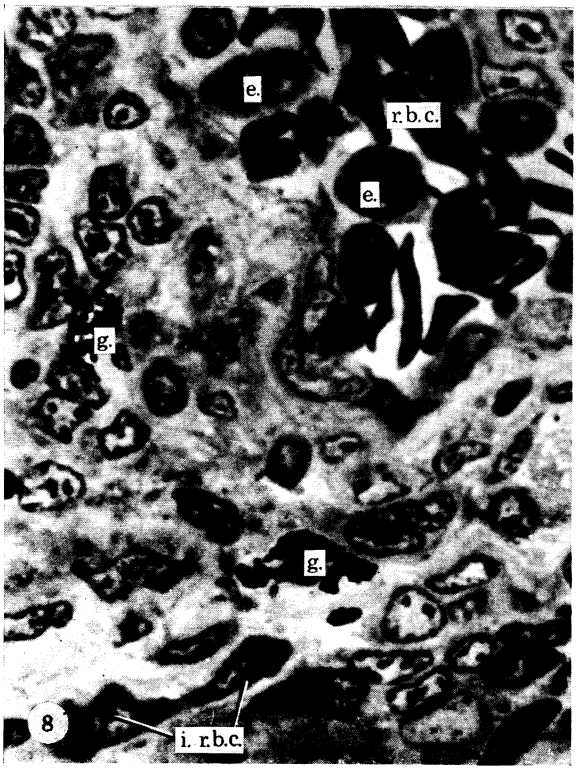

FIGURES 5–8. Thymic cortex and medulla. Azur II stained 1 μm thick sections of araldite-embedded material (all magn. × 1600).

FIGURE 5. Cortex. Adult male in postnuptial moult. Three large macrophages (m.) contain ingested pyknotic cells (p.). Some small lymphocytes present (l.) but many cells are lymphocyte-like (l.-l.). Some larger cells (*) might be transitional cells; there is one cell in mitosis (mit.).

FIGURE 6. Cortex. Adult female with enlarging thymic lobes. Immature erythrocyte (i.r.b.c.) shows a clear zone in the cytoplasm which may contain the golgi. The basophilic erythroblasts (b.) have rounded nuclei. The large cell (*) might be a blast cell. l, lymphocyte.

FIGURE 7. Medulla from the same gland. Long cilia (c.) project into the lumen of the ciliated cyst (cy.). Several mucous cells (m.-c.) can be seen; the apical region of one borders the cyst.

FIGURE 8. Medulla from the same gland. A blood vessel containing mature erythrocytes (r.b.c.) and several eosinophils (e.) in one of the connective tissue septa of the lobes. Immature erythrocytes (i.r.b.c.) with rounded, leptochromatic nuclei can be seen at the bottom of the figure, and above are two granulocytes (probably neutrophils) (g.).

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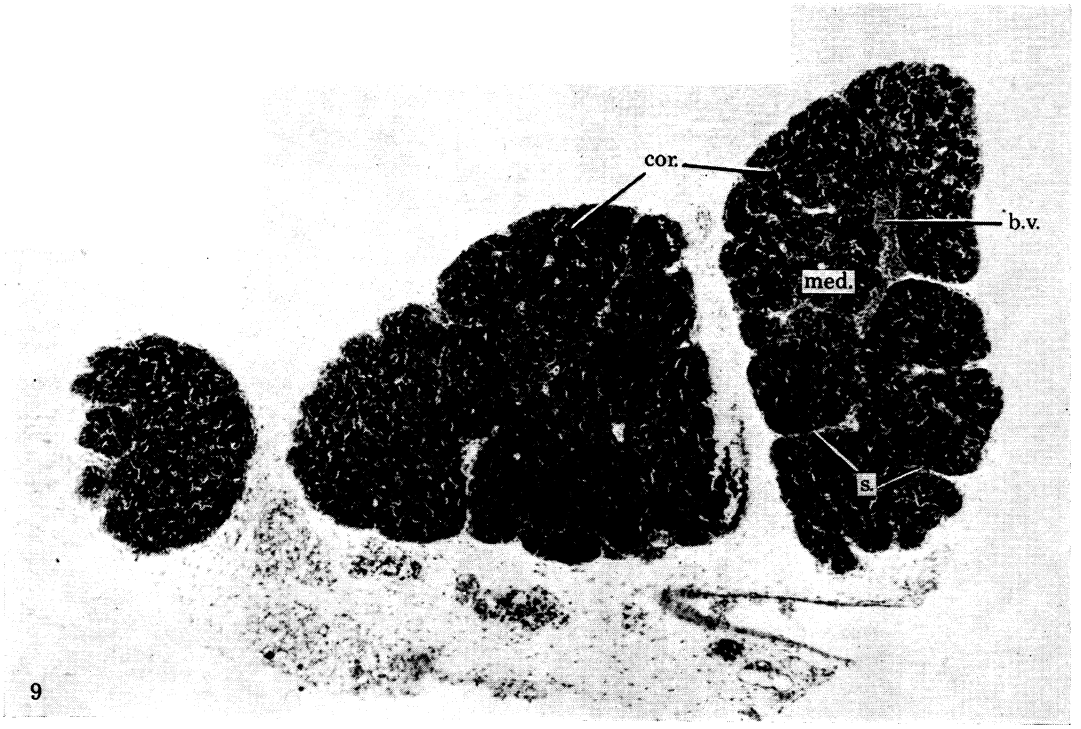

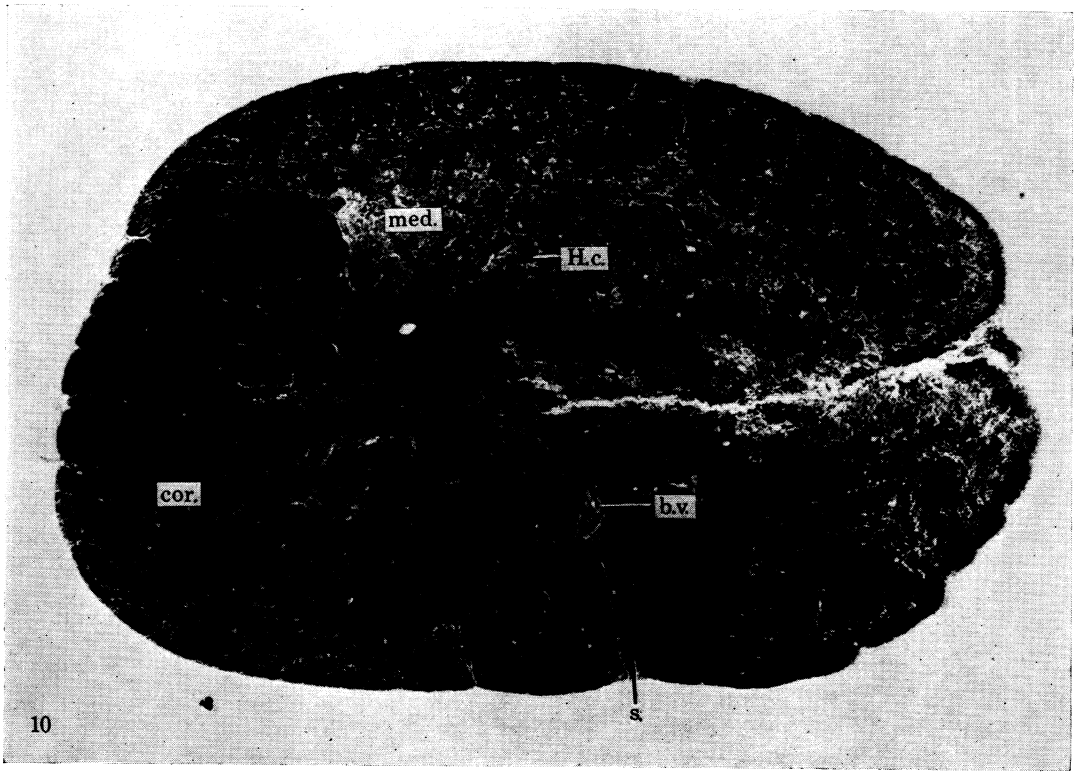

FIGURE 9. Part of three small, enlarging thymic lobes from an embryo just about to hatch. Blood vessels (b.v.) run in septa (s.) which divide the lobes into lobules. There is a small region of medulla (med.) but most of the lobes are composed of cortex (cor.). Masson stained 8 μm thick section (magn. × 48).

FIGURE 10. A fully enlarged thymic lobe from an adult in postnuptial moult. The densely populated cortex (cor.) surrounds a medulla (med.) which contains Hassall's corpuscles (H.c.). A blood vessel (b.v.) surrounded by connective tissue from the septum (s) is deep within the lobe. Masson stained 8 μm thick section (magn. × 48).

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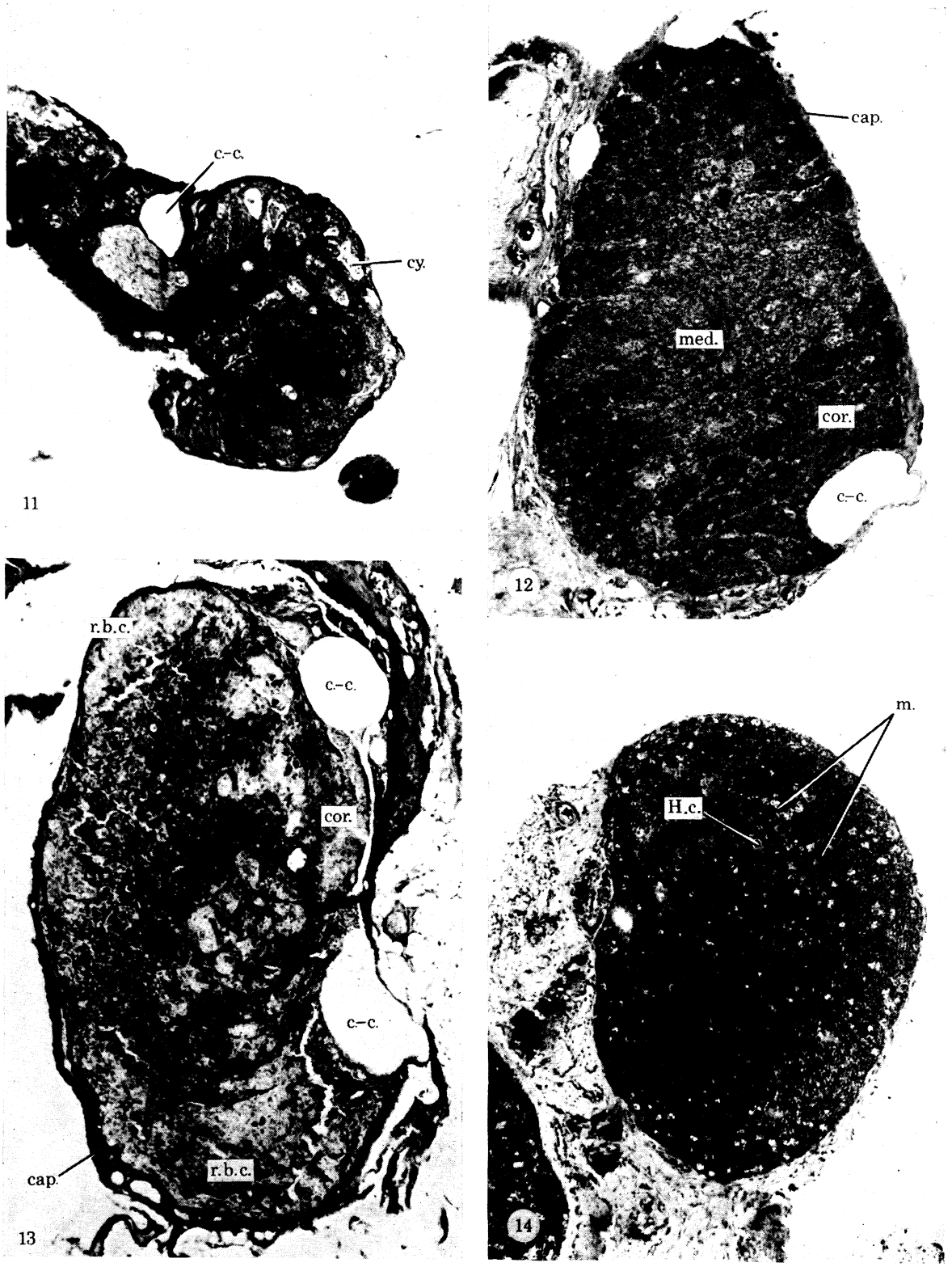

FIGURES 11–14. Thymic lobes from queleas showing different types of development. Masson stained 8 μm thick sections (all magn. × 160).

FIGURE 11. Fully regressed gland from an adult female in postnuptial moult. There is no clearly separated cortex and medulla; large cysts (cy.) and Hassall's corpuscles occur throughout the lobe. A clear channel (c.-c.) can be seen on the left.

FIGURE 12. Enlarging lobe from an adult female in postnuptial moult. A clearly defined cortex (cor.) and medulla (med.) are present. The three large clear channels (c.-c.) are all within the capsule (cap.) of the gland.

FIGURE 13. Thymic lobe from a first-year female in prenuptial moult. Most of the cortex (cor.) is filled with erythrocytes (r.b.c.) which impart a pale colour to this section. The presence of the erythrocytes also makes section cutting difficult and some splitting has occurred. Around the periphery are two clear channels (c.-c.), again within the capsule (cap.).

FIGURE 14. A regressing lobe from an adult female at the end of the postnuptial moult. There are a large number of macrophages (m.) present and some Hassall's corpuscles (H.c.).

