A Review: Comparative Genomics and Physiology of Parity Mode Evolution in Amniotes

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Abstract

Across amniotes, squamates represent the only clade with highly variable parity modes, oviparity (egg-laying) and viviparity (live-birth). Despite this, relatively little is known about how oviparity and viviparity evolve at the genomic and physiological levels in squamates. Within the context of interdisciplinary medical, poultry science, and reproductive biology literature, I review the genomics and physiology of reproduction across five broad processes expected to change during transitions between parity modes—eggshell formation, embryonic retention, placentation, calcium transport, and maternal-fetal immune dynamics. Throughout, I offer alternative perspectives and testable hypotheses regarding proximate causes of parity mode evolution in squamates. This review is the first time that the maternal-fetal immune dynamics of viviparous squamates is considered in the context of the modern medical understanding that embryos are not analogous to allografts (e.g., organ transplants). In the discussion, I present two new pathways through which early Lepidosaurs may have transitioned rapidly between oviparity and viviparity with no intermediate stages. Rather than emphasizing the feasibility of transitions in either direction, I posit that oviparity and viviparity are relatively minor variations of a shared process. I encourage the scientific community to embrace the complex physiology and evolutionary history of reproduction in squamates.

Key Words: reproductive mode, parity modes, e, oviparity, squamates, eggshell deposition, embryonic retention, embryonic calcium transport, maternal-fetal interface, comparative evolutionary physiology.

Contents

I. Introduction

A reappraisal is needed for the conceptual framework used to research the evolution of oviparity (egg-laying) and viviparity (live-birth) in amniotes (birds, non-avian reptiles, and mammals). Squamates (snakes and lizards) are unique amongst amniotes because they have highly variable parity modes (Figure 1). Beginning with the first phylogenetic analyses on the subject, a warm-blooded scientific disagreement has persisted over the labile nature of evolutionary transitions between parity modes (Blackburn, 1999, 2015; de Fraipont, Clobert & Barbault, 1996; Griffith et al., 2015; Harrington & Reeder, 2017; Lee & Shine, 1998; Pyron, 2015; Pyron & Burbrink, 2014, 2015; Recknagel et al., 2018). With modern genomic technologies, it is prudent to acknowledge that the relative difficulty of changing phenotypes cannot be determined from morphology alone or unidentified physiological mechanisms. At least theoretically, any phenotypic change could be facilitated by simple genomic changes (e.g., a single nucleotide polymorphism) or any combination of multi-omic changes to any number of loci. As research begins to reveal the molecular networks involved with parity mode evolution, it is important to avoid bias that could be introduced by assumptions on the feasibility of transitions in either direction.

The earliest estimates predicted that viviparity evolved independently between 90-100 times in squamates (Blackburn, 1982, 1985; Shine, 1985; Blackburn, 1992). These estimates assumed that reversals back to oviparity should be exceedingly rare (hereafter rare-reversal model) (Fitch, 1970; Neill, 1964; Tinkle & Gibbons, 1977). An intermediate phenotype of re-evolving an eggshell may be physiologically unviable, preventing reversals (Blackburn, 1995; Griffith et al., 2015). This was demonstrated when experimentally induced extended egg retention in phrynosomatid lizards resulted in adverse embryonic development attributable to impeded gas exchange imposed by the eggshell (Mathies & Andrews, 1999, 2000; Parker & Andrews, 2006). However, this result may be specific to the clade.

Intermediate phenotypes as fitness valleys assumes 1) eggshells inherently impede gas-exchange and 2) that an eggshell must re-evolve before a reversal back to oviparity is possible (Griffith et al., 2015). Contrarily, eggshells are considered a component of the placenta in viviparous Rough Earth Snakes, *Haldea striatula*, and in viviparous reproductively bimodal Eastern Common Lizards, *Zootoca vivipara* and Yellow-bellied Three-toed Skinks, *Saiphos equalis* (Stewart et al., 2013). Additionally, *Saiphos equalis* is a reproductively bimodal skink that has an oviparous population with incubation times as short as 5 days, thus embryos spend significant time in utero with an eggshell (Smith et al., 2001). Another surprising example of eggshells being compatible with full embryonic development includes a report of a captive tortoise that retained viable eggs until the hatching stage (Kuchling & Hofmeyr, 2022).

An ancestral state reconstruction from 2014 found highly plastic parity modes in squamates, wherein viviparity evolved early and subsequently reversed back to oviparity repeatedly (hereafter labile model) (Pyron & Burbrink, 2014). Several additional ancestral state reconstructions also predict reversals back to oviparity within Squamata (de Fraipont et al., 1996; Fenwick et al., 2011; Harrington & Reeder, 2017; Lee & Shine, 1998; Recknagel et al., 2018). *Saiphos equalis* proved the possibility of reversals when a viviparous individual oviposited an egg prior to birthing fully developed young within the same litter (Laird et al., 2019). The unusual absence of an egg-tooth in oviparous Arabian Sand Boas, *Eryx jayakari* (Lynch & Wagner, 2010; Staub & Emberton, 2002) serves as additional evidence of a reversal, though this has been challenged (Griffith et al., 2015).

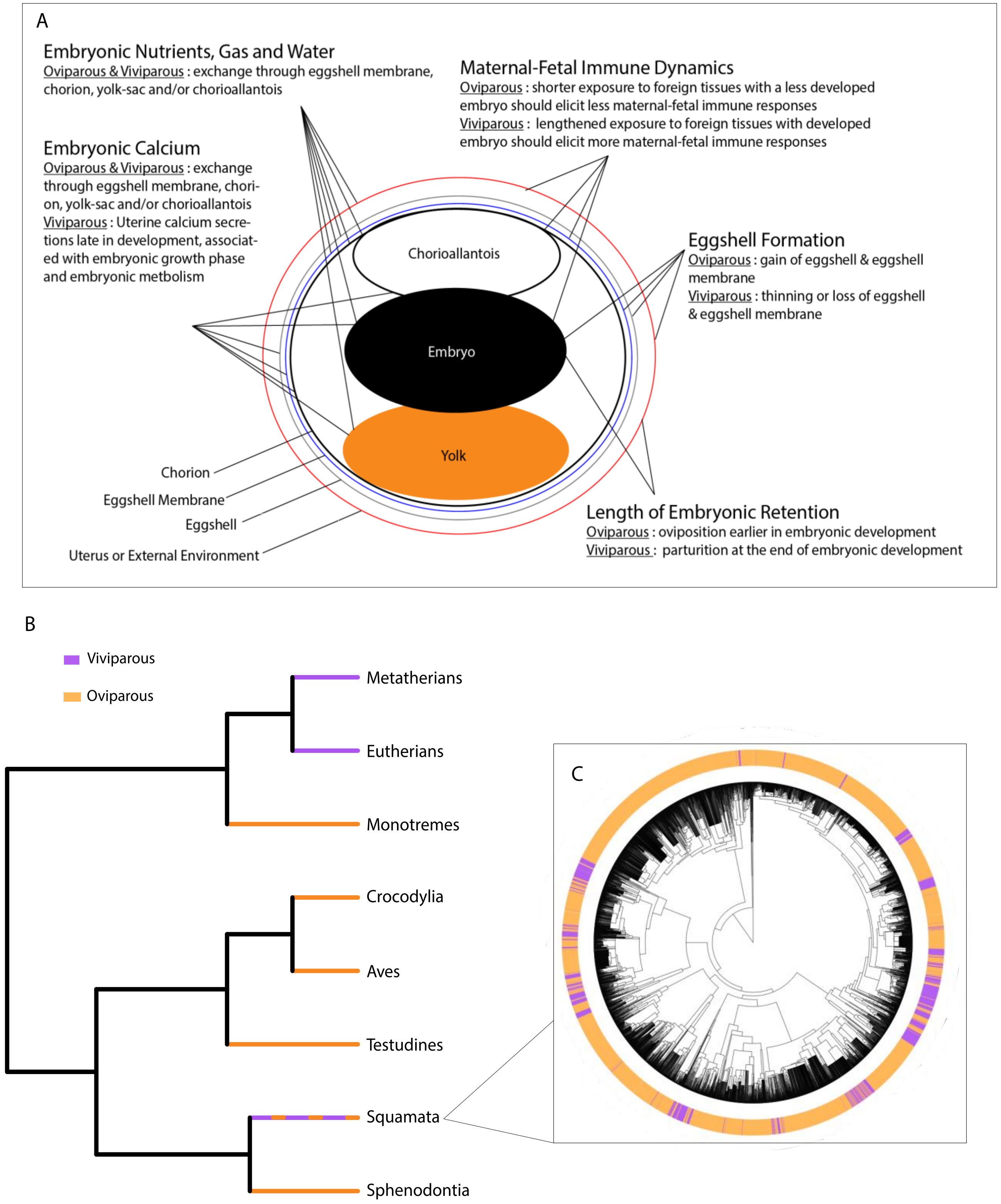
A
Embryonic Nutrients, Gas and Water
Oviparous & Viviparous : exchange through eggshell membrane, chorion, yolk-sac and/or chorioallantois
Maternal-Fetal Immune Dynamics
Oviparous : shorter exposure to foreign tissues with a less developed embryo should elicit less maternal-fetal immune responses
Viviparous : lengthened exposure to foreign tissues with developed embryo should elicit more maternal-fetal immune responses
Embryonic Calcium
Oviparous & Viviparous : exchange through eggshell membrane, chorion, yolk-sac and/or chorioallantois
Viviparous : Uterine calcium secretions late in development, associated with embryonic growth phase and embryonic metbolism
Chorioallantois
Embryo
Yolk
Eggshell Formation
Oviparous : gain of eggshell & eggshell membrane
Viviparous : thinning or loss of eggshell & eggshell membrane
Chorion
Eggshell Membrane
Eggshell
Uterus or External Environment
Length of Embryonic Retention
Oviparous : oviposition earlier in embryonic development
Viviparous : parturition at the end of embryonic development
B
Viviparous
Oviparous
Metatherians
Eutherians
Monotremes
Crocodylia
Aves
Testudines
Squamata
Sphenodontia
C

Figure 1: Schematic demonstrating (A) the anticipated processes that change during transitions between oviparity and viviparity, and the organs associated with those changes, (B) relationships between major amniote clades and their associated reproductive mode, and (C) the variation of reproductive modes across squamates. The squamate phylogeny is adapted from Pyron et al., (2016) and reproductive modes of squamate species from Pyron & Burbrink (2014). In the amniote phylogeny, branch lengths are arbitrary.

An early origin of viviparity for squamates or within different clades of squamates is not unreasonable. The oldest known amniotes (Mesosauridae) were viviparous (Piñeiro et al., 2012). Several basal lineages of diapsids, the clade containing all modern birds and reptiles, were viviparous (Motani et al., 2014). Viviparity may have been common in terrestrial reptiles ~248 mya (Motani et al., 2014). Recently, the first fossil record of viviparity was reported in a snake, *Messelophis variatus*, dating back 47 mya (Chuliver, Scanferla & Smith, 2022). This record compliments fossil records of viviparous lizards and challenges several dominant hypotheses on parity mode evolution including the rare-reversal model and the cold climate hypothesis (Tinkle & Gibbons, 1977).

In squamates, the degree of parity mode variation within a clade varies dramatically for, thus far, non-generalizable environmental, developmental, or genomic reasons (Anderson, Stoyan & Ricklefs, 1987; Blackburn, 2005; Griffith et al., 2017; Griffith & Wagner, 2017; Hodges, 2004; Li et al., 2009; Schwarzkopf & Andrews, 2012; Stewart et al., 2013; Van Dyke et al., 2014; Webb et al., 2006; Zimin et al., 2022). Oviparity and viviparity both entail numerous gains and losses of complex structures and processes (Blackburn, 1992; Lee & Doughty, 1997; Packard et al., 1977; Rothchild, 2003; Shine, 1985; Shine & Bull, 1979; Tinkle & Gibbons, 1977)—some of which are considered at the molecular level for the first time in this review. Using biological evidence gleaned from interdisciplinary literature across amniotes, I explore physiological features of gestation and gravidity, including those that could be exploited to support rapid shifts between parity modes, and those that may facilitate or impede reversals. I do not understand proximate causes of squamate parity mode evolution to adhere to one generalizable model, I advocate for future work to embrace the complexity of this system. I hope this serves as a foundation for further exploration on the genomic evolution of parity modes in squamates.

(1) Terminology

I use the conventional definition of viviparity as retention of eggs until the stage when the embryo is fully developed (Shine, 1985; van Dyke et al., 2014). Oviparity is defined by eggs that develop outside the mother (Stewart, 1997). I use the terms gravidity and gestation to describe the period of internal retention of the embryo in oviparous and viviparous taxa, respectively. Vertebrate placentas are conventionally defined by apposition of maternal and fetal tissues (Mossman, 1937; Stewart & Blackburn, 1988). It is accepted that all viviparous squamates have a chorioallantoic placenta under this definition (Murphy et al., 2009; Stewart & Blackburn, 1988). The avian chorioallantoic membrane and mammalian chorioallantoic placenta are homologous (Metcalfe & Stock, 1993). I sometimes refer to this organ as the chorioallantoic tissue to describe it for both parity modes. Oviposition refers to the process and act of egg-laying, while parturition refers to the process and act of giving birth to live-young.

(1) Main five physiological changes of parity mode transitions

Several physiological features are expected to change during transitions between oviparity and viviparity (Figure 1). I break this down into five physiological features (hereafter Main Five)—1) length of embryonic retention (Murphy & Thompson, 2011; Packard et al., 1977; Thompson & Speake, 2006)—only viviparous mothers retain the embryo for the entirety of development; 2) eggshell deposition (Heulin et al., 2005; Packard et al., 1977; van Dyke et al., 2014)—viviparous embryos generally do not have an eggshell; 3) placental development for maternal-fetal exchange of required water, gas and/or nutrients (Blackburn, 1992, 2015; Guillette & Guillette, 1993; Thompson et al., 2000; Thompson & Speake, 2006); 4) embryonic calcium provisioning (Packard et al., 1985; Shadrix et al., 1994; Thompson & Speake, 2006)—sources of embryonic calcium and timing of uterine calcium secretions generally differs between oviparous and viviparous reproduction; 5) maternal-fetal immune dynamics (Graham et al., 2011; Hendrawan et al., 2017)—viviparous reproduction is associated with maternal and embryonic exposure to foreign tissues, which is likely to require enhanced regulation of maternal-fetal immune systems.

II. Length of Embryonic Retention

Viviparous amniotes retain the embryo until it is fully developed, but oviparous amniotes retain the embryo for a fraction of that time. There are some examples of oviparous squamates with long egg retention, but oviposition still occurs prior to complete embryonic development in these taxa (Heulin et al., 2002). Rather than using precocious hatching and parturition (PH&P), like that of opossums and early viviparous mammals (Wagner et al., 2014), squamates evolve viviparity through extended egg retention (García-Collazo et al., 2012; Guillette & Guillette, 1993; Shine, 1983). Thus, processes affecting the length of embryonic retention are expected to change to support transitions between parity modes (García-Collazo et al., 2012; Guillette & Guillette, 1993; Murphy & Thompson, 2011; Thompson & Speake, 2006).

(1) Parturition & oviposition

The genes and hormones involved with initiating and ending gestation may provide insights into the loci squamates can co-opt to change the length of embryonic retention during parity mode transitions. Parturition and oviposition terminate embryonic retention. Parturition can be divided into four parts (Terzidou, 2007; Vannuccini et al., 2016)—quiescence (Phase 0), activation (Phase 1), stimulation (Phase 2) and involution (Phase 3). In eutherian mammals, several processes contribute to the initiation and termination of gestation including inflammation (Challis et al., 2009; Hansen et al., 2017), maternal recognition of pregnancy (MRP), mechanical stretch of uterine tissues (Sooranna et al., 2004; Shynlova et al., 2008), and fluctuating concentrations of corticotropin-releasing hormone, progesterone, and estrogen (Challis et al., 2000; Condon et al., 2004; Mitchell et al., 1984; Shaw & Renfree, 2001).

(i) Quiescence & sustained progesterone production in reproductive tissues

Extended embryonic retention could be achieved by triggering mechanisms that extend uterine quiescence, inactivity of the uterus. Inhibition of myometrial contractions through sustained progesterone production supports quiescence across different viviparous amniotes (Bazer, 1992; Casey & MacDonald, 1997; Fergusson & Bradshaw, 1991; Ilicic et al., 2017; Murphy & Thompson, 2011; Putnam et al., 1991; Soloff et al., 2011). The corpus luteum (or plurally called corpora lutea), a transient progesterone-producing organ, produces progesterone during gestation (Gemmell, 1995). Extended lifespan of the corpus luteum likely aided the evolution of viviparity in mammals (Amoroso, 1968; Callard et al., 1992; Stouffer & Hennebold, 2015). Thus, early research on squamate viviparity also explored the influence of corpus luteum lifespan. The lifespan of corpora lutea associates with oviparous egg retention and oviposition (Diaz, Alonso-Gomez & Delgado, 1994; Fox & Guillette 1987; Guillette & Guillette 1993; Jones & Guillette 1982). Eggshell formation in oviparous Whiptail lizards, *Cnemidophorus uniparens*, is even disrupted by experimental removal of corpora lutea (Cuellar, 1979). The lifespan of corpora lutea do not consistently correlate with length of embryonic retention in viviparous squamates like it does in mammals (Albergotti & Guillette, 2011; Callard et al., 1992).

Maternal recognition of pregnancy (MRP) refers to the early signaling of the embryo to prevent luteolysis (Thatcher, Meyer, & Danet-Desnoyers, 1995), degradation of the corpus luteum. Luteolysis occurs in the absence of pregnancy. MRP enables continued progesterone production by the corpus luteum to support uterine quiescence during early gestation. An independent evolution of MRP is reported for Macropodidae, a lineage of marsupial mammals (Freyer, Zeller, & Renfree, 2003). MRP has not been explicitly studied in squamates. However, MRP likely happens in squamates, given that corpora lutea do not get degraded in the earliest stages of gravidity/gestation in oviparous or viviparous squamates (Callard et al., 1992; Albergotti & Guillette, 2011).

Different loci are signaled by embryos for MRP across mammals. Human chorionic gonadotropin hormone (hCG) establishes MRP (Ross, 1979; Behrman et al., 1993; Duncan, McNeilly, & Illingworth, 1998; Duncan, 2000; Ticconi et al., 2007). In pigs, MRP is triggered by embryonic signaling of oestrogen (Geisert et al., 1990). Glycoproteins, estradiol (E2) and prostaglandin E2 (PGE2) have been implicated in signaling MRP in horses (Klein & Troedsson, 2011; Klein, 2016). In ruminants, embryonic signaling of IFN-τ establishes MRP (Bazer, 2013; Bazer, Spencer & Ott, 1997; Thatcher et al., 1995). During gestation in the uterus of viviparous African Ocellated skinks, *Chalcides ocellatus*, four receptors for interferon alpha, beta, omega, and gamma are differentially expressed but no expression of IFN-τ was detected compared to non-gestational uterine tissue (Brandley et al., 2012). I was unable to find expression patterns of MRP signaling homologs in other squamate reproductive tissues based on the available literature. Should MRP occur in squamates, it may be signaled by loci that are clade-specific, like in mammals. This makes comparatively evaluating the influence of MRP on the evolution of viviparity an interesting avenue for future research.

