

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

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5

6 **Abstract**

7

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

24

25 *Key Words:* reproductive mode, parity modes, viviparity, oviparity, squamates, eggshell

26 deposition, embryonic retention, embryonic calcium transport, maternal-fetal immune dynamics,

27 comparative evolutionary physiology.

28

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92 **I. Introduction**

93

94 A reappraisal is needed for the conceptual framework used to research the evolution of
95 oviparity (egg-laying) and viviparity (live-birth) in amniotes (birds, non-avian reptiles, and
96 mammals). Squamates (snakes and lizards) are unique amongst amniotes because they have
97 highly variable parity modes. Beginning with the first phylogenetic analyses on the subject, a
98 warm-blooded scientific disagreement has persisted over the labile nature of evolutionary
99 transitions between parity modes (Blackburn, 1999, 2015; de Fraipont et al., 1996; Griffith et al.,
100 2015; Harrington & Reeder, 2017; Lee & Shine, 1998; Pyron, 2015; Pyron & Burbrink, 2014,
101 2015; Recknagel et al., 2018). With modern genomic technologies, it is prudent to acknowledge
102 that the relative difficulty of changing phenotypes cannot be determined from morphology alone
103 or unidentified physiological mechanisms. At least theoretically, any phenotypic change could be
104 facilitated by simple genomic changes (e.g., a single nucleotide polymorphism) or any
105 combination of multi-omic changes to any number of loci. As research begins to reveal the
106 molecular networks involved with parity mode evolution, it is important to avoid bias that could
107 be introduced by assumptions on the feasibility of transitions in either direction.

108 The earliest estimates predicted that viviparity evolved independently between 90-100
109 times in squamates (Blackburn, 1982, 1985; Shine, 1985; Blackburn, 1992). These estimates
110 assumed that reversals back to oviparity should be exceedingly rare (hereafter rare-reversal
111 model) (Fitch, 1970; Neill, 1964; Tinkle & Gibbons, 1977). An intermediate phenotype of re-
112 evolving an eggshell may be physiologically unviable, preventing reversals (Blackburn, 1995;
113 Griffith et al., 2015). This was demonstrated when experimentally induced extended egg
114 retention in phrynosomatid lizards resulted in adverse embryonic development attributable to

115 impeded gas exchange imposed by the eggshell (Mathies & Andrews, 1999, 2000; Parker &
116 Andrews, 2006). However, this result may be specific to the clade.

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

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

137 An early origin of viviparity for squamates or within different clades of squamates is not
138 unreasonable. The oldest known amniotes (Mesosauridae) were viviparous (Piñeiro et al., 2012).
139 Several basal lineages of diapsids, the clade containing all modern birds and reptiles, were
140 viviparous (Motani et al., 2014). Viviparity may have been common in terrestrial reptiles ~248
141 mya (Motani et al., 2014). Recently, the first fossil record of viviparity was reported in a snake,
142 *Messelophis variatus*, dating back 47 mya (Chuliver et al., 2022). This record compliments fossil
143 records of viviparous lizards and challenges several dominant hypotheses on parity mode
144 evolution including the rare-reversal model and the cold climate hypothesis (Tinkle & Gibbons,
145 1977).

146 In squamates, the degree of parity mode variation within a clade varies dramatically for,
147 thus far, non-generalizable environmental, developmental, or genomic reasons (Anderson et al.,
148 1987; Blackburn, 2005; Griffith et al., 2017; Griffith & Wagner, 2017; Hodges, 2004; Li et al.,
149 2009; Schwarzkopf & Andrews, 2012; Stewart et al., 2013; Van Dyke et al., 2014; Webb et al.,
150 2006; Zimin et al., 2022). Oviparity and viviparity both entail numerous gains and losses of
151 complex structures and processes (Blackburn, 1992; Lee & Doughty, 1997; Packard et al., 1977;
152 Rothchild, 2003; Shine, 1985; Shine & Bull, 1979; Tinkle & Gibbons, 1977)—some of which
153 are considered at the molecular level for the first time in this review. Using biological evidence
154 gleaned from interdisciplinary literature across amniotes, I explore physiological features of
155 gestation and gravidity, including those that could be exploited to support rapid shifts between
156 parity modes, and those that may facilitate or impede reversals. I do not understand proximate
157 causes of squamate parity mode evolution to adhere to one generalizable model, I advocate for
158 future work to embrace the complexity of this system. I hope this serves as a foundation for
159 further exploration on the genomic evolution of parity modes in squamates.

160

161 *(1) Terminology*

162 I use the conventional definition of viviparity as retention of eggs until the stage when the
163 embryo is fully developed (Shine, 1985; van Dyke et al., 2014). Oviparity is defined by eggs that
164 develop outside the mother (Stewart, 1997). I use the terms gravidity and gestation to describe
165 the period of internal retention of the embryo in oviparous and viviparous taxa, respectively.
166 Vertebrate placentas are conventionally defined by apposition of maternal and fetal tissues
167 (Mossman, 1937; Stewart & Blackburn, 1988). It is accepted that all viviparous squamates have
168 a chorioallantoic placenta under this definition (Murphy et al., 2009; Stewart & Blackburn,
169 1988). The avian chorioallantoic membrane and mammalian chorioallantoic placenta are
170 homologous (Metcalf & Stock, 1993). I sometimes refer to this organ as the chorioallantoic
171 tissue to describe it for both parity modes. Oviposition refers to the process and act of egg-
172 laying, while parturition refers to the process and act of giving birth to live-young.

173

174 *(1) Main five physiological changes of parity mode transitions*

175 Several physiological features are expected to change during transitions between
176 oviparity and viviparity. I break this down into five physiological features (hereafter Main
177 Five)—1) length of embryonic retention (Murphy & Thompson, 2011; Packard et al., 1977;
178 Thompson & Speake, 2006)—only viviparous mothers retain the embryo for the entirety of
179 development; 2) eggshell deposition (Heulin et al., 2005; Packard et al., 1977; van Dyke et al.,
180 2014)—viviparous embryos generally do not have an eggshell; 3) placental development for
181 maternal-fetal exchange of required water, gas and/or nutrients (Blackburn, 1992, 2015; Guillette
182 & Guillette, 1993; Thompson et al., 2000; Thompson & Speake, 2006); 4) embryonic calcium

183 provisioning (Packard et al., 1985; Shadrix et al., 1994; Thompson & Speake, 2006)—sources of
184 embryonic calcium and timing of uterine calcium secretions generally differs between oviparous
185 and viviparous reproduction; 5) maternal-fetal immune dynamics (Graham et al., 2011;
186 Hendrawan et al., 2017)—viviparous reproduction is associated with maternal and embryonic
187 exposure to foreign tissues, which is likely to require enhanced regulation of maternal-fetal
188 immune systems.

189

190 **II. Length of Embryonic Retention**

191

192 Viviparous amniotes retain the embryo until it is fully developed, but oviparous amniotes
193 retain the embryo for a fraction of that time. There are some examples of oviparous squamates
194 with long egg retention, but oviposition still occurs prior to complete embryonic development in
195 these taxa (Heulin et al., 2002). Rather than using precocious hatching and parturition (PH&P),
196 like that of opossums and early viviparous mammals (Wagner et al., 2014), squamates evolve
197 viviparity through extended egg retention (García-Collazo et al., 2012; Guillette & Guillette,
198 1993; Shine, 1983). Thus, processes affecting the length of embryonic retention are expected to
199 change to support transitions between parity modes (García-Collazo et al., 2012; Guillette &
200 Guillette, 1993; Murphy & Thompson, 2011; Thompson & Speake, 2006).

201

202 *(1) Parturition & oviposition*

203 The genes and hormones involved with initiating and ending gestation may provide insights
204 into the loci squamates can co-opt to change the length of embryonic retention during parity
205 mode transitions. Parturition and oviposition terminate embryonic retention. Parturition can be

206 divided into four parts (Terzidou, 2007; Vannuccini et al., 2016)—quiescence (Phase 0),
207 activation (Phase 1), stimulation (Phase 2) and involution (Phase 3). In eutherian mammals,
208 several processes contribute to the initiation and termination of gestation including inflammation
209 (Challis et al., 2009; Hansen et al., 2017), maternal recognition of pregnancy (MRP), mechanical
210 stretch of uterine tissues (Sooranna et al., 2004; Shynlova et al., 2008), and fluctuating
211 concentrations of corticotropin-releasing hormone, progesterone, and estrogen (Challis et al.,
212 2000; Condon et al., 2004; Mitchell et al., 1984; Shaw & Renfree, 2001).

213

214 (i) *Quiescence & sustained progesterone production in reproductive tissues*

215 Extended embryonic retention could be achieved by triggering mechanisms that extend
216 uterine quiescence, inactivity of the uterus. Inhibition of myometrial contractions through
217 sustained progesterone production supports quiescence across different viviparous amniotes
218 (Bazer, 1992; Casey & MacDonald, 1997; Fergusson & Bradshaw, 1991; Ilicic et al., 2017;
219 Murphy & Thompson, 2011; Putnam et al., 1991; Soloff et al., 2011). The corpus luteum (or
220 plurally called corpora lutea), a transient progesterone-producing organ, produces progesterone
221 during gestation (Gemmell, 1995). Extended lifespan of the corpus luteum likely aided the
222 evolution of viviparity in mammals (Amoroso, 1968; Callard et al., 1992; Stouffer & Hennebold,
223 2015). Thus, early research on squamate viviparity also explored the influence of corpus luteum
224 lifespan. The lifespan of corpora lutea associates with oviparous egg retention and oviposition
225 (Diaz et al., 1994; Fox & Guillette 1987; Guillette & Guillette 1993; Jones & Guillette 1982).
226 Eggshell formation in oviparous Whiptail lizards, *Cnemidophorus uniparens*, is even disrupted
227 by experimental removal of corpora lutea (Cuellar, 1979). The lifespan of corpora lutea do not

228 consistently correlate with length of embryonic retention in viviparous squamates like it does in
229 mammals (Albergotti & Guillette, 2011; Callard et al., 1992).

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

239 Different loci are signaled by embryos for MRP across mammals. Human chorionic
240 gonadotropin hormone (hCG) establishes MRP (Ross, 1979; Behrman et al., 1993; Duncan,
241 McNeilly, & Illingworth, 1998; Duncan, 2000; Ticconi et al., 2007). In pigs, MRP is triggered by
242 embryonic signaling of oestrogen (Geisert et al., 1990). Glycoproteins, estradiol (E2) and
243 prostaglandin E2 (PGE2) have been implicated in signaling MRP in horses (Klein & Troedsson,
244 2011; Klein, 2016). In ruminants, embryonic signaling of IFN- τ establishes MRP (Bazer, 2013;
245 Bazer, et al., 1997; Thatcher et al., 1995). During gestation in the uterus of viviparous African
246 Ocellated skinks, *Chalcides ocellatus*, four receptors for interferon alpha, beta, omega, and
247 gamma are differentially expressed but no expression of IFN- τ was detected compared to non-
248 gestational uterine tissue (Brandley et al., 2012). I was unable to find expression patterns of MRP
249 signaling homologs in other squamate reproductive tissues based on the available literature.
250 Should MRP occur in squamates, it may be signaled by loci that are clade-specific, like in

251 mammals. This makes comparatively evaluating the influence of MRP on the evolution of
252 viviparity an interesting avenue for future research.

253 The evolution of viviparous extended embryonic retention may be sufficiently supported by
254 maintenance of chorioallantoic progesterone production coupled with eggshell loss (Griffith,
255 Brandley et al., 2017). This theory may be broadly applicable across amniotes given that the
256 most recent common ancestor of amniotes likely had a chorioallantois with an endocrine
257 function (Griffith, Chavan et al., 2017). Following death of the corpus luteum during gestation,
258 placental progesterone production supports extended embryonic retention in eutherian mammals
259 (Castracane & Goldzieher, 1986; Ellinwood et al., 1989; Nakajima et al., 1991; Rothchild, 2003;
260 Spencer & Bazer, 2004). Viviparous Italian Three-toed Skinks, *Chalcides chalcides*, shift to
261 chorioallantoic progesterone production following degradation of corpora lutea during gestation
262 (Guarino et al., 1998). The placenta of viviparous Southern Snow Skinks, *Carinascincus*
263 *microlepidotus*, produces minimal progesterone but has a strong capacity to convert
264 pregnenolone to progesterone (Girling & Jones, 2003). Whereas all genes involved with a known
265 biosynthesis pathway for progesterone production are expressed in the placenta of horses, *Equus*
266 *caballus*, only some loci were detected in the chorioallantois of chickens, *Gallus gallus*,
267 viviparous Southern Grass Skinks, *Pseudemoia entrecasteauxii*, and oviparous and viviparous
268 Southeastern Sliders, *Lerista bougainvillii* (Griffith, Brandley et al., 2017). Thus, if
269 chorioallantoic progesterone production has supported multiple origins of viviparity in amniotes,
270 it is not evidenced by a conserved ancestral gene expression pattern (Griffith, Brandley et al.,
271 2017).

272 Other female reproductive tissues in squamates express genes involved with progesterone
273 biosynthesis—StAR-related lipid transfer domain protein 3 (*StARD3*) and hydroxy-delta-5-

274 steroid dehydrogenase (*HSD3B1*). *STARD3* is significantly upregulated in the uterine tissue
275 during pregnancy in viviparous African Ocellated skinks, *Chalcides ocellatus*, along with
276 significant differential expression of seven paralogs (Brandley et al., 2012). Compared to non-
277 gestational samples, *HSD3B1* is significantly upregulated in the uterus during early and late
278 gestation in viviparous individuals of reproductively bimodal *Saiphos equalis* (Foster et al.,
279 2020). Oviparous individuals from the same species did not exhibit this expression pattern
280 (Foster et al., 2020). Activity of *HSD3B1* was detected in the mucosal epithelium of oviparous
281 Eastern Garden Lizards, *Calotes versicolor* (Shanthakumari et al., 1990, 1992), and in the uterine
282 glands of oviparous Keeled Indian Mabuya, *Eutropis carinata* (Mundkur & Sarkar, 1982). Other
283 loci involved with the biosynthesis of progesterone (e.g., steroidogenic acute regulatory protein
284 or cytochrome-P450-family-11-subfamily-A-polypeptide-1) serve as further candidates for
285 exploring the relationship between organ-specific patterns of progesterone production and the
286 evolution of extended embryonic retention in viviparous squamates. Biosynthesis of
287 progesterone may also occur through an unknown biosynthesis pathway in squamate
288 reproductive tissues (Griffith, Brandley et al., 2017).

289 For progesterone to prevent myometrial contractions and support quiescence, there must be
290 progesterone receptors (PGRs) in the uterus (Mesiano et al., 2011; Young et al., 2011). In
291 humans, progesterone responsiveness is related to specific ratios of PGRs, *PR-A* and *PR-B*, in
292 myometrial cells (Young et al., 2011). Minimal research exists on PGR expression in squamate
293 reproductive tissues. One study found that in the uterus of the yolk-sac in viviparous Southern
294 Grass Skinks, *Pseudemoia entrecasteauxii*, one progesterone receptor, *PGRMC2*, is upregulated
295 compared to non-gestational uterine tissue (Griffith et al., 2016); Another progesterone receptor,
296 *PGR*, is downregulated in the uterus of the chorioallantoic placenta and yolk sac placenta

297 compared to non-gestational uterine tissue (Griffith et al., 2016). Downregulation of both *PGR*
298 and *PGRMC2* in the uterus during gestation was detected in viviparous *Chalcides ocellatus*
299 (Brandley et al., 2012). Measuring expression of PGRs and their ratios in uteruses of oviparous
300 and viviparous squamates may provide insights on mechanisms of extended embryonic retention.

301

302 (ii) *Activation & progesterone withdrawal*

303 The activation stage of parturition is marked by the withdrawal, or functional withdrawal, of
304 progesterone leading to an estrogen dominated response during the next state, stimulation
305 (Bakker et al., 2017; Fergusson & Bradshaw, 1991). Progesterone may withdraw in response to
306 environmental stimuli in reptiles during parturition (Shine & Guillette, 1988). In mammals,
307 activation is marked by increasing concentrations of corticotropin-releasing hormone and
308 contraction associated proteins (CAPs) including connexin-43, prostaglandins, oxytocin
309 receptors, prostanoid receptors and cell signaling proteins (Bakker et al., 2017; Ilicic et al., 2017;
310 Leadon et al., 1982; Pashen & Allen, 1979; Whittle et al., 2000). Pro-inflammatory cytokines
311 and chemokines, prostaglandin synthase-2 (*COX-2*, also referred to as *PTGS2*), and NF- κ B also
312 influence activation in mammals (Christiaens et al., 2008; Lappas et al., 2002; Lappas & Rice,
313 2007; Lindström & Bennett, 2005; Olson, 2003; Terzidou, 2007).

314 Some similar patterns are associated with oviposition in birds. In chickens, *Gallus gallus*,
315 prostaglandin F (PGF) concentrations increase in the hours leading up to oviposition (Takahashi
316 et al., 2004). Experimental injection of oxytocin and arginine vasotocin, similar
317 neurohypophyseal peptides, revealed that uterine tissues of chickens, *Gallus gallus*, maintain
318 responsiveness to oxytocin but are more sensitive toward arginine vasotocin (Ewy, 1969).
319 Murphy & Thompson (2011) provide a rather exhaustive list of resources on progesterone and

320 estrogen assays across oviparous and viviparous squamates. Future research should consider
321 exploring parallels between mechanisms of activation in mammals and squamates. Any process
322 that can trigger or stall activation should lead to extended embryonic retention.

323

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

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

333 Physical stretching of the uterus causes an influx of calcium and sodium, altering the action
334 potential and enabling contractions (Kao & McCullough, 1975). Calcium further activates
335 voltage gated calcium channels on myometrial cell membranes, enhancing the influx of calcium
336 ions, mediating the force and speed of myometrial contractility (Arrowsmith & Wray, 2014;
337 Wray et al., 2015). The influence of uterine overdistention on oviposition and parturition in birds
338 and non-avian reptiles has not yet been examined, to our knowledge. However, differentially
339 expressed genes functionally enriched the GO term for “voltage-gated calcium channel activity”
340 in uterine tissues during gravidity and gestation in oviparous and viviparous *Saiphos equalis*
341 (Foster et al., 2020). A uterine response to overdistention is among the many possible
342 explanations for this. It may be important to consider the influence of uterine overdistention on

343 squamate parity mode transitions, because should bioelectrical responses to uterine
344 overdistention be a common feature of vertebrate parturition, lessened distention may be a hurdle
345 to reverse back to oviparity.

346 Uterine overdistention may additionally influence parturition by triggering the “inflammatory
347 pulse” that activates further myometrial contractility (Adams Waldorf et al., 2015). At this time,
348 there is an influx of uterine and embryonic pro-inflammatory genes and immune cells (Adams
349 Waldorf et al., 2015; Charpigny et al., 2003; Marvin, 2002; McEvoy & Tetrokalashvili, 2018;
350 Mesiano et al., 2002; Park et al., 2005; Romero et al., 1994; Terzidou, 2007; Welbergen et al.,
351 2008). The inflammatory responses associated with uterine contractions in humans involve
352 actions of prostaglandins (PGs), oxytocin, corticotropin-releasing hormone, cytokines, and
353 neutrophils (Adams Waldorf et al., 2015; De Rensis et al., 2012; Gibb, 1998; McEvoy &
354 Tetrokalashvili, 2018; Olson & Hertelendy, 1983; Park et al., 2005; Romero et al., 1994; Sykes
355 et al., 2014; Terzidou, 2007).

356 The cycling concentrations of a neuropeptide, corticotropin-releasing hormone (CRH),
357 supports parturition in humans. This has been compared to a biological clock that is initiated at
358 early stages of gestation (Lockwood, 2004; McLean & Smith, 2001). Increased production of
359 CRH facilitates parturition by interacting with CRH receptors, CRH-R1 and CRH-R2, which
360 promote myometrial relaxation or contractility, respectively (Campbell et al., 1987; Li & Challis,
361 2005; Petraglia et al., 1995; Yuan & López Bernal, 2007). Altered regulation, phenotype or
362 function of loci that function as biological clocks, like CRH, may have a particularly strong
363 influence on evolutionary changes to length of embryonic retention, a trait inherently related to
364 time.

365 Placental CRH production has only been identified in primates thus far (Challis et al., 2005;
366 Emanuel et al., 1994; Florio et al., 2002; Grammatopoulos et al., 1994; Grammatopoulos et al.,
367 1996; Karteris et al., 1998; Mendelson, 2009; Robinson et al., 1989; Torricelli et al., 2007).
368 Placental CRH production may, therefore, be unique to primates. Alternatively, absence of
369 placental CRH production in other taxa may be an artifact of bias sampling. The amino acid
370 sequence of CRH is highly conserved in vertebrates (Noy et al., 2017), indicating there is a
371 possibility for shared function across diverse taxa. Like CRH cycling in mammals, timely
372 fluctuations of a neuropeptide that stimulates uterine contractions, arginine vasotocin (AVT),
373 enables oviposition in birds, turtles, and lizards (Ewy, 1969; Fergusson & Bradshaw, 1991;
374 Guillette Jr & Jones, 1980; Jones et al., 1987; Rzasa, 1978; Srivastava et al., 2007; Wu et al.,
375 2019).

