JOURNAL OF EXPERIMENTAL ZOOLOGY 293:141–170 (2002)

The Reptilian Oviduct: A Review of Structure and Function and Directions for Future Research

JANE E. GIRLING*
School of Zoology, University of Tasmania, Hobart, Tasmania, Australia 7001

ABSTRACT The reptilian oviduct is a complex organ with a variety of functions (albumen production, eggshell production, placentation, oviposition or parturition, and sperm storage), depending on the parity mode of the species in question. These functions are under complex physiological control, the details of which are far from understood. The aims of this review are to summarise the information available concerning the structure and functions of the reptilian oviduct and to highlight areas in particular need of further research. *J. Exp. Zool. 293:141–170, 2002.* © 2002 Wiley-Liss, Inc.

The reptilian oviduct is a fascinating organ and its multiple functions reflect the variety of reproductive patterns exhibited by this diverse group of animals. The oviduct acts as a conduit for the egg between ovulation and oviposition or parturition. It acts as a site for fertilisation and, in some species, sperm storage. It may provide an oocyte with albumen and a multilayered eggshell. Alternatively, the oviduct may function with extraembryonic membranes to form placental interactions providing gas and water exchange, and in some cases nutrient transfer, between the mother and embryo(s).

Although the oviduct has long been an organ of interest, understanding of its functions is still in its infancy. This is especially apparent when compared with the advances made for other vertebrate groups, specifically the eutherian mammals. There are large gaps in our knowledge of a variety of issues, particularly relating to the endocrine control and molecular and biochemical nature of the oviduct.

The aims of this review are to (1) summarise the information available concerning the reptilian oviduct, and (2) identify areas in need of further research. There are four living orders of reptiles to be considered: Crocodilia (crocodiles, alligators, caimans, and gavials), Sphenodontia (tuatara), Squamata (lizards [including skinks, geckos, agamids, etc.], snakes, and amphisbaenians), and Testudines (turtles and tortoises, which will collectively be called turtles in the following discussion). The Sphenodontia and Squamata make up the Lepidosauria. Only limited data concerning oviductal structure in Sphenodontia are available, so tuatara are not considered in detail here. However, tuatara are believed to exhibit a typically reptilian oviduct with numerous uterine glands (Osawa, 1898; Gabe and Saint Girons, '64; Fox, '77). Fox ('77) provided a detailed summary of early information concerning the structure of the oviduct in reptiles. To avoid excessive repetition, information summarised here will predominantly use data that became available after 1977. An extensive recent review has also been provided by Blackburn ('98a), who discussed oviductal structure and function in squamate species from a phylogenetic perspective. Some overlap with this valuable paper is unavoidable, but I aim here to provide a summary of the knowledge available concerning the oviduct in reptiles as a whole. It must be remembered, however, that these summaries are based on information from a relatively small number of species. Any generalisations must be tempered with the realisation that much more information is required to provide a full picture of the reptilian oviduct.

TERMINOLOGY

Terminology concerning the oviduct varies in a potentially confusing manner, even warranting a paper discussing the relative merits of *oviductal* versus *oviducal* as the adjectival form of *oviduct* (Smith et al., '89). Smith et al. ('89) concluded that *oviductal* was the preferred form, and, for the sake

*Correspondence to: Jane Girling, School of Zoology, University of Tasmania, GPO Box 252-05, Hobart, Tasmania, Australia 7001. E-mail: Jane.Girling@utas.edu.au

Received 7 May 2001; Accepted 24 January 2002
Published online in Wiley InterScience (www.interscience.wiley.com). DOI: 10.1002/jez.10105

of consistency, this term will be used throughout this paper.

The oviduct can be divided into several different regions that differ in their structure and function (Fig. 1A). The terminology used to identify these regions varies, which can lead to some confusion, particularly when interspecific comparisons are being made. The terms identified in the following text will be used consistently throughout this paper. Starting anteriorly, the regions include (a) the infundibulum, (b) the uterine tube (also known as the tuba, glandular region, albumen-secreting portion, magnum), (c) the isthmus (aglandular segment, intermediate region), (d) the uterus (shell-forming region), and (e) the vagina (cervix). The different regions are not recognised in all reptilian species, and additional regions may also be included. In descriptions of several squamate species, the infundibulum and uterine tube are not differentiated (Halpert et al.,'82; Adams and Cooper,'88; Aldridge, '92; Shanthakumari et al.,'92), and the uterus is divided into anterior and posterior regions (Guillette and Jones,'85b; Guillette et al.,'89). In the crocodilians studied to date, the infundibulum and the uterus may each be separated into anterior and posterior portions (Palmer and Guillette,'92). The different regions will be discussed in more detail in the following text.

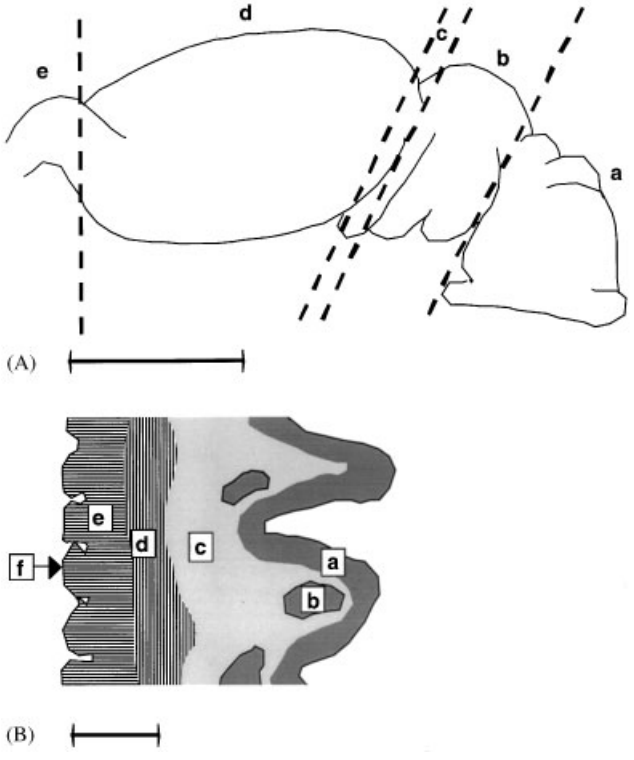

Fig. 1. (**A**) Gross morphology of gekkonid oviduct drawn from dissection of *Hoplodactylus maculatus*. a: infundibulum; b: uterine tube; c: isthmus; d: uterus; e: vagina. Bar=5 mm. (**B**) Schematic diagram of cross section through oviduct illustrating different tissue types. a: epithelium; b: shell gland; c: connective tissue; d: circular muscle; e: longitudinal muscle; f: serosa (mucosa=a+b+c; muscularis=d+e). Bar=100 μm.

The oviduct can also be differentiated into different tissue layers in cross section (Fig. 1B). The innermost layer or mucosa (endometrium) consists of an epithelial layer lining the lumen of the oviduct plus its underlying lamina propria. The lamina propria consists of connective tissue and any glands that may be present. Under the mucosa is the muscularis (myometrium), which consists of an inner circular and an outer longitudinal muscle layer. The oviduct is enclosed within the serosa (perimetrium), a continuation of the peritoneum. Obviously, these layers differ in structure between the different oviductal regions. The terms *endometrium, myometrium*, and *perimetrium* more correctly relate specifically to uterine tissues but have been used to describe oviductal tissues in general in the reptilian literature. In this review, I will use *mucosa*, *muscularis*, and *serosa* for all regions.

PARITY MODE AND NUTRIENT PROVISION TO EMBRYOS

In the following discussion, it will be necessary to highlight differences in oviductal structure and function that directly relate to the parity mode, or the method of nutrient provision to embryos, of the species in question. In the context of this discussion, oviparity is defined as the laying of eggs containing embryos that require a period of development outside of the female's reproductive tract (Guillette,'93). Viviparity, on the other hand, is defined as the retention of the embryo within the uterus of the mother until development is complete and birth can occur (Guillette,'93). The term *gravid* refers to oviparous females containing oviductal eggs prior to oviposition. The term *gestation* refers to the period of time when embryos are within the oviduct of viviparous females prior to parturition.

Viviparity is believed to have evolved within the squamate reptiles over 100 times (Blackburn,'82,'85; Shine,'85). However, within the crocodilians, turtles, and sphenodontians, all species are oviparous. The ecological and physiological factors concerned with the evolution of viviparity in squamate reptiles have been widely debated (e.g., Packard et al., '77,'89; Angelini and Ghiara,'84; Shine and Guillette,'88; Shine,'89,'95; Callard et al.,'92; Guillette, '93; Blackburn,'95; Andrews and Mathies, 2000).

The hypothesised sequence of physiological and morphological changes allowing the evolution of viviparity can be summarised as follows (Packard et al., '77; Callard et al., '92; Guillette, '93). To allow viviparity to evolve, the embryo must be retained within the uterus of the mother for longer and longer time periods. While in the mother, there is a need for gas and water exchange; hence the evolution of a placenta. This requires a reduction in eggshell thickness to allow closer association of uterine and embryonic tissues. It is obvious, therefore, that the evolution of viviparity in reptilian species is intimately associated with changes in oviductal structure and function.

Two sources of nutrient provision to embryos are seen in reptiles. In the first of these, *lecithotrophy*, embryos receive their nutrients predominantly from the yolk supplied during vitellogenesis. Most reptiles, both viviparous and oviparous, exhibit lecithotrophy. The supply of nutrients via a placenta is termed *placentotrophy* and is exhibited in only a few reptilian species studied to date (Blackburn et al., '84; Thompson and Stewart, '94; Thompson et al.,'99c).

HISTOLOGY OF THE OVIDUCT

The reptilian oviduct includes all structures of the female reproductive tract derived from the embryonic Müllerian duct (Wake, '85). In general, the oviducts are paired structures, one lying dorsally on either side of the body (Fox,'77). Rarely, one oviduct has been lost; for example, the left oviduct is absent in the skink *Lipinia rouxi* (Greer and Mys, '87), and in the southeastern crown snake, *Tantilla coronata*, the left oviduct is vestigial, although females do have a functional left and right ovary (Aldridge, '92). The oviducts may be different lengths on each side of the body (Perkins and Palmer, '96), presumably to make efficient use of body space during gravidity or gestation.

The following is a summary of the structure and histology of the different oviductal regions during the vitellogenic period when oviducts are fully developed in preparation for gravidity or gestation.

Infundibulum

The most anterior region of the oviduct, the infundibulum, tends to be a slender, flaccid region. It receives the ovulated egg from the ovary via a funnel-shaped ostium opening to the coelomic cavity. Prior to ovulation, the infundibulum migrates toward the ovary where the ostium surrounds the developing oocyte. This process has been observed in several squamate species (Cuellar, '70) and means that the ostium is ideally placed to receive ovulated oocytes. The luminal epithelium of the ostium is made up predominantly of ciliated cells (e.g., Girling et al., '97, '98); do ciliated cells function in the positioning of the ostium around the oocyte? Whether the oviduct is directly involved in stimulating the ovulation process is unknown.

The epithelium of the infundibulum consists of an even mix of ciliated and nonciliated cells; the mucosa is usually thrown into folds that gradually increase in height toward the uterine tube (Botte, '73; Palmer and Guillette, '88, '92; Uribe et al., '88; Picariello et al., '89; Sarker et al., '95; Perkins and Palmer, '96 ; Girling et al., '97, '98) (Fig. 2). In some species, the change in the mucosa is considered sufficient to divide the infundibulum into anterior and posterior regions (e.g., the gopher tortoise, *Gopherus polyphemus*; Palmer and Guillette, '88). Despite the availability of detailed descriptions of the infundibulum, however, there is very little discussion of the functions of this oviductal region.

The infundibulum is obviously a secretory region. In the Florida scrub lizard, *Sceloporus woodi*, deposition of secretory material begins immediately upon entry of the egg into the oviduct (Palmer et al., '93). Evidence for this came from an egg observed only halfway inside the ostium; material was already deposited on the egg, but only on the portion inside the oviduct (Palmer et al., '93). The function of these secretions, however, is yet to be investigated. Very little is known of the nature of secretions produced by the infundibulum. Nonciliated cells of the epithelium may stain for carbohydrate or carbohydrate-protein substances with Periodic Acid-Schiff reagent (PAS) (Botte,'73; Guillette et al.,'89; Picariello et al.,'89 ; Girling et al., '97, '98). In three species of gecko—New Zealand's common gecko, *Hoplodactylus maculatus*; the leaf-tailed gecko, *Saltuarius wyberba*; and the Mediterranean gecko, *Hemidactylus turcicus*—positive carbohydrate staining corresponded to numerous secretory granules of varying electron density in the apical regions of cells (Girling et al.,'98). Some nonciliated cells exhibited apical protrusions into the lumen. In the case of *H. turcicus*, the nuclei were positioned within these protrusions, giving the appearance that the cells were about to slough off into the lumen. In the viviparous black swamp snake, *Seminatrix pygaea*, numerous lipid droplets were observed in the infundibular epithelial cells (Sever et al., 2000).

Bleb cells have been noted in several species. In the gopher tortoise, *Gopherus polyphemus*, bleb cells were found at the base of folds in the posterior

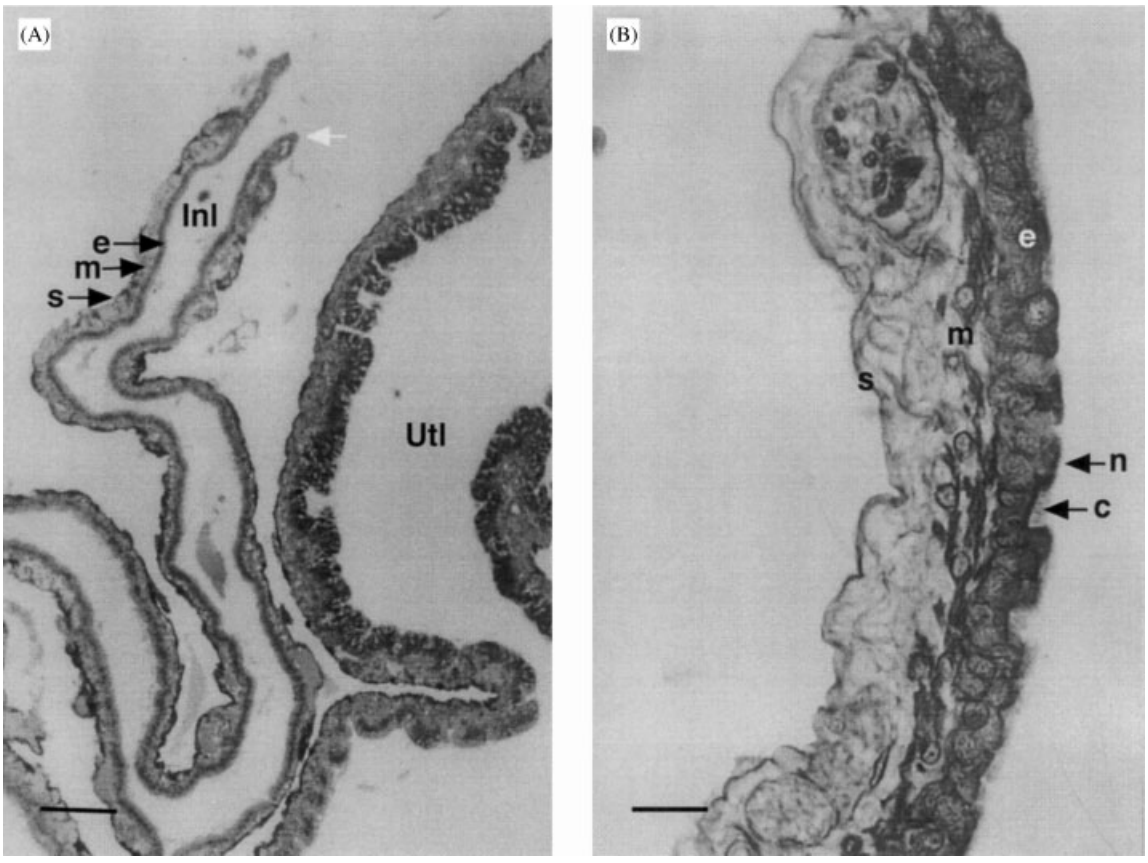

Fig. 2. Photomicrographs of infundibulum. (**A**) Infundibulum from the viviparous gecko *Hoplodactylus maculatus*. Tissues have been stained with haematoxylin and eosin and alcian blue. Note that the epithelium lining the infundibulum extends over the lip of the ostium (white arrow) and merges with the serosa. Bar=200 μm. (**B**) Infundibulum from the oviparous gecko *Saltuarius wyberba*. Tissues have been stained with Mallory's trichrome. Bar=20 μm. c: ciliated cell; e: epithelium; Inl: lumen of the infundibulum; m: muscularis; n: nonciliated cell; s: serosa; Utl: lumen of the uterine tube. Photos courtesy of Dr. A. Cree.

infundibulum (Palmer and Guillette, '88). These cells had a smooth apical surface and did not stain positively for carbohydrate. Bleb cells were also observed in the infundibulum of the geckos *H. maculatus*, *S. wyberba*, and *H. turcicus* using light microscopy (Girling et al., '97, '98). When tissues were observed using transmission electron microscopy, it was suggested that the most likely candidate for bleb cells in these geckos were cells with a fine, apical membrane protruding into the lumen. The protrusions contained fine, nongranular material, and the cytoplasm below the bleb resembled that of other nonciliated cells. In fact, numerous small bleblike and other protrusions were noted on the apical surface of epithelial cells from all three gecko species (Girling et al.,'98). The function of these bleb cells is unknown, but Palmer and Guillette ('88) suggested that they may be involved in apocrine or merocrine secretion. Apical protrusions in the infundibulum are ideally placed to secrete materials directly onto the ovulated egg prior to the egg being surrounded by albumen and shell membranes.

Uterine tube

In squamates, the mucosa of the uterine tube is formed into folds of connective tissue covered with epithelial cells (Fig. 3A; Botte,'73; Uribe et al.,'88; Picariello et al.,'89; Palmer et al.,'93; Perkins and Palmer,'96 , Girling et al.,'97,'98). The epithelium lining the lumen of the uterine tube consists of both columnar ciliated and nonciliated cells. The staining properties of the epithelial cells differ from those in the infundibulum, suggesting a difference in function between the regions. However, the function of the uterine tube in squamate reptiles is unknown.

