Female reproductive anatomy and development of ovarian follicles in *Miniopterus fraterculus*

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The uterus of *Miniopterus fraterculus* (Thomas & Swan 1906) is bicornuate and asymmetrical, the right uterine horn being larger than the left in parous and nulliparous females. Ovarian and uterine function is asymmetrical; 94% of observed ovulations originated in the left ovary and all implantations occurred in the right uterine horn. Growth and development of ovarian follicles follow the typical eutherian mammalian pattern. The preovulatory Graafian follicle differs from that of most hibernating verspertilionids in that the cumulus oophorus is relatively small. Two types of follicular atresia occur. The first type, in which the stratum granulosum degenerates before degeneration of the oocyte, occurs in multilaminar follicles. The second type occurs in primary and early secondary follicles and is characterized by the oocyte showing the first signs of regression.
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Miniopterus fraterculus (Thomas & Swann 1906) het 'n bikornaatuterus wat asimmetries is met die regterhoring groter as die linker een. Die funksie van beide ovarium en uterus is asimmetries, deurdat 94% van die waargenome ovulerings in die linker ovarium ontstaan het, en alle implanterings in die regterhoring van die uterus plaasgevind het. Groei en ontwikkeling van die follikels in die ovarium kom ooreen met die kenmerkende patroon in die eutheria. Die preovulatoriese follikel van Graaf verskil van dié van meeste hibernerende vespertilionidae daarin dat die cumulus oophorus relatief klein is. Twee tipes follikulêre atresia kom voor in *M. fraterculus*. Die eerste tipe is waar die stratum grànulosum degenereer voordat degenerasie van die oösiet plaasvind, en word aangetref in multilaminêre follikels. Die tweede tipe kom voor in primêre en vroeë sekondêre follikels en hier word die eerste tekens van regressie in die oösiet gevind.
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The growth and development of ovarian follicles have been described for *Myotis lucifugus* (Guthrie & Jeffers 1938 a,b; Wimsatt 1944); *Myotis grisescens* (Guthrie, Jeffers & Smith 1951); *Myotis myotis* and *Myotis emarginatus* (Sluiter & Bouman 1951); *Pipistrellus hesperus* (Krutzch 1975); *Eptesicus fuscus* (Wimsatt 1944); and *Miniopterus schreibersi* (Van der Merwe 1979). In those species of the family Vespertilionidae in which ovulation occurs at the end of a period of hibernation the cells of the cumulus oophorus show a marked hypertrophy. In *P. hesperus*, which does not undertake prolonged periods of hibernation (Krutsch 1975), and *M. schreibersi*, in which ovulation occurs before hibernation (Van der Merwe 1979), the cells of the cumulus oophorus do not show any marked hypertrophy. *Miniopterus fraterculus*, the species under study, is a hibernating vespertilionid, and as in *M. schreibersi* ovulation occurs before hibernation.

Although a large number of follicles begin development in mammals, only a few reach the preovulatory stage, the majority regressing at an earlier stage. This process of follicular atresia has been described in *M. lucifugus* (Guthrie & Jeffers 1938a); *M. grisescens* (Guthrie, Jeffers & Smith 1951); and *M. schreibersi* (Van der Merwe 1979). In the present study the female reproductive tract, follicular growth and development, and follicular atresia in *M. fraterculus* is described.

Materials and Methods

During 1977, 51 female *M. fraterculus* were collected on a regular monthly basis from several caves in the Natal Midlands area. Specimens were killed in the laboratory by asphyxiation with carbon dioxide and the reproductive tract was removed under a dissecting microscope. The length and width of the two uterine horns and the dimensions of the ovaries were measured with an eye-piece graticule and a dissecting microscope. The tissues were fixed in Bouin's fluid and stored in 70% alcohol. Following routine embedding sections were cut at 5,0 μm and routinely stained with Ehrlich's haematoxylin and counter-stained with eosin.

