Original Paper

Structure of the Ovaries of the Nimba Otter Shrew, *Micropotamogale lamottei*, and the Madagascar Hedgehog Tenrec, *Echinops telfairi*

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Abstract

The otter shrews are members of the subfamily Potamogalinae within the family Tenrecidae. No description of the ovaries of any member of this subfamily has been published previously. The lesser hedgehog tenrec, *Echinops telfairi,* is a member of the subfamily Tenrecinae of the same family and, although its ovaries have not been described, other members of this subfamily have been shown to have ovaries with non-antral follicles. Examination of these two species illustrated that non-antral follicles were characteristic of the ovaries of both species, as was clefting and lobulation of the ovaries. Juvenile otter shrews range from those with only small follicles in the cortex to those with 300- to 400-μm follicles similar to those seen in non-pregnant and pregnant adults. As in other species, most of the growth of the oocyte occurred when follicles had one to two layers of granulosa cells. When larger follicles became atretic in the Nimba otter shrew, hypertrophy of the theca interna produced nodules of glandular interstitial tissue. In the tenrec, the hypertrophying theca interna cells in most large follicles appeared to undergo degeneration. Both species had some follicular fluid in the intercellular spaces between the more peripheral granulosa cells. It is suggested that this fluid could aid in separation of the cumulus from the remaining granulosa at ovulation. The protruding follicles in lobules and absence of a tunica albuginea might also facilitate ovulation of non-antral follicles. Ovaries with a thin-absent tunica albuginea and follicles with small-absent antra are widespread within both the Eulipotyphla and in the Afrosoricida, suggesting that such features may represent a primitive condition in ovarian development. Lobulated and deeply crypted ovaries are found in both groups but are not as common in the Eulipotyphla making inclusion of this feature as primitive more speculative.

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Introduction

The order of insectivores has long been considered to include more diverse groups than other Eutherian orders. Recently the moles, shrews and hedgehogs have been separated into the order Eulipotyphla within the superorder Laurasiatheria [Murphy et al., 2001], whereas the tenrecs, otter shrews and golden moles have been included in the order Afrosoricida within the superorder Afrotheria [Stanhope et al., 1998]. Separation of these groups of primitive animals into different superorders has renewed interest in the various species. In the past the ovarian

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structure of the tenrecs has received special attention because of the lack of an antrum in the preovulatory and ovulating follicles [Strauss, 1938a, 1950]. Eversion of the corpora lutea and intraovarian fertilization, reported for *Setifer*, *Hemicentetes* and *Tenrec ecaudatus* [Strauss, 1938b; Mossman and Duke, 1973; Nicoll and Racey, 1985] are considered to be related to ovulation from non-antral follicles.

In the current study ovaries of a member of the subfamily Potamogalinae of the family Tenrecidae, the Nimba otter shrew *(Micropotamogale lamottei)*, and a previously unexamined member of the subfamily Tenrecinae, the lesser hedgehog tenrec *(Echinops telfairi)*, have been examined with regard to similarities and dissimilarities of structure of these organs to that of previously described species. This material became available during studies of possible interrelationships of placental structure in Afrotherian species [Carter, 2001; Carter et al., 2004].

Fig. 1. Lobulated and clefted ovary of an otter shrew in early pregnancy. The surrounding bursa has a mucosa of the oviductal type. cl = Corpus luteum; mf = mature follicle; arrow = isolated lobule. Bar = 500 μm.
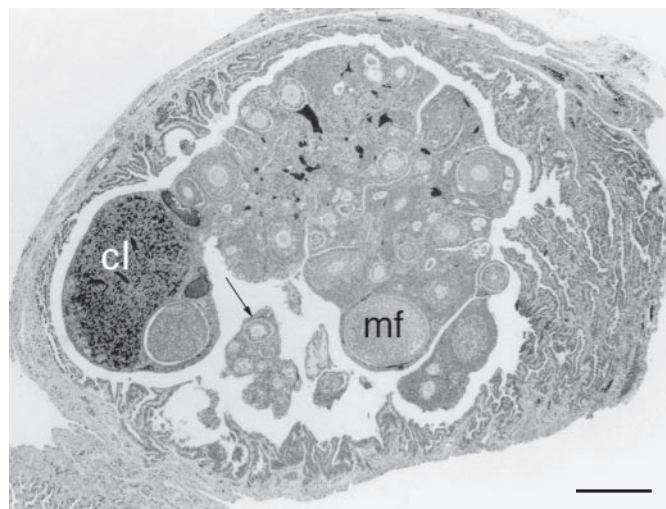
Materials and Methods

Nimba otter shrews *(M. lamottei)* that had been trapped and drowned in bow nets on the Ivory Coast were preserved in formalin by the fishermen. The dissected female reproductive tracts were subsequently placed in 80% alcohol and later shipped to Denmark and the United States for histological examination. Ovaries of 20 animals (6 pregnant and 6 nonpregnant adults, and 8 juveniles) were embedded and sectioned. In most cases one ovary was embedded in plastic for thin sectioning and one ovary in paraplast for serial sectioning. Sections of the paraplast-embedded material were stained with hematoxylin and eosin; sections of the plastic-embedded material were stained with Azure B. Most of the ovaries showed satisfactory preservation for general histological observation despite the suboptimal conditions of preservation and extended storage time.

Ovaries were obtained from 3 pregnant tenrecs *(Echinops telfairi)* in a colony held at the Department of Anatomy, University of Munich. The colony is housed and maintained as described previously [Künzle, 1998]. The ovaries were fixed in paraformaldehyde followed by glutaraldehyde and postfixed in osmium, then embedded in plastic. The blocks were then both thick and thin sectioned for light- and electron-microscopic observation. Additional ovaries from a pregnant female and 2 nonpregnant adult females were embedded in paraffin and sectioned for light microscopy.

Results

General Features of the Ovary of the Nimba Otter Shrew, M. lamottei

The ovaries of the Nimba otter shrew are slightly flattened ovoid structures lying close to the sides of the uterine horns and situated in a complete ovarian bursa (fig. 1).

The bursa is composed of folds of oviductal-type mucosa, with a surface epithelium of ciliated cells and a few interspersed nonciliated (secretory) cells. The ovary is covered by a thin surface epithelium that intrudes into the ovary as clefts. There is no distinct tunica albuginea underlying the surface epithelium. In adult ovaries the clefts result in a lobular structure of the cortex. The vasculature and lymphatic vessels communicate with the ovary directly from the short mesovarium, radiating in the medulla out to the cortical lobules.

