STUDIES ON THE EMBRYOLOGY OF MICROCHIROPTERA, PART VI.

Structure of the Placenta in the Indian Vampire Bat, *Lyroderma lyra lyra* (Geoffroy)–(Megadermatidae).

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(Communicated by Prof. M. A. Moghe, F.N.I.)

(Received October 10; read November 25, 1949.)

I. Introduction.

Very little is known of the life-history, development and placentation of the family Megadermatidae. According to Blanford (1881) *Megaderma (Lyroderma) lyra lyra* is the only species commonly found in India. The only bit of information from that source is that 'Hodgson has observed that in this species males greatly exceed the females in numbers'.....'Anderson found the young adhering to the abdominal teats and moving about from them to the pectoral mammae'..... 'Hodgson found a single young in many pregnant females examined by him at the end of February.' This information is obviously very insufficient.

In this paper I propose to record a few observations on the reproductive system and to describe the foetal membranes and the structure of the placenta. The material at my disposal is not sufficient and I cannot describe the sex-cycle or the early development of this bat.

II. Material and Methods.

The bats were collected from old houses and cowsheds in two villages—Lakhani and Shipewada—in Bhandara district, Central Provinces, India. The specimens were brought to the laboratory in cages. The reproductive structures and the mammary glands of the females were fixed in Bouin's fixative, the pregnant uteri were slit open or punctured to allow the penetration of the fixative. After dehydration they were sectioned at a thickness of 10μ and stained with Ehrlich's haematoxylin and counterstained with eosin. In cases of the males the reproductive organs, kidneys and the suprarenals were fixed. In addition to Bouin's fixative, which was used as a routine fixative, Carnoy's fluid, Sanfelice's formula and formalin were also employed to fix the testes.

III. Observations and Conclusions.

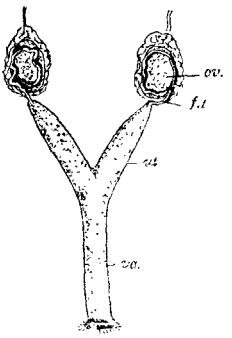
The following table gives the data of collections (specimens were collected during 1947 and 1948):—

	Males.	Females.
February	7	7
March	4	6
July	10	5
August	5	11
October	2	13
November	0	1
Total ..	28	43

(*a*) *The female reproductive structures:*—

The ovaries are flattened structures, ellipsoidal in shape and having a diameter of 0·4 mm. in section. The ovary is enclosed inside a complete ovarian capsule, hence the corpus luteum does not project beyond the surface of the ovary.

The Fallopian tube arises from the lateral side of the ovarian capsule, has a circuitous course and emerges as a fine tube from the caudal aspect of the ovarian capsule. The uterine cornua are symmetrically placed in the form of the two limbs of a 'V' across the median line. In the non-pregnant females the two horns are equally well developed, and each has a length of 0·8 cm. Pregnancy occurs only in one horn. The vagina has a length of 1·2 cm. (Text fig. 1.)



TEXT-FIGURE 1.

The female genitalia in *Lyroderma lyra lyra* (Geoffroy). *Ov.*: ovary; *f.t.*: fallopian tube. *Ut.*: uterus; *vg.*: vagina.

There are a pair of pectoral mammae each with a single teat. There are also a pair of pubic teats without any pubic mammary glands. The pubic nipples are well developed in the case of the parous forms and measures in length 1·3 cm. while in the case of the virgin females the pubic nipples are small and are not more than 0·6 cm. in length. The pubic nipples are covered with fine fur. It has been suggested by Harrison Matthews (1937) that they increase greatly in size during the first pregnancy and lactation, and having once developed they do not return to their original condition. He, therefore, suggests that the large size of the pubic nipples is a sure indication of the sexual maturity of the female bats.