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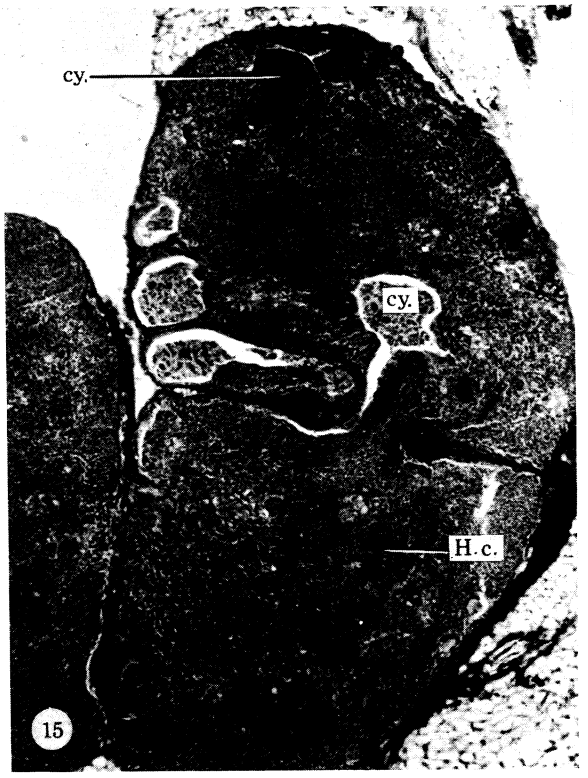

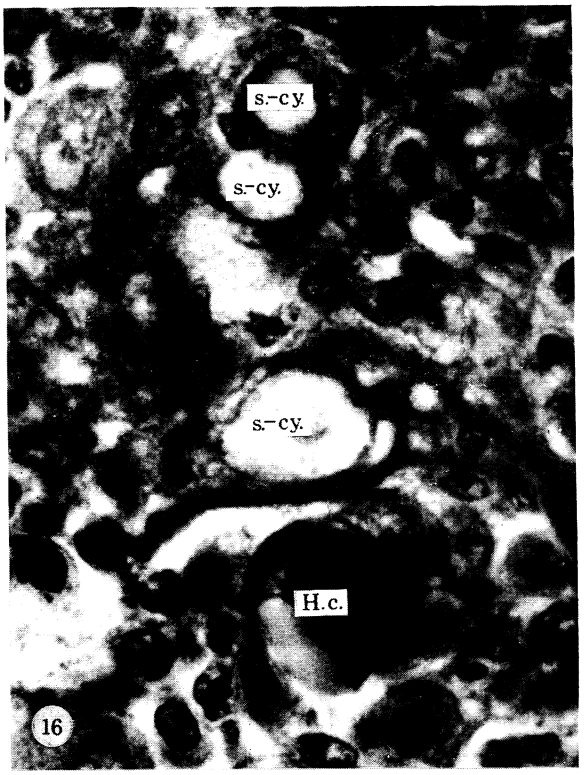

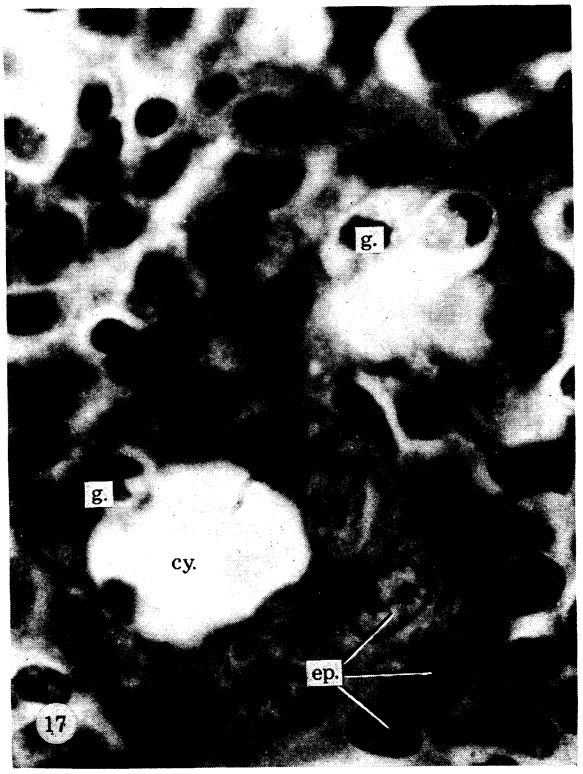

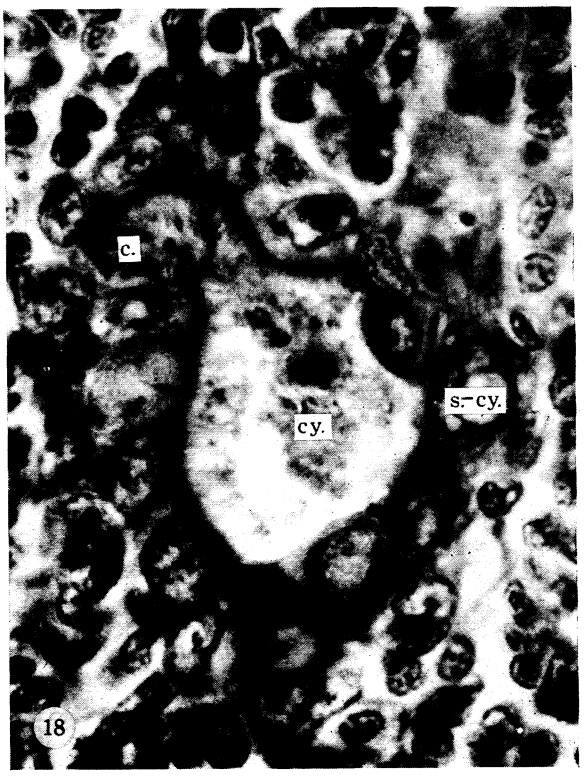

FIGURE 15. Regressing lobe from an adult female in prenuptial moult. Several very large cysts (cy.) contain cell debris. Large late Hassall's corpuscles are also present (H.c.). Masson stained 8 μm thick sections (magn. × 100).

FIGURE 16. Medulla of an enlarged lobe from an adult female in a breeding colony with chicks. Some small cysts (s.-cy.) are intracellular and some intercellular. An early Hassall's corpuscle (H.c.), cut tangentially, shows the cells which surround the outside (magn. × 1600).

FIGURE 17. Cysts in the medulla of an enlarging lobe from a male chick. The granulocytes (g.) appear to be in small compartments around the cysts (cy.). The distinctive nuclei of the epithelial reticular cells (ep.) are clearly shown (magn. × 1600).

FIGURE 18. A ciliated (c.) cyst (cy.) in the medulla of an enlarging lobe from an adult male in a breeding colony with chicks. Nearby is a cell with an intracellular cyst (s.-cy.) (magn. × 1600).

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TABLE 2. A SUMMARY OF THE HISTOLOGICAL OBSERVATIONS ON THE THYMIC LOBES OF ADULTS AND JUVENILES OF *QUELEA QUELEA*

(+, present; ++, common; +++, abundant, and −, absent for each feature under consideration. The lobes are classified as v.s., very small; s.e., slightly enlarged; m.e., moderately enlarged; e., enlarged; v.e., very enlarged. Details of these groups are found in the text.)

	young				adults											
	s.e.	m.e.	e.	v.e.	v.s.	s.e.	m.e.	e.	e.	m.e.	s.e.	s.e.	v.s.	v.s.		
	enlarging				enlarging				regressing			effete		re-gressed		
cortex	+	+	+	+		+	+	+	+	+	+	+				
mitosis	+	+	+	+		+	+	+	+	−	−	−	−	−		
pyknotic cells	+	+	+	+	+	+	+	+		+		+	+			
immature r.b.cs			+	+		+	+	+	+			+	+			
mature r.b.cs			+	+		+	+	+	+			+				
granulocytes			+	+		+		+	+	+		+	+			
blood vessels full			+	+				+	+	+						
early Hassall's corp.	+	+	+	+												
late Hassall's corp.			+	+			+	+	+	+		+	+			
small cysts	+	+	+	+			+									
large cysts				+				+	+	+				+		
active macrophages		+	+	+		+				+	+	+	+			
fibroblasts					+						+			+		

in some lobes there were late Hassall's corpuscles. The cortex in some lobes was, at least in some regions, filled with mature erythrocytes to the almost complete exclusion of other cell types. Strands of reticular cells could be seen between erythrocytes, and blood vessels packed with erythrocytes ramified both cortex and medulla. Pyknotic cells, lymphocyte-like cells and immature erythrocytes were common in some regions, mainly in the cortex, but also in the medulla in some lobes. Lobes with many pyknotic cells often contained large macrophages that had pyknotic cells and erythrocytes within the cytoplasmic inclusions.

Fully regressed lobes were found in adults at the end of the prenuptial moult, in adults in colonies when the young were independent and in certain individuals whilst in postnuptial moult. Late Hassall's corpuscles were conspicuous in the medulla of the lobes but the cortex in many glands was composed of fibroblasts and some glands contained regions where fibroblasts were the predominant cell type.

Slightly enlarged lobes

Twenty-five lobes were examined. Lobes taken from adult birds were all slightly larger (1–2 mm long) but otherwise similar to the very small lobes described previously.

Developing glands in embryos were taken from eggs about to hatch. Each lobe was clearly lobulated and each lobule contained a small central medulla surrounded by a cortex of mainly small lymphocytes (figure 9). Cell densities were higher under the capsule (Kendall, in press) where there were many cells in mitosis. Early Hassall's corpuscles were present in the medulla. The constituent cells contained small, clear intracellular vesicles (3–4 μm diameter).

Moderately enlarged lobes

Thirty lobes were examined. Lobes of this size were found in some adults at all times of the year but they were particularly numerous in adults in breeding colonies after eggs had been laid. Macroscopically the lobes were pinkish in colour and measured 2–3 mm long. Histologically two types of lobes were recognized: enlarging and regressing lobes. Enlarging lobes (figure 12) were those with cortical cells in mitosis and numerous immature erythrocytes. Mitosis of medullary cells was found in both types of lobe.

Enlarged lobes

Thirty-one lobes were examined. These lobes (4–5 mm long) were found in nestlings growing the juvenile plumage; in young in postjuvenile moult (very small percentage only); they were prevalent in adults in breeding colonies after egg laying and in adults during postnuptial moult.

Enlarged lobes in nestling chicks were lobulated although the lobules were partially obscured by the cortical tissue which was greater in extent than in the smaller lobes of chicks. All the lobes examined contained cells in mitosis, and the cortex of most contained low numbers of pyknotic cells, immature erythrocytes and mature erythrocytes amongst large numbers of small lymphocytes and lymphocyte-like cells. Blood vessels within the lobes were full of erythrocytes. In addition to these vessels there were other vessels with round patent lumens which ramified through the lobes. The lumens were up to 30 μm in diameter and lined with squamous epithelium possibly surrounded by a thin loose connective tissue. Continuity of these vessels with the outside of the gland was difficult to prove despite searching many serial sections. No cells were ever found within the lumen of the vessels.

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In lobes taken from adult birds, the distinction between enlarging and regressing lobes was not great as many of the lobes exhibited different appearances in different parts. In general the cortex was conspicuous and contained large numbers of lymphocyte-like cells, pyknotic cells, immature erythrocytes and mature erythrocytes, the proportions of each cell type varying considerably from region to region within a lobe and from lobe to lobe within one bird. In all lobes some arteries and all veins were full of erythrocytes, mature or immature, all closely packed together. It appeared as though the erythrocytes might be developing within the vessels as well as within the lobes. The medulla in some glands also appeared to be erythropoietic and contained late Hassall's corpuscles.

Thymic lobes taken from females which had just laid eggs were of a particularly striking appearance. Macroscopically the lobes were bright red in colour and served by prominent thymic blood vessels. Sections of these lobes indicated that the medulla of the lobes was normal but that the cortex was largely filled with immature and mature erythrocytes (similar to the lobe shown in figure 13). At low powers, the erythrocytes appeared to be within very large vessels but on detailed examination the walls of the vessels were found to be connective tissue septa which normally ramified through the cortex and medulla. Small vessels (up to 35 μm diameter) within the gland and veins on the periphery were filled with blood. In the cortex, the erythrocytes were closely packed together (figures 2, 3 and 4) to the almost complete exclusion of any other cell types. When other cells were found they were difficult to identify. All were larger than small lymphocytes, some might have been epithelial reticular cells, some granulocytes and others plasma cells. Within a given region of a lobe most of the erythrocytes were at a similar stage of development. Thus the entire cortex of these lobes appeared to be erythropoietic.

Many of these lobes contained large vessels similar to those described as present in thymic lobes of chicks. These vessels, however, were connected to the outside of the lobes as they could be seen in the connective tissue of the sheath where they branched and spread around the lobes. The larger vessels (lumens up to 100 μm diameter) were always distended, and no cells were ever observed within them. It is suggested that they might be fine ramifications of the extensive air-sac system of the bird (figures 11–13).

Very enlarged lobes

Twenty lobes were examined. These very large lobes were only found in juveniles and a few adults in breeding colonies.

Samples were taken from chicks 5–7 days and 17–19 days after hatching. Although the same size, the lobes of younger chicks were different from those of older chicks. Lobes from chicks 5–7 days old were similar to the enlarged lobes just described, except that the Hassall's corpuscles of the medulla were larger with a pronounced central region, and some lobes contained large ciliated cysts full of cells and cell debris.

Very enlarged lobes from chicks 17–19 days old also had a medulla with late Hassall's corpuscles but the cortex lacked the compact cellular appearance typical of lobes from younger chicks. The cortex consisted of low numbers of small and medium lymphocytes with some immature erythrocytes, a few mature erythrocytes, many pyknotic cells and large prominent macrophages. The macrophages contained many phagocytosed particles amongst which could be recognized pyknotic cells and erythrocytes. Macrophage numbers in the cortex and medulla had not increased very much, but each cell was very large and imparted

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a pale colour to the stained sections of the lobe. Many of the lobes examined also contained large lakes of material which might have been haemoglobin, but did not stain very well for it. Not all of the lobes in one bird were similar, some were more like the lobes of younger chicks and others closely resembled regressed glands with many fibroblasts in the cortex.

The very enlarged lobes from breeding birds in colonies were lobulated and similar to the very enlarged lobes from 5–7 day old chicks except that there were more cells in mitosis and the lobes had many immature and mature erythrocytes in the cortex. It is possible that these were from breeding first-year adults.

Discussion

Although it was not possible to follow the thymus size changes and associated histological developments in any one bird, we were able to sample from a very large population and to correlate the histology of the lobes with the physiological state of the individuals in the samples. Macroscopically the thymus lobes in adults change in size during most breeding sessions and during some moults (Ward & Kendall 1975). We have therefore in this study regarded the thymic lobes as being capable of enlargement and regression. Furthermore at two stages in the life cycle of the birds we were able to sample the same population on subsequent dates: when the eggs hatched and the young were confined to the nest; and when the adults were closely associated with the highly synchronized colonies. We can thus suggest a cycle of events (figure 19) which accounts for the observations reported here.