Juvenile Stages of the Otter Shrew

Ovaries were obtained from 8 animals ranging in weight from 19.5 to 44 g and considered to be juveniles. When examined with a dissecting microscope, 3 of the ovaries were smooth, 4 had a lumpy exterior surface, and 1 showed only one or two rounded protuberances. The smooth ovaries averaged 2.18 × 1.40 mm; the remaining ovaries averaged 2.13 × 1.58 mm. The animals in the first group weighed 30 g or less and had thin endometria with short undilated glands, whereas those in the last group averaged 38 g and had more glandular development in their endometria. Histological examination of the ovaries also showed a range of development (fig. 2). The ovaries that were smooth in outline showed a cortex with multiple small follicles ranging from primordial follicles to those with three or four layers of granulosa cells (fig. 2A). These ovaries that were not lobed nevertheless
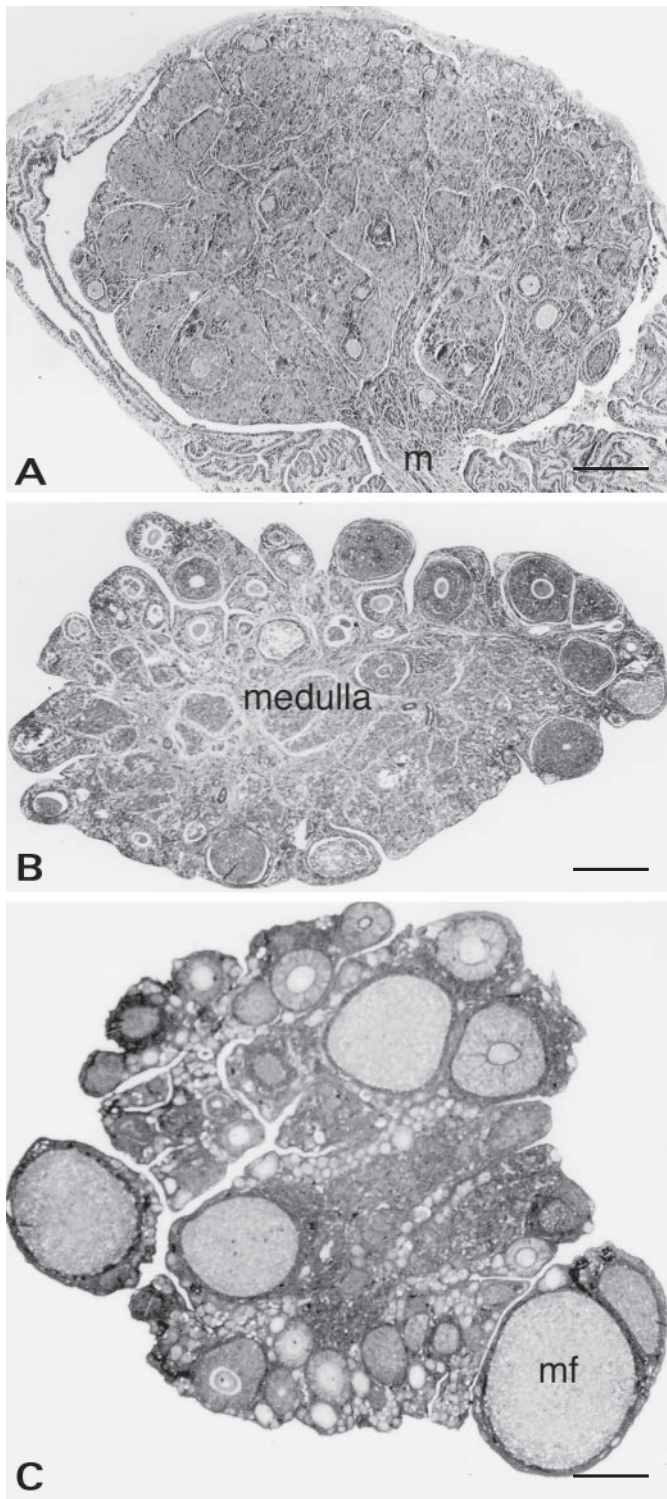
had numerous cortical clefts. Few of the follicles in this group reached more than 200 μm in diameter. The ovaries of one female had only a few large follicles (fig. 2B), whereas the other juvenile females had several large follicles varying from 300 to 400 μm in diameter (fig. 2C). The ovaries with greater follicular development also showed more extensive clefts as well as lobulation. In this respect they resembled nonpregnant adult ovaries.

Separation of the cortex and medulla was not clear in most of the ovaries. In the group with smaller follicles much of the glandular interstitial tissue appeared to be associated with the medulla rather than the cortex. In the ovaries of juvenile females with larger follicles, however, there was an abundance of glandular interstitial tissue in clusters within the cortex, indicating that much of this interstitial tissue derived from atretic follicles (fig. 3).

Adult, Nonpregnant Otter Shrews

Of the ovaries of 6 nonpregnant adult animals, only 2 had corpora lutea. All had large follicles, multiple clefts, and lobules. Sections through the medulla showed lobules radiating from this area (fig. 4A); sections through the cortex showed multiple isolated lobules (fig. 4B). Some of the lobules appeared to center on one or two large follicles or, in the case of 1 animal, a single corpus luteum (fig. 4C); closer examination usually revealed the presence of multiple constituents in each lobule. Some of the smaller projections contained only small follicles, interstitial cells and connective tissue. The healthy follicles in these animals reached 400 μm or slightly more. Despite the multiple layers of granulosa cells, none of the follicles had an antrum. The granulosa cells associated with the zona pellucida tended to be more columnar and were closely associated with one another without intercellular spaces (fig. 5A). However, the more peripheral granulosa often had intercellular spaces with some apparent follicular fluid although there was no tendency for accumulation of fluid into either a single or segmented antrum. Healthy follicles had only a thin theca interna with a few glandular cells. Most of the glandular interstitial tissue seen appeared to be derived from follicular atresia (fig. 5B).

Fig. 2. Ovaries of juvenile otter shrews. **A** Ovary of the most immature type showing little follicular development and large areas of glandular interstitial tissue. m = Mesovarium; paraffin section. Bar = 500 μm. **B** Ovary showing moderate follicular development and lobulation of the cortex surrounding a medulla with abundant glandular interstitial tissue. Bar = 300 μm. **C** Section through the cortex of an ovary showing extensive follicular development, including some follicles that reach mature follicle (mf) dimensions. Bar = 220 μm.
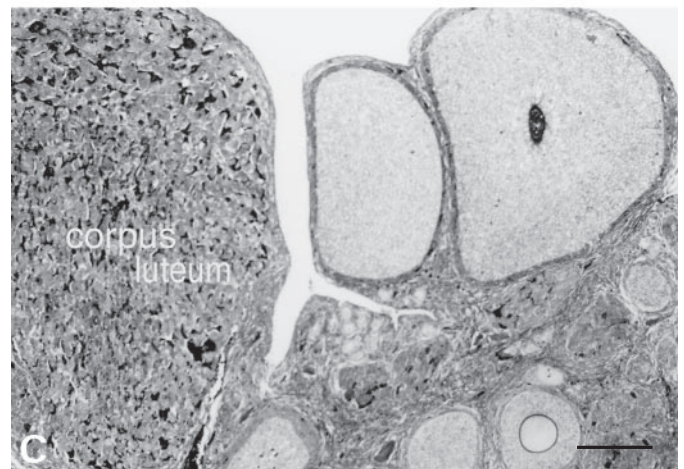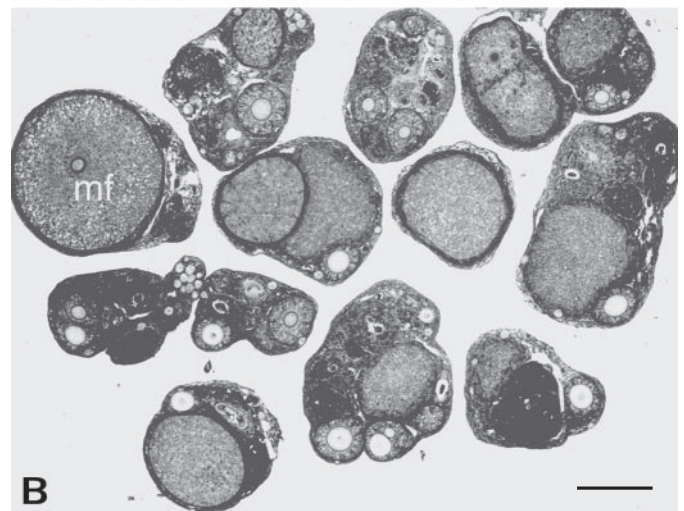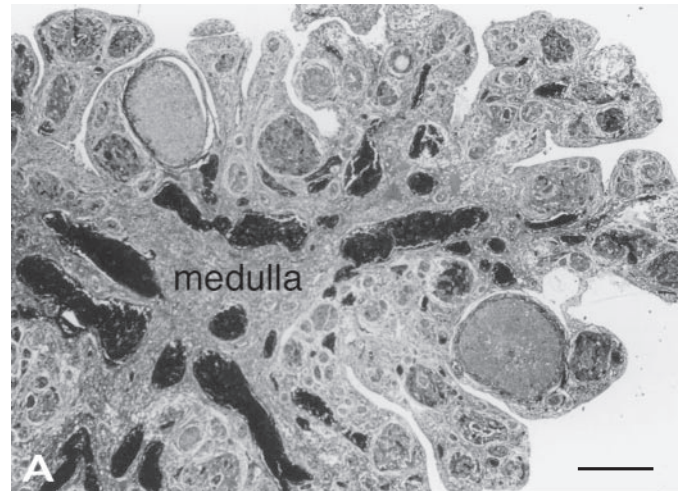
Ovaries of Pregnant Otter Shrews