(*b*) *Number of embryos in litter:*—

The physiological asymmetry of the genitalia of the Chiroptera is a well-established fact. (Wood Jones, 1917; Harrison Matthews, 1937 and 42; Wimsatt, 1945). In most species, which have been studied, only one young is brought forth in each litter and pregnancy usually occurs in the right horn. (Duval, 1895; Wood Jones 1917; Guthrie, 1933; Baker and Bird, 1936; Harrison Matthews, 1937; Wimsatt, 1945). In extreme cases like *Rhinolophus hipposideros* (Harrison Matthews, 1937) the left horn does not even produce mature ova, indicating the final stage in the functional degeneration of the left part of the genitalia. Only in the case of the members belonging to the family Phyllostomatidae there is a simplex uterus as in *Glossophaga soricina* (Hamlett, 1934 and 1935) and *Artibeus jamaicensis parvipes* (Wislocki and Fawcett, 1941). Perfect bilateral symmetry with both the horns bearing embryos is found in some Vespertilionid bats such as *Vesperugo leisleri* (Ramaswami, 1933), *Scotophilus wroughtoni* and *S. temminki* (Gopalakrishna, 1947). In *Lyroderma lyra lyra* there is a single young in each litter, either in the

left horn or in the right horn. It was observed that in every pregnant female the ovary on the same side as the side of pregnancy had the corpus luteum. Furthermore the ovary on the other side showed no signs of degeneration.

There is another fact of considerable interest which I desire to record. Of the 13 females collected during February and March (pregnancies were observed only during these two months) 10 were pregnant. Of the 10 pregnant females 4 bore pregnancy in the right horn and 6 in the left horn of the uterus. These specimens which showed pregnancy in right horn had small public teats while those that had pregnancy in the left horn had large pubic teats. The small number of my collections does not encourage me to offer any opinion at present on the statement made by Harrison Matthews (1937) in explanation of this fact.

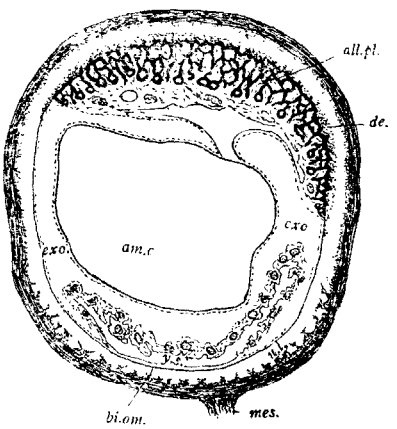
IV. Placentation.

(*a*) *Arrangement of foetal membranes*:—

The stage of development, on which this account is based, is an advanced stage of development collected in February. The foetus shows the beginnings of the ossification of the long bones, and the foetal erythrocytes are enucleate. The foetal membranes have attained their definitive disposition and final structural differentiation. The uterus has a diameter of 2·2 cm. in the transverse axis and 2·7 cm. in the tubo-cervical axis.

The general topography of the foetal membranes is indicated in text-fig. 2. There is a discoidal chorio-allantioic placenta on the antimesometrial side of the uterus. The allantoic diverticulum is situated slightly to one side of the median line. The allantois carrying foetal vessels spreads fanwise at the base of the placenta.

The yolk-sac occurs in the section as a crescentic space on the mesometrial side. The vascular splanchnopleure is separated from the bilaminar ophalopleure by a slit-like space. The bilaminar omphalopleure does not come into contact with the uterine wall, hence a small part of the uterine lumen persists on the mesometrial side of the uterus. The connection between the foetal gut and the yolk-sac cavity is lost as the yolk stalk has become solid.



Text-figure 2.

A diagrammatic transverse section of the gestation sac to show the arrangement of the foetal membranes in *Lyroderma lyra lyra* (Geoffroy). *all. pl.*: allantoic placenta; *am. c.*: amniotic cavity; *bi. on.*: bilaminar omphalopleure; *de.*: decidua; *exo.*: exocoelom; *mes.*: mesometrium; *u.l.*: uterine lumen; *y.sc.*: yolk-sac.