Examination of thymic lobes from embryos and young chicks showed that the individual lobes were small before hatching and rapidly increased to maximum size over the next few weeks prior to the attainment of sexual maturity. This is consistent with the known situation for birds (Romanoff 1960) and for mammals (Romer 1966). The lobes were differentiated into cortex and medulla prior to the birds hatching and there was a growth of both regions with the overall increase in size.

The major cellular component was the small lymphocyte which was more dense in the cortex than in the medulla, and the presence of pyknotic cells and some erythrocytes is in agreement with most workers. Hassall's corpuscles consisted of only a few epithelial cells in the thymic lobes of embryos but they were large and prominent in the enlarged lobes of juveniles. Very enlarged lobes of juveniles contained some erythrocytes free in the stroma of the gland, but not in such large numbers as are seen in adult thymic lobes. The cortex contained many lymphocytes, lymphocyte-like, erythroid cells and erythrocytes together with pyknotic cells. The blood vessels in and around the lobes were packed full of both immature and mature erythrocytes. At this stage of the bird's development (up to 19 days after hatching) the immature erythrocytes in the lobes could have come from circulating immature erythrocytes in the blood. However, particularly after this when immature forms of erythrocytes were found in the cortex of the thymic lobes, many of the surrounding cells were no longer typical small lymphocytes but were lymphocyte-like or possibly early erythroid cells. Terni (1924) suggested that the avian thymus is erythropoietic at this stage and from our observations in this study and the examination of the electron micrographs (Kendall & Frazier, in preparation) we consider that the thymus may be a site of erythropoiesis.

Signs of regression from an enlarged state were seen in the lobes of juveniles in which there was a partial invasion of the cortex by fibroblasts and clear phagocytic activity of macrophages. The macrophages contained engulfed pyknotic cells and erythrocytes.

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Completely regressed glands lacked the organization of a cortex and medulla, contained predominantly small lymphocytes, large well developed Hassall's corpuscles, were often partially invaded by fibroblasts, and contained few, if any, cells in mitosis. We suggest that small lobes in a fully regressed condition containing groups of cells in mitosis are lobes which are about to become enlarged. When mitosis was widespread in the lobes then there was usually some degree of organization of a cortex and medulla. Mitosis was greater in the subcapsular region as Sainte-Marie & Leblond (1964) found in rats. Some enlarging lobes had late Hassall's corpuscles, others had only small groups of cells which probably represented early Hassall's corpuscles. There was no sign of erythropoiesis in the lobes and the blood vessels were not particularly conspicuous.

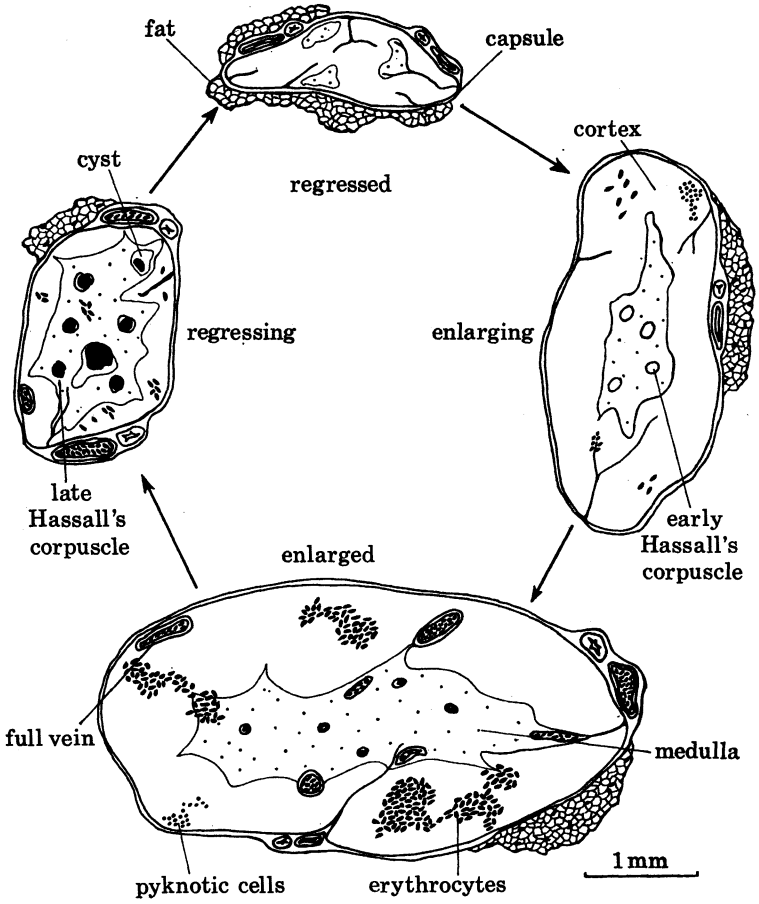

FIGURE 19. Diagram of a suggested cycle of events which accounts for the histology of the thymic lobes examined in this study.

Moderately enlarged lobes of adults and first-year birds were pinkish or red macroscopically. Internally the blood vessels were prominent and the lobes resembled those found in young chicks, except that the tissue was not lobulated. The cortex was also more variable within one lobe; some regions were composed mainly of small lymphocytes, other regions of lymphocyte-like cells and others of immature or mature erythrocytes. The medulla often showed mitosis and contained similar cells to those of the cortex. We suggest that these moderately enlarged and enlarged lobes are actively producing erythrocytes which we assume enter the general blood circulation.

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Enlargement from a fully regressed condition to an enlarged state can be very rapid. In one breeding colony none of the lobes in the adults were enlarged at the end of egg laying, but 4 days later 42% of the adults had enlarged thymic lobes and this percentage rose to 60% 3 days after this (Ward & Kendall 1975). These enlarged glands were those in which erythropoiesis was synchronized and clearly evident.

Where synchrony of development does occur, there may be a massive efflux of mature erythrocytes and a collapse of the lobe afterwards (since there are few cortical cells left). Some glands partially collapse as we have found erythrocytes apparently trapped in the glands and degenerating there. If enlargement is not so rapid or synchronized perhaps there is a steady output of erythrocytes and a relatively steady regression of the lobe to a small size again. It may then take some time for effete glands to deal with the cellular debris and to become ready for further enlargement. We suggest that the Hassall's corpuscles and ciliated cysts are involved in this as regressing glands contained many late Hassall's corpuscles in the medulla but small enlarging glands did not. Blau (1967) has suggested that the function of Hassall's corpuscles is to clear the thymus of unwanted cell types. Regression in these quelea lobes is very different from the age involution of man (Bloom & Fawcett 1968) where there is a slow infiltration of the gland with fat cells over many months or years.

Several important facts emerge from this study of the thymic lobes of *Quelea quelea*. Mitotic figures were not a constant feature of all lobes examined. Erythroid cells, present in enlarging and enlarged lobes as free cells (not contained in blood vessels), were normally present in small numbers and in some individuals they formed the major cell type of the cortex. Both immature (myelocytes) and mature granulocytes were observed in enlarging and enlarged lobes. Pyknotic cells were a constant feature of many enlarging and enlarged lobes although they were almost entirely absent from lobes that contained predominantly erythroid cells in the cortex. These facts will now be discussed in relation to the current concepts concerning the thymus.

The rate of mitosis in the thymus gland is known to be greater than in other lymphoid organs (Miller & Osoba 1967). In foetal mice the mitotic index amongst thymic cells is high, falls immediately after birth and remains relatively high for over one year (Metcalf 1962) but the examination of serial sections in this study indicates that there are some lobes which have very high mitosis rates and others in which mitotic figures are rare (quantitative studies on mitosis rates are being considered elsewhere – Kendall, in press). These observations are consistent with the thesis of thymus enlargement and regression, but inconsistent with the concept of the adult thymus having a steady but decreasing mitosis rate during a gradual involution with age (Andreasen & Christensen 1949).

Enlarging glands with high mitosis rates in the cortex had few erythroid cells or pyknotic cells. Enlarging and enlarged lobes with few mitotic figures almost always had some erythroid cells in the cortex, and in the case of adults in breeding colonies the numbers were high. Erythroid cells are not normally considered to be typical of thymic tissue although Albert, Wolf & Pryjma (1965) and Albert, Wolf, Pryjma & Vasquez (1965) present evidence for erythropoiesis in the mouse thymus, and Terni (1924) considered that the avian thymus was erythropoietic in embryos. The presence of early erythroid cells and immature erythrocytes suggest to us that these cells are developing *in situ*. Which cells are the precursors of these erythroid cells and their origin is beyond the scope of this study of wild material, but the presence of myelocytes and granulocytes which have a myeloblast as the primitive stem cell

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(Pease 1956) suggests that the stem cells could be myeloid in origin. Abe, Sasaki & Ito (1973) showed that the cortical small lymphocytes of mice are morphologically similar to the majority of lymphocytes in the bone marrow and liver, and Ford *et al.* (1966) and Micklem, Ford, Evans & Gray (1966) showed that the stem cells of thymic lymphocytes are derived from myeloid origins. The thymic lobes of *Quelea quelea*, at times when mitotic figures were prevalent in the cortex, contained predominantly small lymphocytes or lymphocyte-like cells. Larger cells which may have been transitional cells were also found. Following mitosis many cells were erythroid. Thus the possibility that the small lymphocyte is either a stem cell or is on the line of cells which ultimately culminate in the erythrocyte needs to be fully investigated.

Pyknotic cells are usually regarded as dying cells. Metcalf (1964), found a close correlation between the number of pyknotic cells and the thymus mass changes, and suggested that most of these cells were dying from natural causes. Miller & Osoba (1967) suggest that lymphocytes disintegrate rather than become pyknotic. In this study pyknotic cells were recorded in the lobes whenever erythroid cells were also present (small lobes had few if any pyknotic or erythroid cells). The stains employed suggest that the pyknotic cells may arise shortly after mitosis and that most stain as erythroid cells. Since the cortex of some lobes contained mainly erythroid cells and few pyknotic cells, and other lobes many pyknotic cells and few erythroid cells, it is possible that, following mitosis, the resultant cells may differentiate towards erythrocytes or become pyknotic. Thus the numbers of pyknotic cells within the gland may reflect the action of a control mechanism concerning the ultimate numbers of erythrocytes.

It is difficult to estimate how many erythrocytes could be produced by one thymic lobe, and even more difficult to estimate the contribution from all the thymic lobes in one bird. In growing young most of the lobes in one bird were of a similar size, but in adults the variation in one bird was great. Furthermore, if the erythrocytes produced are destined to enter the blood stream then the numbers seen in the lobes give no indication of the rate of formation of erythrocytes. Nor is it known for how long the lobes remain enlarged or producing erythrocytes. An analysis of 27 lobes from adults in breeding colonies showed that for 4–5 weeks all but 3 (2 very small and 1 enlarging lobe) had erythrocytes present in the lobe (Kendall, in press). The erythrocyte contribution to the blood could be very large.

In queleas enlargement of the thymic lobes occurred in young, in adults during breeding sessions, and during moult (Ward & Kendall 1975). In young, enlargement occurred during periods of rapid growth (young attain adult masses and dimensions by 3 weeks of age). In adults in breeding colonies the enlargement coincided with a period of rapid recovery of protein and fat which was lost from the bird during nest building, mating and egg laying. During moult, growth of feathers is underway. All of these processes no doubt require a good complement of erythrocytes in the bird.

We would like to thank all the staff at the Centre for Overseas Pest Research and St Thomas's Hospital Medical School for help in the preparation of this paper. Particular thanks are due to Dr P. Ward who made the study possible, and also to Mr W. W. Page and Mr G. G. Pope for technical assistance.