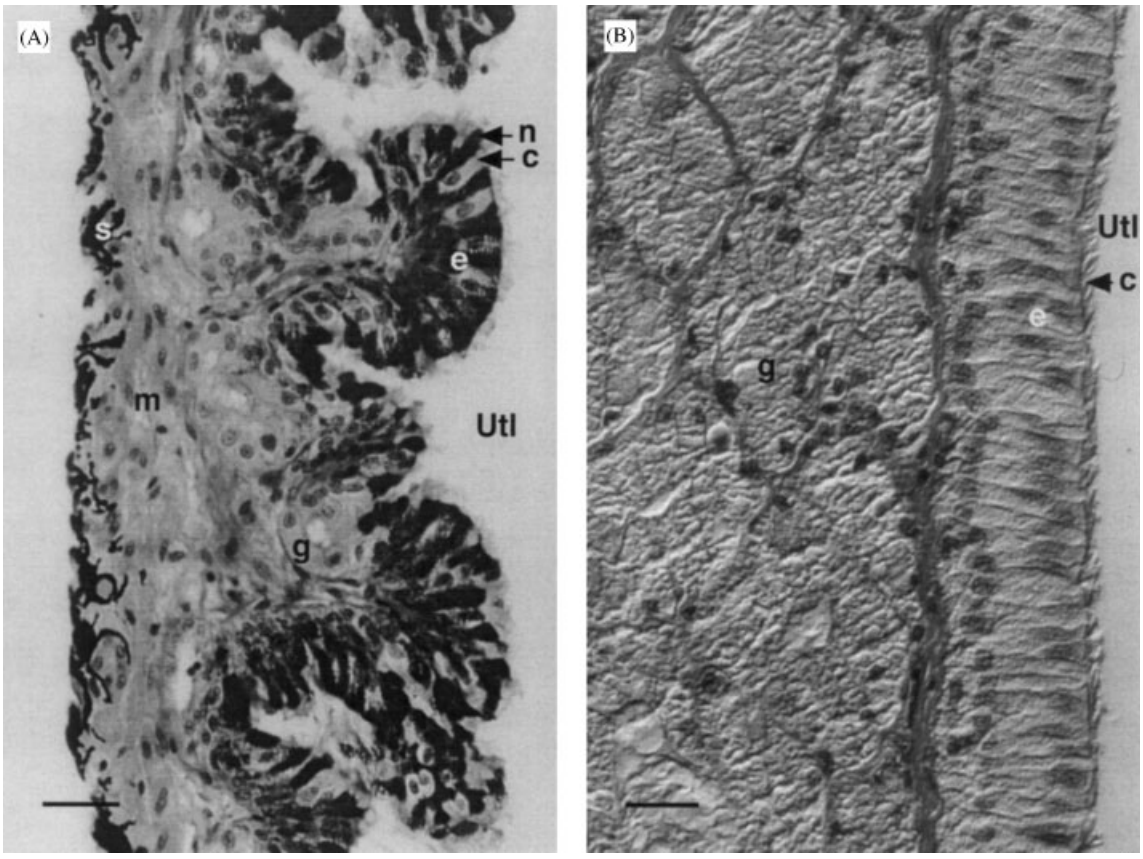

Fig. 3. Photomicrographs of uterine tube. (**A**) Uterine tube from the viviparous gecko *Hoplodactylus maculatus*. Tissues have been stained with haematoxylin and eosin and alcian blue. Bar=40 μm. (**B**) Uterine tube from the alligator *Alligator mississippiensis*. Tissues have been stained with Mallory's trichrome. Bar=5 μm. c: ciliated cell; e: epithelium; g: gland; m: muscularis, n: nonciliated cell, s: serosa; Utl: lumen of the uterine tube. Photos courtesy of Dr. A. Cree (**A**) and Prof. L. J. Guillette, Jr. (**B**).

The uterine tube of squamates does produce secretory material. In most squamates examined to date, nonciliated cells stain positively for carbohydrate and carbohydrate-protein substances with PAS and for acid mucosubstances with Alcian blue. In the wall lizard *Podarcis* (*Lacerta*) *sicula* (Botte, '73) and the gecko species studied by Girling et al. ('98), tests indicated that the staining product was not glycogen. The bases of mucosal folds in the posterior uterine tube form glandular crypts (in both oviparous and viviparous species). Although epithelial cells lining the crypts do not stain positively with various carbohydrate stains, gland cells do contain numerous secretory granules. In some species, these crypts are involved in sperm storage.

The uterine tube of turtles and crocodilians is responsible for the production of albumen: egg white proteins that surround the egg prior to oviposition in turtles and crocodilians, but not in squamates. As in squamates, a simple columnar epithelium of ciliated and nonciliated cells is present, the nonciliated cells of which stain positively with PAS for carbohydrate substances (Palmer and Guillette, '88; Abrams Motz and Callard, '91; Sarker et al., '95). The mucosa, however, is packed with numerous glands that occupy 80–90% of the total thickness of the uterine tube and that are presumably responsible for albumen production. These glands may be compound tubulo-alveolar, branched tubular, or branched acinar (Fig. 3B; Palmer and Guillette, '88; Abrams Motz and Callard, '91; Sarker et al., '95). In the American alligator, *Alligator mississippiensis*, gland cells contained spherical granules of varying electron density (Palmer and Guillette,'92), and the surface of gland cells was covered with numerous microvilli.

Isthmus

As an intermediate region between the uterine tube and the uterus, the isthmus often appears to share similarities with both its neighbouring regions. It is also a region that is often short and

ignored in published descriptions, particularly in squamate species. It may be that the isthmus is better considered as a transitional area in squamates, rather than a separate region in its own right. In addition, as pointed out by Blackburn ('98a), the use of the term *isthmus* in squamates should not be taken to imply homology with the isthmus in birds and chelonians.

In the gecko species *H. maculatus*, *S. wyberba*, and *H. turcicus*, the isthmus was not visible with the naked eye and it was morphologically similar to both the uterine tube and the uterus (Girling et al., '98). However, a cytologically distinct isthmus was present that, unlike the epithelium of neighbouring regions, did not stain with either PAS or Alcian blue. In the gecko *Tarentola m. mauritanica*, the epithelium of both the isthmus and the uterine tube stained positively with both PAS and Alcian blue, and the mucosal glands of the isthmus resembled those in the uterine tube and the uterus (Picariello et al.,'89).

The isthmus of the gopher tortoise, *Gopherus polyphemus*, was aglandular (Palmer and Guillette, '88), whereas in the soft-shelled turtle, *Lissemys p. punctata*, tubular alveolar glands similar to those in the uterine tube were seen, but only at the time of ovulation (Sarker et al.,'95).

Uterus

The typical uterus of an oviparous squamate has a columnar epithelium with both ciliated and nonciliated cells (Fig. 4A; Uribe et al., '88; Guillette et al.,'89; Picariello et al.,'89; Palmer et al.,'93; Perkins and Palmer,'96; Girling et al.,'98). Staining of nonciliated cells for carbohydrate substances produces different results in different species. This may relate to the different types of eggshell produced by the uterus in different species. Unlike that of the uterine tube, the epithelium of the uterus overlays a thick *lamina propria* containing numerous mucosal glands (tubulo-alveolar, tubular, branched saccular or branched acinar) that contain numerous secretory granules and function in eggshell production. Beneath the mucosa are the inner layer of circular and outer layer of longitudinal muscle that function to expel the egg during oviposition (Fig. 4a; Uribe et al.,'88; Guillette et al., '89; Picariello et al., '89; Palmer et al., '93; Perkins and Palmer,'96; Girling et al.,'98).

The uterus of turtles is very similar to that described for oviparous squamates (see preceding text; Aitken and Solomon,'76; Palmer and Guillette, '88; Abrams Motz and Callard,'91; Sarker et al.,'95); however, in the American alligator, *Alligator mississippiensis*, the uterus was divided into two functionally separate regions (Fig. 4C,D). In *A. mississippiensis*, the mucosal glands of the anterior uterus were branched tubular glands with short ducts connecting them to the lumen (Palmer and Guillette, '92). Gland cells were cuboidal and contained numerous electron-dense granules. The posterior uterus also had numerous glands in the mucosa. However, these gland cells lacked the extensive distribution of electron dense granules (Palmer and Guillette, '92). The differing structure of these regions reflects the different process of eggshell production exhibited by crocodilians (discussed later).

In *Lerista* (*Sphenomorphus*) *fragilis*, a skink exhibiting incipient viviparity (i.e., it lays eggs that hatch within hours of oviposition), the uterus contained very few, but well-developed, mucosal glands (Guillette, '92). This illustrates the difference in uterine structure that is seen with the transition from oviparity to viviparity and its associated loss of the eggshell. Viviparous squamates have very few glands within the mucosa (Fig. 4B), although the gland cells still contain secretory granules of varying electron densities. The uterus in viviparous species, as in oviparous species, has an epithelium made up of a mix of ciliated and nonciliated cells (Guillette and Jones,'85 b; Girling et al.,'97,'98; Corso et al., 2000; Sever et al., 2000), and the mucosa is well vascularised with numerous blood vessels under the epithelial layer.

Histochemical properties and the numbers of secretory granules in glandular cells vary between different species of reptiles, presumably reflecting the different structure and thickness of eggshell membranes among species. In the gecko *Tarentola m. mauritanica* (Picariello et al.,'89) and the wall lizard *Podarcis* (*Lacerta*) *sicula* (Botte,'73), the glandular cells stained positively for keratin and also for S-S and SH- groups. Some ultrastructural information is available for the green turtle, *Chelonia mydas* (Aitken and Solomon, '76). Glandular cells contained variable numbers of uniformly electron-dense, membrane-bound secretory granules. The luminal surface of gland cells sometimes had microvilli or exhibited blebbing, and golgi apparatus and rough endoplasmic reticulum (RER) were prominent within the cells. In the oviparous gecko *Hemidactylus turcicus* (which produces a hard, calcareous eggshell), the uterine gland cells contained loosely packed secretory granules, whereas in the oviparous gecko *Saltuarius wyberba* (which is thought to produce a soft, parchmentlike eggshell), the granules were tightly packed (Girling et al.,'98).

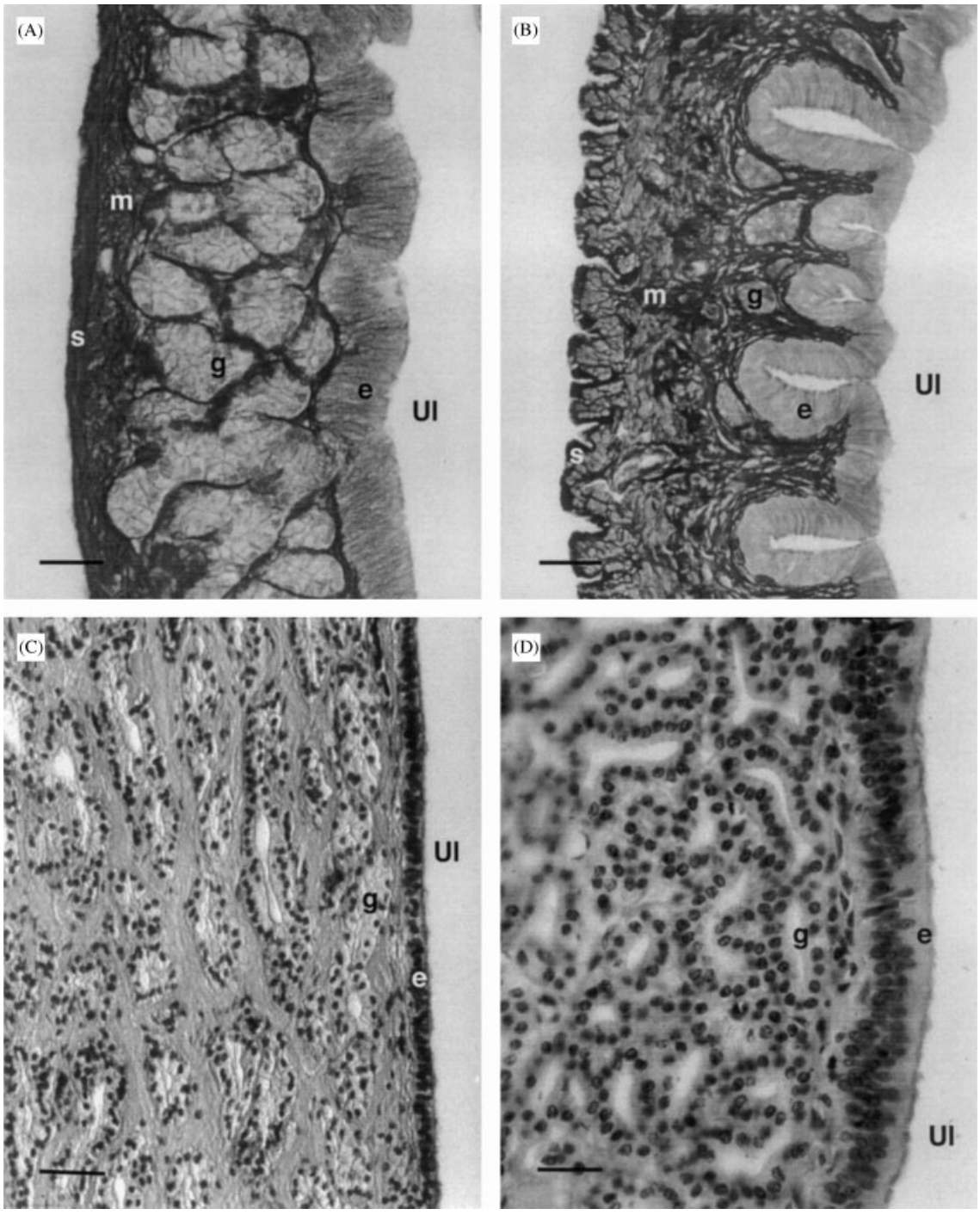

Fig. 4. Photomicrographs of uterus. (**A**) Uterus from the oviparous gecko *Hemidactylus turcicus*. Bar=40 m. (**B**) Uterus from the viviparous gecko *Hoplodactylus maculatus*. Bar=75 μm. (**C**) Anterior and (**D**) posterior uterus from the alligator *Alligator mississippiensis*. (C) and (D): Bar=5 μm. Tissues have all been stained with Mallory's trichrome. e: epithelium; g: gland; m: muscularis; s: serosa; Ul: lumen of the uterus. Photos courtesy of Dr. A. Cree (A, B) and Prof. L.J. Guillette, Jr. (C,D).

The secretory granules in the few glands present in the viviparous gecko *Hoplodactylus maculatus* were smaller and more electron dense then those in either *H. turcicus* or *S. wyberba* (Girling et al.,'97,'98).

Vagina

The most posterior region of the oviduct, which leads out to the common urogenital or cloacal opening, is called the vagina (Fig. 5; Botte, '73; Palmer

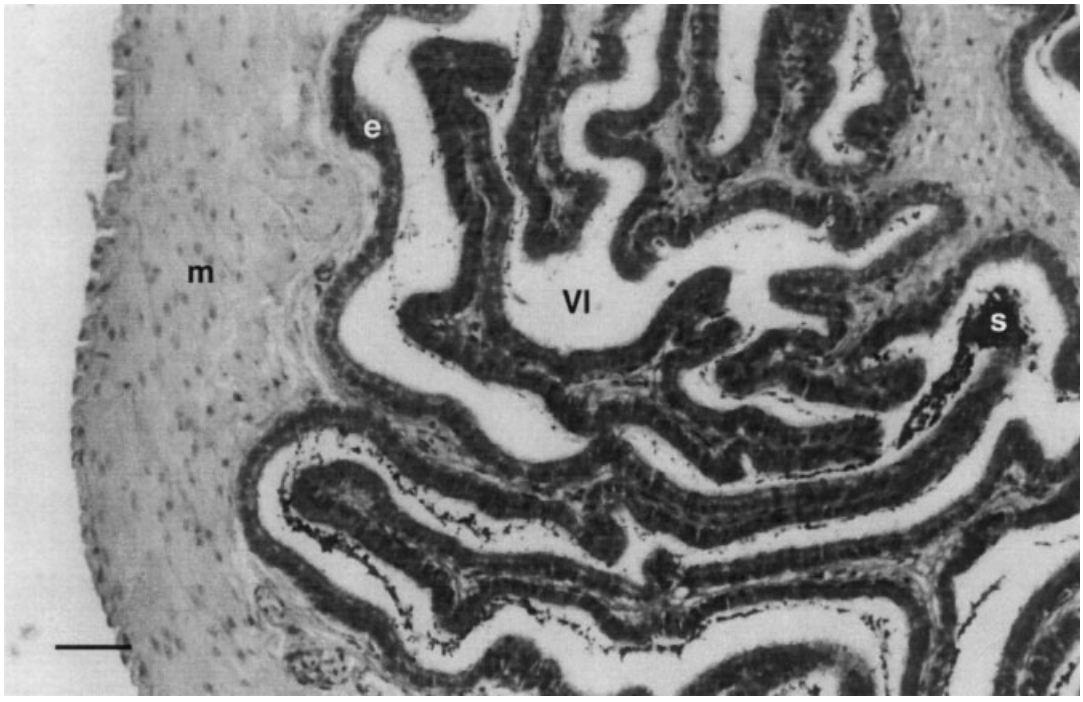

Fig. 5. Photomicrograph of the vagina from the oviparous gecko *Saltuarius wyberba*. Tissues have been stained with haematoxylin and eosin and alcian blue. Note the sperm in the lumen. e: epithelium; m: muscularis; s: sperm; Vl: lumen of vagina. Bar=75 μm. Photo courtesy of Dr. A. Cree.

and Guillette,'88; Picariello et al.,'89; Abrams Motz and Callard,'91; Palmer et al.,'93; Perkins and Palmer,'96 ; Girling et al.,'97,'98). The vagina is a thick, muscular region that acts as a sphincter during gravidity or gestation. The mucosa is thrown into deep folds that effectively reduce the volume of the vaginal lumen. The folds may reduce in height more posteriorly (Botte,'73 ; Girling et al.,'97,'98) or, as in Florida scrub lizard, *Sceloporus woodi*, the trend was reversed and folds increased in height more posteriorly (Palmer et al., '93). Cuellar ('66) suggested that the folds may be needed to increase the mucosal surface area during oviposition or parturition.

The mucosal epithelium is heavily ciliated (Sever et al., 2000). Ciliated cells may function in sperm transport or the movement of mucus and debris from the oviduct. Nonciliated cells, which stain positively for carbohydrate substances, contain numerous secretory granules (Girling et al., '97, '98). In New Zealand's common gecko, *Hoplodactylus maculatus*, goblet cells were also present and were filled with secretory granules that appeared to coalesce (Girling et al., '98). The vagina is usually aglandular, although glands, or glandlike crypts between the mucosal folds, may be present in the anterior vagina of some species and are associated with sperm storage.

HORMONAL CONTROL OF SEASONAL OVIDUCTAL DEVELOPMENT

As with other reproductive organs, the oviduct undergoes changes over the course of a reproductive cycle. These changes can be correlated with seasonal hormone patterns. Development of the oviduct occurs during the vitellogenic or preovulatory period in preparation for gravidity or gestation and is associated with an increase in the height and secretory nature of epithelial tissues. Mucosal glands and the muscularis also become hypertrophied at this time, and there may be a general increase in vascularity.

