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REPRODUCTION AND THE FEMALE REPRODUCTIVE CYCLE IN THE TROPICAL AMERICAN VAMPIRE BAT, DESMODUS ROTUNDUS MURINUS

WILLIAM A. WIMSATT AND HAROLD TRAPIDO
Laboratory of Histology and Embryology, Department of Zoology, Cornell University and Gorgas Memorial Laboratory, Panama

TWENTY FIGURES

Although 17 families of bats are currently recognized (Simpson, '45) the reproductive habits of less than half of them have thus far been investigated. Bats in which the reproductive habits are known fall into one of two groups: (1) those in which the phenomena of reproduction follow the general mammalian pattern, characterized, among other features, by restricted sexual seasons and coincidence of copulation and ovulation;[1] and (2) bats in which there is a prolonged storage of viable spermatozoa in the vagina or uterus of the female, the normal time of copulation, which first occurs in the fall, being separated by several months from the time when ovulation takes place in the spring.[2] Male bats

[1] This group includes most of the families of bats concerning which information is available, as follows: Megachiroptera — Pteropidae, Kohlbrugge ('13), Baker and Baker ('36), Groome ('40); Microchiroptera — Nycteridae, Mathews ('41); Megadermatidae, Mathews ('41), Gopalakrishna ('50); Phyllostomatidae, Hamlett ('34, '35); tropical Vespertilionidae, Baker and Bird ('36), Mathews ('41), Gopalakrishna ('47, '48); Molossidae, Howell ('19), Hartmann and Cuyler ('27), Sherman ('37).

[2] This group apparently includes only temperate zone, hibernating representatives of two families of the Microchiroptera, as follows: Rhinolophidae, Rollinat and Trouessart (1897), Courrier ('27), Mathews ('37); Vespertilionidae, Rollinat and Trouessart (1896), Grosser ('03), Courrier ('22, '27), Nakano ('28), Redenz ('29), Guthrie ('33), Miller ('39), Deanesly and Warwick ('39), Wimsatt ('42, '44a, b). Hartmann ('33) and Baker and Bird ('36) present extensive reviews of earlier work on reproduction in bats.

of the first group display a typical reproductive periodicity which coincides with that of the female. In males of the second group the same is true for a month or so immediately preceding the fall copulations, after which spermatogenesis ceases. These males are unique, however, in that the spermatogenic and interstitial cells do not have a complementary rhythm. Although spermatogenesis ceases in the early fall, the epididymides and accessory organs remain fully developed, spermatozoa are stored in the epididymides until spring, and the animals retain the ability to copulate throughout the winter. At least one family, the Vespertilionidae, comprises species belonging to both groups. Tropical representatives of this family belong to the first group, whereas the hibernating forms of the temperate zone, with one exception, belong to the second group. The exception is the European species Miniopterus Schreibersii, in which ovulation and fertilization occur in the fall coincident with copulation, but even this species makes some concession to the reduced metabolic levels of hibernation in that development of the ovum is markedly retarded during the period of dormancy, with the result that gestation is several months longer than in tropical representatives of the genus (Baker and Bird, '36).

The details of the reproductive cycle are best known in hibernating bats of the temperate zones (representatives of the Vespertilionidae and Rhinolophidae), and in a few tropical species (representatives of the Vespertilionidae, Phyllostomatidae and Molossidae) which have been most available to investigators. With regard to the other families mentioned many of the details are lacking, and the reproductive pattern has been deduced from a study of relatively few specimens.

Concerning the reproductive phenomena of the 10 families of bats not previously mentioned,[3] either no information whatever is available, or it is too meager to permit conclusions.

[3] These comprise the Rhinopomatidae, Emballonuridae, Noctilionidae, Hipposideridae, Desmodontidae, Natalidae, Furipteridae, Thyropteridae, Myzopodidae and Mystacinidae. Most of these families are tropical or semi-tropical in distribution.

It has been our good fortune to obtain specimens of the tropical American vampire bat, Desmodus rotundus murinus, a representative of one of these uninvestigated families. The specimens were obtained at various times of the year from the Chilibrillo caves in Panama, and from a hollow tree in the forest near Juan Mina, Canal Zone. The true sanguivorous bats of the American tropics comprise a separate family of the Microchiroptera, the Desmodontidae, consisting, according to Simpson ('45), of two genera, Desmodus and Diphylla. A third genus, Diaemus, which was recognized by earlier taxonomists (Miller, '07), has been given subgeneric status by Simpson and included in the genus Desmodus. The genus Desmodus thus contains two species, the genus Diphylla only one.

It is surprising, in view of the economic importance of the vampire bat as a transmitter of rabies and equine trypanosomiasis, the interest aroused by its blood-feeding habits, and its reasonable availability, that most basic aspects of its life history still remain uninvestigated. The present paper is intended to provide information concerning reproduction in this little known family. Principal emphasis will be placed upon the reproductive cycle of the female, but some aspects of reproduction in the male will also be presented. While our material and field observations are not as complete as we might wish, they are adequate to have enabled us to work out the general pattern of reproduction in Desmodus, and we have found it to have several unique features.

MATERIAL AND METHODS

Our material is summarized in table 1, together with dates of collection and other facts pertinent to reproduction in Desmodus.

The microscopic observations are based upon serial sections (cut in paraffin at 5 and 8 μ) of the ovaries, testes, and female reproductive tracts. Most of the tissues were fixed in 10% formalin, Bouin's, Zenker's and Helly's fluids, and an absolute alcohol-formalin mixture.

TABLE 1

Summary of sectioned material

NO	COLLECTION DATE	SEX	AGE	REPRODUCTIVE STATUS Females	Males	NO.	COLLECTION DATE	SEX	AGE	REPRODUCTIVE STATUS Females	Males
A	4/9/45	♀	Ad	Pregnant, implantation		22	5/5/46	♀	Ad.	Pregnant, 8mm. embryo	
B	"	"	"	" free blastocyst		23	"	"	"	Proestrus, late	
C	"	"	"	" neural plate		24	"	"	Imm.	Sexually immature	
4	"	"	"	" 15mm embryo		25	"	"	Ad	Proestrus, late	
5	"	"	"	" 28mm "		26	"	"	"	" "	
6	5/13/45	"	Imm	Sexually immature		27	"	♂	"		Active
7	"	♂	"		Inactive*	27a	"	"	Imm.		Inactive
8	"	"	"		"	27b	"	"	Ad.		Active
9	"	"	Ad.		Active*	28	11/28/46	"	"		"
10	7/14/45	♀	"	Pregnant, 41mm embryo		29	"	"	"		"
11	"	"	"	Estrus, post partum		30	"	♀	Ad.	Puerperium	
12	"	"	"	Proestrus, early		31	"	"	"	Pregnant, 2mm embryo	
13	"	"	"	" "		32	"	"	"	" 27mm "	
14	"	♂	"		Active	33	2/9/47	"	"	" 41mm. "	
15	"	"	"		"	34	"	"	"	Proestrus, early	
16	"	"	New-born		Inactive	35	"	"	"	Pregnant, morula	
17	2/3/46	♀	Ad.	Pregnant, implantation		36	"	"	"	" 2mm embryo	
18	"	"	"	" cleaving ovum		37	"	"	"	" 12mm "	
19	"	"	"	Proestrus, early		38	"	♂	"		Active
20	"	"	"	" "							
21	"	"	"	" "							

* The term "active" indicates that spermatogenesis was occurring and sperm were present in the epididymis. Neither was observed in "inactive" males.