The ovaries examined from the pregnant animals were the largest of the group, averaging 3.70 × 1.89 mm. They were extensively clefted, and their lobulation was quite irregular due to the greater size of corpora lutea than of large follicles (fig. 1, 6A). In none of the females were more corpora lutea than fetuses seen. An occasional corpus luteum was slightly cup-shaped. The surface epithelium overlying the corpus luteum was thin and there were numerous underlying fibroblasts but little apparent intercellular material between the surface epithelium and the lutein cells. All of the corpora lutea were highly vascularized with sinusoidal capillaries forming a meshwork between lutein cells (fig. 6B). The corpora lutea were ovoid and varied from 0.7 mm in width to over 1.6 mm in length. The lutein cells varied from 14 to 16 μm in greatest width in one of the earlier pregnancies to 18–20 μm in the other ovaries. Direct evidence of eversion was not seen and no sperm were encountered within the corpora lutea. Although there was variation in the shape of individual lutein cells within the corpora lutea, no clusters of smaller cells or differences in cells at the periphery were found. Therefore there was no morphological evidence of lutein cells derived from the theca interna as opposed to the granulosa. Corpora albicantia were completely reorganized, indicating that they were not recent (fig. 7A).
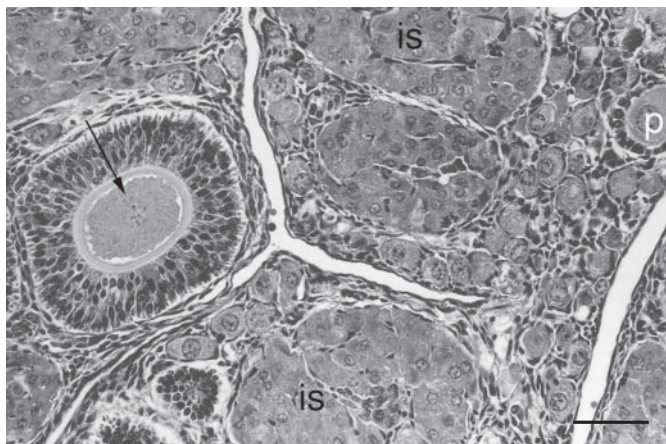

Fig. 3. Ovary of a juvenile otter shrew. Note the robust glandular interstitial cells in clusters (is). Note also the increase in size of the oocyte from the primary follicle (p) and the follicle with 2–3 layers of granulosa cells (arrow). An extensive cleft lined by a thin surface epithelial layer branches in the center. Bar = 50 μm.
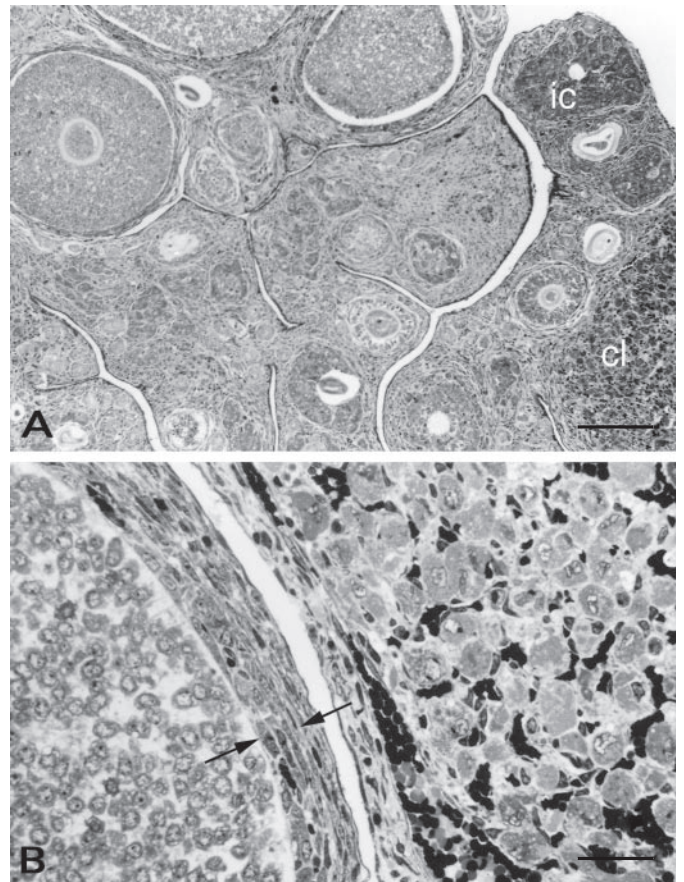

Fig. 4. Ovaries of adult nonpregnant otter shrews. **A** Numerous lobules, many with follicles of different sizes, radiate from the richly vascularized medulla. Bar = 300 μm. **B** Section through the cortex, showing the individual lobules. Note that even the lobule with the mature follicle (mf) contains other tissue in addition to the follicle. Bar = 300 μm. **C** The lobule on the left contains a young corpus luteum; the lobule on the right contains two large follicles. Bar =125 μm.
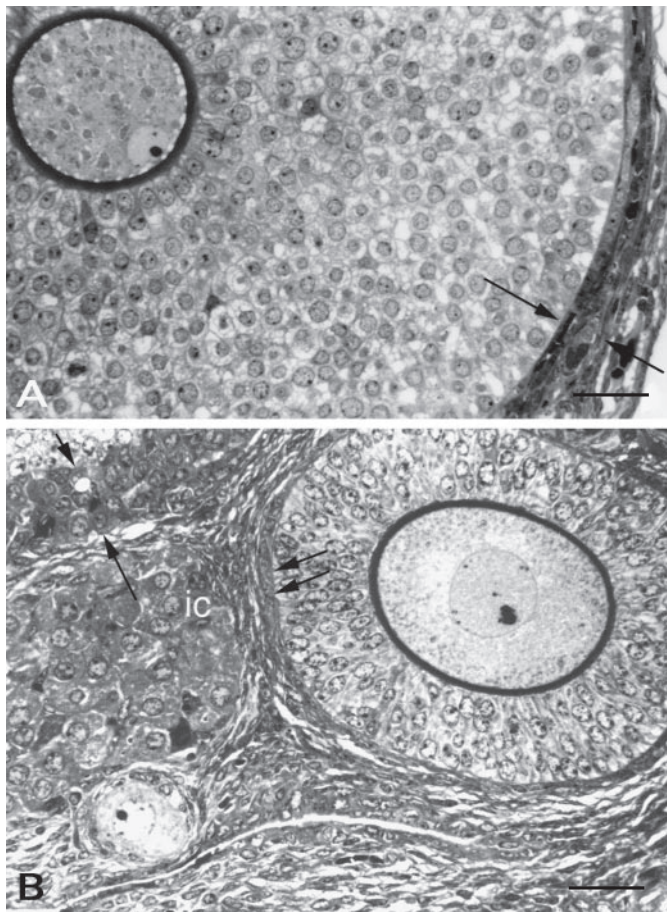
Fig. 5. Ovaries of adult nonpregnant otter shrews. **A** Mature follicle. The nucleus of the oocyte is eccentrically placed. The granulosa cells near the zona pellucida are densely packed; the more peripheral granulosa cells have small intercellular spaces. The theca interna (between arrows) is thin and is overlain by a thin layer of connective tissue and surface epithelium. Bar = 30 μm. **B** A primary follicle lies between the cleft on the lower left and a cluster of interstitial cells (ic). Note that, although the follicle on the right has 3–4 layers of granulosa cells, the theca interna (double arrows) is thin. Hypertrophying thecal cells of a follicle in early atresia appear between the arrows on the left. Bar =30 μm.