376 Prostaglandin E₂ (PGE₂) and prostaglandin F_{2α} (PGF_{2α}) influence, respectively, uterine
377 contractions and cervical relaxation for oviposition/parturition across many amniotes including
378 humans, *Homo sapiens* (Gibb 1998; Terzidou 2007), domestic pigs (De Rensis et al. 2012),
379 domestic chickens (Hertelendy et al., 1974; Olson et al., 1986), and Loggerhead Sea turtles
380 (Guillette et al., 1991). Injections of PGF_{2α} and PGE₂ induce parturition in viviparous Yarrow's
381 Spiny lizards, *Sceloporus jarrovi*, and Raukawa geckos, *Woodworthia maculatus* (Cree &
382 Guillette, 1991; Guillette et al., 1992). However, no injected dosages of PGF_{2α} or PGE₂ induced
383 oviposition in oviparous Collard lizards, *Crotaphytus collaris*, Eastern Fence lizards, *Sceloporus*
384 *undulatus*, Six-lined racerunners, *Aspidoscelis sexlineatus*, or Striped Plateau lizards, *Sceloporus*
385 *virgatus* (Guillette et al., 1991). It is interesting that injections of PGF_{2α} and PGE₂ induced
386 parturition in viviparous lizards but did not induce oviposition in oviparous lizards studied.
387 Given this, it is plausible that regulatory or functional changes to PGF_{2α} and/or PGE₂ in

388 squamates could facilitate changes to the length of embryonic retention to support transitions
389 between reproductive modes. However, induction of parturition with $\text{PGF}_{2\alpha}$ in viviparous
390 *Woodworthia maculatus* only worked with pre-treatment of β -adrenoceptor (Cree & Guillette,
391 1991).

392 $\text{PGF}_{2\alpha}$ decreases progesterone concentrations during stimulation (De Rensis et al., 2012). In
393 humans, biosynthesis of PGs is driven largely by the enzyme cyclooxygenase (*COX*)-2 rather
394 than *COX-1* (i.e., prostaglandin synthase-2 and -1) (Slater et al., 1995, 1999). This helps
395 maintain the decreased progesterone/estrogen ratio of stimulation. In ovariectomized viviparous
396 Garter snakes, *Thamnophis*, increased estrogen stimulated thickness of uterine epithelial cells
397 and glandular activity, whereas administration of progesterone had little influence on uterine
398 histology (Mead et al., 1981). Uterine pig models revealed that estrogen stimulates involuntary
399 contractions and relaxation of the uterus (Mueller et al., 2006).

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

411 A few studies consider the role of cytokines on squamate reproduction but not during
412 oviposition or parturition (Hendrawan et al., 2017; Paulesu et al., 1995, 2005, 2008). Some
413 studies detected expression of cytokines during late gestation (Foster et al., 2020; Gao et al.,
414 2019; Recknagel et al., 2021). TNF- α related activity was only detected at this time in viviparous
415 Tussock Cool-skinks, *Pseudemoia entrecasteauxii*, which were found to downregulate TNF- α
416 induced proteins (*TNFAIP6* and *TNFAIP8L2*) in the ‘uterus of the chorioallantoic placenta’ and
417 *TNFAIP6*, *TNFAIP1*, and *TNFAIP2* in the ‘uterus of the yolk-sac placenta’ compared to not
418 gestational uterine tissues (Griffith et al., 2016). Activity of TNF- α in reproductive tissues
419 during gestation in viviparous Italian Three-toed skinks, *Chalcides chalcides*, and reproductively
420 bimodal European common lizards, *Zootoca vivipara*, was associated with maternal-fetal
421 immune dynamics (Paulesu et al., 1995, 2005, 2008; Hendrawan et al., 2017).

422 Altered expression or phenotype of contractility agonists, oxytocin receptors and estrogen
423 receptors, and contractility antagonists, progesterone receptors and β -adrenergic receptors
424 (McEvoy & Tetrokalashvili, 2018) may also change the length of embryonic retention to support
425 transitions between parity modes. Differences in length of embryonic retention in oviparous and
426 viviparous agamas, *Phrynocephalus przewalskii* and *Phrynocephalus vlangalii*, appears to be
427 driven by regulatory differences of prostaglandins, *COX-2*, an AVT receptor (*MTR*), β -adrenergic
428 receptors, and estrogen receptors. During oviposition, *P. przewalskii*, exhibited the following:
429 promotion of contractions through downregulation of *ADRB2*, and upregulation of *COX-2* and
430 prostaglandin, and absent (potentially lost) expression of two estrogen receptors (*ESR1* and
431 *ESR2*) and the AVT receptor, *MTR* (Gao et al., 2019). During the stage of gestation
432 corresponding to oviposition, viviparous sister-species, *P. vlangalii*, exhibited the following
433 pattern: inhibition of contractions caused by upregulation of β -adrenergic receptor (*ADRB2*) and

434 downregulation of two estrogen receptors (*ESR1*, *ESR2*), an *MTR*, *COX-2*, and prostaglandin
435 (Gao et al., 2019). Some viviparous squamates, *Saiphos equalis*, *Chalcides ocellatus*, and
436 *Pseudemoia entrecasteauxii*, share some of these expression patterns (*COX-2*, *MTR*, and *ADRB*,
437 respectively) thought to be involved with extended embryonic retention in viviparous *P.*
438 *vlangalii* (Brandley et al., 2012; Foster et al., 2020; Gao et al., 2019; Griffith et al., 2016).
439 However, no species shared the same profile for these loci as *P. vlangalii*. However, tissue
440 sampling across species was done at different developmental stages across the four studies.

441 Recently, in humans, the only Classical Major Histocompatibility Antigen (C-MHC)
442 expressed by trophoblasts (specialized placental cells) was associated with parturition when it
443 was discovered that HLA-C is significantly increased during laboring term and preterm placentas
444 compared to non-laboring placentas (Hackmon et al., 2017). The authors suggested a mechanism
445 where fetal HLA-C open conformers on the placenta provoke inflammation of maternal tissues,
446 leading to parturition (Hackmon et al., 2017). Expression of MHC alloantigens, foreign antigens
447 to the host, by fetal cells is also associated with parturition in cows and horses (Benedictusa et
448 al., 2015; Davies et al., 2004; Joosten et al., 1991; Rapacz-Leonard et al., 2018). Around one
449 month prior to parturition in cows, endometrial epithelium thins and eventually disappears
450 completely, putting the antigen-presenting trophoblasts (Adams et al., 2007) in contact with
451 maternal connective tissue of the endometrium (Grunert, 1986; Podhalicz-Dzięgielewska et al.,
452 2000). Fetal MHC alloantigens are proposed to promote the loosening of maternal and fetal
453 tissues (Benedictusa et al., 2015; Ginther, 1979). MHC molecules are expressed during gestation
454 and gravidity in some squamates (Murphy & Thompson, 2010) but their role in oviposition or
455 parturition has not yet been considered to my knowledge. Identifying the presence or absence of
456 MHC alloantigens on embryonic tissues before and during parturition across more diverse taxa

457 may reveal how ubiquitous the influence of embryonic MHC molecules is on parturition and
458 oviposition.

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

463

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

465 Circadian rhythm and temperature-specific influences on reproduction may uniquely
466 influence the molecular processes of oviposition and parturition in birds and non-avian reptiles,
467 respectively. The physiology of avian oviposition is dependent on a circadian schedule
468 (Williams, 2012). A general model of an “open period”, when eggs are laid are separated by
469 “laying gaps” (Williams, 2012). Chicken ovulation and oviposition cycles leave an 8-hour open
470 period where luteinizing hormone (LH) and progesterone can surge, initiating ovulation and
471 continuing the cycle. At the extreme, the ancient murrelet, *Synthliboramphus antiquus*, oviposits
472 a two-egg clutch on seven-day intervals (Williams, 2012). Longer laying intervals have been
473 associated with longer intervals between initiation of yolk development (Astheimer & Grau,
474 1990).

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

480

481 *(3) Pre-term birth and embryonic retention mechanisms*

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

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

496

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

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

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

514

515 **III. Eggshell Deposition**

516

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

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

539

540 *(1) Mineral composition of eggshells*

541 The different mineral compositions of eggshells across amniotes may provide insight into the
542 differing physiological conditions and evolutionary histories under which they are formed (Table
543 1.1). Taxa use a polymorph of calcium carbonate—calcite, aragonite or vaterite—to develop the
544 eggshell (Hincke et al., 2012). Amorphous calcium carbonate (ACC) is a transient non-
545 crystalline precursor phase of calcite and aragonite that is important for many calcification
546 processes in invertebrates (Hincke et al., 2012). It was recently shown to control avian eggshell
547 mineralization (Rodríguez-Navarro et al., 2015).

548 In birds, the organic components of uterine fluid promote the formation of calcite
 549 (Hernández-Hernández, Gomez-Morales et al., 2008; Hernández-Hernández, Rodriguez, et al.,
 550 2008; Nys, 2008). Most amniotes use this polymorph (Hernández-Hernández, Gomez-Morales et
 551 al., 2008; Hernández-Hernández, Rodriguez, et al., 2008; Legendre et al., 2022; Nys, 2008).
 552 However, turtle eggshells are predominately developed with aragonite (Mikhailov, 1997). The
 553 eggshell of most squamates consists of an inner fibrous protein layer overlain by calcium
 554 carbonate that can be a single layer or scattered crystals (Packard & DeMarco, 1991).

555 There are differing accounts on the microstructure of monotreme eggshells and further
 556 studies are needed to determine secondary homology (Legendre et al., 2022). Nonetheless, they
 557 are described as proteinaceous, permeable, and flexible (Hughes, 1984). Marsupials lack an
 558 eggshell but have an eggshell coat that is secreted by the epithelial cells and endometrial glands
 559 early on in embryonic development prior to implantation (Roberts et al., 1994; Roberts & Breed,
 560 1996). This may provide a boundary that immunologically protects the embryo (Roberts &
 561 Breed, 1996).

562 **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: <ul style="list-style-type: none"> • 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

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

565
 566
 567 (2) Uterine glands & the evolution of parity modes

568 Eggshell deposition occurs in the uterus where the uterine glands secrete precursors of the
569 eggshell (Girling, 2002; Guillette et al., 1989; Jonchere et al., 2010; Nys et al., 2004; Picariello et
570 al., 1989; Stewart & Eday, 2010). Uterine glands are critical for gravidity/gestation in both
571 oviparous and viviparous amniotes (Braz et al., 2018; Burton et al., 2002; Cooke et al., 2013).
572 For example, in humans, uterine glands provide histiotrophic nutrition to the early embryo
573 (Burton et al., 2002). In reptiles, precursors for the proteinaceous eggshell membrane are
574 secreted by the uterine glands (Corso et al., 2000; Heulin et al., 2005; Palmer et al., 1993).
575 Calcium secretion can also involve uterine epithelial cells (Herbert et al., 2006; Thompson et al.,
576 2007). Uterine epithelium of the soft-shelled turtle, *Lissemys punctata punctata*, and the eastern
577 collard skink, *Chrotaphytus collaris* (Guillette et al., 1989; Sarkar et al., 1995), stain positive for
578 calcium.

579 Viviparous squamates have an absent or reduced eggshell membrane to facilitate gas
580 exchange (Blackburn, 1993; Braz et al., 2018; Corso et al., 2000; Girling et al., 1997; Guillette &
581 Jones, 1985; Heulin, 1990; Hoffman, 1970; Palmer et al., 1993; Qualls, 1996; Stewart, 1990).
582 Some squamates are encased in the thin membrane through the entirety of development like the
583 viviparous lizard, *Zootoca vivipara* (Heulin, 1989). Others have the membrane only in the early
584 stages of embryonic development like in garter snakes *Thamnophis radix* and *T. sirtalis*
585 (Blackburn & Lorenz, 2003). Calcium deposits are detected on the outer surface of the
586 membrane throughout development in other viviparous lizards (Stewart et al., 2013).

587 The size or density of eggshell glands and their secretory granules correlate with eggshell
588 thickness in several amniotes. In chickens, variation in size, spacing, and neutron density of
589 eggshell glands may be important for eggshell structure (Guillette & Jones, 1985). In the
590 reproductively bimodal lizard, *Zootoca vivipara*, viviparous individuals have a uterine glandular

591 layer that is less developed during the stage of eggshell deposition compared to oviparous
592 individuals (Heulin et al., 2005). Additionally, in *Lerista fragilis*, which lays eggs that hatch
593 within just hours of oviposition, the uterus contains very few mucosal glands (Guillette, 1992).
594 In the fence lizard, *Sceloporus a. aeneus*, the irregular surface of the eggshell was attributed to
595 the irregular spacing of shell glands (Guillette & Jones, 1985). In an oviparous gecko,
596 *Hemidactylus turcicus*, their eggshell glands have loosely packed secretory granules that produce
597 a hard, calcareous shell (Girling et al., 1998). In another oviparous gecko, *Saltuarius wyberba*,
598 their secretory granules are tightly packed, and their shell is soft and parchmentlike (Girling et
599 al., 1998). In a viviparous relative, *Hoplodactylus maculatus*, there are far fewer eggshell glands,
600 and where there are glands, the secretory granules are smaller and more electron dense (Girling
601 et al., 1997, 1998). Smaller eggshell gland size during or after vitellogenesis is also found in
602 other viviparous squamates compared to oviparous counterparts (Braz et al., 2018; Gao et al.,
603 2019; Heulin et al., 2005). In the reproductively bimodal Yellow Bellied Three-toed skink,
604 *Saiphos equalis*, the density of eggshell glands plays a role in eggshell thickness (Stewart et al.,
605 2010). To my knowledge, in monotremes the relationship between eggshell thickness and shell
606 gland size, density or compaction of secretory granules has not been explored.

607

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

609 Presumably because of the influence it has on food production, the process of eggshell
610 formation has been studied most extensively in chickens (Hincke et al., 2012). The avian
611 eggshell is formed in a cell-free environment, and it is the fastest calcifying process known to
612 biology (Hincke et al., 2012; Rodríguez-Navarro et al., 2015). During eggshell formation in
613 birds, the egg is bathed in uterine fluid containing a supersaturation of ionized calcium and

614 bicarbonate ions (Nys et al., 1991). Transport of calcium in the uterus correlates with plasma
615 membrane Ca^{2+} -ATPase (*PMCA*) activity and with concentrations of calbindin-D28K within
616 shell gland epithelial cells (Herbert et al., 2006; Wasserman et al., 1991). This leads to the
617 spontaneous precipitation of calcium carbonate into calcite (Hincke et al., 2012). In the
618 oviparous lizard, *Lampropholis guichenoti*, immunofluorescence microscopy revealed activity of
619 *PMCA* in the uterus at the time of eggshell calcification (Herbert et al., 2006; Thompson et al.,
620 2007).

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

630 Organic aggregates are deposited onto the shell membrane, creating mammillary knobs.
631 Mammillary knobs are a distinct layer between the outer eggshell membrane and the calcified
632 shell matrix layer (Hamilton, 1986). These are characteristic of Archelosaur eggshells (Legendre
633 et al., 2022; Zelenitsky et al., 2002; Zelenitsky & Modesto, 2003). Part of the mammillary knobs,
634 called basal caps, are embedded into the outer eggshell membrane fibers (Tyler, 1965). These
635 basal caps serve as regions of crystal initiation where ACC is deposited (Gautron et al., 2021)
636 and converted into calcite crystals with no intermediate phase (Rodríguez-Navarro et al., 2015).

637 Cones are formed that radiate in all upward directions, extending up to the shell matrix layer
638 (Tyler, 1965). A keratan sulfate proteoglycan, “mammillan”, has been implicated in the
639 composition of mammillary knobs, but it remains uncharacterized (Fernandez et al., 2001;
640 Hincke et al., 2012). The role of homologs of “mammillan” in eggshell formation in squamates
641 may reveal more about the evolutionary history of the eggshell in amniotes.

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

658 In chickens, ovotransferrin is present in the eggshell membrane and basal cap-layer (Gautron,
659 Hincke, Panhéleux et al., 2001). Ovotransferrin promotes the development of elongated crystals

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

667 Over 500 proteins are found in the chicken eggshell matrix (Mann, Maček, & Olsen, 2006;
668 Mikšík et al., 2007, 2010). Ovocleidin-116 (*OC116*), ovocalyxin-36 (*OCX36* or *BPIFB4*),
669 ovocalyxin-21 (*OCX21*), and ovocleidin-17 (*OC17*) are important for avian eggshell formation
670 (Hernández-Hernández, Gomez-Morales et al., 2008; Jonchere et al., 2010; Tian et al., 2010).
671 For example, ovocalyxin-21 may serve as a chaperone protein along with the protein
672 endoplasmic (ENPL) to facilitate proper folding of the eggshell matrix (Jonchere et al., 2010).
673 *OC116*, *OC36*, *OCX21*, and *OC17* are some of the most differentially expressed genes during
674 eggshell calcification in chickens (Gautron et al., 2007; Hincke et al., 1999, 2012; Jonchere et al.,
675 2010). Originally considered avian-specific, several homologs have now been identified in non-
676 avian reptiles and mammals (Le Roy et al., 2021).

677 *OCX36* and other BPI family B proteins (also called *LPLUNCs*) are now thought to have a
678 common origin in vertebrates with multiple duplication events (Gautron et al., 2007; Tian et al.,
679 2010). Orthologs of *OCX36* are found in Archelosauria (turtles, crocodiles, and birds) and
680 Monotremata (egg-laying mammals) (Le Roy et al., 2021). In birds, *OCX36* plays a role in innate
681 immune responses and is found in high concentrations in the inner eggshell membrane (Gautron
682 et al., 2007, 2011; Tian et al., 2010).

683 *OC116* is homologous to mammalian *MEPE* 539, which plays a role in bone and teeth
684 mineralization (Bardet et al., 2010; Le Roy et al., 2021). In birds, *OC116* influences shell
685 thickness, elastic modulus, and egg shape (Dunn et al., 2009; Le Roy et al., 2021; Romé & Le
686 Roy, 2016). *OC116* was identified in a crocodile, *Crocodylus siamensis*, proteome (Le Roy et al.,
687 2021; Mikšík et al., 2018). Synteny analysis across seven turtle species and platypus
688 (*Ornithorhynchus anatinus*) revealed absence of *MEPE/OC116* (Le Roy et al., 2021).

689 Associating expression patterns with the timing of eggshell deposition has revealed
690 squamate-specific candidates for shell formation. One hundred and forty-eight genes were highly
691 expressed in the uterus of the oviparous lizard, *Phrynocephalus przewalskii*, during the stage of
692 eggshell gland formation (Gao et al., 2019). Seven of these genes—*HYPOUI*, *KCNMA1*, *P4HB*,
693 *PRDX4*, *PTN*, *RRBP1* and *TRAMI*—are also purported to be important for eggshell calcification
694 in chickens (Brionne et al., 2014). Given this overlap across species that diverged over 300
695 million years ago (Shen et al., 2011), these are excellent candidates for further exploration. Other
696 genes and lncRNAs are purported to be important for the quality of eggshell formation in hens—
697 *FGF14*, *COL25A1*, *GPX8*, and several members of the solute carrier protein (*SLC*) gene family
698 (Yang et al., 2020). Research into lncRNAs activity in squamate reproductive tissues during
699 embryonic development represents another valuable track for research.

700 During oviparous gravidity in *Saiphos equalis* two GO terms associated with calcium
701 homeostasis are enriched by the set of upregulated genes (Foster et al., 2020). However, most of
702 these genes are associated with regular cellular responses to calcium and even those associated
703 with calcium transport are upregulated in both early and late stages of gravidity (Foster et al.,
704 2020). Their role in eggshell formation in this uniquely labile species is therefore ambiguous.

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

713 In an oviparous agama lizard, *Phrynocephalus przewalskii*, several genes were associated
714 with eggshell gland development (Gao et al., 2019), an important process for secretion of
715 eggshell precursors. Three of the 148 genes highly expressed in *P. przewalskii* were also highly
716 expressed a viviparous relative, *P. vlangalii*, at this time, suggesting differences in eggshell
717 gland development requires regulatory changes to dozens of genes (Gao et al., 2019). Table 1.2
718 compares loci associated with eggshell formation and shell gland development in squamates to
719 that of birds. A wealth of candidate loci for eggshell deposition are differentially expressed in
720 viviparous squamates during gestation (Table 1.2). These genes may function in calcium
721 transport through the chorioallantois instead (Stewart & Eday, 2010).

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

728

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

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

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

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

750 Differential expression of *BMPRI1B* is associated with differences in eggshell quality in
751 chickens (Yang et al., 2020). Another study associated stage-specific high-expression of
752 *BMPRI1B* with the stage corresponding to extended embryonic retention and placentation in
753 *Phrynocephalus vlangalii* (Gao et al., 2019). They identified a co-expression network of highly
754 expressed genes, including *BMPRI1B*, that they associated with placentation (Gao et al., 2019).
755 *BMPRI1B* also reaches significant levels of differential expression in uterine tissues of other
756 gestating viviparous lizards, *Chalcides ocellatus* and *Pseudemoia entrecasteauxii*, compared to
757 non-gestational uterine tissue (Brandley et al., 2012; Griffith et al., 2016). Receptors for *BMPs*
758 are also expressed in the uterus during gestation in other viviparous lizards, *Phrynocephalus*
759 *vlangalii* and *Pseudemoia entrecasteauxii* (Gao et al., 2019; Griffith et al., 2016).

