PART I

THE OVARY
CHAPTER 1

COMPARATIVE STUDIES ON THE STRUCTURE OF THE OVARY OF

CALOTUS VERSICOLOR, HEMI DACTYIUS FLAVIVIRIDIS AND

CHAMAELEON CALCARATUS
INTRODUCTION

The ovary of reptiles, besides producing ova, synthesizes and releases hormones that play a role in reproduction. Its morphology and structure in a number of reptiles have been extensively studied (Loyez, 1960; Brindell, 1960; Betz, 1963; Varma, 1970; Varma and Guraya, 1970; Guraya, 1976). The studies prior to 1900 have been reviewed by Loyez (1906). Betz (1963) has made a comprehensive study on the ovarian histology of the diamond-backed snake, Matrix rhombifera and he has reviewed the earlier information on the ovarian histology and morphology of reptiles. The ovarian histology of the garden lizard, Calotes versicolor has also been described (Varma, 1970; Guraya and Varma, 1975).

The reptilian ovary mainly consists of two elements, (1) the ovarian follicles in different phases of growth and development and (2) the ovarian stroma formed of connective tissue, blood vessels and interstitial gland cells. Depending upon the phases of the reproductive cycle, three types of follicles, namely, normal follicles, atretic follicles and postovulatory follicles or corpora lutea are encountered. After ovulation, the follicle transforms into a postovulatory follicle and continues to be active for a varying
period of time in different reptilian species. A large number of follicles other than those which do not ovulate, undergo degenerative changes called follicular atresia. Very little attention has been given to the study of follicular atresia in the ovaries of nonmammalian vertebrates (Saidapur, in press). The occurrence of follicular atresia has been reported in the ovary of some reptilian species (cited in Setz, 1963; Saidapur, in press).

Many variations in the process of follicular atresia in the ovaries of vertebrates have been noticed. Based on these variations, several types of atresia, namely, previtellogenic, yolky, glandular, bursting, haemorrhagic and cystic types have been recognised. Several of these types have been observed in the ovaries of birds (Dominic, 1961; Sripino, 1973; Bhujia, 1977). Cystic atresia seems to be of common occurrence in fishes (Shenbag and Nadkarni, unpublished observations). Previtellogenic atresia has been studied in detail in the rat ovary (Ingram, 1962). In the snake, Natrix rhombifera, bursting and yolky atresia have been observed (Setz, 1963) while only the yolky type has been reported in the ovary of C. versicolor (Verma, 1970; Verma and Guraya, 1973).

Opinions on the significance of follicular atresia are diverse (Saidapur, in press). Recent histochemical
studies indicate that follicular atresia may be related to the contribution of interstitial cells to the ovarian stroma (Guraya, 1976; Saidapur, in press). However, interstitial stromal cells are reported to be absent from the ovaries of viviparous snakes, Bothrops Crotalus, Xenodon (Fraenkel et al., 1940) and H. rhombifera (Betz, 1963).

Postovulatory follicles of reptiles contain luteal cells, the origin of which is not decisively known. In most reptilian species, the luteal cells are derived from granulosa cells while in Lacerta agilis (Hoff, 1924) and Terrapene carolina (Altland, 1951) contribution from the theca interna to the luteal elements has been claimed (Derry and Rowlands, 1962). The evidence that they produce progesterone is only circumstantial (Brambell, 1960; Callard, 1966; Klicka and Mahmoud, 1972; Verson, 1972; Guraya, 1965,1976) and somewhat conflicting. Callard (1966) histochemically demonstrated the presence of \( \Delta^5-3\beta \) -HSDH (delta 5 3 beta-hydroxysteroid dehydrogenase), a key enzyme in the biosynthesis of steroid hormones, in the luteal bodies of Natricus sigodon pictiventris while he did not notice any difference in the rate of in vitro conversion of pregnenolone to progesterone in both the pregnant and the nonpregnant specimens of this species. Klicka and Mahmoud (1972) found that the homogenate of the corpora
lutea of Chelydra serpentina serpentina has the ability of
in vitro conversion of pregnanolone to progesterone. Histo-
chemical demonstration of lipids in the luteal cells of
lizards and snakes has been attributed to the steroid
producing ability of the luteal cells in reptiles (Guraya,
1976). Retention of eggs or embryos in the genital tract
of reptiles seems to be correlated with the longevity of
the corpus luteum (Harrison Matthews and Marshall, 1960;
Investigations so far made on the endocrine role of post-
ovulatory follicles and their maintenance in reptiles have
yielded conflicting results (Miller, 1959; Yaron, 1972). It
is against this background that the ovarian histology of the
lizards, C. versicolor, Hemidactylus flaviviridis and
Chamaeleon calcaratus was studied in the present work in an
attempt to have a better understanding of follicular atresia,
origin of interstitial gland cells of the ovarian stroma
and the luteinised cells of the corpus luteum in reptiles.
In addition, the information gained from the present histo-
logical study is used as a prerequisite for identifying
steroidogenic cells in the ovaries of reptiles described in
Chapter 3.
The commonly available reptiles around Dharwad (15° 17'N and 75° 3'E) are:

1. the garden lizard, *Calotes versicolor*
2. Wall lizard, *Hemidactylus flaviviridis*
3. the chameleon, *Chamaeleon calcaratus*
4. the oviparous skink, *Nabuya carinata*
5. the chelonians belonging to genera, *Geomyda* and *Helosoma*
6. the snakes of the genera, *Ptyas, Naja, Natrix* and *Typhlops.*

Of these reptiles, the first two are available in adequate numbers in their natural habitat throughout the year. Further, the garden lizards of both the sexes show nuptial colouration of reddish golden hue on the crest and the gular region during the breeding season and thus it is easy to catch sexually mature specimens. The chameleon is available with difficulty and that too in small number. Therefore, we selected the garden lizard, *C. versicolor* for a detailed histological study of the gonads. Further, the histological study of the ovaries of two more reptiles, the wall lizard, *H. flaviviridis* and *C. calcaratus* was investigated for the sake of comparative study of
Live specimens of *C. versicolor*, *H. flaviviridis* and *C. calcaratus* were locally collected and were sacrificed within a day or two after their arrival into the laboratory. The histological study on the ovary of *C. versicolor* was carried out once a month for one year with a view to avail the ovarian elements in different phases of the annual reproductive cycle. The preliminary observations on the structure of the ovary of *H. flaviviridis* showed that histology of *H. flaviviridis* ovary did not vary much from that of *C. versicolor*. Therefore, the ovary of *H. flaviviridis* was studied once in three months for a year in order to ascertain the changes during different phases of its annual cycle. The specimens of *C. calcaratus* were available only during June to September and that too in a small number. The structure of their ovary revealed that the chameleons were in breeding phase during these months. A few specimens showed eggs in the oviducts.

Live specimens of *C. versicolor*, *H. flaviviridis* and *C. calcaratus* were suddenly decapitated and the ovaries were removed and pieces of ovaries were fixed either in Bouin's fixative or Zenker's fluid overnight. Routine paraffin sections of 5 to 7 μm thickness were cut and stained with
Harris haematoxylin and counterstained with eosin. The sections obtained from the tissue fixed in Zenker's fixative, were stained with Mallory's triple stain prepared by using oxalic acid, for determining the tissue elements of the ovary.

**OBSERVATIONS**

The ovary of these lizards is an oblong bunch-like organ situated on the dorsal side of the abdominal cavity anterior to the kidney. Each ovary is attached to meso-dorsal peritoneum on either side of the intestinal mesentery. The ovary is formed of bunches of round follicles of varying sizes and growth, the large follicles being disposed towards the anteroposterior extremities and the small ones being disposed in the middle region of the ovary.

**Germinal epithelium**: It consists of patches of cells disposed towards the free edges of the ovarian stroma nearby the area of the attachment of the ovary to the abdominal peritoneum (Fig. 1.1). These cells give rise to primordial follicles that show primordial germinal cells surrounded by three of connective tissue fibres and cells (Figs. 1.2, 1.3). One of the primordial cells is larger than the rest and it is called auxocyte that later becomes oocyte after vitellogenesis (Fig. 1.3).
Normal follicles: Normal or growing follicles are formed of connective tissue theca, granulosa and the large oocyte (Figs. 1.4, 1.5). The theca of small follicles up to 0.4 mm diameter is not distinguishable into theca externa and theca interna and it is relatively thin. The theca of the medium sized follicles from 0.4 mm to 3.0 mm in diameter is differentiated into theca externa and theca interna through the two thecal layers are not distinctly regioned. The theca externa comprises mainly of connective tissue fibres and a few fibroblasts whereas the theca interna contains a large number of fibrocytes. In addition, the theca interna is richly vascularised. Next to theca is the cellular granulosa layer. The cells of this layer are of three types, small, intermediate and large pyriform cells (Fig. 1.6). The distribution and number of these cell types vary with the size or growth of the follicles. Small cells are present only in small follicles. Intermediates as well as pyriform cells occur in the follicles of medium size. The pyriform cells are so large that they occupy the entire width of the granulosa layer. These are holocrine gland cells. In large ovulatory follicles (3.0 mm to 8.0 mm) the granulosa layer is rather thin and it is made up of a single layer of low cuboidal cells. The zona pellucida separates granulosa from the oocyte and it consists of striated zona striata or radiata and the vitelline membrane. Similarly
membrana propria separates granulosa from theca interna.