Fig. 6. Ovary of pregnant otter shrew. **A** Highly clefted portion of the cortex. A corpus luteum (cl) is in the lower right, and glandular interstitial cells (ic) from an atretic follicle in the upper right. The spaces surrounding the granulosa cells of the follicles in the upper left are artifactual, whereas the clefts are lined by epithelial cells. Bar = 125 μm. **B** Parts of two lobules showing a richly vascularized corpus luteum on the right and a mature normal follicle on the left. Note the thin theca interna between arrows. Bar = 30 μm.

The ovaries had numerous healthy follicles, the largest reaching slightly over 400 μm in diameter but again lacking an antrum. The healthy follicles had a thin theca interna with a few thecal gland cells vascularized by small capillaries (fig. 6B). Atretic follicles showed not only hypertrophy of the thecal gland cells but also persistence of some of the granulosa cells, and often a remnant of the zona pellucida could be seen in the center of these follicles (fig. 7B). There appeared to be more atretic follicles in these animals than in the nonpregnant animals. Only rarely did an atretic follicle appear luteinized with a large

vascularized granulosa as well as hypertrophied thecal glandular cells. The numbers of healthy and atretic small follicles and the clusters of glandular interstitial cells derived from atretic follicles appeared similar to those of the ovaries of nonpregnant adult animals.
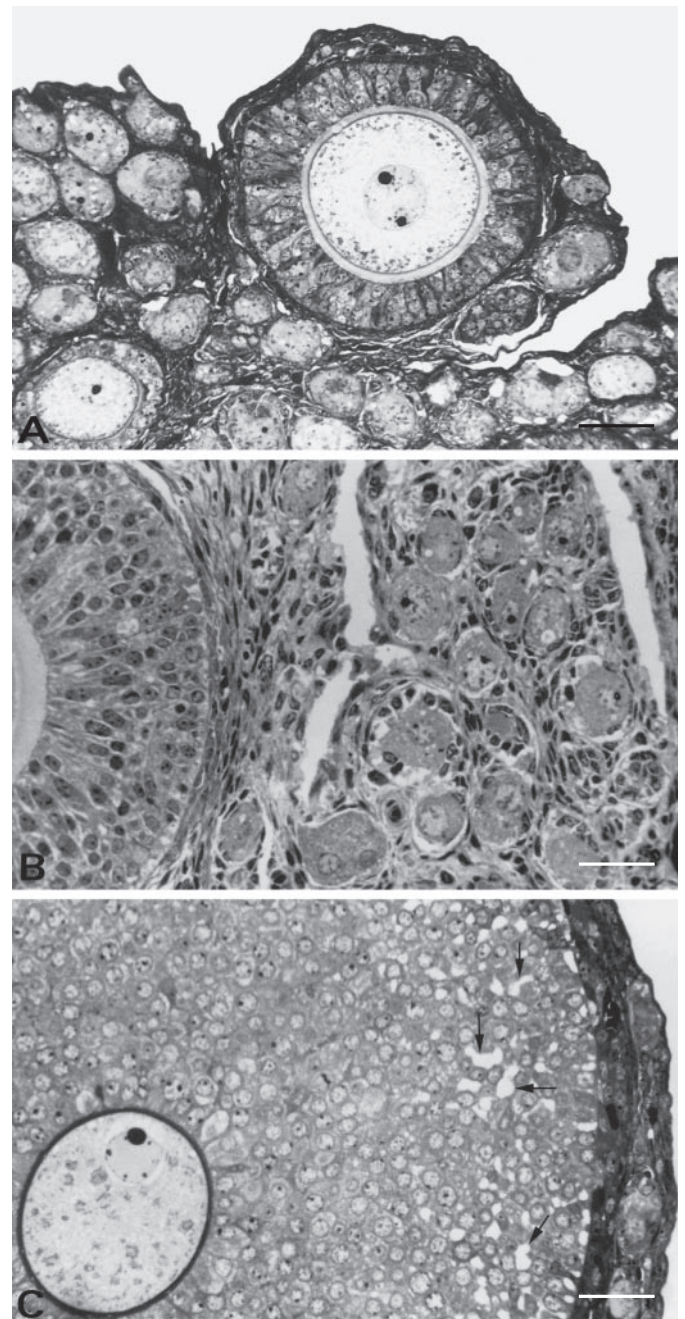
Development of the Follicle

Groups of primary oocytes could be found in all of the ovaries, often near the surface. Even within the clusters, however, the oocytes were organized into primordial follicles (fig. 8A, B). In the juvenile ovaries many follicles

Fig. 7. Ovary of pregnant otter shrew. **A** A corpus albicans lies beneath the thin surface epithelium. Bar = 50 μm. **B** An atretic follicle containing a collapsed oocyte and zona pellucida is on the left. Note the hypertrophied cells in the thickened theca interna (ti), compared with the thin theca interna (arrows) in the normal follicle (upper right). Bar = 30 μm.

with one to several layers of granulosa cells were present in the cortex. Oocytes in clustered or in isolated primordial follicles measured 18–22 μm in diameter. No evidence of neoformation of oocytes was observed. Neither mitotic figures nor predictyate meiotic stages were seen in any cells that might be putative germ cells. Most of the growth of the oocyte occurred when the follicles were either one to two or three layers in thickness. These oocytes reached 60–62 μm in diameter. A distinct zona pellucida could be discerned when the single layer of granulosa cells

Fig. 8. Stages of follicle development in the otter shrew. **A** Numerous follicles in the margin of the cortex: note the difference in size of the oocyte between the numerous primordial follicles and the early secondary follicle in the center. Both the oocyte and the zona pellucida have achieved as much as two thirds of their growth by this stage. Bar = 30 μm. **B** The lobule to the right contains numerous primordial follicles; all of the follicles have separate oocytes, not oocyte clusters. A normal intermediately sized follicle (220 μm) is on the left. Bar = 30 μm. **C** A healthy mature follicle. Note the numerous intercellular spaces in the peripheral granulosa (arrows). The dark theca interna remains thin in normal mature follicles, and there is no antrum. Bar = 30 μm.
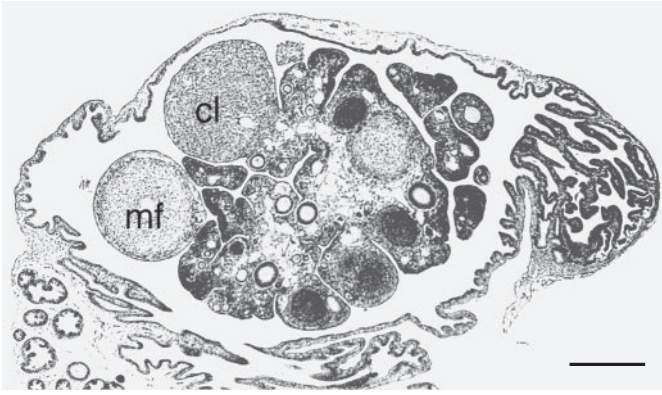
Fig. 9. Ovary of a tenrec in early pregnancy. Note the complete bursa and the extensive lobulation. A mature follicle (mf) and a corpus luteum (cl) are in conspicuous lobules (paraffin section). Bar = 500 μm.