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

765 *SLIT* genes are purported to be involved with folding the eggshell matrix in chickens
766 (Jonchere et al., 2010). The *SLIT2* gene encodes a protein that provides a structural framework
767 for protein-protein interactions (Jonchere et al., 2010; Marillat et al., 2002). *SLIT2* is among the
768 50 most downregulated genes in the uterus during pregnancy in the viviparous African ocellated
769 skink, *Chalcides ocellatus*, compared to non-pregnancy (Brandley et al., 2012). However, in the
770 uterus of the yolk-sac placenta in the viviparous skink, *Pseudemoia entrecasteauxii*, *SLIT2* is
771 upregulated compared to non-reproductive uterine tissue (Griffith et al., 2016). *SLIT3* is
772 differentially expressed during the stage of placentation in the viviparous agama lizard,

773 *Phrynocephalus vlangalii* (Gao et al., 2019). *SLIT* genes also play a role in axonal pathfinding
774 and neuronal migration in rats (Marillat et al., 2002). *SLIT2* was associated with reproduction in
775 humans (Chen, Chu et al., 2015). Future research on their function in squamate reproductive
776 tissues during embryonic development may reveal if *SLIT* genes influence parity eggshell
777 formation.

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

787

788 (5) Eggshell formation termination

789 When eggshell formation is terminated, the egg is still bathed in the supersaturated
790 calcium and bicarbonate ion fluid (Hincke et al., 2012). Some component(s) of the terminal
791 uterine fluid may prevent precipitation of calcium carbonate (Gautron et al., 1997), such as
792 phosphate anions (Lin & Singer, 2005). The presence of phosphorous in the superficial layers of
793 the chicken shell suggest that phosphorous may be the factor preventing the deposition of calcite
794 crystals in the terminal stage (Blackburn, 2000, 1992; Stewart, 2013). Additionally, the high
795 concentration of *OCX32* in the outer eggshell and cuticle, suggest that the gene may inhibit

796 proteinaceous crystal growth in the terminal stage of eggshell calcification (Gautron, Hincke,
797 Mann et al., 2001). It is informative to both viviparous reproduction and the basal cap hypothesis
798 that exposure to precursors of the eggshell does not necessitate eggshell deposition. The
799 influence of phosphate anions and *OCX32* on inhibition of calcium carbonate precipitation on the
800 eggshell membrane of viviparous squamate embryos has not been examined to my knowledge.

801

802 *(6) Rotating the egg for eggshell deposition*

803 Oviparous amniotes rotate the egg for calcium deposition and viviparous mammals rotate the
804 embryos for parturition. One hurdle to reversing back to oviparity may be re-evolving oviductal
805 musculature and rotation of the egg for shell deposition (Griffith et al., 2015). However, given
806 the complex muscular of the uterus that allows for multidirectional force for parturition, it is
807 difficult to determine the degree of difficulty for re-evolving egg-rotation. Cadherins (Wu et al.,
808 2011) and hormonal signaling (Biazik et al., 2012) may influence uterine elasticity and its ability
809 to rotate the developing embryo. Genes that enrich the GO term for “voltage-gated calcium
810 channel activity” are also useful candidates for investigating uterine rotation associated with
811 eggshell formation because voltage-gated calcium channels effect the action potential of cells
812 and can cause muscle contractions.

813

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

815 The process of eggshell deposition is more resolved in birds compared to non-avian reptiles
816 and monotremes (Choi et al., 2018; Frankenberg & Renfree 2018; Hallman et al., 2015; Schleich
817 & Kästle 1988). As more whole genomes become accessible, it would be interesting to explore if
818 non-avian amniotes utilize a similar genetic toolkit for eggshell deposition. I described some

819 overlaps that can be gleaned from the literature, which prove as curious candidates for further
820 research. Of particular interest are ovacalixins and ovoclidesins (*OCX36*, *OC116* and *OC17*) (Le
821 Roy et al., 2021), and the homologs for avian eggshell matrix proteins identified in the *Anolis*
822 *carolinensis* genome (Alföldi et al., 2011; Tian et al., 2010). Some genes purported to be
823 important for eggshell calcification in chickens were also associated with eggshell gland
824 formation in an oviparous lizard, *Phrynocephalus przewalskii*—*HYPOU1*, *KCNMA1*, *P4HB*,
825 *PRDX4*, *PTN*, *RRBP1* and *TRAMI* (Brionne et al., 2014; Gao et al., 2019).

826 It is unclear why Archelosaurs and Lepidosaurians evolved divergent processes for forming
827 their eggshells, which are also morphologically dissimilar. One possibility is that viviparity
828 evolved early in the history of Lepidosaurians, as estimated for squamates (Pyron & Burbrink,
829 2014). Theoretically, it should be relatively simple to transition from oviparity to viviparity if the
830 ancestral oviparous amniotes had an eggshell microstructure like that of dinosaurs and modern
831 birds. Under that scenario, alteration to basal caps in the mammillary layer would prevent the
832 deposition of calcium before it begins (basal cap hypothesis). Alternatives to this possibility are
833 that divergent eggshells and eggshell deposition processes evolved through selective pressure,
834 genetic drift, or both.

835

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

837

838 The evolutionary pressures on fluid allocation, gas exchange and nutrient transport should
839 differ between oviparous and viviparous taxa because their sources of all or some of these
840 resources differ (Blackburn, 1992; Bonnet et al., 2001, 2017; van Dyke et al., 2014). In
841 viviparity, maternal gas and water are accessed through the chorioallantois, which is especially

842 important in the latter half of development (van Dyke et al., 2014; Carter, 2012). Nutrients can
843 be available from the yolk, maternal transfer, or both yolk and maternal transfer. Where amniotes
844 other than squamates can rely on the albumen for fluid allocation, squamates lack an albumen
845 (Blackburn & Stewart, 2021). Their eggshells are specially adapted to exchange fluids with the
846 environment (Blackburn & Stewart, 2021). Oviparous taxa regulate gas exchange through pores
847 in their eggshells (Badham, 1971; Brown & Shine 2005; Ji & Du, 2001; Packard, 1991).

848

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

850 The embryonic membranes regulate embryonic fluid transport, nutrient supply, respiration,
851 immunity, and waste (Brace, 1997; Burton & Tullett, 1985; Ferner & Mess, 2011; Ostergard,
852 1970; Packard & Packard, 1980). Fluids are important for the developing embryo because they
853 prevent desiccation and compression (Ferner & Mess, 2011; Ostergard, 1970; Packard &
854 Packard, 1980). Over-abundance or under abundance of embryonic sac fluids leads to
855 reproductive failure (Chamberlain et al., 1984; Fedakâr et al., 2016; Hadi et al., 1994; Mercer et
856 al., 1984). Without substantial amounts of water, converting yolk nutrients to somatic tissue is
857 impossible (Noble, 1991; Packard, 1991; Thompson et al., 2004). Oxygen flux in embryonic
858 mammals is largely determined by oxygen-diffusing capacity of the placenta, the rates of blood
859 flow in the umbilical and uterine arteries, and the oxygen capacities and affinities of fetal and
860 maternal blood (Carter, 2009). Reptilian and mammalian blood vessels differ in basic
861 characteristics such as capillary density, capillary surface, and oxygen diffusion gradients
862 (Pough, 1980).

863 Patterns of embryonic nutrient exchange can be broadly categorized into lecithotrophy,
864 obtaining nutrients from the yolk, and placentrophy or matrotrophy, obtaining nutrients from the

865 mother. Taxa belonging to Archelosauridae are lecithotrophic. The ancestral state of mammals
866 was most likely oviparous matrotrophy that later evolved into viviparous matrotrophy in therians
867 (Blackburn, 2005). The ancestral state of reptiles was likely lecithotrophy (Blackburn, 2005).
868 Most viviparous squamates are lecithotrophic, some are lecithotrophic and matrotrophic, and a
869 few have specializations for substantial matrotrophy (Blackburn, 1985b; Stewart & Thompson,
870 1993; Thompson, Stewart et al., 1999). Even lecithotrophic viviparous squamates appear to
871 exhibit some degree of matrotrophic nutrient provisioning (Blackburn, 2005; Stewart, 1990,
872 2020; Swain & Jones, 1997, 2000; Thompson, Stewart et al., 1999; Thompson & Speake, 2006).
873 Reversals may be most unlikely in lineages that have specialized placentas for substantial
874 nutrient exchange because they would need to re-evolve lecithotrophy. Highly matrotrophic
875 squamates are extremely rare (Blackburn, 2015a).

876

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

878 Vitellogenesis is the process of yolk formation in the oocyte, providing the embryo with a
879 valuable source of nutrients, primarily through the accumulation of precursor proteins to yolk,
880 vitellogenins. Vitellogenin is produced in the liver, called hepatic vitellogenesis, and transported
881 to the maturing ovum (Ho, 1987). Vitellogenins were lost in all mammals except monotremes
882 (Brawand et al., 2008). They are a primary source of nutrition for other amniotes. Functionally
883 similar to vitellogenin, caseins have persisted in all mammalian milks (Brawand et al., 2008).
884 Glycodelin was also detected in the epithelium of the secondary yolk-sac of humans during the
885 first trimester, suggesting the organ may retain a role in nutrient provisioning during early
886 pregnancy (Burton et al., 2002) but otherwise does not contribute nutritionally. In the yolk-sac of
887 bats, dogs, and non-human primates the mesoderm derived layer is absorptive and may transfer

888 substances from the exocoelomic cavity (Enders et al., 1976; Freyer & Renfree, 2009; King &
889 Wilson, 1983; Lee et al., 1983).

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

902 Ancestral sauropsid morphology and yolk processing likely resembled that of non-avian
903 sauropsids (Blackburn, 2021). A series of recent papers on non-avian sauropods, covering
904 species of snakes, lizards, crocodiles, and turtles, indicate that these taxa utilize similar
905 developmental pathways of yolk-sac formation and yolk processing that differs from birds
906 (Blackburn, 2021; Blackburn et al., 2019; Elinson et al., 2014; Elinson & Stewart 2014; Stinnett
907 et al., 2011). Across these taxa, a bilaminar/trilaminar omphalopleure overgrows the yolk mass,
908 and the yolk mass gets invaded by proliferating endodermal cells that phagocytose the yolk
909 material. These cells form clumps, progressively filling the yolk mass. Small blood vessels
910 derived from yolk sac vasculature invade the yolk sac cavity and the endodermal cells arrange in

911 monolayers around these vessels, forming “spaghetti bands” (Blackburn, 2021). The yolk sac of
912 *Pantherophis guttatus* and other non-avian sauropsids may serve as models for the transition
913 between the egg of anamniotes and amniotes (Elinson & Stewart, 2014; Elinson et al., 2014)

914 A major difference between avian and non-avian sauropsid yolk-sac formation is therefore
915 the morphology and extent of vascularization and cellularization in the yolk sac cavity (Starck,
916 2021). Birds have a yolk-sac with absorptive endodermal lining that digests nutrients and send
917 them into blood circulation (Starck, 2021) whereas snakes, lizards, turtles, and crocodylians have
918 a yolk sac that becomes invaded by endodermal cells that proliferate and phagocytose yolk
919 material (Blackburn, 2021). In these taxa, yolk material becomes cellularized, digested, and
920 transported by vitelline vessels to the developing embryo (Blackburn, 2021). Factors involved
921 with cellularization of the yolk-sac are proposed to include cell cycle regulators and structural
922 proteins (Elinson et al., 2014). Generation of these cells are suspected to be reliant on processes
923 of angiogenesis and are likely transcriptionally active (Elinson et al., 2014).

924 As discussed in a previous section, progesterone inhibits myometrial contractility, but it also
925 inhibits estrogen-induced hepatic vitellogenin synthesis (Custodia-Lora, Novillo, & Callard,
926 2004; Callard et al., 1992). Variable progesterone concentrations in circulation throughout
927 gestation in viviparous squamates may reflect a trade-off to allow estrogen expression to support
928 hepatic vitellogenin synthesis during embryonic development, thus supporting nutrient
929 provisioning during the lengthened embryonic retention. Although hepatic vitellogenesis usually
930 ceases during gestation, vitellogenin synthesis and mother-to-embryo transfer was detected in
931 one viviparous fish, *Xenotoca eiseni*, during gestation (Iida et al., 2019). Future research should
932 consider the timing of vitellogenin synthesis throughout the reproductive cycle in gestating and
933 non-gestating viviparous squamates to investigate this further.

934

935 *(3) Evolutionary history of placentrophy in mammals & squamates*

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

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

956 Nutrient provisioning through placentrophy is obligate for embryonic development in only
957 five lineages of squamates, all of which are scincid lizards (Blackburn, 2000; Flemming &
958 Blackburn, 2003; Ramírez-Pinilla et al., 2011). *Pseudemoia pagenstecheri*, a lizard with a highly
959 specialized placenta, out-performs lecithotrophic oviparous close relatives in the relative amount
960 of nutrients it transfers to the embryo (Stewart et al., 2009). Some *Mabuya* lizards have highly
961 specialized placenta, relying almost entirely on maternally supplied materials (Thompson &
962 Speake, 2002). *Pseudemoia entrecasteauxii* is a moderately matrotrophic viviparous lizard, with
963 roughly half of embryonic nutrient uptake from the yolk and half through a specialized cyto-
964 epitheliochorial placenta (Adams et al., 2005; Speake et al., 2004; Stewart & Thompson, 1993,
965 2009). Specializations of the chorioallantoic placenta for nutrient provisioning in some
966 squamates include elaborate specializations for uterine secretion and absorption, including
967 placentomes, chorionic areolae, hypertrophied uterine mucosa, and chorionic epithelia modified
968 for absorption (Blackburn, 2005).

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

977

978 (4) *Squamate viviparity eggshells, and gas exchange*

979 In squamates, specializations for gas exchange across the chorioallantoic placenta include
980 decreased diffusion distance between maternal and fetal capillaries, uterine vascularity, shell
981 membrane deterioration, and modifications of both fetal and maternal blood properties (Attaway,
982 2000; Blackburn, 1998, 2005; Blackburn & Lorenz, 2003; Blackburn & Vitt, 2002; Stewart and
983 Brasch, 2003). Absence of the eggshell may be necessary for adequate gas exchange during
984 viviparous gestation. However, in some viviparous squamates and oviparous squamates with
985 prolonged egg retention the eggshell is considered part of the placenta (Linville et al., 2010;
986 Stewart et al., 2013). Thus, a calcified eggshells remains compatible with viviparity, at least in
987 these lineages. Pores in the eggshell may support sufficient gas and fluid exchange in viviparous
988 squamates as they do for oviparous eggs.

989

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

991 Water transport in animals is regulated by a family of molecular water channels called
992 aquaporins (*AQs* or *AQPs*) (Borgnia et al., 1999). In humans, *AQP1*, *AQP3*, *AQP4*, *AQP8* and
993 *AQP9* are found in the placenta but further research is needed to understand how these influence
994 water fluxes between maternal and fetal tissues (Damiano, 2011). Transcriptomic analysis on
995 uterine tissue of the gestating, viviparous skink, *Chalcides ocellatus*, reveal differential
996 expression of *AQP1*, *AQP3*, *AQP5*, *AQP6*, *AQP8*, *AQP9* and *AQP11* when compared to non-
997 gestating uteruses (Brandley et al., 2012). In birds, *AQP1* is expressed in the chorioallantoic
998 membrane, and it is suggested to influence angiogenesis throughout embryonic development
999 (Ribatti et al., 2002). In a viviparous lizard, *Pseudemoia entrecasteauxii*, *AQP8* and *AQP9* were
1000 more highly expressed in the chorioallantoic placenta compared to the yolk-sac placenta (Griffith
1001 et al., 2016). During gestation and gravidity in both oviparous and viviparous populations of the

1002 reproductively bimodal skink, *Saiphos equalis*, several genes involved with water homeostasis
1003 are upregulated including *AQP1*, *AQP3* and *AQP12B* (Foster et al., 2020). In uteruses of *Saiphos*
1004 *equalis*, *AQP5* and *AQP8* are upregulated during oviparous late gestation compared to viviparous
1005 late gestation. In sheep, *AQP3* is differentially expressed during gestation, where it serves a dual
1006 role of water transport to the embryo and fetal urea export (Johnston et al., 2000). This is similar
1007 to the function of *AQP9* in humans (Damiano, 2011). Immunocytochemistry reveals that *AQP1*
1008 and *AQP3* are expressed in the uterus of the highly placentrophic South American scincid lizard,
1009 *Mabuya sp.* (Wooding et al., 2010).

1010 Some molecules are implicated in the regulation of aquaporins including insulin (INS),
1011 human chorionic gonadotropin (HcG), cyclic adenosine monophosphate (cAMP) and cystic
1012 fibrosis transmembrane conductance regulator (CFTR) (Castro-Parodi et al., 2008; Damiano,
1013 2011). Genes predicted to be involved with reproduction in *Anolis carolinensis* are enriched for
1014 the GO term for cAMP-mediated signaling (Alföldi, Di Palma, et al., 2011). Further comparative
1015 research should be done to elucidate the functional differences of aquaporins in oviparous and
1016 viviparous amniotes and how they relate to the differing conditions under which these embryos
1017 develop.

1018 Genes involved embryonic oxygen transport precede the origin of amniotes. Hemoproteins
1019 arose in evolutionary history well before they were used for placental oxygen transfer (Hardison
1020 1998). In mammals, adult (Alpha: HBA; Beta: HBB, HBD) and embryonic hemoglobins (Alpha:
1021 HBZ, HBA; Beta: HBE, HBG, and HBH) are involved with oxygen transport (Carter, 2012).
1022 Some of these are unique to eutherian mammals following a series of duplication events (Opazo
1023 et al., 2008). However, fetal hemoglobins are found in turtles, lizards, and snakes (Pough, 1980).
1024 HBA, HBB and HBM are all significantly downregulated in the uterine tissue of the viviparous

1025 African Ocellated Skink, *Chalcides ocellatus*, during gestation compared to non-gestation
1026 (Brandley et al., 2012). The oxygen demands of reptile embryos are relatively low until stage 30,
1027 when most oviparous taxa oviposit (Shine & Thompson, 2006). In viviparous and oviparous
1028 species with long egg retention, embryonic demand for maternal provision of oxygen and
1029 removal of CO₂ increases at this stage (Ferguson & Deeming, 1991).

1030 Improper water, gas and nutrient exchange can occur due to poor chorioallantoic blood flow
1031 (Wootton et al., 1977). Thus, viviparous taxa require greater degrees of vascularization and
1032 vasodilation to facilitate enhanced requirements for maternal resources compared to oviparous
1033 taxa. Rather than increasing the size of the placenta, increasingly dense blood vessels can support
1034 fetal growth without compromising space for embryonic growth as occurs in some pigs (Ford,
1035 1997; Vonnahme et al., 2002). Embryonic vascularization and vasodilation are dependent on
1036 signals from the endoderm (Jin et al., 2005; Vokes & Krieg, 2002; Wilt, 1965). In oviparous
1037 individuals of *Saiphos equalis*, populations with extended egg retention, there is expansion of the
1038 uterine vascular bed and thickening of the chorioallantoic tissue that supports increased
1039 embryonic growth in the later portion of oviparous gravidity (Parker et al., 2010). In the
1040 viviparous scincid lizard, *Eulamprus quoyii*, angiogenesis, the formation of new blood vessels,
1041 and expansion of the vessel-dense elliptical area of the uterus is associated with supporting
1042 increased embryonic oxygen demand (Murphy et al., 2010).

1043 Several protein-coding genes are known to be involved with angiogenesis, vascularization,
1044 and vasodilation in utero. One study that examined expression patterns across chickens
1045 (oviparous), horses (viviparous), two viviparous squamates, and one oviparous squamate found
1046 that no examined genes for angiogenesis showed a viviparity-specific expression pattern
1047 (Griffith, Brandley et al., 2017). However, other than the chicken, the only oviparous taxa

1048 included in this study was a reproductively bimodal skink, *Lerista bougainvillii* (Griffith,
1049 Brandley et al., 2017).

1050 In the uterine tissue of gestating viviparous skinks and rats, several genes for angiogenesis
1051 are upregulated—*EPAS1*, *HIF1A* and *VEGFA* (Brandley et al., 2012; Whittington et al., 2015,
1052 2017). Other proteins involved in vascularization and vasodilation in utero include members of
1053 the vascular endothelial growth factor (*VEGF*) gene family, VEGF receptors (*VEGFRs*),
1054 placental growth factor (*PGF*) and nitric oxide synthase (*NOS*) (Blomberg et al., 2010; Chen,
1055 Wang et al., 2015; Gilbert, 2010; Reynolds et al., 2006; Risau, 1997; Torry et al., 2003;
1056 Vonnahme et al., 2001). In *Saiphos equalis*, different homologs of *NOS* experience different
1057 patterns of gene expression across the oviparous and viviparous stages of gestation/gravidity
1058 (Foster et al., 2020). One homolog of *NOS* is upregulated during oviparous late gestation, and
1059 another is upregulated during viviparous late gestation (Foster et al., 2020). Several genes
1060 involved with angiogenesis and vascular morphogenesis are downregulated in the pre-
1061 implantation uterus of a marsupial, the Fat Tailed Dunnart, *Sminthopsis crassicaudata*—
1062 *ADGRA2*, *ADGRB2*, *ANGPTL1*, *EPHB4*, *ISM1*, *PDZRN3*, *RHOJ*, *TNMD*, and *VEGFD*
1063 (Whittington et al., 2018).

1064 In humans, immune factors are also responsible for increasing embryonic blood supply.
1065 Embryonic non-classical MHC class I molecule, HLA-G, and uterine natural killer (uNK) cells
1066 support increased embryonic blood supply (Moffett & Loke, 2006; Rajagopalan et al., 2006). A
1067 similar pattern of utilizing immune properties to support embryonic blood supply has not been
1068 yet identified in squamates.