The evolution of viviparous extended embryonic retention may be sufficiently supported by maintenance of chorioallantoic progesterone production coupled with eggshell loss (Griffith, Brandley et al., 2017). This theory may be broadly applicable across amniotes given that the most recent common ancestor of amniotes likely had a chorioallantois with an endocrine function (Griffith, Chavan et al., 2017). Following death of the corpus luteum during gestation, placental progesterone production supports extended embryonic retention in eutherian mammals (Castracane & Goldzieher, 1986; Ellinwood et al., 1989; Nakajima et al., 1991; Rothchild, 2003; Spencer & Bazer, 2004). Viviparous Italian Three-toed Skinks, *Chalcides chalcides,* shift to chorioallantoic progesterone production following degradation of corpora lutea during gestation (Guarino et al., 1998). The placenta of viviparous Southern Snow Skinks, *Carinascincus microlepidotus*, produces minimal progesterone but has a strong capacity to convert pregnenolone to progesterone (Girling & Jones, 2003). Whereas all genes involved with a known biosynthesis pathway for progesterone production are expressed in the placenta of horses, *Equus caballus*, only some loci were detected in the chorioallantois of chickens, *Gallus gallus*, viviparous Southern Grass Skinks, *Pseudemoia entrecasteauxii*, and oviparous and viviparous Southeastern Sliders, *Lerista bougainvillii* (Griffith, Brandley et al., 2017). Thus, if chorioallantoic progesterone production has supported multiple origins of viviparity in amniotes, it is not evidenced by a conserved ancestral gene expression pattern (Griffith, Brandley et al., 2017).

Other female reproductive tissues in squamates express genes involved with progesterone biosynthesis—StAR-related lipid transfer domain protein 3 (*StARD3*) and hydroxy-delta-5-steroid dehydrogenase (*HSD3B1*). *STARD3* is significantly upregulated in the uterine tissue during pregnancy in viviparous African Ocellated skinks, *Chalcides ocellatus*, along with significant differential expression of seven paralogs (Brandley et al., 2012). Compared to non-gestational samples, *HSD3B1* is significantly upregulated in the uterus during early and late gestation in viviparous individuals of reproductively bimodal *Saiphos equalis* (Foster et al., 2020). Oviparous individuals from the same species did not exhibit this expression pattern (Foster et al., 2020). Activity of *HSD3B1* was detected in the mucosal epithelium of oviparous Eastern Garden Lizards, *Calotes versicolor* (Shanthakumari et al., 1990, 1992), and in the uterine glands of oviparous Keeled Indian Mabuya, *Eutropis carinata (*Mundkur & Sarkar, 1982). Other loci involved with the biosynthesis of progesterone (e.g., steroidogenic acute regulatory protein or cytochrome-P450-family-11-subfamily-A-polypeptide-1) serve as further candidates for exploring the relationship between organ-specific patterns of progesterone production and the evolution of extended embryonic retention in viviparous squamates. Biosynthesis of progesterone may also occur through an unknown biosynthesis pathway in squamate reproductive tissues (Griffith, Brandley et al., 2017).

For progesterone to prevent myometrial contractions and support quiescence, there must be progesterone receptors (PGRs) in the uterus (Mesiano et al., 2011; Young et al., 2011). In humans, progesterone responsiveness is related to specific ratios of PGRs, *PR-A* and *PR-B*, in myometrial cells (Young et al., 2011). Minimal research exists on PGR expression in squamate reproductive tissues. One study found that in the uterus of the yolk-sac in viviparous Southern Grass Skinks, *Pseudemoia entrecasteauxii*, one progesterone receptor, *PGRMC2,* is upregulated compared to non-gestational uterine tissue (Griffith et al., 2016); Another progesterone receptor, *PGR*, is downregulated in the uterus of the chorioallantoic placenta and yolk sac placenta compared to non-gestational uterine tissue (Griffith et al., 2016). Downregulation of both *PGR* and *PGRMC2* in the uterus during gestation was detected in viviparous *Chalcides ocellatus* (Brandley et al., 2012). Measuring expression of PGRs and their ratios in uteruses of oviparous and viviparous squamates may provide insights on mechanisms of extended embryonic retention.

(ii) Activation & progesterone withdrawal

The activation stage of parturition is marked by the withdrawal, or functional withdrawal, of progesterone leading to an estrogen dominated response during the next state, stimulation (Bakker, Pierce, & Myers, 2017; Fergusson & Bradshaw, 1991). Progesterone may withdraw in response to environmental stimuli in reptiles during parturition (Shine & Guillette, 1988). In mammals, activation is marked by increasing concentrations of corticotropin-releasing hormone and contraction associated proteins (CAPs) including connexin-43, prostaglandins, oxytocin receptors, prostanoid receptors and cell signaling proteins (Bakker et al., 2017; Ilicic et al., 2017; Leadon et al., 1982; Pashen & Allen, 1979; Whittle et al., 2000). Pro-inflammatory cytokines and chemokines, prostaglandin synthase-2 (*COX-2,* also referred to as *PTGS2*), and NF-κB also influence activation in mammals (Christiaens et al., 2008; Lappas et al., 2002; Lappas & Rice, 2007; Lindström & Bennett, 2005; Olson, 2003; Terzidou, 2007).

Some similar patterns are associated with oviposition in birds. In chickens, *Gallus gallus*, prostaglandin F (PGF) concentrations increase in the hours leading up to oviposition (Takahashi et al., 2004). Experimental injection of oxytocin and arginine vasotocin, similar neurohypophyseal peptides, revealed that uterine tissues of chickens, *Gallus gallus*, maintain responsiveness to oxytocin but are more sensitive toward arginine vasotocin (Ewy, 1969). Murphy & Thompson (2011) provide a rather exhaustive list of resources on progesterone and estrogen assays across oviparous and viviparous squamates. Future research should consider exploring parallels between mechanisms of activation in mammals and squamates. Any process that can trigger or stall activation should lead to extended embryonic retention.

(iii) Stimulation & electrical gradients, inflammation, and hormonal regulation

Mechanical stretch, electrical gradients, inflammatory processes, and hormonal regulation contribute to stimulation, the phase when contractions, cervical ripening and dilation occur (McEvoy & Tetrokalashvili, 2018; Ravanos et al., 2015). Stimulation involves contributions from maternal and fetal tissues. As early as 460 BC there was uncertainty over the proportional influence of mother or fetus on the initiation of parturition. Hippocrates proposed that the fetus initiates parturition by pushing its feet on the fundus of the uterus (Thorburn, 1987). Although the reality is not so cartoonish, mechanical stretch of the uterus from the growing embryo plays a role in parturition (Lefebvre et al., 1995; Tamizian & Arulkumaran, 2004).

Physical stretching of the uterus causes an influx of calcium and sodium, altering the action potential and enabling contractions (Kao & McCullough, 1975). Calcium further activates voltage gated calcium channels on myometrial cell membranes, enhancing the influx of calcium ions, mediating the force and speed of myometrial contractility (Arrowsmith & Wray, 2014; Wray et al., 2015). The influence of uterine overdistention on oviposition and parturition in birds and non-avian reptiles has not yet been examined, to our knowledge. However, differentially expressed genes functionally enriched the GO term for "voltage-gated calcium channel activity" in uterine tissues during gravidity and gestation in oviparous and viviparous *Saiphos equalis* (Foster et al., 2020). A uterine response to overdistention is among the many possible explanations for this. It may be important to consider the influence of uterine overdistention on squamate parity mode transitions, because should bioelectrical responses to uterine overdistention be a common feature of vertebrate parturition, lessened distention may be a hurdle to reverse back to oviparity.

Uterine overdistention may additionally influence parturition by triggering the "inflammatory pulse" that activates further myometrial contractility (Adams Waldorf et al., 2015). At this time, there is an influx of uterine and embryonic pro-inflammatory genes and immune cells (Adams Waldorf et al., 2015; Charpigny et al., 2003; Marvin, 2002; McEvoy & Tetrokalashvili, 2018; Mesiano et al., 2002; Park et al., 2005; Romero et al., 1994; Terzidou, 2007; Welbergen et al., 2008). The inflammatory responses associated with uterine contractions in humans involve actions of prostaglandins (PGs), oxytocin, corticotropin-releasing hormone, cytokines, and neutrophils (Adams Waldorf et al., 2015; De Rensis et al., 2012; Gibb, 1998; McEvoy & Tetrokalashvili, 2018; Olson & Hertelendy, 1983; Park et al., 2005; Romero et al., 1994; Sykes et al., 2014; Terzidou, 2007).

The cycling concentrations of a neuropeptide, corticotropin-releasing hormone (CRH), supports parturition in humans. This has been compared to a biological clock that is initiated at early stages of gestation (Lockwood, 2004; McLean & Smith, 2001). Increased production of CRH facilitates parturition by interacting with CRH receptors, CRH-R1 and CRH-R2, which promote myometrial relaxation or contractility, respectively (Campbell et al., 1987; Li & Challis, 2005; Petraglia et al., 1995; Yuan & López Bernal, 2007). Altered regulation, phenotype or function of loci that function as biological clocks, like CRH, may have a particularly strong influence on evolutionary changes to length of embryonic retention, a trait inherently related to time.

Placental CRH production has only been identified in primates thus far (Challis et al., 2005; Emanuel et al., 1994; Florio et al., 2002; Grammatopoulos, Milton & Hillhouse, 1994; Grammatopoulos et al., 1996; Karteris et al., 1998; Mendelson, 2009; Robinson et al., 1989; Torricelli et al., 2007). Placental CRH production may, therefore, be unique to primates. Alternatively, absence of placental CRH production in other taxa may be an artifact of bias sampling. The amino acid sequence of CRH is highly conserved in vertebrates (Noy et al., 2017), indicating there is a possibility for shared function across diverse taxa. Like CRH cycling in mammals, timely fluctuations of a neuropeptide that stimulates uterine contractions, arginine vasotocin (AVT), enables oviposition in birds, turtles, and lizards (Ewy, 1969; Fergusson & Bradshaw, 1991; Guillette Jr & Jones, 1980; Jones et al., 1987; Rzasa, 1978; Srivastava et al., 2007; Wu et al., 2019).

Prostaglandin E_2 (PGE_2) and prostaglandin F2α ($PGF_{2\alpha}$) influence, respectively, uterine contractions and cervical relaxation for oviposition/parturition across many amniotes including humans, *Homo sapiens* (Gibb 1998; Terzidou 2007), domestic pigs (De Rensis et al. 2012), domestic chickens (Hertelendy et al., 1974; Olson et al., 1986), and Loggerhead Sea turtles (Guillette et al., 1991). Injections of $PGF_{2\alpha}$ and PGE_2 induce parturition in viviparous Yarrow's

Spiny lizards, *Sceloporus jarrovi*, and Raukawa geckos, *Woodworthia maculatus* (Cree & Guillette, 1991; Guillette et al., 1992). However, no injected dosages of $PGF_{2\alpha}$ or PGE_2 induced oviposition in oviparous Collard lizards, *Crotaphytus collarus*, Eastern Fence lizards, *Sceloporus undulatus*, Six-lined racerunners, *Aspidoscelis sexlineatus*, or Striped Plateau lizards, *Sceloporus virgatus* (Guillette et al., 1991). It is interesting that injections of $PGF_{2\alpha}$ and PGE_2 induced parturition in viviparous lizards but did not induce oviposition in oviparous lizards studied. Given this, it is plausible that regulatory or functional changes to $PGF_{2\alpha}$ and/or PGE_2 in squamates could facilitate changes to the length of embryonic retention to support transitions between reproductive modes. However, induction of parturition with $PGF_{2\alpha}$ in viviparous *Woodworthia maculatus* only worked with pre-treatment of β-adrenoeceptor (Cree & Guillette, 1991).

$PGF_{2\alpha}$ decreases progesterone concentrations during stimulation (De Rensis et al., 2012). In humans, biosynthesis of PGs is driven largely by the enzyme cyclooxygenase (*COX*)-*2* rather than *COX-1* (i.e., prostaglandin synthase-2 and -1) (Slater et al., 1995, 1999). This helps maintain the decreased progesterone/estrogen ratio of stimulation. In ovariectomize viviparous Garter snakes, *Thamnophis*, increased estrogen stimulated thickness of uterine epithelial cells and glandular activity, whereas administration of progesterone had little influence on uterine histology (Mead et al., 1981). Uterine pig models revealed that estrogen stimulates involuntary contractions and relaxation of the uterus (Mueller et al., 2006).

The softening of the cervix is important during the stimulation stage of parturition. A hormone related to insulin, *relaxin*, promotes myometrial softening in humans, *Homo sapiens*, domestic pigs, and turtles (Mercado-Simmen et al., 1982; Sorbera et al., 1988; Weiss & Goldsmith, 2001). The cervix also gets softer by actions of PGE_2. PGE_2 activates pro-inflammatory cytokines, interleukin (IL)-8 and tumor necrosis factor (TNF)-α, which activates the collagenases and matrix metalloproteinases for cervical softening (Bakker et al., 2017). This causes a positive feedback loop between IL-8 and PGE_2 synthesis (Denison et al., 1998; Denison, Calder & Kelly, 1999; Terzidou, 2007; Li et al., 2010). Upregulated of IL-8 is also promoted by the protein complex NF-kB during parturition in humans (Elliott, 2001). Similar patterns were observed during parturition in mice (Condon et al., 2004) and baboons (Mendelson & Condon, 2005).

A few studies consider the role of cytokines on squamate reproduction but not during oviposition or parturition (Hendrawan et al., 2017; Paulesu et al., 1995, 2005, 2008). Some studies detected expression of cytokines during late gestation (Foster et al., 2020; Gao et al., 2019; Recknagel et al., 2021). TNF-α related activity was only detected at this time in viviparous Tussock Cool-skinks, *Pseudemoia entrecasteauxii,* which were found to downregulate TNF-α induced proteins (*TNFAIP6* and *TNFAIP8L2*) in the 'uterus of the chorioallantoic placenta' and *TNFAIP6*, *TNFAIP1*, and *TNFAIP2* in the 'uterus of the yolk-sac placenta' compared to not gestational uterine tissues (Griffith et al., 2016). Activity of TNF-α in reproductive tissues during gestation in viviparous Italian Three-toed skinks, *Chalcides chalcides*, and reproductively bimodal European common lizards, *Zootoca vivipara*, was associated with maternal-fetal immune dynamics (Paulesu et al., 1995, 2005, 2008; Hendrawan et al., 2017).

Altered expression or phenotype of contractility agonists, oxytocin receptors and estrogen receptors, and contractility antagonists, progesterone receptors and β-adrenergic receptors (McEvoy & Tetrokalashvili, 2018) may also change the length of embryonic retention to support transitions between parity modes. Differences in length of embryonic retention in oviparous and viviparous agamas, *Phrynocephalus przewalskii* and *Phrynocephalus vlangalii,* appears to be driven by regulatory differences of prostaglandins, *COX-2*, an *AVT* receptor (*MTR*), β-adrenergic receptors, and estrogen receptors. During oviposition, *P. przewalskii*, exhibited the following: promotion of contractions through downregulation of *ADRB2*, and upregulation of *COX-2* and prostaglandin, and absent (potentially lost) expression of two estrogen receptors (*ESR1* and *ESR2*) and the AVT receptor, *MTR* (Gao et al., 2019). During the stage of gestation corresponding to oviposition, viviparous sister-species, *P. vlangalii*, exhibited the following pattern: inhibition of contractions caused by upregulation of β-adrenergic receptor (*ADRB2*) and downregulation of two estrogen receptors (*ESR1*, *ESR2*), an *MTR*, *COX-2*, and prostaglandin (Gao et al., 2019). Some viviparous squamates, *Saiphos equalis, Chalcides ocellatus*, and *Pseudemoia entrecasteauxii*, share some of these expression patterns (*COX-2*, *MTR*, and *ADRB*, respectively) thought to be involved with extended embryonic retention in viviparous *P. vlangalii* (Brandley et al., 2012; Foster et al., 2020; Gao et al., 2019; Griffith et al., 2016). However, no species shared the same profile for these loci as *P. vlangalii*. However, tissue sampling across species was done at different developmental stages across the four studies.

Recently, in humans, the only Classical Major Histocompatibility Antigen (C-MHC) expressed by trophoblasts (specialized placental cells) was associated with parturition when it was discovered that HLA-C is significantly increased during laboring term and preterm placentas compared to non-laboring placentas (Hackmon et al., 2017). The authors suggested a mechanism where fetal HLA-C open conformers on the placenta provoke inflammation of maternal tissues, leading to parturition (Hackmon et al., 2017). Expression of MHC alloantigens, foreign antigens to the host, by fetal cells is also associated with parturition in cows and horses (Benedictusa, Koets & Ruttena, 2015; Davies et al., 2004; Joosten et al., 1991; Rapacz-Leonard et al., 2018). Around one month prior to parturition in cows, endometrial epithelium thins and eventually disappears completely, putting the antigen-presenting trophoblasts (Adams et al., 2007) in contact with maternal connective tissue of the endometrium (Grunert, 1986; Podhalicz-Dzięgielewska et al., 2000). Fetal MHC alloantigens are proposed to promote the loosening of maternal and fetal tissues (Benedictusa et al., 2015; Ginther, 1979). MHC molecules are expressed during gestation and gravidity in some squamates (Murphy & Thompson, 2010) but their role in oviposition or parturition has not yet been considered to my knowledge. Identifying the presence or absence of MHC alloantigens on embryonic tissues before and during parturition across more diverse taxa may reveal how ubiquitous the influence of embryonic MHC molecules is on parturition and oviposition.

Involution (phase 3) occurs after the embryo(s) is released. In eutherian involution, the placenta detaches, and the uterus shrinks. This is supported by actions of prostaglandins (Husslein, 1984) and oxytocin (Terzidou, 2007). It seems unlikely for processes of involution to be related to evolutionary changes to the length of embryonic retention.

(2) Unique qualities of oviposition and parturition in birds and non-avian reptiles

Circadian rhythm and temperature-specific influences on reproduction may uniquely influence the molecular processes of oviposition and parturition in birds and non-avian reptiles, respectively. The physiology of avian oviposition is dependent on a circadian schedule (Williams, 2012). A general model of an “open period”, when eggs are laid are separated by “laying gaps” (Williams, 2012). Chicken ovulation and oviposition cycles leave an 8-hour open period where luteinizing hormone (LH) and progesterone can surge, initiating ovulation and continuing the cycle. At the extreme, the ancient murrelet, *Synthliboramphus antiquus*, oviposits a two-egg clutch on seven-day intervals (Williams, 2012). Longer laying intervals have been associated with longer intervals between initiation of yolk development (Astheimer & Grau, 1990).

