THE INVOLUTION OF THE THYMUS OF THE LIZARD, *CALOTES VERSICOLOR* (DAUD.)

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Contents

Introduction

Although the thymus resembles lymph nodes in its physiological and pathological reactions (Gyllensten, 1953), it differs from them in its morphology, histology and embryonic development. One of the striking points of resemblance of thymus and lymph nodes is in their involution with age (Andrew and Andrew, 1948). The prevailing view held by many investigators (Hammar, 1927; James, 1939; Smith and Louise, 1941; Gregoire, 1943; Baillif, 1949; Feldman, 1951; Smith *et al.*, 1952*b*) is that during involution of the thymus there is shrinkage accompanied by replacement of parenchymal tissue by connective and adipose tissues. Andrew and Andrew (1948) have reported that the atrophic process of the cervical lymph nodes of rat involves loss of parenchymal tissues, without any replacement by connective or adipose tissues, leading to the formation of large cavities of 'astonishing size'. According to Baillif (1951) the destruction of lymph nodes involves dissolution of lymphocytes, stromal cells and fibres, thus forming dilated cystic nodes which are at first multilocular, but later reduced to an unilocular sac. The present study was undertaken to determine if the thymus of *Calotes versicolor* behaves as the lymph nodes do during involution. It was found that in several respects the thymus of this species resembles on the one hand the thymus of mammals, while on the other it recalls the condition seen in amphibia.

Material and Methods

No attempts were made to rear the lizards in the laboratory but the animals were prepared for study directly after collection from the field. Examination was made of the contents of the alimentary canal in every case to make sure that the lizards had been well fed and all those that showed a paucity of food were discarded. For the purpose of this study twenty-four lizards weighing from 6 grams to 77 grams were used. The thymus was dissected out and fixed in Zenker's formol-acetic and

Bouin's fluids. Sagittal sections in paraffin were cut at 7 μ and 10 μ, and stained in Delafield's haematoxylin-eosin, Mallory's triple and Heidenhain's iron-haematoxylin. Shorr's differential stain as modified by Svihla (see Hartman, 1944) was also used.

OBSERVATIONS

To begin with it will be appropriate to review the morphology of the thymus of *Calotes versicolor* (specimens weighing 22–56 grams) with special attention to the structures concerned in involution. The size, shape and histological appearance of the thymus vary greatly depending on the age and weight of the animals. The thymus of *Calotes versicolor* is made up of an anterior oval and a posterior more rounded lobe separated by interlobar connective tissue (Fig. 1). Each lobe is surrounded by a fibrous capsule. There is an outer cortex and inner medulla. The cortex is composed of medium and small sized thymocytes (lymphocytes). The medulla consists of thymocytes, reticular cells forming medullary cords, basophilic granulocytes (foamy cells) unicellular Hassall's corpuscles, multinucleated plasmodial masses and sinusoids. All the intra-thymic blood vessels are surrounded by perivascular connective tissue which is continuous with the capsule.

Group 1. (Specimens weighing 6 to 18 grams.)

The thymus of seven specimens in this weight group was examined. In these young animals the thymus is small. The cortex can be differentiated from the medulla, but medulla appears more extensive (Fig. 1). The capsule is uniformly thick and is made of fibroblasts and a few mast cells. Thymocytes predominate in the cortex and are closely packed. The medulla consists of many unicellular Hassall's corpuscles with vesicular nuclei indicating a relationship to the reticular cells. Their cytoplasm shows concentric striations (Fig. 10). The multinucleated plasmodial masses arise by fusion of reticular cells. Generally these masses undergo degeneration. Dissolution of cytoplasm takes place first at the periphery and it later extends inwards. Lacunae are thus formed with central degenerating tissues (Figs. 11 and 12). The lacunae are small and lined by flattened reticulum resembling the endothelial wall of a blood vessel. Basophilic granulocytes are few. No macrophages are seen.

Group 2. (Specimens weighing 22 to 56 grams.)