Seasonal changes in oviductal tissues have been reported in numerous reptilian species (e.g., the whiptail lizards *Cnemidophorus inornatus* and *C. neomexicanus*, Christainsen,'73 ; the lacertid lizard *Lacerta vivipara*, Gavaud, '86 ; the agamid lizard *Uromastyx hardwickii*, Nawaz, '87 ; New Zealand's common gecko, *Hoplodactylus maculatus*, Girling et al., '97). Seasonal changes may simply be noted as changes in the weight of oviductal tissue, with predicably, maximum weight occurring during the period of reproductive activity (vitellogenesis and gravidity/gestation) (Botte, '73; van Wyk, '84; Picariello et al., '89; van Wyk, '94). Similarly, oviductal

weight increases significantly with sexual maturity (Sen and Maiti, '90). Another common measure of oviductal hypertrophy is an increase in oviductal diameter and/or diameter of uterine glands such as that seen during the reproductive cycle of the agamid lizard *Calotes versicolor* (Shanthakumari et al., '92). In the New Zealand common gecko, epithelial cell height reached a maximum in late vitellogenic females before declining in pregnant females (Girling et al.,'97).

In the painted turtle, *Chrysemys picta*, the tubuloalveolar glands of the uterine tube and the uterus showed significant growth in the preovulatory period (Abrams Motz and Callard, '91). This occurred concurrently with maximal plasma levels of both estradiol and progesterone (Callard et al.,'78). The thickness of oviductal tissues was maintained in postovulatory animals while progesterone levels were high, although glandular contents and granules from epithelial cells were discharged from the uterine tube. After oviposition, the uterine tube and uterus showed significant regression concurrent with a drop to basal levels of estradiol and progesterone (Callard et al., '78; Abrams Motz and Callard,'91).

In the gopher tortoise, *Gopherus polyphemus*, epithelial cell height and the thickness of the mucosa increased in the uterine tube and the uterus during vitellogenesis (Palmer and Guillette, '90). During gravidity, the epithelium remained hypertrophied, but the thickness of the uterine mucosa declined. Oviductal hypertrophy during vitellogenesis corresponded to elevated plasma estradiol concentrations. During gravidity, plasma progesterone concentration peaked.

A particularly detailed description of the reproductive cycle is available for the soft-shelled turtle, *Lissemys p. punctata* (Sarker et al.,'95,'96). Ovarian activity was divided into several different phases: preparatory, recrudescent, breeding, regressive, and quiescent. The breeding phase was further subdivided into preovulatory, ovulatory, postovulatory, and postlaying stages. Plasma estradiol concentrations rose slowly through the preparatory and recrudescent phases, were high in preovulatory females, and reached a peak in ovulatory females (Sarker et al.,'96). Concentrations declined sharply following ovulation, declined further in the postoviposition phase, and were basal in regressive and quiescent phases. Plasma progesterone concentrations remained low throughout the reproductive cycle, except in the breeding phase. They were low in the preovulatory stage, increased during the ovulatory stage, reached their peak in the postovulatory phase, and declined again following oviposition (Sarker et al., '96). Mean absolute and weight-specific oviductal weights (without eggs) were also considered in relation to these reproductive phases (Sarker et al.,'96). Weights remained low in the preparatory phase. They gradually increased during the recrudescent phase and peaked in the postovulatory stage of the breeding phase. Following oviposition, weights decreased sharply and remained low throughout the regressive and quiescent phases. These reductions in weight were associated with reductions in epithelial cell height, glandular size, and secretory activity in both epithelial and glandular tissues (Sarker et al.,'95).

The anole lizard *Anolis pulchellus* is an unusual example because it lays several clutches a year but only a single egg per clutch; ovulations alternate between the ovaries (Ortiz and Morales, '74). The oviducts undergo cyclic glandular degeneration and regeneration of new glands. This cycle accelerates while an egg is in the oviduct. As secretion occurs, glands break down quickly, but at the same time growth of new glands is occurring (Ortiz and Morales,'74). A comparable process of glandular degeneration and partial development of new glands was seen in oviductal tissue cultured in vitro. These processes occurred more quickly in oviductal tissue cultured in the presence of ovarian tissue (Ortiz and Morales,'74).

These examples illustrate differences in oviductal structure and plasma hormone levels that occur over reproductive cycles. The differences complicate consideration of which, and how, hormones control oviductal function. Interspecific variability is always a factor and may cause problems to researchers searching for a common pattern of control.

Control of oviductal development is a complex affair involving both direct and indirect input from components of the hypothalamo-hypophysial -ovarian and adrenal axes. Administration of exogenous hormones to nonreproductive or surgically manipulated females has been used to analyse the actions of hormones within oviductal tissue. However, to date, no one has administered gonadotropin-releasing hormone (GnRH) to reptiles to analyse the potential effects on oviductal tissue; in fact, there is very little information concerning GnRH in reptiles at all (Licht and Porter,'87).

Some attention, however, has been paid to the actions of gonadotropins on oviductal function. In crocodilians and turtles, two gonadotropins similar to mammalian follicle-stimulating hormone

(FSH) and luteinising hormone (LH) have been identified, whereas in squamates there appears to be a single gonadotropin with uncertain homologies with mammalian FSH and LH (Licht, '83). Little is known of the seasonal fluctuations of gonadotropins in reptiles, although in the cobra *Naja naja*, females exhibit a bimodal profile of plasma gonadotropin with peaks during midwinter and in spring (correlating with vitellogenesis) (Bona-Gallo et al.,'80).

In sexually quiescent *Podarcis* (*Lacerta*) *sicula* (wall lizard, Botte and Basile,'74) and early vitellogenic blue spiny lizards [*Sceloporus serrifer* (*cyanogenys*), Callard et al., '72] and painted turtles (*Chrysemys picta*, Klicka and Mahmoud, '77), ovarian activity and oviductal development were stimulated by the administration of pregnant mare serum (PMS, contains equine placental gonadotropin). In ovariectomised female *P. sicula*, administration of PMS caused no morphological changes in oviductal tissues, but there was an increase in DNA and protein content and an increase in alkaline phosphatase activity (Botte and Basile,'74). In postpartum blue spiny lizards, no effects of PMS were observed (Callard et al., '72). FSH, or FSH and LH, when administered to ovariectomised Indian house geckos, *Hemidactylus flaviviridis*, resulted in an increase in epithelial cell height and high activity of the enzymes Δ^5-3B-HSD and G-6-PP (Haider, '85). These changes did not occur in females treated with LH only. In reproductively inactive females of the skink *Lygosoma laterale*, daily administration of FSH, PMS, or human chorionic gonadotropin (hCG) caused an increase in oviductal weight (Jones, '69). These results suggest that gonadotropins may have direct or indirect effects on oviductal tissue without interaction with ovarian hormones such as estradiol.

However, the evidence to date suggests that estradiol, secreted by the ovary during vitellogenesis, is the main substance controlling oviductal development in preparation for gravidity or gestation. The oviductal development seen during vitellogenesis has often been mimicked in sexually quiescent or juvenile females by treatment with exogenous estradiol. Administration of estradiol typically causes oviductal hypertrophy with an increase in the number and size of mucosal glands, increased height and secretory activity in luminal and glandular epithelia, and increased oviductal vascularity (Prasad and Sanyal, '69; Christainsen, '73; Veith, '74; Abrams Motz and Callard,'91). Similarly, in ovariectomised females treated with exogenous estradiol, development of the oviduct is usually observed (Yaron,'72; Callard and Klotz,'73; Mead et al.,'81 ; Girling et al., 2000). The initial ovariectomy causes regression of oviductal tissues including a reduction in glandular activity and a reduction in epithelial cell height and secretory activity (Callard et al., '72; Mead et al.,'81; Haider,'85 ; Girling et al., 2000). Administration of exogenous estradiol then results in oviductal hypertrophy.

Although oviductal development was noted in ovariectomised *Thamnophis elegans* (garter snake) after estradiol treatment, this was only partial development, in comparison to that of naturally vitellogenic females (Mead et al., '81). This may mean that the time frame was insufficient to cause complete development or that factors other than estradiol may also be important in oviductal development.

Oviductal development has also been induced by various androgens in several reptilian species. In the whiptail lizards *Cnemidophorus inornatus* and *C. neomexicanus*, limited oviductal hypertrophy was induced with testosterone or testosterone propionate (Christainsen, '73). In the gecko *Hemidactylus flaviviridis*, only slight (but significant) oviductal hypertrophy was induced by estradiol, but a greater increase in oviductal weight was noted after treatment with testosterone propionate, methyl testosterone, or 19-nortestosterone (Prasad and Sanyal,'69). Testosterone also stimulated some oviductal hypertrophy in the spiny tailed lizard, *Uromastyx hardwickii* (Akhtar,'88), but not to the same extent as estradiol. Since testosterone is a precursor for estradiol synthesis, it may be that localised conversion of plasma testosterone to estradiol within the oviduct may stimulate oviductal development (Guillette et al.,'97).

Plasma concentrations of testosterone have been measured over the reproductive cycle in females of a few reptilian species. A peak of testosterone is noted around the time of ovulation in some reptilian species (e.g., Callard et al.,'78; Whittier et al., '87; Guillette et al., '97; Edwards and Jones, 2001), whereas in others testosterone is low or nondetectable over the entire reproductive cycle (Moore et al., '85; van Wyk, '94). As yet, little attention has been paid to the reasons for the different patterns of plasma testosterone observed in female reptiles.

In the garter snake *Thamnophis sirtalis*, females emerged from hibernation in the spring with low plasma concentrations of sex steroids (Whittier et al., '87). After mating, plasma estradiol concentrations increased rapidly over a 24-hr period and then declined over the next two weeks. Thus, estradiol levels dropped several weeks before ovulation.

This meant that vitellogenesis and oviductal development were maintained when estradiol concentrations were at their lowest. Testosterone, however, increased just before ovulation, but only in those females that ovulated. This raises a question about the role that testosterone plays in oviductal growth. Intact snakes were treated with estradiol, testosterone (aromatisable), or 5a-dihydrotestosterone (DHT, nonaromatisable; Whittier, '92). Females in all treatment groups exhibited an increase in oviductal mass with an associated increase in epithelial cell height and area compared to control females. DHT also drastically altered the oviductal morphology in comparison to other groups, with an increase in the number of pockets and blind-folding in the mucosal wall, suggesting that DHT is unlikely to play a role in normal oviductal development. An interesting point is that no androgen receptors could be detected in oviductal tissues of *T. sirtalis* (Whittier et al., '91), suggesting that the effects of androgens on oviductal tissues are not mediated by an androgen receptor mechanism in this species. However, androgen receptor and aromatase activity have been identified in the oviduct of the slider turtle *Trachemys scripta* (Smith et al.,'95).

Another sex steroid hormone of interest is progesterone. Progesterone is secreted primarily by the corpus luteum (Veith,'74; Arslan et al.,'78) and has been implicated in regulation of several oviductal functions. Of particular interest is the role that progesterone plays in maintaining gestation (see later). Progesterone may also act during oviductal growth, but research to date does not provide consistent information. In the viviparous saurian lizard, *Xantusia vigilis*, there was no significant difference in oviductal weight between ovariectomised females treated with vehicle solution and those treated with progesterone (Yaron,'72). An increase in oviductal weight was seen in ovariectomised females treated with estradiol, but this increase was less than in females treated with both estradiol and progesterone. A similar pattern was seen in the garter snake *Thamnophis elegans*, except that progesterone administered concurrently with estradiol produced effects no different from those of estradiol alone (Mead et al., '81). In the whiptail lizard *Sceloporus serrifer* (*cyanogenys*), progesterone administered concurrently with PMS prevented the oviductal development seen in females treated with PMS only (Callard et al.,'72).

Prolactin (an adenohypophysial hormone) is yet another hormone that has been considered briefly in relation to oviductal activity. In the green anole, *Anolis carolinensis*, injections of ovine prolactin depressed oviductal weights in vitellogenic females, but not in sexually quiescent females (Hensgen et al.,'80). Injection of prolactin did not inhibit oviductal development in females treated with exogenous estradiol, but it did diminish the ability of ovine FSH to stimulate oviductal growth in vitellogenic females (Hensgen et al., '80). Hensgen et al. ('80) suggested that these results indicated that prolactin acts on the ovary by suppressing growth and steroid biosynthesis of smaller ovarian follicles and that reproductive status can influence prolactin effects. Possible diurnal and seasonal fluctuations in prolactin have not been investigated because a prolactin assay has not been developed for reptilian species.

In summary, oviductal tissue shows seasonal changes that correlate with seasonal hormone cycles. Estradiol, which has its highest plasma concentrations during vitellogenesis, appears to be the main influence controlling the development of the oviduct in preparation for gravidity/gestation. The hypertrophy of the oviduct seen in vitellogenic females can be mimicked in sexually quiescent females or ovariectomised females if exogenous estradiol is administered. Estradiol does not act in isolation, however, and other hormones (gonadotropins, androgens, progesterone, prolactin) may influence oviductal development. Other hormonal and neural influences act to cause parturition/oviposition, and these will be discussed later.

Sex steroid receptors

That sex steroids act directly on oviductal tissue is implied by the presence of sex steroid receptor proteins. Estrogen receptors (ERs) have been identified in the oviduct of several reptilian species (turtles: *Chrysemys picta*: Salhanick et al.,'79; Giannoukos and Callard, '96 ; squamates: viviparous snake *Thamnophis sirtalis parietalis*: Whittier et al., '87; oviparous lizard *Podarcis s. sicula*: Paolucci et al., '92; Paolucci and DiFiore, '94 ; crocodilians: *Alligator mississippiensis*: Vonier et al., '97). Ovariectomy significantly decreased ER concentration in the painted turtle, *C. picta* (Giannoukos and Callard,'96), and the wall lizard, *P. s. sicula*. In ovariectomised *P. s. sicula*, estradiol treatment increased ER concentration and induced an ER shift from the cytosol into the nuclei (Paolucci et al., '92). Estrogen receptor levels in ovariectomised females were not restored by any steroid regime in *C. picta* (Giannoukos and Callard,'96).

Estrogen receptor quantity may change over a reproductive cycle. In the wall lizard *P. s. sicula*, ER concentration significantly increased as the

oviduct developed, supporting a role for estradiol in oviductal stimulation (Paolucci et al.,'92). Ovariectomised or postovulatory females had little oviductal ER-mRNA in comparison to estrogen-treated or vitellogenic female *Cnemidophorus uniparens* (whiptail lizard, Young et al.,'95).

Progesterone receptors (PRs) have also been identified in reptilian oviductal tissue (squamates: viviparous snake, *Nerodia* sp.: Kleis-San Francisco and Callard,'86 ; oviparous lizard *Podarcis s. sicula*: Paolucci and DiFiore,'94 ; turtles: *Chrysemys picta*: Ho and Callard, '84; *Chelydra serpenta*: Mahmoud et al., '86 ; Giannoukos and Callard, '96 ; crocodilians: *Alligator mississippiensis*: Vonier et al.,'97). It appears there are two isoforms, PR-A and PR-B (Reese and Callard,'89; Paolucci and DiFiore,'94). PR-B, but not PR-A, is under estrogenic control and shows seasonal changes. Immunocytochemical analysis identified PRs in the nuclei of uterine epithelium, submucosal glands, and smooth muscle in the painted turtle, *C. picta* (Giannoukos and Callard,'96).

Numbers of oviductal PRs change over a reproductive cycle, with the highest concentrations appearing during vitellogenesis (Ho and Callard, '84). In the snapping turtle, *Chelydra serpentina*, no PRs were detected during the postovulatory phase, when plasma progesterone concentrations were high and the corpora lutea were active (Mahmoud et al.,'86). Estrogen priming did not increase PRs at this time. In the postoviposition phase, PRs were detectable only after estrogen priming. During vitellogenesis, however, PRs were detectable without estrogen priming. Both cytosolic and nuclear PRs increased significantly during vitellogenesis in the viviparous snake *Nerodia* sp. (Kleis-San Francisco and Callard,'86). Levels of cytosolic PR then declined, but nuclear PR did not decline until the second trimester of gestation. In a unisexual whiptail lizard, *Cnemidophorus uniparens*, ovariectomised or postovulatory females had little oviductal PR-mRNA in comparison to estrogen-treated or vitellogenic females (Young et al.,'95). The presence of PRs on the oviduct during vitellogenesis suggests that progesterone acts on the oviduct during development, despite the inconclusive results from treatment experiments. Reduced receptor concentration during gravidity/gestation, when plasma concentrations are at their peak, however, suggests reduced effects of progesterone directly on the oviduct at this time.

To date, androgen receptors have only been identified in the oviduct of a single reptilian species, the turtle *Trachemys scripta* (Smith et al.,'95). Seasonal changes in the number of androgen receptors, or potential changes following hormonal manipulation, have not been investigated.

In summary, estrogen and progesterone receptors have been identified in representative species of turtles, squamates, and crocodilians. Concentrations of these receptors vary over a reproductive cycle and may be influenced by surgical and hormonal manipulation. Thus, receptivity of oviductal tissues to various hormones will change depending on the interaction between changing hormone and hormone-receptor levels. To date, androgen receptors have been detected in the oviducts of one species of reptile only.

Enzyme activity

In addition to steroid hormone receptors, certain key enzymes involved in the biosynthesis of steroid hormones have been identified in the oviduct of several reptilian species. For instance, activity of Δ^5-3β-hydroxysteroid dehydrogenase (HSD; involved in the conversion of pregnenolone to progesterone) and 17β-HSD (involved in oxidative interconversions of various estrogenic and androgenic steroids) was measured in the uterine glands of the skink *Mabuya carinata* (Mundkur and Sarkar, '82) and in the mucosal epithelium of the agamid lizard *Calotes versicolor* (Shanthakumari et al., '90, '92). Various other metabolic enzymes were also detected in the uterine glands of *M. carinata* (glucose-6-phosphate dehydrogenase, $NADH_2$ diaphorase, and lactate dehydrogenase; Mundkur and Sarkar,'82).

For most of the steroidogenic and metabolic enzymes measured in the oviparous lizard *C. versicolor*, the highest activity occurred during the reproductive phase with a decrease following breeding (Shanthakumari et al.,'92). Beta-glucuronidase was an exception, with the highest activity occurring in the regressed oviduct. Enzymatic activity showed some variation among the different regions of the oviduct. For example, acid phosphatase activity was higher in the uterine regions than in either the infundibulum or vagina. Shanthakumari et al., ('92) argued that the presence of these enzymes is evidence that the oviduct is a site of steroid metabolism and secretory activity, while the seasonal changes in their activity suggest they may be under the control of estrogenic hormones. Beta-glucuronidase is a lysosomal enzyme, so the inverse activity may relate to tissue degeneration following breeding (Shanthakumari et al., '92). The results from Shanthakumari et al. ('92), however, are not consistent with the findings

for the viviparous snake *Natrix sipedon pictiventris*. In this species, the highest levels of β-glucuronidase were detected during pregnancy and the lowest levels were detected postpartum (Callard and Leathem,'70).

A similar suite of enzymes (see preceding text, Shanthakumari et al.,'92) to those measured in the mucosal epithelium were also found in the epithelium of uterovaginal sperm pockets of the agamid lizard *C. versicolor* (Shanthakumari et al.,'90) and the rock lizard *Psammophilus dorsalis* (Srinivas et al.,'95). It is not known whether these enzymes have a role in sperm storage.