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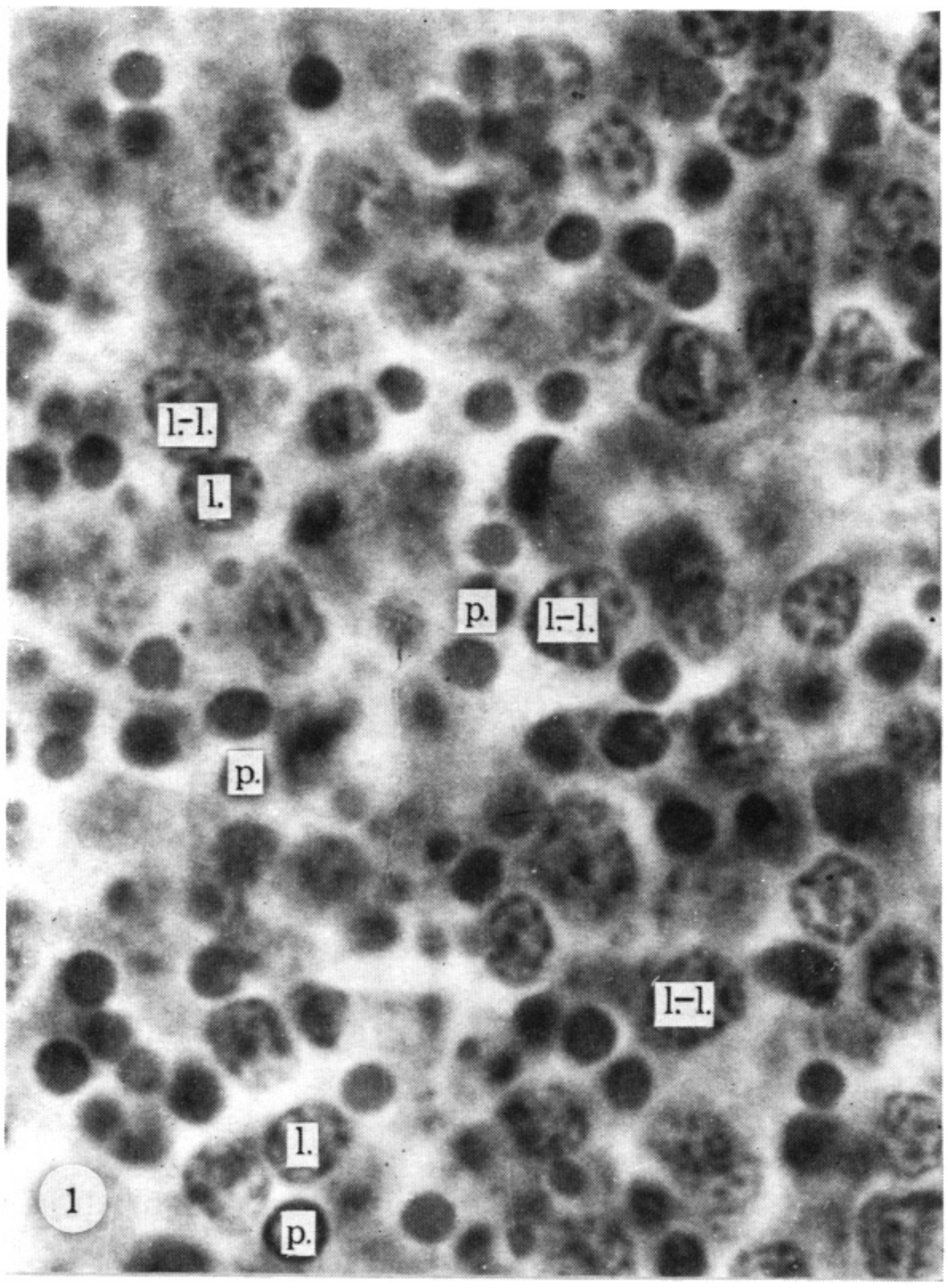
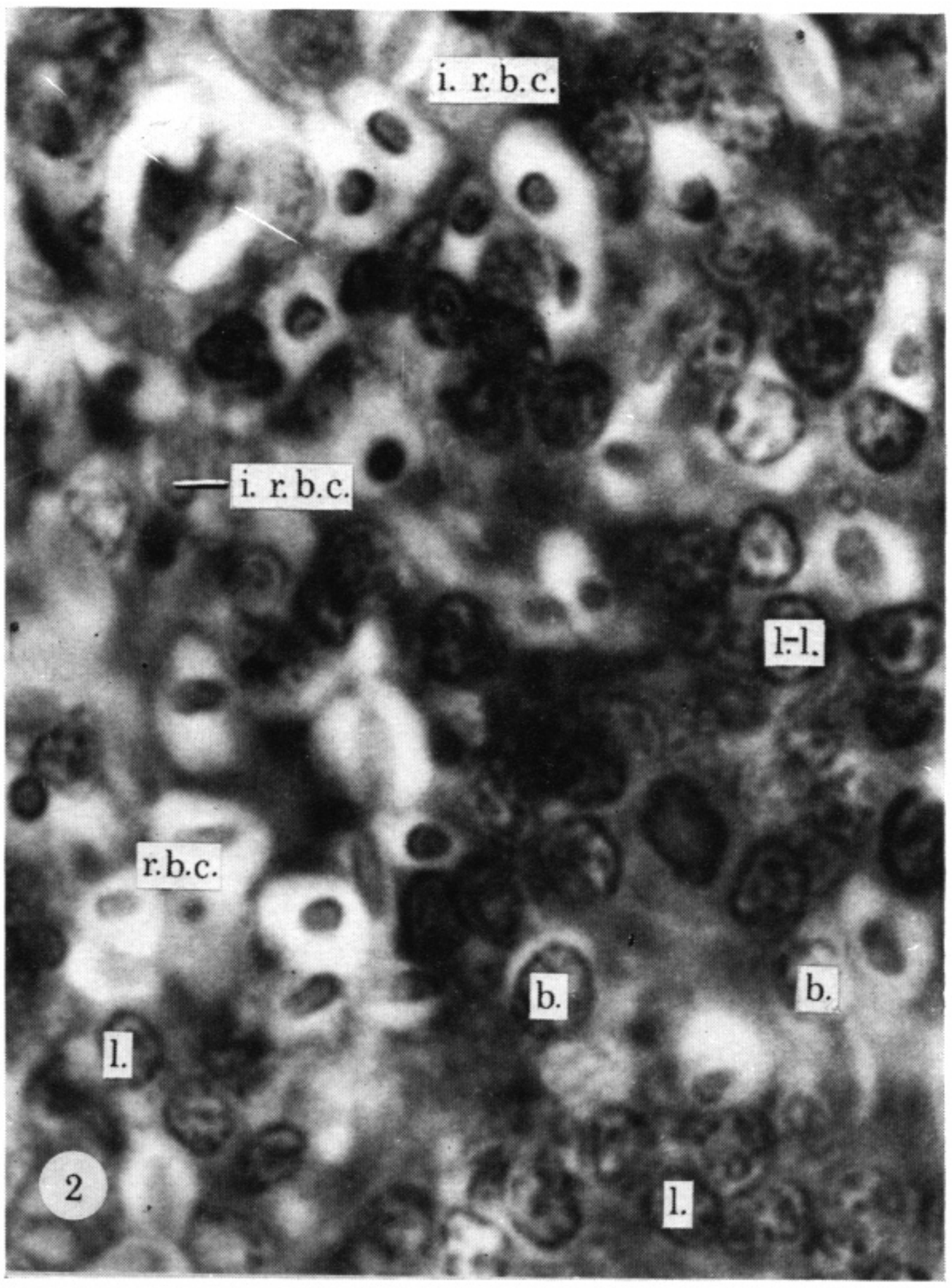
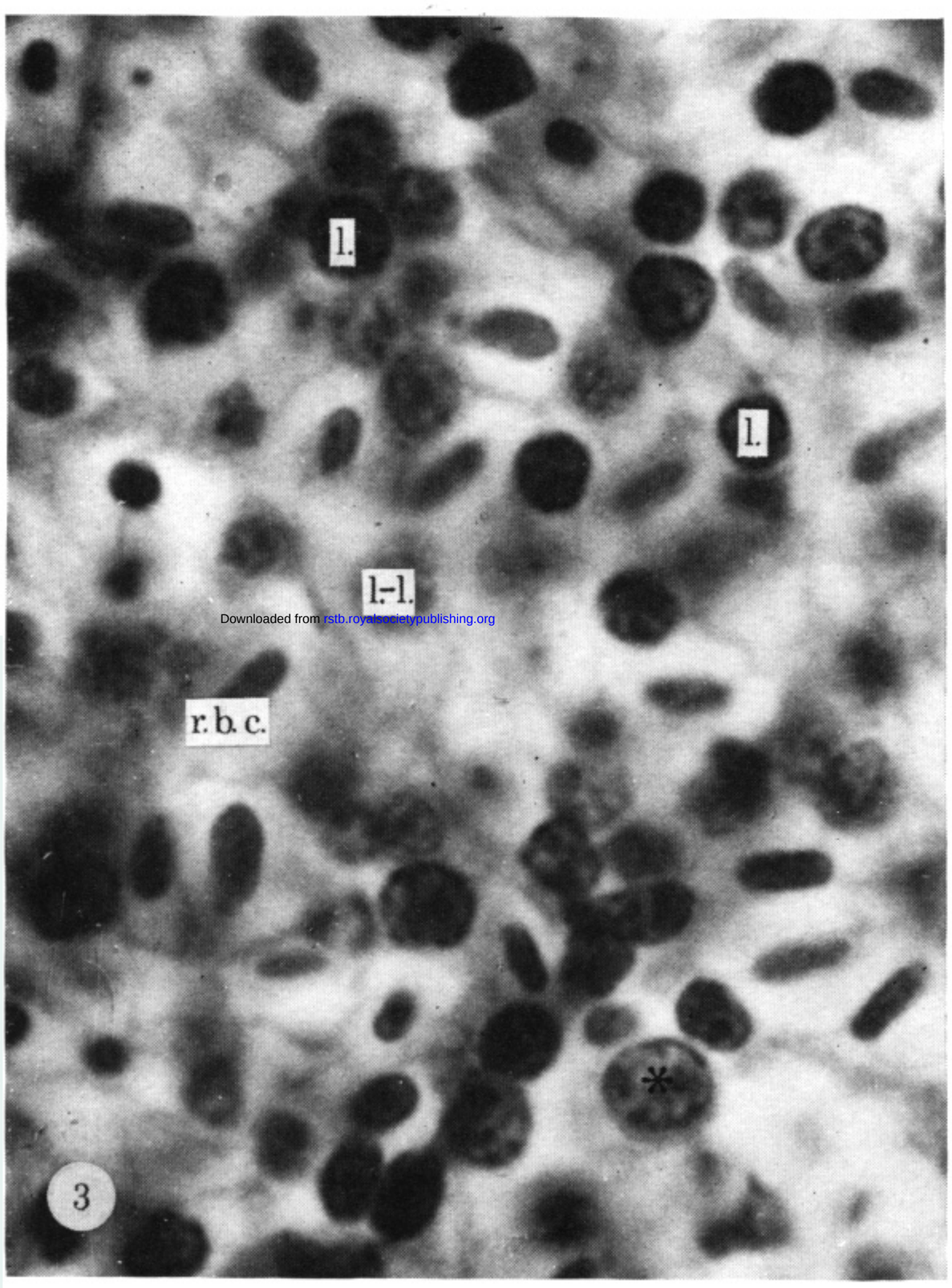
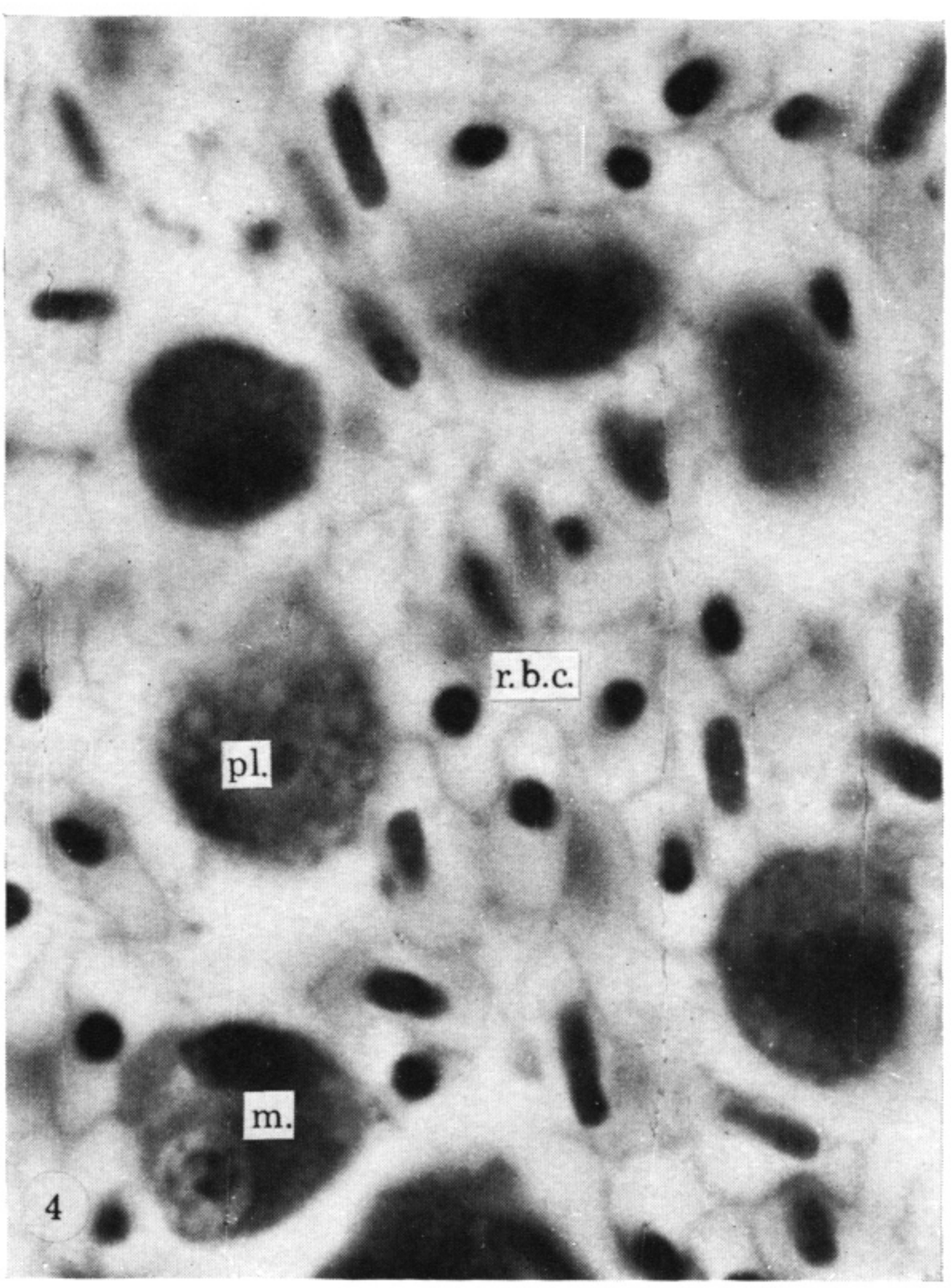