The general disposition of the foetal membranes in *Lyroderma lyra lyra* resembles that of most of the insectivorous bats so far studied. A decidua capsularis, as has been described in some of the Phyllostomatid bats (Hamlett, 1934 and 1935; Wislocki and Fawcett, 1941), is absent from *Lyroderma lyra lyra.*

(*b*) *Finer structure of the Placenta* :—

The microscopic structure of the allantoic placenta resembles that of most of the species of microchiroptera so far known, and is typically labyrinthine and haemochorial. The placenta is made up of a system of hollow syncytiotrophoblastic cords containing maternal blood which occurs in the core of the placental cords. The cords form a plexiform labyrinth and the spaces between the cords are occupied by the allantoic mesenchyme and foetal blood vessels. At the base of the placental disc (i.e. on the foetal surface) large lacunae containing maternal blood and surrounded by syncytiotrophoblast can be seen (Pl. VI, Fig. 1).

The trophoblastic cords are zigzag and traversed by a hollow core containing maternal blood, and are lined on the interior by a row of darkly staining nuclei, spherical in shape and belonging to the syncytiotrophoblast. The cords are clear and distinct towards the base of the placenta, while towards the periphery, due to their intense interjunction, they appear to be in the form of a network. The trophoblastic cords have a uniform thickness. In a cross-section of a cord, or under higher magnifications, the histological details of the cords can be clearly made out (Pl. VI, Fig. 2). The cytoplasm is disposed mostly towards the periphery and the central space is lined by a distinct row of spherical nuclei. These nuclei appear to be in direct contact with the maternal blood; in other words, they appear to form the innermost layer of the cord, but under the oil immersion objective a thin layer of cytoplasm can be clearly made out over the layer of these nuclei. Outside this layer of nuclei there is a larger area of hyaline cytoplasm with very few nuclei scattered here and there. These nuclei are flattened and lightly staining.

The allantoic mesenchyme and the foetal blood vessels enter the placental region from the base. They occur in between the trophoblastic cords in the meshes of the network, and extend almost about three-quarters of the thickness of the placenta.

The junctional zone between the placenta and the decidua is very clear because in this region the trophoblast forms a continuous syncytial covering to the placenta. This syncytial shell is pierced here and there by the maternal vessels which enter the placenta from the uterine side.

The zone of separation of the parturient is clearly marked out at this stage. The decidual covering round the placenta occurs as a thin layer of loose connective tissue with plenty of areoli. The space which occurs between the decidua and the uterine wall is, probably, an artefact due to shrinkage.

The maternal vessels enter the placental disc from the antimesometrial side. Up to the point where they penetrate the placenta, i.e. up to the margin of the syncytiotrophoblastic shell, the maternal vessels maintain the endothelial lining. But after the vessels enter the placental labyrinth the endothelial lining is lost, and the vessels continue down towards the base of the placenta forming the core to the trophoblastic cords. Thus the maternal vascularization of the placenta is very simple —each capillary continuing as the hollow core of the trophoblastic cord up to the base of the placenta. Some of these tubes can be seen as enlarged spaces at the base of the placenta, each space surrounded by the syncytiotrophoblast. The endothelial lining of the maternal capillaries is lost as soon as they enter the placental zone.

Thus in the placenta the foetal blood is separated from the maternal blood by (*a*) the foetal endothelium, (*b*) the allantoic mesenchyme, and (*c*) the trophoblast.

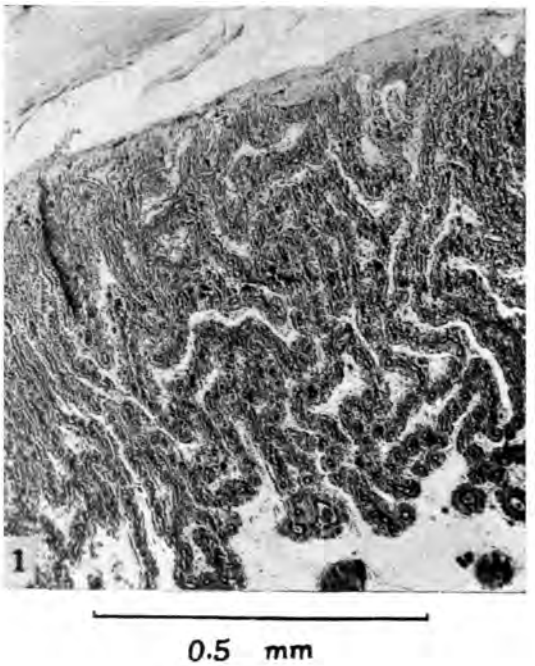


FIG. 1.