had become tall cuboidal, and the zona was a thick structure in follicles that had obtained two layers of granulosa cells. These latter follicles showed the first patches of theca interna and a thin but complete theca was seen in follicles that had matured further. Fibroblasts were intermixed with this cell population with little or no theca externa. In follicles of 400 μm in diameter the oocyte reached 80–87 μm in diameter (fig. 8C). Hypertrophy of the thecal glandular cells in atresia of large follicles resulted in large cuboidal cells in spheres and clusters. Although these cells were clearly much larger than the original thecal cells, they were appreciably smaller than lutein cells.

Ovaries of the Tenrec, E. telfairi

The ovaries were situated in a complete ovarian bursa. Although the bursa was lined by cuboidal to columnar ciliated and secretory cells, only a few areas showed oviduct-like folding of the mucosa (fig. 9).

The ovary was covered by a surface epithelium that was low cuboidal and dipped into the cortex as clefts and surrounded occasional lobules. There was no well-formed tunica albuginea, but in some areas there were a number of fibroblasts near the surface (fig. 10). The cortex had clusters of primary oocytes with interspersed epithelial cells as well as numerous primordial follicles and follicles of various sizes (fig. 11). The largest follicles observed reached 330–430 μm. There were no antra in such follicles but there was some follicular fluid between the granulosa cells near the basement membrane of the follicle
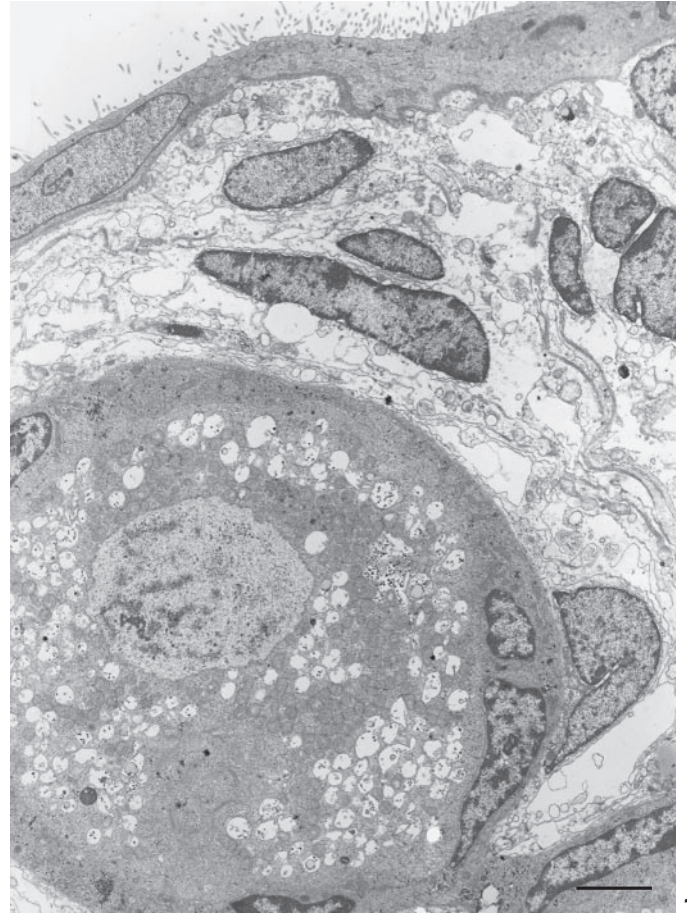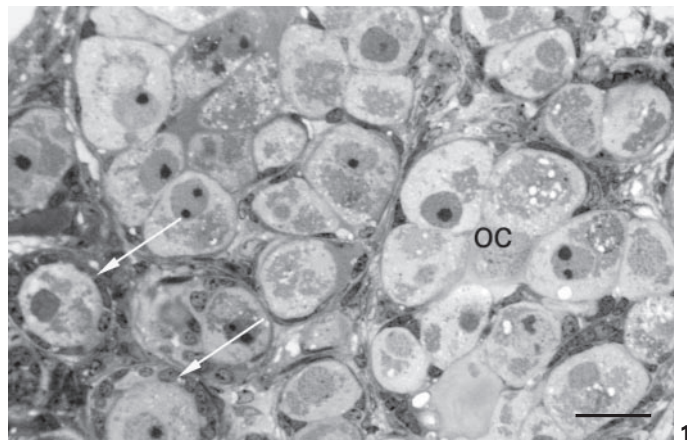
**Fig. 10.** Electron micrograph of a section through the margin of the cortex of a tenrec ovary. The surface epithelium lies over loose connective tissue rather than a dense tunica albuginea. A healthy primary follicle surrounded by a complete but thin layer of granulosa cells is in the lower left. Bar = 2.35 μm.