Differing from birds, oviparous squamates retain eggs longer than the ovarian cycle (Tinkle & Gibbons, 1977). This suggests that oviparous squamates may rely on different molecular mechanisms to support oviposition than birds. Non-avian reptiles are unique in that they are the only ectothermic amniotes. This makes them uniquely reliant on temperature for embryonic retention and associated embryonic signaling to indicate the stage of embryonic development.

(3) Pre-term birth & embryonic retention mechanisms

The literature on pre-term birth may be a fruitful avenue of research to inform understanding on the evolutionary genomics of embryonic retention length. Rapid increases in CRH are associated with preterm labor in humans, and slow increases are associated with post-term labor (Ellis et al., 2002; Torricelli et al., 2006). Injections of RU486, a progesterone receptor (PGR) antagonist, promoted pre-term labor in rhesus macaques but the progression of physiological activity differed from normal parturition (Haluska et al., 1987). Examining homologs of loci involved with human pre-term birth in squamate taxa may be illuminating.

In humans, pregnancy loss from infection follows distorted ratios of immune factors at the maternal-fetal interface (Arenas-Hernandez et al., 2016; Chaturvedi et al., 2015; Chattopadhyay et al., 2010). Future research on the evolution of lengthened embryonic retention to support viviparity may benefit from exploring ratios of immune cells in the uterus and embryonic tissues during term and pre-term pregnancy in squamates. I direct researchers to the literature on the reptile immune system and immune cell ratios at the maternal fetal interface during term and pre-term mammalian pregnancy for further exploration (Yang et al., 2019; Zimmerman, 2010, 2020).

(4) Discussion and future directions—embryonic retention and parity mode evolution

The physiological processes involved with the start of gestation (maternal recognition of pregnancy) and the end of gestation (oviposition and parturition) in birds and mammals provide insights into the loci squamates may co-opt to alter length of embryonic retention during transitions between parity modes. Given the role of uterine overdistention in mammalian parturition, a lack of uterine overdistention may be one hurdle for reversals back to oviparity.

Unsurprisingly, hormones like estrogen and progesterone, play important roles in oviposition/parturition across amniotes. Further processes to be examined in squamates include signaling of homologous loci for MRP, placental progesterone production, novel pathways for biosynthesis of progesterone, fluctuating ratios of progesterone receptors, the lifespan of the corpus luteum across a broader range of taxa, production and circulation of homologs for AVT and CRH or other similarly structured loci, expression of fetal alloantigens and inflammatory cytokines in utero, and the influence of uterine overdistention on contractions. Understanding the evolutionary physiology and genomics of embryonic retention in oviparous and viviparous squamates will benefit from focused attention on reproductively bimodal species (Whittington et al., 2022) and from genomics/physiological research across more taxa that vary in reproductive modes.

III. Eggshell Deposition

Oviparous amniotic embryos develop within an eggshell that is at least partially mineralized, whereas viviparous embryos generally do not. Evolutionary transitions between parity modes therefore requires changes to the process of eggshell deposition. Some have suggested that the amniote eggshell originated multiple times (Aoki, 1993). The history of research on the evolutionary morphology of the amniote egg is important for future comparative research (Blackburn & Stewart, 2021). Primarily, the eggshell serves as physical protection and calcium reserve (Stewart & Ecay 2010; Stewart et al., 2009). The eggshell matrix contains immune properties (Mine et al., 2003) and pores that enable gas exchange and water uptake (Packard et al., 1982).

Birds have hard calcareous eggshells. Other than two lineages of geckos with hard shells, oviparous squamates have parchment-shelled eggs with a thin layer of calcium deposits on the outer surface of the shell membrane (Blackburn & Stewart, 2021; Choi et al., 2018). Monotremes have an eggshell but far less has been documented about its structure compared to other amniotes (Legendre et al., 2022). The structure and physiological mechanisms involved with eggshell calcification are most well resolved in birds (Choi et al., 2018; Francesch et al., 1997; Jonchere et al., 2010, 2012; Mikšík et al., 2010; Rose-Martel, Du, & Hincke, 2012). Homologous processes do not support eggshell deposition in tuatara or squamates (Choi et al., 2018). Viviparous squamates lack an eggshell, absorb the eggshell during gestation, or have a thin layer of calcium deposits (Schleich & Kästle, 1988; Stewart et al., 2013). Evolutionary loss of the eggshell may evolve through gradual thinning. However, this does not explain highly labile transitions, within a single clutch for example (Laird et al., 2019). Other evolutionarily labile traits in squamates include venom and limb evolution (Sites et al., 2011).

(1) Mineral composition of eggshells

The different mineral compositions of eggshells across amniotes may provide insight into the differing physiological conditions and evolutionary histories under which they are formed (Table 1.1). Taxa use a polymorph of calcium carbonate—calcite, aragonite or vaterite—to develop the eggshell (Hincke et al., 2012). Amorphous calcium carbonate (ACC) is a transient non-crystalline precursor phase of calcite and aragonite that is important for many calcification processes in invertebrates (Hincke et al., 2012). It was recently shown to control avian eggshell mineralization (Rodríguez-Navarro et al., 2015).

In birds, the organic components of uterine fluid promote the formation of calcite (Hernández-Hernández, Gomez-Morales et al., 2008; Hernández-Hernández, Rodriguez, et al., 2008; Nys, 2008). Most amniotes use this polymorph (Hernández-Hernández, Gomez-Morales et al., 2008; Hernández-Hernández, Rodriguez, et al., 2008; Legendre et al., 2022; Nys, 2008). However, turtle eggshells are predominately developed with aragonite (Mikhailov, 1997). The eggshell of most squamates consists of an inner fibrous protein layer overlain by calcium carbonate that can be a single layer or scattered crystals (Packard & DeMarco, 1991).

There are differing accounts on the microstructure of monotreme eggshells and further studies are needed to determine secondary homology (Legendre et al., 2022). Nonetheless, they are described as proteinaceous, permeable, and flexible (Hughes, 1984). Marsupials lack an eggshell but have an eggshell coat that is secreted by the epithelial cells and endometrial glands early on in embryonic development prior to implantation (Roberts et al., 1994; Roberts & Breed, 1996). This may provide a boundary that immunologically protects the embryo (Roberts & Breed, 1996).

Table 1.1. Amniote Eggshell Ultrastructures

Taxon	**Eggshell ultrastructure**
Testudoid (turtle)	Radial aragonite with organic core at base
Crocodiloid	Tabular, arranged in wedges of calcite with no organic core
Squamate	Two types:

	- rigid-shelled eggs with well-developed crystalline layer (dibamid and gekkonid lizards). Stem-like crystals grow downward making for a rigid shell - flexible-shelled eggs with parchment-like shell of fibrils overlaid with little thin crystal caps or no crystalline material (other squamates)
Ornithoid (avian)	Calcite with a clear boundary between lower and upper parts. Mammillary layer defines the lower portion of the shell, with calcite crystals that radiate upwards
Monotreme	Distensible, permeable and highly proteinaceous

Note: Adapted from Choi et al., (2018); Frankenberg & Renfree, (2018); Hallman & Griebeler, (2015); Hincke et al., (2012); Schleich & Kästle, (1988); Trauth & Fagerberg, (1984)

(2) Uterine glands & the evolution of parity modes

Eggshell deposition occurs in the uterus where the uterine glands secrete precursors of the eggshell (Girling, 2002; Guillette, Fox & Palmer, 1989; Jonchere et al., 2010; Nys et al., 2004; Picariello et al., 1989; Stewart & Ecay, 2010). Uterine glands are critical for gravidity/gestation in both oviparous and viviparous amniotes (Braz et al., 2018; Burton et al., 2002; Cooke et al., 2013). For example, in humans, uterine glands provide histiotrophic nutrition to the early embryo (Burton et al., 2002). In reptiles, precursors for the proteinaceous eggshell membrane are secreted by the uterine glands (Corso, Delitala & Carcupino, 2000; Heulin et al., 2005; Palmer et al., 1993). Calcium secretion can also involve uterine epithelial cells (Herbert, Thompson & Lindsay, 2006; Thompson et al., 2007). Uterine epithelium of the soft-shelled turtle, *Lissemys punctata punctata*, and the eastern collard skink, *Chrotaphytus collaris* (Guillette et al.,1989; Sarkar et al., 1995), stain positive for calcium.

Viviparous squamates have an absent or reduced eggshell membrane to facilitate gas exchange (Blackburn, 1993; Braz et al., 2018; Corso et al., 2000; Girling et al., 1997; Guillette & Jones, 1985; Heulin, 1990; Hoffman, 1970; Palmer et al., 1993; Qualls, 1996; Stewart, 1990). Some squamates are encased in the thin membrane through the entirety of development like the viviparous lizard, *Zootoca vivipara* (Heulin, 1989). Others have the membrane only in the early stages of embryonic development like in garter snakes *Thamnophis radix* and *T. sirtalis*

(Blackburn & Lorenz, 2003). Calcium deposits are detected on the outer surface of the membrane throughout development in other viviparous lizards (Stewart et al., 2013).

The size or density of eggshell glands and their secretory granules correlate with eggshell thickness in several amniotes. In chickens, variation in size, spacing, and neutron density of eggshell glands may be important for eggshell structure (Guillette & Jones, 1985). In the reproductively bimodal lizard, *Zootoca vivipara*, viviparous individuals have a uterine glandular layer that is less developed during the stage of eggshell deposition compared to oviparous individuals (Heulin et al., 2005). Additionally, in *Lerista fragilis,* which lays eggs that hatch within just hours of oviposition, the uterus contains very few mucosal glands (Guillette, 1992). In the fence lizard, *Sceloporus a. aeneus,* the irregular surface of the eggshell was attributed to the irregular spacing of shell glands (Guillette & Jones, 1985). In an oviparous gecko, *Hemidactylus turcicu*s, their eggshell glands have loosely packed secretory granules that produce a hard, calcareous shell (Girling et al., 1998). In another oviparous gecko, *Saltuarius wyberba,* their secretory granules are tightly packed, and their shell is soft and parchmentlike (Girling et al., 1998). In a viviparous relative, *Hoplodactylus maculatus*, there are far fewer eggshell glands, and where there are glands, the secretory granules are smaller and more electron dense (Girling, Cree & Guillette, 1997; Girling, Cree & Guillette, 1998). Smaller eggshell gland size during or after vitellogenesis is also found in other viviparous squamates compared to oviparous counterparts (Braz et al., 2018; Gao et al., 2019; Heulin et al., 2005). In the reproductively bimodal Yellow Bellied Three-toed skink, *Saiphos equalis*, the density of eggshell glands plays a role in eggshell thickness (Stewart et al., 2010). To my knowledge, in monotremes the relationship between eggshell thickness and shell gland size, density or compaction of secretory granules has not been explored.

(3) *Evolutionary implications of the physiology of eggshell formation*

Presumably because of the influence it has on food production, the process of eggshell formation has been studied most extensively in chickens (Hincke et al., 2012). The avian eggshell is formed in a cell-free environment, and it is the fastest calcifying process known to biology (Hincke et al., 2012; Rodríguez-Navarro et al., 2015). During eggshell formation in birds, the egg is bathed in uterine fluid containing a supersaturation of ionized calcium and bicarbonate ions (Nys et al., 1991). Transport of calcium in the uterus correlates with plasma membrane Ca^{2+}-ATPase (*PMCA*) activity and with concentrations of calbindin-D28K within shell gland epithelial cells (Herbert et al., 2006; Wasserman et al., 1991). This leads to the spontaneous precipitation of calcium carbonate into calcite (Hincke et al., 2012). In the oviparous lizard, *Lampropholis guichenoti*, immunofluorescence microscopy revealed activity of *PMCA* in the uterus at the time of eggshell calcification (Herbert et al., 2006; Thompson et al., 2007).

Eggshell deposition begins with the eggshell membrane. Two unciliated cell types in the uterus contribute to eggshell membrane formation in a viviparous skink, *Chalcides ocellatus tiligugu* (Corso et al., 2000). One of these secretes sulfated glycosaminoglycans, forming the amorphous inner component of the shell membrane (Corso et al., 2000). The second cell type secretes acidic glycoproteins, responsible for building the outer layers of the shell membrane (Corso et al., 2000). Simple alveolar glands in the lamina propria secrete collagen fibers (Corso et al., 2000). Inhibition of fiber formation or cross-linking, typically caused by aminopropionitrile or a copper deficiency, causes distorted formations of the eggshell membrane in birds (Arias et al., 1997; Chowdhury & Davis, 1995; Hincke et al., 2012).

Organic aggregates are deposited onto the shell membrane, creating mammillary knobs. Mammillary knobs are a distinct layer between the outer eggshell membrane and the calcified shell matrix layer (Hamilton, 1986). These are characteristic of Archelosaur eggshells (Legendre et al., 2022; Zelenitsky et al., 2002; Zelenitsky & Modesto, 2003). Part of the mammillary knobs, called basal caps, are embedded into the outer eggshell membrane fibers (Tyler, 1965). These basal caps serve as regions of crystal initiation where ACC is deposited (Gautron et al., 2021) and converted into calcite crystals with no intermediate phase (Rodríguez-Navarro et al., 2015). Cones are formed that radiate in all upward directions, extending up to the shell matrix layer (Tyler, 1965). A keratan sulfate proteoglycan, “mammillan”, has been implicated in the composition of mammillary knobs, but it remains uncharacterized (Fernandez et al., 2001; Hincke et al., 2012). The role of homologs of “mammillan” in eggshell formation in squamates may reveal more about the evolutionary history of the eggshell in amniotes.

Parsimony would suggest that all oviparous amniotes shared an ancestral process of eggshell formation. In Archelosaurs (birds, crocodiles, and turtles) the process of eggshell formation occurs from the bottom up as described above. In Lepidosaurs (tuatara and squamates) studied thus far, eggshell formation occurs via a top town process, where crystals grow inward toward the center of the egg (Choi et al., 2018). The strikingly divergent structure and directionality of eggshell formation between Archelosauria and Lepidosauria suggests clade-specific mechanisms arose through genetic drift (Schiffman & Ralph, 2022) or that their eggshells are a result of convergence (Aoki, 1993). An early evolution of viviparity in Lepidosaurs could explain convergent evolution of eggshells. One ancestral state reconstruction estimated an early origin of viviparity in squamates (Pyron & Burbrink, 2014). Two Triassic diapsids (Sauropterygia) may have even been reproductively bimodal (Motani et al., 2014), which is otherwise only known from ten extant squamates (Whittington, 2022). If a version of the avian eggshell was the ancestral microstructure of oviparous amniotes, the loss of basal caps could result in a rapid loss of the eggshell and thus a relatively fast transition to viviparity (the basal cap hypothesis). More information is needed on the eggshell microstructure of early squamates and amniotes to determine the evolutionary history.

In chickens, ovotransferrin is present in the eggshell membrane and basal cap-layer (Gautron, Hincke, Panhéleux et al., 2001). Ovotransferrin promotes the development of elongated crystals (Gautron, Hincke, Panhéleux et al., 2001). The resulting shell matrix is made up of the crystal layer and cuticle (Hamilton, 1986). On the inner portion of the eggshell, it is unclear what prevents growing crystalized cones from extending into the inner membrane or the albumen. Collagen type X has been implicated (Arias et al., 1993, 1997; Hincke et al., 2012). The role of collagen type X in the formation of squamate eggshells is worth further consideration given their top-down process of calcification. The only non-avian eggshell matrix protein, pelovaterin, was identified in the soft-shell turtle (Lakshminarayanan et al., 2005).

Over 500 proteins are found in the chicken eggshell matrix (Mann, Maček, & Olsen, 2006; Mikšík et al., 2007, 2010). Ovocleidin-116 (*OC116*), ovocalyxin-36 (*OCX36* or *BPIFB4*), ovocalyxin-21 (*OCX21*), and ovocleidin-17 (*OC17*) are important for avian eggshell formation (Hernández-Hernández, Gomez-Morales et al., 2008; Jonchere et al., 2010; Tian et al., 2010). For example, ovocalyxin-21 may serve as a chaperone protein along with the protein endoplasmin (ENPL) to facilitate proper folding of the eggshell matrix (Jonchere et al., 2010). *OC116*, *OC36*, *OCX21*, and *OC17* are some of the most differentially expressed genes during eggshell calcification in chickens (Gautron et al., 2007; Hincke et al., 1999, 2012; Jonchere et al., 2010). Originally considered avian-specific, several homologs have now been identified in non-avian reptiles and mammals (Le Roy et al., 2021).

OCX36 and other BPI family B proteins (also called *LPLUNC*s) are now thought to have a common origin in vertebrates with multiple duplication events (Gautron et al., 2007; Tian et al., 2010). Orthologs of *OCX36* are found in Archelosauria (turtles, crocodiles, and birds) and Monotremata (egg-laying mammals) (Le Roy et al., 2021). In birds, *OCX36* plays a role in innate immune responses and is found in high concentrations in the inner eggshell membrane (Gautron et al., 2007, 2011; Tian et al., 2010).

OC116 is homologous to mammalian *MEPE* 539, which plays a role in bone and teeth mineralization (Bardet et al., 2010; Le Roy et al., 2021). In birds, *OC116* influences shell thickness, elastic modulus, and egg shape (Dunn et al., 2009; Le Roy et al., 2021; Romé & Le Roy, 2016). *OC116* was identified in a crocodile, *Crocodylus siamensis*, proteome (Le Roy et al., 2021; Mikšík et al., 2018). Synteny analysis across seven turtle species and platypus (*Ornithorhynchus anatinus*) revealed absence of *MEPE/OC116* (Le Roy et al., 2021).

Associating expression patterns with the timing of eggshell deposition has revealed squamate-specific candidates for shell formation. One hundred and forty-eight genes were highly expressed in the uterus of the oviparous lizard, *Phrynocephalus przewalskii*, during the stage of eggshell gland formation (Gao et al., 2019). Seven of these genes—*HYPOU1, KCNMA1, P4HB, PRDX4, PTN, RRBP1 and TRAM1*—are also purported to be important for eggshell calcification in chickens (Brionne et al., 2014). Given this overlap across species that diverged over 300 million years ago (Shen et al., 2011), these are excellent candidates for further exploration. Other genes and lncRNAS are purported to be important for the quality of eggshell formation in hens—*FGF14, COL25A1, GPX8,* and several members of the solute carrier protein (*SLC*) gene family

(Yang et al., 2020). Research into lncRNAs activity in squamate reproductive tissues during embryonic development represents another valuable track for research.