Twelve specimens were examined. The thymus is large and has reached its maximum size. The capsule is compact, but thin, except at the region where the trabeculae enter the parenchyma of the gland. The mast cells are numerous and large, having coarse basophilic granules. The cortex is compact, more extensive than medulla, and is composed chiefly of thymocytes (Fig. 2). The thymocytes are more numerous than in the younger animals (group 1). Their accumulation is particularly great in the cranial and caudal ends of the gland. Mitotic figures are abundant in the cortical region, but degenerating thymocytes are also common. Degeneration consists in the breaking down of thymocytes into deeply staining spheroidal bodies (Fig. 13) resembling in all respects the 'Tingible Körper' of lymphocytes (Andrew and Andrew, 1948). These finally undergo karyolysis and are disposed off by phagocytes. Thus there appear many clear rounded patches in the cortex where groups of thymocytes have undergone complete degeneration (Fig. 2). Pycnotic thymocytes also occur all over the cortex. There are a few abnormal mitoses in anaphase showing chromosomal bridges (Fig. 13).

The medulla is loose and contains medium and small thymocytes, unicellular Hassall's corpuscles, multinucleated plasmodial masses, lacunae with or without degenerating tissues, granulocytes and macrophages (Figs. 12, 15, 16). The trabeculae, though narrow, extend deep into the parenchyma. The reticular cells have vesicular nuclei and are predominant in this region. The multinucleated plasmodial masses are undergoing cytolysis forming large lacunae (Figs. 12 and 16). The unicellular Hassall's corpuscles are generally scattered throughout the gland, but are found in conspicuously large numbers in the medulla. Their cytoplasm is acidophilic and exhibits concentric striations (Figs. 14 and 16). A few corpuscles have vacuoles in their cytoplasm (Fig. 14).

The basophilic granulocytes are generally in groups and occur near the multinucleated plasmodial masses and blood vessels. Each cell is large and swollen with many basophilic granules (Fig. 15). In preparations stained with iron-haematoxylin these cells appear yellow, but after Mallory's triple stain they are coloured pale blue and appear light green when stained with Shorr's method. Some granulocytes have few granules but others have many, depending perhaps on the physiological condition of the cell as well as of the gland. The granulocytes are large in number and also the granules appear numerous.

The macrophages are found in large numbers in the vicinity of the lacunae containing degenerating masses. They are polymorphic cells with vesicular nuclei indicating that they are probably derived from reticular cells. Their cytoplasm contains black, brown or golden yellow pigment and phagocytosed inclusions (Fig. 16).

Group 3. (Specimens weighing 58 to 77 grams.)

