DEVELOPMENT OF THE CORPUS LUTEUM IN THE INDIAN LEAF-NOSED BAT, *HIPPOSIDEROS SPEORIS* (SCHNEIDER)

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ABSTRACT

The extrovert corpus luteum of *Hipposideros speoris* is formed by the evagination of the ruptured follicle. It develops rapidly reaching its maximum development by the time the blastocyst is implanted, after which it undergoes rapid regression until it disappears altogether by the time the chorio-allantoic placenta is formed. It is umbrella shaped during early stages of its development, but soon becomes converted into a large, nearly spherical, vascular ball connected to the rest of the ovary by a short, narrow isthmus. During this period the granulosa cells of the ruptured follicle hypertrophy and become vacuolated. During its regression there is a progressive shrinkage and devacuolation of the luteal cells accompanied by an invasion of the luteal tissue by the cells of the ovarian stroma and of the theca folliculi. The time relationship between the stages of development of the corpus luteum and the development of the embryo suggest that the endocrine functions of the corpus luteum are completely taken over by the placenta at an early stage of pregnancy in this bat.

INTRODUCTION

THE corpus luteum of bats, which have been so far described, can be recognized into three types : (1) The intra-ovarian corpus luteum which develops within the confines of the ovary. The development of this type of corpus luteum is characterized by the occurrence of a central fluid-filled cavity, which has been referred to as the central blood clot by some workers, in the ovulated follicle for some time after the release of the ovum. This cavity is progressively invaded and occupied by the hypertrophied luteal cells. Such a type of corpus luteum has been noticed in most of the bats so far studied[1-9]. (2) Extrovert corpus luteum, in which ovulation is immediately followed by the evagination of the ovulated follicle. Consequently, there is no central cavity in the follicle after the release of the ovum. Such a corpus luteum has been described in the British horse-shoe bats[10], *Rhinopoma kinneari*[11], *Megaderma lyra lyra* and *Hipposideros fulvus fulvus*[12]. (3) Pedunculated corpus luteum, which not only grows out of the confines of the ovary but there is a central cavity during the early stages of its development. This central cavity persists for some time, but is soon filled up by the hypertrophy of the granulosa cells of the ruptured follicle. At the height of its development the corpus luteum appears like a large solid ball of cells attached to the ovary by a stalk. Such a corpus luteum was noticed in *Rhinolophus rouxi*[13]. Whereas the details of development of the intra-ovarian corpus luteum[1,4,7] and some details of the development of the pedunculated corpus luteum[13] have been described, there is as yet no report on the manner of development of the extrovert corpus luteum. A true extrovert corpus luteum is, in fact, rare among mammals and has been shown to occur only in a few mammals[14-17] apart from the few bats mentioned above. Even in these mammals the manner of development of the extrovert corpus luteum has not been fully described.

MATERIALS AND METHODS

Specimens of *Hipposideros speoris* were collected at frequent intervals in and around Chandrapur in Maharashtra from 5th November 1977 until 14th May 1980. Many female specimens at various stages of pregnancy were also collected at Bangalore during the period from November 1977 to May 1979. The female genitalia were fixed either in Rossman's fixative or neutral formalin. The ovaries of the pregnant females were sectioned after following the usual procedure of dehydrating through graded ethanol, clearing in xylene and embedding in paraffin. The sections were stained either with Ehrlich's haematoxylin and counterstained with eosin or with Heidenhain's iron haematoxylin.

OBSERVATIONS

The breeding habits of *Hipposideros speoris* appears to differ at different latitudes as revealed by the following facts. Whereas conception commenced in the middle of November in a sharply defined period at Bangalore, the specimens in and around Chandrapur conceived at any time between the third week of December and the middle of March. Hence, while all pregnant females collected on a given date between November and May in and around Bangalore carried conceptuses at nearly the same stage of development and all the females in the colony delivered within a span of 8 to 16 days, the pregnant females collected in and around Chandrapur on any date between December and the following May carried conceptuses at different stages of development, and the period of parturition in the colony extended from the first week of May to the last week of July.

The pre-ovulatory follicle of *Hipposideros speoris* differs from that of all other species of bats so far described in the details of its structure. In sectional views of the pre-ovulatory follicle (Fig. 1) the ovum, surrounded by a circlet of one or two layers of cumulus cells, appears to lie freely in the antrum near about the centre of the follicle. A few cells also appear to lie scattered freely in the antrum. However, examination of serial sections reveals that several radiating strands of cells, which extend in a zig-zag manner, connect the cumulus layer with the granulosa layer at several places and the cells, which appear freely scattered in the antrum, belong to these irregular crooked strands.