During oviparous gravidity in *Saiphos equalis* two GO terms associated with calcium homeostasis are enriched by the set of upregulated genes (Foster et al., 2020). However, most of these genes are associated with regular cellular responses to calcium and even those associated with calcium transport are upregulated in both early and late stages of gravidity (Foster et al., 2020). Their role in eggshell formation in this uniquely labile species is therefore ambiguous.

In oviparous individuals of another reproductively bimodal skink, *Lerista bougainvillii*, only two genes are significantly differentially expressed in the gravid uterine tissue compared to non-gravid uterine tissue (Griffith et al., 2016). No genes are differentially expressed in the gravid uterine tissue of the oviparous garden skink, *Lampropholis guichenoti*, compared to non-gravid uterine tissue (Griffith et al., 2016). The genes involved in the shelling process in these species may not involve changes in expression from the non-gravid state. However, this study only measured gene expression at one developmental stage, making it difficult to infer if regulatory changes influence eggshell formation.

In an oviparous agama lizard, *Phrynocephalus przewalskii*, several genes were associated with eggshell gland development (Gao et al., 2019), an important process for secretion of eggshell precursors. Three of the 148 genes highly expressed in *P. przewalskii* were also highly expressed a viviparous relative, *P. vlangalii*, at this time, suggesting differences in eggshell gland development requires regulatory changes to dozens of genes (Gao et al., 2019). Supplementary table 2 compares loci associated with eggshell formation and shell gland development in squamates to that of birds. A wealth of candidate loci for eggshell deposition are differentially expressed in viviparous squamates during gestation (Supplementary Table 2).

These genes may function in calcium transport through the chorioallantois instead (Stewart & Ecay, 2010).

The dissimilarity in uterine gene expression profiles across lizards during gravidity suggests there may be multiple ways oviparous squamates shell their eggs. Given the variation already observed, the physiology of eggshell deposition in squamates should be considered in a phylogenetic context and under the different evolutionary history inferred by ancestral state reconstructions (Blackburn, 1999; de Fraipont et al., 1996; Griffith et al., 2015; Harrington & Reeder, 2017; Pyron & Burbrink, 2014).

(4) Pleiotropy of genes and proteins involved with eggshell deposition

Some genes associated with eggshell deposition have pleiotropic effects within species or have different effects in oviparous vs. viviparous amniotes. Osteopontin (*SPP1*) is found in bone and kidneys, and transports calcium to other tissues in the body (Pines et al., 1995). It is highly expressed in the chicken uterus during calcification (Jonchere et al., 2010) but supports pregnancy recognition and implantation in sheep (Bazer et al., 2011). Improper functioning of *SPP1* in the uterus leads to cracked and abnormal shells (Arazi et al., 2009; Hincke et al., 2008).

When expressed in the uterus, some bone morphogenic protein-coding genes (*BMP*s) aid eggshell calcification (Jonchere et al., 2010). BMPs are part of the *TGF-β* superfamily and are involved with the formation of new cartilage and bone, and with biomineralization in corals and mollusks (Canalis et al., 2003; Lelong et al., 2000; Zoccola et al., 2009). Chordin (*CHRD*) is an antagonist of the *BMP* pathway. *BMP*-binding endothelial regulatory protein (*BMPER*) and *CHRD* are expressed in the chicken uterus during the stage of eggshell calcification (Jonchere et al. 2010). Regulation of *BMPs* by *CHRD* is essential for early embryogenesis and adult homoeostasis.

BMPER and seven *BMP*s are expressed during gestation in *Chalcides ocellatus*, a viviparous skink (Brandley et al., 2012). Most of these are upregulated (Brandley et al. 2012). *BMP* genes are expressed during both gravidity and non-gravidity in oviparous *Lerista bougainvillii* and *Lampropholis guichenoti* (Griffith et al., 2016). *BMP2* is upregulated in oviparous late gestation compared to viviparous late gestation in the reproductively bimodal lizard, *Saiphos equalis* (Foster et al., 2020).

Differential expression of *BMPR1B* is associated with differences in eggshell quality in chickens (Yang et al., 2020). Another study associated stage-specific high-expression of *BMPR1B* with the stage corresponding to extended embryonic retention and placentation in *Phrynocephalus vlangalii* (Gao et al., 2019). They identified a co-expression network of highly expressed genes, including *BMPR1B*, that they associated with placentation (Gao et al., 2019). *BMPR1B* also reaches significant levels of differential expression in uterine tissues of other gestating viviparous lizards, *Chalcides ocellatus* and *Pseudemoia entrecasteauxii,* compared to non-gestational uterine tissue (Brandley et al., 2012; Griffith et al., 2016). Receptors for *BMP*s are also expressed in the uterus during gestation in other viviparous lizards, *Phrynocephalus vlangalii* and *Pseudemoia entrecasteauxii* (Gao et al., 2019; Griffith et al., 2016).

The potential role of these genes in squamate eggshell formation remains unclear. *BMP*s influence on dorsal-ventral axis patterning during early embryogenesis and growth of skeletal structures in post-natal tissues (Medeiros & Crump, 2012). It may be difficult to disentangle their roles in embryonic development, placental development, and eggshell deposition. Future research on them may inform scientific understanding of parity mode evolution.

SLIT genes are purported to be involved with folding the eggshell matrix in chickens (Jonchere et al., 2010). The *SLIT2* gene encodes a protein that provides a structural framework for protein-protein interactions (Jonchere et al., 2010; Marillat et al., 2002). *SLIT2* is among the 50 most downregulated genes in the uterus during pregnancy in the viviparous African ocellated skink, *Chalcides ocellatus,* compared to non-pregnancy (Brandley et al., 2012). However, in the uterus of the yolk-sac placenta in the viviparous skink, *Pseudemoia entrecasteauxii*, *SLIT2* is upregulated compared to non-reproductive uterine tissue (Griffith et al., 2016). *SLIT3* is differentially expressed during the stage of placentation in the viviparous agama lizard, *Phrynocephalus vlangalii* (Gao et al., 2019). *SLIT* genes also play a role in axonal pathfinding and neuronal migration in rats (Marillat et al., 2002). *SLIT2* was associated with reproduction in humans (Chen, Chu et al., 2015). Future research on their function in squamate reproductive tissues during embryonic development may reveal if *SLIT* genes influence parity eggshell formation.

Podocalyxin (*PODXL*) is a sialoprotein associated with eggshell calcification in chickens (Jonchere et al., 2010). However, in a viviparous agama lizard, *Phrynocephalus vlangalii,* a weighted gene correlation network analysis associated *PODXL* with uterine structural changes (Gao et al., 2019). The gene may play a role in placentation in these species given that it was also differentially expressed in the uterus during the stage of placentation (Gao et al., 2019). Interestingly, *PODXL* is downregulated in the uterus of the yolk-sac placenta in another viviparous skink, *Pseudemoia entrecasteauxii* (Griffith et al., 2016). Based on its role in chickens and *P. vlangalii*, *PODXL* is a good candidate for further research on the molecular evolution of eggshell formation and placentation in squamates.

(5) Eggshell formation termination

When eggshell formation is terminated, the egg is still bathed in the supersaturated calcium and bicarbonate ion fluid (Hincke et al., 2012). Some component(s) of the terminal uterine fluid may prevent precipitation of calcium carbonate (Gautron, Hincke & Nys, 1997), such as phosphate anions (Lin & Singer, 2005). The presence of phosphorous in the superficial layers of the chicken shell suggest that phosphorous may be the factor preventing the deposition of calcite crystals in the terminal stage (Blackburn, 2000, 1992; Stewart, 2013). Additionally, the high concentration of *OCX32* in the outer eggshell and cuticle, suggest that the gene may inhibit proteinaceous crystal growth in the terminal stage of eggshell calcification (Gautron, Hincke, Mann et al., 2001). It is informative to both viviparous reproduction and the basal cap hypothesis that exposure to precursors of the eggshell does not necessitate eggshell deposition. The influence of phosphate anions and *OCX32* on inhibition of calcium carbonate precipitation on the eggshell membrane of viviparous squamate embryos has not been examined to my knowledge.

(6) Rotating the egg for eggshell deposition

Oviparous amniotes rotate the egg for calcium deposition and viviparous mammals rotate the embryos for parturition. One hurdle to reversing back to oviparity may be re-evolving oviductal musculature and rotation of the egg for shell deposition (Griffith et al., 2015). However, given the complex muscular of the uterus that allows for multidirectional force for parturition, it is difficult to determine the degree of difficulty for re-evolving egg-rotation. Cadherins (Wu et al., 2011) and hormonal signaling (Biazik et al., 2012) may influence uterine elasticity and its ability to rotate the developing embryo. Genes that enrich the GO term for “voltage-gated calcium channel activity” are also useful candidates for investigating uterine rotation associated with eggshell formation because voltage-gated calcium channels effect the action potential of cells and can cause muscle contractions.

(7) Discussion & future directions—eggshell deposition and parity mode evolution

The process of eggshell deposition is more resolved in birds compared to non-avian reptiles and monotremes (Choi et al., 2018; Frankenberg & Renfree 2018; Hallman et al., 2015; Schleich & Kästle 1988). As more whole genomes become accessible, it would be interesting to explore if non-avian amniotes utilize a similar genetic toolkit for eggshell deposition. I described some overlaps that can be gleaned from the literature, which prove as curious candidates for further research. Of particular interest are ovacalyxins and ovoclideins (*OCX36*, *OC116* and *OC17*) (Le Roy et al., 2021), and the homologs for avian eggshell matrix proteins identified in the *Anolis carolinensis* genome (Alföldi et al., 2011; Tian et al., 2010). Some genes purported to be important for eggshell calcification in chickens were also associated with eggshell gland formation in an oviparous lizard, *Phrynocephalus przewalskii—HYPOU1, KCNMA1, P4HB, PRDX4, PTN, RRBP1* and *TRAM1* (Brionne et al., 2014; Gao et al., 2019).

It is unclear why Archelosaurs and Lepidosaurs evolved divergent processes for forming their eggshells, which are also morphologically dissimilar. One possibility is that viviparity evolved early in the history of Lepidosaurs, as estimated for squamates (Pyron & Burbrink, 2014). Theoretically, it should be relatively simple to transition from oviparity to viviparity if the ancestral oviparous amniotes had an eggshell microstructure like that of dinosaurs and modern birds. Under that scenario, alteration to basal caps in the mammillary layer would prevent the deposition of calcium before it begins (basal cap hypothesis). Alternatives to this possibility are that divergent eggshells and eggshell deposition processes evolved through selective pressure, genetic drift, or both.

IV. Placentation & Transport of Embryonic Water, Gas, and Nutrients

The evolutionary pressures on fluid allocation, gas exchange and nutrient transport should differ between oviparous and viviparous taxa because their sources of all or some of these resources differ (Blackburn, 1992; Bonnet et al., 2001; Bonnet, Naulleau & Shine, 2017; van Dyke et al., 2014). In viviparity, maternal gas and water are accessed through the chorioallantois, which is especially important in the latter half of development (van Dyke et al., 2014; Carter, 2012). Nutrients can be available from the yolk, maternal transfer, or both yolk and maternal transfer. Where amniotes other than squamates can rely on the albumen for fluid allocation, squamates lack an albumen (Blackburn & Stewart, 2021). Their eggshells are specially adapted to exchange fluids with the environment (Blackburn & Stewart, 2021). Oviparous taxa regulate gas exchange through pores in their eggshells (Badham, 1971; Brown & Shine 2005; Ji & Du, 2001; Packard, 1991).

(1) Anatomy & methods of water, gas & nutrient provisioning

The embryonic membranes regulate embryonic fluid transport, nutrient supply, respiration, immunity, and waste (Brace, 1997; Burton & Tullett, 1985; Ferner & Mess, 2011; Ostergard, 1970; Packard & Packard, 1980). Fluids are important for the developing embryo because they prevent desiccation and compression (Ferner & Mess, 2011; Ostergard, 1970; Packard & Packard, 1980). Over-abundance or under abundance of embryonic sac fluids leads to reproductive failure (Chamberlain et al., 1984; Fedakâr et al., 2016; Hadi, Hodson & Strickland, 1994; Mercer et al., 1984). Without substantial amounts of water, converting yolk nutrients to somatic tissue is impossible (Noble, 1991; Packard, 1991; Thompson et al., 2004). Oxygen flux in embryonic mammals is largely determined by oxygen-diffusing capacity of the placenta, the rates of blood flow in the umbilical and uterine arteries, and the oxygen capacities and affinities of fetal and maternal blood (Carter, 2009). Reptilian and mammalian blood vessels differ in basic characteristics such as capillary density, capillary surface, and oxygen diffusion gradients (Pough, 1980).

Patterns of embryonic nutrient exchange can be broadly categorized into lecithotrophy, obtaining nutrients from the yolk, and placentrophy or matrotrophy, obtaining nutrients from the mother. Taxa belonging to Archelosauridae are lecithotrophic. The ancestral state of mammals was most likely oviparous matrotrophy that later evolved into viviparous matrotrophy in therians (Blackburn, 2005). The ancestral state of reptiles was likely lecithotrophy (Blackburn, 2005). Most viviparous squamates are lecithotrophic, some are lecithotrophic and matrotrophic, and a few have specializations for substantial matrotrophy (Blackburn, 1985b; Stewart & Thompson, 1993; Thompson, Stewart et al., 1999). Even lecithotrophic viviparous squamates appear to exhibit some degree of matrotrophic nutrient provisioning (Blackburn, 2005; Stewart, 1990, 2020; Swain & Jones, 1997, 2000; Thompson, Stewart et al., 1999; Thompson & Speake, 2006). Reversals may be most unlikely in lineages that have specialized placentas for substantial nutrient exchange because they would need to re-evolve lecithotrophy. Highly matrotrophic squamates are extremely rare (Blackburn, 2015a).

(2) Evolutionary history of yolk-sac formation and yolk processing

Vitellogenesis is the process of yolk formation in the oocyte, providing the embryo with a valuable source of nutrients, primarily through the accumulation of precursor proteins to yolk, vitellogenins. Vitellogenin is produced in the liver, called hepatic vitellogenesis, and transported to the maturing ovum (Ho, 1987). Vitellogenins were lost in all mammals except monotremes (Brawand, Wahli & Kaessmann, 2008). They are a primary source of nutrition for other amniotes. Functionally similar to vitellogenin, caseins have persisted in all mammalian milks (Brawand et al., 2008). Glycodelin was also detected in the epithelium of the secondary yolk-sac of humans during the first trimester, suggesting the organ may retain a role in nutrient provisioning during early pregnancy (Burton et al., 2002) but otherwise does not contribute nutritionally. In the yolk-sac of bats, dogs, and non-human primates the mesoderm derived layer is absorptive and may transfer substances from the exocoelomic cavity (Enders et al., 1976; Freyer & Renfree, 2009; King & Wilson, 1983; Lee et al., 1983).

The morphology of the yolk-sac and process of vitellogenesis differs between birds and non-avian reptiles. In birds, during the process of meroblastic cleavage, the zygote’s cells divide while the yolk component does not. The yolk forms a large, fluid, non-cellularized mass surrounded by the extraembryonic yolk sac. The formation of the yolk-sac placenta in birds has the following pattern—first the bilaminar omphalopleure forms and then trilaminar omphalopleure; blood vessels move into folds of the extraembryonic endoderm, becoming stratified epithelium; the folds carrying the blood vessels reach the peripheral regions of the yolk only and the center of the yolk mass remains uncellularized (Starck, 2021). Intensive development of hemopoietic tissue surrounding the blood vessels during most of embryonic development, thus far, appears to be unique to birds (Starck, 2021). Compared to non-avian sauropsids, the unique pattern of yolk processing in birds facilitates faster embryonic development (Blackburn, 2021).

Ancestral sauropsid morphology and yolk processing likely resembled that of non-avian sauropsids (Blackburn, 2021). A series of recent papers on non-avian sauropods, covering species of snakes, lizards, crocodiles, and turtles, indicate that these taxa utilize similar developmental pathways of yolk-sac formation and yolk processing that differs from birds (Blackburn, 2021; Blackburn et al., 2019; Elinson et al., 2014; Elinson & Stewart 2014; Stinnett et al., 2011). Across these taxa, a bilaminar/trilaminar omphalopleure overgrows the yolk mass, and the yolk mass gets invaded by proliferating endodermal cells that phagocytose the yolk material. These cells form clumps, progressively filling the yolk mass. Small blood vessels derived from yolk sac vasculature invade the yolk sac cavity and the endodermal cells arrange in monolayers around these vessels, forming “spaghetti bands” (Blackburn, 2021). The yolk sac of *Pantherophis guttatus* and other non-avian sauropsids may serve as models for the transition between the egg of anamniotes and amniotes (Elinson & Stewart, 2014; Elinson et al., 2014)

A major difference between avian and non-avian sauropsid yolk-sac formation is therefore the morphology and extent of vascularization and cellularization in the yolk sac cavity (Starck, 2021). Birds have a yolk-sac with absorptive endodermal lining that digests nutrients and send them into blood circulation (Starck, 2021) whereas snakes, lizards, turtles, and crocodilians have a yolk sac that becomes invaded by endodermal cells that proliferate and phagocytose yolk material (Blackburn, 2021). In these taxa, yolk material becomes cellularized, digested, and transported by vitelline vessels to the developing embryo (Blackburn, 2021). Factors involved with cellularization of the yolk-sac are proposed to include cell cycle regulators and structural proteins (Elinson et al., 2014). Generation of these cells are suspected to be reliant on processes of angiogenesis and are likely transcriptionally active (Elinson et al., 2014).

As discussed in a previous section, progesterone inhibits myometrial contractility, but it also inhibits estrogen-induced hepatic vitellogenin synthesis (Custodia-Lora, Novillo, & Callard, 2004; Callard et al., 1992). Variable progesterone concentrations in circulation throughout gestation in viviparous squamates may reflect a trade-off to allow estrogen expression to support hepatic vitellogenin synthesis during embryonic development, thus supporting nutrient provisioning during the lengthened embryonic retention. Although hepatic vitellogenesis usually ceases during gestation, vitellogenin synthesis and mother-to-embryo transfer was detected in one viviparous fish, *Xenotoca eiseni*, during gestation (Iida et al., 2019). Future research should consider the timing of vitellogenin synthesis throughout the reproductive cycle in gestating and non-gestating viviparous squamates to investigate this further.

(3) Evolutionary history of placentrophy in mammals & squamates

Traditionally, it was thought that placentrophy evolved after viviparity in squamates (Packard, Tracy, & Roth, 1977; Shine & Bull, 1979). Further research demonstrated that placentrophy and viviparity evolved simultaneously (incipient matrotrophy) in mammals and may have in squamates (Blackburn, 1985, 1992, 2005, 2006; Stewart & Ecay, 2010). The incipient matrotrophy model relies on evidence that 1) uterine provisioning of nutrients predates the origin of viviparity (Blackburn 1985, 1992, 2006), 2) uterine and embryonic tissues have a close anatomical and physiological association in viviparous taxa and 3) some degree of placental transfer of organic and inorganic molecules is common in all viviparous taxa (Stewart & Ecay, 2010). In squamates, the potential for incipient matrotrophy and evolution of placentrophy after viviparity is supported (Stewart & Ecay, 2010). Facultative placental nutrient provisioning and incipient matrotrophy may have driven the evolution of squamates with substantial matrotrophic nutrient provisioning (Stewart, 2020; Swain & Jones, 2000).