Fig. 11. Oocytes in the cortex of a tenrec ovary. Note that the oocytes on the right are in clusters (oc) and are not always separated by epithelial cells. In the lower left are two primary follicles with a surrounding layer of granulosa cells. Bar = 20 μm.
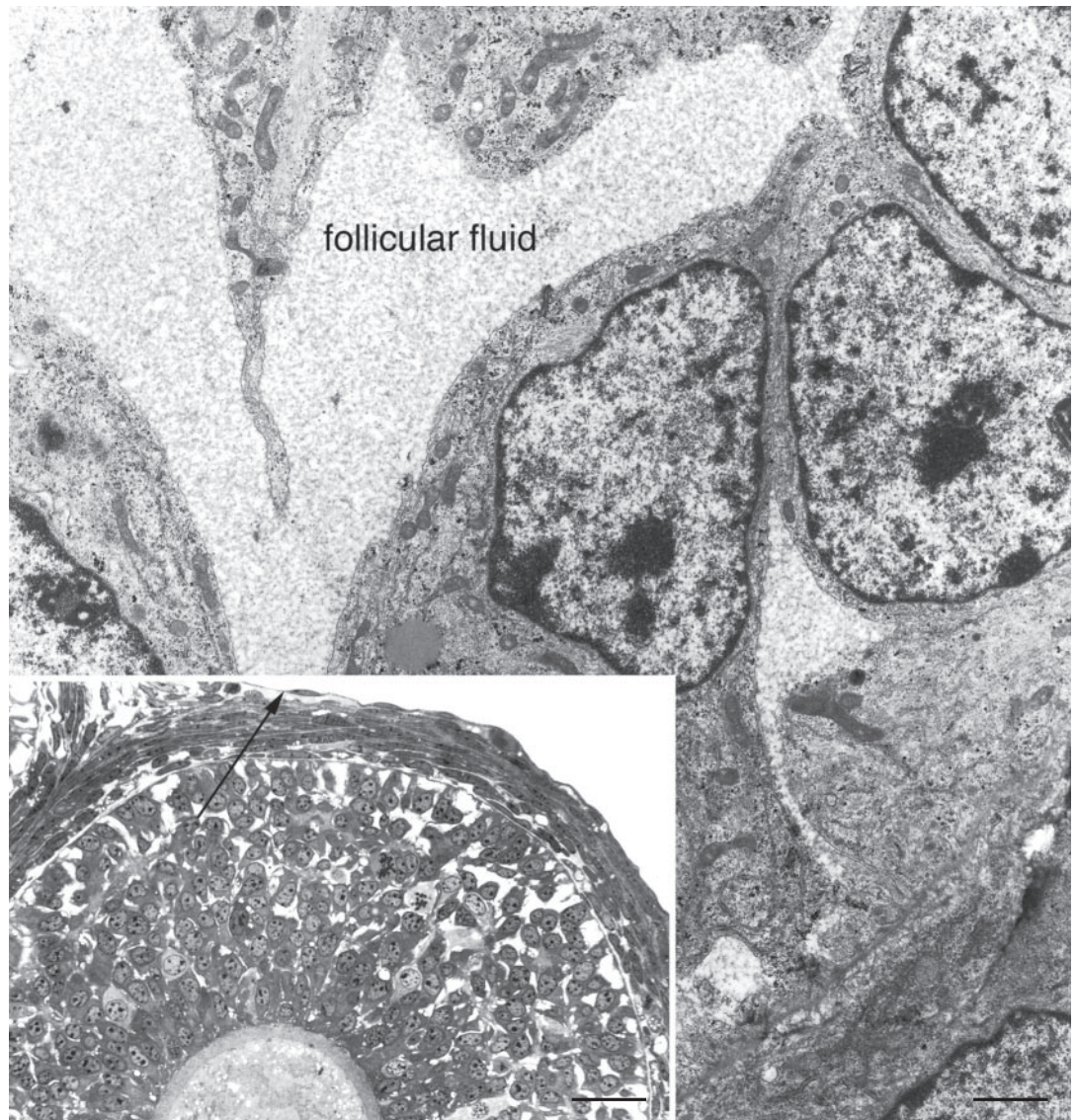
Fig. 12. Tenrec ovary (pregnant). Electron micrograph of the edge of a mature follicle. Note the flocculent follicular fluid between these peripheral granulosa cells. Bar = 1.5 µm. **Inset** Healthy mature follicle showing follicular fluid between the peripheral granulosa cells and more compact arrangement of cumulus cells. The glandular cells of the theca interna are vacuolated. Note the extreme thinness of the surface epithelium overlying the follicle (arrow). Bar = 30 µm.

(fig. 12). Healthy large follicles had a thin theca interna with a few glandular cells and small capillaries. Primary oocytes were approximately 22–26 µm when first incorporated into follicles. The zona pellucida developed and the oocytes grew to 60 µm within primary follicles. The oocytes reached a diameter of 80–88 µm in the largest follicles. An occasional large follicle in early stages of atresia showed hypertrophy of the theca interna cells (fig. 13A). This appeared to be accompanied by a fatty degeneration of both these cells and granulosa cells. Rarely an atretic follicle showed signs of luteinization, with vascularization and hypertrophy of the granulosa as well as the thecal cells (fig. 13B).

The medulla of the ovary was richly vascularized with both blood and lymphatic vessels. Epithelial cells, many arranged into rete tubules, extended from the medulla
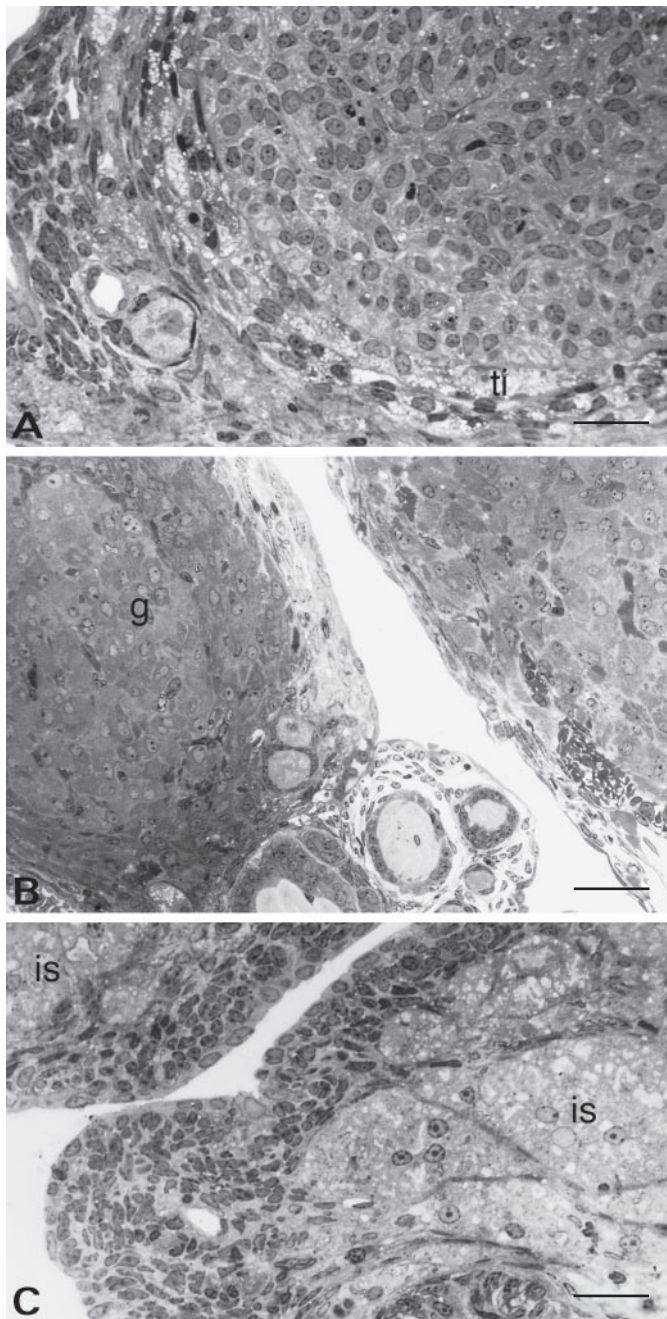
Fig. 13. Tenrec ovary (pregnant). **A** Section of a large follicle in early atresia. Although there is some hypertrophy of the theca interna (ti), the cells have numerous lipid droplets. Bar = 30 μm. **B** A portion of a corpus luteum is on the right; on the left is a rare luteinizing follicle. The hypertrophied theca interna cells have little lipid and the granulosa (g) has been vascularized. Bar = 50 μm. **C** The two cortical lobules seen here have numerous fibroblasts beneath the surface but little extracellular matrix. In the center of each lobule are large glandular interstitial cells (is) of a type thought to be of embryonic origin. Bar = 30 μm.
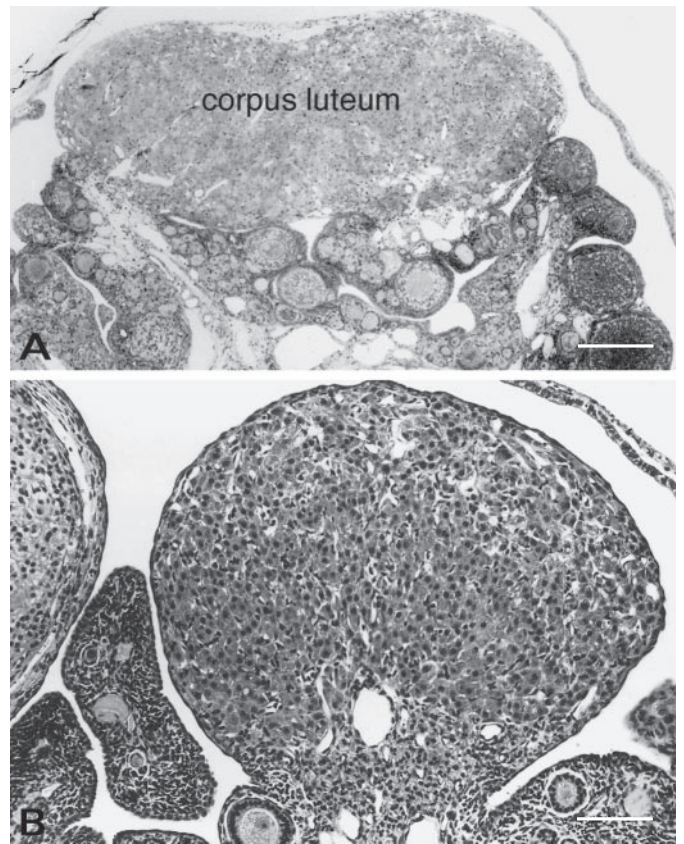
Fig. 14. Tenrec ovary (pregnant). **A** Margin of the cortex, showing a cup-shaped corpus luteum adjacent to the ovarian bursa. Bar = 300 μm. **B** Higher magnification of the corpus luteum seen in figure 9. Note that there is little more than a thin layer of surface epithelium overlying the greater circumference of the corpus luteum. Bar = 125 μm.