1069 Lipids are a main energy source for embryos. Lipoprotein lipase (LPL) is an important
1070 enzyme in lipid transport. LPL is significantly expressed on the syncytiotrophoblasts, specialized

1071 placental cells, of humans (Lindegaard et al., 2005) and the endometrium of cows (Forde et al.,
1072 2011), and pigs (Ramsay et al., 1991), where it plays a role in lipid mobilization. A viviparous
1073 lizard, *Pseudemoia entrecasteauxii*, increases capacity for lipid transport toward the end of
1074 pregnancy (Griffith, Ujvari et al., 2013). The uterine tissue of the yolk-sac placenta in this
1075 species had significantly higher expression of LPL than the uterine tissues of the chorioallantoic
1076 placenta (Griffith, Ujvari et al., 2013), leading the authors to suggest that the yolk-sac placenta is
1077 the major site of lipid transport. LPL expression was not detected during pregnancy in the
1078 viviparous skink, *Chalcides ocellatus* (Blackburn, 1992; Brandley et al., 2012). Instead, lipid
1079 transport may be facilitated by fatty acid binding proteins in this species (Chmurzyńska, 2006;
1080 Brandley et al., 2012). These are also active on mammalian placenta (Haggarty, 2002).

1081 Apolipoproteins are also suitable candidates for transport of fatty acids, cholesterol and
1082 phospholipids. Five of these (*APOA1*, *APOA2*, *APOA4*, *APOE*, and *APOM*) and *APOA1BP* are
1083 significantly upregulated in the pregnant uterus of the viviparous skink, *Chalcides ocellatus*
1084 (Brandley et al., 2012). *APOA1BP* is also upregulated in the uterus of the chorioallantoic
1085 placenta and yolk-sac placenta compared to non-gestational uterine tissues in *Pseudemoia*
1086 *entrecasteauxii* (Griffith et al., 2016). Additionally, upregulation of 136 genes that encode solute
1087 carrier proteins (SLCs) in the pregnant uterus of *Chalcides ocellatus* are associated with
1088 transport of inorganic ions, metals, glucose, amino acids, peptides, fatty acids, and carboxylic
1089 acids (Brandley et al., 2012).

1090 Cathepsins and phospholipases are important for uterine secretions for embryonic
1091 development in horses, pigs, sheep and cattle (Bazer, 1975; Satterfield et al., 2007; Song et al.,
1092 2010). Cathepsins are present in yolk sacs of humans and mice. They function to degrade
1093 proteins to free amino acids (Cindrova-Davies et al., 2017). Two genes for cathepsin L (*CTSL1*

1094 and *CTSL2*) are upregulated in the uterus during gestation in *Chalcides ocellatus* (Brandley et al.,
1095 2012). *CTSL* is also upregulated in the uterus during the pre-implantation phase in the Fat-Tailed
1096 Dunnart, *Sminthopsis crassicaudata* (Whittington et al., 2018), and in the uterus of the
1097 chorioallantoic placenta and uterus of the yolk sac placenta during gestation in *Pseudemoia*
1098 *entrecasteauxii* (Griffith et al., 2016).

1099 In viviparous individuals of the reproductively bimodal lizard, *Saiphos equalis*, many genes
1100 for cellular adhesion are upregulated during late gestation (Foster et al., 2020). The authors
1101 postulated that this helps facilitate maternal-fetal signaling and paracellular transport (Foster et
1102 al., 2020). Gao et al. (2019) identified a set of genes in *Phrynocephalus vlangualii* that were
1103 differentially expressed in the uterus during the stage of placentation and these enriched GO
1104 terms functionally related to the process of placentation. This included an estrogen receptor
1105 (*ESR1*) and two growth factor receptors (*GHR* and *IGF1R*) (Gao et al., 2019).

1106 Finally, the proteomes of the ovary and placenta from obligately placentrophic *Mabuya*
1107 lizards can further serve as a useful resource for examining nutrient provisioning in squamates
1108 (Hernández-Díaz et al., 2017). In the placenta they found protein expression involved with
1109 nutrient metabolism, transport, protein synthesis, and embryonic development (Hernández-Díaz
1110 et al., 2017).

1111

1112 (6) Uterine glands: adenogenesis, placenta development and histotrophy

1113 In addition to their role in eggshell deposition in oviparous taxa, uterine glands also secrete
1114 growth factors and cytokines that support placental development in mammals. In humans, these
1115 include transforming growth factor- β (TGF- β), epidermal growth factor (EGF), vascular
1116 endothelial growth factor (VEGF), and leukemia inhibitory factor (LIF) (Hempstock et al.,

1117 2004). In eutherians, TGF- β supports placental development by regulating proliferation and
1118 invasion rates of placental cells lines (Caniggia et al., 2000; Hempstock et al., 2004; Lafontaine
1119 et al., 2011).

1120 Histotrophy (also called histiotrophy) occurs when nutrients are secreted into the uterine
1121 lumen from vesicles of the columnar epithelial cells of the uterus and taken up by the embryo.
1122 Histotrophic nutrient provisioning is documented across amniotes including marsupials
1123 (Whittington et al., 2018), several ungulate taxa (Bazer et al., 2011; Han et al., 2016; Gao et al.,
1124 2009), humans (Burton et al., 2002), and squamates (Thompson et al., 2004). In humans,
1125 histotrophic nutrient provisioning occurs during the first trimester. The intervillous space is filled
1126 with fluid containing uterine gland secretions that get phagocytosed by the syncytiotrophoblasts
1127 and are the initial nutrient source for the fetus (Burton et al., 2002). Two of these glycoproteins
1128 are epithelial mucin (*MUC1*) and glycodelin A (*GdA*) (Burton et al., 2002). Interestingly, the
1129 *MUC15* gene is upregulated during gravidity/gestation in the uterus of oviparous and viviparous
1130 *Saiphos equalis* individuals (Foster et al., 2020). This also occurs in the chorioallantoic placenta
1131 of *Pseudemoia entrecasteauxii* during gestation (Griffith et al., 2016). Several mucins are
1132 expressed in the uterus in non-gravid and gravid samples from oviparous individuals of *Lerista*
1133 *bougainvillii* and *Lampropholis guichenoti* (Griffith et al., 2016).

1134 A survey of viviparous squamates with modest to extensive placentrophy revealed
1135 prevalence of histotrophic nutrient provisioning rather than hemotrophy, transfer of nutrients
1136 between maternal and fetal blood streams (Blackburn 2015). Embryos of *Chalcides chalcides*
1137 have extensive placentrophy that supports substantial maternal nutrient provisioning and
1138 histotrophy (Blackburn, 2015a). Histotrophy may lessen parent-offspring conflict and give the
1139 mother the control over nutrient provisioning compared to hemotrophy (Blackburn, 2015b).

1140 *Chalcides ocellatus* has less extensive placentrophy than *C. chalcides* but the gestating uterus
1141 still illustrates expression of many genes associated with organic and inorganic nutrient transport
1142 (Blackburn, 2015a). Multiple *TGF-β* loci are differentially expressed in the uterus during
1143 gestation in *C. ocellatus*, however most these are downregulated compared to non-gestational
1144 uterine tissue (Murphy et al., 2012). The influence of *TGF-β* on placental development and
1145 nutrient provisioning in *Chalcides spp.* remains to be explored to my knowledge. A TGF-β
1146 receptor (*TGFBRI*) was associated with placental development in *Phrynocephalus vlangalii*
1147 (Gao et al., 2019).

1148 Essential to histotrophy is adenogenesis, the generation of endometrial glands. Adenogenesis
1149 allows for the secretion of histotrophs. The period of early development during which
1150 adenogenesis occurs is highly variable among vertebrates but it is required for embryonic
1151 survival (Gray et al., 2001, 2002; Spencer & Bazer, 2004). Some genes involved with
1152 adenogenesis in sheep are insulin-like growth factor 1 (*IGF-1*), *IGF-2*, *PAX2*, *LHX1* (also known
1153 as *LIM1*) and *EMX2*, genes in the abdominal-B HOXA cluster, members of both *Wnt* and
1154 Hedgehog (*Hh*) gene families (Fazleabas et al., 2004), prolactin (*PRL*), fibroblast growth factor 7
1155 (*FGF7*), *FGF10*, *FGFR2IIIb*, hepatocyte growth factor (*HGF*), a receptor tyrosine kinase (*c-*
1156 *Met*), and cadherins (Fazleabas, 2007).

1157 In the gestating uterus of *Chalcides ocellatus*, insulin-like growth factor-binding protein 5
1158 (*IGFBP5*) is one of the most significantly downregulated genes compared to non-gestational
1159 uterine tissue (Brandley et al., 2012). *IGFBP5* is evolutionarily conserved and multifunctional,
1160 with an important role in regulating IGF signaling, including that of *IGF-1* and *IGF-2* (Duan &
1161 Allard, 2020). Other than adenogenesis in sheep, IGFs serve an important role in the growth of

1162 fetal and maternal tissues in mammals. There is a long history of research on this subject (Yan-
1163 Jun et al., 1996; Gibson et al., 2001; Kampmann et al., 2019).

1164 Genes involved with histotrophic secretion in the marsupial *Sminthopsis crassicaudata*
1165 include *AP4SI*, *HYOUI*, and *SRPRA* (Whittington et al., 2018). Nutrient transporters
1166 significantly upregulated at this time are *APOL6* (cholesterol transport (Baardman et al., 2013)),
1167 *PLA2G10* (hydrolysis of fatty acids during pregnancy (Miele et al., 1987)) and a wealth of SLCs
1168 (solute carrier proteins for nucleoside sugar, ions, anions, glucose, fatty acids, calcium and zinc
1169 (Whittington et al., 2018)). In a reproductively bimodal skink, *Saiphos equalis*, *PLA2G10* is
1170 upregulated during viviparous late gestation compared to oviparous late gestation (Foster et al.,
1171 2020). Upregulation of SLCs also occurs in the viviparous skink *Chalcides ocellatus* (Brandley
1172 et al., 2012; Van Dyke et al., 2014) and in the uterus during pregnancy in the grey short-tailed
1173 opossum, *Monodelphis domestica* (Hansen et al., 2016).

1174 Uterine glands are also important for secretions of eggshell precursors. I speculate that genes
1175 involved with adenogenesis of shell glands may be similarly used to support histotrophic nutrient
1176 provisioning, but further research is necessary. Specialized uterine areolar glands are found in
1177 some *Mabuya* lizards, a genus with oviparous species and viviparous species that utilize
1178 placentrophy and histotrophy (Brandley et al., 2012; Corso et al., 1988, 2000; Jerez & Ramírez-
1179 Pinilla, 2001; Ramírez-Pinilla, 2006; Vieira et al., 2007; Visser, 1975). Transcriptomic research
1180 focused on histotrophic nutrient provisioning, placental development, and secretions of eggshell
1181 precursors in oviparous and viviparous *Mabuya spp.* would complement the morphological
1182 literature on the genus

1183

1184 (7) *Discussion & future directions—embryonic nutrients, gas, and water supply*

1185 Many genes for placental functions in mammals have deep origins in vertebrates (Rawn &
1186 Cross, 2008). Across amniotes, there is overlap in hormones and proteins (SLC superfamily,
1187 insulin-like growth factors, aquaporins and solute carrier proteins, etc.) involved in uterine
1188 remodeling, placentation, and placental transport. Identifying a viviparity-specific expression
1189 profile would require measuring expression at stage-specific times across taxa that share the
1190 same form of water, gas, or nutrient provisioning. A viviparity-specific profile may not be the
1191 biological reality. Table 1.3 illustrates how loci mentioned in text for water, gas, and nutrient
1192 transport are expressed in reproductive tissues of squamates during gestation and gravidity.

1193 If specific genes or physiological processes impact more than one of the Main Five
1194 categories, it could have a disproportionate influence on transitions. The solute carrier (*SLC*)
1195 gene superfamily is estimated to be involved with both nutrient transport (Brandley et al., 2012;
1196 Whittington et al., 2018) and eggshell deposition (Yang et al., 2020). Adenogenesis is essential
1197 for histotrophic nutrient provisioning and secretion of eggshell precursors. Additionally,
1198 progesterone production influences both uterine quiescence, which is an important state to
1199 maintain in lengthened embryonic retention, and it also inhibits hepatic vitellogenesis, an
1200 important process for lecithotrophic nutrient provisioning. Thus, examining the role of *SLC* gene
1201 superfamily members, processes of adenogenesis, and progesterone production during
1202 embryonic development in oviparous and viviparous squamate may reveal how interconnected
1203 the Main Five are.

1204

1205 **V. Embryonic Calcium Provisioning**

1206

1207 The embryonic growth stage requires the greatest demand of calcium (Ecay et al., 2017;
1208 Packard & Packard, 1984; Stewart & Ecay, 2010). To support this, peak uterine concentrations
1209 of calcium are highest during either eggshell deposition or during the embryonic growth stage, in
1210 oviparous and viviparous taxa, respectively (Linville et al., 2010; Stewart et al., 2009).
1211 Regardless of parity mode, embryonic metabolism drives calcium uptake (Packard & Packard,
1212 1984). The calcium source(s) utilized have clade-specific implications on the genomic and/or
1213 physiological changes required to transition between parity modes.

1214

1215 *(1) Phylogenetic context of embryonic calcium sources*

1216 Calcium can be acquired by the embryo in three forms: calcium carbonate in the eggshell,
1217 calcium bound to proteins and lipids in the yolk, and/or free ionic calcium from maternal
1218 delivery through the placenta (Stewart & Ecay, 2010). These correspond with five calcium
1219 mobilization patterns: 1) Birds, turtles and crocodiles predominately depend on the eggshell; 2)
1220 Many squamates, regardless of parity mode, predominately depend on the yolk; 3) Some
1221 squamates are intermediately reliant on the eggshell and yolk; 4) Some viviparous squamates are
1222 intermediately reliant on the yolk and placenta; and 5) therian mammals and some viviparous
1223 squamates predominately depend on the placenta (Hoenderop, Nilius, & Bindels, 2005; Jenkins
1224 & Simkiss, 1968; Kovacs, 2015; Packard, 1994; Packard & Seymour, 1997; Stewart et al., 2009,
1225 2009; Stewart & Ecay, 2010; Thompson, Stewart et al., 1999; Thompson, Stewart, & Speake,
1226 2000; Ramírez-Pinilla, 2006). Unlike birds, oviparous squamates do not sequester calcium from
1227 the eggshell into the yolk during incubation (Packard, 1994).

1228

1229 *(2) Hypotheses on calcium mobilization and the evolution of parity modes*

1230 It was hypothesized that predominant reliance on eggshell calcium should constrain lineages
1231 to oviparity because the evolution of viviparity would result in a lost calcium source (hereafter
1232 eggshell calcium constraint hypothesis) (Stewart & Ecy, 2010; Packard et al., 1977; Packard &
1233 Packard, 1984). This hypothesis suggested that viviparity should only evolve in lineages
1234 predominately reliant on yolk calcium (Packard et al., 1977; Packard & Packard, 1984).
1235 Fittingly, birds, turtles and crocodylians generally rely on eggshell calcium, and they are
1236 constrained to oviparity (Anderson et al., 1987). The eggshell calcium constraint hypothesis is
1237 supported by many viviparous squamates that rely heavily on yolk calcium, including *Nerodia*
1238 *rhomboifera*, the diamondback water snake, and *Niveoscincus metallicus*, the metallic skink
1239 (Stewart & Castillo, 1984; Thompson, Speake et al., 1999).

1240 However, subsequent research revealed that viviparity is not constrained by a prerequisite
1241 reliance on yolk calcium. Calcium placentrophy contributes substantially to embryonic
1242 development in several viviparous squamates including *Pseudemoia entrecasteauxii*, *Eulamprus*
1243 *quoyi*, *Zootoca vivipara*, *Saiphos equalis*, and an unidentified species of *Mabuya* lizard (Ecy et
1244 al., 2017; Linville et al., 2010; Ramírez-Pinilla, 2006; Ramírez-Pinilla et al., 2011; Stewart &
1245 Thompson, 1993; Thompson, 1977). These taxa, with the exception of *Zootoca vivipara*, are in
1246 the family Scincidae (Burbrink et al., 2020), which is also the family with the most independent
1247 origins of viviparity in squamates (Blackburn, 1982, 1999; Pyron & Burbrink, 2014). Oviparous
1248 scincid skinks studied thus far are intermediately reliant on eggshell and yolk calcium (Linville
1249 et al., 2010; Shadrix et al., 1994; Stewart et al., 2009; Stewart & Thompson, 1993; Thompson et
1250 al., 2001).

1251 To understand the breadth of physiological conditions from which oviparity and viviparity
1252 evolve in squamates, future research should examine calcium transport in other lineages. Studies

1253 focused on snakes would be particularly informative given the sparse literature on them.
1254 *Helicops angulatus*, a reproductively bimodal water snake from South America, is an ideal
1255 model for this (Braz et al., 2018). Thus far, many oviparous snakes are known to be
1256 intermediately reliant on yolk and eggshell calcium. This has not precluded viviparity from
1257 evolving in these lineages.

1258 The presence of embryos during extended embryonic retention may trigger positive feedback
1259 stimuli for continued uterine calcium secretions (Stewart & Eca, 2010), which may support
1260 incipient calcium matrotrophy. This is postulated to resemble the hormonal and mechanical
1261 stress mechanisms implicated in avian eggshell formation and uterine calcium secretions (Bar,
1262 2009a; Stewart & Eca, 2010). The influx of calcium late in viviparous gestation may be
1263 triggered in part by embryonic growth that over distends the uterus. This is seen in mammals
1264 when uterine overdistention triggers influx of calcium and sodium to support parturition (Kao &
1265 McCullough, 1975).

1266 Dramatic changes to activity in chorioallantois should not be required during parity mode
1267 transitions because these homologous tissues (Metcalf & Stock, 1993) transport calcium
1268 regardless of parity mode (Eca et al., 2004; Tuan & Scott, 1977; Tuan & Knowles, 1984; Tuan
1269 et al., 1978, 1986). Specialized placental structures in some viviparous squamates enhance
1270 calcium provisioning but specialization is not required for placental calcium transport (Stewart et
1271 al., 2009; Stewart & Eca, 2010; Thompson et al., 2000). Loss of chorioallantoic calcium
1272 transporting capacity would be disadvantageous to either parity mode. Growing research reveals
1273 that, like mammals, placentrophy and viviparity can evolve concurrently in squamates
1274 (Blackburn, 2015a; Eca et al., 2017; Stewart & Eca, 2010).

1275 Extending evidence for these hypotheses across the squamate phylogeny, incipient calcium
1276 matrotrophy should support origins of viviparity when viviparity arises in close phylogenetic
1277 proximity to oviparous taxa with embryos that depend intermediately or predominately on
1278 eggshell calcium; Origins of viviparity in close phylogenetic proximity to oviparous taxa with
1279 embryos that depend on lecithotrophic calcium provision should remain reliant on yolk calcium.
1280 This provides a framework from which researchers can infer how viviparous calcium transport
1281 may evolve in different lineages. Measurements of the proportional contribution of different
1282 calcium sources during development has only been done in select taxa (Packard, 1994; Stewart,
1283 2013; Stewart & Blackburn, 2014; Stewart & Eca, 2010). Collection of this data across the
1284 squamate phylogeny may enable assignment of these hypotheses to specific clades.

1285 Embryonic calcium source could have implications on the physiological changes required to
1286 transition between parity modes. Reliance on yolk calcium should render, essentially, no
1287 mechanistic changes for calcium transport. Incipient calcium matrotrophy may require regulatory
1288 changes in the uterus, like timing of calcium secretions (Griffith et al., 2015). However,
1289 regardless of parity mode 1) the uterus secretes calcium, 2) the chorioallantois transports calcium
1290 and 3) embryonic metabolism drives uptake of calcium. Assuming maternal tissue remains
1291 responsive to embryonic metabolism, the joint evolution of matrotrophic calcium provisioning
1292 with viviparity may also require little to no physiological adjustments.

1293 The diversity of embryonic calcium provisioning patterns in viviparous squamates may not
1294 be fully explained by the eggshell calcium constraint hypothesis (Packard et al., 1977; Packard &
1295 Packard, 1984) or incipient calcium matrotrophy (Stewart & Eca, 2010). Both hypotheses
1296 implicitly assume that viviparity equates to a lost eggshell. In one viviparous squamate, *Haldea*
1297 *striatula*, and in viviparous populations of two reproductively bimodal lizards, *Zootoca vivipara*

1298 and *Saiphos equalis*, the calcified eggshell is considered as a component of the placenta (Stewart,
1299 2013). Some other viviparous squamates have transient calcified patches on their embryonic
1300 membranes (Blackburn, 1998; Heulin, 1990, 2005; Qualls, 1996) suggesting that uterine calcium
1301 secreting capabilities in early gestation may be retained in some viviparous lineages. In the case
1302 of reversals, it remains unknown how the uterus shifts back to early calcium secretions after
1303 ovulation (Blackburn, 2015b; Griffith et al., 2015). Reversals may be most feasible within
1304 viviparous clades that evolved through incipient calcium matrotrophy because the calcium
1305 secreting capacity of the uterus is certainly retained.

1306

1307 *(3) Embryonic calcium provisioning mechanisms*

1308 In vertebrates, specialized tissues that recover environmental calcium and transport it into
1309 blood circulation maintain conserved mechanisms for intracellular calcium transport (Bronner
1310 2003; Hoenderop et al., 2005). These include the uterus, chorioallantoic tissues, and yolk
1311 splanchnopleure (Bronner, 2003; Hoenderop et al., 2005; Stewart, 2013). Uterine and embryonic
1312 tissues may be proto-adapted for the maternal-embryonic calcium provisioning (Coleman &
1313 Terepka, 1972; Ecaj et al., 2017; Packard & Packard, 1984; Packard, 1994; Stewart & Ecaj,
1314 2010).