Placentation and implantation are not homologous in mammals compared to squamates (Griffith, van Dyke & Thompson, 2013). Several placental specializations for gas and nutrient exchange are unique to mammals including erosion of the uterine mucosa, extensively invasive implantation, hemochorial contact, retention of a vascularized choriovitelline membrane, and countercurrent patterns of blood flow (Blackburn, 2005). This enables extensive exchange of nutrients in addition to water and gas. The vast majority of viviparous squamates have the most superficial type of chorioallantoic placenta called epitheliochorial placenta (Blackburn 1993, 2005; Thompson et al., 2004). They use this primarily for gas exchange (Thompson et al., 2004).

Nutrient provisioning through placentrophy is obligate for embryonic development in only five lineages of squamates, all of which are scincid lizards (Blackburn, 2000; Flemming & Blackburn, 2003; Ramírez-Pinilla et al., 2011). *Pseudemoia pagenstecheri,* a lizard with a highly specialized placenta, out-performs lecithotrophic oviparous close relatives in the relative amount of nutrients it transfers to the embryo (Stewart et al., 2009). Some *Mabuya* lizards have highly specialized placenta, relying almost entirely on maternally supplied materials (Thompson & Speake, 2002). *Pseudemoia entrecasteauxii* is a moderately matrotrophic viviparous lizard, with roughly half of embryonic nutrient uptake from the yolk and half through a specialized cyto-epitheliochorial placenta (Adams et al., 2005; Speake et al., 2004; Stewart & Thompson, 1993, 2009). Specializations of the chorioallantoic placenta for nutrient provisioning in some squamates include elaborate specializations for uterine secretion and absorption, including placentomes, chorionic areolae, hypertrophied uterine mucosa, and chorionic epithelia modified for absorption (Blackburn, 2005).

Mammalian placenta-specific genes have deep origins in vertebrates (Rawn & Cross, 2008). Placentation to support viviparity likely employs genes that are ancestral to the chorioallantois. However, one study that looked at placentation and gene expression across a small sample of divergent amniotes found only one gene with a placentrophy-specific pattern of gene expression, *DIO3* (Griffith, Brandley et al., 2017). In mammals, this is an imprinted gene and preferentially paternally expressed. The authors suggest that the gene may increase offspring resource uptake during pregnancy in the horse and a viviparous lizard, *Pseudemoia entrecasteauxii*, where it is recruited to the placenta (Griffith, Brandley et al., 2017).

(4) Squamate viviparity eggshells, and gas exchange

In squamates, specializations for gas exchange across the chorioallantoic placenta include decreased diffusion distance between maternal and fetal capillaries, uterine vascularity, shell membrane deterioration, and modifications of both fetal and maternal blood properties (Attaway, 2000; Blackburn, 1998, 2005; Blackburn & Lorenz, 2003; Blackburn & Vitt, 2002; Stewart and Brasch, 2003). Absence of the eggshell may be necessary for adequate gas exchange during viviparous gestation. However, in some viviparous squamates and oviparous squamates with prolonged egg retention the eggshell is considered part of the placenta (Linville et al., 2010; Stewart et al., 2013). Thus, a calcified eggshells remains compatible with viviparity, at least in these lineages. Pores in the eggshell may support sufficient gas and fluid exchange in viviparous squamates as they do for oviparous eggs.

(5) Loci involved with embryonic water, gas, and nutrient exchange

Water transport in animals is regulated by a family of molecular water channels called aquaporins (*AQ*s or *AQP*s) (Borgnia et al., 1999). In humans, *AQP1, AQP3, AQP4, AQP8* and *AQP9* are found in the placenta but further research is needed to understand how these influence water fluxes between maternal and fetal tissues (Damiano, 2011). Transcriptomic analysis on uterine tissue of the gestating, viviparous skink, *Chalcides ocellatus*, reveal differential expression of *AQP1, AQP3, AQP5, AQP6, AQP8, AQP9* and *AQP11* when compared to non-gestating uteruses (Brandley et al., 2012). In birds, *AQP1* is expressed in the chorioallantoic membrane, and it is suggested to influence angiogenesis throughout embryonic development (Ribatti et al., 2002). In a viviparous lizard, *Pseudemoia entrecasteauxii, AQP8* and *AQP9* were more highly expressed in the chorioallantoic placenta compared to the yolk-sac placenta (Griffith et al., 2016). During gestation and gravidity in both oviparous and viviparous populations of the reproductively bimodal skink, *Saiphos equalis*, several genes involved with water homeostasis are upregulated including *AQP1, AQP3* and *AQP12B* (Foster et al., 2020). In uteruses of *Saiphos equalis, AQP5* and *AQP8* are upregulated during oviparous late gestation compared to viviparous late gestation. In sheep, *AQP3* is differentially expressed during gestation, where it serves a dual role of water transport to the embryo and fetal urea export (Johnston et al., 2000). This is similar to the function of *AQP9* in humans (Damiano, 2011). Immunocytochemistry reveals that *AQP1* and *AQP3* are expressed in the uterus of the highly placentrophic South American scincid lizard, *Mabuya sp.* (Wooding et al., 2010).

Some molecules are implicated in the regulation of aquaporins including insulin (INS), human chorionic gonadotropin (HcG), cyclic adenosine monophosphate (cAMP) and cystic fibrosis transmembrane conductance regulator (CFTR) (Castro-Parodi et al., 2008; Damiano, 2011). Genes predicted to be involved with reproduction in *Anolis carolinensis* are enriched for the GO term for cAMP-mediated signaling (Alföldi, Di Palma, et al., 2011). Further comparative research should be done to elucidate the functional differences of aquaporins in oviparous and viviparous amniotes and how they relate to the differing conditions under which these embryos develop.

Genes involved embryonic oxygen transport precede the origin of amniotes. Hemoproteins arose in evolutionary history well before they were used for placental oxygen transfer (Hardison 1998). In mammals, adult (Alpha: HBA; Beta: HBB, HBD) and embryonic hemoglobins (Alpha: HBZ, HBA; Beta: HBE, HBG, and HBH) are involved with oxygen transport (Carter, 2012). Some of these are unique to eutherian mammals following a series of duplication events (Opazo et al., 2008). However, fetal hemoglobins are found in turtles, lizards, and snakes (Pough, 1980). HBA, HBB and HBM are all significantly downregulated in the uterine tissue of the viviparous African Ocellated Skink, *Chalcides ocellatus*, during gestation compared to non-gestation (Brandley et al., 2012). The oxygen demands of reptile embryos are relatively low until stage 30, when most oviparous taxa oviposit (Shine & Thompson, 2006). In viviparous and oviparous species with long egg retention, embryonic demand for maternal provision of oxygen and removal of CO_2 increases at this stage (Ferguson & Deeming, 1991).

Improper water, gas and nutrient exchange can occur due to poor chorioallantoic blood flow (Wootton et al., 1977). Thus, viviparous taxa require greater degrees of vascularization and vasodilation to facilitate enhanced requirements for maternal resources compared to oviparous taxa. Rather than increasing the size of the placenta, increasingly dense blood vessels can support fetal growth without compromising space for embryonic growth as occurs in some pigs (Ford, 1997; Vonnahme et al., 2002). Embryonic vascularization and vasodilation are dependent on signals from the endoderm (Jin et al., 2005; Vokes & Krieg, 2002; Wilt, 1965). In oviparous individuals of *Saiphos equalis*, populations with extended egg retention, there is expansion of the uterine vascular bed and thickening of the chorioallantoic tissue that supports increased embryonic growth in the later portion of oviparous gravidity (Parker et al., 2010). In the viviparous scincid lizard, *Eulamprus quoyii*, angiogenesis, the formation of new blood vessels, and expansion of the vessel-dense elliptical area of the uterus is associated with supporting increased embryonic oxygen demand (Murphy et al., 2010).

Several protein-coding genes are known to be involved with angiogenesis, vascularization, and vasodilation in utero. One study that examined expression patterns across chickens (oviparous), horses (viviparous), two viviparous squamates, and one oviparous squamate found that no examined genes for angiogenesis showed a viviparity-specific expression pattern (Griffith, Brandley et al., 2017). However, other than the chicken, the only oviparous taxa included in this study was a reproductively bimodal skink, *Lerista bougainvillii* (Griffith, Brandley et al., 2017).

In the uterine tissue of gestating viviparous skinks and rats, several genes for angiogenesis are upregulated—*EPAS1*, *HIF1A* and *VEGFA* (Brandley et al., 2012; Whittington et al., 2015, 2017). Other proteins involved in vascularization and vasodilation in utero include members of the vascular endothelial growth factor (*VEGF*) gene family, VEGF receptors (*VEGFR*s), placental growth factor (*PGF*) and nitric oxide synthase (*NOS*) (Blomberg et al., 2010; Chen, Wang et al., 2015; Gilbert, 2010; Reynolds et al., 2006; Risau, 1997; Torry et al., 2003; Vonnahme et al., 2001). In *Saiphos equalis*, different homologs of *NOS* experience different patterns of gene expression across the oviparous and viviparous stages of gestation/gravidity (Foster et al., 2020). One homolog of *NOS* is upregulated during oviparous late gestation, and another is upregulated during viviparous late gestation (Foster et al., 2020). Several genes involved with angiogenesis and vascular morphogenesis are downregulated in the pre-implantation uterus of a marsupial, the Fat Tailed Dunnart, *Sminthopsis crassicaudata*—*ADGRA2*, *ADGRB2*, *ANGPTL1*, *EPHB4*, *ISM1*, *PDZRN3*, *RHOJ*, *TNMD*, and *VEGFD* (Whittington et al., 2018).

In humans, immune factors are also responsible for increasing embryonic blood supply. Embryonic non-classical MHC class I molecule, HLA-G, and uterine natural killer (uNK) cells support increased embryonic blood supply (Moffett & Loke, 2006; Rajagopalan et al., 2006). A similar pattern of utilizing immune properties to support embryonic blood supply has not been yet identified in squamates.

Lipids are a main energy source for embryos. Lipoprotein lipase (LPL) is an important enzyme in lipid transport. LPL is significantly expressed on the syncytiotrophoblasts, specialized placental cells, of humans (Lindegaard et al., 2005) and the endometrium of cows (Forde et al., 2011), and pigs (Ramsay et al., 1991), where it plays a role in lipid mobilization. A viviparous lizard, *Pseudemoia entrecasteauxii,* increases capacity for lipid transport toward the end of pregnancy (Griffith, van Dyke & Thompson, 2013). The uterine tissue of the yolk-sac placenta in this species had significantly higher expression of LPL than the uterine tissues of the chorioallantoic placenta (Griffith, van Dyke & Thompson, 2013), leading the authors to suggest that the yolk-sac placenta is the major site of lipid transport. LPL expression was not detected during pregnancy in the viviparous skink, *Chalcides ocellatus* (Blackburn, 1992; Brandley et al., 2012). Instead, lipid transport may be facilitated by fatty acid binding proteins in this species (Chmurzyńska, 2006; Brandley et al., 2012). These are also active on mammalian placenta (Haggarty, 2002).

Apolipoproteins are also suitable candidates for transport of fatty acids, cholesterol and phospholipids. Five of these (*APOA1*, *APOA2*, *APOA4*, *APOE*, and *APOM*) and *APOA1BP* are significantly upregulated in the pregnant uterus of the viviparous skink, *Chalcides ocellatus* (Brandley et al., 2012). *APOA1BP* is also upregulated in the uterus of the chorioallantoic placenta and yolk-sac placenta compared to non-gestational uterine tissues in *Pseudemoia entrecasteauxii* (Griffith et al., 2016). Additionally, upregulation of 136 genes that encode solute carrier proteins (SLCs) in the pregnant uterus of *Chalcides ocellatus* are associated with transport of inorganic ions, metals, glucose, amino acids, peptides, fatty acids, and carboxylic acids (Brandley et al., 2012).

Cathepsins and phospholipases are important for uterine secretions for embryonic development in horses, pigs, sheep and cattle (Bazer, 1975; Satterfield et al., 2007; Song et al., 2010). Cathepsins are present in yolk sacs of humans and mice. They function to degrade proteins to free amino acids (Cindrova-Davies et al., 2017). Two genes for cathepsin L (*CTSL1* and *CTSL2*) are upregulated in the uterus during gestation in *Chalcides ocellatus* (Brandley et al., 2012). *CTSL* is also upregulated in the uterus during the pre-implantation phase in the Fat-Tailed Dunnart, *Sminthopsis crassicaudata* (Whittington et al., 2018), and in the uterus of the chorioallantoic placenta and uterus of the yolk sac placenta during gestation in *Pseudemoia entrecasteauxii* (Griffith et al., 2016).

In viviparous individuals of the reproductively bimodal lizard, *Saiphos equalis*, many genes for cellular adhesion are upregulated during late gestation (Foster et al., 2020). The authors postulated that this helps facilitate maternal-fetal signaling and paracellular transport (Foster et al., 2020). Gao et al. (2019) identified a set of genes in *Phrynocephalus vlangalii* that were differentially expressed in the uterus during the stage of placentation and these enriched GO terms functionally related to the process of placentation. This included an estrogen receptor (*ESR1*) and two growth factor receptors (*GHR* and *IGF1R*) (Gao et al., 2019).

Finally, the proteomes of the ovary and placenta from obligately placentrophic *Mabuya* lizards can further serve as a useful resource for examining nutrient provisioning in squamates (Hernández-Díaz et al., 2017). In the placenta they found protein expression involved with nutrient metabolism, transport, protein synthesis, and embryonic development (Hernández-Díaz et al., 2017).

(6) Uterine glands: adenogenesis, placenta development and histotrophy

In addition to their role in eggshell deposition in oviparous taxa, uterine glands also secrete growth factors and cytokines that support placental development in mammals. In humans, these include transforming growth factor-β (TGF-β), epidermal growth factor (EGF), vascular endothelial growth factor (VECG), and leukemia inhibitory factor (LIF) (Hempstock et al., 2004). In eutherians, TGF-β supports placental development by regulating proliferation and invasion rates of placental cells lines (Caniggia et al., 2000; Hempstock et al., 2004; Lafontaine et al., 2011).

Histotrophy (also called histiotrophy) occurs when nutrients are secreted into the uterine lumen from vesicles of the columnar epithelial cells of the uterus and taken up by the embryo. Histotrophic nutrient provisioning is documented across amniotes including marsupials (Whittington et al., 2018), several ungulate taxa (Bazer et al., 2011; Han et al., 2016; Gao et al., 2009), humans (Burton et al., 2002), and squamates (Thompson et al., 2004). In humans, histotrophic nutrient provisioning occurs during the first trimester. The intervillous space is filled with fluid containing uterine gland secretions that get phagocytosed by the syncytiotrophoblasts and are the initial nutrient source for the fetus (Burton et al., 2002). Two of these glycoproteins are epithelial mucin (*MUC1*) and glycodelin A (*GdA*) (Burton et al., 2002). Interestingly, the *MUC15* gene is upregulated during gravidity/gestation in the uterus of oviparous and viviparous *Saiphos equalis* individuals (Foster et al., 2020). This also occurs in the chorioallantoic placenta of *Pseudemoia entrecasteauxii* during gestation (Griffith et al., 2016). Several mucins are expressed in the uterus in non-gravid and gravid samples from oviparous individuals of *Lerista bougainvillii* and *Lampropholis guichenoti* (Griffith et al., 2016).

A survey of viviparous squamates with modest to extensive placentrophy revealed prevalence of histotrophic nutrient provisioning rather than hemotrophy, transfer of nutrients between maternal and fetal blood streams (Blackburn 2015). Embryos of *Chalcides chalcides* have extensive placentrophy that supports substantial maternal nutrient provisioning and histotrophy (Blackburn, 2015a). Histotrophy may lessen parent-offspring conflict and give the mother the control over nutrient provisioning compared to hemotrophy (Blackburn, 2015b).

Chalcides ocellatus has less extensive placentrophy than *C. chalcides* but the gestating uterus still illustrates expression of many genes associated with organic and inorganic nutrient transport (Blackburn, 2015a). Multiple *TGF-β* loci are differentially expressed in the uterus during gestation in *C. ocellatus*, however most these are downregulated compared to non-gestational uterine tissue (Murphy et al., 2012). The influence of *TGF-β* on placental development and nutrient provisioning in *Chalcides spp.* remains to be explored to my knowledge. A TGF-β receptor (*TGFBR1*) was associated with placental development in *Phrynocephalus vlangalii* (Gao et al., 2019).

Essential to histotrophy is adenogenesis, the generation of endometrial glands. Adenogenesis allows for the secretion of histotrophs. The period of early development during which adenogenesis occurs is highly variable among vertebrates but it is required for embryonic survival (Gray et al., 2001, 2002; Spencer & Bazer, 2004). Some genes involved with adenogenesis in sheep are insulin-like growth factor 1 (*IGF-1*), *IGF-2, PAX2*, *LHX1* (also known as *LIM1*) and *EMX2*, genes in the abdominal-B HOXA cluster, members of both *Wnt* and Hedgehog (*Hh*) gene families (Fazleabas et al., 2004), prolactin (*PRL*), fibroblast growth factor 7 (*FGF7*), *FGF10*, *FGFR2IIIb*, hepatocyte growth factor (*HGF*), a receptor tyrosine kinase (*c-Met)*, and cadherins (Fazleabas, 2007).

In the gestating uterus of *Chalcides ocellatus*, insulin-like growth factor–binding protein 5 (*IGFBP5*) is one of the most significantly downregulated genes compared to non-gestational uterine tissue (Brandley et al., 2012). *IGFBP5* is evolutionarily conserved and multifunctional, with an important role in regulating IGF signaling, including that of *IGF-1* and *IGF-2* (Duan & Allard, 2020). Other than adenogenesis in sheep, IGFs serve an important role in the growth of fetal and maternal tissues in mammals. There is a long history of research on this subject (Yan-Jun et al., 1996; Gibson et al., 2001; Kampmann et al., 2019).

Genes involved with histotrophic secretion in the marsupial *Sminthopsis crassicaudata* include *AP4S1, HYOU1,* and *SRPRA* (Whittington et al., 2018). Nutrient transporters significantly upregulated at this time are *APOL6* (cholesterol transport (Baardman et al., 2013)), *PLA2G10* (hydrolysis of fatty acids during pregnancy (Miele et al., 1987)) and a wealth of SLCs (solute carrier proteins for nucleoside sugar, ions, anions, glucose, fatty acids, calcium and zinc (Whittington et al., 2018)). In a reproductively bimodal skink, *Saiphos equalis, PLA2G10* is upregulated during viviparous late gestation compared to oviparous late gestation (Foster et al., 2020). Upregulation of SLCs also occurs in the viviparous skink *Chalcides ocellatus* (Brandley et al., 2012; Van Dyke et al., 2014) and in the uterus during pregnancy in the grey short-tailed opossum, *Monodelphis domestica* (Hansen, Schilkey & Miller, 2016).