Shanthakumari et al. ('92) suggested that acid phosphatase was the best indicator of secretory activity in uterine glands. Alkaline and acid phosphatase activity were also present in the oviducts of the wall lizard *Podarcis* (*Lacerta*) *sicula* during the preovulatory and ovulatory phases (Botte,'73) and in the oviducts of the snake *N. s. pictiventris* (Callard and Leatham,'70). Activity was present in the epithelium of the infundibulum and uterine tube, while in the uterus, activity was present in shell glands. Along the entire oviduct, the walls of blood vessels were rich in phosphatase activity, and Botte ('73) suggested that the presence of phosphatase activity indicated that these enzymes are involved with secretion and also in the exchange between blood vessels and the mucosa.

In summary, numerous steroidogenic and metabolic enzymes have been identified in the reptilian oviduct, but to date, only in squamate species. Their activities change over the course of a reproductive cycle, providing further evidence that the oviduct is a site of secretory activity and steroid metabolism.

Growth factors

In recent years, numerous growth factors and cytokines have been identified in mammalian species. These substances act in an autocrine, paracrine, and endocrine manner to produce a response. The continuing work to identify these polypeptides and their binding proteins and receptors, and to determine their function and mechanism of action, has resulted in a large literature. Growth factors obviously play a vital role in reproduction, including the actions of the oviduct, as well as in other bodily functions.

Research on growth factors and cytokines in reptilian species has only just begun. The growth factor that has received the most attention to date is insulin-like growth factor (IGF). Both IGF-I and IGF-II have been identified in skeletal tissue of a gecko (Bautista et al.,'90). IGF-I has been detected in the plasma of the American alligator, *Alligator mississippiensis*, and the slider turtle, *Trachemys scripta* (Crain et al.,'90). Maximal plasma levels of IGF-I were observed during gravidity in *A. mississippiensis*, correlating with high plasma progesterone concentrations (Guillette et al., '96). It was proposed that high levels of IGF-I in gravid females may be due to the synthesis of IGF-I for incorporation into eggs and that IGF-I may also act to stimulate uterine secretion. Both IGF-I and IGF-II have been found in the albumen of fully shelled eggs in utero from *A. mississippiensis* (Guillette and Williams, '91). IGF-I immunoreactivity was noted in the mucosal glands of the uterine tube and uterus, and in the uterine luminal epithelium and its secretions, in the alligator *A. mississippiensis* and the gopher tortoise *Gopherus polyphemus* (Palmer and Guillette, '91; Cox and Guillette, '93). In mammals, IGF-I has been implicated as a possible mediator of estradiol-induced proliferation of the female reproductive tract, as well as having involvement in placental interactions and embryonic development (Simmen and Simmen, '91; Wang and Chard,'92).

Epidermal growth factor (EGF) is also believed to act as a facilitator of estrogen action and causes proliferation of mouse, rabbit, and human endometrial cells (Cooke et al.,'86; Haining et al.,'91; Nelson et al.,'91 ; Smith,'94) . In studies of reptiles, EGF immunoreactivity has been identified in the mucosal glands and the luminal epithelium of the uterus in the American alligator, *A. mississippiensis* (Palmer and Guillette,'91).

In the Mediterranean gecko, *Hemidactylus turcicus*, both exogenous IGF-I and EGF induced hypertrophy of the oviduct in ovariectomised females (Cox,'94). Epithelial cell height was significantly increased in comparison to control females, but was only 25% of the height measured in estradiol-treated females. In IGF-I–treated females, mucosal thickness and gland diameter were 71 and 83%, respectively, of that observed in estradiol-treated females. In EGF-treated females, mucosal thickness and gland diameter were only 50 and 65% of that recorded in estradiol-treated females. The major difference between treatments appeared to be in the number and density of secretory granules produced. These results suggest that IGF-I and EGF can influence oviductal development (but to a lesser extent than estradiol) and that they do not act in isolation.

Interleukin-I (IL-I) has also been found in reptiles; IL-I and its specific membrane receptor

(IL-1R tI) have been identified using immunocytochemistry in the oviductal epithelium of the skink *Chalcides chalcides* during prepregnancy, early gestation, and postpartum (Paulesu et al., '95). Immunoreactivity was much higher in the pregnant than in the pre- and postpregnant uterus. IL-Iα and IL-Iβ immunoreactivity was observed in the placenta of *C. chalcides* during midgestation, particularly at the basal region of cells. Immunoreactivity was noted in uterine epithelium, but only in a small number of cells; however, there was clear immunoreactivity in uterine connective tissue. Just prior to parturition, the epithelium showed strong staining, particularly around the nuclei and at the apical portion of cells where apocrine secretion appeared to be occurring. Although the technique used cannot differentiate between absorbed and secreted IL-I, the results to date suggest that IL-I may be involved in placentation. In mammals, it has been suggested that, among other actions, IL-I inhibits the proliferation of stromal and epithelial endometrial cells, is proinflammatory, and induces production of prostaglandin-E_2 (see Tabibzadeh, '94 for summary).

In addition to EGF, IGF-I and -II, and interleukins (considered in preceding text), the list of growth factors and cytokines identified in mammals includes (among others) transforming growth factor α and β, fibroblast growth factors, and colony-stimulating factors. It is inappropriate to discuss here all the possible oviductal interactions of growth factors and cytokines that have been identified in mammalian species. Reviews that summarise the current information are available (e.g., Simmen and Simmen, '91; Murphy and Barron, '93; Smith, '94; Tabibzadeh, '94). It is appropriate, however, to identify how these peptides cause effects in the reproductive tract of mammals and where continued study in reptiles will be invaluable to the study of oviductal action. Growth factors are involved in the development of the oviduct in association with the hypothalamo-pituitary axis, acting in a mitogenic and angiogenic fashion. It appears that this development is differentially regulated; a whole suite of factors may be necessary for complete development and regression. Production of oviductal secretions (mucus, albumen, shell membranes) and their release at the appropriate time may well involve growth factors. Maternal growth factors, synthesised by the oviduct or transported via the oviduct, may be essential for complete embryonic development. Growth factors of foetal origin may be involved in regional differentiation of the oviduct associated with placentation and may also be necessary to maintain gestation and later to trigger parturition.

In summary, EGF, IGF-I and -II, and IL-I have been identified in the reptilian oviduct. EGF and IGF are believed to act as facilitators of estradiol-induced proliferation. IL-I is believed to have a role in placentation. There are numerous areas in which these growth factors, and others yet to be identified in reptiles, may be important in the control of various oviductal functions. It will be necessary to characterise the chemical properties of these growth factors, their receptors and binding proteins, before a clearer view of their function(s) in reptiles can be established.

FUNCTIONS OF THE OVIDUCT

Functions of the luminal epithelium

The luminal epithelium has secretory potential in all regions of the oviduct. The secretions include albumen, components of the eggshell, and materials involved with placentation and sperm storage. These will be discussed more fully in the following text. Three cell types are found in the luminal epithelium: ciliated, microvillous nonciliated, and bleblike nonciliated cells. The function of ciliated cells is presumably to maintain movement of mucus and cellular debris down the oviduct (Palmer and Guillette, '88). Cilia may also aid in the movement of sperm and potentially the ovulated egg. Apical protrusions and blebbing from ciliated cells have been noted (Girling et al., '97), suggesting that ciliated cells may also have some secretory function.

Microvillous nonciliated cells are presumably mucus-producing, mucus being necessary to keep the lumen of the oviduct moist and clean (Aitken and Solomon, '76; Leese, '88). The oviductal lumen is continuous with the animal's exterior (via the urogenital sinus) and so is vulnerable to contamination. Whether oviductal secretions contain antibacterial, antifungal, or antiviral properties has not yet been investigated in reptiles.

Bleblike nonciliated cells have been identified in a small number of species only (Palmer and Guillette, '88 ; Girling et al., '97, '98), and their function is unknown. Palmer and Guillette ('88) suggested they may be involved in apocrine or merocrine secretion.

Sperm storage and fertilisation

Sperm storage has been noted in numerous squamates and chelonians, and it has been suggested for at least one crocodilian (dwarf caiman, *Paleosuchus palpebrosus*, Davenport, '95). Reviewers such as

Birkhead and Mollar ('93) have considered the evolutionary implications of such storage. Sperm storage may be obligatory in some species due to asynchronous reproductive cycles in males and females. It allows copulation to be separated from fertilisation. Sperm storage may also be advantageous because it extends the reproductive period available to females, it may contribute to sperm competition and/or multiple paternity within a single clutch (Schuett, '92; Birkhead and Mollar, '93; Gist and Fischer, '93), it may reduce the risk of predation by reducing copulation frequency (Conner and Crews, '80), and it may act as insurance against not finding a partner because of low densities or slow movement (Birkhead and Mollar, '93).

Sites of sperm storage appear to be restricted to the anterior vagina and/or the anterior oviductal regions (usually the posterior uterine tube). For instance, in the oviparous ringneck snake *Diadophis punctatus*, two sites for sperm storage were noted (Perkins and Palmer, '96). After mating took place in either the autumn or spring, sperm were stored in folds of the mucosa in the anterior vagina. During the early stages of vitellogenesis, sperm traveled up through the uterine lumen to glands in the posterior uterine tube. A similar pattern was observed in the viviparous gecko, *Hoplodactylus maculatus* (Girling et al., '97).

Sperm storage in the anterior vagina has been reported for several reptilian species (Cuellar, '66; Halpert et al., '82; Shanthakumari et al., '90; Palmer et al., '93). Sites for sperm storage are often formed from crypts between folds of the vaginal mucosa (e.g., the rock lizard, *Psammophilus dorsalis*, Srinivas et al., '95). In the green anole, *Anolis carolinensis*, sperm storage occurred in tubular outgrowths of the anterior vagina (Fox, '63; Conner and Crews, '80).

Storage in the posterior uterine tube is also common. This site of storage has been identified in several gekkonid species (e.g., Picariello et al., '89; Murphy-Walker and Haley, '96 ; Girling et al., '97). Sperm storage was also noted in the infundibulum (including uterine tube) of the geckos *Phyllodactylus homolepidurus* and *Coleonyx variegatus* (Cuellar, '66) and geckos belonging to the *Heteronotia binoei* complex (Whittier et al., '94). Sperm storage tubules, which communicate with the oviductal lumen via ducts, have been identified in the posterior uterine tube of various species of turtle representing several families (Gist and Jones, '89; Gist and Congdon, '98).

Ultrastructural information concerning sperm storage sites is available for the box turtle, *Terrapene carolina* (Gist and Fischer, '93). In this species, sperm storage sites were identified in the posterior uterine tube (Hattan and Gist, '75; Gist and Fischer, '93). The tubules containing sperm, which were no different from others in the uterine tube, were surrounded by six to eight secretory cells that contained numerous membrane-bound vesicles (Gist and Fischer, '93). Microvilli were present on the apical membranes, and prominent junctional complexes were present on the lateral membranes. Sperm were not in contact with the oviductal tissues. In the black swamp snake, *Seminatrix pygaea*, sperm were noted in glands in the posterior infundibulum (tube included; Sever and Ryan, '99). The histology of these storage regions did not differ from that of surrounding tissue. The similarities between sperm-carrying and non-sperm-carrying tubules suggests that their function as sperm storage structures may be fortuitous. Gist and Jones ('87) pointed out that sperm storage structures are characteristically unspecialised, except, of course, for the presence of sperm.

Although the morphology of sperm storage structures may not differ from that of the surrounding oviduct, biochemical and physiological differences may play a role in sperm maintenance. In the majority of papers available, sperm are described as being in groups in the sperm storage sites, without direct connection to the oviductal tissue (Fox, '63; Gist and Jones, '89; Shanthakumari et al., '90; Gist and Fischer, '93). However, in the keeled earless lizard, *Holbrookia propinqua*, the sperm were considered to be directly associated with or partially embedded in oviductal tissue (Adams and Cooper, '88), and in the lacertid lizard, *Acanthodactylus scutellatus hardyi*, some sperm were noted in the intercellular spaces between and in the cytoplasm of gland cells (Bou-Resli et al., '81). This suggests that in the majority of cases, either the oviduct must secrete, or the male semen must supply, any substances associated with sperm maintenance.

In the rock lizard, *Psammophilus dorsalis*, discrete granules resembling those found in the vas deferens were found associated with sperm in the anterior vagina (Srinivas et al., '95). These granules stained positively for carbohydrate (PAS) and also for acid phosphatase. In the agamid lizard *Calotes versicolor*, sperm were mixed with a PAS-positive homogeneous mixture, although it is not known whether this was of oviductal origin or from the male (Shanthakumari et al., '90). The sperm in *C. versicolor* were stored in pockets in the uterovaginal region. The epithelium of these pockets resembled that of the oviductal epithelium and

stained positively for proteins and carbohydrates. Activity of various steroidogenic and metabolic enzymes was also detected in the epithelium (Shanthakumari et al., '90).

In the red-sided garter snake, *Thamnophis sirtalis parietalis*, 6 weeks into the period of winter dormancy the epithelial cells of the vagina (where sperm storage occurs) hypertrophied and stained strongly for carbohydrate (Halpert et al., '82). The vaginal epithelial border sloughed off and associated with the stored sperm as it moved anteriorly through the oviduct. After 20 weeks in dormancy, the sperm were found in storage tubules in the posterior uterine tube. Halpert et al. ('82) called this the carrier matrix and suggested that it facilitated transport of the sperm anteriorly and may function as a nutritional store. A carrier matrix of mucoid substances, desquamated epithelium, lipids, and membranous structures was also associated with sperm in the posterior oviductal regions of the black swamp snake, *Seminatrix pygaea*, following a recent mating (Sever and Ryan, '99). This suggested an active role by the oviduct of this species in sperm transport and maintenance.

Another factor to consider is how sperm are transported within the oviduct and how sperm are released from storage sites. In the green anole, *Anolis carolinensis*, sperm entered the storage tubules (in the anterior vagina) 2–6 hr after insemination (Conner and Crews, '80). Small amounts of sperm reached the uterine tube 6–24 hr after mating. It was suggested by Halpert et al. ('82) that the direction of ciliary beating may be reversed during vitellogenesis to aid the movement of sperm up to the oviduct toward the infundibulum. Halpert et al. ('82) also hypothesised that ovulation may trigger the release of sperm from storage sites in the uterine tube. As the eggs pass though the uterine tube, the glands containing sperm are stretched, which causes the release of sperm into the lumen. This idea, however, does not explain how sperm from vaginal sites were released.

That stored sperm are capable of fertilisation is indicated by the fact that females of several species that have been kept in captivity without males for prolonged periods can still produce viable clutches (for instance, the keeled earless lizard, *Holbrookia propinqua*, Adams and Cooper, '88). As an extreme example, delayed fertilisation and the production of a fully developed embryo occurred in the file snake *Acrochordus javanicus* after 7 years in captivity (Mangusson, '79). However, Fox ('77) advised caution in assuming sperm storage from delayed fertilisation because parthenogenesis occurs in some species. In the gecko *Hemidactylus frenatus*, females maintained in isolation for a period of 1 year produced, on average, seven clutches, suggesting a minimum period of sperm storage of 36 weeks (Murphy-Walker and Haley, '96). Hatchlings included males, thus excluding the possibility of parthenogenesis being responsible for the additional clutches.

The site of fertilisation in reptilian species has yet to be determined. Fertilisation must presumably occur before albumen or shell membranes cover the ovulated oocyte. Eggs are coated with oviductal secretions as soon as they enter the infundibular ostium (Palmer et al., '93). This suggests that fertilisation must occur in either the infundibulum or uterine tube, and sperm have been observed in storage sites in both these regions. For instance, in a gecko from the *Heteronotia binoei* complex that was in the process of ovulation, nests of sperm were observed in the oviductal wall of the infundibulum that surrounded the unshelled ovum (Whittier et al., '94). This suggests that fertilisation occurs in the infundibulum of this species.

Thus, although storage of sperm has been noted in several species, the contribution(s) of the oviduct to sperm maintenance is unknown. The oviduct may do no more than provide a site for sperm storage, but it may also have nutritional and/or protective functions. We do not know the mechanism by which sperm are released from storage sites in either the vagina or anterior oviductal regions, nor whether the oviduct plays a role in the movement of sperm up the oviduct to the site of fertilisation. The site of fertilisation is yet another unknown, and research analysing the oviduct and egg at timed periods following ovulation would be appropriate.

Albumen production

The eggs of turtles and crocodilians are covered with a thick layer of albumen (egg white proteins) at oviposition, whereas lepidosaurian (tuatara and squamates) eggs apparently lack such a layer (Packard et al., '88). Reptilian albumen, like that of birds, is believed to have various antimicrobial, nutritive, supporting, cushioning, and water-binding properties essential for the developing embryo (Palmer and Guillette, '91). It also provides an important reservoir of water, which in birds is secreted by the shell gland as "plumping fluid." Packard et al. ('88) suggested that the absence of an albumen layer in lepidosaurians means that the eggs contain insufficient water when they are oviposited to support the embryos until they hatch. However, significant

water intake by the egg in the oviduct of the anole lizard *Anolis pulchellus* has been reported (Cordeno-López and Morales,'95).

It is thought that the uterine tube is responsible for secretion of the albumen layer. The uterine tube of the turtle and crocodilian oviduct is homologous with the avian magnum, which is known to secrete albumen (Aitken and Solomon,'76). Using tritiated leucine and explant cultures, it was shown that the uterine tube of *Pseudemys s. scripta* is capable of synthesising and secreting albumen proteins in vitro (Palmer and Guillette,'91). Additionally, antibodies to whole fowl albumen and purified ovalbumen showed cross-reactivity to reptilian albumen proteins and bound to mucosal glands in the uterine tube of the American alligator, *A. mississippiensis* (Palmer and Guillette,'91).

Despite there being no albumen layer in lepidosaurians, various albumens have been detected in the eggs of some squamates (the ringneck snake *Diadophis punctatus*; the whiptail lizards *Sceloporus woodi*, *S. virgatus*, and *S. scalaris*; and the anole lizard *Norops* (*Anolis*) sagrei; Palmer and Guillette, '91). It is not known, however, whether these proteins are of oviductal or ovarian origin. Synthesis of avidin (an avian albumen protein) was detected in the oviduct of the wall lizard *Podarcis* (*Lacerta*) *sicula* (Botte et al.,'74; Botte and Granata, '77). Estradiol, or estradiol and progesterone, stimulated avidin synthesis in the uterine tube. Testosterone also increased avidin synthesis, but was less potent. However, without a distinct albumen layer, the question arises as to whether and where these proteins are incorporated into the egg.

As in other lepidosaurians, there is no structural distinction between the yolk and albumen layer in the anole lizard *Anolis pulchellus* (Cordeno-López and Morales,'95). Electrophoresis showed no qualitative difference between the follicle and the egg, suggesting that, at least in *A. pulchellus*, there are no proteins of oviductal origin in the egg (Cordeno-López and Morales,'95).