The rupture of the follicle releasing the ovum is accompanied by the eversion of the granulosa layer through the point of rupture so that the granulosa layer becomes turned inside out (Fig. 2). Hence, the early corpus luteum has the shape of an umbrella connected to the ovary at the centre by a short stem—the isthmus. The corpus luteum is, therefore, outside the ovary from the beginning of its formation and there is no central cavity in the middle of the ruptured follicle. The rapid enlargement of the corpus luteum also results in the further reflection of the borders of the corpus luteum backwards over the sides of the ovary (Fig. 3). It reaches its maximum size just prior to implantation of the blastocyst, when the corpus luteum mushrooms out into a nearly spherical ball, which is considerably larger than the rest of the ovary to which it is attached by a short, narrow isthmus (Fig. 4). The commencement of the regression of the corpus luteum synchronizes with the formation of the early trophoblastic placenta, after which it appears progressively to shrink in size (Figs. 5 and 6) until it occurs as a small stump projecting from the surface of the ovary with a small part embedded within the ovary at the time when the chorio-vitelline placenta is well established (Fig. 7). The corpus luteum disappears altogether by the time the chorio-allantoic placenta is formed.

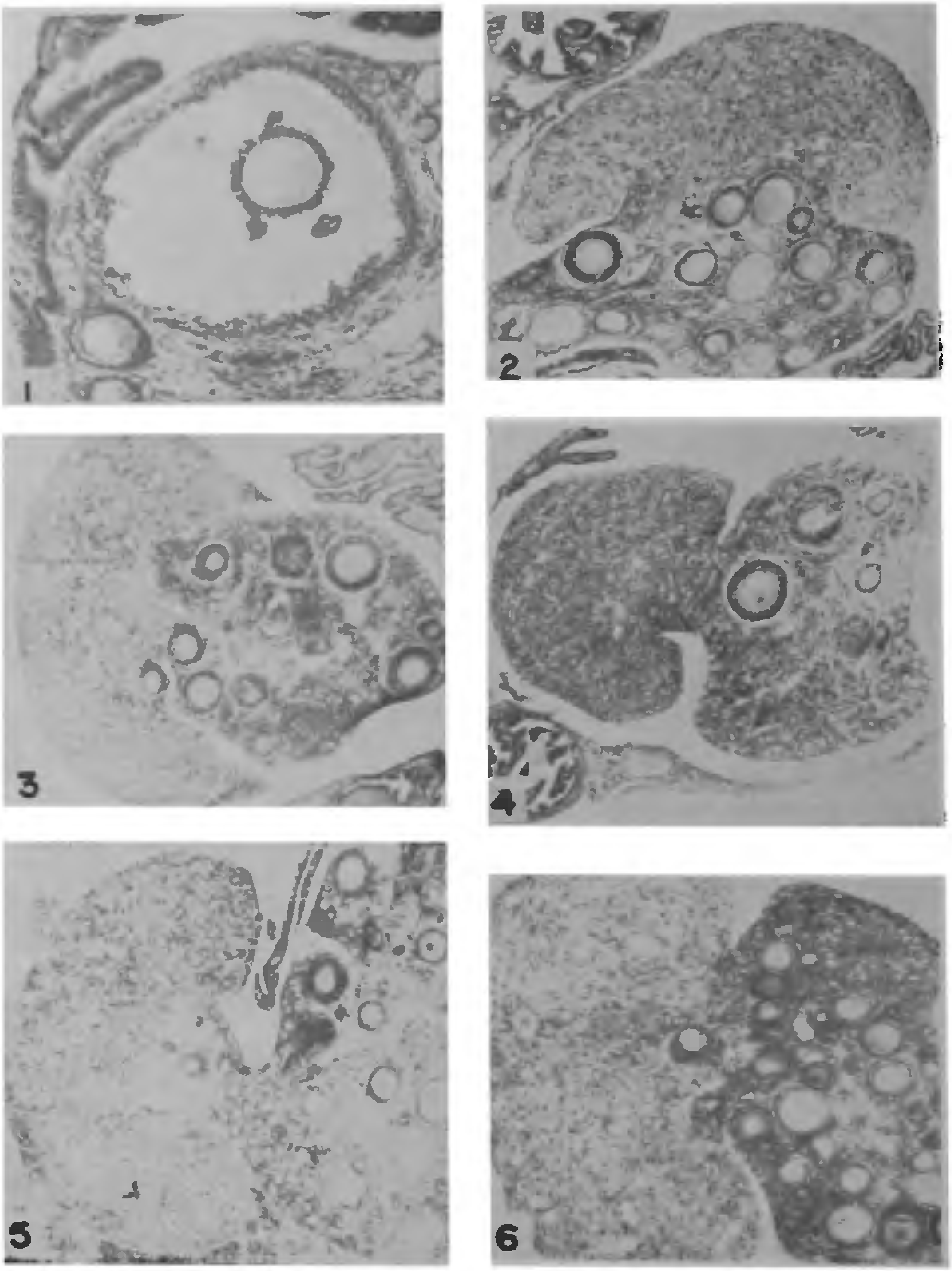
The histological changes in the corpus luteum can be recognized into three distinct phases. The first phase consists of an enormous hypertrophy and vacuolation of the granulosa cells (Fig. 8) accompanied by the invasion of the corpus luteum by numerous blood capillaries from the ovarian stroma through the isthmus. Since the entire Graafian follicle is turned inside out, and the corpus luteum has an umbrella shape, the theca folliculi, which originally surrounded the pre-ovulatory follicle, occurs in the form of a lining of small cells with darkly staining fusiform nuclei on the concave surface of the umbrella, whereas the hypertrophied luteinized cells themselves form the covering on the convex surface of the umbrella. A thick mass of cells derived from the thecal cells of the follicle occurs along the edge of the umbrella (Fig. 9). The first phase corresponds to the period between ovulation and hatching of the unilaminar blastocyst out of the zona pelucida.