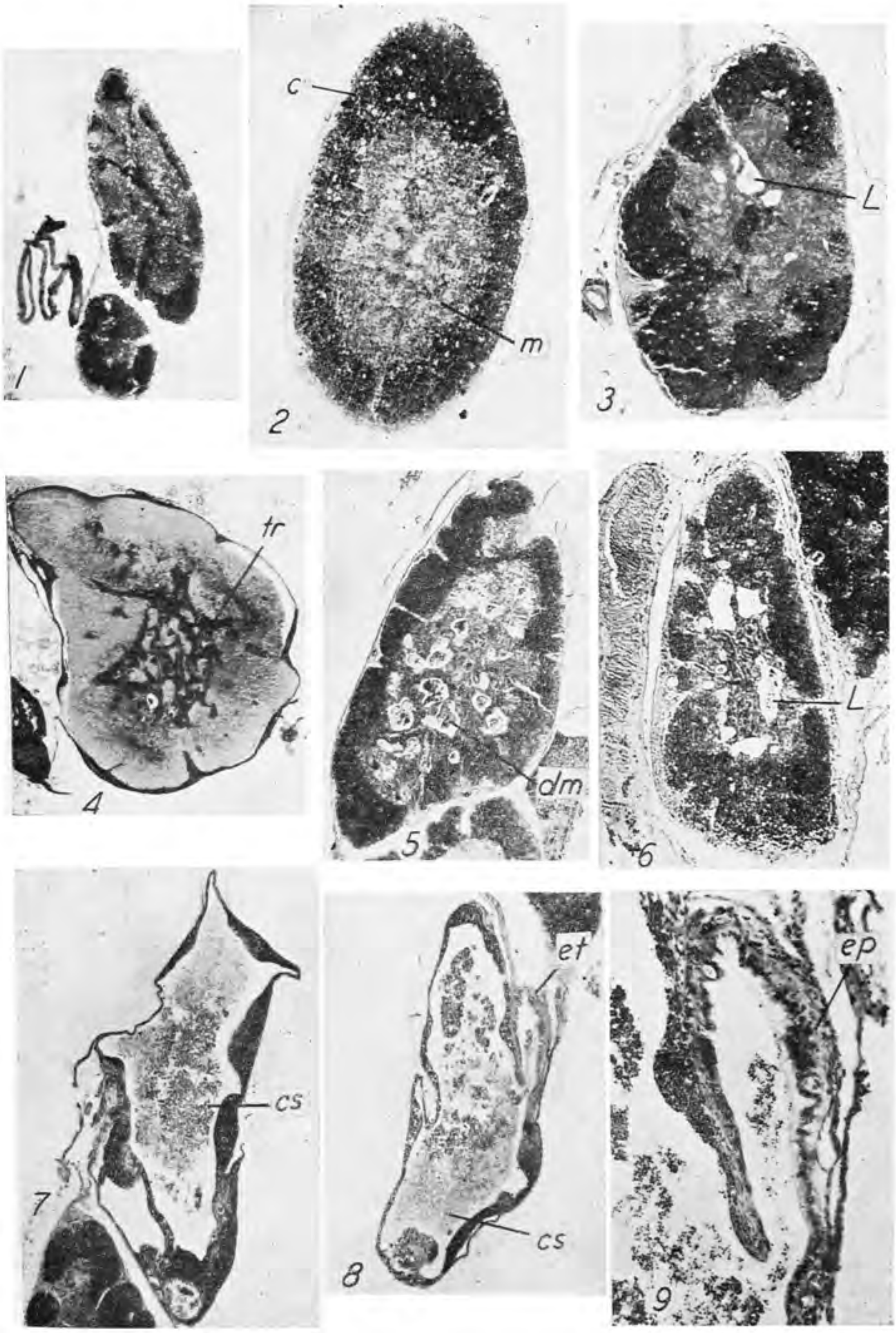
In the three specimens examined in this weight group, the conspicuous features of the thymus are the increase of connective tissue in the parenchyma and the presence of large spheroidal and ovoidal cavities in the medulla with or without degenerating masses (Figs. 3, 5 and 6).

The capsule is thick as compared with that in the preceding groups. This thickening is due to increase in number of fibres and their separation. The mast cells are large in number and size. Many trabeculae enter into the parenchyma from all sides of the gland and form a network in the medullary region (Figs. 3, 4, 5 and 6).

The medulla is extensive and the medullary cords reach the capsule at several places (Figs. 3 and 6). Thus there is a tendency to hyperplasia of reticular cells as a result of which the cortex is greatly reduced (Figs. 3 and 5). The lacunae have increased in number and size (Figs. 5) and are lined not only by flattened reticulum but also by the fibres (Figs. 6 and 17). Many of them now open into lymph vessels and thus are aptly called sinusoids, though they have originally arisen as products of liquefaction of the plasmodial masses. These plasmodial masses are partially or completely absorbed as involution proceeds (Figs. 5 and 6). As there are many thymocytes in blood vessels of the capsule and as the trabeculae, which are highly vascularized, enclose the cortical tissues, it seems reasonable to conclude that the thymocytes have migrated into the blood stream and that their place is taken by hypertrophied medulla.

Group 4. (Specimens weighing 54 and 56 grams.)

Among the animals studied there were two which weighed 54 and 56 grams, but which displayed in their thymus such outstanding characteristics that they have been dealt with separately. The thymus in these animals has undergone complete involution. The most striking feature is the presence of a large cavity occupying practically the entire gland except for a few patches of cortical tissue and reticular cells (Figs. 7 and 18). The cystic space is lined by flattened reticulum. In certain places the cavity extends up to the capsule (Fig. 7). It seems to involve not only the medulla but also large areas of the cortex and is filled with fluid coagulum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containing free thymocytes, a few reticular cells, unicellular Hassall's corpuscles and macrophages (Figs. 7 and 18). The basophilic granulocytes are few in number.