FIG. 2.

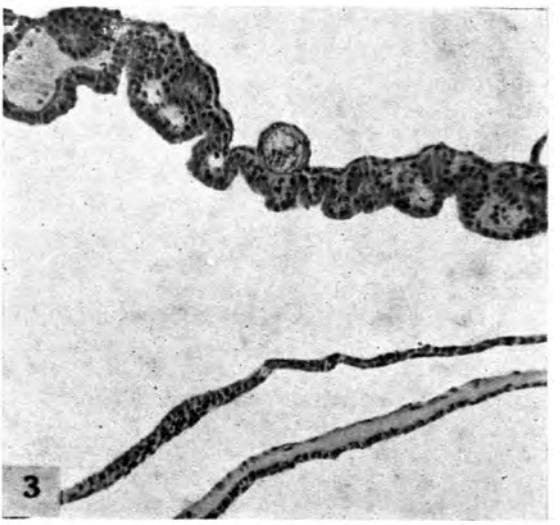


FIG. 3.

(For explanation of Plate, *see* page 98.)

All these structures are foetal in origin, and hence it conforms to the haemochorial type of relationship.

(c) *The Yolk-sac:*

The yolk-sac is large and occurs as a semicircular space on the mesometrial side, and extends to the lateral side to a slight extent. The splanchnopleure is supplied by vitelline vessels and the foetal erythrocytes are enucleate. At this stage the vascular splanchnopleure has no placental significance because it does not have any point of contact with the uterine tissue. (Pl. VI, Fig. 3.) On the mesometrial side the bilaminar omphalopleure still persists. There is no decidua capsularis.

V. Summary.

1. The physiological asymmetry of the female genitalia in the case of *Lyroderma lyra lyra* is well recognized, because only one horn of the uterus becomes pregnant. It may be the right or the left. A single young is born in each litter.

2. Foetal membranes: ALLANTOIC PLACENTA.—*Disposition*: Antimesometial. *Shape*: Discoidal. *Type*: Labyrinthine. *Finer morphology*: Haemochorial. YOLK-SAC.—Large. The vascular splanchnopleure is extensive. The bilaminar omphalopleure persists. DECIDUA.—A thin layer of decidua is shed at birth. There is no decidua capsularis.

Acknowledgement.

I am very grateful to Prof. M. A. Moghe, Head of the Department of Zoology, College of Science, Nagpur, for his very valuable guidance and encouragement throughout this work. My thanks are also due to Mr. R. V. Ektatey, Zamindar of Lakhani, for his keen interest in collecting the bats and sending them to my laboratory.

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Explanations of Plate VI.

(All figures are photomicrographs.)

Fig. 1. Part of the allantoic placenta. The syncytiotrophoblastic cords are distinct only towards the foetal surface, while on the uterine surface the cords get intermingled. The spaces between the cords contain the allantoic mesenchyme and foetal vessels. A few foetal capillaries are seen at the base of the placenta. Note a thin layer a decidua covering the placenta.

Fig. 2. Magnified picture of a part of the allantoic placenta to show the details of the syncytiotrophoblastic cords. The cords are clearly seen to be tubular and the lumen of the tube contains maternal blood. The nuclei of the syncytiotrophoblast form a continuous lining to the lumen of the cords.

Fig. 3. A part of the yolk-sac wall enlarged. The figure includes the persistent bilaminar omphalopleure and also the vascular splanchnopleure, which has invaginated over the bilaminar omphalopleure. The yolk-sac cavity occurs between these two layers. (Magnification same as plate figure 2).