The oocyte is a large cell that occupies the centre of the follicle. It is formed of the germ vesicle or the egg nucleus and the ooplasm. There is a large vacuole near the germ vesicle (Fig. 1.4). The ooplasm contains yolk granules and fat droplets; the disposition of which varies with the size or age of the oocytes. In small oocytes, the yolk granules and fat droplets occur immediately around the germ vesicle and they are well spread out. They appear midway between the germ vesicle and the periphery of the oocyte in the medium-sized follicles. In fully grown follicles, they appear more concentrated and disposed towards the vitelline membrane.

Postovulatory follicles: The postovulatory follicles or the luteal bodies are the follicles from which the ova are discharged. These show highly thickened and vascularised theca that surrounds the granulosa lutein cells. A newly formed corpus luteum shows collapsed thecal capsule lined inside by irregular layers of luteinised granulosa cells (Fig. 1.7). In the corpus luteum of the next stage, theca is thicker and more vascularised with granulosa luteal cells filling the central space (Fig. 1.9). There is an over-all increase in the size of the corpus luteum due to hypertrophy of luteal cells and without any apparent increase
in the number of these cells as indicated by the absence of mitotic figures in them. The trabeculae or stroma of connective tissue cells, fibres and blood spaces of the theca from the site of the rupture of follicles extend into the luteal area amidst the luteinised cells. Thus the interior of the postovulatory follicles shows the luteinised granulosa cells interspersed with trabeculae of connective tissue and blood sinuses derived from the theca at the site of rupture (Fig. 1.8). The luteal bodies after remaining active for some time, undergo degeneration to form structures similar to mammalian corpora albicorns (Figs. 1.10, 1.11). The luteal cells become highly vacuolated and later disappear completely. The thecal remnants of corpora albicorns seem to merge with the ovarian stroma.

Atretic follicles: Follicular atresia in the ovary

C. vermicular causes at any stage of the follicular growth. Many variations in the process of follicular atresia have been noticed (Figs. 1.12-1.16). In the early stage of atresia, the granulosa cells become polymorphic and they are dispersed in many layers (Figs. 1.5, 1.12, 1.13, & 1.17). The yolk granules and fat droplets which assume various sizes, are unevenly spread out in the ooplasm. Thus the ooplasm shows a disorganised appearance.

During yolky atresia, zona pellucida and membranes
propria collapse and the granulosa cells which are detached, are seen in the ooplasm (Fig. 1.16). In glandular atresia, membrane propria remains intact and the granulosa cells are not detached. Hence granulosa and theca interna in the follicles undergoing glandular atresia appear rugose and make inroads into the ooplasm after the collapse of vitelline membrane and zona radiata (Fig. 1.12). Cystic atresia is identified by the presence of shrunken oocyte, other follicular elements remaining as in normal follicles. Large ovarian follicles replete with yolk, appear to undergo bursting atresia (Figs. 1.14, 1.15, & 1.18) which is similar to glandular atresia except that the theca ruptures and yolk content is extruded into the ovarian stroma where it forms ectopic yolk masses. Some follicles appear to undergo haemorrhagic atresia as made out from the presence of haemorrhage in the region of theca interna and granulosa and even at the peripheral region of the ooplasm (Fig. 1.13). It was not possible to ascertain the occurrence of previtellogenic atresia in the ovary of C. versicolor.

Ovarian stroma: The ovarian stroma mostly consists of connective tissue, blood vessels, smooth muscles and interstitial gland cells. It appears to undergo cyclic changes as seen by changes in its histology. In all the three lizards of the present investigations, the ovary did
not show central cavity. However, small empty spaces (Figs. 1, 1, 1.10 & 1.16) are markedly seen during the period of regression of the breeding cycle. During the period of regeneration and prior to onset of the breeding phase, the stroma appears highly glandular (Fig. 1.19) and there is an increase in the number of stromal interstitial gland cells. Besides these elements, the remnants of the atretic follicles, corpora lutea, corpora albicans, ectopic yolk masses may also be encountered in the ovarian stroma.