It is interesting to note the presence of an epithelial tubular structure opening into the cystic space of the thymus (Fig. 8). It is lined externally by the capsule and internally by vacuolated cuboidal epithelial cells (Fig. 9). This epithelial lining is continuous with the internal lining of the cavity of the thymus (Figs. 8 and 9). In the lumen of the tube are thymocytes which have migrated from the cystic space of the thymus.

Discussion

The involution of the thymus of *Calotes versicolor* offers many points of interest, particularly in its resemblance to lymph nodes. It has been known for a long time that during sexual maturity and old age the lymph nodes undergo atrophy. During this process the parenchymal elements of the nodes are replaced by connective and adipose tissues (Hellman, 1930; Krumbhaar, 1942). According to Andrew and Andrew (1948) and Baillif (1951) on the other hand, the atrophy is due, not to a replacement of the original cell elements by new ones, but to a total loss of cells resulting in cavity formation. The thymus of *Calotes versicolor* involutes by a process essentially similar to this.

Andrew and Andrew (1948) have stated that it is possible to identify with considerable accuracy the nodes of young, middle aged and senile rats. An application of their observations to the findings in *Calotes versicolor* seems possible. For, in this animal, the changes in the thymus so characteristically reflect their age groups that I have ventured to suggest a classification into (*a*) juvenile, (*b*) middle aged, (*c*) old and (*d*) senile forms, depending on the structural changes in the thymus. Thus animals weighing 6 to 18 grams are considered as juvenile, 22 to 56 grams, middle aged, 56 to 77 grams, old and 54 to 56 grams as senile animals. In *Calotes versicolor* during the early period of involution there is a certain amount of infiltration of connective tissue from the capsule into the parenchyma of the thymus (Figs. 3, 5 and 6); but later there is a definite loss of both cortical as well as medullary tissues leading to the formation of large cavities (Figs. 5, 6 and 7) in the thymus of old and senile animals. The loss of parenchymal tissue cannot be attributed either to infiltration of or to replacement by connective and adipose tissues as stated by Hammar (1927), Baillif (1949), Feldman (1951) and Smith *et al.* (1952), because no such replacement or infiltration of tissues is seen during involution. On the contrary, the loss of parenchymal tissues is so great that it leads to the formation of large cavities where there is neither overgrowth nor replacement of other tissues. Figures 7 and 8 which represent stages of almost complete involution, are interesting, in that they do not show any evidences of overgrowth or infiltration. The involution of the thymus of *Calotes versicolor*, therefore, strongly recalls the atrophic process of lymph nodes of rats described by Andrew and Andrew (1948) and Baillif (1951).

In the normal thymus of rat, the capsule is thin (Baillif, 1949) but at the time of involution it becomes a thick coat of loosely matted sheath of fibres. In the lymph nodes of this animal also, a similar change has been reported (Andrew and Andrew, 1948). It is a matter of interest that in *Calotes versicolor*, the capsule of the thymus which remains thin in the normal thymus, becomes a thickened sheath of fibres during involution (Fig. 6).

The flat cells lining the wall of the sinuses of the lymph nodes have been described by Ribbert (1907) as endothelium. According to his view the sinuses have been derived from the lymphatics of the nodes. Downey (1915 and 1922) sees intimate anatomical relations between the flat cells of the sinus wall and reticular cells of the lymph nodes and postulates that 'these sinuses develop not from preformed embryonic lymphatics but arise as independent blind cavities in the mesenchyme of the lymph node primordium'. The cavities later fuse with afferent and efferent lymph vessels. Jordan and Looper (1928) described in the thymus of the box turtle a closely graded series of the formation of the sinuses from the degeneration of reticular cells. Andrew and Andrew (1948) are of the opinion that the cystic spaces in the lymph nodes of rats also arise 'as areas of cell and fiber loss in the more compact tissues of medullary cords or of the cortex'. The present author has observed that in the thymus of *Microhyla ornata* (in press) the sinusoid spaces (lacunae) arise by dissolution of the hypertrophied reticular cells.