All microscopic measurements were made with an eyepiece micrometer. Mean follicular diameter was calculated from two measurements taken at right angles to each other, one of which was always the largest diameter. The oocyte diameter was calculated from two measurements taken in the same planes as those used for the follicle. The diameter of the follicle included the theca folliculi and the diameter of the oocyte excluded the zona pellucida. Regression lines for the growth of primary, secondary and Graafian follicles were calculated.

Results

Female reproductive anatomy

The gross external morphology of the reproductive tract of *Miniopterus fraterculus* resembled that described for *M. minor* and *M. dasythrix* (Matthews 1941; = *M. schreibersi natalensis*, fide Hayman & Hill 1977); and *M. australis* and *M. schreiversi* (Richardson 1977). The uterus of *M. fraterculus* was bicornuate with the right uterine horn longer than the left. The oviducts were coiled and the ostia opened beneath the ovaries. The ovary and part of the oviduct were enclosed in an ovarian capsule.

The ovaries were bilaterally flattened, ovoid structures, the right ovary being generally larger than the left. The mean measurements of ovaries from five parous bats collected in February were

Right ovary 0,85 mm × 0,62 mm × 0,47 mm.
Left ovary 0,80 mm × 0,51 mm × 0,45 mm.

The uterine horns were lined by a columnar epithelium, as was the upper end of the corpus of the uterus. The region of the corpus of the uterus, above the cervix, was lined by a ciliated epithelium.

In nulliparous females the uterine horns were short and thin, the right being slightly more robust than the left. In parous non-pregnant females the right uterine horn was approximately three times longer and wider than the left. The left uterine horn of parous females was longer than in nulliparous females, a result of the fetus occupying both uterine horns during the later stages of pregnancy.

Changes in uterine horn dimensions of *M. fraterculus* during 1977 are shown in Fig. 1. Up to September, expansion of the uterus was restricted to the right uterine horn, but from late September onward the fetus occupied both uterine horns so that individual horn length could no longer be measured.

Development of ovarian follicles

The following details of follicular development are based on measurements and observations made on the ovaries from bats collected throughout the year. In the present study four types of follicle have been recognized; primordial; primary; secondary and tertiary or Graafian.

Primordial follicles

The primordial follicle consisted of an oocyte surrounded by a single layer of fusiform or low cuboidal cells. These follicles formed tight clusters around the periphery of the ovary, and as such it was difficult to determine where a particular follicle began or ended. The mean diameter of primordial follicles with fusiform follicular cells was 20,0 ± 1,8 μm. Hypertrophy of the follicular cells and growth of the oocyte resulted in an increase in the mean follicular diameter to 24,0 ± 1,4 μm. The oocyte nucleus nearly filled the oocyte of the primordial follicle and as such its position can only be described as central.

Primary follicles

The distinction between primordial and primary follicles is a tenuous one. While large primordial follicles have low cuboidal follicular cells, follicles with large cuboidal cells are regarded as being primary. In *M. fraterculus* follicles with a mean diameter of 36,0 ± 2,4 μm had large cuboidal follicular cells and were regarded as primary (Fig. 3A).

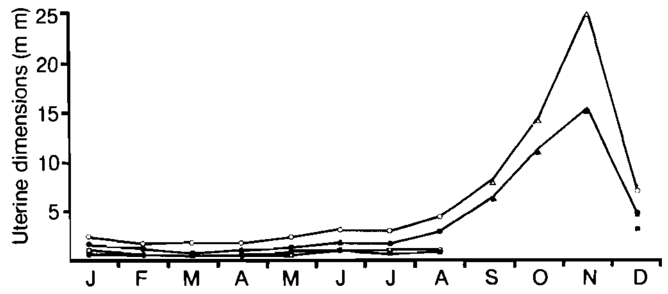

Fig. 1 Monthly changes in uterine horn dimensions.
○ Mean right uterine horn length
○ Mean right uterine horn width
● Mean left uterine horn length
○ Mean left uterine horn width
△ Mean total length of uterine horns
▲ Mean total width of uterine horns.
Sample size for all measurements was four.