Consecutive slides in each series were variously stained in Harris' hematoxylin and eosin, Heidenhain's iron hematoxylin, eosin and methylene blue, the Mallory azan and Masson trichrome stains, and the Bodian protargol silver technique as modified by Dawson and Barnett ('43).

OBSERVATIONS AND DISCUSSION

Some general aspects of the reproductive cycle

Sexual season. The vampire bat, Desmodus rotundus murinus, apparently has no well-defined sexual season, but appears to breed throughout the year. This conclusion is based upon the following 4 lines of evidence. (a) Pregnant females were captured throughout the year (table 1), whereas in bats with restricted sexual seasons pregnant specimens may be obtained during only a few consecutive weeks or months of the year. (b) A group of females collected at any one time may include individuals in all stages of the breeding cycle, namely, non-pregnant, pregnant and lactating specimens, whereas in bats having restricted sexual seasons all females tend to be in the same stage of the breeding cycle at any given time.[4] (c) Immature specimens have been collected throughout the year, whereas they are obtainable during only part of the year in bats with restricted sexual seasons. (d) Males in full sexual activity, as indicated by the occurrence of spermatogenesis, and the presence of spermatozoa in the epididymis, have been collected throughout the year, whereas in bats with a restricted sexual season the

[4] Indicative in this connection is the following spread of weights (in grams) of specimens of Desmodus collected all on the same date, November 28, 1946, at the Chilibrillo caves.

1. male, 11.5 (newborn)	6. male, 32.5	11. female, 41.0
2. male, 15.5	7. male, 38.0	12. male, 41.0
3. male, 21.5	8. male, 39.0	13. male, 41.5
4. male, 27.5	9. female, 40.0	14. female, 46.5
5. male, 27.5	10. male, 40.5	15. female, 48.5

This series represents practically the entire range of post-natal growth, from the newborn (11.5 gm), to the full adult (probably 38 gm and over). The first 6 specimens were clearly immatures, but were, nevertheless, in different stages of growth, indicating the lack of close correspondence in their birth dates.

male displays a seasonal reproductive periodicity which coincides with that of the female.

In the above respects Desmodus may be unique among the Microchiroptera. All other species concerning which information is available have been described as monestrous, and as having a restricted sexual season, usually in the early spring (cf. Hartmann and Cuyler, '27; Hamlett, '34; Baker and Bird, '36; Sherman, '37; Mathews, '41; Gopalakrishna, '47), but, in a few instances, in the fall (Hartmann, '33; Guthrie, '33; Wimsatt, '44a, b, '45).

After the original draft of this paper had been completed we were fortunate to uncover a reference by Verteuil and Urich ('36) in which the authors draw conclusions concerning the breeding cycle of Desmodus which are in complete accord with our own observations. They state (p. 326) that "Desmodus produces only one young at a time. The period of gestation has not yet been positively ascertained, but it is not less than 3 months. Bats with advanced embryos have been caught in January, June and September, and young bats were also born in captivity in November, whilst half-grown bats were observed in January and September. From the above data it seems obvious that breeding goes on all the year around."

Estrous cycle. Among the Microchiroptera a polyestrous[5] condition is apparently rare, for with but one exception,[6], all

[5] The terms "monestrous" and "polyestrous" have often been used ambiguously. In this paper we follow the definition of Heape ('00), Marshall ('22) and Asdell ('46). A "monestrous" condition is one in which estrus does not recur during the sexual season. If there are two or more sexual seasons per year separated by periods of anestrum, and only one estrous cycle occurs in each season, the monestrous condition still prevails. A "polyestrous" condition is one in which there is a recurrence of diestrous cycles during one or more sexual seasons, or throughout the year.

[6] Mathews ('41) collected females of the African bat Nycteris luteola (Nycteridae) which carried fetuses of approximately "half term," and which were at the same time in full lactation. He states that the ovaries and genital tracts gave every indication of being prepared for another pregnancy shortly after the birth of the young. He concludes that the species has two, and possibly three, pregnancies in rapid succession, and that the conditions described are ". . . compatible with the suggestion that this species may be polyestrous. . ."

species thus far investigated have been shown to be monestrous. Although conclusive proof that Desmodus is polyestrous has not been obtained, our observations do furnish presumptive evidence that this is the case, and definitely show, in any event, that the vampire may experience more than one estrous cycle per year. First, the year-around sexual activity of Desmodus already described is strongly suggestive of a polyestrous condition. Secondly, we possess two specimens which clearly demonstrate that one breeding cycle may follow closely upon a preceding one. The first of these is a female (specimen B, table 1) which contains a young blastocyst in an oviduct, and a new corpus luteum in the ovary of the same side. The opposite ovary contains a prominent fibrous scar (fig. 16) which is clearly the remnant of a degenerate corpus luteum, but whether of pregnancy, psuedopregnancy or diestrum cannot be definitely determined. How quickly such a scar might disappear entirely we are unable to say, but it is unlikely that a long time would be required, otherwise similar scars would be more often observed in our material. The current pregnancy probably was initiated soon after the termination of a previous pregnancy (considered most likely), pseudopregnancy, or sterile diestrous period, for it is exceedingly unlikely that an old corpus luteum would persist through a period of anestrum.

The second specimen is similar, but even more conclusive than the first. There can be no question that this specimen either was in estrus or had just passed through it, for the uterine lumen and glands are filled with spermatozoa (fig. 20), indicating that copulation had occurred recently. The uterus is hyperplastic and the glands are prominent, although to a lesser degree than in the previous specimen, which displays a characteristic progestational reaction. The uterus apparently had not yet come under the influence of progesterone. Furthermore, there is good reason to believe that this second specimen is a parturient one, for one horn of the uterus is appreciably larger than the other,[7] and contains in its somewhat dilated lumen a mass of debris of epithelial and connective tissue origin, and large numbers of leucocytes and red blood cells. The opposite, smaller, horn contains none of this material. Furthermore the ovary on the side of the larger cornu contains a degenerating corpus luteum consisting for the most part of fibrous tissue, but still containing scattered small nests of clearly recognizable lutein cells (fig. 18). It is unfortunate that in this critical specimen the opposite ovary and oviduct, on the side of the smaller cornu, were somehow lost, for this ovary must have contained a follicle which, if not recently ruptured, was nearing rupture. The presence of sperm, and the condition of the uterus, make this seem a certainty. This specimen, in which estrus has occurred in a still parturient individual, and the previous one, in which the same phenomenon presumably also occurred slightly earlier, demonstrate conclusively that Desmodus may, at least on occasion, experience a post-partum estrus, a phenomenon which is suggestive of a polyestrous condition. Thus Desmodus and the African bat Nycteris[8] are unique among the Microchiroptera thus far investigated in having more than one estrous cycle each year and in displaying the phenomenon of post-partum estrus.