into the mesovarium. These tubules appeared solid by light microscopy but by electron microscopy could be seen to have a microvillous internal border but not a patent lumen. A few large interstitial cells containing numerous lipid droplets could be found in the medulla. Similarly such large lipid-filled cells were sometimes in the center of lobules in the cortex, especially those that lacked large follicles (fig. 13C). This distribution suggests that these were fetal interstitial cells in origin rather than contributions from atretic follicles, the latter apparently undergoing degeneration or dedifferentiation at this stage in the reproductive cycle.

The corpora lutea were large and some of them were slightly cupped towards the surface epithelium, perhaps indicating partial eversion (fig. 14). Other corpora protruded in a manner similar to those identified as re-cov-

ered by surface epithelium in *Setifer* and *Centetes* by Strauss [1938b]. However, no sperm were found in any of the corpora lutea, so there was no indication of intrafollicular fertilization. These corpora measured approximately 1.7 mm in length and 0.67 mm in width. All had a complete layer of surface epithelium with an underlying layer of sparse connective tissue (fig. 15A). The lutein cells varied in intensity of staining; they were approximately 20 μm in diameter in the mature corpus luteum (fig. 15B). No clusters of cells that might be considered derived from the theca interna were found in the corpora. The lutein cells had areas of microvilli, mitochondria with some villiform cristae, a great deal of smooth endoplasmic reticulum, but both free polyribosomes and patches of rough endoplasmic reticulum (fig. 16). A few dense granules were seen both in the cytoplasm and near the Golgi zones. In one of the ovaries there appeared to be luteinization of a nonovulated follicle in the form of hypertrophied and vascularized granulosa and theca cells.

Discussion

The ovaries of the Nimba otter shrew, *M. lamottei,* have several features similar to those of the tenrec, *E. telfairi.* Most notable is the absence of antral follicles. Both species, however, seem to have intercellular spaces between the more peripheral granulosa cells in the larger follicles. Electron micrographs of follicles of the tenrec show that there is a small amount of follicular fluid present between granulosa cells rather than the spacing being a shrinkage artifact. The ovaries of both the Nimba otter shrew and tenrec were folded and fissured. Those of the otter shrew had much more glandular interstitial tissue of the thecal type than did the tenrec. Clusters of primary oocytes that had not yet been incorporated into primordial follicles were characteristic of the tenrec but not the otter shrew ovaries.

The oocytes of mature follicles of both species examined here were larger than those reported for *Hemicentetes semispinosus* [Bluntschli, 1937] and were approximately the same size as those reported for the greater hedgehog tenrec, *Setifer setosus* [Strauss, 1938a]. There was no evidence of polyovulation in either of the species examined, in contrast to the situation reported in the streaked tenrec *H. semispinosus* [Strauss, 1938b] and *Tenrec ecaudatus* [Nicoll and Racey, 1985] and in the elephant shrew, *Elephantulus myurus* [van der Horst and Gillman, 1941]. Polyovulation is also variable in different elephant shrew species [Tripp, 1971].
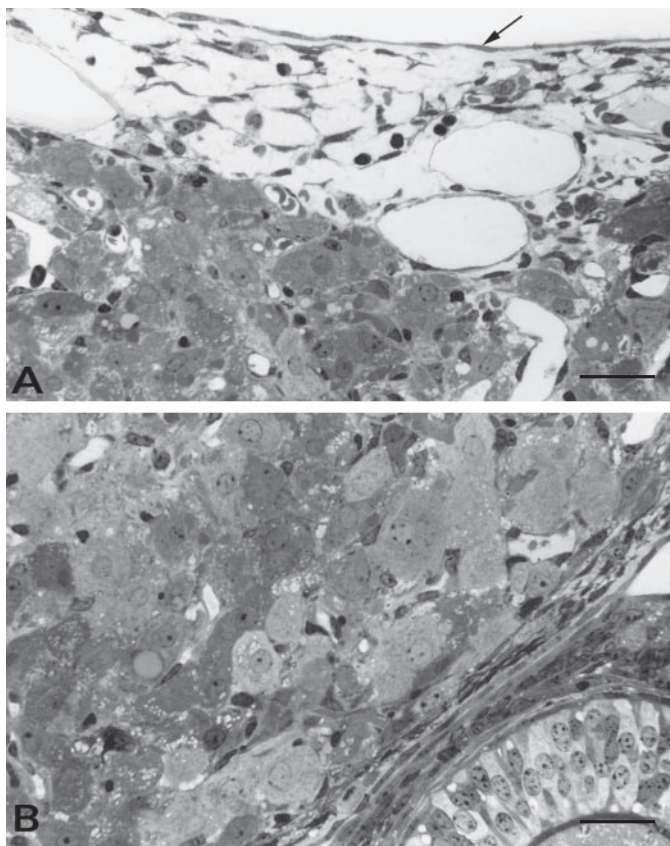
Fig. 15. A Higher magnification micrograph of the depressed area over the corpus luteum seen in figure 14A. Note the squamous nature of the surface epithelium (arrow) and the loose connective tissue between the epithelium and the lutein cells. The blood vessels appear largely empty in this perfusion-fixed specimen. Bar = 30 μm. **B** A corpus luteum of early pregnancy is on the left. There is variation in density of the individual lutein cells but there is no indication of clusters of different cell types. An early secondary follicle is in the lower right. Bar = 30 μm.