Uterine glands are also important for secretions of eggshell precursors. I speculate that genes involved with adenogenesis of shell glands may be similarly used to support histotrophic nutrient provisioning, but further research is necessary. Specialized uterine areolar glands are found in some *Mabuya* lizards, a genus with oviparous species and viviparous species that utilize placentrophy and histotrophy (Brandley et al., 2012; Corso et al., 1988, 2000; Jerez & Ramírez-Pinilla, 2001; Ramírez-Pinilla, 2006; Vieira et al., 2007; Visser, 1975). Transcriptomic research focused on histotrophic nutrient provisioning, placental development, and secretions of eggshell precursors in oviparous and viviparous *Mabuya spp*. would complement the morphological literature on the genus

(7) Discussion & future directions—embryonic nutrients, gas, and water supply

Many genes for placental functions in mammals have deep origins in vertebrates (Rawn & Cross, 2008). Across amniotes, there is overlap in hormones and proteins (SLC superfamily, insulin-like growth factors, aquaporins and solute carrier proteins, etc.) involved in uterine remodeling, placentation, and placental transport. Identifying a viviparity-specific expression profile would require measuring expression at stage-specific times across taxa that share the same form of water, gas, or nutrient provisioning. A viviparity-specific profile may not be the biological reality. Supplementary Table 3 illustrates how loci mentioned in text for water, gas, and nutrient transport are expressed in reproductive tissues of squamates during gestation and gravidity.

If specific genes or physiological processes impact more than one of the Main Five categories, it could have a disproportionate influence on transitions. The solute carrier *(SLC)* gene superfamily is estimated to be involved with both nutrient transport (Brandley et al., 2012; Whittington et al., 2018) and eggshell deposition (Yang et al., 2020). Adenogenesis is essential for histotrophic nutrient provisioning and secretion of eggshell precursors. Additionally, progesterone production influences both uterine quiescence, which is an important state to maintain in lengthened embryonic retention, and it also inhibits hepatic vitellogenesis, an important process for lecithotrophic nutrient provisioning. Thus, examining the role of *SLC* gene superfamily members, processes of adenogenesis, and progesterone production during embryonic development in oviparous and viviparous squamate may reveal how interconnected the Main Five are.

V. Embryonic Calcium Provisioning

The embryonic growth stage requires the greatest demand of calcium (Ecay et al., 2017; Packard & Packard, 1984; Stewart & Ecay, 2010). To support this, peak uterine concentrations of calcium are highest during either eggshell deposition or during the embryonic growth stage, in oviparous and viviparous taxa, respectively (Linville et al., 2010; Stewart et al., 2009). Regardless of parity mode, embryonic metabolism drives calcium uptake (Packard & Packard, 1984). The calcium source(s) utilized have clade-specific implications on the genomic and/or physiological changes required to transition between parity modes.

(1) Phylogenetic context of embryonic calcium sources

Calcium can be acquired by the embryo in three forms: calcium carbonate in the eggshell, calcium bound to proteins and lipids in the yolk, and/or free ionic calcium from maternal delivery through the placenta (Stewart & Ecay, 2010). These correspond with five calcium mobilization patterns: 1) Birds, turtles and crocodiles predominately depend on the eggshell; 2) Many squamates, regardless of parity mode, predominately depend on the yolk; 3) Some squamates are intermediately reliant on the eggshell and yolk; 4) Some viviparous squamates are intermediately reliant on the yolk and placenta; and 5) therian mammals and some viviparous squamates predominately depend on the placenta (Hoenderop, Nilius, & Bindels, 2005; Jenkins & Simkiss, 1968; Kovacs, 2015; Packard, 1994; Packard & Seymour, 1997; Stewart et al., 2009, 2009; Stewart & Ecay, 2010; Thompson, Stewart et al., 1999; Thompson, Stewart, & Speake, 2000; Ramírez-Pinilla, 2006). Unlike birds, oviparous squamates do not sequester calcium from the eggshell into the yolk during incubation (Packard, 1994).

(2) Hypotheses on calcium mobilization and the evolution of parity modes

It was hypothesized that predominant reliance on eggshell calcium should constrain lineages to oviparity because the evolution of viviparity would result in a lost calcium source (hereafter eggshell calcium constraint hypothesis) (Stewart & Ecay, 2010; Packard et al., 1977; Packard & Packard, 1984). This hypothesis suggested that viviparity should only evolve in lineages predominately reliant on yolk calcium (Packard et al., 1977; Packard & Packard, 1984). Fittingly, birds, turtles and crocodilians generally rely on eggshell calcium, and they are constrained to oviparity (Anderson et al., 1987). The eggshell calcium constraint hypothesis is supported by many viviparous squamates that rely heavily on yolk calcium, including *Nerodia* *rhombifera*, the diamondback water snake, and *Niveoscincus metallicus*, the metallic skink (Stewart & Castillo, 1984; Thompson, Speake et al., 1999).

However, subsequent research revealed that viviparity is not constrained by a prerequisite reliance on yolk calcium. Calcium placentrophy contributes substantially to embryonic development in several viviparous squamates including *Pseudemoia entrecasteauxii*, *Eulamprus quoyi*, *Zootoca vivipara*, *Saiphos equalis*, and an unidentified species of *Mabuya* lizard (Ecay et al., 2017; Linville et al., 2010; Ramírez-Pinilla, 2006; Ramírez-Pinilla et al., 2011; Stewart & Thompson, 1993; Thompson, 1977). These taxa, with the exception of *Zootoca vivipara*, are in the family Scincidae (Burbrink et al., 2020), which is also the family with the most independent origins of viviparity in squamates (Blackburn, 1982, 1999; Pyron & Burbrink, 2014). Oviparous scincid skinks studied thus far are intermediately reliant on eggshell and yolk calcium (Linville et al., 2010; Shadrix et al., 1994; Stewart et al., 2009; Stewart & Thompson, 1993; Thompson et al., 2001).

To understand the breadth of physiological conditions from which oviparity and viviparity evolve in squamates, future research should examine calcium transport in other lineages. Studies focused on snakes would be particularly informative given the sparse literature on them. *Helicops angulatus*, a reproductively bimodal water snake from South America, is an ideal model for this (Braz et al., 2018). Thus far, many oviparous snakes are known to be intermediately reliant on yolk and eggshell calcium. This has not precluded viviparity from evolving in these lineages.

The presence of embryos during extended embryonic retention may trigger positive feedback stimuli for continued uterine calcium secretions (Stewart & Ecay, 2010), which may support incipient calcium matrotrophy. This is postulated to resemble the hormonal and mechanical stress mechanisms implicated in avian eggshell formation and uterine calcium secretions (Bar, 2009a; Stewart & Ecay, 2010). The influx of calcium late in viviparous gestation may be triggered in part by embryonic growth that over distends the uterus. This is seen in mammals when uterine overdistention triggers influx of calcium and sodium to support parturition (Kao & McCullough, 1975).

Dramatic changes to activity in chorioallantois should not be required during parity mode transitions because these homologous tissues (Metcalfe & Stock, 1993) transport calcium regardless of parity mode (Ecay, Stewart & Blackburn, 2004; Tuan & Scott, 1977; Tuan & Knowles, 1984; Tuan et al., 1978, 1986). Specialized placental structures in some viviparous squamates enhance calcium provisioning but specialization is not required for placental calcium transport (Stewart et al., 2009; Stewart & Ecay, 2010; Thompson et al., 2000). Loss of chorioallantoic calcium transporting capacity would be disadvantageous to either parity mode. Growing research reveals that, like mammals, placentrophy and viviparity can evolve concurrently in squamates (Blackburn, 2015a; Ecay et al., 2017; Stewart & Ecay, 2010).

Extending evidence for these hypotheses across the squamate phylogeny, incipient calcium matrotrophy should support origins of viviparity when viviparity arises in close phylogenetic proximity to oviparous taxa with embryos that depend intermediately or predominately on eggshell calcium; Origins of viviparity in close phylogenetic proximity to oviparous taxa with embryos that depend on lecithotrophic calcium provision should remain reliant on yolk calcium. This provides a framework from which researchers can infer how viviparous calcium transport may evolve in different lineages. Measurements of the proportional contribution of different calcium sources during development has only been done in select taxa (Packard, 1994; Stewart, 2013; Stewart & Blackburn, 2014; Stewart & Ecay, 2010). Collection of this data across the squamate phylogeny may enable assignment of these hypotheses to specific clades.

Embryonic calcium source could have implications on the physiological changes required to transition between parity modes. Reliance on yolk calcium should render, essentially, no mechanistic changes for calcium transport. Incipient calcium matrotrophy may require regulatory changes in the uterus, like timing of calcium secretions (Griffith et al., 2015). However, regardless of parity mode 1) the uterus secretes calcium, 2) the chorioallantois transports calcium and 3) embryonic metabolism drives uptake of calcium. Assuming maternal tissue remains responsive to embryonic metabolism, the joint evolution of matrotrophic calcium provisioning with viviparity may also require little to no physiological adjustments.

The diversity of embryonic calcium provisioning patterns in viviparous squamates may not be fully explained by the eggshell calcium constraint hypothesis (Packard et al., 1977; Packard & Packard, 1984) or incipient calcium matrotrophy (Stewart & Ecay, 2010). Both hypotheses implicitly assume that viviparity equates to a lost eggshell. In one viviparous squamate, *Haldea striatula*, and in viviparous populations of two reproductively bimodal lizards, *Zootoca vivipara* and *Saiphos equalis*, the calcified eggshell is considered as a component of the placenta (Stewart, 2013). Some other viviparous squamates have transient calcified patches on their embryonic membranes (Blackburn, 1998; Heulin, 1990, 2005; Qualls, 1996) suggesting that uterine calcium secreting capabilities in early gestation may be retained in some viviparous lineages. In the case of reversals, it remains unknown how the uterus shifts back to early calcium secretions after ovulation (Blackburn, 2015b; Griffith et al., 2015). Reversals may be most feasible within viviparous clades that evolved through incipient calcium matrotrophy because the calcium secreting capacity of the uterus is certainly retained.

(3) Embryonic calcium provisioning mechanisms

In vertebrates, specialized tissues that recover environmental calcium and transport it into blood circulation maintain conserved mechanisms for intracellular calcium transport (Bronner 2003; Hoenderop et al., 2005). These include the uterus, chorioallantoic tissues, and yolk splanchnopleure (Bronner, 2003; Hoenderop et al., 2005; Stewart, 2013). Uterine and embryonic tissues may be proto-adapted for the maternal-embryonic calcium provisioning (Coleman & Terepka, 1972; Ecay et al., 2017; Packard & Packard, 1984; Packard, 1994; Stewart & Ecay, 2010).

In birds, a sub-compartment of the mammillary layer of the eggshell is the calcium reserve body (Chien et al., 2009), which contains microcrystals of calcite that get dissolved and transported as calcium to the embryo (Chien et al., 2009). Calcium is eroded from the eggshell by acid released from villus cavity cells (VCCs) in chorioallantoic membrane (Anderson, Gay, and Schraer, 1981; Narbaitz et al., 1981; Packard & Lohmiller, 2002; Simkiss, 1980). This increases the carbonic anhydrase activity of the cells enabling calcium to be released into the cavity between the eggshell and the chorionic epithelium, where it is taken up by capillary covering cells (CCCs) in chorioallantoic membrane (Coleman & Terepka, 1972). In some species this erosion leads to a gradual weakening of the eggshell that facilitates hatching (Chien, Hincke & McKee, 2008; Nys et al., 2004). In chickens, transcalcin, a calcium binding protein, is credited for the calcium transporting capacity of the chorioallantoic membrane (Tuan & Knowles, 1984; Tuan & Ono, 1986; Tuan & Scott, 1977; Tuan et al., 1978, 1986). The presence of VCCs and CCCs in the chorioallantois of viviparous squamates would indicate a known route through which calcium can be absorbed.

Transcellular calcium transport has been modeled as a three-step process involving proteins calbindin-D9K, calbindin-D28K, and the highly calcium-specific ion channels of the transient receptor potential vanilloid gene family (*TRPV5* and *TRPV6*) (Stewart & Ecay, 2010). Across vertebrates, this machinery is shared in epithelial tissues with significant roles in calcium transport (Hoenderop et al., 2005). Estrogen and vitamin D3 have regulatory roles in this process.

Calbindin-D9K, calbindin-D28K, *TRPV5*, and *TRPV6* is involved with calcium exchange in multiple organs of birds, squamates, and mammals. Broadly, activity of calbindin-D9K and/or calbindin-D28K is associated with patterns of calcium absorption in the mammalian kidney and uterus (Bindels, 1993; Luu et al., 2004), murine uterus and placenta (Lafond & Simoneau, 2006; Koo et al., 2012), and chicken duodenum and uterus (Bar, 2009b; Yang et al., 2013). In humans, calbindin-D9K and calbindin-D28K are critical to the active transport of Ca2+ across placental cells (Faulk & McIntyre, 1983; Belkacemi, Simoneau & Lafond, 2002; Belkacemi et al., 2004). A study on rats suggests that calbindin-D9K increases by over 100-fold in the last 7 days of gestation (Glazier et al., 1992), when the embryo gains >99% of calcium (Comar, 1956). *TRPV6* is involved with maternal-fetal calcium transport in mice (Suzuki et al., 2008). Increased *TRPV6* and calbindin-D28K expression occurs during eggshell formation in chickens (Yang et al., 2013). Given the involvement of these loci in both eggshell deposition and embryonic calcium transport, squamates may have exploited this pathway to support transitions.

In several highly matrotrophic lizards, embryonic uptake of calcium is associated with placental expression of calbindin-D28K (Stewart et al., 2009; Stinnett et al., 2011, 2012). In both oviparous and viviparous embryos of *Zootoca vivipara*, sharp increase in calcium uptake in late development coincides with increased calbindin-D28K and PMCA by the chorioallantois

(Stewart et al., 2009, 2011). In oviparous corn snakes, *Pantherophis guttatus*, expression of calbindin-D28K in the yolk-sac and chorioallantoic membrane coincides with growth of these tissues and calcium transport activity (Ecay et al., 2004). The chorioallantois of other lizards and snakes transport calcium to the embryo and express calbindin-D28K and PMCA (Blackburn, 2004; Ecay et al., 2004; Stewart et al., 2010; Stinnett et al., 2012).

Viviparous embryos of *Zootoca vivipara*, a reproductively bimodal lizard, incubated *ex utero* respond to availability of calcium by increasing expression of calbindin-D28K (Ecay et al., 2017). In this species, embryonic recognition of environmental calcium stimulates a transcellular calcium transporting mechanism and may also alter chorioallantoic membrane paracellular permeability to calcium (Ecay et al., 2017). The authors proposed that there is a calcium sensing receptor (CaSR) on chorionic epithelial cells to support this in both oviparous and viviparous *Zootoca vivipara* embryos (Ecay et al., 2017), similar to the CaSRs expressed by vertebrate cells involved in calcium homeostasis (Brennan et al., 2013).

As mentioned earlier, PMCA activity is associated with eggshell deposition in birds and oviparous squamates (Bar, Rosenberg, & Hurwitz, 1984; Hincke et al., 2012; Wasserman et al., 1991). PMCA is also crucial for calcium transport in late embryonic development in rats (Glazier et al., 1992). In viviparous scincid lizards, *Niveoscincus metallicus*, *N. ocellatus*, and *Pseudemoia spenceri*, PMCA was expressed in uterine glandular and surface epithelia during pregnancy but only *P. spenceri* expressed it throughout gestation (Herbert et al., 2006). When PMCA was not detected by immunoblotting in the yolk splanchnopleure of *Haldea striatula*, a viviparous snake that relies predominately on yolk calcium (Stewart, 1989; Fregoso, Stewart, & Ecay, 2010), NCXs were proposed as an alternative transporter of calcium (Fregoso et al., 2012). NCXs are important for placental calcium transport in humans (Belkacemi et al., 2005).

Calciotropic hormones, those involved with calcium transport, and phosphotropic hormones, those involved with phosphorous transport, operate via an interconnected pathway (Andrukhova et al., 2016; Biber, Hernando & Forster, 2013; Blaine, ChoncholLevi. 2015; Erben & Andrukhova, 2015). Phospho- and calciotropic hormones are important regulators of fetal serum mineral concentrations (Kovacs, 2015). Evidence from viviparous amniotes suggests that these are suitable candidates for embryonic calcium provisioning. In mice, genes encoding parathyroid hormone (*PTH*) and *PTH*-related peptide (*PTHrP*) are important regulators of placental calcium transport (Kovacs et al., 1996; Simmonds et al., 2010). A non-exhaustive list of additional candidates for embryonic calcium provisioning include fibroblast growth factor 23 (Bar, 2009a; Erben & Andrukhova, 2015; Stewart & Ecay, 2010), the annexin gene family (Matschke et al., 2006), carbonic anhydrase (Narbaitz et al., 1981; Tuan & Knowles, 1984), and calcium binding proteins (CaBPs) can be found in the referenced literature.

(4) Discussion & future directions—calcium provisioning and parity mode evolution

Generalized hypotheses to explain how squamate parity modes evolve are not universally applicable (Hodges, 2004; Li et al., 2009; Packard et al., 1977; Stewart & Ecay, 2010). However, they can be used as a framework to infer the most likely form of embryonic calcium provisioning used in specific lineages. This was discussed in detail in section two. Phylogenetic frameworks like this enable researchers to make broader testable hypotheses about the evolutionary history of calcium provisioning in specific clades. Implications gleaned from taxon-specific studies can be explored in distantly related analogous groups. Additionally, I speculated that lineages with incipient calcium matrotrophy may more feasibly reversal to oviparity because of continued role of uterus in calcium provisioning.

Loci involved with calcium transport in uterine and embryonic tissues have been described across mammals, birds, and reptiles. Like other amniotes, activity of calbindin-D28K and PMCA supports embryonic calcium provisioning across diverse oviparous and viviparous squamates. Their involvement with both eggshell deposition and embryonic calcium provisioning makes these particularly interesting candidates for parity mode evolution. The regulatory influence of other molecules in calcium transport, like *PTH*, *PTHrP* and NCXs has not been evaluated thoroughly in squamates. Additional reviews on mechanisms of embryonic calcium provisioning in squamates can be found in the literature (Stewart, 2013; Stewart & Blackburn, 2014; Stewart & Ecay, 2010).