Gestation. The gestation period of Desmodus is unknown, but there are indications that it is comparatively long. Ditmars and Greenhall ('35) obtained a female of the species which was kept isolated from the moment of its capture, and which gave birth to a living fetus after a little over three months in captivity. Mister Lawrence H. Dunn (personal communication) describes an adult female collected at the Chilibrillo caves on March 23, 1933, which was kept isolated from males, and which on August 26, 1933, gave birth to a living fetus. This remarkable record indicates that the gesta-

[7] The bicornuate uterus of Desmodus is symmetrical in form. Only in pregnant and parturient individuals is one cornu (that in which the ovum is, or was lodged) larger than the other.

[8] See footnote 6, page 420.

tion period may be in excess of 5 months — an unusual duration for a bat the size of Desmodus.[9]

The relatively enormous size attained by the fetus at birth is suggestive of a long gestation period. In one of our specimens judged to be near term the fetus measured 41 mm, crown-rump, and this in a species in which the adult is scarcely 90 mm in length.

Number of young. In comparison with most other small mammals bats are strikingly non-prolific. Most species are monestrous, and perhaps the majority produce but one offspring each year. A few species regularly produce two young at a time, and the red bat (Lasiurus borealis) of the United States, has been reported to produce on occasion as many as 4 (Lyon, '03), but in general, among bats, multiple births are exceptional. The secretive habits and surprising longevity (Trapido, '46) of bats are factors which no doubt enable them to maintain their numbers despite a relatively low reproductive potential.

Desmodus follows the pattern of the majority of bats in that it typically produces no more than one offspring at each pregnancy, for no specimen has yet been obtained which carried more than a single fetus. Apparently, in most instances only a single ovum is released at ovulation, for there is usually

[9] Data assembled from the literature suggest that among bats some direct correlation exists between the length of gestation and the size of the animals. It also reveals a tendency for the gestation period to be longer in tropical than in temperate zone species. Among smaller bats the gestation period varies from about 44 days in Pipistrellus pipistrellus (Deanesly and Warwick, '39) to between 50 and 60 days in Myotis lucifugus (Wimsatt, '45). Both of these vespertilionid bats live in temperate latitudes. In a small semi-tropical (central Florida) mollossid bat, Tadarida cynocephala, gestation lasts somewhat longer, 11 to 12 weeks (Sherman, '37), and in Miniopterus australis, a small tropical (New Hebrides) vespertilionid bat, it lasts just over three months (Baker and Bird, '36). A larger vespertilionid bat, Scotophilus wroughtoni, from tropical India, has a gestation period of 105 to 115 days (Gopalakrishna, '47). Among the largest bats, the old world fruit-eating bats of the family Pteropidae, estimates of gestation length range in different species from 4 to 6½ months (Baker and Baker, '36), the longer periods being found in the larger species. For most Pteropidae, however, the Bakers postulate a gestation period of 5 months. These bats are many times the size of Desmodus.

present only one corpus luteum of pregnancy. In this respect Desmodus differs from some American vespertilionid bats, which normally bear but one or two offspring, but which characteristically ovulate excess ova. The latter may develop to the point of completing implantation, but they are eventually resorbed (cf. Wimsatt, '45).

Two observations, however, indicate that in Desmodus occasionally more than one ovum may be shed. Firstly, biovular follicles are occasionally observed in the ovaries (fig. 17). If one of these matured, two ova would be released, but presumably only one corpus luteum would be formed. Practically, however, biovular follicles are so scarce that the principle of estimating the number of ova released on the basis of the number of corpora lutea in the ovaries may be applied to a large series of specimens with little danger of significant error. Secondly, we possess a specimen which contains a single implanted embryo, but which has in the ovary on the side of the pregnant horn two functional corpora lutea which are identically developed (fig. 19). It is most reasonable to assume that two follicles matured, and that two ova were shed, but that one either failed to develop further, or was resorbed early in its development. It is not considered at all likely that one of the corpora lutea represents an unruptured "luteinized" follicle. General appearances, and the character of the luteinization process in the ovaries of Desmodus do not make such a suggestion plausible.

Despite the two exceptions described, the majority of our specimens demonstrate that multiple ovulations are not typical in Desmodus, and it appears most likely that in the occasional instances in which more than one ovum is shed, usually only one of them survives gestation. The relatively enormous size attained by the fetus would, if more than one were present, presumably cause a deleterious crowding in the uterus and impose an excessive physiological strain on the mother. Accordingly, it is our opinion that multiple births, if they ever occur in Desmodus, are rare.

The number of young that a female of the species might produce in a lifetime cannot of course be determined accurately, but on the basis of certain assumptions a theoretical maximum figure can be arrived at which would probably never be exceeded, and which at least gives some indication of the maximum reproductive potential of the species. Since one fetus is produced at each pregnancy, and one breeding cycle probably requires between 5 and 6 months, and assuming that Desmodus is actually polyestrous, a theoretical maximum of two offspring might be produced during one year. Trapido ('46) has assembled longevity records which permit us to assume a 12-year minimum life span for the species. Assuming further, by analogy with other bats, that young females become sexually mature in time to bear one offspring in their first year, and that they produce the theoretical maximum for 11 years thereafter, each female might produce in her lifetime, under optimal conditions, a maximum of about 24 offspring.[10] By way of comparison, Myotis lucifugus of the eastern United States, which probably lives about as long as Desmodus (data from unpublished banding records), produces only one offspring per year, so that each female can beget in a lifetime a theoretical maximum of only about 12 offspring. A factor limiting the growth of Desmodus populations is their susceptibility to equine trypanosomiasis and rabies, diseases of which they are proven natural vectors. They are particularly susceptible to equine trypanosomiasis and ordinarily the disease proves fatal to them in less than a month, although there are records of recovery (Clark, '48).

[10] There is some possibility that the gestation period may last appreciably longer than the 5 to 6 months here estimated. In a personal communication dated January 24, 1952, Mr. Lawrence H. Dunn writes, "I left Panama about the first week in February, 1934, and I think that a baby vampire was born shortly after that, somewhere within two weeks to about three months after I left. . . I don't remember who informed me of the fact, but I remember deciding then that the gestation period must be not far from nine months. . . It is my impression that the vampires have a period of from six to nine months for. . . gestation. . ." If Mr. Dunn is correct in this, on the basis of the assumptions in the above paragraph Desmodus might produce a maximum of 4 young every three years or about 16 in a lifetime.

Sperm storage in the female. We have obtained no evidence that spermatozoa are ever stored for long periods in the uterus of Desmodus, as occurs, for example, in the hibernating bats of temperate zones. Spermatozoa were not observed in the uterus of any of our mature, non-pregnant specimens, and prolonged storage is therefore considered highly improbable. Not only do the factors of the breeding cycle in the male and the female indicate otherwise, but storage appears to be an adaptation to the hibernating habit, and would seem to serve no useful purpose in a tropical, non-hibernating species.

Microscopic analysis of the female reproductive cycle

In Desmodus both ovaries are functional, for vesicular follicles are observed in each, and the corpus luteum of pregnancy has been found, in different individuals, in both right and left ovaries. In this respect Desmodus differs from a small number of other Microchiroptera (e.g., Tadarida cynocephala, cf. Sherman, '37; Rhinolophus hipposideros minutus, cf. Mathews, '37) in which only one ovary, usually the right one,[11] is functional. Furthermore, there is some indication that the two ovaries might function alternately in a rhythmical manner. In the first place, in two specimens in early pregnancy which appear to have experienced a post-partum estrus, the degenerate and viable corpora lutea are in opposite ovaries. Secondly, although the ovaries of specimens in early proestrum contain approximately equal numbers of growing vesicular follicles, those of two specimens presumed to be in late proestrum display an imbalance in vesicular follicle content. In each case one ovary is larger than the other and contains the greater number of vesicular follicles, which are also noticeably larger than those in the smaller, less active ovary.