Two structures appeared during primary follicular growth; the zona pellucida and the theca folliculi. In follicles with a mean diameter of 50,4 ± 1,7 μm, the zona pellucida appeared as a thin acidophilicly stained line around the oocyte, and the theca folliculi as a thin layer of fusiform cells surrounding the follicles. With continued hypertrophy the cuboidal follicular cells became increasingly columnar in shape and follicles with a mean diameter of 56,0 ± 2,4 μm had conspicuously columnar follicular cells.

Many of the primary follicles were oval in shape, the result of two factors. Firstly, in many cases the oocyte was oval and secondly the follicular cells at opposite poles were more columnar than those at the sides. As the follicular cells became increasingly columnar their nuclei assumed a peripheral position leaving a band of clear cytoplasm between the oocyte and the nuclei.

Secondary follicles

Secondary follicles were characterized by the production of a second and subsequent cell layers in the stratum granulosum. Follicles with a mean diameter of 70,0 ± 4,2 μm had begun to produce a second cell layer and cell divisions were apparent in the follicular cells. It was noted in several secondary follicles that the production of the second cell layer began at two opposite poles, accentuating the oval shape.

The theca folliculi and zona pellucida were fully developed in late secondary follicles. The theca folliculi was comprised of fusiform cells which ran parallel to the stratum granulosum, and a few capillaries.

In some follicles some of the thecal cells had lost their fusiform shape and had come to resemble the interstitial cells. In no follicles did this differentiation represent a division of the theca folliculi into a cellular theca interna and a fibrous theca externa.

Graafian follicles

Graafian follicles were characterized by the presence of an antrum in the stratum granulosum. In *M. fraterculus* there

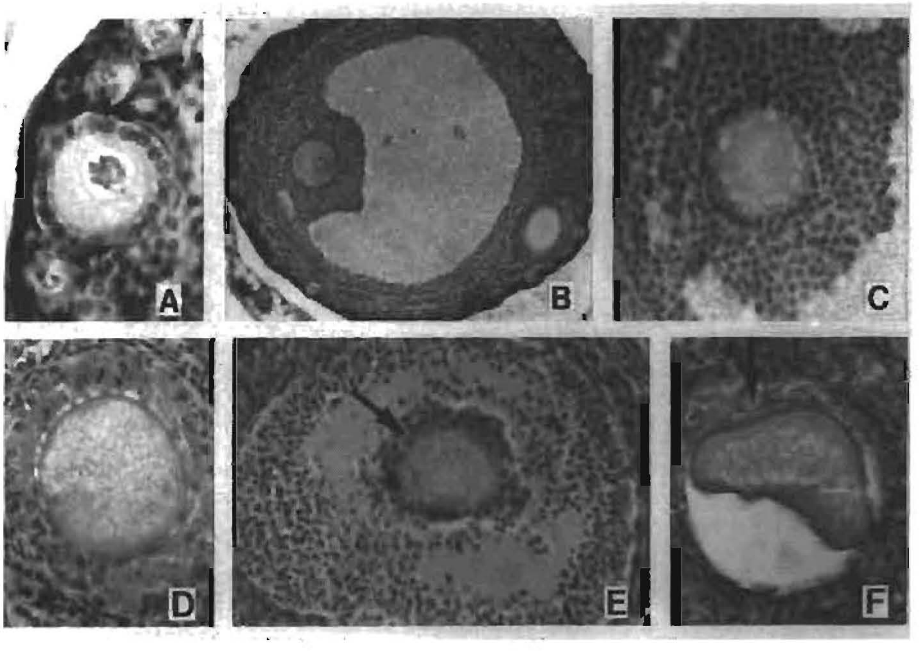

Fig. 3 A = Typical early primary follicle. Note the cuboidal follicular cells and position of follicle adjacent to the edge of the ovary (×625).
B = Preovulatory Graafian follicle showing the relatively small size of the cumulus oophorus (×102).
C = Section through the ovum-bearing mass of a preovulatory Graafian follicle showing the breaking away of the oocyte-bearing mass from the stratum granulosum at the hilus (×210).
D = Secondary follicle undergoing the first stage of type I regression. Note that the oocyte is intact although the majority of follicular cells have degenerated (×315).
E = Early Graafian follicle undergoing an early stage of type I regression. Note the ring of apparently normal cells around the oocyte (×250).
F = Primary follicle undergoing the first stage of type II regression. Note that the oocyte is misshapen and that some of the thecal cells are undergoing luteinization (arrowed) (×705).

was a variation in follicular diameter when the antrum first appeared. The smallest follicle with a developing antrum had a diameter of 131,0 μm, while the largest had a diameter of 158,0 μm. The antrum first appeared as one or more spaces between the follicular cells which coalesced to form the definitive antrum.