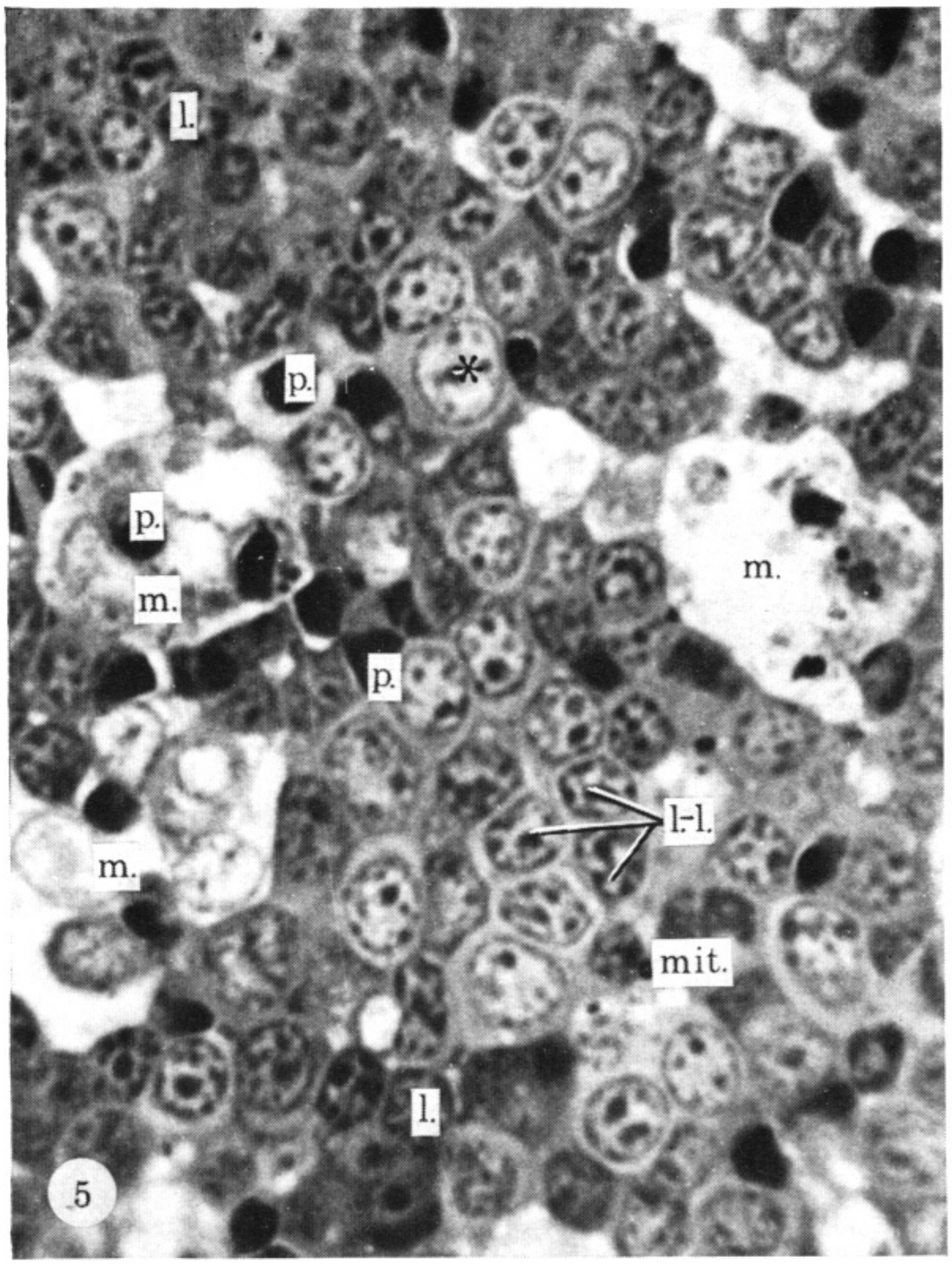
FIGURES 1–4. Thymic cortex of queleas. Masson stained 8 μm thick sections (all × 1600).

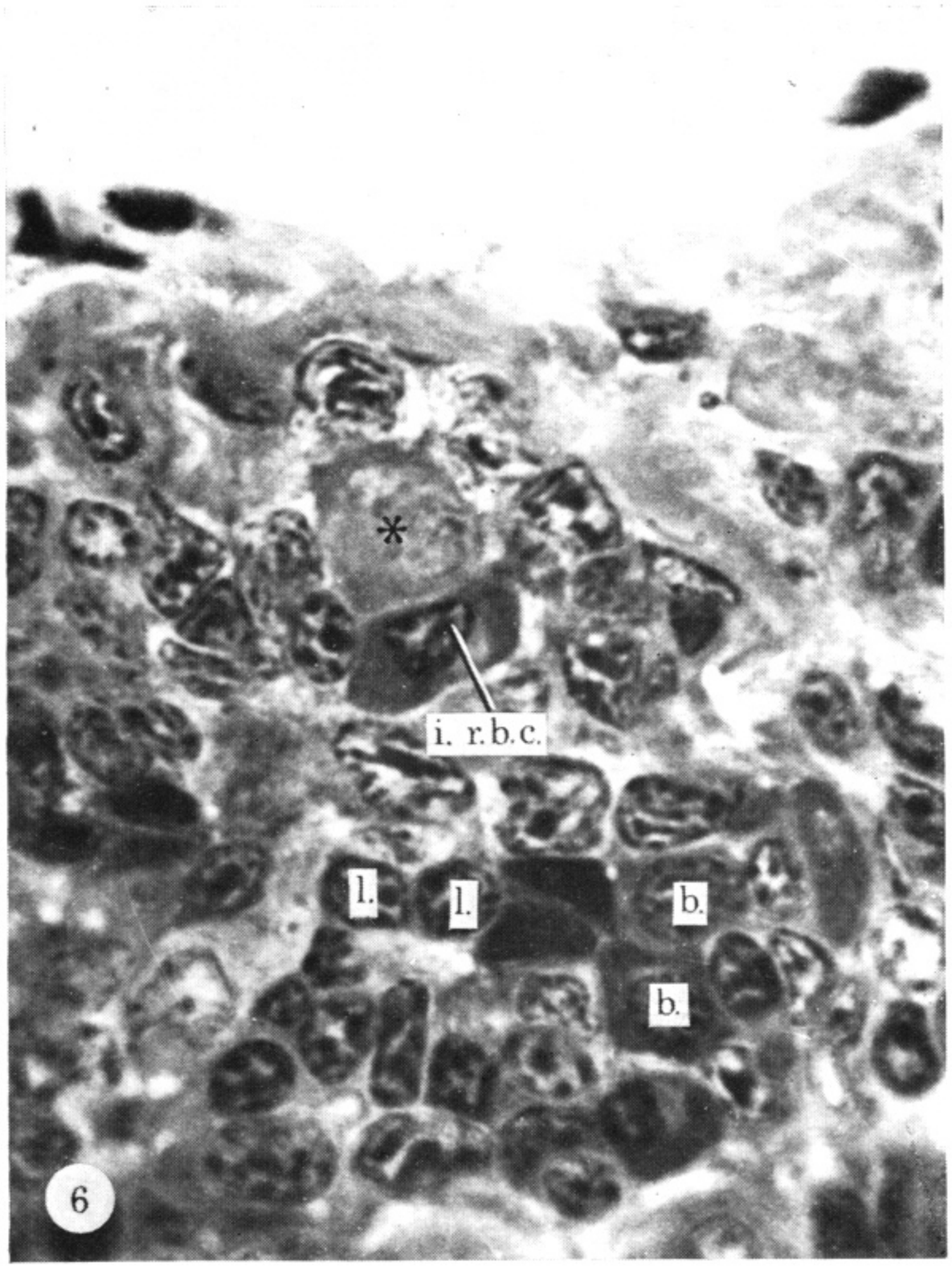
FIGURE 1. Six day old chick. Most of the cells are lymphocytes (l.), lymphocyte-like (l.-l.) or pyknotic (p.). Several pyknotic cells have small unstained spheres attached.

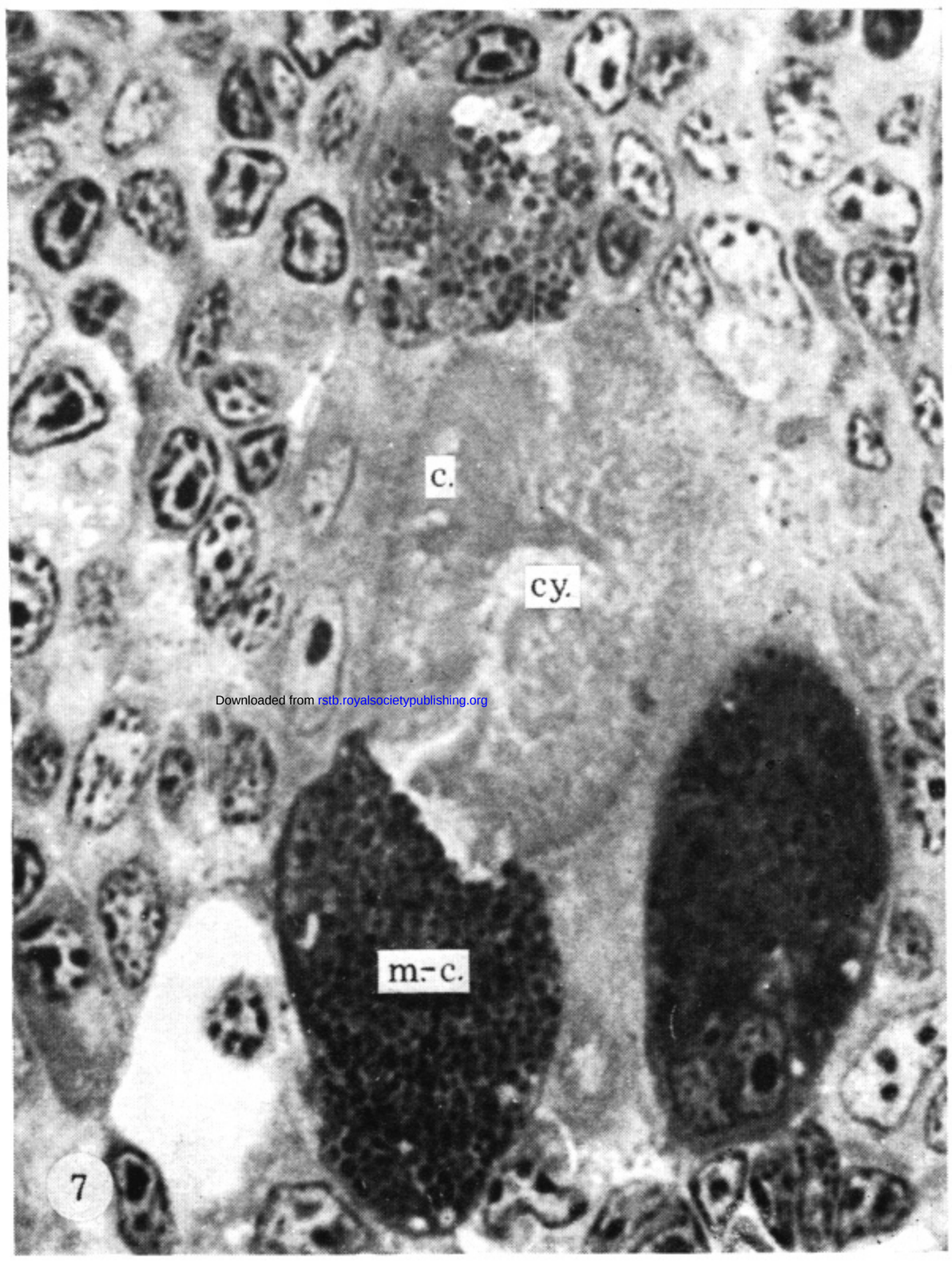
FIGURE 2. Adult female from breeding colony with eggs. The thymic lobe was enlarged and appeared red in colour. Lymphocytes (l.), lymphocyte-like cells (l.-l.), fairly mature erythrocytes (r.b.c.), immature erythrocytes (i.r.b.c.) and basophilic erythroblasts (*b*) are present.

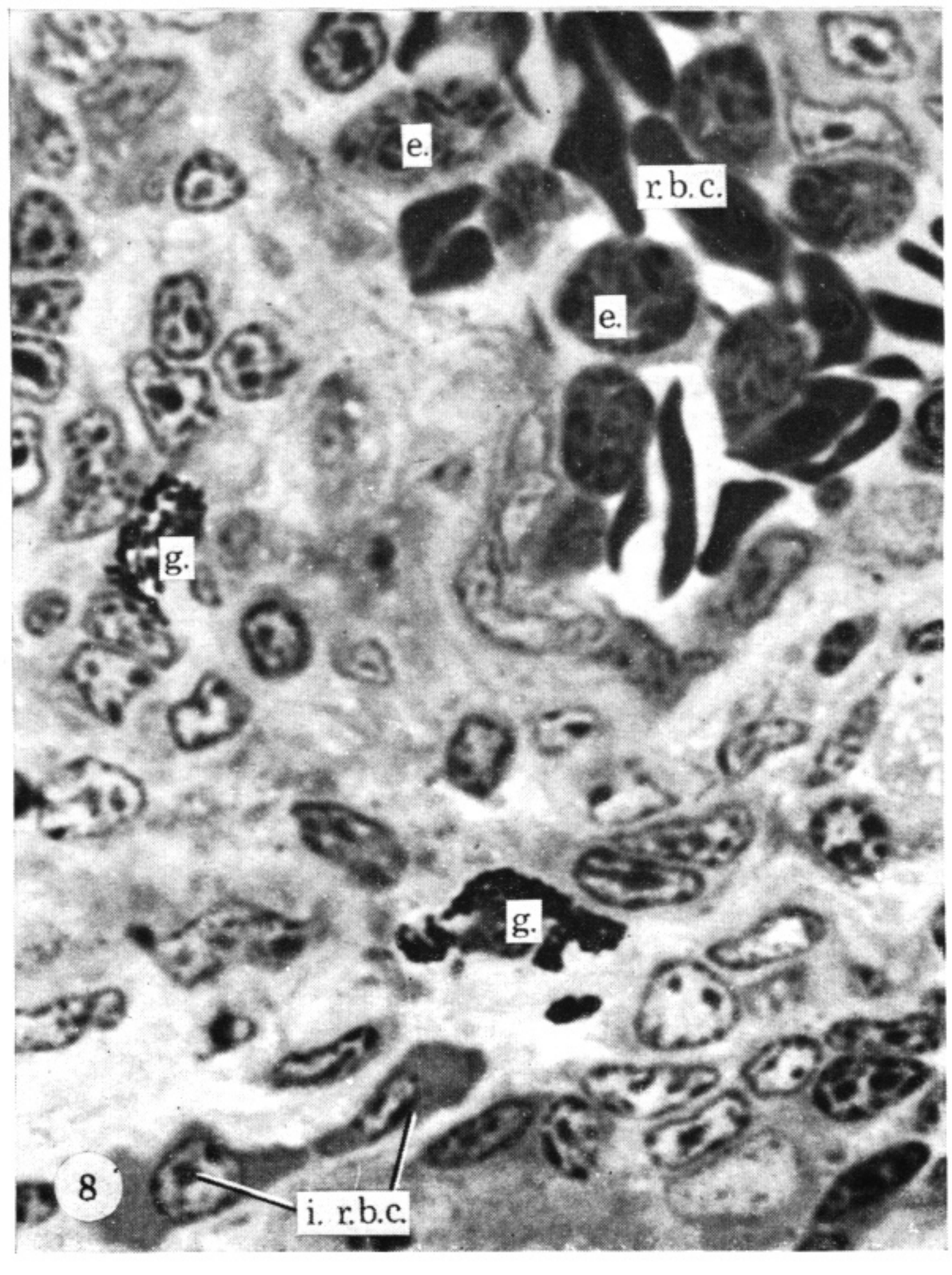
FIGURE 3. Adult female captured from a feeding flock, caged overnight during which time she laid an egg, and killed next morning. Most of the cortex consists of erythrocytes (r.b.c.) with some lymphocytes (l.) and lymphocyte-like cells (l.-l.) and one larger cell (*) which might be a transitional cell.