[11] An interesting exception is Miniopterus dasythrix, an African vespertilionid bat in which the fetus is always lodged in the right cornu of the uterus, but the corpus luteum is consistently observed in the left ovary. The right ovary, however, does not appear to be physiologically atrophied (Mathews, '41).

The cycle of activity in the ovaries of Desmodus follows the pattern of other estrous mammals, except that corpora lutea have not been observed in non-pregnant specimens. The absence of spurious corpora lutea could conceivably indicate that a nervous stimulus is required before ovulation can occur, but this is considered unlikely by analogy with numerous other bats in which ovulation is known to be spontaneous (Wimsatt, '42, 44a, b, and others). Furthermore, it is entirely probable that the absence (or perhaps scarcity) of corpora lutea in non-pregnant animals may merely be a consequence of the habits of Desmodus which are such as to ensure almost continuous contact between males and females. The animals live during the day in small colonies comprised of individuals of both sexes. There seems little likelihood that females in heat will miss being inseminated, and therefore little probability that ovulation would not be followed by pregnancy.

Whether conditions of pseudopregnancy, or diestrum, would ensue in the event that fertilization did not occur, our material does not permit us to say. It would be of interest to determine this point in isolated captive females. Conditions suggestive of pseudopregnancy have, to the best our our knowledge, been described in only one species of bat, Glossophaga soricina, of the Phyllostomatidae (Hamlett, '34, '35).[12]

Structure of the immature ovary. We possess serial sections of the ovaries of two immature specimens. The ovaries are smaller than in the adult and the demarcation between

[12] The species has a restricted breeding season, during which Hamlett ('34) collected mature, non-pregnant females with corpora lutea in the ovaries. Some of these specimens he described as being "pseudopregnant," and others as "menstruating." The menstrual bleeding takes place from a degenerating hypertrophied endometrium (of pseudopregnancy), and according to Hamlett ('34) is identical to menstruation in Primates except in point of frequency. Since the species has only one estrous cycle per year there is opportunity for only one bleeding each year. Hamlett makes no mention of changes in the mammary glands or behavior phenomena which accompany typical pseudopregnancy in such mammals as the dog and rabbit, and there is perhaps some question as to whether the phenomenon he describes in Glossophage is to be intrepreted as pseudopregnancy as usually defined (cf. Asdell, '46), or as a purely diestrous phase which will shortly be succeeded by anestrum.

cortical and medullary areas is not sharply defined (fig. 3). Vesicular follicles [13] are absent, and only a few secondary follicles are present near the center of the organ. These consist of primary oöcytes which have not yet attained maximum size, surrounded by not more, and usually less than three layers of follicular cells (fig. 4). Primary follicles are abundant, however, and vary in size, the smaller ones lying nearer the surface of the ovary (fig. 3). The oöcytes are surrounded by a single layer of flattened follicular cells, except that these are cuboidal in the largest growing primary follicles. The nuclei of oöcytes in primary follicles are always centrally situated, but have become slightly eccentric in the larger secondary follicles. The oöcyte does not attain full size during the primary follicle stage.

Follicular atresia is prominent among the secondary follicles, but was not observed among the primary ones. It is characterized initially by the hypertrophy and apparent luteinization of the stromal cells (of the theca interna) immediately surrounding the layer of follicular cells. There is thus formed an encircling zone of interstitial tissue 3 or 4 cells wide about the atretic follicle. Interstitial cells are not conspicuous elsewhere in the ovarian stroma and it is presumed that they are formed only in accompaniment of follicular atresia, and that they also rapidly disappear. A similar condition is observed in the adult ovary (fig. 10). In atretic secondary follicles of the immature ovary the oöcyte most often degenerates completely before the follicular cells disappear, and follicles in advanced atresia are identified as nests of follicular and interstitial cells. In atretic vesicular

[13] In this study ovarian follicles are classified as one of three types — primary, secondary and vesicular (Graafian). Primary follicles are those in which the ovum is surrounded by a single layer of follicle cells, including not only primordial follicles in which the follicle cells are squamous in form, but also early growing follicles in which the ovum has begun to enlarge and the follicle cells have hypertrophied. Secondary follicles are growing follicles in which the ovum is surrounded by two or more layers of follicle cells. With the appearance of clefts, presaging the formation of the antrum, the follicle is designated a vesicular follicle.

follicles of adult ovaries, on the other hand, the granulosal layer disappears long before the ovum does.

A conspicuous feature of both the immature and adult ovary of Desmodus is the prominence of the germinal epithelium (figs. 1, 2, 10). The latter is composed of cuboidal and columnar cells which contain relatively large, oval nuclei. A careful examination of this epithelium in the immature ovary has revealed unmistakable evidence of activity which indicates that it is a source of ova and follicle cells in the post-natal period. At various places in the epithelium may be observed localized areas in which the cells have hypertrophied, and perhaps proliferated, to form small oval or circular masses which bulge into the underlying stroma (fig. 1). Eventually, one of the cells in each of these masses outstrips the others in growth with the result that the smaller ones are crowded outward and become flattened about the more rapidly enlarging cell at the center. When this stage has been reached the cellular complex protrudes conspicuously into the stroma, and its primary follicular character is unmistakable. With further development the follicle loses its contact with the germinal epithelium and moves deeper into the stroma. Small globular masses and short cords of epithelioid cells which are also frequently observed in the stroma immediately beneath the germinal epithelium (fig. 2) likewise appear to have been derived by proliferation or invagination of the germinal epithelium, and constitute an additional source of primary follicles.

Structure of the adult ovary. The ovary of the adult differs from that of the immature specimen only in that it is larger and displays a different follicular composition, varying in accord with the stages of the breeding cycle. The general follicular content of the adult ovary probably approaches most closely to that of the immature ovary immediately after parturition, at which time there is an absence of vesicular follicles and a paucity of larger secondary follicles. At this period, however, a degenerate corpus luteum is invariably present.

The initiation of an estrous cycle is indicated by an increase in the number of secondary follicles and the gradual transformation of some of them into vesicular follicles (fig. 5). We possess 7 adult specimens in which vesicular follicles are present in both ovaries, and which, because the sizes of the largest follicles vary in different individuals, are presumed to be in various stages of proestrum. This conclusion is supported by the fact that in the different specimens there is a direct relation between the sizes of the largest follicles and the degree of endometrial hyperplasia. In those specimens in which antra are just beginning to appear in the largest follicles, hyperplasia of the endometrium is not obvious. In specimens in which the largest vesicular follicles are of medium size, however, there is some elongation and increase of the uterine glands, as well as a thickening of the endometrium. In two specimens in late proestrum in which the vesicular follicles are very large and about to enter the period of preovulatory growth, hyperplasia of the endometrium is very marked; mitotic figures are numerous in both the epithelial and connective tissue constituents, and the endometrium has appreciably thickened.