VI. Maternal-Fetal Immune Dynamics

Medawar (1953) pointed out the paradigm between the peripheral body's normal attack response to allografts (foreign tissue) and uterine tolerance to embryos (Medawar, 1953). This was inspired by earlier work by Ray Owen (Owen, 1945). Stricter regulation of the maternal and fetal immune systems is expected for viviparous reproduction because of contact between uterine and embryonic tissues. Oviparity may pose less of an immunological challenge. Medawar suggested barriers, inertness and/or immunosuppression enable pregnancy. This formed the foundation of decades of medical research on immune dynamics between maternal, embryonic, and paternal immune factors in utero.

In recent years, there was a call for a reappraisal of Medawar's paradigm (Chaouat, 2010, 2016; Moffett & Loke, 2004, 2006; Mor et al., 2011; Stadtmauer & Wagner, 2020b; Yoshizawa 2016). Moffett & Loke (2006) caution against conceptualizing embryos as analogs of allografts.

This perspective has yet to reach the evolutionary literature on parity mode evolution (Graham et al., 2011; Gao et al., 2019; Murphy & Thompson, 2011; Van Dyke, Brandley, & Thompson, 2014; Murphy, Thompson, & Belov, 2009).

The uterine immune system has a distinct evolutionary history from the periphery. The uterine immune environment enables cooperative dynamics with foreign tissues. It supports fertilization and early embryonic development. This should have started evolving, distinct from the periphery, since internal fertilization first originated. To demonstrate this, I discuss the changing landscape of immunological research at the maternal-fetal interface and apply it to the current knowledge on uterine and embryonic immune responses during viviparous gestation in squamates.

Most literature on maternal-fetal immune dynamics limits itself to mammals. Squamates may serve as a better comparative model for understanding the evolution of the uterine immune system. Active research on the peripheral reptilian immune system (Zimmerman et al., 2010, 2020) and uterine immune activity in squamates (Graham et al., 2011; Hendrawan et al., 2017; Murphy et al., 2009; Paulesu et al. 1995, 2008, 2005) will support future insights on this.

(1) Comparing amniote immune systems

Cellular components of the innate immune system are conserved across jawed vertebrates (De et al., 2007; Uribe et al., 2011; Zimmerman et al., 2010). The general machinery of the adaptive immune system is ancient despite divergences and convergences across all domains of life (Ghosh et al., 2011; Morales et al., 2017; Müller et al., 2018; Rimer et al., 2014). Diversification of antigen receptor genes likely occurred independently in a lineage-specific fashion (Boehm et al., 2018). Compared to mammals, the avian immune system requires less antigen (Larsson et al., 1998). Birds also have faster but shorter antibody responses, potentially due to their higher body temperatures (Jurd, 1994).

Reptiles have the same general components of the mammalian immune system (Zimmerman, 2020). However, the reptilian immune system may not fit neatly into the two arms of mammalian immune systems—innate and adaptive (Zimmerman, 2010; 2020). Expanding upon this is beyond the scope of this review, but it is worth considering in future comparative research. I refer readers to articles by Zimmerman et al. (2010, 2020) and Ghorai et al. (2018), and the books by Williams (2012) and Davison et al. (2008) for more information on reptilian and avian immune systems.

(2) Medawar's paradigm

Tolerance toward the foreign fetus was postulated to occur through immunological inertness, immunosuppression or immunotolerance mechanisms (Medawar, 1953). Theoretically, immunotolerance could be established if there are relatively small quantities of alloantigens present, resulting in regulatory responses rather than activating responses (Pradeu, 2011). Contradicting this, the larger the alloantigen difference between the mother and embryo the bigger and healthier the placentae in rats (Chaouat et al., 2010). In humans, divergent HLA profiles between mother and embryo do not lead to detrimental immune responses (Tilburgs, Scherjon, & Claas, 2010). Instead, cooperative inflammatory responses between maternal and fetal tissues support reproduction (Stadtmauer et al., 2020). In humans, microchimeric cell populations, presence of cells from one individual in another genetically distinct individual, are now considered a normal expectation of pregnancy (Nelson, 2012).

In his 1991 Nobel Lecture, Medawar acknowledged that maternal and embryonic tissues have regular exposure to alloantigens (Medawar, 1991). It has become clear that the maternal immune system actively responds to fetal alloantigen rather than responding solely with ignorance or anergy (Arck & Hecher, 2013). Neither maternal immunosuppression/privilege nor embryonic inertness/immaturity fully explain immune dynamics during gestation in mammals, including those with the simple epitheliochorial placentation (Chaouat et al., 2010; Chavan, Griffith & Wagner, 2017; Moffett & Loke, 2004, 2006; Stadtmauer & Wagner, 2020).

(3) Perspectives on the evolution of the uterine immune system

Viviparous reproduction existed eons before the origin of mammals and no evidence suggests there was immune conflict within these taxa (Chaouat, 2016). Placentrophy existed as far back as the invertebrate clade Bryozoa (Ostrovsky, 2013; Schwaha et al., 2019), suggesting an ancient history for supportive maternal-fetal immune dynamics. Differing from Medawar's paradigm, Polly Matzinger, who proposed the 'danger model' for the immune system (Matzinger, 2007), wrote "Reproduction cannot be a danger. It does not make evolutionary sense" (Chaouat, 2016).

In mammals, immunological cells at the maternal-fetal interface may not function through self-non-self-discrimination, as they are understood to function in the rest of the body (Chaouat, 2016; Moffett & Loke 2004, 2006). The 'maternal-fetal interface' may be better conceptualized as 'maternal-fetal intra-action' given the dynamics between maternal and fetal immune systems in mammals (Yoshizawa, 2016). It is unclear if these insights apply to other viviparous amniotes.

In mammals, immune factors in the uterus and placenta appear to be specifically evolved to support maternal-fetal immune dynamics. Several cell types have unique functions and/or phenotypes in utero—uterine NK (uNK) cells, uterine macrophages, uterine T regulatory cells

(Faas & de Vos, 2017; Mold et al., 2008, 2010; Mold & McCune, 2011). An immunosuppressive antigen, HLA-G, is almost exclusively expressed by trophoblasts (Faulk & Temple, 1976; Kovats et al., 1990; Rajagopalan & Long, 2012; Rouas-Freiss et al., 1997). Taken from an evolutionary perspective, this suggests that the uterine immune system in viviparous mammals evolved unique responses to allogenic tissues that differ from the periphery. Whether the evolution of this system predates mammals remains to be explored, to my knowledge.

Some suggest that viviparous reproduction is immunologically compatible in species with less active adaptive immune system. In these clades, innate immune cells, like uNK cells, may be sufficient to regulate immune responses during pregnancy (Moffett & Loke, 2004; Chaouat, 2016). Determining whether viviparity is immunologically compatible in squamates, or if they require specialized immune responses in utero, requires further investigation. Nonetheless, uterine tissue of oviparous and viviparous skinks expresses maternal antigens prior to and during gravidity and gestation (Murphy et al., 2009). Viviparous species in this study have a unique expression profile of MHC antigens which may ‘hide’ the embryo from the maternal immune system (Murphy et al., 2009).

(4) Implications of the reptilian immune system and morphology on parity mode evolution

Ectothermic reptiles may inherently have a more tolerogenic uterine environment compared to mammals due to their slower antibody response. It can take up to six weeks to reach peak concentrations (Ingram & Molyneux, 1983; Grey, 1963; Marchalonis et al., 1969; Pye et al., 2001; Origgi et al., 2001; Work et al., 2000). A slower metabolism also makes several reptiles more tolerogenic to pathogens (Ghorai & Priyam, 2018).

During pregnancy in the viviparous skink, *Chalcides ocellatus*, there is a reduced response to in vitro exposure to mitogens concanavalin A (Con A), phytohemagglutinin (PHA), and *Escherichia coli* lipopolysaccharide (LPS) (Saad & El Deeb, 1990). Oviparous lizards exhibit immune activation tradeoffs during reproductive cycles (Cox, Peaden, & Cox, 2015; Durso & French, 2018; French, Johnston, & Moore, 2007; Uller, Isaksson, & Olsson, 2006).

In the majority of viviparous squamates, the eggshell membrane is absorbed during pregnancy (Yaron, 1985; Blackburn, 1993). Whether the eggshell membrane elicits immune responses prior to absorption remains to be examined to my knowledge. Viviparous squamates, at minimum, have epitheliochorial placentation. In mammals, epitheliochorial placentation is sufficient to cause immunorecognition from the mother. Specialized placental cells, trophoblasts, may be more common in other viviparous amniotes than previously recognized (Blackburn, 2015a). In mammals, trophoblasts are antigen presenting and actively participate in maternal-fetal immune dynamics.

A few viviparous squamates have placentas with characteristics similar to placentas found in eutherian mammals—syncytialized cells layers, specialized zones such as areolae and placentomes, or cellular invasion of maternal tissues by the fetus (Blackburn & Flemming, 2012; Jerez & Ramírez-Pinilla, 2001; Vieira et al., 2007). The increased contact here may require more tightly regulated immune dynamics at the maternal-fetal interface compared to other viviparous squamates.

(5) The inflammation paradox

In mammals, implantation may have evolved from an ancestral inflammatory attachment reaction (Griffith, Chavan et al., 2017). Inflammation is the most crucial system to support implantation, but it is also the greatest threat to the continuation of pregnancy (Chavan et al., 2017). This phenomenon is called the inflammation paradox. In humans, immune cells including uterine macrophages, T cells of multiple subtypes, uterine natural killer (uNK) cells, dendritic cells, and natural killer T (NKT) cells increase until implantation and remain abundant in the uterus throughout first trimester (Bulmer et al., 1991; Bulmer, Williams & Lash, 2010). Early implantation in humans is characterized by high pro-inflammatory T helper (Th)-1 cells and cytokines (IL-6, IL-8, and TNFα) (Koga & Mor, 2008; Yoshinaga, 2008). The exploitation of inflammatory mechanisms for eutherian implantation and the shift toward non-inflammatory activity to maintain pregnancy may have been key in enabling extended embryonic retention of eutherians (Griffith, Chavan et al., 2017).

How the inflammation paradox applies to viviparous squamates is unclear, given that placentation in squamates and mammals in not homologous (Griffith, Van Dyke, & Thompson, 2013). In extrauterine pregnancies of mammals with non-invasive placentas, the embryo will invade extrauterine tissue because it is not inhibited by uterine secretions (Vogel, 2005; Samuel & Perry, 1972). However, in *Pseudemoia entrecasteauxii*, a viviparous skink that also has a non-invasive placenta, extrauterine pregnancy does not result in invasive implantation of extrauterine tissues (Griffith, Van Dyke, & Thompson, 2013). The inherent invasive nature of mammalian embryos outside of the uterus, compared to the non-invasive nature of viviparous squamate embryos studied thus far, suggests that the parent-offspring conflict and the inflammation paradox may be less pronounced in viviparous squamates compared to viviparous mammals.

(6) Inertness and barriers at the maternal-fetal interface

The uterine environment is not inert or sterile (Agostinis et al., 2019; Erlebacher, 2013; Moffett & Loke, 2006; Munoz-Suano, Hamilton, & Betz, 2011; Murphy, Thompson, & Belov, 2009; Terzidou, 2007; Yoshimura, Okamoto, & Tamura, 1997). In humans, the decidual layer of the uterus during pregnancy is comprised of ~40% leukocytes (Ander, Diamond, & Coyne, 2019; Manaster & Mandelboim, 2010). This cellular subpopulation has 70% uNK cells, 10-20% antigen presenting cells (APCs) including macrophages and dendritic cells, and 3-10% T cells of several subtypes (Abrahams et al., 2004; Hanna et al., 2006; Kämmerer et al., 2006; Le Bouteiller & Piccinni, 2008; Liu et al., 2017; Manaster & Mandelboim, 2010; Moffett-King, 2002; Moffett & Loke, 2006; Roussev et al., 2008). There is an abundance of decidual large granular lymphocytes (LGLs), CD3-NK cells and CD3+ activated cytotoxic T cells, in the human uterus, that have cytotoxic properties and produce cytokines, and these are affected by fetal MHC molecules (Rieger, 2002).

Avian and non-avian reptiles have also immunocompetent cells in their oviducts. T and B cells are present in chicken ovary where they are stimulated by estrogen (Barua & Yoshimura, 1999; Withanage et al., 2003; Zettergren & Cutlan, 1992). Other immunocompetent cells in the chicken oviduct include IgG+, IgA+ and CD3+ (Yoshimura, Okamoto, & Tamura, 1997). Immune competent cells located throughout the mucosal tissue of avian oviductal segments including macrophages, antigen presenting cells (APCs) expressing MHC class II antigens, helper T cells and cytotoxic T cells, and premature B cells (Das, Isobe, & Yoshimura, 2008).

Inert barriers between maternal and fetal tissues may ‘hide’ the embryo. In oviparous taxa, the eggshell may serve as a barrier. However, the antimicrobial properties of the eggshell matrix in birds demonstrate that even the eggshell is not inert. The FAS ligand, also called APO-1 or CD95, in humans and rodent embryonic tissue was proposed to serve as a barrier because it causes apoptosis of surrounding maternal immune cells (Kayisli et al., 2003; Makrigiannakis et al., 2008).

Medawar suggested that an impermeable placenta strictly regulates molecular exchanges, preventing rejection of the embryo (Medawar, 1991). Synctiotrophoblasts lack cellular junctions and thus it was postulated to serve as this barrier (Ander et al., 2019). However, the growing data on bidirectional cellular traffic of APCs, even in mammals with noninvasive placentas, rejected this hypothesis (Bakkour et al., 2014; Burlingham, Bracamonte-Baran, & Burlingham, 2014; Fujiki et al., 2008; Turin et al., 2007).

(7) T cell populations and mammalian viviparity

In mammals, immune-dynamics at the maternal-fetal interface are established through innate and adaptive immune responses. There is a delicate balance between ratios of Th1, Th2, Th17, Tregs and memory T cells at the maternal-fetal interface in eutherian mammals during gestation (Chaouat et al., 1997; Kieffer et al., 2019; Peck & Mellins, 2010; Saito et al., 2010; Wu et al., 2014). A shift in utero from T helper type 1 (Th1) cells to T helper type 2 (Th2) cells during gestation in mammals equates to a shift from pro-inflammation to anti-inflammation. The galectin proteins, GAL-13 and GAL-14, expressed by syncytiotrophoblasts, bind to T cells where they inhibit activation, induce apoptosis, and enhance interleukin-8 (IL-8) production (Balogh et al., 2019).

Growing research is revealing the central role of Tregs at the maternal-fetal interface during pregnancy in mammals (Teles et al., 2013; Wienke et al., 2019). Tregs play a central role in immunosuppression in mammals (Attias, Al-Aubodah, & Piccirillo, 2019). Differentiation of Tregs is governed by the transcription factor, *FOXP3* (Ramsdell & Rudensky, 2020).

Alloantigen-dependent, uterine T cell signaling, and immunocompetent embryonic cells and their products facilitate enhanced regulatory phenotypes of immune cells overall (Ander et al., 2019).

The T-cell dependent adaptive immune system of mammals is unique. This may have prompted their intricate balance of Treg mediators of immunotolerance at the maternal-fetal interface (Chaouat, 2016). Birds rely more heavily on B cells. In non-avian reptiles, T helper cells are functional, but the presence and function of other T cell subsets is unclear (Zimmerman, 2020; Zimmerman, Vogel, & Bowden, 2010). The potential role of T cells and Tregs in viviparous squamate gestation should not be discounted. Treg-like cells have been identified in a pufferfish, *Tetraodon nigroviridis* (Wen et al., 2011), suggesting that Tregs may have an ancient evolutionary history.

(8) Progesterone, cytokines, and maternal-fetal immune dynamics

In addition to the role of progesterone in uterine quiescence (embryonic retention) and hepatic vitellogenesis (nutrient provisioning), it also plays a role in maternal-fetal immune dynamics. In the uterus of pregnant mammals, progesterone concentrations are associated with altered B cell immunoglobin secretion, inhibition of NK-cell mediated cytotoxicity and the shift from Th1 (pro-inflammatory) to Th2 (anti-inflammatory) dominated immune responses (Druckmann & Druckmann, 2005). Progesterone is also associated with immunomodulatory effects (Ortega Brown et al., 1990). During gestation in *Agkistrodon piscivorus*, a viviparous pit viper, progesterone concentrations are associated with decreased complement performance (Graham et al., 2011), a portion of the immune system that promotes inflammation, among other immune functions.

In humans, progesterone induced protein (PIBF) is transported by placental extravillous trophoblasts to maternal lymphocytes causing the induction of interleukin-10 (IL-10) production, contributing to the Th2 dominant responses (Szekeres-Bartho, Šućurović, & Mulac-Jeričević, 2018). IL-10 is a potent anti-inflammatory cytokine that is produced by multiple cell types (Zimmerman, Bowden, & Vogel, 2014). It is associated with Th2 response, and it inhibits Th1 responses. The phenotype of uterine macrophages is affected by trophoblasts when they secrete IL-10 and macrophage colony-stimulating factor (M-CSF) (Svensson-Arvelund et al., 2021). IL-10 inhibits IFN-γ and increases in response to infection in chickens (Giansanti, Giardi, & Botti, 2006; Rothwell et al. 2004). In the uterus of the oviparous skink, *Lampropholis guichenoti*, during gravidity and non-gravidity, IL-10 is expressed (Griffith et al., 2016).

Proinflammatory cytokines may be downregulated during reproductive periods to limit maladaptive immune responses to the foreign fetus (Zimmerman, Vogel, & Bowden, 2010). In mammals, IL-1 allows release of hormones in human trophoblasts (Felice Petraglia et al., 1990; Masuhiro et al., 1990; Yagel et al., 1989), facilitates implantation (Haimovici, Hill, & Anderson, 1991; Hill, 1992; Tartakovsky & Ben-Yair, 1991), and influences the initiation of labor (Romero et al., 1989, 1992). Regulation of the proinflammatory cytokines tumor necrosis factor (TNF) and interleukin 1B (IL-1β) is of particular importance in eutherian pregnancy (Haider & Knöfler, 2009; Paulesu, Romagnoli, & Bigliardi, 2005; Saito et al., 2010; Tayade et al., 2006).

The uterine tissue of two reproductively bimodal squamates—viviparous individuals of *Chalcides chalcides,* and oviparous and viviparous individuals of *Zootoca vivipara*—express IL-1β (Paulesu et al., 1995, 2005; Romagnoli et al., 2003). In the uterus of the viviparous skink, *Pseudemoia entrecasteauxii*, during gestation regulation of TNF and IL-1β at the transcriptional and post-translation levels, respectively, may reduce inflammation (Hendrawan et al., 2017). The pro-inflammatory function of IL-1β in *Pseudemoia entrecasteauxii* may play a role developing a more complex placenta (Hendrawan et al., 2017). The placenta of *Chalcides chalcides* expresses pro-inflammatory cytokines, IL-1α and IL-1β, at specific times during gestation (Paulesu et al., 1995). During gestation, *Chalcides ocellatus* also differentially expresses 27 other interleukins and interleukin related products (Brandley et al., 2012).