FIGURE 4. Adult female from breeding colony with young chicks. The cortex is almost entirely composed of erythrocytes (r.b.c.). The other cells are difficult to identify but may be plasma cells (pl.) or macrophages (m.).









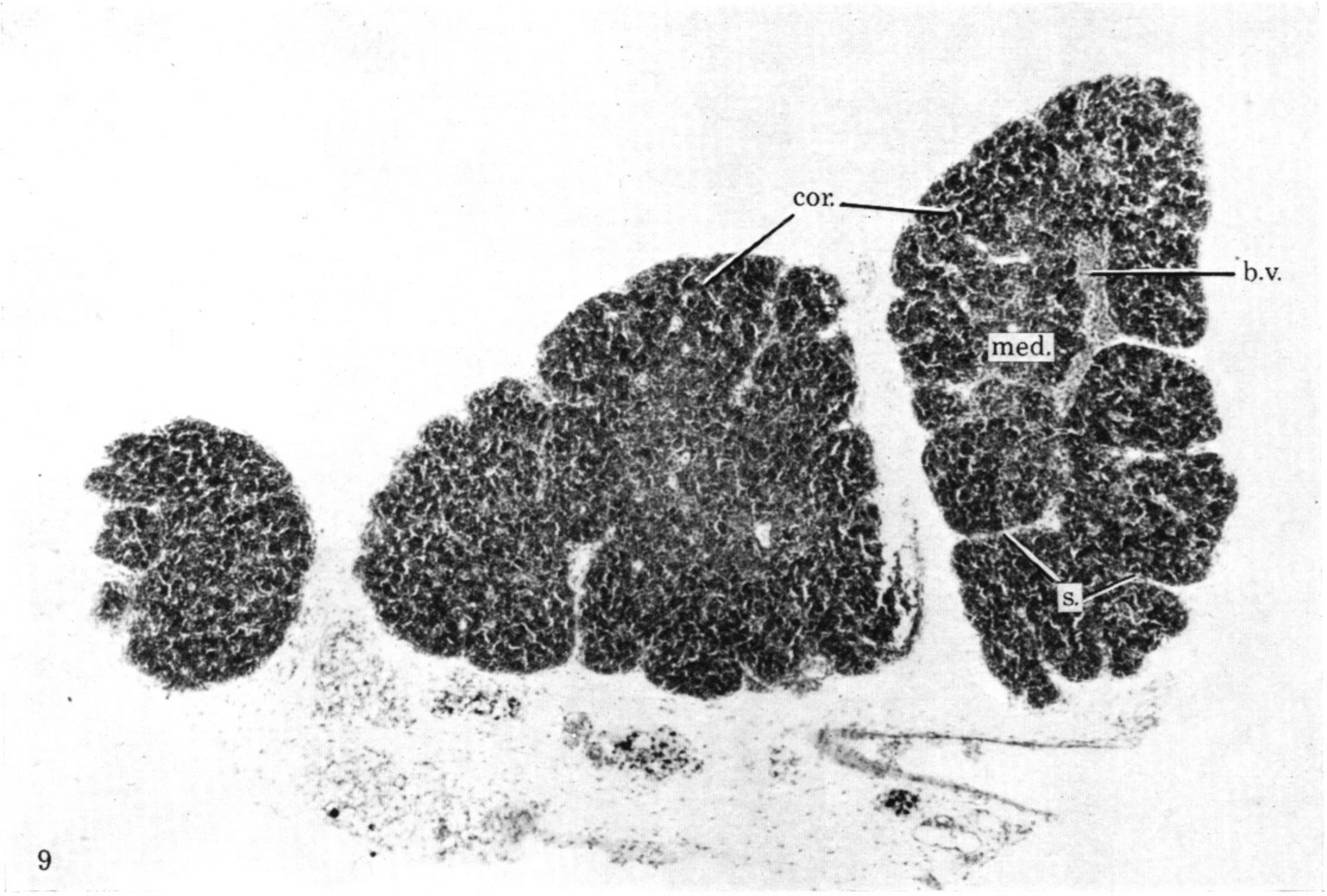
FIGURES 5–8. Thymic cortex and medulla. Azur II stained 1 μm thick sections of araldite-embedded material (all magn. × 1600).

FIGURE 5. Cortex. Adult male in postnuptial moult. Three large macrophages (m.) contain ingested pyknotic cells (p.). Some small lymphocytes present (l.) but many cells are lymphocyte-like (l.-l.). Some larger cells (*) might be transitional cells; there is one cell in mitosis (mit.).

FIGURE 6. Cortex. Adult female with enlarging thymic lobes. Immature erythrocyte (i.r.b.c.) shows a clear zone in the cytoplasm which may contain the golgi. The basophilic erythroblasts (b.) have rounded nuclei. The large cell (*) might be a blast cell. l, lymphocyte.

FIGURE 7. Medulla from the same gland. Long cilia (c.) project into the lumen of the ciliated cyst (cy.). Several mucous cells (m.-c.) can be seen; the apical region of one borders the cyst.

FIGURE 8. Medulla from the same gland. A blood vessel containing mature erythrocytes (r.b.c.) and several eosinophils (e.) in one of the connective tissue septa of the lobes. Immature erythrocytes (i.r.b.c.) with rounded, leptochromatic nuclei can be seen at the bottom of the figure, and above are two granulocytes (probably neutrophils) (g.).



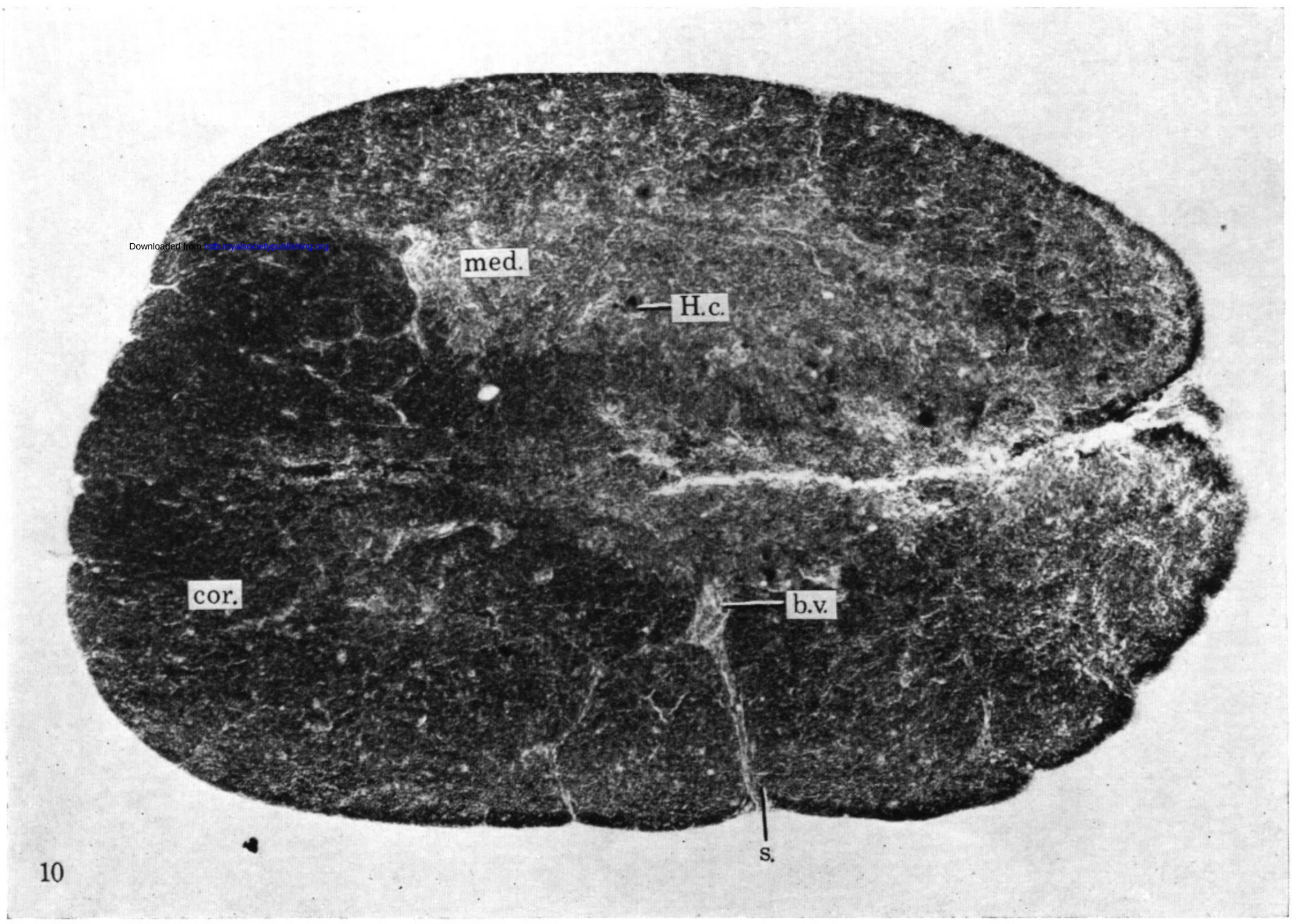
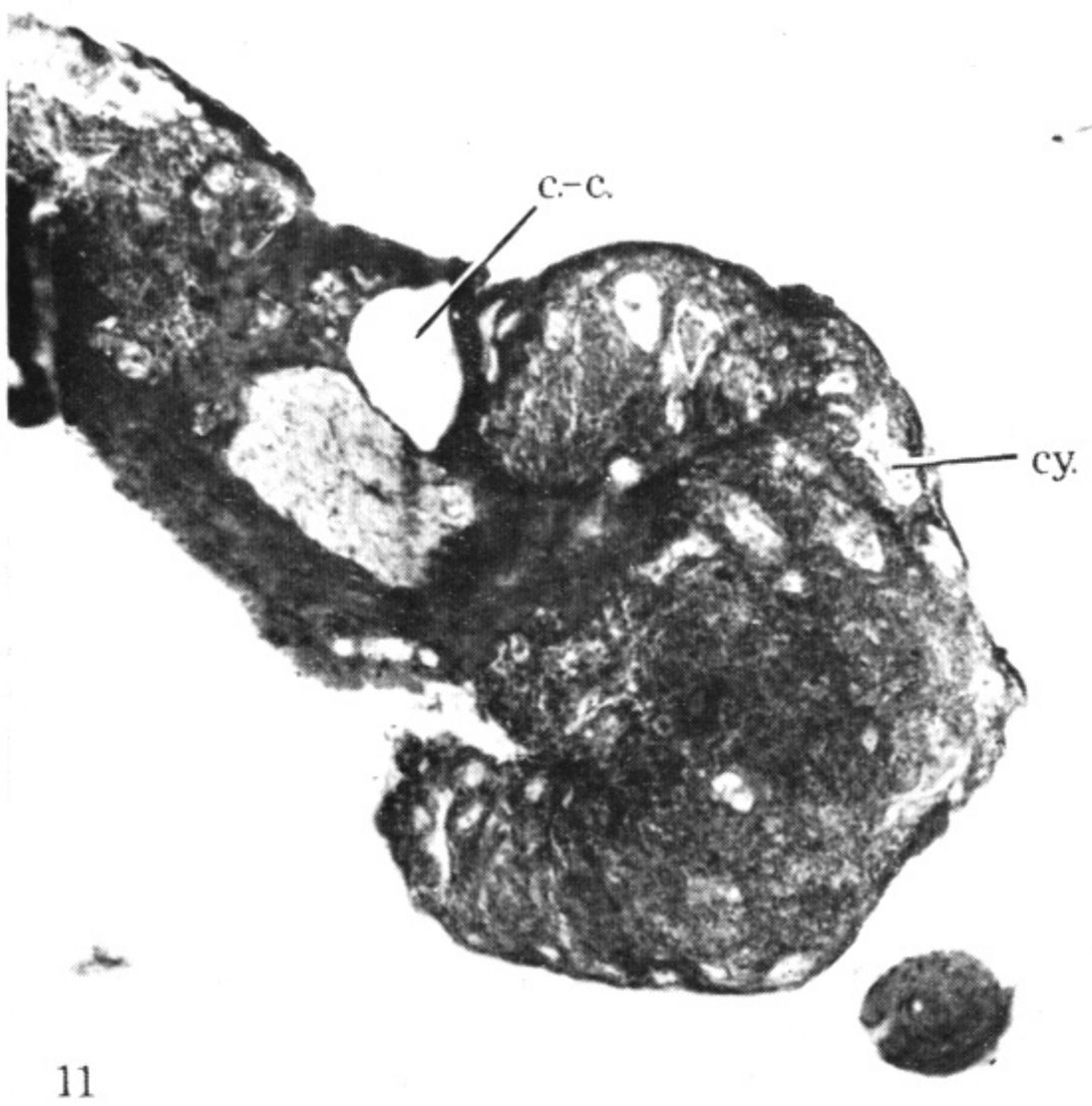


FIGURE 9. Part of three small, enlarging thymic lobes from an embryo just about to hatch. Blood vessels (b.v.) run in septa (s.) which divide the lobes into lobules. There is a small region of medulla (med.) but most of the lobes are composed of cortex (cor.). Masson stained 8 μm thick section (magn. × 48).

FIGURE 10. A fully enlarged thymic lobe from an adult in postnuptial moult. The densely populated cortex (cor.) surrounds a medulla (med.) which contains Hassall's corpuscles (H.c.). A blood vessel (b.v.) surrounded by connective tissue from the septum (s) is deep within the lobe. Masson stained 8 μm thick section (magn. × 48).