**DISCUSSION**

The previtellogenic follicles in *C. versicolor*, *H. flaviviridis* and *C. calcaratus* are formed from primordial germ cells surrounded by the ovarian stromal connective tissue. This feature is also observed in the snake, *N. rhombifera* (Betz, 1963) and the lizard, *C. versicolor* (Verna, 1970). One of the germ cells enlarges to differentiate into an auxocyte that comes to occupy the centre of the previtellogenic follicle. The auxocyte undergoes vitellogenesis and enlarges further to become an oocyte. During the process of vitellogenesis, plenty of yolk granules and fat droplets appear in the cytoplasm of the auxocyte, now called the oocyte. The remaining germ cells inside the previtellogenic
follicle however, continue as granulosa cells around the enlarged oocyte. The increase in size of the follicle during and after vitellogenesis seems to be mainly due to increase in the size of the oocyte concurrent with the increase in the number of cells in the granulosa layer as judged from the occurrence of mitotic figures in the granulosa cells. In mammals, it has been reported that the vitellogenic material is partly synthesized in the liver and transported through the vascular system and partly synthesized within the ovary (Chester Jones et al., 1972). There are however, no reports on this aspect in the reptilian ovary. Our histological observations, because of its limited scope do not permit us to draw any conclusive inference on this question. The appearance of vitellogenic material first in the neighbourhood of the germ vesicle and its subsequent shift towards the periphery of the ooplasm strongly suggests that these substances, at least in part, are synthesized within the oocytes. In addition, the germ vesicle has been shown to synthesize proteins (Guraya, 1965) some of which might serve as enzymes during the synthesis of yolk granules and fat droplets. The occurrence of proteins, phospholipids and triglycerides in granulosa cells (Guraya, 1965; Vazma and Gurya, 1973) may also indicate the endogenous synthesis of vitellogenic substances within the ovary of reptiles.
The small cells of the granulosa layer appear first during the growth of the ovarian follicles while the intermediate and pyriform cells make their appearance later in large follicles. Based on the observations of occasional mitotic figures in small cells of granulosa, it may be inferred that the small cells are the oldest among the granulosa cells and that intermediate and pyriform cells are derived from the small cells as a result of differentiation. This observation conforms to views of Betz (1963) who has reported a similar observation on the ovary of \textit{N. rhombifera}. Pyriform cells are the large unicellular holocrine gland cells that establish communication with the ooplasm and they seem to transport their content across zona pellucida and discharge them into ooplasm. Electron microscopic studies have shown that the oocyte and the granulosa cells in reptiles develop microvilli that extend into one another (Blanc, 1971; Hubert, 1971 cited in Guraya, 1976). Zona radiata seen under the light microscope is the region where microvilli occur. Thus the occurrence of zona radiata in the ovary of reptiles indicates the existence of microvilli. The granulosa of large preovulatory follicles in the three reptiles comprises of a single layer of low cuboidal cells as in \textit{N. rhombifera} (Betz, 1963) and \textit{H. flaviviridis} (Guraya and Verma, 1976). Zona
pellucida is reduced owing to the resorption of zona radiata prior to ovulation.

The postovulatory follicles in the three lizards show a highly thickened and vascularised connective tissue theca that encapsulates the luteinised granulosa cells. In newly ruptured follicles, the luteal cells are disposed along the inside surface of the theca and later they fill the cavity inside the ovulated follicles. The thecal elements from the site of rupture or the stigma fold inside, become regenerative and proliferate off their elements that intersperse amidst the luteal cells. The reports on the origin of luteal cells, whether they arise from theca or granulosa or from both, are not unequivocal. The luteal cells in the ovaries of Thamnophis and Potamophis have been claimed to arise from granulosa only (Franchi, 1962). Boyd (1941) who has reviewed the relevant literature on the subject and made a detailed study of the postovulatory follicles in Lacerta vivipara and Hoplodactylus maculatus has also made a similar observation. Contrary to this observation, thecal contribution to the luteal elements has been claimed in certain oviparous and viviparous reptiles (Weekes, 1934; Miller, 1959). The origin of luteal cells from granulosa could not be ascertained in the histological study on the ovary of N. rhombifera (Betz, 1963). In the
lizards, *C. versicolor* and *H. flaviviridis*, the luteal cells are seen to arise from granulosa and the thecal elements form the trabeculae or the connective tissue septa amidst the luteinised granulosa cells.