1315 In birds, a sub-compartment of the mammillary layer of the eggshell is the calcium reserve
1316 body (Chien et al., 2009), which contains microcrystals of calcite that get dissolved and
1317 transported as calcium to the embryo (Chien et al., 2009). Calcium is eroded from the eggshell
1318 by acid released from villus cavity cells (VCCs) in chorioallantoic membrane (Anderson et al.,
1319 1981; Narbaitz et al., 1981; Packard & Lohmiller, 2002; Simkiss, 1980). This increases the
1320 carbonic anhydrase activity of the cells enabling calcium to be released into the cavity between

1321 the eggshell and the chorionic epithelium, where it is taken up by capillary covering cells (CCCs)
1322 in chorioallantoic membrane (Coleman & Terepka, 1972). In some species this erosion leads to a
1323 gradual weakening of the eggshell that facilitates hatching (Chien et al., 2008; Nys et al., 2004).
1324 In chickens, transcalcin, a calcium binding protein, is credited for the calcium transporting
1325 capacity of the chorioallantoic membrane (Tuan & Knowles, 1984; Tuan & Ono, 1986; Tuan &
1326 Scott, 1977; Tuan et al., 1978, 1986). The presence of VCCs and CCCs in the chorioallantois of
1327 viviparous squamates would indicate a known route through which calcium can be absorbed.

1328 Transcellular calcium transport has been modeled as a three-step process involving proteins
1329 calbindin-D9K, calbindin-D28K, and the highly calcium-specific ion channels of the transient
1330 receptor potential vanilloid gene family (*TRPV5* and *TRPV6*) (Stewart & Ecaj, 2010). Across
1331 vertebrates, this machinery is shared in epithelial tissues with significant roles in calcium
1332 transport (Hoenderop et al., 2005). Estrogen and vitamin D3 have regulatory roles in this
1333 process.

1334 Calbindin-D9K, calbindin-D28K, *TRPV5*, and *TRPV6* is involved with calcium exchange in
1335 multiple organs of birds, squamates, and mammals. Broadly, activity of calbindin-D9K and/or
1336 calbindin-D28K is associated with patterns of calcium absorption in the mammalian kidney and
1337 uterus (Bindels, 1993; Luu et al., 2004), murine uterus and placenta (Lafond & Simoneau, 2006;
1338 Koo et al., 2012), and chicken duodenum and uterus (Bar & Hurwitz, 1979; Bar, 2009b; Yang et
1339 al., 2013). In humans, calbindin-D9K and calbindin-D28K are critical to the active transport of
1340 Ca²⁺ across placental cells (Faulk & McIntyre, 1983; Belkacemi et al., 2002; Belkacemi et al.,
1341 2004). A study on rats suggests that calbindin-D9K increases by over 100-fold in the last 7 days
1342 of gestation (Glazier et al., 1992), when the embryo gains >99% of calcium (Comar, 1956).
1343 *TRPV6* is involved with maternal-fetal calcium transport in mice (Suzuki et al., 2008). Increased

1344 *TRPV6* and calbindin-D28K expression occurs during eggshell formation in chickens (Yang et
1345 al., 2013). Given the involvement of these loci in both eggshell deposition and embryonic
1346 calcium transport, squamates may have exploited this pathway to support transitions.

1347 In several highly matrotrophic lizards, embryonic uptake of calcium is associated with
1348 placental expression of calbindin-D28K (Stewart et al., 2009; Stinnett et al., 2011, 2012). In both
1349 oviparous and viviparous embryos of *Zootoca vivipara*, sharp increase in calcium uptake in late
1350 development coincides with increased calbindin-D28K and PMCA by the chorioallantois
1351 (Stewart et al., 2009, 2011). In oviparous corn snakes, *Pantherophis guttatus*, expression of
1352 calbindin-D28K in the yolk-sac and chorioallantoic membrane coincides with growth of these
1353 tissues and calcium transport activity (Ecay et al., 2004). The chorioallantois of other lizards and
1354 snakes transport calcium to the embryo and express calbindin-D28K and PMCA (Blackburn,
1355 2004; Ecay et al., 2004; Stewart et al., 2010; Stinnett et al., 2012).

1356 Viviparous embryos of *Zootoca vivipara*, a reproductively bimodal lizard, incubated *ex utero*
1357 respond to availability of calcium by increasing expression of calbindin-D28K (Ecay et al.,
1358 2017). In this species, embryonic recognition of environmental calcium stimulates a transcellular
1359 calcium transporting mechanism and may also alter chorioallantoic membrane paracellular
1360 permeability to calcium (Ecay et al., 2017). The authors proposed that there is a calcium sensing
1361 receptor (CaSR) on chorionic epithelial cells to support this in both oviparous and viviparous
1362 *Zootoca vivipara* embryos (Ecay et al., 2017), similar to the CaSRs expressed by vertebrate cells
1363 involved in calcium homeostasis (Brennan et al., 2013).

1364 As mentioned earlier, PMCA activity is associated with eggshell deposition in birds and
1365 oviparous squamates (Bar et al., 1984; Hincke et al., 2012; Wasserman et al., 1991). PMCA is
1366 also crucial for calcium transport in late embryonic development in rats (Glazier et al., 1992). In

1367 viviparous scincid lizards, *Niveoscincus metallicus*, *N. ocellatus*, and *Pseudemoia spenceri*,
1368 PMCA was expressed in uterine glandular and surface epithelia during pregnancy but only *P.*
1369 *spenceri* expressed it throughout gestation (Herbert et al., 2006). When PMCA was not detected
1370 by immunoblotting in the yolk splanchnopleure of *Haldea striatula*, a viviparous snake that
1371 relies predominately on yolk calcium (Stewart, 1989; Fregoso, Stewart, & Eca, 2010), NCXs
1372 were proposed as an alternative transporter of calcium (Fregoso et al., 2012). NCXs are
1373 important for placental calcium transport in humans (Belkacemi et al., 2005).

1374 Calcitropic hormones, those involved with calcium transport, and phosphotropic hormones,
1375 those involved with phosphorous transport, operate via an interconnected pathway (Andrukhova
1376 et al., 2016; Biber et al., 2013; Blaine et al., 2015; Erben & Andrukhova, 2015). Phospho- and
1377 calcitropic hormones are important regulators of fetal serum mineral concentrations (Kovacs,
1378 2015). Evidence from viviparous amniotes suggests that these are suitable candidates for
1379 embryonic calcium provisioning. In mice, genes encoding parathyroid hormone (*PTH*) and *PTH*-
1380 related peptide (*PTHrP*) are important regulators of placental calcium transport (Kovacs et al.,
1381 1996; Simmonds et al., 2010). A non-exhaustive list of additional candidates for embryonic
1382 calcium provisioning include fibroblast growth factor 23 (Bar, 2009a; Erben & Andrukhova,
1383 2015; Stewart & Eca, 2010), the annexin gene family (Matschke et al., 2006), carbonic
1384 anhydrase (Narbaitz et al., 1981; Tuan & Knowles, 1984), and calcium binding proteins (CaBPs)
1385 can be found in the referenced literature.

1386

1387 (4) Discussion & future directions—calcium provisioning and parity mode evolution

1388 Generalized hypotheses to explain how squamate parity modes evolve are not universally
1389 applicable (Hodges, 2004; Li et al., 2009; Packard et al., 1977; Stewart & Eca, 2010). However,

1390 they can be used as a framework to infer the most likely form of embryonic calcium provisioning
1391 used in specific lineages. This was discussed in detail in section two. Phylogenetic frameworks
1392 like this enable researchers to make broader testable hypotheses about the evolutionary history of
1393 calcium provisioning in specific clades. Implications gleaned from taxon-specific studies can be
1394 explored in distantly related analogous groups. Additionally, I speculated that lineages with
1395 incipient calcium matrotrophy may more feasibly reversal to oviparity because of continued role
1396 of uterus in calcium provisioning.

1397 Loci involved with calcium transport in uterine and embryonic tissues have been described
1398 across mammals, birds, and reptiles. Like other amniotes, activity of calbindin-D28K and PMCA
1399 supports embryonic calcium provisioning across diverse oviparous and viviparous squamates.
1400 Their involvement with both eggshell deposition and embryonic calcium provisioning makes
1401 these particularly interesting candidates for parity mode evolution. The regulatory influence of
1402 other molecules in calcium transport, like *PTH*, *PTHrP* and *NCXs* has not been evaluated
1403 thoroughly in squamates. Additional reviews on mechanisms of embryonic calcium provisioning
1404 in squamates can be found in the literature (Stewart, 2013; Stewart & Blackburn, 2014; Stewart
1405 & Ecaj, 2010).

1406

1407 **VI. Maternal-Fetal Immune Dynamics**

1408

1409 Medawar (1953) pointed out the paradigm between the peripheral body's normal attack
1410 response to allografts (foreign tissue) and uterine tolerance to embryos (Medawar, 1953). This
1411 was inspired by earlier work by Ray Owen (Owen, 1945). Stricter regulation of the maternal and
1412 fetal immune systems is expected for viviparous reproduction because of contact between uterine

1413 and embryonic tissues. Oviparity may pose less of an immunological challenge. Medawar
1414 suggested barriers, inertness and/or immunosuppression enable pregnancy. This formed the
1415 foundation of decades of medical research on immune dynamics between maternal, embryonic,
1416 and paternal immune factors in utero.

1417 In recent years, there was a call for a reappraisal of Medawar's paradigm (Chaouat, 2010,
1418 2016; Moffett & Loke, 2004, 2006; Mor et al., 2011; Stadtmauer & Wagner, 2020b; Yoshizawa
1419 2016). Moffett & Loke (2006) caution against conceptualizing embryos as analogs of allografts.
1420 This perspective has yet to reach the evolutionary literature on parity mode evolution (Graham et
1421 al., 2011; Gao et al., 2019; Murphy & Thompson, 2011; Van Dyke, Brandley, & Thompson,
1422 2014; Murphy, Thompson, & Belov, 2009).

1423 The uterine immune system has a distinct evolutionary history from the periphery. The
1424 uterine immune environment enables cooperative dynamics with foreign tissues. It supports
1425 fertilization and early embryonic development. This should have started evolving, distinct from
1426 the periphery, since internal fertilization first originated. To demonstrate this, I discuss the
1427 changing landscape of immunological research at the maternal-fetal interface and apply it to the
1428 current knowledge on uterine and embryonic immune responses during viviparous gestation in
1429 squamates.

1430 Most literature on maternal-fetal immune dynamics limits itself to mammals. Squamates may
1431 serve as a better comparative model for understanding the evolution of the uterine immune
1432 system. Active research on the peripheral reptilian immune system (Zimmerman et al., 2010,
1433 2020) and uterine immune activity in squamates (Graham et al., 2011; Hendrawan et al., 2017;
1434 Murphy et al., 2009; Paulesu et al. 1995, 2008, 2005) will support future insights on this.

1435

1436 *(1) Comparing amniote immune systems*

1437 Cellular components of the innate immune system are conserved across jawed vertebrates
1438 (De et al., 2007; Uribe et al., 2011; Zimmerman et al., 2010). The general machinery of the
1439 adaptive immune system is ancient despite divergences and convergences across all domains of
1440 life (Ghosh et al., 2011; Morales et al., 2017; Müller et al., 2018; Rimer et al., 2014).
1441 Diversification of antigen receptor genes likely occurred independently in a lineage-specific
1442 fashion (Boehm et al., 2018). Compared to mammals, the avian immune system requires less
1443 antigen (Larsson et al., 1998). Birds also have faster but shorter antibody responses, potentially
1444 due to their higher body temperatures (Jurd, 1994).

1445 Reptiles have the same general components of the mammalian immune system (Zimmerman,
1446 2020). However, the reptilian immune system may not fit neatly into the two arms of mammalian
1447 immune systems—innate and adaptive (Zimmerman, 2010; 2020). Expanding upon this is
1448 beyond the scope of this review, but it is worth considering in future comparative research. I
1449 refer readers to articles by Zimmerman et al. (2010, 2020) and Ghorai et al. (2018), and the
1450 books by Williams (2012) and Davison et al. (2008) for more information on reptilian and avian
1451 immune systems.

1452

1453 *(2) Medawar's paradigm*

1454 Tolerance toward the foreign fetus was postulated to occur through immunological inertness,
1455 immunosuppression or immunotolerance mechanisms (Medawar, 1953). Theoretically,
1456 immunotolerance could be established if there are relatively small quantities of alloantigens
1457 present, resulting in regulatory responses rather than activating responses (Pradeu, 2011).
1458 Contradicting this, the larger the alloantigen difference between the mother and embryo the

1459 bigger and healthier the placentae in rats (Chaouat et al., 2010). In humans, divergent HLA
1460 profiles between mother and embryo do not lead to detrimental immune responses (Tilburgs,
1461 Scherjon, & Claas, 2010). Instead, cooperative inflammatory responses between maternal and
1462 fetal tissues support reproduction (Stadtmauer et al., 2020). In humans, microchimeric cell
1463 populations, presence of cells from one individual in another genetically distinct individual, are
1464 now considered a normal expectation of pregnancy (Nelson, 2012).

1465 In his 1991 Nobel Lecture, Medawar acknowledged that maternal and embryonic tissues
1466 have regular exposure to alloantigens (Medawar, 1991). It has become clear that the maternal
1467 immune system actively responds to fetal alloantigen rather than responding solely with
1468 ignorance or anergy (Arck & Hecher, 2013). Neither maternal immunosuppression/privilege nor
1469 embryonic inertness/immaturity fully explain immune dynamics during gestation in mammals,
1470 including those with the simple epitheliochorial placentation (Chaouat et al., 2010; Chavan et al.,
1471 2017; Moffett & Loke, 2004, 2006; Stadtmauer & Wagner, 2020).

1472

1473 *(3) Perspectives on the evolution of the uterine immune system*

1474 Viviparous reproduction existed eons before the origin of mammals and no evidence suggests
1475 there was immune conflict within these taxa (Chaouat, 2016). Placentrophy existed as far back as
1476 the invertebrate clade Bryozoa (Ostrovsky, 2013; Schwaha et al., 2019), suggesting an ancient
1477 history for supportive maternal-fetal immune dynamics. Differing from Medawar's paradigm,
1478 Polly Matzinger, who proposed the 'danger model' for the immune system (Matzinger, 2007),
1479 wrote "Reproduction cannot be a danger. It does not make evolutionary sense" (Chaouat, 2016).

1480 In mammals, immunological cells at the maternal-fetal interface may not function through
1481 self-non-self-discrimination, as they are understood to function in the rest of the body (Chaouat,

1482 2016; Moffett & Loke 2004, 2006). The ‘maternal-fetal interface’ may be better conceptualized
1483 as ‘maternal-fetal intra-action’ given the dynamics between maternal and fetal immune systems
1484 in mammals (Yoshizawa, 2016). It is unclear if these insights apply to other viviparous amniotes.

1485 In mammals, immune factors in the uterus and placenta appear to be specifically evolved to
1486 support maternal-fetal immune dynamics. Several cell types have unique functions and/or
1487 phenotypes in utero—uterine NK (uNK) cells, uterine macrophages, uterine T regulatory cells
1488 (Faas & de Vos, 2017; Mold et al., 2008, 2010; Mold & McCune, 2011). An immunosuppressive
1489 antigen, HLA-G, is almost exclusively expressed by trophoblasts (Faulk & Temple, 1976;
1490 Kovats et al., 1990; Rajagopalan & Long, 2012; Rouas-Freiss et al., 1997). Taken from an
1491 evolutionary perspective, this suggests that the uterine immune system in viviparous mammals
1492 evolved unique responses to allogenic tissues that differ from the periphery. Whether the
1493 evolution of this system predates mammals remains to be explored, to my knowledge.

1494 Some suggest that viviparous reproduction is immunologically compatible in species with
1495 less active adaptive immune system. In these clades, innate immune cells, like uNK cells, may be
1496 sufficient to regulate immune responses during pregnancy (Moffett & Loke, 2004; Chaouat,
1497 2016). Determining whether viviparity is immunologically compatible in squamates, or if they
1498 require specialized immune responses in utero, requires further investigation. Nonetheless,
1499 uterine tissue of oviparous and viviparous skinks expresses maternal antigens prior to and during
1500 gravidity and gestation (Murphy et al., 2009). Viviparous species in this study have a unique
1501 expression profile of MHC antigens which may ‘hide’ the embryo from the maternal immune
1502 system (Murphy et al., 2009).

1503

1504 *(4) Implications of the reptilian immune system and morphology on parity mode evolution*

1505 Ectothermic reptiles may inherently have a more tolerogenic uterine environment compared
1506 to mammals due to their slower antibody response. It can take up to six weeks to reach peak
1507 concentrations (Ingram & Molyneux, 1983; Grey, 1963; Marchalonis et al., 1969; Pye et al.,
1508 2001; Origgi et al., 2001; Work et al., 2000). A slower metabolism also makes several reptiles
1509 more tolerogenic to pathogens (Ghorai & Priyam, 2018).

1510 During pregnancy in the viviparous skink, *Chalcides ocellatus*, there is a reduced response to
1511 in vitro exposure to mitogens concanavalin A (Con A), phytohemagglutinin (PHA), and
1512 *Escherichia coli* lipopolysaccharide (LPS) (Saad & El Deeb, 1990). Oviparous lizards exhibit
1513 immune activation tradeoffs during reproductive cycles (Cox, Peadar, & Cox, 2015; Durso &
1514 French, 2018; French, Johnston, & Moore, 2007; Uller, Isaksson, & Olsson, 2006).

1515 In the majority of viviparous squamates, the eggshell membrane is absorbed during
1516 pregnancy (Yaron, 1985; Blackburn, 1993). Whether the eggshell membrane elicits immune
1517 responses prior to absorption remains to be examined to my knowledge. Viviparous squamates,
1518 at minimum, have epitheliochorial placentation. In mammals, epitheliochorial placentation is
1519 sufficient to cause immunorecognition from the mother. Specialized placental cells, trophoblasts,
1520 may be more common in other viviparous amniotes than previously recognized (Blackburn,
1521 2015a). In mammals, trophoblasts are antigen presenting and actively participate in maternal-
1522 fetal immune dynamics.

1523 A few viviparous squamates have placentas with characteristics similar to placentas found in
1524 eutherian mammals—syncytialized cells layers, specialized zones such as areolae and
1525 placentomes, or cellular invasion of maternal tissues by the fetus (Blackburn & Flemming, 2012;
1526 Jerez & Ramírez-Pinilla, 2001; Vieira et al., 2007). The increased contact here may require more

1527 tightly regulated immune dynamics at the maternal-fetal interface compared to other viviparous
1528 squamates.

1529

1530 (5) *The inflammation paradox*

1531 In mammals, implantation may have evolved from an ancestral inflammatory attachment
1532 reaction (Griffith, Chavan et al., 2017). Inflammation is the most crucial system to support
1533 implantation, but it is also the greatest threat to the continuation of pregnancy (Chavan et al.,
1534 2017). This phenomenon is called the inflammation paradox. In humans, immune cells including
1535 uterine macrophages, T cells of multiple subtypes, uterine natural killer (uNK) cells, dendritic
1536 cells, and natural killer T (NKT) cells increase until implantation and remain abundant in the
1537 uterus throughout first trimester (Bulmer et al., 1991, 2010). Early implantation in humans is
1538 characterized by high pro-inflammatory T helper (Th)-1 cells and cytokines (IL-6, IL-8, and
1539 TNF α) (Koga & Mor, 2008; Yoshinaga, 2008). The exploitation of inflammatory mechanisms
1540 for eutherian implantation and the shift toward non-inflammatory activity to maintain pregnancy
1541 may have been key in enabling extended embryonic retention of eutherians (Griffith, Chavan et
1542 al., 2017).

1543 How the inflammation paradox applies to viviparous squamates is unclear, given that
1544 placentation in squamates and mammals is not homologous (Griffith, Van Dyke, & Thompson,
1545 2013). In extrauterine pregnancies of mammals with non-invasive placentas, the embryo will
1546 invade extrauterine tissue because it is not inhibited by uterine secretions (Vogel, 2005; Samuel
1547 & Perry, 1972). However, in *Pseudemoia entrecasteauxii*, a viviparous skink that also has a non-
1548 invasive placenta, extrauterine pregnancy does not result in invasive implantation of extrauterine
1549 tissues (Griffith, Van Dyke, & Thompson, 2013). The inherent invasive nature of mammalian

1550 embryos outside of the uterus, compared to the non-invasive nature of viviparous squamate
1551 embryos studied thus far, suggests that the parent-offspring conflict and the inflammation
1552 paradox may be less pronounced in viviparous squamates compared to viviparous mammals.