The expression of IL-34 in a marsupial, the fat-tailed dunnart, during pre-implantation (Whittington et al., 2018) may have an immunosuppressive function to help tolerate potential contact of maternal and fetal tissues when the embryonic shell coat disintegrates (Lindau et al., 2015; Roberts & Breed, 1994; Selwood, 2000). In chickens, IL-34 regulates Th1 and Th17 cytokine production (Truong et al., 2018). During gestation in *Pseudemoia entrecasteauxii,* IL-16 and IL-1α are expressed in addition to three receptors for Th17 family cytokines—IL-17RA, IL-17RC, and IL-17RA (Griffith, Brandley, et al., 2016, 2017). In the yolk sac of *Pseudemoia entrecasteauxii* during pregnancy interleukin related molecules, *ILDR1*, *IRAK1*, and *SIGIRR*, are differentially expressed (Griffith et al., 2016). This profile suggests the presence of tricellular tight junctions and/or tricellulin (Higashi et al., 2013; Ikenouchi et al., 2005), and regulation of toll-like receptors (TLRs) and/or IL-1R signaling (Kawagoe et al., 2008; Lin, Lo, & Wu, 2010; Muzio et al., 1997).

(9) The major histocompatibility complex and maternal-fetal immune dynamics

A substantial amount of literature on maternal-fetal immune dynamics was initially focused on uNK cells. Uterine NK cells have a distinct phenotype and function from peripheral NK cells. They have several activating receptors (Manaster & Mandelboim, 2010) but do not exert cytolytic functions on embryonic trophoblasts that they are in contact with (King, Birkby, &

Loke, 1989). Allorecognition of embryonic placental cells by uNK cells is a key regulator of the maternal-fetal immune mechanisms that support placentation in mammals (Moffett et al., 2014). When cells lose their ability to express any HLAs, uNK cells are shown to kill them (Hunt et al., 2005; Ishitani et al., 2003; King, Allen et al., 2000).

In humans, expression of the classical MHC class I (C-MHCI) molecule HLA-C, and nonclassical MHC class I (NC-MHCI) molecules HLA-E, HLA-F and HLA-G on trophoblasts inhibit uNK cell-mediated cytotoxicity (Hunt et al., 2003; King, Burrows et al., 2000). Differing from this, mismatched HLA-C profiles trigger rejection of the transplanted organs (Petersdorf et al., 2014). Selection for balanced polymorphisms in HLA-C alleles and their killer immunoglobin receptors (KIRs) is proposed to be driven by reproductive success, rather than immune recognition of pathogens (Trowsdale & Betz, 2006). Dimorphisms of HLA-C emerged recently within primates (Adams & Parham, 2001).

Similar patterns in MHC profiles have been explored in other viviparous amniotes. C-MHCI antigen, H2-K, is expressed on giant trophoblast cells of mice and this is attributed to trophoblast-induced uterine vasculature transformation (Arcellana-Panlilio & Schultz, 1994; ChatterJee-Hasrouni & Lala, 1982; Hedley et al., 1989; King et al., 1987; Sellens, Jenkinson, & Billington, 1978). H2-D antigen is co-expressed with H2-K in virtually all their other nucleated cells (Madeja et al., 2011). However, H2-K expressing trophoblasts lack H2-D expression. This parallels the expression patterns of C-MHC molecules at the maternal-fetal interface in humans and may be an evolutionarily conserved pattern (Madeja et al., 2011).

In humans, NC-MHCI molecule, HLA-G, is especially tolerogenic (Carosella et al., 2015; González et al., 2012; Hviid et al., 2004; Kovats et al., 1990). In adults, HLA-G is almost exclusively expressed by fetal trophoblasts compared to adult cells (Faulk & Temple, 1976;

King, Burrows et al., 2000; Kovats et al., 1990; Rajagopalan & Long, 2012; Rouas-Freiss et al., 1997). It supports immunotolerance at the maternal-fetal interface (Rebmann et al., 2014). The role of HLA-G in supporting tolerogenic responses to organ transplants appears to be an exploitation of its role in immunotolerance in the utero during pregnancy (Rebmann et al., 2014). HLA-G is upregulated by several molecules that serve essential roles during gestation including progesterone (Yie, Xiao, & Librach, 2006; Yie et al., 2006), IFN-α, IFN-β, and IFN-γ (Rebmann et al. 2003; Lefebvre et al., 2001; Ugurel et al., 2001; Yang, Geraghty, & Hunt, 1995), and IL-10 and TGF-β (Cadet et al., 1995; Moreau et al., 1999).

A similar NC-MHCI gene to HLA-G exists in horses (Davies et al., 2006) where it likely functions to protect the embryo from NK-cell mediated attack (Ott et al., 2014). NC-MHC molecules with similar structure to HLA-G are also found in Rhesus monkeys (Boyson et al., 1997) and baboons (Stern et al. 1987). Mice have two NC-MHCI genes that are expressed on the surface of their placentas and on pre-implanted embryos (Product, Warner, & Goldbard, 1987; Sipes et al., 1996).

In the gestating uterus of the viviparous skink, *Pseudemoia entrecasteauxii*, four putative C-MHCI and two putative NC-MHCI molecules are expressed (Murphy, Thompson, & Belov, 2009). This pattern resembles the C-MHCI and NC-MHCI expression profiles of mammals, suggesting that this viviparous skink utilizes a similar physiological mechanism to ‘hide’ the embryo (Murphy, Thompson, & Belov, 2009). One of the putative NC-MHCI loci (Psen-160Ut/Psen-78G) has a substitution at position 150 where a tryptophan is substituted for a leucine (Murphy, Thompson, & Belov, 2009). When Psen-160Ut/Psen-78G was aligned to NC-MHCI loci of vertebrates ranging from fish to eutherian mammals, tryptophan was conserved at position 150 except in Psen-160Ut/Psen-78G and HLA-G (Murphy, Thompson, & Belov, 2009).

Whether this reflects an evolutionary history associated with immune tolerance at the maternal-fetal interface in *Pseudemoia entrecasteauxii* requires further investigation.

MHCI genes are also expressed in reproductive tissues of oviparous skinks (*Ctenotus taeniolatus* and *Lampropholis guichenoti*) during non-reproductive periods and during late gravidity (Murphy, Thompson, & Belov, 2009). A similar pattern is found in viviparous skinks *Eulamprus tympanum*, *Niveoscincus metallicus*, *Pseudemoia entrecasteauxii* and the reproductively bimodal skink *Saiphos equalis* which all express MHCI genes at non-reproductive periods and during late pregnancy/gravidity (Murphy, Thompson, & Belov, 2009).

Differential expression of immune factors in an oviparous lizard with long egg-retention, *Saiphos equalis* included complement component genes (*C3*, *C9*) and genes relating to MHC loci (*H2-EA*) (Foster et al., 2020). These were also differentially expressed in viviparous individuals of this species during gestation (Foster et al., 2020). Lengthened egg retention occurs in some oviparous squamates. If it requires regulation of the uterine immune environment, then this has important implications for the evolution of viviparity in squamates.

The butyrophilin subfamily 1 member A (*BTN1A1*) is located in the MHCI region of the genome in mammals (Trowsdale, 2011). *BTN1A1* is differentially expressed in the uterus during gestation in a viviparous lizard, *Chalcides ocellatus* (Brandley et al., 2012). *BTN1A1* may have important antimicrobial properties in chicken eggshells (Mann, Maček, & Olsen, 2006). In mammals BTN1A1 is the major protein associated with fat droplets in milk (Jeong et al., 2009).

(10) *Microchimerism and maternal-fetal immune dynamics*

Billingham, Brent and Medawar suggested the concept of actively acquired immunologic tolerance during pregnancy almost 70 years ago (Billingham, Brent, & Medawar, 1953).

Subsequent research over the following decades revealed that substantial transfer of proteins, parasites and even immunologically active cells occurs between mother and embryo (Adams & Nelson, 2004; Axiak-Bechtel et al., 2013; Bakkour et al., 2014; Burlingham, 2010; Fujiki et al., 2008; Gitlin et al., 1965; Khosrotehrani et al., 2005; Owen, 1945; Remington et al., 2006; Turin et al., 2007). Microchimerism, where there is <0.1% donor chimeras in host tissue, is relatively pervasive among eutherians during pregnancy. It plays a role in establishing tolerance to non-inherited antigens. For example, cell populations from the mother that are transferred into embryonic lymph nodes enable the establishment of embryonic Tregs that are tolerogenic toward non-inherited maternal antigens (Mold et al., 2008).

Microchimeric cellular populations are transferred across all placental types (Axiak-Bechtel et al., 2013; Bakkour et al., 2014; Fujiki et al., 2008; Khosrotehrani et al., 2005; Turin et al., 2007). Fetal and maternal cells persist for decades after birth across a range of tissues in mother and offspring, respectively (Adams & Nelson, 2004; Bakkour et al., 2014; Bayes-Genis et al., 2005; Bianchi et al., 1996; Evans et al., 1999; Jonsson et al., 2008; Stevens et al., 2004). There is even a call in the immunology literature to shift from the conventional paradigm of "self vs other" to instead consider the "self" as inherently chimeric (Nelson, 2012). Given that epitheliochorial placentation is sufficient to illicit microchimeric cell populations, the occurrence of similar bidirectional cellular traffic is a reasonable possibility in viviparous squamates.

(11) Paternal alloantigens

Under tenants gleaned from transplant medicine, the maternal immune system would illicit an attack response as early as insemination when maternal tissues are exposed to paternal alloantigens (Borziak et al., 2016; Schumacher & Zenclussen, 2015; Seavey & Mosmann, 2006).

Instead, maternal cells immunologically recognize them at this time without attack (Schumacher & Zenclussen, 2015; Seavey & Mosmann, 2006; Zenclussen et al., 2010). Treg expansion, a process with major influence on maternal-fetal immunotolerance in mammals, is proposed to be driven by several different factors found in seminal plasma (Baratelli et al., 2005; Clark, Fernandez, & Banwatt, 2008; Teles et al., 2013). Mothers may maintain fetal-specific Tregs with memory of the paternal alloantigens (Schober et al., 2012), expediting Treg response in future pregnancies with the same father (Rowe et al., 2012).

Alloantigen exposure at the time of insemination is not restricted to mammals. Seminal fluid of chickens contains two MHC I paternal alloantigens and one MHC II alloantigen (Borziak et al., 2016). It also contains proteins involved in immunity and antimicrobial defenses (Borziak et al., 2016). In hens, evidence suggests that a protective local immunity to pathogens is established after exposure to semen but the mechanisms for this remain unclear (Reiber & Conner, 1995; Reiber, Conner, & Bilgili, 1995).

In mammals, paternal alloantigens and cytokines in seminal fluid drive immune tolerance (Schjenken & Robertson, 2014). Mammalian seminal plasma contains immune-factors (Kelly, 1995; Schjenken & Robertson, 2014)—TGF-β (Breuss et al., 1993; Chu & Kawinski, 1998; Slater & Murphy, 1999), IL-8 (Gutsche et al., 2003), and soluble IL-2 receptor (Srivastava, Lippes, & Srivastava, 1996), prostaglandin E2 (PGE2) and 19-hydroxyprostaglandin E (19-hydroxy PGE) (Denison et al., 1999b), soluble tumor necrosis factor (TNF) receptors (Liabakk et al., 1993), receptors for the Fc portion of γ-globulin, spermine (Evans, Lee, & Flugelman, 1995), and complement inhibitors (Kelly, 1995). In horses and pigs, respectively, the proteins CRISP3 (Doty et al., 2011), PSP-I and PSP-II (Rodriguez-Martinez et al., 2010), act as signaling agents in seminal fluid.

Secretions of growth factors, cytokines and chemokines from cervical and endometrial tissues immediately following insemination generates a proinflammatory environment that likely aids in implantation. In the utero-vaginal junction of chickens and the utero-tubal junction of pigs, several genes were shared following mating compared to non-mating and these genes were involved with immune-modulation (*IFIT5*, *IFI16*, *MMP27*, *ADAMTS3*, *MMP3*, *MMP12*) and pH-regulation (*SLC16A2*, *SLC4A9*, *SLC13A1*, *SLC35F1*, *ATP8B3*, *ATP13A3*), a process essential for implantation (Atikuzzaman et al., 2017, 2015). Instead of mounting an attack, it appears that the uterine immune system and paternal loci work cooperatively to support pregnancy in mammals and gravidity in birds. Whether this applies to reptiles, and how it may influence immune dynamics involved with squamate parity mode evolution, deserves investigation.

(12) Discussion and future directions—maternal-fetal immune dynamics & the evolution of parity modes

Immune processes appear to be important for both oviparity and viviparity—as evidenced here, in part, by overlapping expression profiles of immune genes in female reproductive tissues of chickens and pigs, expression of paternal antigens in avian seminal fluid, and uterine expression of maternal antigens in oviparous and viviparous skinks. This highlights the scientific advances made since Medawar’s paradigm, when embryos were treated as analogs to allografts. Nonetheless, viviparity is associated with complex immune dynamics between maternal, fetal and paternal tissues. Unique MHC expression profiles were also identified in some viviparous skinks compared to oviparous relatives (Murphy et al., 2009).

Substantial immunological changes in species with less active adaptive immune systems may not be necessary (Chaouat, 2016). Oviparous and viviparous *Zootoca vivipara* have remarkably similar cytokine expression during gravidity and gestation (Paulesu et al., 2005). Labile parity modes in squamates may be supported if they are more heavily reliant on the innate immune system for reproduction. However, reptiles may not have distinguished innate and adaptive immune systems (Zimmerman et al., 2020). It remains difficult to resolve how this all applies to the evolution of viviparity in squamates without studying immune gene activity during gestation and gravidity in more taxa.

Changes to loci that serve overlapping functions across the Main Five may have a disproportionate influence on transitions between parity modes. In this section I reviewed two molecules, *TGF*-β and progesterone, that exert influence on multiple Main Five categories. Progesterone influences uterine quiescence (embryonic retention), hepatic vitellogenesis (nutrient provisioning) and regulation of inflammatory responses in utero (maternal-fetal immune dynamics). Genes in the TGF-β family play a role in placental development and maternal-fetal immune dynamics. TGF-β is implicated in placental development in eutherians (Hempstock et al., 2004; Caniggia et al., 2000; Lafontaine et al., 2011). A TGF-β receptor protein (TGFBR1) was associated with placental development in *Phrynocephalus vlangalii* (Gao et al., 2019). In humans TGF-β upregulates tolerogenic HLA-G in utero and is an immune factor in mammalian seminal fluid. Multiple gene in the TGF-β family are also differentially expressed during gestation in other viviparous lizards, *Pseudemoia entrecasteauxii* and *Saiphos equalis* (Foster et al., 2020; Griffith et al., 2016). Examining the functions of TGF-β and progesterone across other amniotes may reveal insights into how these molecules influence the evolution of parity modes.

In mammals, inflammation appears to be involved with two of the Main Five processes—regulation of maternal-fetal immune dynamics and embryonic retention. It is intriguing to consider the implications this has for the interconnectedness of the Main Five. Greater interconnectedness would suggest that changes to few loci involved with the Main Five could cause a cascading effect to support more labile transitions between parity modes.

Implantation and parturition in therian mammals evolved from a shared inflammatory attachment reaction (Hansen et al., 2017). The process of implantation has important implications for maternal-fetal exchanges of inorganic and organic material and maternal-fetal immune dynamics. Given that inflammation is associated with implantation and parturition implicates it in gas, water, and nutrient provisioning (including calcium here), maternal-fetal immune dynamics and length of embryonic retention. However, implantation in mammals and viviparous squamates is not homologous (Griffith, Van Dyke, & Thompson, 2013). Therefore, it is difficult to make inferences about how substantial the influence of inflammation is on the evolution of parity modes in squamates. Nonetheless, the abundant literature on uterine inflammatory processes during human pregnancy and the evolution of inflammatory processes that supported the evolution of viviparity in mammals (Challis et al., 2009; Chavan, Griffith, & Wagner, 2017; Mor et al., 2011; Griffith, Chavan et al., 2017; Stadtmauer & Wagner, 2020d) serve as indispensable resources for exploring the role of inflammation in squamate viviparity.

I resist expanding on this further in viviparous reptiles given the need for more research on the reptile immune system overall (Zimmerman, 2020). I suspect that the immune system plays a central role in dictating the plasticity of parity modes in some Squamata clades. However, further work is necessary to validate this.

VII. Discussion

(1) Two new mechanisms for transitions between oviparity and viviparity, without intermediate stages, stand out. These are meant as tools to be broadened and challenged with the goal of advancing scientific insight on the subject.

   a. The genomics and physiology of amniote parity mode evolution does not preclude an origin of viviparity in the MRCA of Lepidosaurs. I propose the following mechanism—a change to the phenotype or function of basal caps instantaneously prevented calcium carbonate deposition (basal cap hypothesis); the eggshell loss enabled uterine exposure to chorioallantoic progesterone production (extending embryonic retention) and incipient calcium matrotrophy (supporting embryonic development); the growing embryo increasingly over distended the uterus triggering parturition of a fully developed offspring. This is one way to imagine viviparity evolving in the MRCA of Lepidosaurs.
   b. A reversal back to oviparity may evolve most easily within viviparous clades with substantial maternal calcium provisioning through the following sequence of events—calcium secretions in utero stick to the outer embryonic membrane instead of being absorbed by the chorioallantois; oviposition can then occur in one of two ways 1) the death of corpora lutea or 2) the calcified eggshell blocks a threshold of chorioallantoic progesterone production from reaching uterine tissue; the calcified eggshell provides embryonic calcium that is transported upon embryonic metabolic demand.

(2) Changes to gene(s) or physiological processes associated with more than one of the Main Five should disproportionately influence parity mode evolution—*SLC* gene superfamily, TGF-β, *BMPR1B*, progesterone, *PMCA*, calbindin-D28K, *SPP1*, sustained functioning of the corpora lutea and inflammation.

(3) Growing evidence in the medical literature suggests that immune system interactions at the maternal-fetal interface in mammals did not evolve simply through tolerance, evasion, or suppression (Chaouat, 2016; Chavan, Griffith, & Wagner, 2017; Moffett & Loke, 2004, 2006). Instead, maternal-fetal immune dynamics have a deep evolutionary history that enables both embryo and mother interact cooperatively (Yoshizawa, 2016). Future research on squamate parity mode evolution should consider maternal-fetal immune dynamics in this context.

(4) Ectothermy influences parity mode evolution in squamates because it entails slower antibody responses and a greater reliance on climatic conditions for embryonic development, thus involving maternal behavior and unique pressure on embryos to signal parturition.

(5) Advancing bioinformatics approaches are extending the horizon for studies on the genomics of complex trait evolution (Capecci et al., 2020; Halfon, 2017; M’barek et al., 2019; Mittal & Hasija, 2020).

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