The origin of the sinusoid spaces in the thymus of *Calotes versicolor* conforms to the process described by Downey (1915 and 1922) in the mammalian lymph nodes, by Jordan and Looper (1928) in the thymus of the box turtle and by Andrew and Andrew (1948) in the cervical lymph nodes of rats. These spaces arise by liquefaction of the hypertrophied reticular cells. At first the cells form multinucleated plasmodial masses (Fig. 11). Frequently dissolution of their cytoplasm takes place at the periphery and extends inwards forming lacunae lined by flattened reticulum with central degenerating masses (Figs. 5, 6, 11 and 12). These lacunae in older forms open into lymph vessels and are called sinuses (Fig. 17). They widen up gradually in old and senile animals forming large cystic spaces (Figs. 6 and 7).

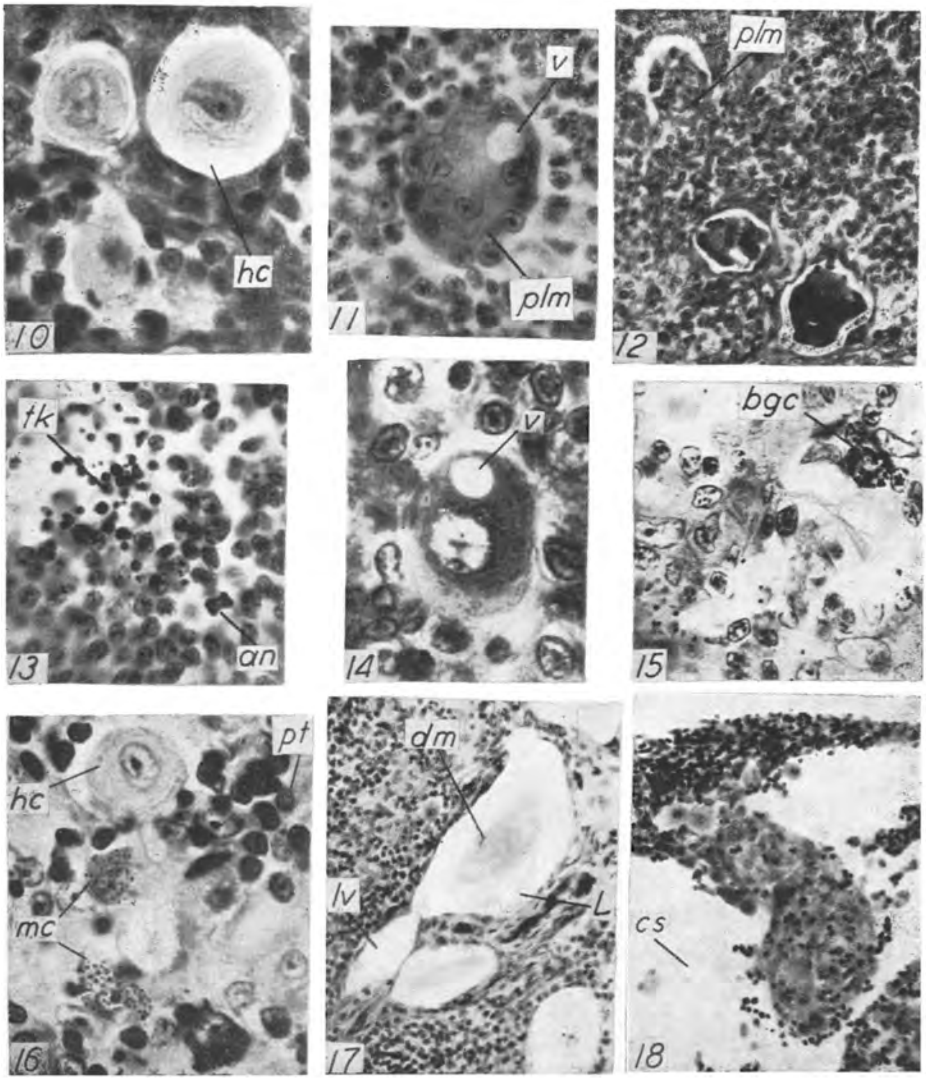
The unicellular Hassall's corpuscles have been described as sarcolytes by Mayer (1888), Schaffer (1893) and Pensa (1902). Hammar (1905), Jordan and Looper (1928) and Fabrizio and Charipper (1941) consider them as modified reticular cells. In the thymus of *Calotes versicolor* these corpuscles resemble to a great extent the reticular cells. Jordan and Looper (1928) describe in the thymus of the box turtle the occurrence of vacuoles in the sub-peripheral region of the corpuscles; later, with the coalescence of the vacuoles, an exoplasmic area is separated from the endoplasmic nucleated portion. I find in my material vacuoles in the peripheral region of the corpuscle but have not noticed their coalescence as in that of the box turtle thymus (Fig. 14).