Vesicular follicles are most numerous in earlier stages of proestrum (figs. 5, 8) and gradually decline in numbers as estrus approaches. The two ovaries may contain from 20 to 40 small vesicular follicles (including atretic ones) early in the proestrous period, and usually less than half this number in late proestrum. Furthermore, at all stages of proestrum some of the largest follicles, as well as many of the smaller ones, become atretic. As proestrum progresses, therefore, many of the vesicular follicles degenerate, some early before they attain any considerable size (fig. 6), others later, after significant growth (fig. 10). In our two latest proestrus specimens the number of non-atretic vesicular follicles is reduced to 4 to 8 in each, with an approximately equal number of obviously atretic ones. In each of these specimens, furthermore, one of the non-atretic follicles is conspicuously larger than the others (fig. 9), and since estrus is apparently imminent, this largest follicle in each of the two specimens is presumably the one which will experience preovulatory growth and ovulation. Following ovulation the degeneration of the remaining unruptured follicles is extremely rapid, for in specimens containing late cleaving ova in the oviducts vesicular follicles have entirely disappeared from the ovaries, and even the remaining secondary follicles are in advanced atresia.

We possess only one specimen, already described (p. 421), which was either in estrus, or had just passed through it, when killed. Since the ovary which presumably contained a preovulatory or newly-ruptured follicle was lost, it has not been possible to determine whether extrusion of the first polar body precedes ovulation as in other bats (Wimsatt, '44b), or follows rupture of the follicle as is known to occur in the hamster (Ward, '46) and some Canidae (Asdell, '46).

Before describing the condition of the ovaries during pregnancy we shall present a brief description of the vesicular follicle in Desmodus. Small and medium vesicular follicles are characterized by a thick granulosal layer, which becomes relatively reduced, however, as the antrum continues to enlarge (figs. 6, 7, 9). The cumulus oophorus is eccentric, and broadly attached to the granulosa at one side as in most other mammals, rather than being supported within the antrum by cellular retinacula as in Myotis lucifugus (Wimsatt, '44b). Only in late proestrum do the follicular cells at the base of the cumulus loosen, presaging the freeing of this body from the granulosa (fig. 9). Furthermore, the cumulus cells resemble the granulosa cells, as in most mammals, and do not display the peculiar hypertrophy characteristic of the cumulus cells of hibernating vespertilionid bats (Wimsatt, '44b) which most certainly represents a physiological adaptation to the survival of the follicle over the several months of hibernation (Wimsatt, '49). In all other respects the follicles of Desmodus resemble those of other mammals.

During pregnancy the ovaries of Desmodus are completely devoid of vesicular follicles, or large secondary follicles, which indicates that the species does not ovulate during this period. Throughout gestation, follicles become atretic when they reach a late primary or early secondary stage. Atresia is also observed among the smaller primary follicles, and the latter are far less numerous than in the ovaries of immature or proestrous specimens. Evidence of proliferation in the germinal epithelium was not observed in specimens in advanced pregnancy.

The corpus luteum of pregnancy is relatively very large and occupies almost the entire ovary (fig. 15). As a consequence, the ovary bearing the corpus is always much larger than the opposite one, appearing oftentimes to have two or three times the volume of the latter. Another unusual feature is the rapidity with which the corpus luteum develops. Corpora lutea of pregnancy of different ages are illustrated in figures 11 to 15 inclusive. The only specimen in which a central cavity is still present within the corpus (fig. 11) is one in which a cleaving ovum of approximately 6 cells lies in the oviduct of the same side. Already, however, the original cavity has been invaded by connective tissue, and the lutein cells nearer the periphery of the body have attained near-definitive size. In two other, slightly more advanced specimens, containing in the oviducts a morula and a small blastocyst respectively, the follicular cavity has become completely filled with connective tissue, and reduced in diameter over the preceding specimen by the hypertrophy of the innermost lutein cells (figs. 12, 13). Both the corpus luteum as a whole, and the individual lutein cells, appear to have attained maximum size. Older corpora lutea are similar to these, except that the fibrous central area is ultimately completely filled in with lutein cells (figs. 14, 15). Mitotic figures were not observed within the corpora lutea, and it is probable that most of their increase in size is attributable to the hypertrophy of the individual lutein cells. Evidence that thecal cells participate in the formation of lutein cells was not obtained.

In routine histological preparations the cytoplasm of the lutein cells has a homogeneous texture during the earlier half of pregnancy. In all of our older specimens, however, the cells are vacuolated. In younger vacuolated specimens the vacuoles are of approximately equal size and completely fill the cytoplasmic area, giving the cell a foamy appearance similar to that of the cells of the fascicular zone of the adrenal cortex. In more advanced specimens the vacuoles are of irregular size and distribution. There is little doubt that the vacuoles represent the sites of lipid droplets. Their accumulation in the lutein cells, and especially their irregular form in later stages, may, in Desmodus, as in other mammals, be associated with a decreasing secretory activity of the corpus luteum, although this has not been demonstrated.

The rapid morphological development of the corpus luteum is apparently accompanied by an equally rapid physiological development, for while the fertilized ovum is still within the oviduct a progestational reaction occurs in the uterus which is far more conspicuous than that in any other bat thus far described (cf. Wimsatt, '44c). These changes will be described in detail in a later paper dealing with the early embryology and placentation of Desmodus.

Unfortunately, in the collection of material for this study the vaginae were not preserved, so we are unable at present to describe the histological changes of the vaginal mucosa during the estrogenic and progestational phases of the reproductive cycle.

SUMMARY AND CONCLUSIONS

This paper presents observations on the breeding habits and the female reproductive cycle of Desmodus rotundus murinus, a true vampire bat inhabiting Central America, and a member of a family of Microchiroptera, the Desmodontidae, the reproduction of which has not heretofore been described.

Desmodus is unique among bats thus far investigated in that it has no well-defined sexual season, and apparently breeds throughout the year. The species is also unusual among bats in that it appears to be polyestrous, and does, at least on occasion, experience a post-partum estrus. A similar condition has been described thus far in only one other bat, Nycteris luteola of the Nycteridae (Mathews, '41), but even this species differs from Desmodus in that its recurrent estrous periods occur during only a part of the year, that is, it is "seasonally polyestrous." All other Microchiroptera thus far studied are clearly monestrous.

The gestation period in Desmodus is comparatively long for a bat of its size, and is known with certainty to require at least 5 months. Only a single fetus is born of each pregnancy. It may be lodged in either horn of the uterus, which is symmetrically developed, and is relatively enormous at birth. Ordinarily only a single ovum is released at ovulation, but it may come from either of the two ovaries. Occasionally more than one ovum may be released, either by the rupture of more than one follicle, or by the rupture of a polyovular follicle, but such second ova apparently fail to implant.

The structural characteristics of the ovary at various stages of the estrous cycle and pregnancy are described. There is some evidence which indicates that the ovaries may function alternately in producing ova in successive breeding cycles. The origin of ova and follicular cells from the germinal epithelium has been observed.

The vesicular (Graafian) follicle, and the growth of the corpus luteum of pregnancy are described briefly. The latter is characterized by its rapid morphological and physiological development, and its large size. Vesicular follicles are absent during pregnancy. Corpora lutea have not been observed in non-pregnant specimens, and it is therefore not known whether a failure of fertilization would be followed by pseudopregnancy, or a sterile diestrous period. We have no evidence that Desmodus ever experiences anestrum.