1553

1554 *(6) Inertness and barriers at the maternal-fetal interface*

1555 The uterine environment is not inert or sterile (Agostinis et al., 2019; Erlebacher, 2013;
1556 Moffett & Loke, 2006; Munoz-Suano, Hamilton, & Betz, 2011; Murphy, Thompson, & Belov,
1557 2009; Terzidou, 2007; Yoshimura, Okamoto, & Tamura, 1997). In humans, the decidual layer of
1558 the uterus during pregnancy is comprised of ~40% leukocytes (Ander, Diamond, & Coyne, 2019;
1559 Manaster & Mandelboim, 2010). This cellular subpopulation has 70% uNK cells, 10-20%
1560 antigen presenting cells (APCs) including macrophages and dendritic cells, and 3-10% T cells of
1561 several subtypes (Abrahams et al., 2004; Hanna et al., 2006; Kämmerer et al., 2006; Le
1562 Bouteiller & Piccinni, 2008; Liu et al., 2017; Manaster & Mandelboim, 2010; Moffett-King,
1563 2002; Moffett & Loke, 2006; Roussev et al., 2008). There is an abundance of decidual large
1564 granular lymphocytes (LGLs), CD3-NK cells and CD3+ activated cytotoxic T cells, in the
1565 human uterus, that have cytotoxic properties and produce cytokines, and these are affected by
1566 fetal MHC molecules (Rieger, 2002).

1567 Avian and non-avian reptiles have also immunocompetent cells in their oviducts. T and B
1568 cells are present in chicken ovary where they are stimulated by estrogen (Barua & Yoshimura,
1569 1999; Withanage et al., 2003; Zettergren & Cutlan, 1992). Other immunocompetent cells in the
1570 chicken oviduct include IgG+, IgA+ and CD3+ (Yoshimura, Okamoto, & Tamura, 1997).

1571 Immune competent cells located throughout the mucosal tissue of avian oviductal segments

1572 including macrophages, antigen presenting cells (APCs) expressing MHC class II antigens,
1573 helper T cells and cytotoxic T cells, and premature B cells (Das, Isobe, & Yoshimura, 2008).

1574 Inert barriers between maternal and fetal tissues may 'hide' the embryo. In oviparous taxa,
1575 the eggshell may serve as a barrier. However, the antimicrobial properties of the eggshell matrix
1576 in birds demonstrate that even the eggshell is not inert. The FAS ligand, also called APO-1 or
1577 CD95, in humans and rodent embryonic tissue was proposed to serve as a barrier because it
1578 causes apoptosis of surrounding maternal immune cells (Kayisli et al., 2003; Makrigiannakis et
1579 al., 2008).

1580 Medawar suggested that an impermeable placenta strictly regulates molecular exchanges,
1581 preventing rejection of the embryo (Medawar, 1991). Syncytiotrophoblasts lack cellular junctions
1582 and thus it was postulated to serve as this barrier (Ander, Diamond, & Coyne, 2019). However,
1583 the growing data on bidirectional cellular traffic of APCs, even in mammals with noninvasive
1584 placentas, rejected this hypothesis (Bakkour et al., 2014; Burlingham, Bracamonte-Baran, &
1585 Burlingham, 2014; Fujiki et al., 2008; Turin et al., 2007).

1586

1587 *(7) T cell populations and mammalian viviparity*

1588 In mammals, immune-dynamics at the maternal-fetal interface are established through
1589 innate and adaptive immune responses. There is a delicate balance between ratios of Th1, Th2,
1590 Th17, Tregs and memory T cells at the maternal-fetal interface in eutherian mammals during
1591 gestation (Chaouat et al., 1997; Kieffer et al., 2019; Peck & Mellins, 2010; Saito et al., 2010; Wu
1592 et al., 2014). A shift in utero from T helper type 1 (Th1) cells to T helper type 2 (Th2) cells
1593 during gestation in mammals equates to a shift from pro-inflammation to anti-inflammation. The
1594 galectin proteins, GAL-13 and GAL-14, expressed by syncytiotrophoblasts, bind to T cells

1595 where they inhibit activation, induce apoptosis, and enhance interleukin-8 (IL-8) production
1596 (Balogh et al., 2019).

1597 Growing research is revealing the central role of Tregs at the maternal-fetal interface
1598 during pregnancy in mammals (Teles et al., 2013; Wienke et al., 2019). Tregs play a central role
1599 in immunosuppression in mammals (Attias, Al-Aubodah, & Piccirillo, 2019). Differentiation of
1600 Tregs is governed by the transcription factor, *FOXP3* (Ramsdell & Rudensky, 2020).

1601 Alloantigen-dependent, uterine T cell signaling, and immunocompetent embryonic cells and their
1602 products facilitate enhanced regulatory phenotypes of immune cells overall (Ander, Diamond, &
1603 Coyne, 2019).

1604 The T-cell dependent adaptive immune system of mammals is unique. This may have
1605 prompted their intricate balance of Treg mediators of immunotolerance at the maternal-fetal
1606 interface (Chaouat, 2016). Birds rely more heavily on B cells. In non-avian reptiles, T helper
1607 cells are functional, but the presence and function of other T cell subsets is unclear (Zimmerman,
1608 2020; Zimmerman, Vogel, & Bowden, 2010). The potential role of T cells and Tregs in
1609 viviparous squamate gestation should not be discounted. Treg-like cells have been identified in a
1610 pufferfish, *Tetraodon nigroviridis* (Wen et al., 2011), suggesting that Tregs may have an ancient
1611 evolutionary history.

1612

1613 (8) *Progesterone, cytokines, and maternal-fetal immune dynamics*

1614 In addition to the role of progesterone in uterine quiescence (embryonic retention) and
1615 hepatic vitellogenesis (nutrient provisioning), it also plays a role in maternal-fetal immune
1616 dynamics. In the uterus of pregnant mammals, progesterone concentrations are associated with
1617 altered B cell immunoglobulin secretion, inhibition of NK-cell mediated cytotoxicity and the shift

1618 from Th1 (pro-inflammatory) to Th2 (anti-inflammatory) dominated immune responses
1619 (Druckmann & Druckmann, 2005). Progesterone is also associated with immunomodulatory
1620 effects (Ortega Brown et al., 1990). During gestation in *Agkistrodon piscivorus*, a viviparous pit
1621 viper, progesterone concentrations are associated with decreased complement performance
1622 (Graham et al., 2011), a portion of the immune system that promotes inflammation, among other
1623 immune functions.

1624 In humans, progesterone induced protein (PIBF) is transported by placental extravillous
1625 trophoblasts to maternal lymphocytes causing the induction of interleukin-10 (IL-10) production,
1626 contributing to the Th2 dominant responses (Szekeres-Bartho, Šućurović, & Mulac-Jeričević,
1627 2018). IL-10 is a potent anti-inflammatory cytokine that is produced by multiple cell types
1628 (Zimmerman, Bowden, & Vogel, 2014). It is associated with Th2 response, and it inhibits Th1
1629 responses. The phenotype of uterine macrophages is affected by trophoblasts when they secrete
1630 IL-10 and macrophage colony-stimulating factor (M-CSF) (Svensson-Arvelund et al., 2021). IL-
1631 10 inhibits IFN- γ and increases in response to infection in chickens (Giansanti, Giardi, & Botti,
1632 2006; Rothwell et al. 2004). In the uterus of the oviparous skink, *Lampropholis guichenoti*,
1633 during gravidity and non-gravidity, IL-10 is expressed (Griffith et al., 2016).

1634 Proinflammatory cytokines may be downregulated during reproductive periods to limit
1635 maladaptive immune responses to the foreign fetus (Zimmerman, Vogel, & Bowden, 2010). In
1636 mammals, IL-1 allows release of hormones in human trophoblasts (Felice Petraglia et al., 1990;
1637 Masuhiro et al., 1990; Yagel et al., 1989), facilitates implantation (Haimovici, Hill, & Anderson,
1638 1991; Hill, 1992; Tartakovsky & Ben-Yair, 1991), and influences the initiation of labor (Romero
1639 et al., 1989, 1992). Regulation of the proinflammatory cytokines tumor necrosis factor (TNF)

1640 and interleukin 1B (IL-1 β) is of particular importance in eutherian pregnancy (Haider & Knöfler,
1641 2009; Paulesu, Romagnoli, & Bigliardi, 2005; Saito et al., 2010; Tayade et al., 2006).

1642 The uterine tissue of two reproductively bimodal squamates—viviparous individuals of
1643 *Chalcides chalcides*, and oviparous and viviparous individuals of *Zootoca vivipara*—express IL-
1644 1 β (Paulesu et al., 1995, 2005; Romagnoli et al., 2003). In the uterus of the viviparous skink,
1645 *Pseudemoia entrecasteauxii*, during gestation regulation of TNF and IL-1 β at the transcriptional
1646 and post-translation levels, respectively, may reduce inflammation (Hendrawan et al., 2017). The
1647 pro-inflammatory function of IL-1 β in *Pseudemoia entrecasteauxii* may play a role developing a
1648 more complex placenta (Hendrawan et al., 2017). The placenta of *Chalcides chalcides* expresses
1649 pro-inflammatory cytokines, IL-1 α and IL-1 β , at specific times during gestation (Paulesu et al.,
1650 1995). During gestation, *Chalcides ocellatus* also differentially expresses 27 other interleukins
1651 and interleukin related products (Brandley et al., 2012).

1652 The expression of IL-34 in a marsupial, the fat-tailed dunnart, during pre-implantation
1653 (Whittington et al., 2018) may have an immunosuppressive function to help tolerate potential
1654 contact of maternal and fetal tissues when the embryonic shell coat disintegrates (Lindau et al.,
1655 2015; Roberts & Breed, 1994; Selwood, 2000). In chickens, IL-34 regulates Th1 and Th17
1656 cytokine production (Truong et al., 2018). During gestation in *Pseudemoia entrecasteauxii*, IL-
1657 16 and IL-1 α are expressed in addition to three receptors for Th17 family cytokines—IL-17RA,
1658 IL-17RC, and IL-17RA (Griffith, Brandley, et al., 2016, 2017). In the yolk sac of *Pseudemoia*
1659 *entrecasteauxii* during pregnancy interleukin related molecules, *ILDRI*, *IRAK1*, and *SIGIRR*, are
1660 differentially expressed (Griffith et al., 2016). This profile suggests the presence of tricellular
1661 tight junctions and/or tricellulin (Higashi et al., 2013; Ikenouchi et al., 2005), and regulation of

1662 toll-like receptors (TLRs) and/or IL-1R signaling (Kawagoe et al., 2008; Lin, Lo, & Wu, 2010;
1663 Muzio et al., 1997).

1664

1665 *(9) The major histocompatibility complex and maternal-fetal immune dynamics*

1666 A substantial amount of literature on maternal-fetal immune dynamics was initially focused
1667 on uNK cells. Uterine NK cells have a distinct phenotype and function from peripheral NK cells.
1668 They have several activating receptors (Manaster & Mandelboim, 2010) but do not exert
1669 cytolytic functions on embryonic trophoblasts that they are in contact with (King, Birkby, &
1670 Loke, 1989). Allorecognition of embryonic placental cells by uNK cells is a key regulator of the
1671 maternal-fetal immune mechanisms that support placentation in mammals (Moffett et al., 2014).
1672 When cells lose their ability to express any HLAs, uNK cells are shown to kill them (Hunt et al.,
1673 2005; Ishitani et al., 2003; King, Allen et al., 2000).

1674 In humans, expression of the classical MHC class I (C-MHCI) molecule HLA-C, and
1675 nonclassical MHC class I (NC-MHCI) molecules HLA-E, HLA-F and HLA-G on trophoblasts
1676 inhibit uNK cell-mediated cytotoxicity (Hunt et al., 2003; King, Burrows et al., 2000). Differing
1677 from this, mismatched HLA-C profiles trigger rejection of the transplanted organs (Petersdorf et
1678 al., 2014). Selection for balanced polymorphisms in HLA-C alleles and their killer
1679 immunoglobulin receptors (KIRs) is proposed to be driven by reproductive success, rather than
1680 immune recognition of pathogens (Trowsdale & Betz, 2006). Dimorphisms of HLA-C emerged
1681 recently within primates (Adams & Parham, 2001).

1682 Similar patterns in MHC profiles have been explored in other viviparous amniotes. C-MHCI
1683 antigen, H2-K, is expressed on giant trophoblast cells of mice and this is attributed to
1684 trophoblast-induced uterine vasculature transformation (Arcellana-Panlilio & Schultz, 1994;

1685 Chatterjee-Hasrouni & Lala, 1982; Hedley et al., 1989; King et al., 1987; Sellens, Jenkinson, &
1686 Billington, 1978). H2-D antigen is co-expressed with H2-K in virtually all their other nucleated
1687 cells (Madeja et al., 2011). However, H2-K expressing trophoblasts lack H2-D expression. This
1688 parallels the expression patterns of C-MHC molecules at the maternal-fetal interface in humans
1689 and may be an evolutionarily conserved pattern (Madeja et al., 2011).

1690 In humans, NC-MHCI molecule, HLA-G, is especially tolerogenic (Carosella et al., 2015;
1691 González et al., 2012; Hviid et al., 2004; Kovats et al., 1990). In adults, HLA-G is almost
1692 exclusively expressed by fetal trophoblasts compared to adult cells (Faulk & Temple, 1976;
1693 King, Burrows et al., 2000; Kovats et al., 1990; Rajagopalan & Long, 2012; Rouas-Freiss et al.,
1694 1997). It supports immunotolerance at the maternal-fetal interface (Rebmann et al., 2014). The
1695 role of HLA-G in supporting tolerogenic responses to organ transplants appears to be an
1696 exploitation of its role in immunotolerance in the utero during pregnancy (Rebmann et al., 2014).
1697 HLA-G is upregulated by several molecules that serve essential roles during gestation including
1698 progesterone (Yie, Xiao, & Librach, 2006; Yie et al., 2006), IFN- α , IFN- β , and IFN- γ (Rebmann
1699 et al. 2003; Lefebvre et al., 2001; Ugurel et al., 2001; Yang, Geraghty, & Hunt, 1995), and IL-10
1700 and TGF- β (Cadet et al., 1995; Moreau et al., 1999).

1701 A similar NC-MHCI gene to HLA-G exists in horses (Davies et al., 2006) where it likely
1702 functions to protect the embryo from NK-cell mediated attack (Ott et al., 2014). NC-MHC
1703 molecules with similar structure to HLA-G are also found in Rhesus monkeys (Boyson et al.,
1704 1997) and baboons (Stern et al. 1987). Mice have two NC-MHCI genes that are expressed on the
1705 surface of their placentas and on pre-implanted embryos (Product, Warner, & Goldbard, 1987;
1706 Sipes et al., 1996).

1707 In the gestating uterus of the viviparous skink, *Pseudemoia entrecasteauxii*, four putative C-
1708 MHCI and two putative NC-MHCI molecules are expressed (Murphy, Thompson, & Belov,
1709 2009). This pattern resembles the C-MHCI and NC-MHCI expression profiles of mammals,
1710 suggesting that this viviparous skink utilizes a similar physiological mechanism to ‘hide’ the
1711 embryo (Murphy, Thompson, & Belov, 2009). One of the putative NC-MHCI loci (Psen-
1712 160Ut/Psen-78G) has a substitution at position 150 where a tryptophan is substituted for a
1713 leucine (Murphy, Thompson, & Belov, 2009). When Psen-160Ut/Psen-78G was aligned to NC-
1714 MHCI loci of vertebrates ranging from fish to eutherian mammals, tryptophan was conserved at
1715 position 150 except in Psen-160Ut/Psen-78G and HLA-G (Murphy, Thompson, & Belov, 2009).
1716 Whether this reflects an evolutionary history associated with immune tolerance at the maternal-
1717 fetal interface in *Pseudemoia entrecasteauxii* requires further investigation.

1718 MHCI genes are also expressed in reproductive tissues of oviparous skinks (*Ctenotus*
1719 *taeniolatus* and *Lampropholis guichenoti*) during non-reproductive periods and during late
1720 gravidity (Murphy, Thompson, & Belov, 2009). A similar pattern is found in viviparous skinks
1721 *Eulamprus tympanum*, *Niveoscincus metallicus*, *Pseudemoia entrecasteauxii* and the
1722 reproductively bimodal skink *Saiphos equalis* which all express MHCI genes at non-
1723 reproductive periods and during late pregnancy/gravidity (Murphy, Thompson, & Belov, 2009).

1724 Differential expression of immune factors in an oviparous lizard with long egg-retention,
1725 *Saiphos equalis* included complement component genes (*C3*, *C9*) and genes relating to MHC loci
1726 (*H2-EA*) (Foster et al., 2020). These were also differentially expressed in viviparous individuals
1727 of this species during gestation (Foster et al., 2020). Lengthened egg retention occurs in some
1728 oviparous squamates. If it requires regulation of the uterine immune environment, then this has
1729 important implications for the evolution of viviparity in squamates.

1730 The butyrophilin subfamily 1 member A (*BTN1A1*) is located in the MHCI region of the
1731 genome in mammals (Trowsdale, 2011). *BTN1A1* is differentially expressed in the uterus during
1732 gestation in a viviparous lizard, *Chalcides ocellatus* (Brandley et al., 2012). *BTN1A1* may have
1733 important antimicrobial properties in chicken eggshells (Mann, Maček, & Olsen, 2006). In
1734 mammals *BTN1A1* is the major protein associated with fat droplets in milk (Jeong et al., 2009).

1735

1736 (10) *Microchimerism and maternal-fetal immune dynamics*

1737 Billingham, Brent and Medawar suggested the concept of actively acquired immunologic
1738 tolerance during pregnancy almost 70 years ago (Billingham, Brent, & Medawar, 1953).
1739 Subsequent research over the following decades revealed that substantial transfer of proteins,
1740 parasites and even immunologically active cells occurs between mother and embryo (Adams &
1741 Nelson, 2004; Axiak-Bechtel et al., 2013; Bakkour et al., 2014; Burlingham, 2010; Fujiki et al.,
1742 2008; Gitlin et al., 1965; Khosrotehrani et al., 2005; Owen, 1945; Remington et al., 2006; Turin
1743 et al., 2007). Microchimerism, where there is <0.1% donor chimeras in host tissue, is relatively
1744 pervasive among eutherians during pregnancy. It plays a role in establishing tolerance to non-
1745 inherited antigens. For example, cell populations from the mother that are transferred into
1746 embryonic lymph nodes enable the establishment of embryonic Tregs that are tolerogenic toward
1747 non-inherited maternal antigens (Mold et al., 2008).

1748 Microchimeric cellular populations are transferred across all placental types (Axiak-Bechtel
1749 et al., 2013; Bakkour et al., 2014; Fujiki et al., 2008; Khosrotehrani et al., 2005; Turin et al.,
1750 2007). Fetal and maternal cells persist for decades after birth across a range of tissues in mother
1751 and offspring, respectively (Adams & Nelson, 2004; Bakkour et al., 2014; Bayes-Genis et al.,
1752 2005; Bianchi et al., 1996; Evans et al., 1999; Jonsson et al., 2008; Stevens et al., 2004). There is

1753 even a call in the immunology literature to shift from the conventional paradigm of “self vs
1754 other” to instead consider the “self” as inherently chimeric (Nelson, 2012). Given that
1755 epitheliochorial placentation is sufficient to illicit microchimeric cell populations, the occurrence
1756 of similar bidirectional cellular traffic is a reasonable possibility in viviparous squamates.

1757

1758 (11) *Paternal alloantigens*

1759 Under tenants gleaned from transplant medicine, the maternal immune system would illicit
1760 an attack response as early as insemination when maternal tissues are exposed to paternal
1761 alloantigens (Borziak et al., 2016; Schumacher & Zenclussen, 2015; Seavey & Mosmann, 2006).
1762 Instead, maternal cells immunologically recognize them at this time without attack (Schumacher
1763 & Zenclussen, 2015; Seavey & Mosmann, 2006; Zenclussen et al., 2010). Treg expansion, a
1764 process with major influence on maternal-fetal immunotolerance in mammals, is proposed to be
1765 driven by several different factors found in seminal plasma (Baratelli et al., 2005; Clark,
1766 Fernandez, & Banwatt, 2008; Teles et al., 2013). Mothers may maintain fetal-specific Tregs with
1767 memory of the paternal alloantigens (Schober et al., 2012), expediting Treg response in future
1768 pregnancies with the same father (Rowe et al., 2012).

1769 Alloantigen exposure at the time of insemination is not restricted to mammals. Seminal fluid
1770 of chickens contains two MHC I paternal alloantigens and one MHC II alloantigen (Borziak et
1771 al., 2016). It also contains proteins involved in immunity and antimicrobial defenses (Borziak et
1772 al., 2016). In hens, evidence suggests that a protective local immunity to pathogens is established
1773 after exposure to semen but the mechanisms for this remain unclear (Reiber & Conner, 1995;
1774 Reiber, Conner, & Bilgili, 1995).

1775 In mammals, paternal alloantigens and cytokines in seminal fluid drive immune tolerance
1776 (Schjenken & Robertson, 2014). Mammalian seminal plasma contains immune-factors (Kelly,
1777 1995; Schjenken & Robertson, 2014)—TGF- β (Breuss et al., 1993; Chu & Kawinski, 1998;
1778 Slater & Murphy, 1999), IL-8 (Gutsche et al., 2003), and soluble IL-2 receptor (Srivastava,
1779 Lippes, & Srivastava, 1996), prostaglandin E2 (PGE2) and 19-hydroxyprostaglandin E (19-
1780 hydroxy PGE) (Denison, Grant et al., 1999), soluble tumor necrosis factor (TNF) receptors
1781 (Liabakk et al., 1993), receptors for the Fc portion of γ -globulin, spermine (Evans, Lee, &
1782 Flugelman, 1995), and complement inhibitors (Kelly, 1995). In horses and pigs, respectively,
1783 the proteins CRISP3 (Doty et al., 2011), PSP-I and PSP-II (Rodriguez-Martinez et al., 2010), act
1784 as signaling agents in seminal fluid.