In the largest Graafian follicle which had a diameter of 520,0 μm, the oocyte was surrounded by a cumulus oophorus which was comprised of approximately six cell layers (Fig. 3B). The cells of the layer adjacent to the oocyte appeared to be columnar in shape and the remaining cells were the same size as those of the stratum granulosum.

Although the process of ovulation was not observed in *M. fraterculus*, material collected permits a description of the preovulatory Graafian follicle; two bats collected on 19 May 1977 and one on 2 June 1977 each had a single preovulatory Graafian follicle in its left ovary.

The mean diameter of these three follicles was 490,0 ± 12,4 μm and from observations on these, the preovulatory Graafian follicle appears to have five characteristics:

— In all three follicles the antrum was filled with an acidophilic coagulum, described as the secondary liquor folliculi in the rabbit by Robinson (1918).
— In all three specimens the ovum-bearing mass, which was relatively small when compared to the size of the antrum, was comprised of the oocyte surrounded by the cumulus oophorus of approximately six cell layers. The ovum-bearing mass was attached to the stratum granulosum by the hilus. Mitotic divisions were seen in the cells of the hilus but nowhere else in the cumulus oophorus or stratum granulosum.
— In all three specimens there was a clear breaking away of the ovum-bearing mass from the stratum granulosum at the hilus (Fig. 3C).
— In the specimen collected on 2 June 1977 the oocyte had undergone the first meiotic division.
— In the preovulatory Graafian follicle there was no indication of preovulatory luteinization of the follicular cells and it is assumed that all luteinization occurred after ovulation.

Growth of follicle and ovum

The growth of the follicle and ovum of *M. fraterculus* occurred in two stages. In the first stage, represented by primordial, primary and secondary follicle growth, the follicle and ovum grew at approximately the same rate. In the second stage, represented by growth of the Graafian follicle, significant growth of the oocyte ceased while the follicle continued to grow at an increased rate. These two stages can be seen in Fig. 2, where follicle diameter is plotted against oocyte diameter.

A comparison of the regression lines included in Fig. 2 shows that in primordial and primary follicles the follicle and oocyte grew at approximately the same rate. In secondary follicles the follicle grew more rapidly than the oocyte, due to the production of the second and subsequent cell layers in the stratum granulosum. The regression line for Graafian follicles indicates that while there was a small increase in oocyte diameter, the follicle diameter increased greatly.

The high value of r for primary and secondary follicles

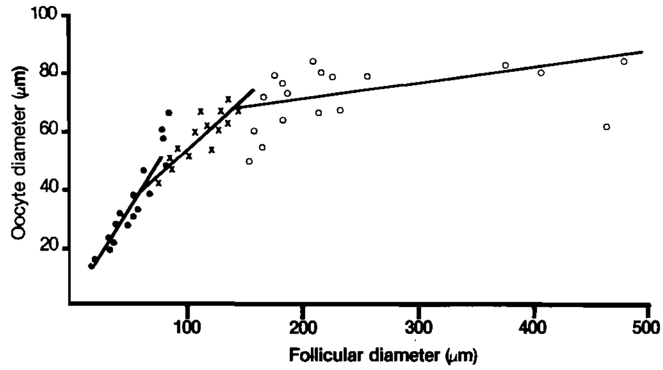

Fig. 2 The relative growth rates of follicle and oocyte during follicular development. Oocyte diameter has been plotted against its follicle diameter for primordial and primary follicles (●), secondary follicles (X), and Graafian follicles (O).