Spermatozoa are not stored for prolonged periods in the female genital tract as occurs in hibernating bats of the temperate zones. The vampire bat is non-hibernating, and sexually active the year around, so there is little need for storage, which seems to have arisen in adaptation to the hibernating habit.

ADDENDUM

While this paper was in press Pearson, Kofoid and Pearson ('52) published a most detailed study of reproduction in the California lump-nosed bat, Corynorhinus (Plecotus?) rafinesquei. The reproductive cycle resembles in general that of other hibernating vespertilionid bats, but the authors fill in many details not previously recorded. Among the most interesting are the following: (a) In Corynorhinus, as in Myotis lucifugus (Wimsatt and Kallen, '52), females may be inseminated while hanging torpid in hibernation. (b) The unique hypertrophy of the cumulus cells surrounding the ovum in the surviving Graafian follicle of hibernation, first described by Wimsatt ('44b, '49), is believed by these authors to be a specific post-copulatory response for it did not occur in hibernating females denied copulation in fall and winter; if this be true, and non-hypertrophied follicles of non-inseminated bats do indeed fail to rupture in the spring, it will necessitate a revision of the generally accepted notion that ovulation in hibernating bats is "spontaneous." (c) Evidence is adduced that there is considerable variability in the length of the gestation period, primarily in response to climatic fluctuations in temperature from place to place and year to year; the estimated extremes (based on colony rather than individual averages) were 76 and 100 days respectively.

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PLATE 1

EXPLANATION OF FIGURES

1 Margin of ovary of an immature specimen showing the germinal epithelium, and within it (arrow) a cluster of hypertrophied cells from which a primary follicle would ultimately develop. × 430.

2 Margin of ovary of immature specimen showing the germinal epithelium, and an invaginated segment of the latter (arrow) of the sort which gives rise to oögenic cords and masses of cells which may frequently be observed immediately beneath the germinal epithelium. × 430.

3 Section of entire ovary of an immature specimen showing the peripheral distribution of primary follicles, the central location of secondary follicles, and the absence of vesicular follicles. × 40.

4 A secondary follicle under higher magnification. Note the multi-layered follicular epithleium and the eccentric position of the nucleus in the oöcyte. × 430.

5 Ovary of adult in early proestrum. Secondary follicles are more numerous than in the immature ovary, and small vesicular follicles are evident. × 60.

6 Ovary of adult in early proestrum. A normal vesicular follicle is visible at the center of the figure. Note the thickness of the granulosa and the eccentric position of the nucleus in the oöcyte. At the upper left may be seen a vesicular follicle in advanced atresia. The granulosa is practically gone, and the theca has formed a conspicuous fibrous cuff about the follicle. In non-atretic follicles the theca is relatively inconspicuous. × 100.

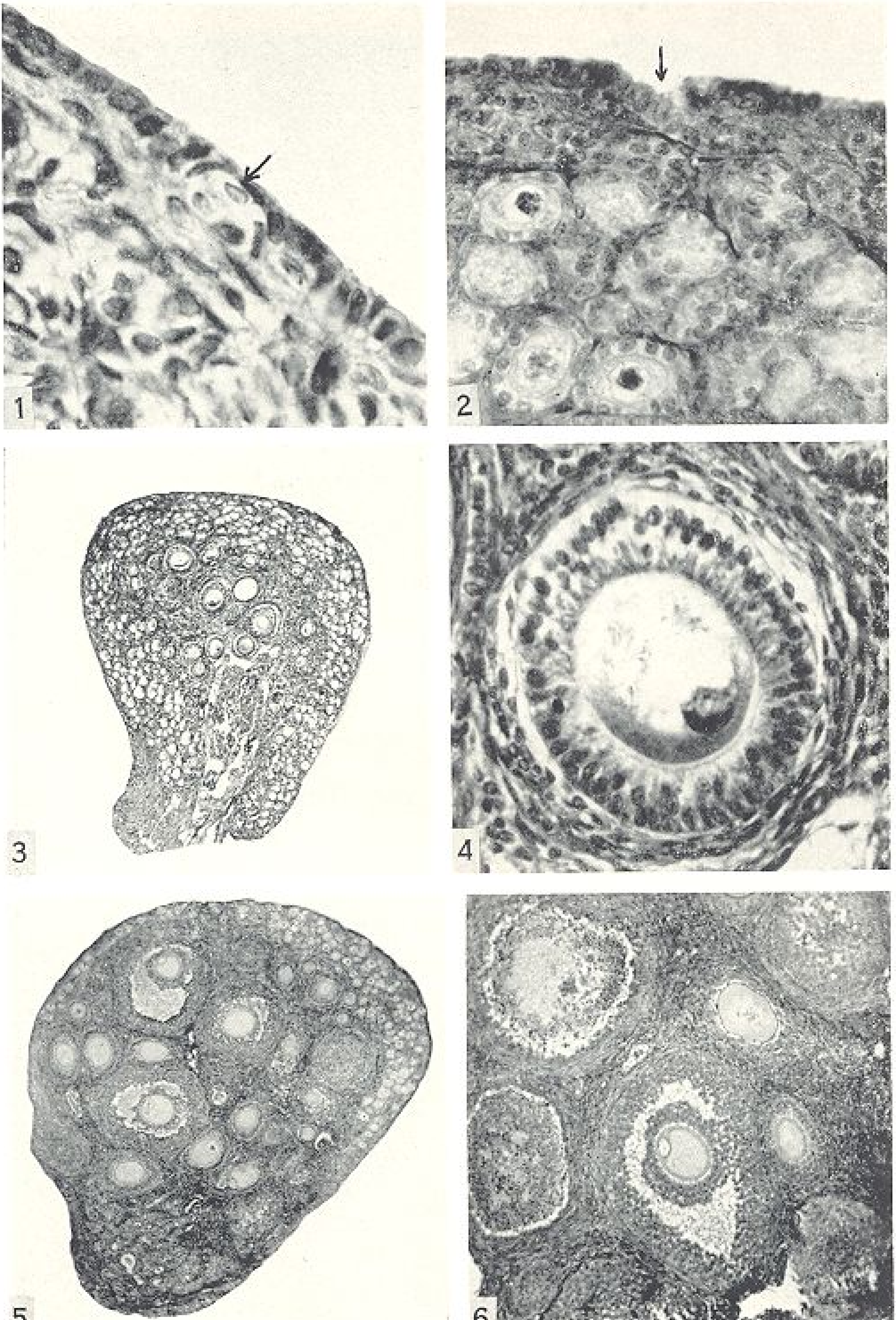
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PLATE 2

EXPLANATION OF FIGURES

7 Ovary of adult in proestrum. A normal vesicular follicle of slightly less than medium size is shown. The granulosa is still relatively thick, the antrum undivided. The attachment of the discus proligerus to one side of the follicle is characteristic of Desmodus, and is one of the features by which it differs from certain hibernating vespertilionid bats in which the discus is suspended within the antrum by cellular retinacula. Note atretic vesicular follicles at lower left and right. × 100.

8 Ovary of adult in mid-proestrum. Note the large number of growing vesicular follicles and two atretic follicles (arrows). × 60.