1785 Secretions of growth factors, cytokines and chemokines from cervical and endometrial
1786 tissues immediately following insemination generates a proinflammatory environment that likely
1787 aids in implantation. In the utero-vaginal junction of chickens and the utero-tubal junction of
1788 pigs, several genes were shared following mating compared to non-mating and these genes were
1789 involved with immune-modulation (*IFIT5*, *IFI16*, *MMP27*, *ADAMTS3*, *MMP3*, *MMP12*) and
1790 pH-regulation (*SLC16A2*, *SLC4A9*, *SLC13A1*, *SLC35F1*, *ATP8B3*, *ATP13A3*), a process
1791 essential for implantation (Atikuzzaman et al., 2017, 2015). Instead of mounting an attack, it
1792 appears that the uterine immune system and paternal loci work cooperatively to support
1793 pregnancy in mammals and gravidity in birds. Whether this applies to reptiles, and how it may
1794 influence immune dynamics involved with squamate parity mode evolution, deserves
1795 investigation.

1796

1797 (12) *Discussion and future directions—maternal-fetal immune dynamics & the*
1798 *evolution of parity modes*

1799 Immune processes appear to be important for both oviparity and viviparity—as evidenced
1800 here, in part, by overlapping expression profiles of immune genes in female reproductive tissues
1801 of chickens and pigs, expression of paternal antigens in avian seminal fluid, and uterine
1802 expression of maternal antigens in oviparous and viviparous skinks. This highlights the scientific
1803 advances made since Medawar’s paradigm, when embryos were treated as analogs to allografts.
1804 Nonetheless, viviparity is associated with complex immune dynamics between maternal, fetal
1805 and paternal tissues. Unique MHC expression profiles were also identified in some viviparous
1806 skinks compared to oviparous relatives (Murphy et al., 2009).

1807 Substantial immunological changes in species with less active adaptive immune systems may
1808 not be necessary (Chaouat, 2016). Oviparous and viviparous *Zootoca vivipara* have remarkably
1809 similar cytokine expression during gravidity and gestation (Paulesu et al., 2005). Labile parity
1810 modes in squamates may be supported if they are more heavily reliant on the innate immune
1811 system for reproduction. However, reptiles may not have distinguished innate and adaptive
1812 immune systems (Zimmerman et al., 2020). It remains difficult to resolve how this all applies to
1813 the evolution of viviparity in squamates without studying immune gene activity during gestation
1814 and gravidity in more taxa.

1815 Changes to loci that serve overlapping functions across the Main Five may have a
1816 disproportionate influence on transitions between parity modes. In this section I reviewed two
1817 molecules, *TGF-β* and progesterone, that exert influence on multiple Main Five categories.
1818 Progesterone influences uterine quiescence (embryonic retention), hepatic vitellogenesis
1819 (nutrient provisioning) and regulation of inflammatory responses in utero (maternal-fetal

1820 immune dynamics). Genes in the TGF- β family play a role in placental development and
1821 maternal-fetal immune dynamics. TGF- β is implicated in placental development in eutherians
1822 (Hempstock et al., 2004; Caniggia et al., 2000; Lafontaine et al., 2011). A TGF- β receptor
1823 protein (TGFBR1) was associated with placental development in *Phrynocephalus vlangalii* (Gao
1824 et al., 2019). In humans TGF- β upregulates tolerogenic HLA-G in utero and is an immune factor
1825 in mammalian seminal fluid. Multiple gene in the TGF- β family are also differentially expressed
1826 during gestation in other viviparous lizards, *Pseudemoia entrecasteauxii* and *Saiphos equalis*
1827 (Foster et al., 2020; Griffith et al., 2016). Examining the functions of TGF- β and progesterone
1828 across other amniotes may reveal insights into how these molecules influence the evolution of
1829 parity modes.

1830 In mammals, inflammation appears to be involved with two of the Main Five processes—
1831 regulation of maternal-fetal immune dynamics and embryonic retention. It is intriguing to
1832 consider the implications this has for the interconnectedness of the Main Five. Greater
1833 interconnectedness would suggest that changes to few loci involved with the Main Five could
1834 cause a cascading effect to support more labile transitions between parity modes.

1835 Implantation and parturition in therian mammals evolved from a shared inflammatory
1836 attachment reaction (Hansen et al., 2017). The process of implantation has important
1837 implications for maternal-fetal exchanges of inorganic and organic material and maternal-fetal
1838 immune dynamics. Given that inflammation is associated with implantation and parturition
1839 implicates it in gas, water, and nutrient provisioning (including calcium here), maternal-fetal
1840 immune dynamics and length of embryonic retention. However, implantation in mammals and
1841 viviparous squamates is not homologous (Griffith, Van Dyke, & Thompson, 2013). Therefore, it
1842 is difficult to make inferences about how substantial the influence of inflammation is on the

1843 evolution of parity modes in squamates. Nonetheless, the abundant literature on uterine
1844 inflammatory processes during human pregnancy and the evolution of inflammatory processes
1845 that supported the evolution of viviparity in mammals (Challis et al., 2009; Chavan, Griffith, &
1846 Wagner, 2017; Mor et al., 2011; Griffith, Chavan et al., 2017; Stadtmauer & Wagner, 2020d)
1847 serve as indispensable resources for exploring the role of inflammation in squamate viviparity.

1848 I resist expanding on this further in viviparous reptiles given the need for more research on
1849 the reptile immune system overall (Zimmerman, 2020). I suspect that the immune system plays a
1850 central role in dictating the plasticity of parity modes in some Squamata clades. However, further
1851 work is necessary to validate this.

1852

1853

1854 **VII. Discussion**

1855

1856 (1) Two new mechanisms for transitions between oviparity and viviparity, without
1857 intermediate stages, stand out. These are meant as tools to be broadened and challenged
1858 with the goal of advancing scientific insight on the subject.

1859 a. The genomics and physiology of amniote parity mode evolution does not preclude
1860 an origin of viviparity in the MRCA of Lepidosauria. I propose the following
1861 mechanism—a change to the phenotype or function of basal caps instantaneously
1862 prevented calcium carbonate deposition (basal cap hypothesis); the eggshell loss
1863 enabled uterine exposure to chorioallantoic progesterone production (extending
1864 embryonic retention) and incipient calcium matrotrophy (supporting embryonic
1865 development); the growing embryo increasingly over distended the uterus

1866 triggering parturition of a fully developed offspring. This is one way to imagine
1867 viviparity evolving in the MRCA of Lepidosauria.

1868 b. A reversal back to oviparity may evolve most easily within viviparous clades with
1869 substantial maternal calcium provisioning through the following sequence of
1870 events—calcium secretions in utero stick to the outer embryonic membrane
1871 instead of being absorbed by the chorioallantois; oviposition can then occur in one
1872 of two ways 1) the death of corpora lutea or 2) the calcified eggshell blocks a
1873 threshold of chorioallantoic progesterone production from reaching uterine tissue;
1874 the calcified eggshell provides embryonic calcium that is transported upon
1875 embryonic metabolic demand.

1876 (2) Changes to gene(s) or physiological processes associated with more than one of the Main
1877 Five should disproportionately influence parity mode evolution—*SLC* gene superfamily,
1878 *TGF-β*, *BMPRII*, progesterone, *PMCA*, calbindin-D28K, *SPP1*, sustained functioning of
1879 the corpora lutea and inflammation.

1880 (3) Growing evidence in the medical literature suggests that immune system interactions at
1881 the maternal-fetal interface in mammals did not evolve simply through tolerance,
1882 evasion, or suppression (Chaouat, 2016; Chavan, Griffith, & Wagner, 2017; Moffett &
1883 Loke, 2004, 2006). Instead, maternal-fetal immune dynamics have a deep evolutionary
1884 history that enables both embryo and mother interact cooperatively (Yoshizawa, 2016).
1885 Future research on squamate parity mode evolution should consider maternal-fetal
1886 immune dynamics in this context.

1887 (4) Ectothermy influences parity mode evolution in squamates because it entails slower
1888 antibody responses and a greater reliance on climatic conditions for embryonic

1889 development, thus involving maternal behavior and unique pressure on embryos to signal
1890 parturition.

1891 (5) Advancing bioinformatics approaches are extending the horizon for studies on the
1892 genomics of complex trait evolution (Capecchi et al., 2020; Halfon, 2017; M'barek et al.,
1893 2019; Mittal & Hasija, 2020).

1894
1895 **VIII. Acknowledgements**

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Table 1.2. Genes Associated with Eggshell Deposition

Gene	Gene Function, GO term or KEGG Pathway	Species with gene associated to eggshell formation	DE in squamate reproductive tissues during gestation
<i>ABCC3</i>	GO:0016817 "hydrolase activity, acting on acid anhydrides" & KEGG: ABC transporters	^A <i>Gallus gallus</i>	^C <i>Chalcides ocellatus</i> (V)
<i>ADORA1</i>	KEGG: Neuroactive ligand-receptor interaction	^A <i>Gallus gallus</i>	
<i>ADRA2A</i>	KEGG: Neuroactive ligand-receptor interaction	^A <i>Gallus gallus</i>	^C <i>Chalcides ocellatus</i> (V); ^D <i>Saiphos equalis</i> (B)
<i>ADRB1</i>	KEGG: Neuroactive ligand-receptor interaction	^A <i>Gallus gallus</i>	^C <i>Chalcides ocellatus</i> (V); ^D <i>Saiphos equalis</i> (B)
<i>AGBL3</i>	GO:0008238 "exopeptidase activity"	^A <i>Gallus gallus</i>	^D <i>Saiphos equalis</i> (B); ^E <i>Pseudemoia entrecasteauxii</i> (V)
<i>AGXT2</i>	KEGG: Glycine, serine and threonine metabolism	^A <i>Gallus gallus</i>	^C <i>Chalcides ocellatus</i> (V); ^E <i>Pseudemoia entrecasteauxii</i> (V)
<i>ALDH3B1</i>	KEGG: Toll-like receptor signaling pathway	^A <i>Gallus gallus</i>	
<i>ANTXR1</i>	GO:0008238 "exopeptidase activity"	^A <i>Gallus gallus</i>	^C <i>Chalcides ocellatus</i> (V)
<i>ANXA5</i>	GO:0005509 "calcium ion binding"	^A <i>Gallus gallus</i>	^C <i>Chalcides ocellatus</i> (V)
<i>AOC3</i>	KEGG: Glycine, serine and threonine metabolism & KEGG: Toll-like receptor signaling pathway	^A <i>Gallus gallus</i>	^D <i>Saiphos equalis</i> (B)
<i>BCMO1</i>	GO:0016020 "membrane"	^A <i>Gallus gallus</i>	
		^A <i>Gallus gallus</i>	^C <i>Chalcides ocellatus</i> (V); ^F <i>Phrynocephalus vlangalii</i> (V); ^E <i>Pseudemoia entrecasteauxii</i> (V)
Table 1.2 (Continued).			
		^A <i>Gallus gallus</i>	
Gene	Gene Function, GO term or KEGG Pathway	Species with gene associated to eggshell formation	DE in squamate reproductive tissues during gestation
<i>C3AR1</i>	GO:0016020 "membrane" & KEGG: Neuroactive ligand-receptor interaction	^A <i>Gallus gallus</i>	

Table 1.2 (Continued).

Gene	Gene Function, GO term or KEGG Pathway	Species with gene associated to eggshell formation	DE in squamate reproductive tissues during gestation
<i>CAB39L</i>	GO:0009605 "response to external stimulus" & GO:0042221 "response to chemical stimulus"	^A <i>Gallus gallus</i>	
<i>CAPN8</i>	GO:0005509 "calcium ion binding"	^A <i>Gallus gallus</i>	
<i>CCDC59</i>	GO:0016020 "membrane"	^A <i>Gallus gallus</i>	^C <i>Chalcides ocellatus</i> (V)
<i>CCR8</i>	GO:0016020 "membrane"	^A <i>Gallus gallus</i>	
<i>CD86</i>	KEGG: Toll-like receptor signaling pathway	^A <i>Gallus gallus</i>	
<i>CDH23</i>	GO:0005509 "calcium ion binding" & GO:0016020 "membrane"	^A <i>Gallus gallus</i>	^D <i>Saiphos equalis</i> (B)
<i>CDH6</i>	GO:0005509 "calcium ion binding"	^A <i>Gallus gallus</i>	^C <i>Chalcides ocellatus</i> (V)
<i>CDHR1</i>	GO:0005509 "calcium ion binding"	^A <i>Gallus gallus</i>	
<i>CDHR3</i>	GO:0005509 "calcium ion binding" & GO:0016020 "membrane"	^A <i>Gallus gallus</i>	^C <i>Chalcides ocellatus</i> (V); ^D <i>Saiphos equalis</i> (B); ^E <i>Pseudemoia entrecasteauxii</i> (V)
<i>CHRNA7</i>	KEGG: Neuroactive ligand-receptor interaction	^A <i>Gallus gallus</i>	
<i>CNRI</i>	GO:0008238 "exopeptidase activity" & GO:0016020 "membrane" & GO:0016817 "hydrolase activity, acting on acid anhydrides" & KEGG: Neuroactive ligand-receptor interaction	^A <i>Gallus gallus</i>	
<i>COL14A1</i>	GO:0016020 "membrane"	^A <i>Gallus gallus</i>	^D <i>Saiphos equalis</i> (B)
<i>COL5A2</i>	GO:0008238 "exopeptidase activity" & GO:0042221 "response to chemical stimulus"	^A <i>Gallus gallus</i>	^C <i>Chalcides ocellatus</i> (V)
<i>COMP</i>	GO:0005509 "calcium ion binding" & KEGG: ECM-receptor interaction & KEGG: Phagosome	^A <i>Gallus gallus</i>	

Table 1.2 (Continued).

Gene	Gene Function, GO term or KEGG Pathway	Species with gene associated to eggshell formation	DE in squamate reproductive tissues during gestation
<i>CPM</i>	GO:0008238 "exopectidase activity"	^A <i>Gallus gallus</i>	^C <i>Chalcides ocellatus</i> (V)
<i>CPNE1</i>	GO:0016020 "membrane"	^A <i>Gallus gallus</i>	^C <i>Chalcides ocellatus</i> (V)
<i>CYBB</i>	KEGG: Phagosome	^A <i>Gallus gallus</i>	^C <i>Chalcides ocellatus</i> (V); ^E <i>Pseudemoia entrecasteauxii</i> (V)
<i>DACH2</i>	GO:0016020 "membrane"	^A <i>Gallus gallus</i>	^C <i>Chalcides ocellatus</i> (V); ^G <i>Anolis carolinensis</i> (O); ^E <i>Pseudemoia entrecasteauxii</i> (V)
<i>DDX60</i>	GO:0016817 "hydrolase activity, acting on acid anhydrides"	^A <i>Gallus gallus</i>	^C <i>Chalcides ocellatus</i> (V)
<i>DGAT2</i>	KEGG: Glycerolipid metabolism	^A <i>Gallus gallus</i>	^C <i>Chalcides ocellatus</i> (V); ^E <i>Pseudemoia entrecasteauxii</i> (V)
<i>DMP1</i>	GO:0009605 "response to external stimulus"	^A <i>Gallus gallus</i>	
<i>E2F7</i>	GO:0005509 "calcium ion binding" & GO:0005667 "transcription factor complex"	^A <i>Gallus gallus</i>	^C <i>Chalcides ocellatus</i> (V); ^E <i>Pseudemoia entrecasteauxii</i> (V)
<i>ERP44</i>	GO:0005509 "calcium ion binding"	^A <i>Gallus gallus</i>	^C <i>Chalcides ocellatus</i> (V)
<i>FBLN7</i>	GO:0005509 "calcium ion binding"	^A <i>Gallus gallus</i>	^D <i>Saiphos equalis</i> (B)
<i>FDPS</i>	GO:0042221 "response to chemical stimulus"	^A <i>Gallus gallus</i>	^C <i>Chalcides ocellatus</i> (V); ^D <i>Saiphos equalis</i> (B)
<i>FGB</i>	GO:0005577 "fibrinogen complex" & GO:0005615 "extracellular space" & GO:0030674 "protein binding, bridging" & GO:0051258 "protein polymerization"	^A <i>Gallus gallus</i>	
<i>FGF14</i>	GO:0016817 "hydrolase activity, acting on acid anhydrides" & GO:0030674 "protein binding, bridging"	^A <i>Gallus gallus</i>	^E <i>Pseudemoia entrecasteauxii</i> (V)
<i>GBP7</i>	GO:0016817 "hydrolase activity, acting on acid anhydrides"	^A <i>Gallus gallus</i>	
<i>GCH1</i>	KEGG: Folate biosynthesis	^A <i>Gallus gallus</i>	^C <i>Chalcides ocellatus</i> (V); ^D <i>Saiphos equalis</i> (B)

Table 1.2 (Continued).

Gene	Gene Function, GO term or KEGG Pathway	Species with gene associated to eggshell formation	DE in squamate reproductive tissues during gestation
<i>GLDC</i>	KEGG: Glycine, serine and threonine metabolism	^A <i>Gallus gallus</i>	^C <i>Chalcides ocellatus</i> (V); ^D <i>Saiphos equalis</i> (B)
<i>GNAT3</i>	GO:0005615 "extracellular space"	^A <i>Gallus gallus</i>	
<i>GPR162</i>	GO:0009055 "electron carrier activity" & GO:0016020 "membrane"	^A <i>Gallus gallus</i>	^C <i>Chalcides ocellatus</i> (V); ^E <i>Pseudemoia entrecasteauxii</i> (V)
<i>GPX8</i>	GO:0042221 "response to chemical stimulus"	^A <i>Gallus gallus</i>	^C <i>Chalcides ocellatus</i> (V); ^E <i>Pseudemoia entrecasteauxii</i> (V)
<i>GRXCR1</i>	GO:0009055 "electron carrier activity"	^A <i>Gallus gallus</i>	
<i>GZMA</i>	KEGG: Neuroactive ligand-receptor interaction	^A <i>Gallus gallus</i>	
<i>HIST1H2B7L1</i>	GO:0005667 "transcription factor complex" & GO:0016591 "DNA-directed RNA polymerase II, holoenzyme"	^A <i>Gallus gallus</i>	
<i>HIST1H2B7L3</i>	GO:0005667 "transcription factor complex" & GO:0016591 "DNA-directed RNA polymerase II, holoenzyme"	^A <i>Gallus gallus</i>	
<i>HIST1H2B8</i>	GO:0005667 "transcription factor complex" & GO:0016591 "DNA-directed RNA polymerase II, holoenzyme"	^A <i>Gallus gallus</i>	
<i>HTR1D</i>	KEGG: Neuroactive ligand-receptor interaction	^A <i>Gallus gallus</i>	
<i>HTR1E</i>	KEGG: Neuroactive ligand-receptor interaction	^A <i>Gallus gallus</i>	
<i>HTR7</i>	GO:0016020 "membrane" & KEGG: Neuroactive ligand-receptor interaction	^A <i>Gallus gallus</i>	^E <i>Pseudemoia entrecasteauxii</i> (V)
<i>IFIH1</i>	KEGG: Herpes simplex infection	^A <i>Gallus gallus</i>	^C <i>Chalcides ocellatus</i> (V)

Table 1.2 (Continued).

Gene	Gene Function, GO term or KEGG Pathway	Species with gene associated to eggshell formation	DE in squamate reproductive tissues during gestation
<i>IRF7</i>	KEGG: Herpes simplex infection & KEGG: Toll-like receptor signaling pathway	^A <i>Gallus gallus</i>	^C <i>Chalcides ocellatus</i> (V)
<i>ITGB4</i>	GO:0016020 "membrane" & KEGG: ECM-receptor interaction	^A <i>Gallus gallus</i>	^C <i>Chalcides ocellatus</i> (V); ^D <i>Saiphos equalis</i> (B); ^E <i>Pseudemoia entrecasteauxii</i> (V)
<i>KCNT2</i>	GO:0016020 "membrane"	^A <i>Gallus gallus</i>	^E <i>Pseudemoia entrecasteauxii</i> (V)
<i>KIAA0319L</i>	GO:0005509 "calcium ion binding"	^A <i>Gallus gallus</i>	^E <i>Pseudemoia entrecasteauxii</i> (V)
<i>KIF18A</i>	GO:0003774 "motor activity" & GO:0016817 "hydrolase activity, acting on acid anhydrides"	^A <i>Gallus gallus</i>	^D <i>Saiphos equalis</i> (B); ^E <i>Pseudemoia entrecasteauxii</i> (V)
<i>KRT19</i>	GO:0003774 "motor activity"	^A <i>Gallus gallus</i>	^C <i>Chalcides ocellatus</i> (V)
<i>KRT6A</i>	GO:0003774 "motor activity" & GO:0005577 "fibrinogen complex" & GO:0005615 "extracellular space" & GO:0016817 "hydrolase activity, acting on acid anhydrides" & GO:0030674 "protein binding, bridging" & "GO:0051258 "protein polymerization"	^A <i>Gallus gallus</i>	^C <i>Chalcides ocellatus</i> (V)
<i>LAMB1</i>	KEGG: ECM-receptor interaction	^A <i>Gallus gallus</i>	^C <i>Chalcides ocellatus</i> (V)
<i>LAMP3</i>	GO:0005667 "transcription factor complex" & GO:0009055 "electron carrier activity" & GO:0016591 "DNA-directed RNA polymerase II, holoenzyme"	^A <i>Gallus gallus</i>	
<i>LEPR</i>	KEGG: Neuroactive ligand-receptor interaction	^A <i>Gallus gallus</i>	^C <i>Chalcides ocellatus</i> (V)
<i>LIPG</i>	KEGG: Glycerolipid metabolism	^A <i>Gallus gallus</i>	^C <i>Chalcides ocellatus</i> (V); ^F <i>Phrynocephalus przewalskii</i> (O)

Table 1.2 (Continued).