The second phase of the development of the corpus luteum coincides with the period when the blastocyst expands in size and establishes contact with the uterus. During this phase numerous cells from the ovarian medulla invade the body of the corpus luteum and come to lie between the large luteal cells (Fig. 10). Likewise, the cells of the theca layer bordering the sub-umbrella surface of the corpus luteum also enter the corpus luteum from several points. The mass of small thecal cells at the margin of the corpus luteum expands over the umbrellar surface so as to form a covering to the umbrellar surface of the corpus luteum. During this phase, when the corpus luteum reaches its maximum size, there is also a considerable increase in the vascularity of the corpus luteum. Hence, at this stage the corpus luteum consists mostly of large cells with vesicular nuclei each with a well-defined nucleolus and a few small cells with darkly staining fusiform nuclei interspersed among the large ones (Fig. 11).

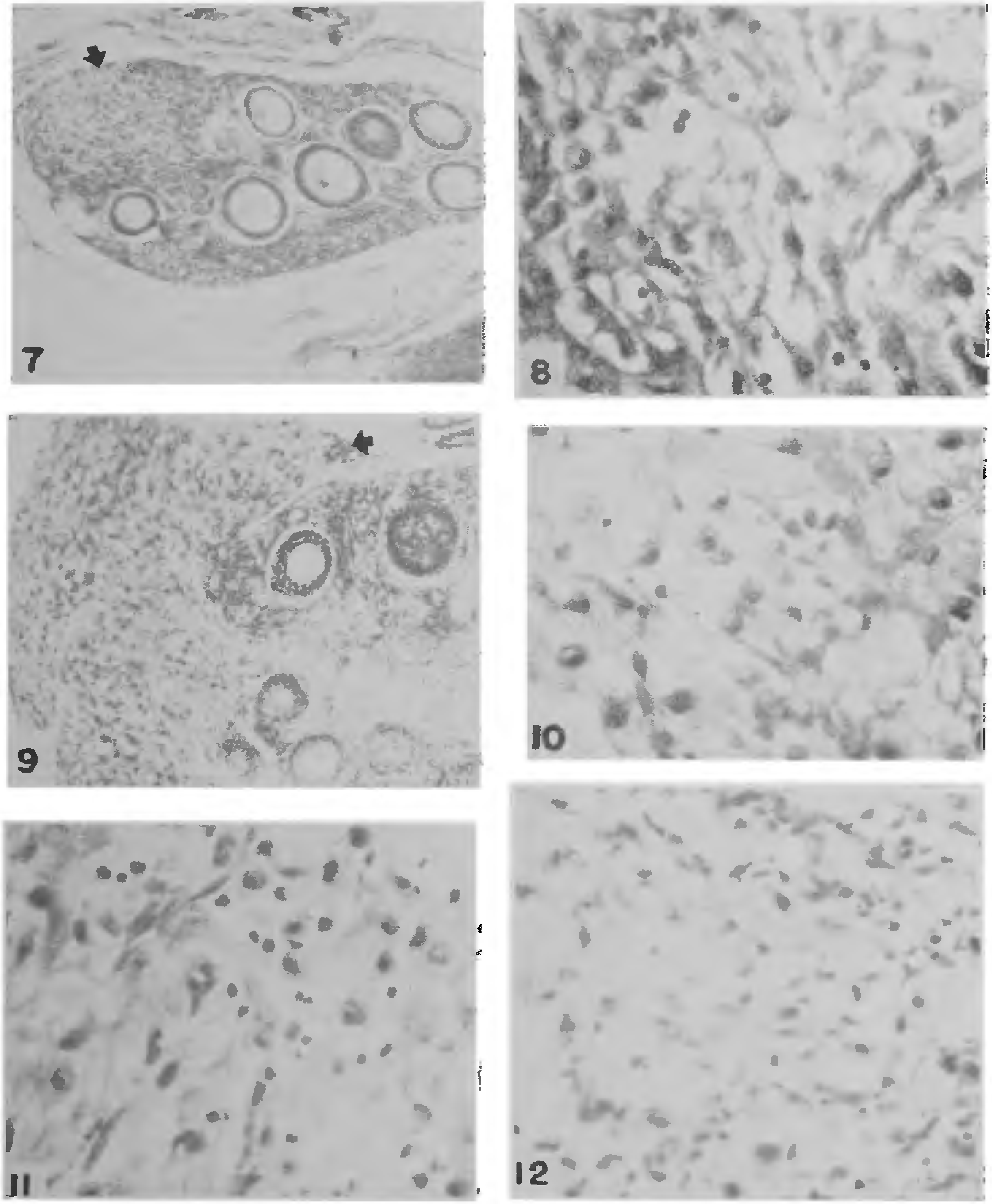
The third phase in the life of the corpus luteum consists in changes leading to its regression and ultimate disappearance, and commences after the blastocyst has become firmly implanted. There is a rapid augmentation of the process of invasion of the corpus luteum by the cells of the ovarian stroma through the isthmus and the thecal cells, which have enveloped the corpus luteum from several points. Concomitantly, the luteal cells lose their vacuolation and become progressively reduced in size. Hence, there is a progressive increase in the number of small darkly staining cells with a progressive reduction in the size of the corpus luteum (Fig. 12). During the final stages of regression, the luteal cells disappear completely and the corpus luteum contains only the small cells.