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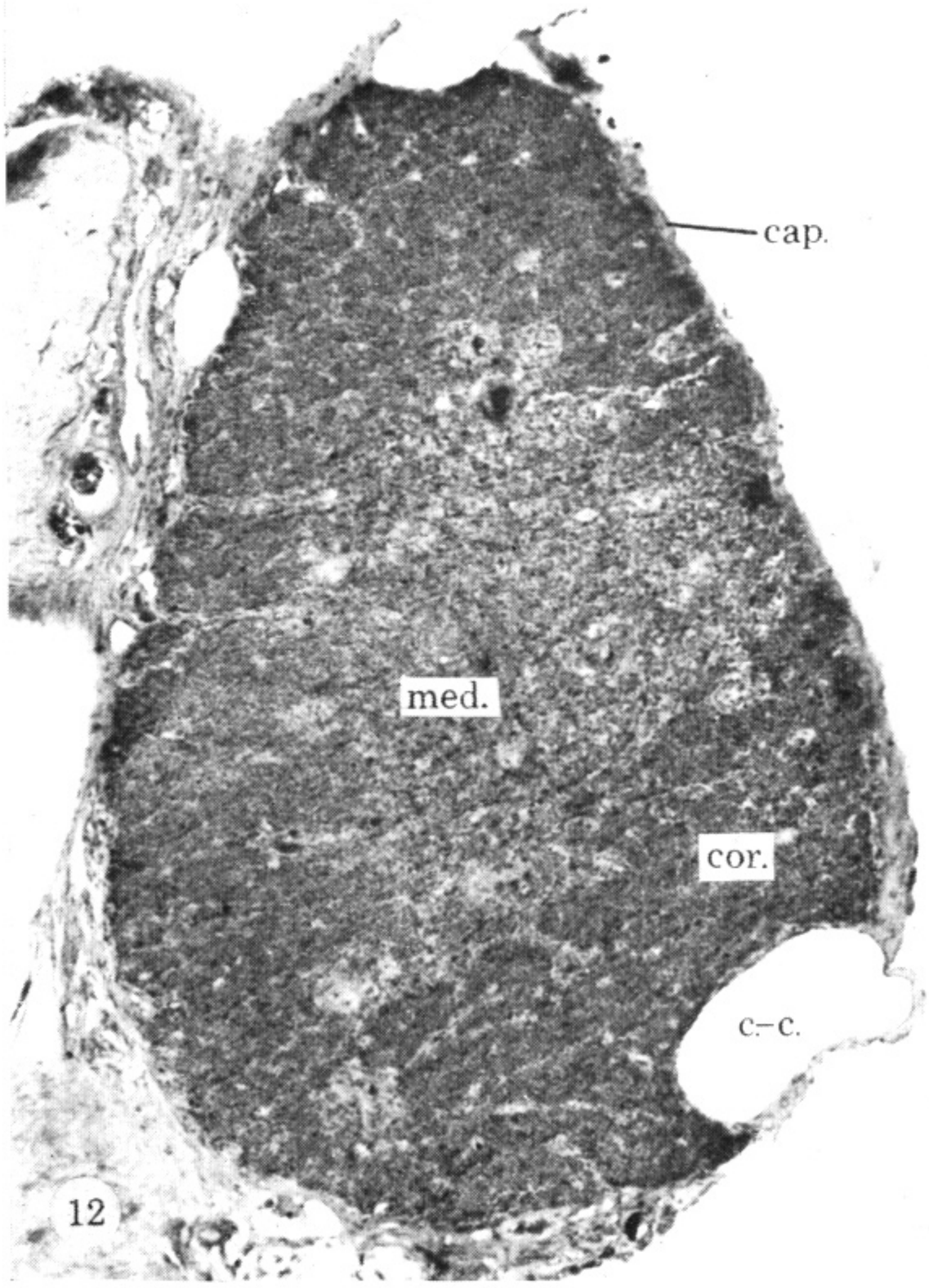

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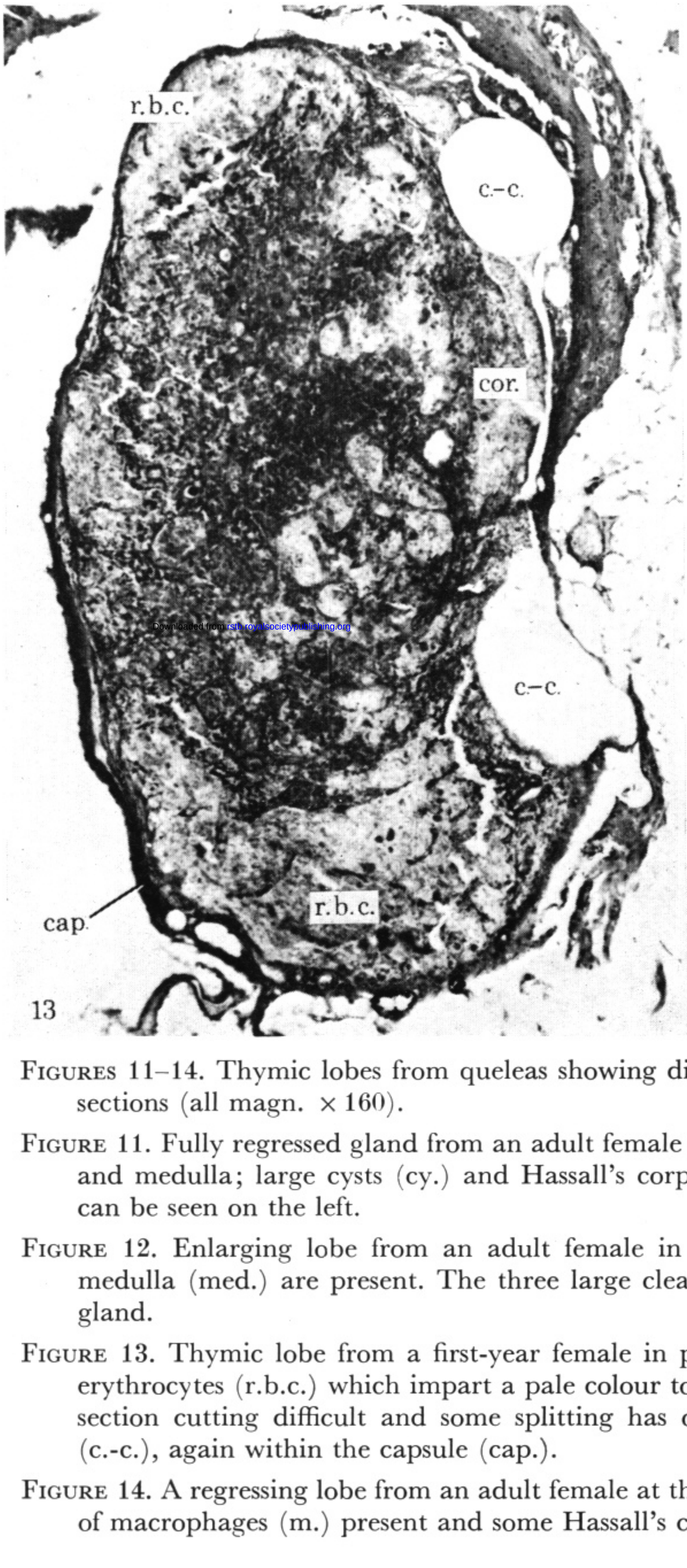

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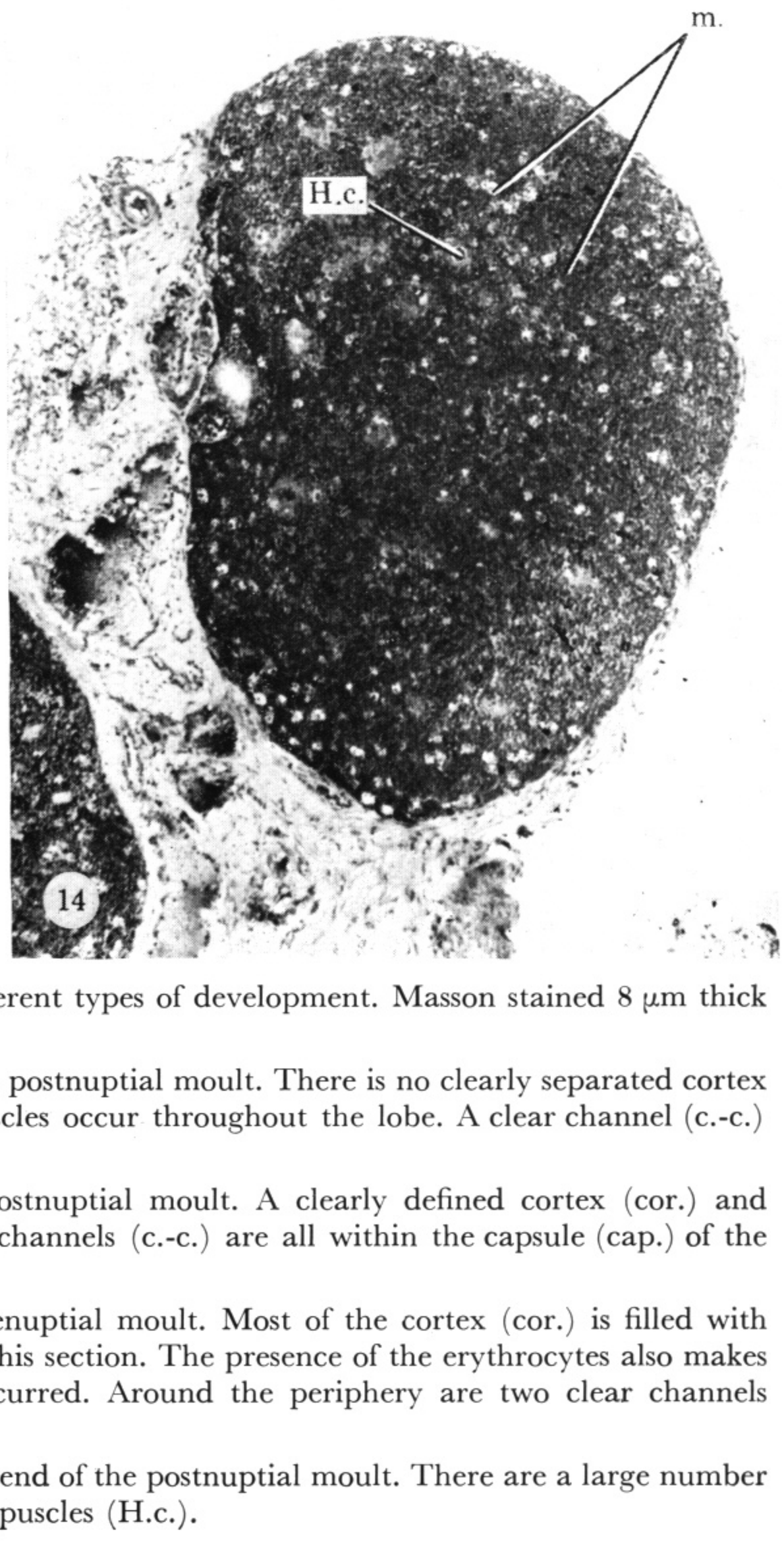

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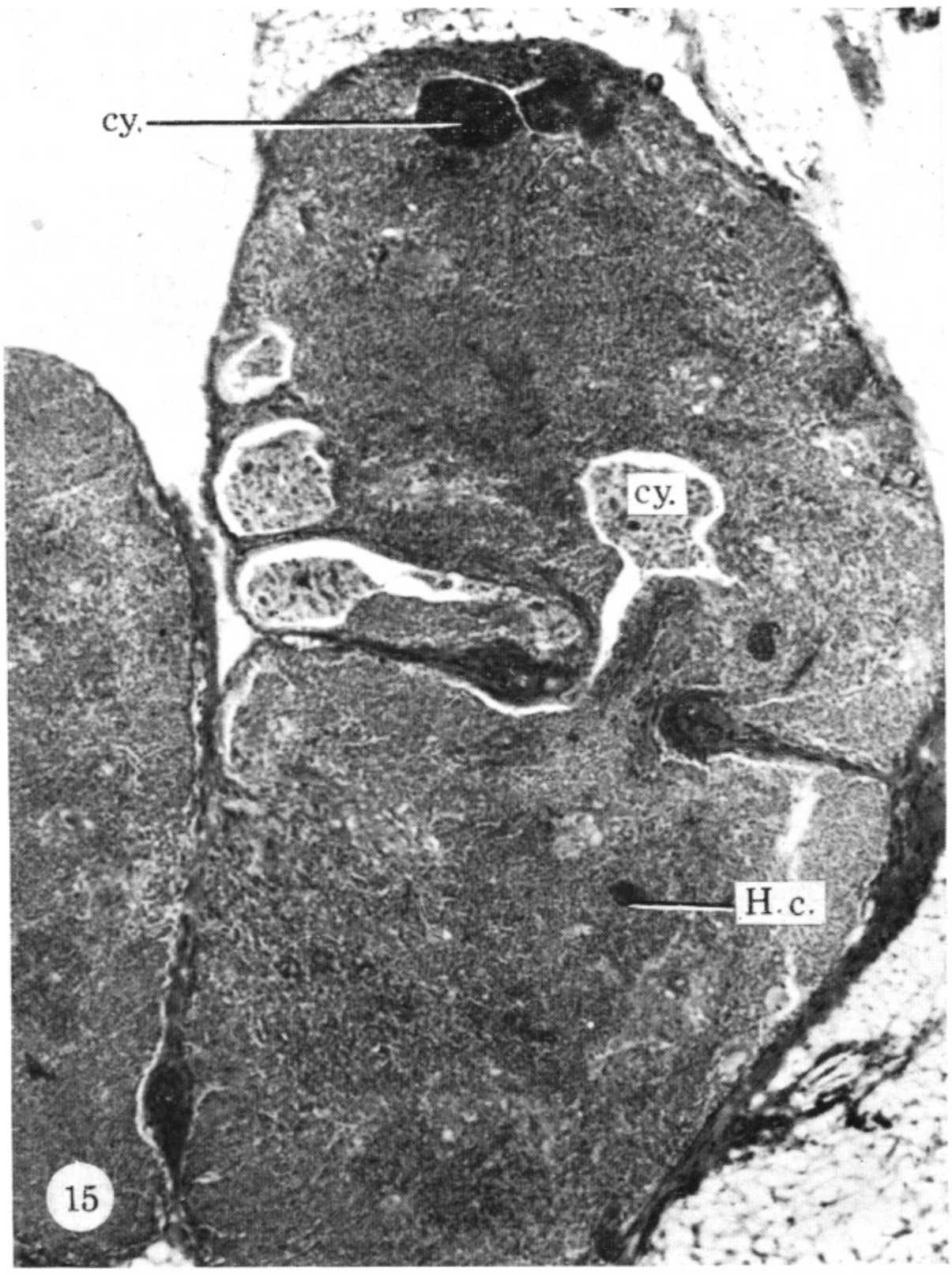
FIGURES 11–14. Thymic lobes from queleas showing different types of development. Masson stained 8 μm thick sections (all magn. × 160).