Follicular atresia is a degenerative process common to all the vertebrate species and the atretic follicles are, as a rule, considered as degenerating follicles with doubtful endocrinial role (Lofts and Bern, 1972; Reinboth, 1972; Dodd, 1972; Varma and Guraya, 1973; Guraya, 1976). Recently, various aspects of follicular atresia in the ovaries of non-mammalian vertebrates have been reviewed by Saidapur (in press). Many variations are known to occur in the process of follicular atresia in different groups of vertebrates (Dominic, 1961; Varma, 1970; Varma and Guraya, 1973; Reinboth, 1972; Dodd, 1972; Guraya, 1976; Bhujle, 1977; Saidapur, in press). Based on these variations several types of atresia, namely, (1) previtellogenic, (2) yolky, (3) glandular, (4) haemorrhagic, (5) bursting and (6) cystic types have been categorised (Dominic, 1961; Crpino, 1973). Previtellogenic atresia has been studied in depth in the ovary of rat (Franchi, 1962). Here, the oocyte degenerates without any invasion of granulosa cells prior to vitellogenesis. Yolky atresia is characterised by the fact that granulosa cells detach from membrane propria and
invade the oocyte and phagocytose its contents. Glandular atresia is very similar to yolky atresia but for the fact that the granulosa cells do not separate from membra propria and the theca with its inner lining of granulosa becomes wavy, making inroads into the ooplasm. In haemorrhagic atresia, haemorrhage occurs in theca interna and the blood elements may spread to granulosa and peripheral region of the ooplasm. Bursting atresia occurs in case of largo follicles heavily laden with yolk. Here, the follicles rupture and the yolk contents of the oocyte are extruded into the ovarian stroma wherein they form ectopic yolk masses. In the teleost studied in our laboratory it is observed that oocyte represses in cystic atresia and the other components remain unaffected as in normal follicles (Shanbhag and Naskarni, unpublished data).

In previous studies on the ovary of C. versicolor, only yolky atresia has been described (Varma, 1970) and yolky and bursting atresia have been reported in the ovary of N. rhombifera (Setz, 1963). Guraya (1976) has made conflicting remarks about follicular atresia in the ovary of C. versicolor in his recent review on the ovaries of nonmammalian vertebrates. He has stated that no follicular atresia has been noticed in the ovaries of C. versicolor. However, he goes on to explain the origin of interstitial
gland cells of the ovarian stroma as from the atretic follicles in *C. versicolor*.

Our observations on follicular atresia in *C. versicolor* and *H. flaviviridia* tend to show that all the types of atresia except previtellogenic type occur in the ovaries. Follicular atresia in these lizards has been observed to take place during any developmental phase of the follicles and also during any phase of the reproductive cycle. In reptiles, the occurrence of atresia during any phase of ovarian growth and its annual cycle has been reported by earlier workers (Betz, 1963; Guraya, 1965; Varma, 1970). Thus our studies show that many types of atresia occur in the ovary of reptiles in which so far only two types i.e. yolky and bursting atresia have been reported.

Considerable attention has been devoted towards the question of origin and role of the interstitial cells of the ovarian stroma of the vertebrates and recent histochemical studies tend to show that interstitial gland cells arise from theca interna and that they are capable of steroid hormone biosynthesis (Guraya, 1976; Saidapur, in press). In *C. versicolor* and *H. flaviviridia*, our observation reveals that the granulosa cells, after invading the ooplasm and phagocytosing its contents disappear, the cells of theca interna, however, continue as interstitial gland cells of
the ovarian stroma in these reptiles. This observation is in agreement with the earlier findings on *H. chondriera* (Betz, 1963) *C. versicolor* (Varma, 1970; Varma and Guraya, 1973a,b) and *H. flaviviridis* (Guraya and Varma, 1976).

Thus the present histological studies on the ovaries of *C. versicolor*, *H. flaviviridis* and *C. calcaratus* indicate that the luteal cells of the postovulatory follicles arise solely from the granulosa cells, connective tissue septa being contributed by the thecal elements. Several types of atresia, namely, glandular, yolk, haemorrhagic, bursting and cystic atresia occur in the ovaries of these lizards. The cells from theca interna of atretic follicles probably transform into interstitial gland cells of the ovarian stroma.