The presence of basophilic granulocytes during involution is of great interest. Jordan and Looper (1928) believe that the appearance of the granulocytes in the thymus of the box turtle is stimulated by tissue destruction and regard them as modified lymphocytes. Baillif (1949) in thymus and Andrew and Andrew (1948) in cervical lymph nodes of the rat consider these granulocytes as modified mast cells. A detailed account of the granulocytes of the thymus of the rat is given recently by Loewenthal and Smith (1952) who call them lipid laden foamy cells.

The basophilic granulocytes are found in large numbers in middle aged and old forms of *Calotes versicolor*. As they occur near the multinucleated plasmodial degenerating masses their appearance is perhaps due to stimulation offered by the degenerating tissues as suggested by Jordan and Looper (1928). Their morphology suggests a resemblance with the foamy cells described by Loewenthal and Smith (1952). The number of granules depends upon the physiological condition of the cells. As these cells are situated far from trabeculae and as they differ from mast cells in their shape it is probable they are derived from thymocytes and not from mast cells as stated by Andrew and Andrew (1948) and Baillif (1949).

Maximow and Bloom (1932) believe that the macrophages are derived from reticular cells. Baillif's (1949) contention is that the intralobular macrophages of the thymus alone are derived from the epithelial stromal cells. Smith *et al.* (1952*a*) are of the opinion that macrophages, reticular cells and lymphocytes are the precursors of the adipose cells and probably they enter into some transient histiocytic condition before becoming fully differentiated fat cells.

Macrophages are present in large numbers in the thymus of middle aged *Calotes versicolor* in the vicinity of the sinusoid spaces (Fig. 16). They are large, polymorphic cells with vesicular nuclei containing cytoplasmic granules (brown, black or yellow) and vacuoles. As they are found in the medullary region of the thymus and as their nuclei resemble those of reticular cells it can be said that they are derived from reticular cells as suggested by Maximow and Bloom (1932) and Baillif (1949).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Whether they are the precursors of adipose cells as stated by Smith *et al.* (1952*a*) is difficult to say.

The presence of epithelial inclusions in the lymph nodes has been noted by Ries (1897), Hellman (1930), Comes (1938) and Andrew and Andrew (1948). These inclusions are normally found in the lymph nodes of the young forms, but tend to disappear with increasing age. In *Calotes versicolor* I have found an epithelial tubular structure in the involuting thymus (Figs. 8 and 9). I am unable to develop any definite view in regard to its origin due to the lack of more complete information.

There is a strong suggestion that the thymus of *Calotes versicolor* behaves like the cervical lymph nodes of rats (Andrew and Andrew, 1948) during involution.

Summary

1. In the thymus of juvenile forms there is a preponderance of medulla over cortex; in middle aged animals, cortex is more extensive; in old age there is again hyperplasia of medulla with a corresponding decrease in cortex.

2. A conspicuous feature in the involuted thymus is the presence of large cavities formed by the dissolution and atrophy of thymo-reticular cells without any replacement by connective or adipose tissues.

3. The capsule thickens during involution. This thickening is effected by increase in number as well as by separation of the capsular fibres.

4. The sinusoid spaces arise by liquefaction of the multinucleated plasmodial masses and they communicate with lymph vessels.

5. The unicellular Hassall's corpuscles are derived from reticular cells of the thymus. Some show the presence of vacuoles in their cytoplasm prior to their liquefaction.

6. The basophilic granulocytes (foamy cells) are formed from thymocytes. They are present in large numbers in middle aged and old forms. They occur near the degenerating plasmodial masses. The number of granules in these cells depends upon the physiological condition of the cell as well as of the gland.

7. The macrophages are found during involution. They are the transformed reticular cells.

8. Occasionally an epithelial tubular structure is present in the involuted thymus.

9. It is suggested that the thymus of *Calotes versicolor* behaves like the cervical lymph nodes of rats during involution.