Y = A + BX.

Primary follicles	Y = 1,56 + 0,63;	r = 0,97; n = 120.
Secondary follicles	Y = 20,04 + 0,32;	r = 0,77; n = 151.
Graafian follicles	Y = 60,47 + 0,04;	r = 0,23; n = 47.

indicates that there was a statistically significant correlation between follicle and oocyte growth rates. The low value of r for Graafian follicles indicates on the other hand that at this stage there was little correlation between oocyte and follicle growth ($p > 0,1$).

Follicular atresia

Two types of follicular atresia occurred in the ovaries of *M. fraterculus*. Type 1 atresia, which occurred in multilaminar follicles, was characterized by the stratum granulosum degenerating before the oocyte. Type 2 atresia, which occurred in primary and early secondary follicles, was characterized by the oocyte and follicular cells degenerating at approximately the same time. In some primary follicles both the oocyte and follicular cells appeared to be degenerating while in others the oocyte appeared to be intact although some of the follicular cells had degenerated.

Type 1 atresia first appeared as a deeply stained, disorganized mass of cells in the stratum granulosum (Fig. 3D). Phagocytes invaded the stratum granulosum and broke down the outer cells leaving a thin layer of apparently normal cells surrounding the oocyte (Fig. 3E). The result of the action of the phagocytes was that the oocyte came to lie in a cavity filled with a non-cellular acidophilic coagulum.

At this stage the cells of the theca folliculi began to divide and hypertrophy, forming the corpora atretica. During periods of follicular atresia each ovary contained three or four of these bodies.

The second type of atresia first appeared as a distortion of the oocyte (Fig. 3F). Phagocytes invaded the oocyte and at the same time the follicular cells began to break down. Breakdown of the oocyte left a collapsed zona pellucida lying in a small cavity.

Type 1 atresia was most common in the ovaries of parous females during the periods of active follicular growth and for a short period after ovulation. Type 2 atresia was most common in the ovaries of nulliparous females, while also occurring in those of adult bats.

Discussion

Reproductive anatomy

Gopalakrishna (1949) has stated that the reproductive organs of the Chiroptera are characterized by their bilateral asymmetry and that symmetry is rare. The bicornuate of *M. fraterculus* is characteristic of all microchiropteran families except the Nycteridae which have a duplex uterus and the Phyllostomatidae (excluding the subfamily Chilonycterinae) which have a simplex uterus (Carter 1970).

There appear to be two types of functional asymmetry in the reproductive organs of bats. In the first type only one ovary and one uterine horn are dominant. In *Rhinolophus ferrumequinum* and *R. hipposideros* (Matthews 1937) only the right ovary is functional and implantation is restricted to the right uterine horn, while in *Hipposideros ater* (Gopalakrishna & Ramakrishna 1977) only the left ovary and left uterine horn are functional.

In the second type, implantation is restricted to one uterine horn while ovulation may occur in either ovary. This type of functional asymmetry has been recorded in *M. myotis* (Sluiter & Bouman 1951) and *Eptesicus regulus* (Kitchener & Halse 1978).

Wimsatt (1979) described four types of reproductive asymmetry in Chiroptera that are basically sub-divisions of the two types given above.

The type of asymmetry seen in *M. fraterculus* falls into the first class since a few cases of ovulation in the right ovary and implantation in the left uterine horn have been recorded (Baker & Bird 1936; Wallace 1978).

There are, on the other hand, species with perfectly symmetrical genitalia. Gopalakrishna (1949) reported that *Scotophilus wroughtoni* has two functional ovaries and that each uterine horn bears a fetus during pregnancy. In general the families Nycteridae (Matthews 1941); Desmodontidae (Wimsatt & Trapido 1952); Emballonuridae (Gopalakrishna 1955); Rhinopomatidae (Kumar 1965); and some members of the genus *Pipistrellus* (Krutzsch 1975) have two functional ovaries and implantation occurs in the corresponding uterine horn. As such members of these families and genera show little reproductive asymmetry.