Thus, there is obviously still some contention surrounding the presence of albumen in squamate species. It appears that several considerations need to be addressed. Does the lack of a distinct albumen layer in lepidosaurians mean that proteins of oviductal origin are not found in the eggs? If oviductal proteins are detected, are they incorporated into the yolk layer or elsewhere? What is the function of these potential oviductal proteins in lepidosaurians? Do they share the same functions as those proposed for albumen in turtles and crocodilians?

Eggshell production

A vital function of the reptilian oviduct in oviparous species is the production of the eggshell. The generalised reptilian eggshell is composed of an inorganic layer of calcium bicarbonate (either calcite or aragonite) with an underlying organic layer(s) that is otherwise known as the shell membrane (see Packard and DeMarco, '91). The innermost layer of the shell membrane, which lies adjacent to the extraembryonic membranes, is known as the inner boundary. Eggshell structure varies widely between species, with the different layers of the eggshell differing in thickness and morphology. The differences in eggshell morphology will presumably be reflected by differences in those oviductal regions responsible for secretion of the eggshell. Several useful and detailed reviews concerning reptilian eggshell structure are available (Packard et al., '82, '88; Packard and Hirsch, '86; Packard and DeMarco,'91). The inner boundary is thought to be secreted by the anterior regions of the oviduct. It is known that oviductal secretions are present on the egg as soon as it enters the infundibular ostium (Palmer et al.,'93), and it has been proposed that the infundibulum is responsible for secretion of the inner boundary (Guillette et al., '89). However, in those species with a layer of albumen present that lies beneath the shell membrane, presumably the uterine tube, isthmus, or uterus must secrete the inner boundary. Cree et al. ('96) suggested that the uterine glands are responsible for secretion of the inner boundary as well as the shell membrane of tuatara, based on similarities between secretory granules observed in the uterine glands of tuatara (and other reptiles) and those forming the inner boundary of the tuatara eggshell. In turtles and lepidosaurians (tuatara and squamates), the uterus is a single region (unlike the crocodilians, in which the uterus is divided into two functionally different regions) that produces both the calcareous and fibrous components of the eggshell. The fibres making up the shell membrane are secreted by the uterine mucosal glands. Once the egg reached the uterus of the whiptail lizard *Sceloporus woodi*, long, proteinaceous fibres were observed extruding from ducts of the mucosal glands (Palmer et al.,'93). Most glands had stopped secreting by 24 hr post ovulation, and the shell membrane was largely complete. In the wall lizard *Podarcis* (*Lacerta*) *sicula* also, secretory material in the form of filaments was noted passing into the lumen of the oviduct from the uterine mucosal glands (Botte, '73). The fibres had the same histochemical

properties as the secretion noted within the glands. Palmer et al. ('93) hypothesised that the formation of the fibrous membrane is similar to that seen in birds. As the proteinaceous material is forced out of the neck of the gland, it coalesces into a fibre. It appears that the orientation of the fibres forming the shell membrane is due, at least in part, to the rotation of the eggs within the oviduct (Packard and DeMarco,'91; Palmer et al.,'93). Guillette et al. ('89) drew attention to the need for additional studies to determine if phylogenetically distinct reptilian species secrete fibres that differ biochemically and/or structurally. In a comparison of two lizard species, Guillette et al. ('89) found that the uterine mucosal glands of the Eastern collared lizard, *Crotaphytus collaris*, produced fibres of a collagen-like material, whereas in the Great Plains skink, *Eumeces obsoletus*, the uterine mucosal glands did not stain for collagen. This highlights the potential difference in chemical composition of the shell membrane between species.

Although eggs of viviparous species lack a complete eggshell, a shell membrane has been reported in several species (Boyd,'42; Girling et al.,'97; Corso et al., 2000). In the viviparous skink *Chalcides ocellatus tiligugu*, two unciliated cell types were distinguished in the uterus (Corso et al., 2000). The first of these secreted sulfated gylcosaminoglycans and were believed to be responsible for secretion of the amorphous inner component of the shell membrane. The second cell type secreted acidic glycoproteins, which were hypothesised to secrete the matrix of the outer layer of the shell membrane.

The source of calcium needed for eggshell production is still unknown, although various clues suggest that the uterine epithelium is responsible. In the turtle *Lissemys p. punctata*, the secretory cells of the uterine epithelium stained positively for calcium throughout the period of gravidity (Sarker et al., '95). In the Eastern collared skink, *C. collaris* also, but not the Great Plains skink, *E. obsoletus*, the uterine epithelium stained intensely for calcium (Guillette et al., '89). The uterine epithelium of the whiptail lizard *Sceloporus woodi* exhibited changes during gravidity that correlated with the period of calcium deposition (Palmer et al., '93). During this period, the apical membranes were greatly distended, the cells were hypertrophied, and the microvilli were less pronounced. There is evidence, however, that does not support the uterine epithelium as the source of calcium. Picariello et al. ('89) used chlorotetracycline chlorhydrate (fluorescent) to monitor Ca^{+} in the oviduct of the gecko *Tarentola m. mauritanica*. During the period of maximum reproductive activity, fluorescence was noted in the basal region of uterine glands, but not in the epithelium. Calcium, however, is essential for mitochondrial function, and, since mitochondria are common in both glandular and epithelial cells, the presence of calcium staining in various regions does not necessarily correspond to calcium secretion for eggshell production.

The extant archosaurs (birds and crocodilians) exhibit similar egg-shelling processes. As with birds, different components of the crocodilian eggshell are secreted in different regions of the oviduct (Palmer and Guillette, '92). In crocodilians, it appears that two spatially distinct regions, the anterior and posterior uterus, are responsible for the production of the shell membrane and the calcareous component, respectively. The anterior uterus of *A. mississippiensis* resembled the isthmus of birds and the uterus of other squamates and chelonians (Palmer and Guillette, '92). The mucosal glands of the posterior uterus in *A. mississippiensis* resembled the glands of the avian shell gland, which is responsible for production of the calcareous component of the eggshell. The cells of the mucosal glands in the posterior uterus may function to secrete calcium ions as well as adding the "plumping water" needed to saturate albumen proteins (Palmer and Guillette,'92).

The structure of reptilian eggshells varies widely between species. Guillette and Jones ('85b) suggested that this difference in structure may relate to the structural organisation of the uterine shell glands. For instance, in the whiptail lizard *Sceloporus a. aeneus*, the shell glands had distinct pores that opened out onto the luminal surface. These pores, however, did not cover the entire surface of the epithelium. The particular arrangement of the pores may contribute to the irregular surface of the eggshell (Guillette and Jones,'85b).

To summarise, little is known about the role of the oviduct in the process of egg shelling in reptiles. Although the oviductal regions where shelling occurs have been determined, few details about processes are available, particularly in regard to calcium secretion. The hormonal mechanisms controlling eggshell production are unknown. Cuellar ('79) observed that deluteinisation disrupted the shelling process in the lizard *Cnemidophorus uniparens*. This suggests a possible role for the corpus luteum and its major hormonal product, progesterone, in the shelling process. Equally, the stress of the process of deluteinisation may have been the casual factor disrupting shelling. More detailed

research determining the hormonal triggers for shelling is needed.

Placentation

A feature considered essential to the evolution of viviparity is the development of a placenta, which is defined as any intimate apposition or fusion of parental to foetal tissues that allows for physiological exchange (Mossman, '37). In viviparous squamates, the extraembryonic membranes (which are also present within the eggshell of oviparous species, e.g., Stewart and Florian, 2000; Fig. 6) provide the foetal component of the placenta, while the uterus provides the parental component. The presence of an ovulated egg distends the uterus so that most of the egg surface is in contact with the uterus. Additionally, since the eggshell is reduced or absent in viviparous species, the uterine epithelium is very closely apposed to the extraembryonic membranes (Blackburn, '93a). The thin shell membrane found in some viviparous species is believed to be due to the few uterine mucosal glands (responsible for secretion of the shell membrane in oviparous species) still present in viviparous species. In the gecko *Hoplodactylus maculatus*, the thin shell membrane was only observed during the early stages of pregnancy (Boyd, '42; Girling et al., '97). The mechanism by which the shell membrane is lost during pregnancy is unknown.

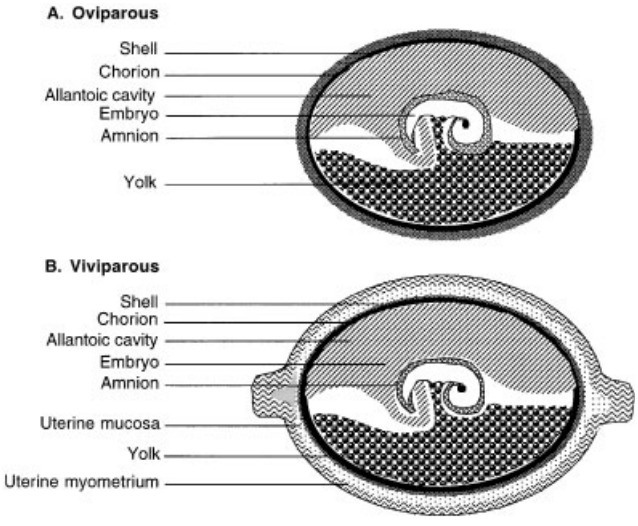

Fig. 6. Diagram illustrating extraembryonic membranes within (**A**) the egg of an oviparous squamate species, and (**B**) the uterus of a viviparous squamate species. The allantoic cavity is surrounded by the allantois and the yolk is enclosed within the vitelline membrane. Apposition of the chorion and the allantois forms the chorioallantoic membrane. Simple placentation forms within the viviparous species when the chorioallantoic membrane (forms chorioallantoic placenta) and vitelline membrane (forms yolksac placenta) lie adjacent to the uterine epithelium. Modified from Guillette, '93.

In the initial stages of placentation in eutherian mammals, a series of changes in the plasma membrane of uterine epithelia occurs in preparation for implantation of the blastocyst (Murphy et al., 2000). These changes, termed the "plasma membrane transformation," include a loss of microvilli resulting in a flattened epithelial surface. After similar changes were observed during early pregnancy in the viviparous skinks *Eulamprus tympanum* and *Niveoscincus metallicus*, Murphy et al. (2000) suggested that the plasma membrane transformation may also be common to viviparous lizards.

Despite detailed morphological descriptions of placental structures in some species that range from apposition of extraembryonic membranes with uterine tissue to complex hypertrophy and interdigitation, no detailed information concerning the function of placental tissues is available. There are detailed reviews of the morphology and ontogeny of placental structure concerning the species studied to date (Yaron, '85; Stewart and Blackburn, '88; Blackburn, '93a; Stewart, '93; Blackburn and Callard, '97; Stewart and Thompson, '96, '98, 2000), and further elaboration here would be redundant. Instead, consistent with the theme of this review, I will focus on the structure and function of the uterus in placentation.

The majority of viviparous squamates ovulate large, yolky eggs and have a conservative yolksac and chorioallantoic placenta. The uterus may well exhibit regional differences in structure associated with the different placental regions. Commonly, the uterus is very thin during pregnancy, particularly the epithelial layer, which may be cuboidal or squamous. Numerous blood vessels are present at the base of the epithelium (Boyd, '42; Stewart, '92) allowing the maternal blood supply to be very close to the foetal blood supply.

Regional hypertrophy of uterine epithelial tissues may occur, as in the development of the omphaloplacenta (yolk-sac placenta; Stewart, '92) in the rough earth snake, *Virginia striatula*. The uterine epithelial cells of the omphaloplacenta (in the region of the isolated yolk mass) were initially cuboidal with a rich vascular system. As the allantois extended into the isolated yolk cleft, the omphalallantoic placenta was formed. The uterine epithelial cells in this region then hypertrophied to form columnar cells arranged on pilae (mucosal folds) that extended from the *lamina propria* (Stewart, '90, '92). Capillaries lay at the base of the mucosal columns.

In this species, the uterus apposed to the other placental regions was heavily vascularised with a squamous epithelium (Stewart,'90,'92).

Only a few squamate species studied to date exhibit advanced forms of placental interaction (Blackburn et al.,'84; Thompson and Stewart,'94; Stewart and Thompson, '98; Flemming and Branch, 2001). These species are predominantly matrotrophic and ovulate small eggs with little or no yolk. In the skinks *Chalcides chalcides* (Blackburn,'93b; Blackburn and Callard, '97) and *Mabuya bistriata* (Vitt and Blackburn,'91), a specialised region of the chorioallantoic placenta called the placentome was present. The uterine mucosa underwent hypertrophy to form branching folds or outgrowths that protruded into deep invaginations of the chorioallantois. The interdigitation of uterine and foetal tissues at the placentome increased the surface area available for physiological exchange (Blackburn,'93b). It was considered most likely that nutrient provision by the placentome was histotrophic, meaning that the hypertrophied uterine epithelium secretes material synthesised from precursors in the maternal blood system (Blackburn, '93b). In the remaining chorioallantoic placenta of *M. bistriata* that was not part of the placentome, chorionic crypts were found (Vitt and Blackburn,'91). These were invaginated pits lined by microvillous columnar cells that were opposed to openings of uterine glands. Secretory material was evident within the crypts, and the cytoplasm of the crypt epithelium contained inclusions that stained identically to uterine secretions.

As yet, the functions of uterine regions associated with different parts of the placenta are unknown. Also unknown is the mechanism that causes the differentiation of the uterus to form placental associations. It is not unreasonable to expect that local paracrine action by the developing extraembryonic membranes acts to cause differentiation. This is a potential area for the action of growth factors.

Obviously vital to placental exchange is the uterine blood supply. Vascularity peaks during gestation (Guillette and Jones, '85b) and gravidity (Masson and Guillette, '87) in viviparous and oviparous species. Masson and Guillette ('87) argued that major changes in the degree of uterine vascularity are not required for the evolution of simple placentation in reptiles. Guillette and Jones ('85 b) suggested that the increased oviductal vascularity seen in viviparous species may be stimulated by hypoxia of the uterus caused by the embryo. As the embryos remove oxygen from the uterine tissue, other existing blood vessels would be stimulated to open and new ones could form.

A placenta is vital for water and gas exchange, and potentially inorganic and organic nutrient exchange, between maternal and foetal tissues (Yaron,'85). Unfortunately, little is known of the exact sites of the physiological exchange or how the oviduct mediates the transfer. Information available to date concerning placental transport in viviparous species is based on comparisons of the composition of ovulated eggs with neonates (Thompson,'81,'82; Stewart et al.,'90; Stewart and Thompson, '93; Thompson et al., '99a,b, '99c, 2000) and on the uptake by embryonic tissues of labeled ions or amino acids and their metabolites (Veith, '74; Thompson, '77; Swain and Jones, '97; Stewart and Thompson, 2000). Blackburn ('94) discussed the relative merits of different methodologies. He concluded that comparison of the composition of eggs and neonates provides the most reliable method of quantifying the source of nutrients for development. The studies using either method suggest that both organic (protein and lipid) and inorganic ions (e.g., calcium, potassium, sodium) can cross the placenta. Most of these experiments have been undertaken in relatively lecithotrophic species, suggesting that transfer of at least some inorganic or organic compounds is a common feature of viviparous squamates (Blackburn, '94). The amount of transfer varies considerably, however, depending on the relative contribution of the yolk to embryonic development and the complexity of placental tissues. In matrotrophic species, considerably more physiological exchange must occur. For example, in *Mabuya heathi*, a skink that ovulates the smallest known reptilian egg ($\approx$1 mm diameter), placental transport accounted for >99% of dry mass increase in neonates (Blackburn et al.,'84). In the viviparous skink *Pseudemoia pagenstecheri*, eggs contained only 51% of the dry matter that is present in neonates (Thompson et al.,'99c).

In mammals, the placenta is a well-known endocrine organ, but as yet there has been little consideration of the potential of the reptilian placenta to synthesise hormones. As with the mammalian placenta (Strauss et al.,'96), the reptilian placenta is ideally situated to utilise steroid precursors contributed by either the mother or the foetus, as well as to be influenced by maternal or foetal hormones. The yolk, which was found to contain androstenedione, estradiol, and testosterone in the American alligator *A. mississippiensis* (Conley et al.,'97), may also supply hormones capable of crossing the placental barrier. In Yarrow's spiny lizard, *Scelo-*

porus jarrovi, several events occurred in the fourth month of pregnancy: the corpus luteum began to degenerate, rapid embryonic growth began, the chorioallantoic placenta formed, and there was a marked increase in plasma progesterone concentrations (Guillette et al., '81). These changes suggested that the corpus luteum is not the only source of progesterone during pregnancy in *S. jarrovi*. Progesterone measured at this time may be secreted by the corpora atretica or the chorioallantoic placenta. In the skink *Chalcides chalcides*, progesterone was produced in vitro by placental tissues, with increased levels produced by tissue from late pregnant females in comparison to females in the early stages of pregnancy (Guarino et al., '98). The potential production of hormones (including growth factors) by placental tissues clearly needs to be addressed.

In summary, most viviparous squamates have a simple placental arrangement that is essential for water and gas exchange, nutrients being supplied predominantly by the yolk. More advanced forms of placentation are found, however, with regional differentiation of the uterine tissues associated with the developing extraembryonic membranes. Little is known about the potential nutrient transfer across the placenta, nor the potential for endocrine interactions between maternal and foetal tissues.

Oviposition or parturition

At the completion of gravidity or gestation, the oviduct plays a role in oviposition or parturition. These processes are achieved by rhythmic contractions of the oviductal muscularis, and they involve various hormones, including arginine vasotocin (AVT) and prostaglandins (PGs), as well as neural factors (Guillette et al., '91b). Females exhibit seasonal variations in spontaneous contractions of the oviduct, with maximal contractility occurring during gravidity or gestation (Abrams Motz and Callard, '88). The trigger for the contractions that cause oviposition or parturition is a topic that has received considerable attention in the reptilian literature, and several detailed reviews are available (Yaron, '72; La Pointe, '77; Jones and Guillette, '82; Guillette et al., '91b; Jones and Baxter, '91).

The neurohypophysial hormone AVT appears to play a major role in the processes of oviposition or parturition. In oviparous and viviparous species, AVT has been shown to induce oviductal contractions in vitro (La Pointe, '69, '77; Guillette and Jones, '80; Cree and Guillette, '91; Fergusson and Bradshaw, '92; Guillette et al., '92) and also to induce oviposition (Guillette and Jones, '82) or parturition (Guillette, '79; Guillette and Jones, '82; Cree and Guillette, '91). Maximal sensitivity of the oviducts to AVT occurred at approximately the same temperature as the preferred body temperature for each species examined by La Pointe ('77).