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Explanation of Figures

Plate II

FIG. 1.—Sagittal section of the thymus of juvenile form (weight, 12 grams) showing an anterior oval and a posterior round lobe. Note the preponderance of medulla over cortex. Heidenhain's haematoxylin. ×28.

FIG. 2.—Sagittal section of the anterior lobe of the thymus of middle aged form (weight, 34 grams) showing accumulation of thymocytes in the cranial and caudal ends of the gland. H.H. ×49.

FIG. 3.—Sagittal section of the anterior lobe of the thymus of old form (weight, 58 grams). The hyperplasia of medullary region and the presence of lacunae are seen. H.H. ×49.

FIG. 4.—Sagittal section of the anterior lobe of the thymus of old form (weight, 62 grams), showing the network of trabeculae in the medullary region. Shorr's differential stain. ×49.

FIG. 5.—Sagittal section of the anterior lobe of the thymus of old form (weight, 71 grams), showing the presence of lacunae with degenerating masses. H.H. ×49.

FIG. 6.—Sagittal section of the anterior lobe of the thymus of old form (weight, 77 grams), showing the presence of cavities in the medullary region. H.H. ×49.

FIG. 7.—Sagittal section of the anterior lobe of the thymus of senile form (weight, 54 grams), wherein the gland has undergone complete involution. Note presence of large cavity occupying the entire gland. H.H. ×49.

FIG. 8.—Sagittal section of the anterior lobe of the thymus of senile form (weight, 54 grams), showing the presence of an epithelial tube. H.H. ×49.

FIG. 9.—A portion of the thymus of senile form (weight, 54 grams) enlarged to show the lining of the epithelial tube. The epithelium is cuboidal and is continuous with the internal lining of the cystic wall. The thymocytes in the epithelial tube have migrated from the cystic space of the thymus. H.H. ×130.

Plate III

FIG. 10.—Unicellular Hassall's corpuscles showing concentric striations. Their nuclei are vesicular. (Thymus of juvenile form; weight, 12 grams.) H.H. × 1400.

FIG. 11.—A portion of the medulla of the thymus of juvenile form (weight 12 grams) enlarged to show the plasmodial mass with the dissolution of its cytoplasm at the periphery. H.H. × 1120.

FIG. 12.—A portion of the medulla of the thymus of middle aged form (weight, 34 grams) enlarged to show the formation of lacunae in the plasmodial masses. Mallory's triple. × 480.

FIG. 13.—A portion of the cortex of the thymus of middle aged form (weight, 34 grams) to show the presence of 'Tingible Körper' and pycnotic thymocytes. An aberrant anaphase is also seen. H.H. × 1120.

FIG. 14.—Unicellular Hassall's corpuscle showing a vacuole in the cytoplasm. Mallory's triple. × 1800.

FIG. 15.—A portion of the medulla of the thymus of middle aged form (weight, 34 grams) enlarged. A basophilic granulocyte with granules is seen near a lacuna. Note the basophilic granules also. Mallory's triple. × 1150.

FIG. 16.—A portion of the medulla of the thymus of middle aged form enlarged (weight, 34 grams). Three macrophages with their pigment granules are seen around a lacuna. A unicellular Hassall's corpuscle is also seen. H.H. × 1150.

FIG. 17.—A portion of the medulla of the thymus of old form (weight, 58 grams) enlarged to show the opening of the lacuna into a lymphatic vessel. H.H. × 310.

FIG. 18.—A portion of the thymus of the senile form (weight, 54 grams) enlarged. The reticular cells, thymocytes and unicellular Hassall's corpuscles are torn away from the wall of the thymus. H.H. × 360.

KEY TO LETTERING

an = Aberrant anaphase.
bgc = Basophilic granulocytes.
c = Cortex.
cs = Cystic space.
dm = Degenerating mass.
ep = Epithelium (Columnar).
et = Epithelial tube.
hc = Hassall's corpuscle.
L = Lacuna.
lv = Lymphatic vessels.
m = Medulla.
mc = Macrophages.
plm = Plasmodial mass.
pt = Pycnotic thymocytes.
tk = Tingible Körper.
tr = Trabecular network.
v = Vacuole.

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