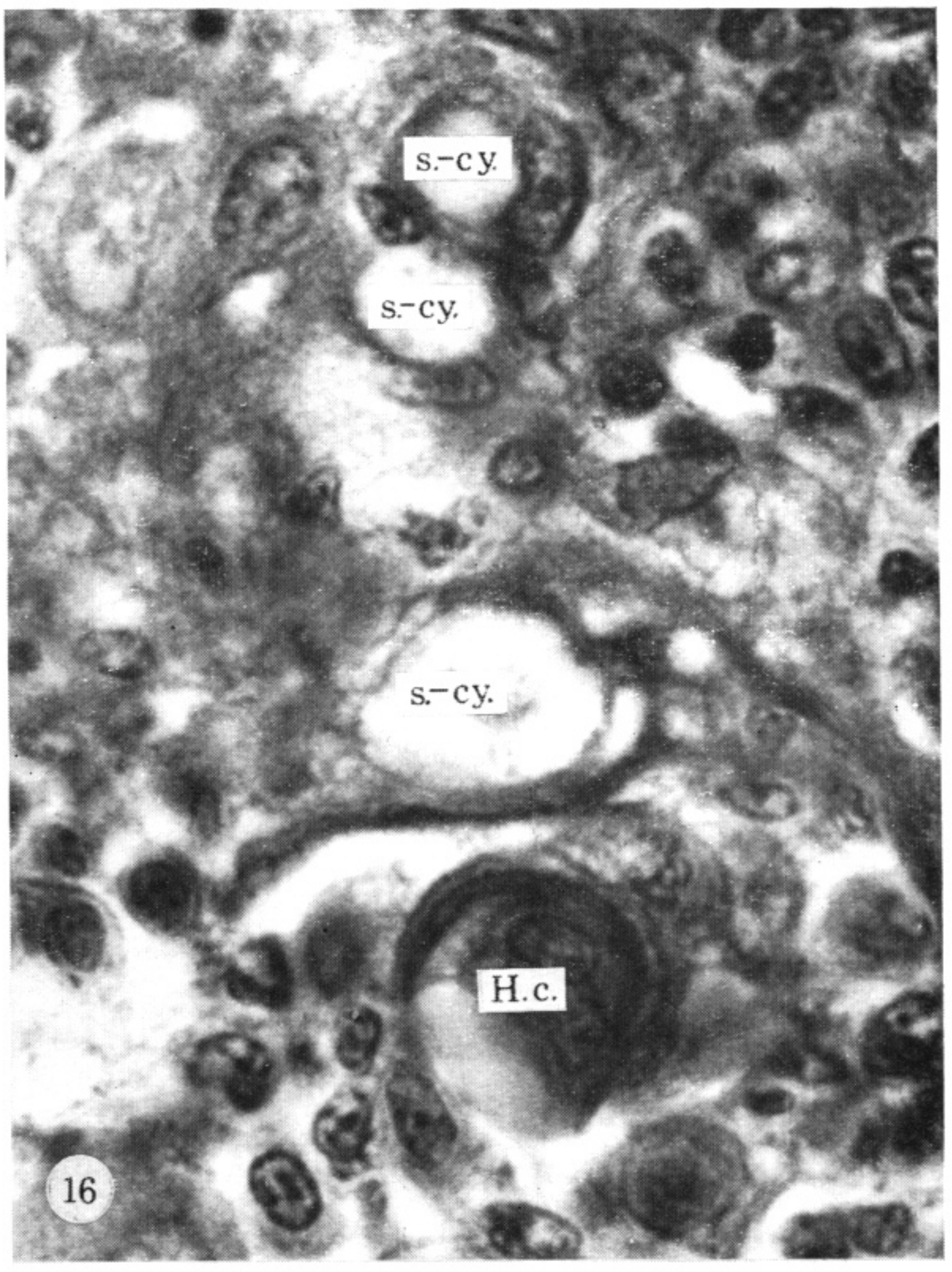
FIGURE 11. Fully regressed gland from an adult female in postnuptial moult. There is no clearly separated cortex and medulla; large cysts (cy.) and Hassall's corpuscles occur throughout the lobe. A clear channel (c.-c.) can be seen on the left.

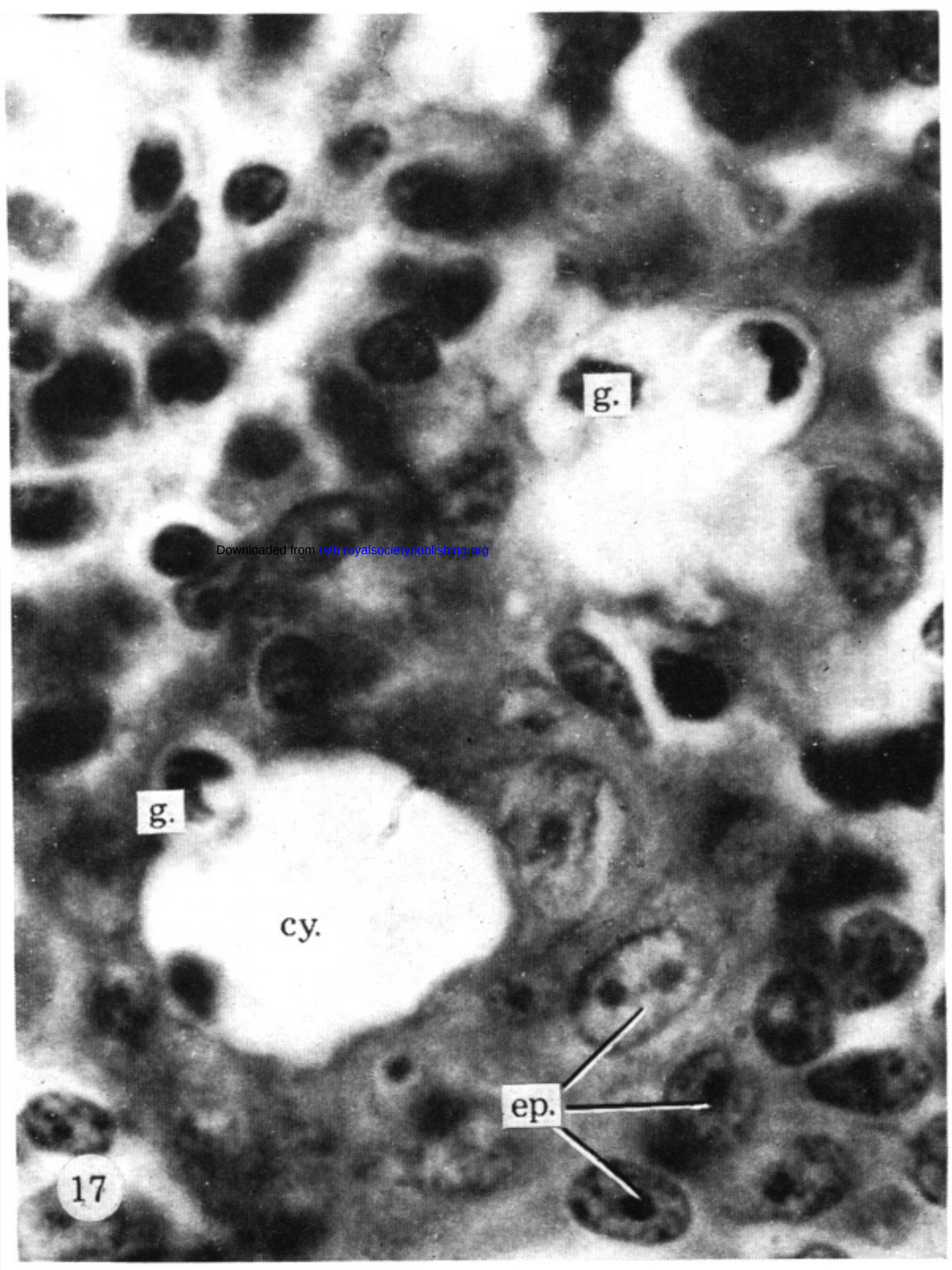
FIGURE 12. Enlarging lobe from an adult female in postnuptial moult. A clearly defined cortex (cor.) and medulla (med.) are present. The three large clear channels (c.-c.) are all within the capsule (cap.) of the gland.

FIGURE 13. Thymic lobe from a first-year female in prenuptial moult. Most of the cortex (cor.) is filled with erythrocytes (r.b.c.) which impart a pale colour to this section. The presence of the erythrocytes also makes section cutting difficult and some splitting has occurred. Around the periphery are two clear channels (c.-c.), again within the capsule (cap.).

FIGURE 14. A regressing lobe from an adult female at the end of the postnuptial moult. There are a large number of macrophages (m.) present and some Hassall's corpuscles (H.c.).







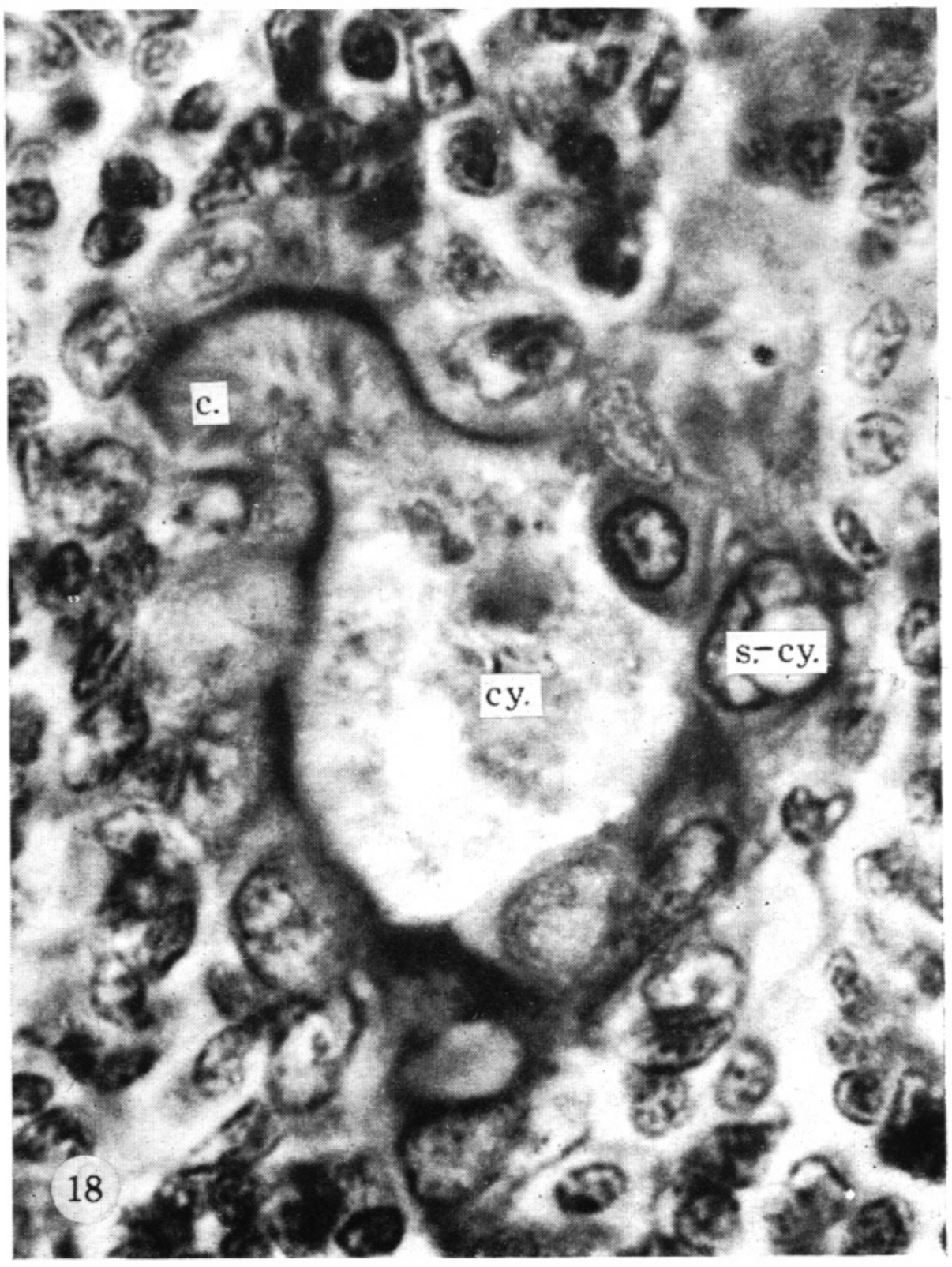


FIGURE 15. Regressing lobe from an adult female in prenuptial moult. Several very large cysts (cy.) contain cell debris. Large late Hassall's corpuscles are also present (H.c.). Masson stained 8 μm thick sections (magn. × 100).

FIGURE 16. Medulla of an enlarged lobe from an adult female in a breeding colony with chicks. Some small cysts (s.-cy.) are intracellular and some intercellular. An early Hassall's corpuscle (H.c.), cut tangentially, shows the cells which surround the outside (magn. × 1600).

FIGURE 17. Cysts in the medulla of an enlarging lobe from a male chick. The granulocytes (g.) appear to be in small compartments around the cysts (cy.). The distinctive nuclei of the epithelial reticular cells (ep.) are clearly shown (magn. × 1600).

FIGURE 18. A ciliated (c.) cyst (cy.) in the medulla of an enlarging lobe from an adult male in a breeding colony with chicks. Nearby is a cell with an intracellular cyst (s.-cy.) (magn. × 1600).