In the Pacific ridley turtle, *Lepidochelys olivacea*, and the loggerhead turtle, *Caretta caretta*, AVT and neurophysin (prohormone) concentrations were low in animals right up until oviposition (Figler et al., '89). Values were consistent with the hypotheses that the AVT-neurophysin complex is released from the neurohypophysis during nesting and that AVT is the physiological regulator of oviductal contractions in sea turtles. Similarly, in the tuatara, *Sphenodon punctatus*, high levels of AVT were recorded during oviposition (Guillette et al., '91d). However, in the viviparous skink, *Trachydosaurus* (*Tiliqua*) *rugosa*, plasma AVT rose approximately 30 days prior to parturition (Fergusson and Bradshaw, '91). If, as suggested, AVT is the physiological regulator of oviductal contraction, another factor(s) must prevent parturition until the appropriate time. The rise in AVT in *T. rugosa* was concurrent with a decrease in plasma progesterone from high levels during midpregnancy to basal levels at parturition as the corpus luteum degenerated (Fergusson and Bradshaw, '91).

Innervation will undoubtably contribute to the mechanisms controlling oviposition or parturition. Adrenergic and peptidergic innervation of the oviduct was analysed in Yarrow's spiny lizard, *Sceloporus jarrovi*, and showed seasonal changes (Rooney et al., '97). Adrenergic neurons were uncommon in the uterus of vitellogenic females, but abundant adrenergic nerve bundles were common in the uterus of gestating females. Rooney et al. ('97) hypothesised that uterine innervation is essential to maintain muscle quiescence during gestation. Both alpha- and beta-adrenergic receptors were present in the uterus of the lizards *Liolaemus gravenhorstii* and *L. tenuis* (Zurich et al., '71). Contractions of uterine tissue in vitro induced by adrenalin or noradrenalin were blocked by dibenzyline (blocks alpha-adrenergic receptors). In contrast, relaxation of uterine tissue in vitro was blocked by dichlorisoproterenol (blocks beta-adrenergic receptors; Zurich et al., '71).

An antibody directed against mammalian galanin was used to indicate that this neuropeptide is present in the oviduct of the oviparous wall lizard *Podarcis s. sicula* (Lammana et al., '99). Galanin immunoreactive neurons were found in all regions of the oviduct, predominantly in the circular muscle layer, with the most significant numbers being

present in the uterus and vagina. Galanin immunoreactive neurons were most common in the oviduct of reproductively active females and nonreproductive individuals treated with 17β-estradiol. Additionally, premature oviposition could be induced in gravid wall lizards *P. s. sicula* by the administration of galanin (Lammana et al., '99). Some galanin immunoreactive neurons also reacted with an antibody directed at vasoactive intestinal polypeptide (VIP). Lammana et al. ('99) hypothesised that galanin and VIP are important in the egg-laying process and act synergistically on oviductal smooth muscle.

Oviposition is often correlated with regression or surgical removal of the corpus luteum in oviparous species (Klicka and Mahmoud,'77; Cuellar,'79), which has led to the suggestion that luteal regression induces AVT secretion (Guillette and Jones, '82; Jones and Guillette,'82). The role of the corpus luteum in parturition in viviparous species is less clear. Considerable difference in the timing of luteal regression exists between species, as does the response to deluteinisation (Xavier, '87; Callard et al.,'92).

The actions of AVT may also be modified by sex steroids. In the skink *T. rugosa*, the strength of uterine contractions in vitro was reduced by pretreatment in vivo with progesterone or estradiol, although the frequency of AVT-induced contractions was enhanced by estradiol pretreatment (Fergusson and Bradshaw,'92). Although the strength of AVT-induced contractions was not significantly different between pregnant and nonpregnant females, spontaneous rhythmic contractions were present only in pregnant females. Ovariectomy did not affect the spontaneous or the AVT-induced contractions in *T. rugosa* (Fergusson and Bradshaw,'92).

Precursor compounds (eicosatrienoic acid and arachidonic acid) for PGs were identified in the oviduct of the viviparous lizard *Sceloporus jarrovi*, and the oviduct in vitro produced compounds that migrated alongside matching PG standards in thin-layer chromatography (Guillette et al., '88). Responsiveness of oviducts to arachidonic acid in vitro indicated that the oviducts were capable of producing PGs (Guillette et al., '91c). Uteri of the American alligator, *A. mississippiensis*, secreted PGF and PGE in vitro (Dubois and Guillette, '92). Secretion of PGs was lowest during gravidity but increased dramatically during oviposition. PG levels were also elevated around the time of oviposition in the tuatara (Guillette et al.,'90). PGs can be produced by the corpus luteum as well as by oviductal tissue of reptiles (Gobbetti et al.,'93). Amounts and types of PG produced by the corpus luteum of the wall lizard *Podarcis s. sicula* varied depending on the reproductive stage of the female (Gobbetti et al.,'93).

Guillette et al. ('91c) treated gravid females of several lizard species with $PGF_{2\alpha}$, PGE_2, or arachidonic acid (PG precursor) in vivo. None of the tested dosages induced oviposition in any of the species examined. However, if oviducts (containing fully shelled eggs) were isolated in culture with $PGF_{2\alpha}$ or arachidonic acid, oviducts did oviposit. Guillette et al. ('91b) hypothesised that PGs can stimulate oviposition in oviparous species but that the action of PGs may be inhibited by oviductal innervation.

In late-pregnant females of the viviparous lizard *Sceloporus jarrovi*, administration of $PGF_{2\alpha}$, PGE_2, or arachidonic acid in vivo, or to cultured oviduct in vitro, stimulated parturition within 2 hr (Guillette et al., '92). Administration of the these compounds to midpregnant females elicited no response in vivo. In oviducts cultured in vitro from midpregnant females, contractions were stimulated by $PGF_{2\alpha}$ but not by arachidonic acid. Similarly, AVT stimulated parturition in vitro in late-pregnant but not midpregnant females. In *S. jarrovi*, where progesterone falls markedly prior to parturition, subcutaneous implants of progesterone significantly delayed parturition (Guillette et al., '91a). Implants of indomethacin, which inhibits synthesis and release of prostaglandins, also delayed parturition and disrupted the normal birth process.

In the gecko *Hoplodactylus maculatus*, AVT, but not $PGF_{2\alpha}$, induced parturition in vivo in late-pregnant females (Cree and Guillette,'91). Pretreatment of females with β-adrenoreceptor antagonist before administration of $PGF_{2\alpha}$ stimulated parturition. Uteri treated in vitro contracted in response to both AVT and $PGF_{2\alpha}$. Pre-exposure of uteri to a β-adrenoreceptor agonist caused relaxation of tissue. However, pre-exposure did not prevent contractions induced by AVT, but it did prevent contractions induced by $PGF_{2\alpha}$. The results support the hypothesis that β-adrenergic stimulation inhibits the contractile response to $PGF_{2\alpha}$ in *H. maculatus* (Cree and Guillette,'91). Beta-adrenergic inhibition of oviposition was also reported in the anole lizard *Anolis carolinensis* (Jones et al.,'83b; Summers et al., '85). The uterus was found to respond to hormonal stimulation once a β-adrenergic agonist was administered or the uterus was surgically denervated.

The green anole, *Anolis carolinensis*, has provided a more complicated puzzle (Guillette and Jones,'85a). *A. carolinensis* ovulates an egg from al-

ternate ovaries approximately every 14 days followed by unilateral uterine contraction and oviposition. AVT did not stimulate oviposition (Guillette and Jones, '82), although oviductal contractions were stimulated by AVT in vitro in ovariectomised females (Guillette and Jones, '80). In naturally cycling females, oviductal contractions stimulated by AVT occurred in oviducts ipsilateral to an ovary in which the corpus luteum was degenerating or absent (Jones et al., '82; Jones and Guillette, '82). If a corpus luteum was present in the ovary on the same side as the oviduct tested, AVT failed to stimulate contraction. Unilateral deluteinisation removed the unilateral inhibition of oviductal contraction. The authors suggested that inhibitory substances may have been secreted by the corpus luteum and delivered to the ipsilateral uterus via small uteroovarian blood vessels (Jones et al., '82; Jones et al., '83a).

In mammals, relaxin (an insulin-like peptide) reaches peak plasma concentrations just prior to birth and causes cervical softening and relaxation of the pelvic ligaments, allowing the pelvis to stretch and expand during parturition (Sherwood, '88). Unfortunately, almost nothing is known about the actions of relaxin in reptilian species. In the turtle *Chrysemys* sp., relaxin significantly decreased the interval between contractions of the uterine muscularis (Sorbera et al., '88). Similarly, in sharks, relaxin depressed contractile activity of the uterine muscularis (Sorbera and Callard, '87). In the viviparous dogfish *Squalus acanthias*, relaxin increased the cervical cross-sectional area, resulting in premature birth (Koob et al., '84). The response to relaxin was specific to the cervix, not being observed in the anterior uterine constriction. Guillette et al. ('91b) suggested that the posterior oviduct of vertebrates (cervix, uterovaginal junction) may act to retain the eggs or embryos in utero because it is under separate control from other regions of the oviduct. The possibility of a functionally separate cervix (vagina) and the potential actions of relaxin needs further research within the reptiles, as well as in other vertebrate groups.

In the lacertid lizard *Lacerta vivipara*, plasma corticosterone concentrations reached a peak in late gestation (Dauphin-Villemant et al., '90). In addition, daily injections of corticosterone during late gestation significantly delayed the timing of parturition in *L. vivipara* (Dauphin-Villemant et al., '90), indicating that corticosterone may be involved in the parturition process. However, in the gecko *Hoplodactylus maculatus*, plasma concentrations of corticosterone did not vary between females in four reproductive conditions (vitellogenic, midpregnant, late-pregnant, and spent) (Girling and Cree, '95). These results do not support a role for corticosterone in maintaining gestation in this species . To my knowledge, no further information concerning the possible role of corticosterone in parturition is available.

It seems, therefore, that the major endocrine and neurological players in the oviposition/parturition process may have been identified, but the details of all the direct or indirect links between mechanisms causing oviductal contraction are still not understood. Guillette et al. ('90) summarised the probable actions of the main players as follows: AVT and prostaglandins induce oviductal contractions needed for oviposition or parturition, β-adrenergic neurons inhibit oviposition or parturition, and AVT seems to be able to override the β-adrenergic inhibition. The possible actions of relaxin and corticosterone need further investigation.

Abortive egg loss

Not all eggs that are ovulated into the oviduct develop successfully. This includes those eggs that are never fertilised. A current area of interest is the process by which abortive eggs are removed from the oviduct of squamate species, particularly the possibility that eggs may be resorbed by the uterine tissues. From a theoretical standpoint, resorption is an ideal method of minimising the loss of nutrients from females that ovulate failed eggs (Blackburn, '98b). It would also allow the female to modulate her reproductive output after ovulation in response to changing environmental conditions. However, to date there is only weak evidence that supports resorption of aborted eggs and does not exclude other alternatives. Alternatives include eggs being retained within the oviduct, or eggs being expelled and extruded from the oviduct via the cloaca (Blackburn, '98). Blackburn et al. ('98) examined the histology of sites of abortive eggs in the skink *Chalcides chalcides* and found no evidence of egg resorption. Uterine histology in these regions is very similar to the histology of the uterus of females in the early stages of pregnancy (pseudostratifed columnar epithelium, shell glands, and modest vascularity). Blackburn et al. ('98) hypothesised that abortive eggs are pushed down and extruded from the oviduct by action of the oviductal musculature. In the viviparous blue tongue lizard, *Tiliqua nigrolutea*, apparently unfertilised eggs are expelled along with full-term embryos at parturition. The eggs are then consumed by the mother (Edwards, '99).

FUTURE RESEARCH

There is considerable scope for further research on the structure and functions of oviductal tissues. Although it is not possible to identify every conceivable question that needs addressing, certain key areas stand out. These key areas, some of which have been alluded to in the preceding discussion, are collated and restated in following text.

The potential functions of the infundibulum have not been analysed in any detail. The infundibulum is the most anterior region of the oviduct, and it exhibits various epithelial cell characteristics, such as apical protrusions and blebbing, that are not understood. The infundibulum is known to be secretory; oviductal secretions coat the egg as soon as it enters the infundibulum, and epithelial cells contain various secretory granules. What is the nature of these secretions? As a working hypothesis, I suggest that the infundibulum secretes the mucus necessary for lubrication as the egg enters the oviduct. This hypothesis does not preclude other possibilities, which need clarification, namely, that the infundibulum may play a role in albumen secretion and that it may be a region that secretes growth factors. The infundibulum is ideally placed to secrete materials directly onto the ovulated egg prior to albumen and shell secretion.

The traditional view of estradiol-mediated oviductal development has been challenged, particularly in certain species. It appears that androgens may play a larger role in oviductal development than has been previously realised. Further characterisation of androgen receptor systems and aromatase activity in various species will be invaluable. I hypothesise that, in certain species (such as the garter snake, *Thamnophis sirtalis*, studied by Whittier et al., '87, '91; Whittier, '92), androgens are capable of maintaining the hypertrophied oviduct after an initial burst of estradiol at the beginning of vitellogenesis, which triggers oviductal development. Whether the androgens are acting directly on the oviduct or are being aromatised to estradiol would need investigation.

Analysis of the actions of growth factors will undoubtably add to our understanding of the reptilian oviduct, and the use of models based on information available for mammals will provide useful working hypotheses. For instance, in mammals it is believed that estradiol-induced uterine development is mediated by EGF. This was based on the observation that hypertrophy of the uterine epithelium observed in vivo could only be elicited in vitro if epithelial tissue was cultured in combination with stromal tissue. This suggested that paracrine factors were in action. Use of in vitro models in reptilian species will be important in determining the process by which estradiol and growth factors stimulate oviductal development. For example, based on the mammalian data, do reptilian epithelial cells cultured in vitro hypertrophy in response to EGF, but not to estradiol?

Another example of a model based on mammalian data that can be applied to reptiles involves IL-I. In mammals, IL-I induces production of prostaglandin-E_2. In the skink *Chalcides chalcides*, immunoreactivity for IL-I was strongest just prior to parturition. I hypothesise that production of IL-I at this time triggers the production of prostaglandins necessary for egg-laying or parturition.

Analysis of egg shelling in reptiles is hampered by our lack of knowledge concerning calcium secretion. The current hypothesis that the epithelium is the most likely source of shell calcium makes intuitive sense. The epithelium, which lines the lumen of the oviduct, is ideally placed to secrete an even layer of calcium over the entire egg. However, further specialised techniques will be required to confirm this hypothesis. Since the mechanism of calcium secretion in oviparous species is unknown, it is difficult to propose how the process may have been lost or changed in viviparous species. In the continuing debate concerning the evolution of viviparity, any information concerning the control of calcium secretion will be vital.

Research analysing the potential nutrient transfer by reptilian placental tissues has begun, but as yet little consideration has been given to the potential hormonal actions of the squamate placenta. In viviparous species, the lifespan of the corpus luteum (the major source of progesterone) varies, and in some species it degenerates well before parturition. The hypothesis by Guillette et al. ('81) that the placenta is another source of progesterone should be investigated. In certain viviparous squamate species, development of the placenta is associated with differential development of the uterus. I hypothesise that growth factors or sex steroids produced by the extraembryonic membranes are responsible for the differential development. Use of immunocytochemical techniques will be useful in identifying the presence and distribution of various hormones in placental tissues. These techniques will be most useful when used along with in vitro techniques to characterise the type and quantity of hormones produced by placental tissues.

The hypothesis by Guillette et al. ('91b) that the vagina may act as a functional cervix with separate

control from other oviductal regions needs further consideration. Again, in vitro techniques will be useful in identifying differential response to AVT, prostaglandin, relaxin, and neural factors among the different oviductal regions.

CONCLUSIONS

The reptilian oviduct is a diverse organ with a range of functions, depending on the reproductive mode of the species in question. The infundibulum initially receives the ovulated egg, and oviductal secretions immediately cover the egg. The exact nature of these secretions is unknown. The uterine tube is responsible for secretion of the albumen layer found in crocodilians and turtles. The role of the uterine tube in lepidosaurians is inconclusive, since no distinct albumen layer is present in their eggs. The uterus secretes the eggshell (both shell membranes and the calcareous components) in oviparous species. Mechanisms of shell secretion, particularly in regard to the production of the calcareous layer, are not well understood. In viviparous species, associations of the uterus with the extraembryonic membranes form the placenta. We still know little about what crosses the placental barrier, particularly potential transport of hormones and growth factors. At the completion of gravidity or gestation, the oviduct musculature contracts to cause oviposition or parturition, a procedure that requires AVT, PGs, and neural factors.

There is considerable potential for future research into this fascinating organ. In particular, improved techniques for identifying endocrine, molecular, and biochemical mechanisms acting in the oviduct will provide useful insight.

ACKNOWLEDGMENTS

Thanks to Alison Cree, Brett Gartrell, Sue Jones, Lou Guillette, and Roy Swain for their useful comments on this manuscript. Thanks also to Alison Cree and Lou Guillette for providing photographs.

LITERATURE CITED

Abrams Motz V, Callard IP. 1988. Seasonal variations in oviductal activity, extensibility, and tensile strength in *Chrysemys picta*. Gen Comp Endocrinol 72:453–460.

Abrams Motz V, Callard IP. 1991. Seasonal variations in oviductal morphology of the painted turtle, *Chrysemys picta*. J Morphol 207:59–71.

Adams CS, Cooper WE Jr. 1988. Oviductal morphology and sperm storage in the keeled earless lizard, *Holbrookia propinqua*. Herpetologica 44:190–197.

Aitken RNC, Solomon SE. 1976. Observations on the ultrastructure of the oviduct of the Costa Rican green turtle (*Chelonia mydas* L.). J Exp Mar Biol Ecol 21:75–90.

Akhtar P. 1988. Effects of steroids on the oviduct of female spiny tailed lizard. Pakistan J Agricult Res 9:120–124.

Aldridge RD. 1992. Oviductal anatomy and seasonal sperm storage in the south-eastern crowned snake (*Tantilla coronata*). Copeia 1992:1103–1106.

Andrews RM, Mathies T. 2000. Natural history of reptilian development: Constraints on the evolution of viviparity. BioScience 50:227–238.

Angelini F, Ghiara G. 1984. Reproductive modes and strategies in vertebrate evolution. Boll Zool 51:121–203.

Arslan M, Zaidi P, Lobo J, Zaidi AA, Qazi MH. 1978. Steroid levels in preovulatory and gravid lizards (*Uromastyxhardwicki*). Gen Comp Endocrinol 34:300–303.

Bautista CM, Mohan S, Baylink DJ. 1990. Insulin-like growth factors I and II are present in the skeletal tissue of ten vertebrates. Metabolism 39:96–100.

Birkhead TR, Mollar AP. 1993. Sexual selection and the temporal separation of reproductive events: Sperm storage data from reptiles, birds and mammals. Biol J Linnean Soc 50:293–311.

Blackburn DG. 1982. Evolutionary origins of viviparity in the Reptilia. I. Sauria. Amphib-Reptilia 3:185–205.

Blackburn DG. 1985. Evolutionary origins of viviparity in the Reptilia. II. Serpentes, Amphisbaenia and Ichthyosauria. Amphib-Reptilia 6:259–291.

Blackburn DG. 1993a. Chorioallantoic placentation in squamate reptiles: Structure, function, development, and evolution. J Exp Zool 266:414–430.