Two factors appear to determine whether or not the bicornuate uterus is symmetrical. If the species produces two or more young per pregnancy, or if both uterine horns and both ovaries are functional and implantation alternates between uterine horns, then the reproductive organs will tend to be symmetrical. If, on the other hand only one ovary or uterine horn is functional, uterine asymmetry will be the rule.

From the above it would appear that uterine asymmetry is the result of reproductive asymmetry but this is not a simple cause-and-effect relationship, since in *M. fraterculus* the nulliparous female shows some uterine asymmetry, suggesting that whatever advantage asymmetry may have has been incorporated into the gene pool.

Development of ovarian follicles

The development of the follicle from an oocyte surrounded by a single layer of fusiform cells to the mature Graafian follicle, as seen in *M. fraterculus*, is characteristic of all eutherian mammals. The cumulus oophorus which surrounds the oocyte in the Graafian follicle is thought to supply the nutritional requirements of the oocyte in those species in which it is shed after hibernation. Wimsatt (1944) noted that in hibernating vespertilionids hypertrophy of the cumulus cells occurs and that in *M. lucifugus* the ovum-bearing mass takes up a large part of the antrum. Although

M. fraterculus is a hibernating vespertilionid ovulation occurs before hibernating and as such it is to be expected that there is little or no hypertrophy of the cumulus cells.

The cells of the theca folliculi originate from the surrounding connective tissue and in some species the theca is divided into an internal and external layer (Matthews, 1937 in *Rhinolophus hipposideros* and *R. ferrumequinum;* Guthrie & Jeffers 1938a in *M. lucifugus*). Gopalakrishna (1955) and van der Merwe (1979) reported that there is no division of the theca folliculi in *Taphozous longimanus* and *M. schreibersi* respectively. This apparent anomally could be the result of the observed differentiation of fibrous thecal cells to a cuboidal interstitial form, so that in some follicles two cell types are apparent in the theca folliculi.

Growth of ovarian follicles

The growth of ovarian follicles in eutherian mammals characteristically occurs in two stages. In the first stage the oocyte and follicle grow at approximately the same rate, while in the second stage, the oocyte ceases to grow and the follicle continues growing at an increased rate. This phenomenon has been recorded by many authors including Brambell (1928) for the mouse; Deanesley (1934) for the hedgehog; Matthews (1937) for *Rhinolophus* species; Wimsatt (1944) for *M. lucifugus;* Gopalakrishna (1949 & 1955) for *S. wroughtoni* and *T. longimanus;* and Van der Merwe (1979) for *M. schreibersi.*

Although previous authors have drawn a single regression line covering primary and secondary follicle growth, the method used in the present study clearly indicates that the first growth stage can be sub-divided into stages representing the growth of primary and secondary follicles. It can be expected that growth rates in these two stages will differ since their growth involves two different processes, cellular hypertrophy in primary follicles and cell division in secondary follicles.

In *M. fraterculus* there is a wide variation in follicular diameter when the antrum first appears. The points in Fig. 2 where the regression lines for secondary and Graafian follicles intersect, which represent the diameter of the mature oocyte on the abscissa, fall approximately in the middle of the range of follicular diameters in which the antrum first appears. It is therefore assumed that in *M. fraterculus* the oocyte reaches maturity at the time the antrum first appears.

Follicular atresia

Van der Merwe (1979) described two types of follicular atresia as occurring in the ovaries of *M. schreibersi.* These two types are similar to those described by Guthrie and Jeffers (1938a) for *M. lucifugus* and *M. grisescens* and for *M. fraterculus* in the present study. Van der Merwe (1979) reported that in the second type of atresia the oocyte degenerated before degeneration of the stratum granulosum, but observations from the present study suggest that the oocyte and follicular cells may degenerate simultaneously.

The production of corpora atretica or interstitial gland tissue from thecal cells during atresia of multilaminar follicles suggests that atresia is not simply a means of removing excess follicles. The interstitial gland tissue is a major steroidogenic centre in the ovary (Mossman & Duke 1973) and as such follicular atresia provides a source of steroidogenic tissue.

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