As in other vertebrates, the histological features of the ovarian elements in reptiles never remain static and they undergo annual cyclic changes concomitant with those of the ambient ecological conditions and the breeding habits. The cyclic changes in the morphology and structure of the ovary in reptiles are described in the next Chapter (2).
SUMMARY

1 The histological structure of the ovary of C. versicolor, H. flaviviridis and C. calcaratus has been described.

2 The structure of the previtellogenic follicle, normal growing follicle, large prevulatory follicle, postovulatory follicle and atretic follicle has been studied.

3 Follicular atresia occurs in various ways and glandular, yolky, haemorrhagic, bursting and cystic types of follicular atresia have been observed in the three reptiles.

4 The luteinised cells seem to originate from the granulosa cells of postovulatory follicles. However, theca contributes to the connective tissue septa that traverse into the luteal body.

5 Interstitial gland cells of the ovarian stroma appear to arise from the theca interna cells of the atretic follicles.
EXPLANATION TO FIGURES

Fig. 1.1 Germinal epithelium (G) from the ovary of C. versicolor and the ovarian stroma replete with glandular interstitial stromal cells (I). X400.

Fig. 1.2 Primordial germ cells (G) and small normal follicles (NF) in the ovary of C. versicolor. Note the ovarian stroma showing connective tissue (T) and interstitial gland cells (I). X400.

Fig. 1.3 Ovary of C. calcaratus showing germ cells and young follicles. The oocyte (A) is seen in one of the newly formed follicles. X400.

Fig. 1.4 Section of the ovary of C. versicolor showing a large normal follicle (NF) and highly vascular stroma (ST). X100.
EXPLANATION TO FIGURES

Fig. 1.5  Ovary of C. versicolor. The normal follicle (NF) shows theca externa (TE), theca interna (TI), granulosa (G), vitelline membrane (V) and the ooplasm (arrow). The other, atretic follicle (AF) shows many layered polymorphic granulosa (G) and wavy and interrupted vitelline membrane (V). X100.

Fig. 1.6  Magnified view of the large normal follicle of C. calcarius. Theca externa (TE), interna (TI), granulosa of small (arrow), intermediate (I) and large pyriform cells (P), vitelline membrane (V), zona radiata (R), zona pellucida (Z) and the ooplasm (O). X400.

Fig. 1.7  Section of the ovary of C. versicolor during regression (September). Follicles in different conditions may be seen (NF=normal follicle; CL=corpus luteum; AF=atretic follicle undergoing cystic atresia; S=ovarian stroma). X100.

Fig. 1.8  Newly formed postovulatory follicle of C. versicolor. (T=theca; G=luteinized granulosa). X100.
EXPLANATION TO FIGURES

Fig. 1.9  Postovulatory follicles of *C. calgaratus* showing theca (T) and granulosa lutein cells (G). X100.

Fig. 1.10  Degenerating corpora lutea from the ovary of *H. flaviviridis* (S=stroma; C=degenerated corpus luteum). X200.

Fig. 1.11  Magnified view of the same. X400.

Fig. 1.12  Atretic follicle of *C. versicolor* showing glandular atresia. Granulosa cells (G) invade the ooplasm (o) without detaching from theca (T). X100.
EXPLANATION TO FIGURES

Fig. 1.13  Hemorrhagic atresia in the ovary of *C. versicolor*. Hemorrhage is seen in vascularized theca interna. Granulosa (G) becomes polymorphic and many layered (O=oo plasma). X100.

Fig. 1.14  Bursting atresia in *C. versicolor*. The granulosa cells (G) form wavy folds and the yolk oozes out through the rupture (R) of the burst follicle. X100.

Fig. 1.15  Bursting atretic follicles of *C. versicolor*. in an advanced stage of degeneration. X100.

Fig. 1.16  Atretic follicle (AF) in the ovary of *C. versicolor* undergoing yolky atresia (S=stroma). X100.
EXPLANATION TO FIGURES

Fig. 1.17  Atriotic follicle (AF) showing glandular atresia in the ovary of C. versicolor (G=granulosa; M=mature; S=stroma). X100.

Fig. 1.18  Section of the entire ovary of C. versicolor showing only atriotic follicles and reduced stroma (S). The section was taken in December. X40.

Fig. 1.19  Ovarian stroma of H. flaviviridis showing chords of interstitial gland cells. X200.