Blackburn DG. 1993b. Histology of the late-stage placentae in the matrotrophic skink *Chalcides chalcides* (Lacertilia; Scincidae). J Morphol 216:179–195.

Blackburn DG. 1994. Standardized criteria for the recognition of embryonic nutritional patterns in squamate reptiles. Copeia 1994:925–935.

Blackburn DG. 1995. Saltonist and punctuated equilibrium models for the evolution of viviparity and placentation. J Theor Biol 174:199–216

Blackburn DG. 1998a. Structure, function, and evolution of the oviducts of squamate reptiles, with special reference to viviparity and placentation. J Exp Zool 282:560–617.

Blackburn DG. 1998b. Resorption of oviductal eggs and embryos in squamate reptiles. Herpetol J 8(2):65–71.

Blackburn DG, Callard IP 1997. Morphogenesis of placental membranes in the viviparous, placentotrophic lizard *Chalcides chalcides* (Squamata: Scincidae). J Morphol 232:35–55.

Blackburn DG, Vitt LJ, Beuchat CA. 1984. Eutherian-like reproductive specializations in a viviparous reptile. Proc Natl Acad Sci 81:4860–4863.

Blackburn DG, Kleis-San Francisco S, Callard IP. 1998. Histology of abortive egg sites in the uterus of a viviparous placentotrophic lizard, the skink *Chalcides chalcides*. J Morphol 235:97–108.

Bona-Gallo A, Licht P, MacKenzie DS, Loft B. 1980. Annual cycles in levels of pituitary and plasma gonadotropin, gonadal steroids and thyroid activity, in the Chinese cobra (*Naja naja*). Gen Comp Endocrinol 42:477–493.

Botte V. 1973. Some aspects of oviduct development in the lizard *Lacerta sicula* in relation to the annual cycle. Boll Zool 40: 315–321.

Botte V, Basile C. 1974. The hormonal control of the oviduct in the lizard *Lacerta sicula* Raf. 2. The effects of PMS administration in normal and ovariectomized animals. Monit Zool Ital 8:55–59.

Botte V, Granata G. 1977. Induction of avidin synthesis by RNA obtained from lizard oviducts. J Endocrinol 73:535–536.

Botte V, Segal SJ, Koide SS. 1974. Induction of avidin synthesis in the oviduct of *Lacerta sicula*, by sex hormones. Gen Comp Endocrinol 23:357–359.

Bou-Resli MN, Bishay LF, Al-Zaid NS. 1981. Observations on the fine structure of the sperm storage crypts in the lizard *Acanthodactylus scutellatus Hardyi*. Arch Biol (Bruxelles) 92:287–298.

Boyd MMM. 1942. The oviduct, foetal membranes, and placentation in *Hoplodactylus maculatus* Gray. Proc Zool Soc Lond. Series A 112:65–104.

Callard IP, Klotz KL. 1973. Sensitivity of parameters of estrogen action in the iguanid lizard *Dipsosaurus dorsalis*. Gen Comp Endocrinol 21:314–321.

Callard IP, Leatham JH. 1970. Biochemical changes in the oviduct of the snake *Natrix sipedon pictiventris*. Comp Biochem Physiol 32:17–22.

Callard IP, Bayne CG, McConnell WF. 1972. Hormones and reproduction in the female lizard *Sceloporus cyanogenys*. Gen Comp Endocrinol 18:175–194.

Callard IP, Lance V, Salhanick AR, Barad D. 1978. The annual ovarian cycle of *Chrysemys picta*: Correlated changes in plasma steroids and parameters of vitellogenesis. Gen Comp Endocrinol 35:245–257.

Callard IP, Fiteti LA, Perez LE, Sorbera LA, Giannoukos G, Klosterman LL, Tsang P, McCracken JA. 1992. Role of the corpus luteum and progesterone in the evolution of vertebrate viviparity. Am Zool 32:264–275.

Christainsen JL. 1973. Natural and artificially induced oviductal and ovarian growth in two species of *Cnemidophorus* (Sauria: Teiidae). Herpetologica 29:195–204.

Conley AJ, Elf P, Corbin CJ, Dubowsky S, Fivizzani A, Lang JW. 1997. Yolk steroids during sexual differentiation in the alligator. Gen Comp Endocrinol 107:191–200.

Conner J, Crews D. 1980 Sperm transfer and storage in the lizard, *Anolis carolinensis*. J Morphol 163:331–348.

Cooke PS, Uchima F-DA, Fujii DK, Bern HA, Cunha GR. 1986. Restoration of normal morphology and estrogen responsiveness in cultured vaginal and uterine epithelia transplanted with stroma. Proc Natl Acad Sci USA 83:2109–2113.

Cordeno-López N, Morales MH. 1995. Lack of proteins of oviductal origin in the egg of a tropical anoline lizard. Physiol Zool 68:512–523.

Corso G, Delitala GM, Carcupino M. 2000. Uterine morphology during the annual cycle in *Chalcides ocellatus tiligugu* (Gmelin) (Squamata: Scincidae). J Morphol 243:153–165.

Cox C, Guillette LJ Jr. 1993. Localization of insulin-like growth factor-I-like immunoreactivity in the reproductive tract of the vitellogenic female American alligator, *Alligator mississippiensis*. Anat Rec 236:635–640.

Cox MC. 1994. Presence and functional role of the polypeptide growth factors insulin-like growth factor I (IGF-I) and epidermal growth factor (EGF) in the reptilian oviduct. Unpublished PhD thesis. University of Florida, Gainesville.

Crain DA, Gross TS, Cox MC, Guillette LJ Jr. 1990. Insulin-like growth factor-I in the plasma of two reptiles: Assay development and validation. Gen Comp Endocrinol 98:26–34.

Cree A, Guillette LJ Jr. 1991. Effect of β-adrenergic stimulation on uterine contraction in response to arginine vasotocin and prostaglandin $F_{2\alpha}$ in the gecko *Hoplodactylus maculatus*. Biol Reprod 44:499–510.

Cree A, Guillette LJ Jr, Reader K 1996. Eggshell formation during prolonged gravidity of the tuatara *Sphenodon punctatus*. J Morphol 230:129–144.

Cuellar HS. 1979. Disruption of gestation and egg shelling in deluteinized oviparous whiptail lizards *Cnemidophorus uniparens* (Reptilia: Teiidae). Gen Comp Endocrinol 39:150–157.

Cuellar O. 1966. Oviductal anatomy and sperm storage structures in lizards. J Morphol 119:7–20.

Cuellar O. 1970. Egg transport in lizards. J Morphol 130:129–136.

Dauphin-Villemant C, Leboulenger F, Vaudry H. 1990. Adrenal activity in the female lizard *Lacerta vivipara* Jacquin during artificial hibernation. Gen Comp Endocrinol 79:201–214.

Davenport M. 1995. Evidence of possible sperm storage in the caiman, *Paleosuchus palpebrosus*. Herpetol Rev 26:14–15.

Dubois DH, Guillette LJ Jr. 1992. Secretion of prostaglandin $F_{2\alpha}$ and E_2 in vitro by the uterus of the American alligator (*Alligator mississippiensis*). J Exp Zool 264:253–260.

Edwards A. 1999. Steroids and reproduction in *Tiliqua nigrolutea*. PhD thesis, University of Tasmania, Hobart, Australia.

Edwards A, Jones SM. 2001. Changes in plasma progesterone, estrogen, and testosterone concentrations throughout the reproductive cycle in female viviparous blue-tongued skinks, *Tiliqua nigrolutea* (Scincidae), in Tasmania. Gen Comp Endocrinol 122:260–269.

Fergusson B, Bradshaw SD. 1991. Plasma arginine vasotocin, progesterone, and luteal development during pregnancy in the viviparous lizard *Tiliqua rugosa*. Gen Comp Endocrinol 82:140–151.

Fergusson B, Bradshaw SD. 1992. In vitro uterine contractions in the viviparous lizard *Tiliqua rugosa*: Effects of gestation and steroid pretreatment in vivo. Gen Comp Endocrinol 86:203–210.

Figler RA, Mackenzie DS, Owens DW, Licht P, Amoss MS. 1989. Increased levels of arginine vasotocin and neurophysin during nesting in sea turtles. Gen Comp Endocrinol 73:223–232.

Flemming AF, Branch WR. 2001. Extraordinary case of matrotrophy in the African skink *Eumecia anchietae*. J Morphol 247:264–287

Fox H. 1977. The urinogenital system of reptiles. In: Gans C, Parsons TS, editors. Biology of the Reptilia. London: Academic Press. p 1–157.

Fox W. 1963. Special tubules for sperm storage in female lizards. Nature 194:500–501.

Gabe M, Saint Girons H. 1964. Contribution a l'histologie de *Sphenodon punctatus* Gray. Paris: Editions du Centre National de la Recherche Scientific.

Gavaud J. 1986. Vitellogenesis in the lizard *Lacerta vivipara* Jacquin II. Vitellogenin synthesis during the reproductive cycle and its control by ovarian steroids. Gen Comp Endocrinol 63:11–23.

Giannoukos G, Callard IP. 1996. Radioligand and immunocytochemical studies of turtle oviduct progesterone and estrogen receptors: Correlations with hormone treatment and oviduct contractility. Gen Comp Endocrinol 101:63–75.

Girling JE, Cree A. 1995. Plasma corticosterone levels are not significantly related to reproductive stage in female common geckos (*Hoplodactylus maculatus*). Gen Comp Endocrinol 100:273–281

Girling JE, Cree A, Guillette LJ Jr. 1997. Oviductal structure in a viviparous New Zealand gecko, *Hoplodactylus maculatus*. J Morphol 234:51–68.

Girling JE, Cree A, Guillette LJ Jr. 1998. Oviductal structure in four species of gekkonid lizard differing in parity mode and eggshell structure. Reprod Fertil Dev 10:139–154.

Girling JE, Guillette LJ Jr, Cree A. 2000. Ultrastructure of the uterus in an ovariectomized gecko (*Hemidactylus turcicus*)

after administration of exogenous estradiol. J Exp Zool 286:76–89.
Gist DH, Congdon JD. 1998. Oviductal sperm storage as a reproductive tactic of turtles. J Exp Zool 282:526–534.
Gist DH, Fischer EN. 1993. Fine structure of the sperm storage tubules in the box turtle oviduct. J Reprod Fertil 97:463–468.
Gist DH, Jones JM. 1987. Storage of sperm in the reptilian oviduct. Scanning Microsc 1:1839–1849.
Gist DH, Jones JM. 1989. Sperm storage within the oviduct of turtles. J Morphol 199:379–384.
Gobbetti A, Zerani M, DiFore MM, Botte V. 1993. $PGF_{2\alpha}$, PGE_2, progesterone and estradiol-17β secretion by the corpus luteum of the oviparous lizard, *Podarcis sicula sicula*. Prostaglandins 45:159–166.
Greer AE, Mys B. 1987. Resurrection of *Lipinia rouxi* (Hediger, 1934) (Reptilia: Lacertilia: Scincidae), another skink to have lost the left oviduct. Amphib-Reptilia 8:417–418.
Guarino FM, Paulesu L, Cardone A, Bellini L, Ghiara G, Angelini F. 1998. Endocrine activity of the corpus luteum and placenta during pregnancy in *Chalcides chalcides* (Reptilia, Squamata). Gen Comp Endocrinol 111:261–270.
Guillette LJ Jr. 1979. Stimulation of parturition in a viviparous lizard (*Sceloporus jarrovi*) by arginine vasotocin. Gen Comp Endocrinol 38:457–460.
Guillette LJ Jr. 1992. Morphology of the reproductive tract in a lizard exhibiting incipient viviparity (*Sphenomorphus fragilis*) and its implications for the evolution of the reptilian placenta. J Morphol 212:163–173.
Guillette LJ Jr. 1993. The evolution of viviparity in lizards. Bioscience 43:742–751.
Guillette LJ Jr, Jones RE. 1980. Arginine vasotocin-induced *in vitro* oviductal contractions in Anolis carolinensis: Effects of steroid hormone pretreatment *in vivo*. J Exp Zool 212:147–152.
Guillette LJ Jr, Jones RE. 1982. Further observations on arginine vasotocin-induced oviposition and parturition in lizards. J Herpetol 16:140–144.
Guillette LJ Jr, Jones RE. 1985a. Local influence of the corpus luteum on oviductal contraction in the lizard, *Anolis carolinensis*. In: Lofts B, Holmes WN, editors. Current trends in comparative endocrinology: Proceedings of the 9th International Symposium on Comparative Endocrinology, Hong Kong. Hong Kong: Hong Kong University Press. p 385–387.
Guillette LJ Jr, Jones RE. 1985b. Ovarian, oviductal, and placental morphology of the reproductively bimodal lizard, *Sceloporus aeneus*. J Morphol 184:85–98.
Guillette LJ Jr, Williams PE. 1991. Detection of insulin-like growth factors I and II in the egg albumen of the American alligator (*Alligator mississippiensis*) using microcapillary electrophoresis. Biol Reprod 44(supplement 1): 58.
Guillette LJ Jr, Moore FL, Spielvogel S. 1981. Luteal development, placentation, and plasma progesterone concentration in the viviparous lizard *Sceloporus jarrovi*. Gen Comp Endocrinol 43:20–29.
Guillette LJ Jr, Herman CA, Dickey DA. 1988. Synthesis of prostaglandins by tissue of the viviparous lizard, *Sceloporus jarrovi*. J Herpetol 22:180–185.
Guillette LJ Jr, Fox SL, Palmer BD. 1989. Oviductal morphology and egg shelling in the oviparous lizards *Crotaphytus collaris* and *Eumeces obsoletus*. J Morphol 201:145–159.
Guillette LJ Jr, Cree A, Gross TS. 1990. Endocrinology of oviposition in the tuatara (*Sphenodon punctatus*): 1. Plasma steroids and prostaglandins during natural nesting. Biol Reprod 43:285–289.
Guillette LJ Jr, DeMarco V, Palmer BD. 1991a. Exogenous progesterone or indomethacin delays parturition in the viviparous lizard *Sceloporus jarrovi*. Gen Comp Endocrinol 81:105–112.
Guillette LJ Jr, Dubois DH, Cree A. 1991b. Prostaglandins, oviductal function and parturient behavior in nonmammalian vertebrates. Am J Physiol 260:R854–R861.
Guillette LJ Jr, Masson GR, DeMarco V. 1991c. Effects of prostaglandin $F_{2\alpha}$, prostaglandin E_2 and arachidonic acid on the induction of oviposition *in vivo* and *in vitro* in oviparous lizards. Prostaglandins 42:533–540.
Guillette LJ Jr, Propper CR, Cree A, Dores RM. 1991d. Endocrinology of oviposition in the tuatara (*Sphenodon punctatus*): II. Plasma arginine vasotocin concentrations during natural nesting. Comp Biochem Physiol 100A:819–822.
Guillette LJ Jr, DeMarco V, Palmer BD, Masson GR. 1992. Effects of arachidonic acid, prostaglandin $F_{2\alpha}$, prostaglandin E_2, and arginine vasotocin on induction of birth *in vivo* and *in vitro* in a viviparous lizard (*Sceloporus jarrovi*). Gen Comp Endocrinol 85:477–485.
Guillette LJ Jr, Cox MC, Crain DA. 1996. Plasma insulin-like growth factor-I concentration during the reproductive cycle of the American alligator (*Alligator mississippiensis*). Gen Comp Endocrinol 104:116–122.
Guillette LJ Jr, Woodward AR, Crain DA, Masson GR, Palmer BD, Cox MC, You-Xiang Q, Orlando E. 1997. The reproductive cycle of the female American alligator (*Alligator mississippiensis*). Gen Comp Endocrinol 108:87–101.
Haider S. 1985. Effects of season, ovariectomy and mammalian gonadotropins on the oviduct of Indian wall lizard *Hemidactylus flaviviridis*. Arch Anat Hist Embr 68:119–126.
Haining REB, Cameron IT, van Papendorp C, Davenport AP, Prentice A, Thomas EJ, Smith SK. 1991. Epidermal growth factor in human endometrium: Proliferative effects in culture and immunocytochemical localisation in normal endometriotic tissues. Hum Reprod 6:1200–1205.
Halpert AP, Garstka WR, Crews D. 1982. Sperm transport and storage and its relation to the annual sexual cycle of the female red-sided garter snake, *Thamnophis sirtalis parietalis*. J Morphol 174:149–159.
Hattan LR, Gist DH. 1975. Seminal receptacles in the eastern box turtle, *Terrapene carolina*. Copeia 1975:505–510.
Hensgen HT, Rainey JM, Gist DH. 1980. Antigonadal effects of prolactin in female *Anolis carolinensis*. Gen Comp Endocrinol 41:22–30.
Ho S-M, Callard IP. 1984. High affinity binding of [^{3}H]R5020 and [^{3}H] progesterone by putative progesterone receptors in cytosol and nuclear extract of turtle oviduct. Endocrinology 114:70–79.
Jones RE. 1969. Effects of mammalian gonadotropins on the ovaries and oviducts of the lizard, *Lygosoma laterale*. J Exp Zool 171:217–222.
Jones RE, Baxter DC. 1991. Gestation, with emphasis on corpus luteum biology, placentation, and parturition. In: Pang PKT, Schreibman MP, editors. Vertebrate endocrinology: Fundamental and biomedical implications. California: Academic Press. p 205–302.
Jones RE, Guillette LJ Jr. 1982. Hormonal control of oviposition and parturition in lizards. Herpetologica 38:80–93.
Jones RE, Guillette LJ Jr, Norman MF, Roth JJ. 1982. Corpus luteum-uterine relationships in the control of uterine contraction in the lizard *Anolis carolinensis*. Gen Comp Endocrinol 48:104–112.

Jones RE, Summers CH, Austin HB, Smith HM, Gleeson TT. 1983a. Ovarian, oviductal, and adrenal vascular connections in female lizards (Genus *Anolis*). Anat Rec 206:247–255.

Jones RE, Summers CH, Lopez KH. 1983b. Adrenergic inhibition of uterine contractions and oviposition in the lizard *Anolis carolinensis*. Gen Comp Endocrinol 51:71–83.

Kleis-San Francisco SK, Callard IP. 1986. Progesterone receptors in the oviduct of a viviparous snake (*Nerodia*): Correlations with ovarian function and plasma steroid levels. Gen Comp Endocrinol 63:220–229.

Klicka J, Mahmoud IY. 1977. The effects of hormones on the reproductive physiology of the painted turtle, *Chrysemys picta*. Gen Comp Endocrinol 31:407–413.

Koob TJ, Laffan JJ, Callard IP. 1984. Effects of relaxin and insulin on reproductive tract size and early fetal loss in *Squalus acanthias*. Biol Reprod 31:231–238.

Lamanna C, Assisi L, Costagliola A, Vittoria A, Botte V, Cecio A. 1999. Galanin in the lizard oviduct: Its distribution and relationship with estrogen, VIP and oviposition. Life Sci 65:91–101.