The extensive lobulation of the ovaries of the Nimba otter shrew is similar to that seen in the European hedgehog, *Erinaceus europaea* (order Eulipotyphla) [Deanesly, 1934], but is also present in the African elephant and hyrax (superorder Afrotheria). An unpublished photograph by J.P. Hill clearly illustrates multiple lobulation in ovaries of the greater otter shrew, *Potamogale velox.* A thin to absent tunica albuginea is characteristic of both the tenrecs and Eulipotyphlan species, including moles and shrews in addition to hedgehogs, as is also a small-absent antrum and small mature follicles [Mossman and Duke, 1973]. A compact mass of granulosa cells around the oocyte lacking follicular fluid is characteristic of many Eu-
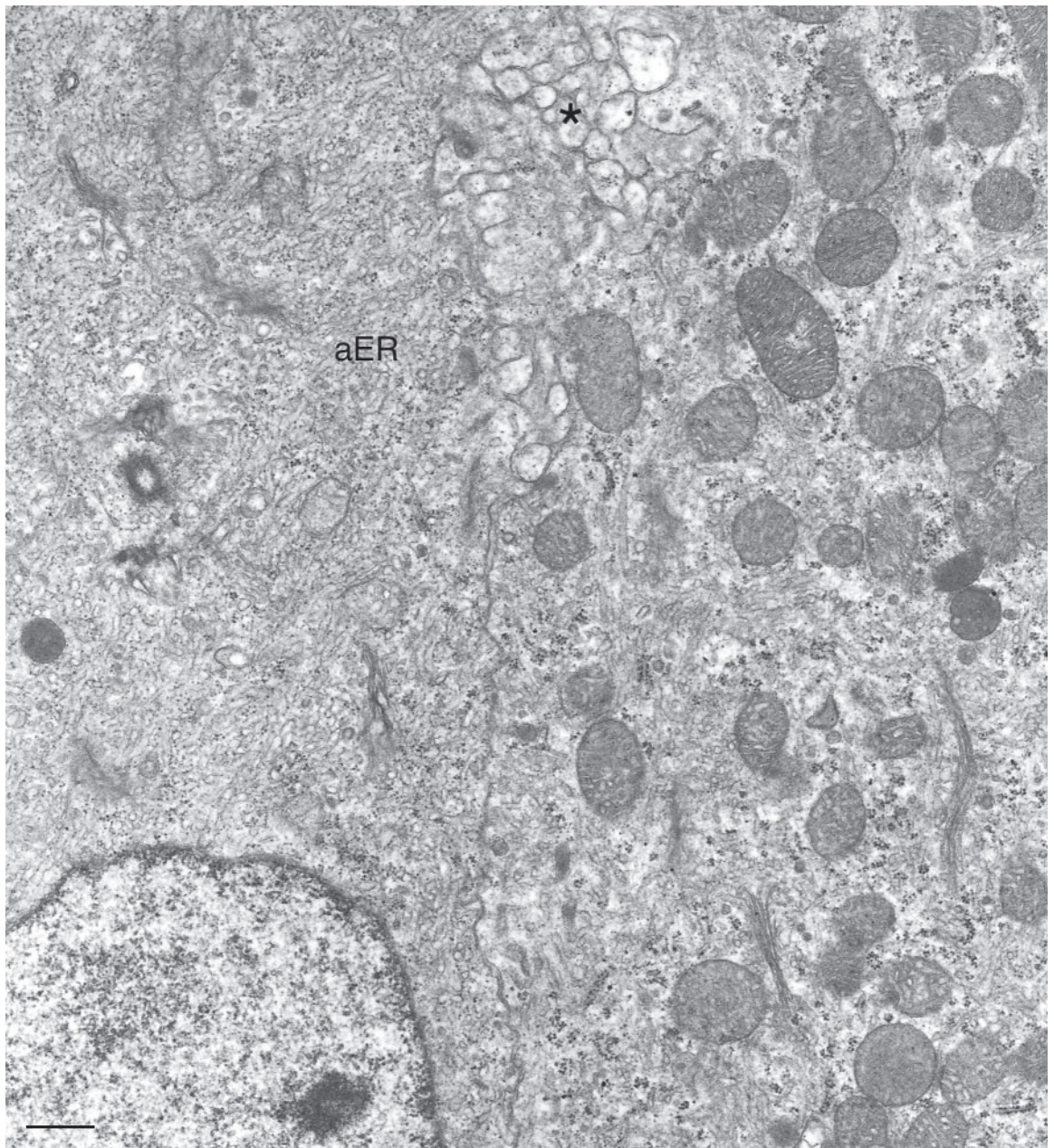
Fig. 16. Electron micrograph through a portion of two lutein cells from a pregnant tenrec. The mitochondrial structure with both tubular and septate cristae, folding of some areas of the cell surface (asterisk) and abundant tubules of agranular endoplasmic reticulum (aER) are typical of lutein cells of many species. Bar = 0.7 μm.

lipotyphlan species [Kaneko et al., 2003]. In the crocidurine species *Suncus murinus* the granulosa cells near the oocyte are distinctly different morphologically with large accumulations of glycogen. These cells do not accumulate follicular fluid even after ovulation [Kaneko et al., 2003]. The white-toothed shrew, *Crocidura russula,* also has glycogen-containing cumulus cells around the oocyte in ter-

tiary follicles [Kress, 1984]. Several shrew species of the genus *Sorex* have mature follicles with small antra [Brambell, 1935; Brambell and Hall, 1936], as does the short tailed shrew, *Blarina brevicauda* [Pearson, 1944] and the musk shrew, *S. murinus* [Dryden, 1969]. In moles, however, a bit larger antrum is formed and follicular fluid accumulates at least in the ovulated cumulus [Bedford et

al., 1999]. The description of follicular fluid in the more peripheral granulosa in both the otter shrew and tenrec is the first report of any intercellular matrix in this location in the Tenricidae, although Landau [1938] reported 'loosening' of the granulosa in follicles in the mature condition. The ovary of the elephant shrew, *E. myurus* (Afrotheria), also has small follicles which lose most of their antral fluid before ovulation and form protruding everted corpora lutea [van der Horst and Gillman, 1940]. Eulipotyphlan species can also form everted corpora lutea, as shown in induced ovulation in the musk shrew, *S. murinus* [Bedford et al., 2004]. The ovaries of elephants and hyraxes (Afrotheria), although lobed and fissured, have larger follicles and a demonstrable tunica albuginea [Perry, 1953; O'Donoghue, 1963; Kayanja and Sale, 1973].

The amount of glandular interstitial tissue is variable within both the Afrosoricida and the Eulipotyphla. The moles in particular show extreme amounts of glandular interstitial tissue including an adrenal-like interstitial tissue in the star-nosed mole, *Condylura cristata* [Mossman and Duke, 1973]. Although it had been suggested that a large amount of glandular interstitial tissue in some of the moles might be related to the masculinization of the female genitalia, this has recently been shown not to be the case [Rubenstein et al., 2003]. The interstitial cells present in juvenile ovaries of *Micropotamogale* were very similar in appearance to the thecal type seen in mature individuals. In other species the similarity between juvenile and thecal-type interstitial cells is apparent at the ultrastructural level, both having features consistent with steroidogenesis [Guraya, 1991]. Because of our incomplete understanding of the function of glandular interstitial tissue and variation in the amount and type in related species, it is not currently possible to correlate observed differences with phylogenetic relationships.

Although no ovulation stages were available from either the otter shrew or the tenrec, it seems probable that there is never a well-developed antrum in follicles of either species. Non-antral follicles in ovaries that lack a well-formed tunica albuginea have been associated with eversion of the corpus luteum in tenrecs [Nicoll and Racey, 1985]. Whether or not such eversion occurs in the two species examined here could not be directly determined, although the cup-shaped structure of some corpora and protruding nature of others suggests such a possibility. The presence of follicular fluid in the peripheral aspect of mature follicles may aid the separation of the cumulus from the residual granulosa cells at ovulation. The location of the large follicles in the extremes of the ovarian lobules may also aid ovulation.

Ovaries with a thin-absent tunica albuginea and follicles with small-absent antra are widespread within both the Eulipotyphla and in the Afrosoricida, suggesting that such features may represent a primitive condition in ovarian development. Lobulated and deeply crypted ovaries are found in both groups but are not as common in the Eulipotyphla making inclusion of this feature as primitive more speculative.

Acknowledgments

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