9 Ovary of adult in late proestrum. The number of vesicular follicles has become reduced. The three smaller ones shown here are atretic (note the fibrous thecal cuffs). The large follicle is normal and is the only one of its size in the two ovaries of this specimen. It appears to have initiated the preovulatory spurt of growth, but the oöcyte has not yet experienced the first maturation division. A loosening of the discus cells is apparent beneath the oöcyte. × 60.

10 Ovary of late proestrum showing a large vesicular follicle undergoing atresia. The granulosa is degenerate and sloughing, the liquor folliculi is undergoing inspissation, and the fibro-cellular thecal cuff characteristic of atretic follicles is well developed. × 100.

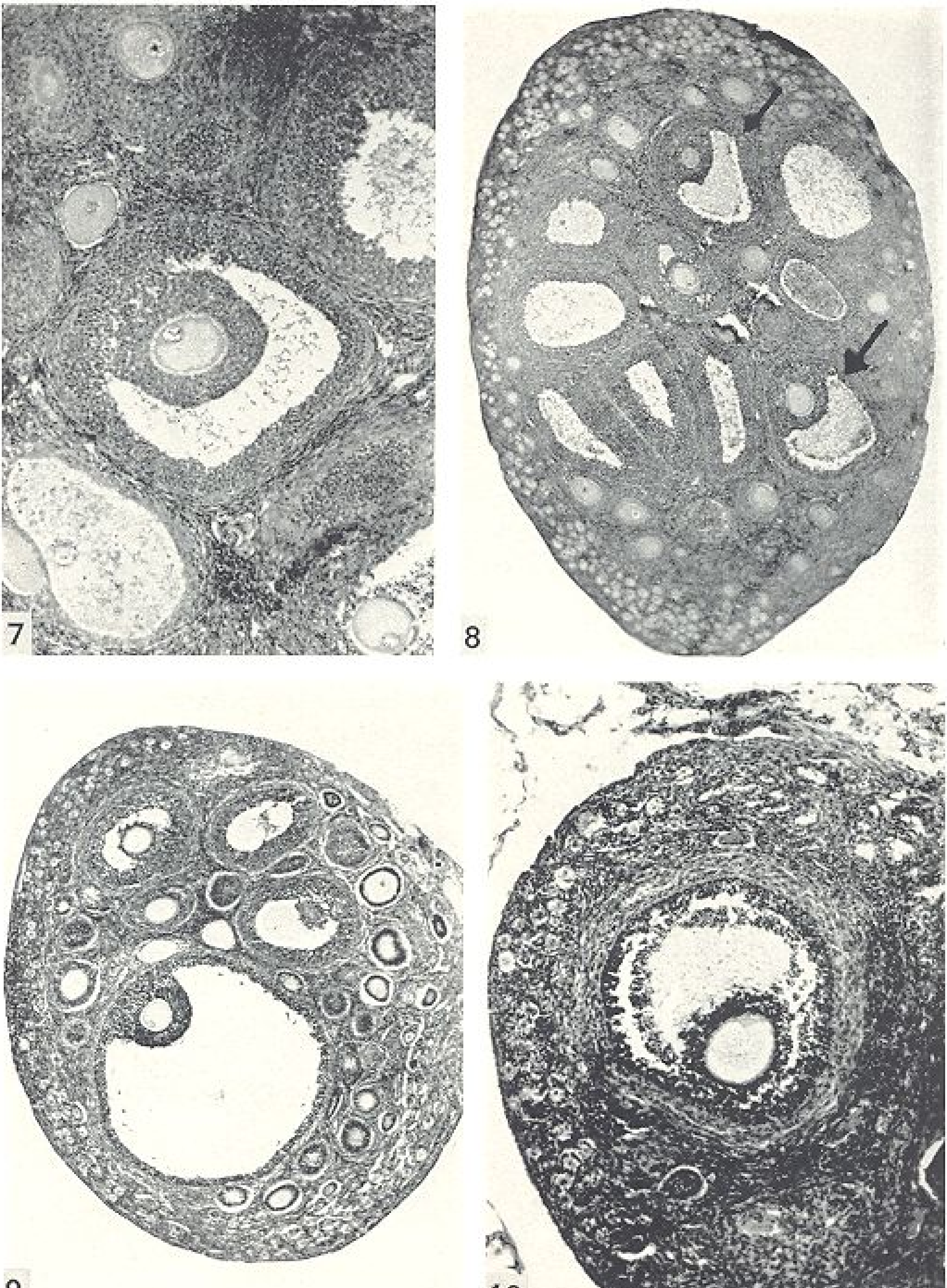
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PLATE 3

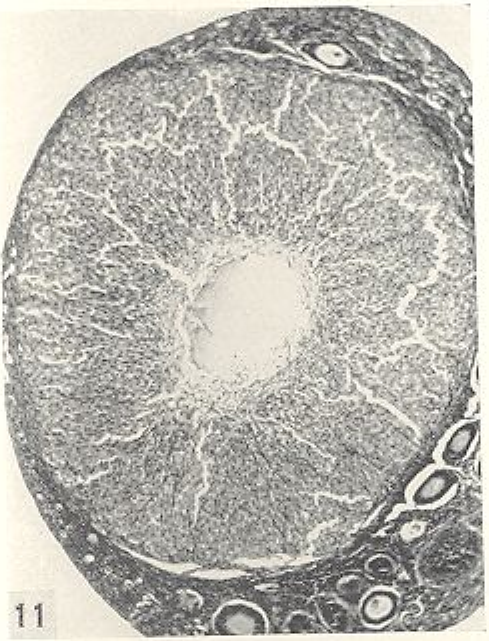
EXPLANATION OF FIGURES

11 Early developing corpus luteum of pregnancy. The oviduct associated with this ovary contained a cleaving ovum of 6 blastomeres. Note that a central cavity is still present in the corpus luteum, but that it is beginning to fill in marginally with connective tissue. The lutein cells near the periphery are larger than those nearer the central cavity. × 60.

12 Early developing corpus luteum of pregnancy at a slightly later stage than the preceding one. The associated oviduct in this instance contained a solid morula of about 40 cells. The central cavity of the corpus has been completely filled in with connective tissue. The lutein cells are appreciably hypertrophied in comparison with the preceding specimen. The irregular cleft is an artifact. × 100.

13 Developing corpus luteum in a specimen in which the associated oviduct contained a small blastocyst. Lutein cells have practically filled in the central cavity and are approaching maximum hypertrophy. × 60.

14 Corpus luteum at the stage of implantation of the blastocyst. The lutein cells are maximally hypertrophied, and evidence of a central cavity is all but obliterated. The corpus occupies almost the entire mass of the ovary. × 60.