La Pointe J L. 1969. Effect of ovarian steroids and neurohypophysial hormones on the oviduct of the viviparous lizard, *Klauberina riversiana*. J Endocrinol 43:197–205.

La Pointe J. 1977. Comparative physiology of neurohypophysial hormone action on the vertebrate oviduct-uterus. Am Zool 17:763–773.

Leese HJ. 1988. The formation and function of oviduct fluid. J Reprod Fertil 82:843–856.

Licht P. 1983. Evolutionary divergence in the structure and function of pituitary gonadotropins of tetrapod vertebrates. Am Zool 23:673–683.

Licht P, Porter DA. 1987. Role of gonadotropin-releasing hormone in regulation of gonadotropin secretion from amphibian and reptilian pituitaries. In: Norris DO, Jones RE, editors. Hormones and reproduction in fishes, amphibians, and reptiles. New York: Plenum Press. p 61–85.

Mahmoud LY, Colás AE, Woller MJ, Cyrus RV. 1986. Cytoplasmic progesterone receptors in uterine tissue of the snapping turtle (*Chelydra serpentina*). J Endocrinol 109:385–392.

Mangusson WE. 1979. Production of an embryo by *Acrochordus javanicus* isolated for seven years. Copeia 1979:744–745.

Masson GR, Guillette LJ Jr. 1987. Changes in oviductal vascularity during the reproductive cycle of three oviparous lizards (*Eumeces obsoletus*, *Sceloporus undulatus* and *Crotaphytus collaris*). J Reprod Fertil 80:361–371.

Mead RA, Eroschenko VP, Highfill DR. 1981. Effects of progesterone and estrogen on the histology of the oviduct of the garter snake, *Thamnophis elegans*. Gen Comp Endocrinol 45: 345–354.

Moore MC, Whittier JM, Crews D. 1985. Sex steroid hormones during the ovarian cycle of an all-female parthenogenetic lizard and their correlation with pseudosexual behaviour. Gen Comp Endocrinol 60:144–153.

Mossman H. 1937. Comparative morphogenesis of the fetal membranes and accessory uterine structures. Contrib Embryol 26:129–247.

Mundkur R, Sarkar HBD. 1982. Localization of some enzymes involved in steroid metabolism in the oviduct of the skink, *Mabuya carinata*. Curr Sci 51:254–255.

Murphy CR, Hosie MJ, Thompson MB. 2000. The plasma membrane transformation facilitates pregnancy in both reptiles and mammals. Comp Biochem Physiol A127:433–439.

Murphy LJ, Barron DJ. 1993. The IGFs and their binding proteins in murine development. Mol Reprod Dev 35:376–381.

Murphy-Walker S, Haley SR. 1996. Functional sperm storage duration in female *Hemidactylus frenatus* (family Gekkonidae). Herpetologica 52:365–373.

Nawaz S. 1987. Morphology and histology of female reproductive organs of *Uromastyxhardwicki* Gray. Biologia (Lahore) 33: 87–96.

Nelson KG, Takahashi T, Bossert NL, Walmer DK, McLachlan JA. 1991. Epidermal growth factor replaces estrogen in the stimulation of female genital-tract growth and differentiation. Proc Natl Acad Sci USA 88:21–25.

Ortiz E, Morales M. 1974. Development and function of the female reproductive tract of the tropical lizard, *Anolis pulchellus*. Physiol Zool 47:207–217.

Osawa G. 1898. Nachtrag zur lehre von den eingeweiden der *Hatteria punctata*. Die weiblichen geschlechtsorgane. Arch Microsc Anat 51:764–794

Packard GC, Tracy CR, Roth JJ. 1977. The physiological ecology of reptilian eggs and embryos, and the evolution of viviparity within the class Reptilia. Biol Rev 55:71–105.

Packard GC, Elinson RP, Gavaud J, Guillette LJ Jr, Lombardi J, Schindler J, Shine R, Tyndale-Biscoe HC, Wake MH, Xavier FDT, Yaron Z. 1989. How are reproductive systems integrated and how has viviparity evolved? In: Wake DB, Roth G, editors. Complex organismal functions: Integration and evolution in vertebrates. New York: John Wiley and Sons. p 281–293.

Packard MJ, DeMarco VG. 1991. Eggshell structure and formation in eggs of oviparous reptiles. In: Deeming DC, Ferguson MWJ, editors. Egg incubation: Its effects on embryonic development in birds and reptiles. Cambridge: Cambridge University Press. p 53–69.

Packard MJ, Hirsch KF. 1986. Scanning electron microscopy of eggshells of contemporary reptiles. Scanning Electron Microsc IV:1581–1590.

Packard MJ, Packard GC, Boardman TJ. 1982. Structure of eggshells and water relations of reptilian eggs. Herpetologica 38:136–155.

Packard MJ, Thompson MB, Goldie KN, Vos M. 1988. Aspects of shell formation in eggs of the tuatara, *Sphenodon punctatus*. J Morphol 197:147–157.

Palmer BD, Guillette LJ Jr. 1988. Histology and functional morphology of the female reproductive tract of the tortoise *Gopherus polyphemus*. Am J Anat 183:200–211.

Palmer BD, Guillette LJ Jr. 1990. Morphological changes in the oviductal endometrium during the reproductive cycle of the tortoise, *Gopherus polyphemus*. J Morphol 204:323–333.

Palmer BD, Guillette LJ Jr. 1991. Oviductal proteins and their influence on embryonic development in birds and reptiles. In: Ferguson MWJ, Deeming DC, editors. Environmental influences on avian and reptilian embryonic development. Cambridge: Cambridge University Press. p 29–46.

Palmer BD, Guillette LJ Jr. 1992. Alligators provide evidence for the evolution of an Archosaurian mode of oviparity. Biol Reprod 46:39–47.

Palmer BD, DeMarco VC, Guillette LJ Jr. 1993. Oviductal morphology and the eggshell formation in the lizard, *Sceloporus woodi*. J Morphol 217:205–217.

Paolucci M, DiFiore MM. 1994. Estrogen and progesterone receptors in lizard *Podarcis s. sicula* oviduct: Seasonal distribution and hormonal dependence. J Exp Zool 269:432–441.

Paolucci M, DiFiore MM, Ciarcia G. 1992. Oviduct 17β-estradiol receptor in the female lizard *Podarcis sicula sicula*, during the sexual cycle: Relation to plasma 17β-estradiol concentration and its binding proteins. Zool Sci 9:1025–1035.

Paulesu L, Romagnoli R, Marchetti M, Cintorino M, Ghiara P, Guarino FM, Ghiara G. 1995. Cytokines in the viviparous reproduction of squamate reptiles: Interleukin-1α (IL-1α) and IL-1β in placental structures of a skink. Placenta 16:193–205.

Perkins MJ, Palmer BD. 1996. Histology and functional morphology of the oviduct of an oviparous snake, *Diadophis punctatus*. J Morphol 227:67–79.

Picariello O, Ciarcia G, Angelini F. 1989. The annual cycle of oviduct in *Tarentola m. mauritanica* L. (Reptilia, Gekkonidae). Amphib-Reptilia 10:371–386.

Prasad MRN, Sanyal MK. 1969. Effect of sex hormones on the sexual segment of kidney and other accessory reproductive organs of the Indian house lizard *Hemidactylus flaviviridis* Ruppell. Gen Comp Endocrinol 12:110–118.

Reese JC, Callard IP. 1989. Two progesterone receptors in the oviduct of the freshwater turtle *Chrysemys picta*. Possible homology to mammalian receptor systems. J Steroid Biochem 33:297–310.

Rooney AA, Donald JA, Guillette LJ Jr. 1997. Adrenergic and peptidergic innervation of the oviduct of *Sceloporus jarrovi* during the reproductive cycle. J Exp Zool 278:45–52.

Salhanick AR, Vito CC, Fox TO, Callard IP. 1979. Estrogen-binding proteins in the oviduct of the turtle, *Chrysemys picta*: Evidence for a receptor species. Endocrinology 105:1388–1395.

Sarker S, Sarker NK, Maiti BR. 1995. Histological and functional changes of oviducal endometrium during seasonal reproductive cycle of the soft-shelled turtle, *Lissemys punctata punctata*. J Morphol 224:1–14.

Sarker S, Sarker NK, Maiti BR. 1996. Seasonal pattern of ovarian growth and interrelated changes in plasma steroid levels, vitellogenesis, and oviductal function in the adult female soft-shelled turtle *Lissemys punctata punctata*. Can J Zool 74:303–311.

Schuett GW. 1992. Is long-term sperm storage an important component of the reproductive biology of temperate pitvipers? In: Campbell JA, Brodie ED Jr, editors. Biology of the pitvipers. Tyler, TX: Selva. p 169–184.

Sen M, Maiti BR. 1990. Histomorphological changes of the ovary and oviduct during sexual maturity in the soft-shelled turtle, *Lissemys punctata punctata*. Zool Anz 225:391–395.

Sever DM, Ryan RJ. 1999. Ultrastructure of the reproductive system of the black swamp snake (*Seminatrix pygaea*): Part I. Evidence for oviducal sperm storage. J Morphol 241:1–18.

Sever DM, Ryan TJ, Morris T, Patton D, Swafford S. 2000. Ultrastructure of the reproductive system of the black swamp snake (*Seminatrix pygaea*). II. Annual oviductal cycle. J Morphol 245:146–160.

Shanthakumari TRS, Sarkar HBD, Shivandappa T. 1990. Histology and histochemistry of the oviductal sperm storage pockets of the agamid lizard Calotes versicolor. J Morphol 203: 97–106.

Shanthakumari TR, Sarker HBD, Shivanandappa T. 1992. Histological, histochemical and biochemical changes in the annual oviduct cycle of the Agamid, *Calotes versicolor*. J Morphol 211:295–306.

Sherwood CD. 1988. Relaxin. In: Knobil E, Neill JD, editors. The physiology of reproduction. New York: Raven, p 585–674.

Shine R. 1985. The evolution of viviparity in reptiles: An ecological analysis. In: Gans C, Billet F, editors. Biology of the Reptilia. Vol. 15. New York: John Wiley and Sons. p 605–694.

Shine R. 1989. Ecological influences on the evolution of vertebrate viviparity. In: Wake DB, Roth G, editors. Complex organismal functions: Integration and evolution in vertebrates. New York: John Wiley and Sons. p 263–278.

Shine R. 1995. A new hypothesis for the evolution of viviparity in reptiles. Am Nat 145:809–823.

Shine R, Guillette LJ Jr. 1988. The evolution of viviparity in reptiles: A physiological model and its ecological consequences. J Theor Biol 132:43–50.

Simmen FA, Simmen RCM. 1991. Peptide growth factors and pro-oncogenes in mammalian conceptus development. Biol Reprod 44:1–5.

Smith HM, Preston MJ, Jones RE. 1989. Oviductal, not oviducal. Anat Rec 223:446–447.

Smith SJ, Palmer BD, Selcer KW. 1995. Androgen receptor and aromatase in the turtle oviduct. Am Zool 35:6A.

Smith SK. 1994. Growth factors in the human endometrium. Hum Reprod 9:936–946.

Sorbera L, Callard I. 1987. Myometrial regulation in elasmobranches. Am Zool 27:80A.

Sorbera L, Giannoukos G, Callard I. 1988. Progesterone and relaxin inhibit turtle myometrium. Am Zool 28:145A.

Srinivas SR, Shivanandappa T, Hedge SN, Sarker HBD. 1995. Sperm storage in the oviduct of the tropical rock lizard, *Psammophilus dorsalis*. J Morphol 224:293–301.

Stewart JR. 1990. Development of the extraembryonic membranes and histology of the placenta in *Virginia striatula* (Squamata: Serpentes). J Morphol 205:33–43.

Stewart JR. 1992. Placental structure and nutritional provision to embryos in predominantly lecithotrophic viviparous reptiles. Am Zool 32:303–312.

Stewart JR. 1993. Yolk sac placentation in reptiles: Structural innovation in a fundamental vertebrate fetal nutritional system. J Exp Zool 266:431–449.

Stewart JR, Blackburn DG. 1988. Reptilian placentation: Structural diversity and terminology. Copeia 1988:839–852.

Stewart JR, Florian JD Jr. 2000. Ontogeny of the extraembryonic membranes of the oviparous lizard, *Eumeces fasciatus* (Squamata: Scincidae). J Morphol 244:81–107.

Stewart JR, Thompson MB. 1993. A novel pattern of embryonic nutrition in a viviparous reptile. J Exp Biol 174:97–108.

Stewart JR, Thompson MB. 1996. Evolution of reptilian placentation: Development of extraembryonic membranes of the Australian scincid lizards, *Bassiana duperreyi* (oviparous) and *Pseudomoia entrecasteauxii* (viviparous). J Morphol 227:349–370.

Stewart JR, Thompson MB. 1998. Placental ontogeny of the Australian scincid lizards *Niveoscincus coventryi* and *Pseudemoia spenceri*. J Exp Zool 282:535–539.

Stewart JR, Thompson MB. 2000. Evolution of placentation among squamate reptiles: Recent research and future directions. Comp Biochem Physiol A127:411–431.

Stewart JR, Blackburn DG, Baxter DC, Hoffman LH. 1990. Nutritional provision to embryos in a predominantly lecithotrophic placental reptile, *Thamnophis ordinoides* (Squamata: Serpentes). Physiol Zool 63:722–734.

Strauss JF III, Martinez F, Kiriakidou M. 1996. Placental steroid hormone synthesis: Unique features and unanswered questions. Biol Reprod 54:303–311.

Summers CH, Austin HB, Jones RE. 1985. Induction of oviposition in cycling *Anolis carolinensis* requires a β-adrenoreceptor blocker and a high dosage of arginine vasotocin. Gen Comp Endocrinol 57:389–392.

Swain R, Jones SM. 1997. Maternal-fetal transfer of ^{3}H-labelled leucine in the viviparous lizard *Niveoscincus metallicus* (Scincidae: Lygosominae). J Exp Zool 277:139–145.

Tabibzadeh S. 1994. Cytokines and the hypothalamic-pituitary-ovarian-endometrial axis. Hum Reprod 9:947–967.

Thompson J. 1977. The transfer of amino acids across the placenta of a viviparous lizard, *Sphenomorphus quoyi*. Theriogenology 8:158.

Thompson J. 1981. A study of the sources of nutrients for embryonic development in a viviparous lizard, *Sphenomorphus quoyii*. Comp Biochem Physiol 70A:509–518.

Thompson J. 1982. Uptake of inorganic ions from the maternal circulation during development of the embryo of a viviparous lizard, *Sphenomorphus quoyii*. Comp Biochem Physiol 71A:107–112.

Thompson MB, Stewart JR. 1994. Egg and clutch size of the viviparous Australian skink, *Pseudomoia pagenstecheri* and the identify of species with type III allantoplacentae. J Herpetol 28:519–521.

Thompson MB, Speake BK, Stewart JR, Russell KJ, McCartney RJ, Surai PF. 1999a. Placental nutrition in the viviparous lizard *Niveoscincus metallicus*: The influence of placental type. J Exp Biol 202:2985–2992.

Thompson MB, Stewart JR, Speake BK, Russell KJ, McCartney RJ. 1999b. Placental transfer of nutrients during gestation in the viviparous lizard, *Pseduemoia spenceri*. J Comp Physiol B 169:319–328.

Thompson MB, Stewart JR, Speake BK, Russell KJ, McCartney RJ, Surai PF. 1999c. Placental nutrition in a viviparous lizard (*Pseudemoia pagenstecheri*) with a complex placenta. J Zool 248:295–305.

Thompson MB, Stewart JR, Speake BK. 2002. Comparison of nutrient transfer across the placenta of lizards differing in placental complexity. Comp Biochem Physiol A127:469–479.

Uribe MCA, Velasco SR, Guillette LJ Jr, Estrada EF. 1988. Oviduct histology of the lizard, *Ctenosaura pectinata*. Copeia 1988:1035–1042.

van Wyk JH. 1984. Physiological changes during the ovarian cycle of the female rock lizard, *Agama atra* (Sauria: Agamaidae). S Afr J Zool 19:253–260.

van Wyk JH. 1994. Physiological changes during the female reproductive cycle of the viviparous lizard *Cordylus giganteus* (Sauria: Cordyliae). Herpetologica 50:480–493.

Veith WJ. 1974. Reproductive biology of *Chamaeleo pumilus pumilus* with special reference to the role of the corpus luteum and progesterone. Zool Afr 9:161–183.

Vitt LJ, Blackburn DG. 1991. Ecology and life history of the viviparous lizard *Mabuya bistriata* (Scincidae) in the Brazilian Amazon. Copeia 1991:916–927.

Vonier PM, Guillette LJ Jr, McLachlan JA, Arnold SF. 1997. Identification and characterization of estrogen and progesterone receptors from the oviduct of the American Alligator (*Alligator mississippiensis*). Biochem Biophys Res Commun 232:308–312.

Wake MH. 1985. Oviduct structure and function in non-mammalian vertebrates. Fortschr Zool 30:427–435.

Wang HS, Chard T. 1992. The role of insulin-like growth factor-I and insulin-like growth factor-binding protein-1 in the control of human fetal growth. J Endocrinol 132:11–19.

Whittier JM. 1992. Effects of sex steroid implants on reproductive tissues of female garter snakes (*Thamnophis sirtalis*). J Morphol 214:43–48.

Whittier JM, Mason RT, Crews D. 1987. Plasma steroid hormone levels of female red-sided garter snake, *Thamnophis sirtalis* parietalis: Relationship to mating and gestation. Gen Comp Endocrinol 67:33–43.

Whittier JM, West NB, Brenner RM. 1991. Immunorecognition of estrogen receptors by monoclonal antibody H222 in reproductive tissues of the red-sided garter snake. Gen Comp Endocrinol 81:1–6.

Whittier JM, Stewart D, Tolley L. 1994. Ovarian and oviductal morphology of sexual and parthenogenetic geckos of the *Heteronotia binoei* complex. Copeia 1994:484–492.

Xavier F. 1987. Functional morphology and regulation of the corpus luteum. In: Norris DO, Jones RE, editors. Hormones and reproduction in fishes, amphibians, and reptiles. New York: Plenum Press. p 241–282.

Yaron Z. 1972. Effects of ovariectomy and steroid replacement on the genital tract of the viviparous lizard, *Xantusia vigilis*. J Morphol 13:313–326.

Yaron Z. 1985. Reptilian placentation and gestation: Structure, function, and endocrine control. In: Gans C, Billet F, editors. Biology of the Reptilia. New York: Wiley and Sons. p 527–603.

Young LJ, Godwin J, Grammer M, Gahr M, Crews D. 1995. Reptilian sex steroid receptors: Amplification, sequence and expression analysis. J Steroid Biochem Mol Biol 55: 261–269.

Zurich L, Paz de la Vega-Lemus Y, Lemus D. 1971. Presence of adrenergic receptors in the uterus of two species of lizards, *Liolaemus gravenhorti* and *Liolaemus tenuis tenuis*. Biol Reprod 5:123–126.