Discussion

From the foregoing it is evident that the corpus luteum of *Hipposideros speoris* has a very short life and occurs only during the first quarter of pregnancy.



Figs. 1–6. Fig. 1. Pre-ovulatory follicle of *Hipposideros speoris*. Note the apparently freely lying ovum surrounded by a circlet of cumulus cells and a few scattered groups of cells in the antrum × 116. Fig. 2. The corpus luteum within a short time after ovulation × 70. Fig. 3. The corpus luteum at the time when the embryo is at late morula stage of development. Note the extension of the corpus luteum over the sides of the ovary × 70. Fig. 4. Corpus luteum just prior to implantation of the blastocyst. Please see text for description × 70. Fig. 5. Corpus luteum when the embryo has a well-developed trophoblastic placenta × 70. Fig. 6. Corpus luteum when the embryo has a non-vascular yolk-sac placenta × 70.



Figs. 7–12. Fig. 7. Corpus luteum at late neural groove stage of the embryo when the chorio-vitelline placenta has been formed. Note the small remains of the regressing corpus luteum (arrow) × 116. Fig. 8. Magnified picture of the part of the early corpus luteum. Note that only large vacuolated cells are present × 450. Fig. 9. Part of the corpus luteum shown in Fig. 3. Note the mass of thecal cells at the margin of the umbrella (arrow) × 116. Fig. 10. Part of the corpus luteum at morula stage of development of the embryo. Note the large luteal cells amidst which there are a few smaller cells with dark nuclei × 450. Fig. 11. Part of the corpus luteum at late implantation stage of the embryo. Note the large number of small cells amidst a few large luteal cells × 450. Fig. 12. Part of the nearly regressed corpus luteum when the embryo has developed a chorio-vitelline placenta. The luteal cells have almost disappeared and there is a large population of small cells with dark fusiform nuclei, × 450.

In this respect this species resembles all other bats in which the corpus luteum is extrovert[11,12] or pedunculated[18]. It is noteworthy that in all these bats the corpus luteum at the peak of its development is considerably larger than the ovary. In the other species of bats the corpus luteum is intra-ovarian and persists throughout pregnancy[1,8,9], and in some monotocous bats experiencing quick succession of pregnancies the corpus luteum persists not only throughout pregnancy but extends to a short period of the succeeding pregnancy[2,6,19] Further, in all the bats possessing an extrovert corpus luteum there is a close time relationship between the development of the corpus luteum and the development of the embryo. The time of maximum development of the corpus luteum coincides with the time of implantation of the blastocyst, after which the corpus luteum regresses rapidly as the placenta becomes established and disappears altogether by the time the chorio-allantoic placenta is established. It is well established that the main function of the corpus luteum is the production of progesterone, which is necessary for the initiation and maintenance of pregnancy[20]. It is also well known that the placenta is also an important source of progresterone[20]. Evidently, the endocrine functions of the corpus luteum are completely taken over by the placenta in those bats in which the corpus luteum is extrovert or pedunculated, whereas in the other bats the corpus luteum and the placenta probably play a complementary role, and therefore, they co-exist after the establishment of the placenta.

ACKNOWLEDGEMENTS

P. A. Ramakrishna and Deepa Bhatia are grateful to the UGC for financial support in various ways for the successful completion of this research work.

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