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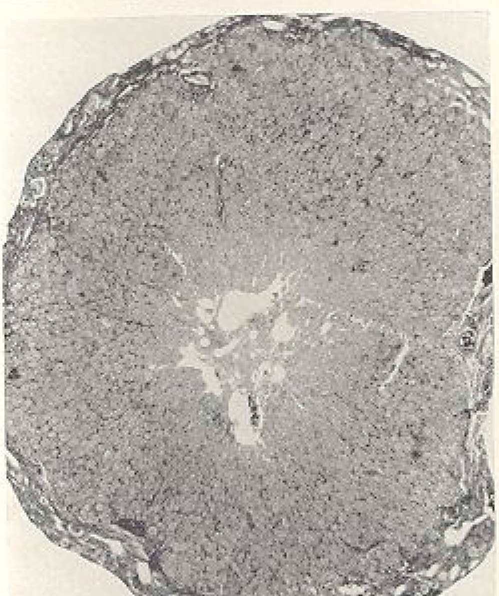

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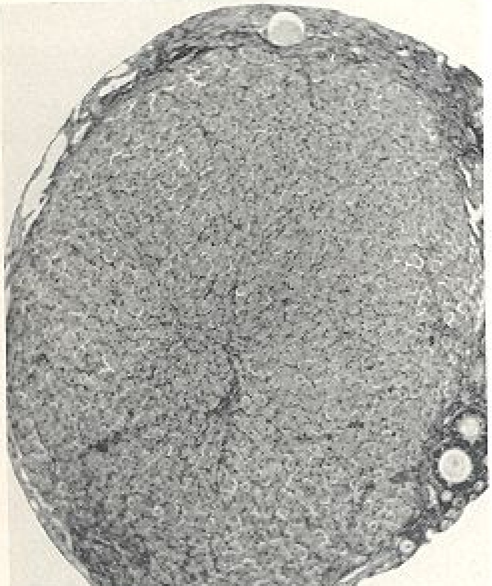

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PLATE 4

EXPLANATION OF FIGURES

15 Corpus luteum at mid-gestation. The organ is large, and gives every appearance of being in full function. The ovary containing it is appreciably larger than its mate. × 40.

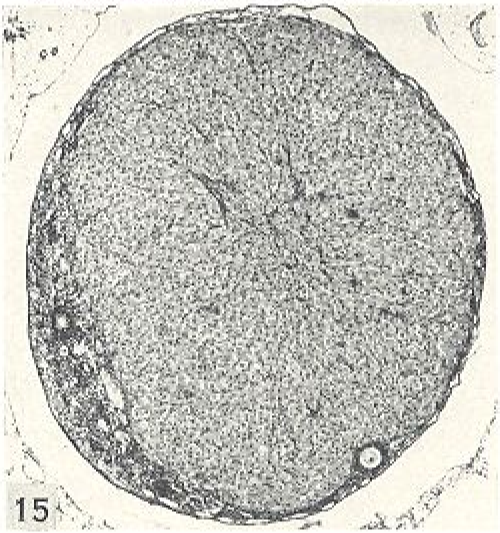
16 Section of the opposite ovary to that shown in figure 13 which contains a new corpus luteum, and in the oviduct of the same side, a small blastocyst. In the ovary figured may be seen a fibrous scar (outlined by arrows) which is the remnant of a degenerate corpus luteum. The probable significance of this is discussed in the text (p. 421). × 60.

17 Ovary at mid-proestrum showing a biovular follicle, which in this instance is in early atresia. × 100.

18 Section of a degenerating corpus luteum of pregnancy in a parturient female. The lutein tissue is being replaced by connective tissue, but scattered lutein cells are still apparent. The opposite ovary of this specimen was lost, but the uterine and glandular lumina contain myriads of spermatozoa (see fig. 20), indicating that copulation had just occurred and that the animal was in estrus when killed. The ovary containing the degenerating corpus possessed no vesicular follicles. As discussed in the text (p. 421) the above combination of factors would seem to indicate the occurrence of a post-partum estrus in Desmodus × 460.

19 Ovary of a specimen containing a single implanting blastocyst in the uterus. The ovary contains, however, two corpora lutea which are equally developed and are separated by a prominent fibrous partition. This condition indicates that in this instance two follicles matured and ruptured rather than the usual one. Only one of the ova, however, survived to the stage of implantation. × 30.

20 Section of the uterus of the parturient specimen in which the degenerate corpus luteum is illustrated in figure 18. Note the abundant spermatozoa in the uterine glands which indicate that the specimen was in estrus when killed. Since the specimen was in the puerperium it is evident that post-partum estrus may occur in Desmodus. × 460.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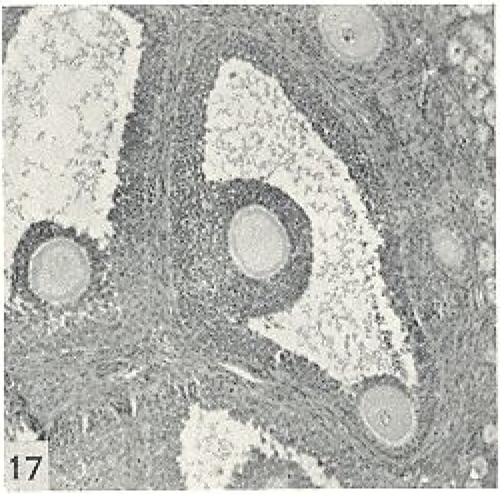
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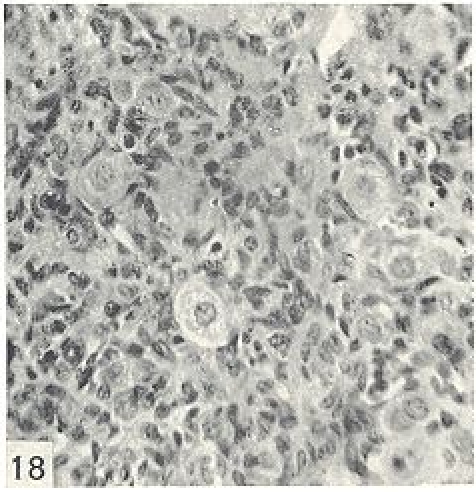
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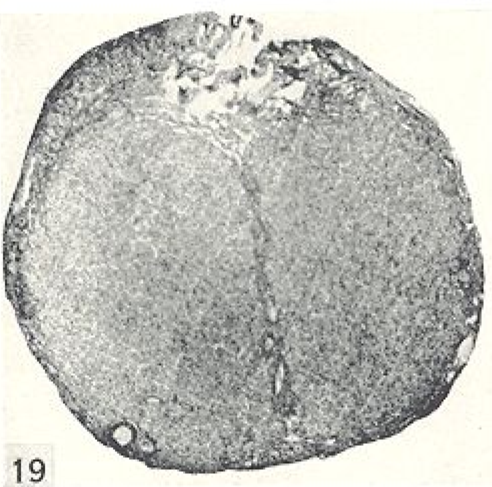
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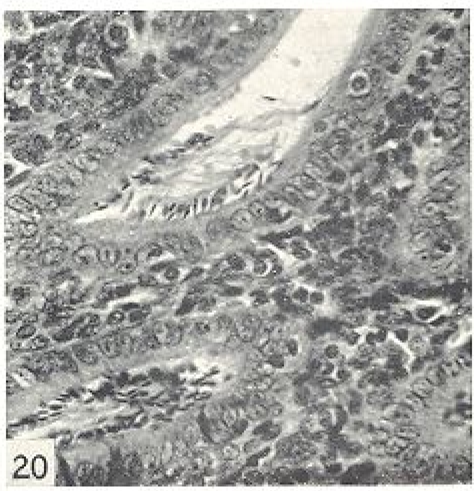
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