Gene	Gene Function, GO term or KEGG Pathway	Species with gene associated to eggshell formation	DE in squamate reproductive tissues during gestation
<i>LZTS1</i>	GO:0003774 "motor activity"	^A <i>Gallus gallus</i>	^E <i>Pseudemoia entrecasteauxii</i> (V)
<i>MASP2</i>	GO:0005509 "calcium ion binding"	^A <i>Gallus gallus</i>	^C <i>Chalcides ocellatus</i> (V)
<i>MEGF6</i>	GO:0005509 "calcium ion binding"	^A <i>Gallus gallus</i>	^C <i>Chalcides ocellatus</i> (V); ^G <i>Anolis carolinensis</i> (O)
<i>MET</i>	GO:0016020 "membrane"	^A <i>Gallus gallus</i>	
<i>MOGAT1</i>	KEGG: Glycerolipid metabolism	^A <i>Gallus gallus</i>	^C <i>Chalcides ocellatus</i> (V)
<i>MST1R</i>	GO:0016020 "membrane"	^A <i>Gallus gallus</i>	^C <i>Chalcides ocellatus</i> (V)
<i>MTNRIA</i>	KEGG: Neuroactive ligand-receptor interaction	^A <i>Gallus gallus</i>	
<i>MX1</i>	GO:0016817 "hydrolase activity, acting on acid anhydrides"	^A <i>Gallus gallus</i>	^C <i>Chalcides ocellatus</i> (V); ^D <i>Saiphos equalis</i> (B)
<i>MYH7</i>	GO:0003774 "motor activity" & "GO:0005577 "fibrinogen complex" & GO:0005615 "extracellular space" & GO:0016817 "hydrolase activity, acting on acid anhydrides" & GO:0030674 "protein binding, bridging" & GO:0030674 "protein binding, bridging" & GO:0051258 "protein polymerization"	^A <i>Gallus gallus</i>	

Table 1.2 (Continued).

Gene	Gene Function, GO term or KEGG Pathway	Species with gene associated to eggshell formation	DE in squamate reproductive tissues during gestation
<i>MYO7B</i>	GO:0003774 "motor activity" & GO:0008509 "anion transmembrane transporter activity" & GO:0009605 "response to external stimulus" & GO:0015103 "inorganic anion transmembrane transporter activity" & GO:0015698 "inorganic anion transport" & GO:0042221 "response to chemical stimulus"	^A <i>Gallus gallus</i>	
<i>MYO7L3</i>	GO:0003774 "motor activity" & GO:0005577 "fibrinogen complex" & GO:0005615 "extracellular space" & GO:0016817 "hydrolase activity, acting on acid anhydrides" & GO:0030674 "protein binding, bridging" & GO:0051258 "protein polymerization"	^A <i>Gallus gallus</i>	
<i>NLRC5</i>	GO:0016817 "hydrolase activity, acting on acid anhydrides"	^A <i>Gallus gallus</i>	
<i>NMI</i>	GO:0016020 "membrane"	^A <i>Gallus gallus</i>	^C <i>Chalcides ocellatus</i> (V)
<i>NR5A2</i>	GO:0042221 ~response to chemical stimulus	^A <i>Gallus gallus</i>	^C <i>Chalcides ocellatus</i> (V); ^D <i>Saiphos equalis</i> (B)
<i>OC3</i>	GO:0005509 "calcium ion binding"	^A <i>Gallus gallus</i>	
<i>OC-116</i>	Avian Eggshell-specific gene	^A <i>Gallus gallus</i>	
<i>OCX-21</i>	Avian Eggshell-specific gene	^A <i>Gallus gallus</i>	
<i>OCX-36</i>	Avian Eggshell-specific gene	^A <i>Gallus gallus</i>	

Table 1.2 (Continued).

Gene	Gene Function, GO term or KEGG Pathway	Species with gene associated to eggshell formation	DE in squamate reproductive tissues during gestation
<i>OCX-32</i>	Avian Eggshell-specific gene	^A <i>Gallus gallus</i>	
<i>PHGDH</i>	KEGG: Glycine, serine and threonine metabolism	^A <i>Gallus gallus</i>	^C <i>Chalcides ocellatus</i> (V); ^E <i>Pseudemoia entrecasteauxii</i> (V)
<i>PHYHIPL</i>	GO:0051258 "protein polymerization"	^A <i>Gallus gallus</i>	^D <i>Saiphos equalis</i> (B)
<i>PLEKHG7</i>	GO:0016817 "hydrolase activity, acting on acid anhydrides"	^A <i>Gallus gallus</i>	^E <i>Pseudemoia entrecasteauxii</i> (V)
<i>PXDN</i>	GO:0042221 "response to chemical stimulus"	^A <i>Gallus gallus</i>	^C <i>Chalcides ocellatus</i> (V); ^D <i>Saiphos equalis</i> (B); ^F <i>Phrynocephalus vlangalii</i> (V); ^E <i>Pseudemoia entrecasteauxii</i> (V)
<i>RASL11B</i>	GO:0016020 "membrane" & GO:0016817 "hydrolase activity, acting on acid anhydrides"	^A <i>Gallus gallus</i>	
<i>RGS18</i>	GO:0008277 "regulation of G- protein coupled receptor protein signaling pathway"	^A <i>Gallus gallus</i>	^C <i>Chalcides ocellatus</i> (V)
<i>RGS20</i>	GO:0008277 "regulation of G- protein coupled receptor protein signaling pathway"	^A <i>Gallus gallus</i>	
<i>SDHB</i>	GO:0009055 "electron carrier activity"	^A <i>Gallus gallus</i>	
<i>SLC20A1</i>	GO:0008509 "anion transmembrane transporter activity" & GO:0015103 "inorganic anion transmembrane transporter activity" & GO:0015698 "inorganic anion transport" & GO:0016020 "membrane"	^A <i>Gallus gallus</i>	^C <i>Chalcides ocellatus</i> (V)

Table 1.2 (Continued).

Gene	Gene Function, GO term or KEGG Pathway	Species with gene associated to eggshell formation	DE in squamate reproductive tissues during gestation
<i>SLC26A3</i>	GO:0008509 "anion transmembrane transporter activity" & GO:0015103 "inorganic anion transmembrane transporter activity" & GO:0015698 "inorganic anion transport" & GO:0016020 "membrane"	^A <i>Gallus gallus</i>	
<i>SLC30A8</i>	GO:0008509 "anion transmembrane transporter activity" & GO:0015103 "inorganic anion transmembrane transporter activity" & GO:0015698 "inorganic anion transport"	^A <i>Gallus gallus</i>	
<i>SLC39A2</i>	GO:0008509 "anion transmembrane transporter activity" & GO:0015103 "inorganic anion transmembrane transporter activity" & GO:0015698 "inorganic anion transport" & "GO:0016020 "membrane"	^A <i>Gallus gallus</i>	^E <i>Pseudemoia entrecasteauxii</i> (V)
<i>SLC43A3</i>	GO:0005615 "extracellular space" & GO:0009605 "response to external stimulus" & GO:0042221 "response to chemical stimulus"	^A <i>Gallus gallus</i>	^E <i>Pseudemoia entrecasteauxii</i> (V)
<i>SLC6A4</i>	GO:0016020 "membrane"	^A <i>Gallus gallus</i>	^C <i>Chalcides ocellatus</i> (V)
<i>SMC4</i>	GO:0016817 "hydrolase activity, acting on acid anhydrides"	^A <i>Gallus gallus</i>	^C <i>Chalcides ocellatus</i> (V); ^E <i>Pseudemoia entrecasteauxii</i> (V)
<i>SOGA2</i>	GO:0005615 "extracellular space" & GO:0016020 "membrane"	^A <i>Gallus gallus</i>	

Table 1.2 (Continued).

Gene	Gene Function, GO term or KEGG Pathway	Species with gene associated to eggshell formation	DE in squamate reproductive tissues during gestation
<i>SOSTDC1</i>	GO:0005615 "extracellular space"	^A <i>Gallus gallus</i>	^C <i>Chalcides ocellatus</i> (V); ^E <i>Pseudemoia entrecasteauxii</i> (V)
<i>SPR</i>	KEGG: Folate biosynthesis	^A <i>Gallus gallus</i>	
<i>STAT1</i>	GO:0016020 "membrane" & KEGG: Herpes simplex infection & KEGG: Toll-like receptor signaling pathway	^A <i>Gallus gallus</i>	
<i>SUSD4</i>	GO:0016020 "membrane"	^A <i>Gallus gallus</i>	^C <i>Chalcides ocellatus</i> (V); ^D <i>Saiphos equalis</i> (B)
<i>SYNPR</i>	GO:0016020 "membrane"	^A <i>Gallus gallus</i>	^E <i>Pseudemoia entrecasteauxii</i> (V)
<i>TAP1</i>	GO:0016817 "hydrolase activity, acting on acid anhydrides" & KEGG: ABC transporters & KEGG: Herpes simplex infection & KEGG: Phagosome	^A <i>Gallus gallus</i>	^C <i>Chalcides ocellatus</i> (V); ^D <i>Saiphos equalis</i> (B)
<i>TAP2</i>	GO:0016817 "hydrolase activity, acting on acid anhydrides" & KEGG: BC transporters & KEGG: Herpes simplex infection & KEGG: Phagosome & KEGG: Phagosome	^A <i>Gallus gallus</i>	
<i>TDH</i>	KEGG: Glycine, serine and threonine metabolism	^A <i>Gallus gallus</i>	^C <i>Chalcides ocellatus</i> (V)
<i>TLR1LA</i>	KEGG: Toll-like receptor signaling pathway	^A <i>Gallus gallus</i>	

Table 1.2 (Continued).

Gene	Gene Function, GO term or KEGG Pathway	Species with gene associated to eggshell formation	DE in squamate reproductive tissues during gestation
<i>TLR2-1</i>	GO:0009605 "response to external stimulus" & GO:0042221 "response to chemical stimulus" & KEGG: Herpes simplex infection & KEGG: Phagosome & KEGG: Toll-like receptor signaling pathway	^A <i>Gallus gallus</i>	
<i>TMEM123</i>	GO:0005667 "transcription factor complex" & GO:0016591 "DNA-directed RNA polymerase II, holoenzyme"	^A <i>Gallus gallus</i>	^C <i>Chalcides ocellatus</i> (V)
<i>TMEM178B</i>	GO:0016020 "membrane"	^A <i>Gallus gallus</i>	
<i>TNR</i>	KEGG: ECM-receptor interaction	^A <i>Gallus gallus</i>	^E <i>Pseudemoia entrecasteauxii</i> (V)
<i>TSPAN13</i>	GO:0016020 "membrane"	^A <i>Gallus gallus</i>	^C <i>Chalcides ocellatus</i> (V)
<i>TUBB6</i>	GO:0051258 "protein polymerization" & KEGG: Phagosome	^A <i>Gallus gallus</i>	^C <i>Chalcides ocellatus</i> (V)
<i>TYRP1</i>	KEGG: Toll-like receptor signaling pathway	^A <i>Gallus gallus</i>	^D <i>Saiphos equalis</i> (B)
<i>UGGT2</i>	GO:0016817 "hydrolase activity, acting on acid anhydrides"	^A <i>Gallus gallus</i>	
<i>VTN</i>	GO:0008238 "exopeptidase activity" & KEGG: ECM-receptor interaction	^A <i>Gallus gallus</i>	^C <i>Chalcides ocellatus</i> (V)
<i>XDH</i>	GO:0009055 "electron carrier activity"	^A <i>Gallus gallus</i>	^C <i>Chalcides ocellatus</i> (V)
<i>ZCCHC11</i>	GO:0009055 "electron carrier activity"	^A <i>Gallus gallus</i>	^C <i>Chalcides ocellatus</i> (V)
<i>ATP13A5</i>	Gene Function: Ca ²⁺ homeostasis	^B <i>Gallus gallus</i>	
<i>ATP2B1</i>	Gene Function: Plasma membrane calcium transporter	^B <i>Gallus gallus</i>	^C <i>Chalcides ocellatus</i> (V); ^E <i>Pseudemoia entrecasteauxii</i> (V)

Table 1.2 (Continued).

Gene	Gene Function, GO term or KEGG Pathway	Species with gene associated to eggshell formation	DE in squamate reproductive tissues during gestation
<i>ATP6V0D2</i>	Gene Function: Proton pump	^B <i>Gallus gallus</i>	^C <i>Chalcides ocellatus</i> (V)
<i>ATP6V1C2</i>	Gene Function: Proton pump	^B <i>Gallus gallus</i>	^C <i>Chalcides ocellatus</i> (V); ^E <i>Pseudemoia entrecasteauxii</i> (V)
<i>ATP6V1G3</i>	Gene Function: Proton pump	^B <i>Gallus gallus</i>	^C <i>Chalcides ocellatus</i> (V)
<i>AVD</i>	Gene Function: Binding biotin	^B <i>Gallus gallus</i>	
<i>CA8</i>	Gene Function: Catalyze HCO ₃ -formation	^B <i>Gallus gallus</i>	^F <i>Phrynocephalus przewalskii</i> (O)
<i>CFTR</i>	Gene Function: Chloride channel	^B <i>Gallus gallus</i>	^C <i>Chalcides ocellatus</i> (V)
<i>CLCN2</i>	Gene Function: Chloride channel	^B <i>Gallus gallus</i>	^C <i>Chalcides ocellatus</i> (V); ^D <i>Saiphos equalis</i> (B)
<i>OVAL</i>	Gene Function: Regulate crystal size	^B <i>Gallus gallus</i>	
<i>PTGS1</i>	Gene Function: Catalyze prostaglandin formation	^B <i>Gallus gallus</i>	^C <i>Chalcides ocellatus</i> (V)
<i>SCNN1A</i>	Gene Function: Epithelial sodium channel	^B <i>Gallus gallus</i>	^C <i>Chalcides ocellatus</i> (V); ^D <i>Saiphos equalis</i> (B)
<i>SCNN1B</i>	Gene Function: Epithelial sodium channel	^B <i>Gallus gallus</i>	^C <i>Chalcides ocellatus</i> (V); ^D <i>Saiphos equalis</i> (B); ^E <i>Pseudemoia entrecasteauxii</i> (V)
<i>SCNN1G</i>	Gene Function: Epithelial sodium channel	^B <i>Gallus gallus</i>	^C <i>Chalcides ocellatus</i> (V); ^D <i>Saiphos equalis</i> (B)
<i>SLC1A1</i>	Gene Function: glutamate transporter	^B <i>Gallus gallus</i>	^C <i>Chalcides ocellatus</i> (V); ^E <i>Pseudemoia entrecasteauxii</i> (V)
<i>SLC25A15</i>	Gene Function: mitochondrial ornithine carrier	^B <i>Gallus gallus</i>	^C <i>Chalcides ocellatus</i> (V); ^D <i>Saiphos equalis</i> (B); ^E <i>Pseudemoia entrecasteauxii</i> (V)
<i>SLC26A4</i>	Gene Function: chloride-iodide transport protein	^B <i>Gallus gallus</i>	^C <i>Chalcides ocellatus</i> (V); ^D <i>Saiphos equalis</i> (B); ^E <i>Pseudemoia entrecasteauxii</i> (V)
<i>SLC31A1</i>	Gene Function: copper transporter	^B <i>Gallus gallus</i>	^C <i>Chalcides ocellatus</i> (V); ^E <i>Pseudemoia entrecasteauxii</i> (V)
<i>SLC34A2</i>	Gene Function: phosphate transporter	^B <i>Gallus gallus</i>	^C <i>Chalcides ocellatus</i> (V); ^E <i>Pseudemoia entrecasteauxii</i> (V)
<i>SLC35F3</i>	Gene Function: thiamine transporter	^B <i>Gallus gallus</i>	^C <i>Chalcides ocellatus</i> (V); ^E <i>Pseudemoia entrecasteauxii</i> (V)
<i>SLC45A3</i>	Gene Function: myelin-enriched sugar	^B <i>Gallus gallus</i>	^C <i>Chalcides ocellatus</i> (V); ^F <i>Phrynocephalus przewalskii</i> (O)

Table 1.2 (Continued).

Gene	Gene Function, GO term or KEGG Pathway	Species with gene associated to eggshell formation	DE in squamate reproductive tissues during gestation
<i>SLC4A1</i>	Gene Function: Bicarbonate transporter	^B <i>Gallus gallus</i>	^C <i>Chalcides ocellatus</i> (V)
<i>SLC4A2</i>	Gene Function: Bicarbonate transporter	^B <i>Gallus gallus</i>	^C <i>Chalcides ocellatus</i> (V); ^E <i>Pseudemoia entrecasteauxii</i> (V)
<i>SLC4A9</i>	Gene Function: Bicarbonate transporter	^B <i>Gallus gallus</i>	^C <i>Chalcides ocellatus</i> (V); ^E <i>Pseudemoia entrecasteauxii</i> (V)
<i>SLC52A3</i>	Gene Function: riboflavin transporter	^B <i>Gallus gallus</i>	^E <i>Pseudemoia entrecasteauxii</i> (V)
<i>SLC5A11</i>	Gene Function: sodium-dependent cotransporter	^B <i>Gallus gallus</i>	
<i>SLC9A8</i>	Gene Function: Sodium/proton exchangers	^B <i>Gallus gallus</i>	^C <i>Chalcides ocellatus</i> (V); ^E <i>Pseudemoia entrecasteauxii</i> (V)
<i>SLCIA3</i>	Gene Function: glutamate transporter, GO:0008509 "anion transmembrane transporter activity" & "GO:0016020 ""membrane"	^{AB} <i>Gallus gallus</i>	^C <i>Chalcides ocellatus</i> (V); ^F <i>Phrynocephalus przewalskii</i> (O)
<i>SPP1</i>	Gene Function: Regulate crystal growth, KEGG: ECM-receptor interaction, KEGG: Toll-like receptor signaling pathway	^{AB} <i>Gallus gallus</i>	
<i>TF</i> (<i>ovotransferrin</i>)	Gene Function: Regulate crystal size	^{AB} <i>Gallus gallus</i>	
<i>ACTN3</i>	GO:0045597 "Positive regulation of cell differentiation"	^F <i>Phrynocephalus przewalskii</i>	
<i>ASCL1</i>	GO:0002065 "Columnar/cuboidal epithelial cell differentiation" & GO:0045597 "Positive regulation of cell differentiation"	^F <i>Phrynocephalus przewalskii</i>	
<i>BAMBI</i>	GO:0022604 "Regulation of cell morphogenesis" & GO:0045597 "Positive regulation of cell differentiation"	^F <i>Phrynocephalus przewalskii</i>	^C <i>Chalcides ocellatus</i> (V)
<i>CDC42EP1</i>	GO:0022604 "Regulation of cell morphogenesis"	^F <i>Phrynocephalus przewalskii</i>	^F <i>Phrynocephalus vlangalii</i> (V)

Table 1.2 (Continued).

Gene	Gene Function, GO term or KEGG Pathway	Species with gene associated to eggshell formation	DE in squamate reproductive tissues during gestation
<i>EPB41L3</i>	GO:0022604 "Regulation of cell morphogenesis"	^F <i>Phrynocephalus przewalskii</i>	^E <i>Pseudemoia entrecasteauxii</i> (V)
<i>EPB42</i>	GO:0022604 "Regulation of cell morphogenesis"	^F <i>Phrynocephalus przewalskii</i>	^C <i>Chalcides ocellatus</i> (V)
<i>EPHA7</i>	GO:0022604 "Regulation of cell morphogenesis" & GO:0022604 "Regulation of cell morphogenesis" & GO:0060562 "Epithelial tube morphogenesis"	^F <i>Phrynocephalus przewalskii</i>	^C <i>Chalcides ocellatus</i> (V); ^E <i>Pseudemoia entrecasteauxii</i> (V)
<i>FGFRL1</i>	GO:0030133 "Transport vesicle"	^F <i>Phrynocephalus przewalskii</i>	^E <i>Pseudemoia entrecasteauxii</i> (V)
<i>HAS2</i>	GO:0022604 "Regulation of cell morphogenesis" & GO:0036120 "Cellular response to platelet-derived growth factor stimulus" & GO:0045597 ""Positive regulation of cell differentiation"	^F <i>Phrynocephalus przewalskii</i>	^C <i>Chalcides ocellatus</i> (V)
<i>HCN1</i>	GO:0045176 "Apical protein localization"	^F <i>Phrynocephalus przewalskii</i>	
<i>IGF1</i>	GO:0043567 "Regulation of insulin-like growth factor receptor signaling pathway" & "GO:0045597 ""Positive regulation of cell differentiation"	^F <i>Phrynocephalus przewalskii</i>	
<i>LOXL2</i>	GO:0045597 "Positive regulation of cell differentiation" & GO:0050673 "Epithelial cell proliferation"	^F <i>Phrynocephalus przewalskii</i>	^D <i>Saiphos equalis</i> (B)
<i>NKX3-1</i>	GO:0043567 "Regulation of insulin-like growth factor receptor signaling pathway" & GO:0050673 "Epithelial cell proliferation"	^F <i>Phrynocephalus przewalskii</i>	

Table 1.2 (Continued).

Gene	Gene Function, GO term or KEGG Pathway	Species with gene associated to eggshell formation	DE in squamate reproductive tissues during gestation
<i>PDE3A</i>	GO:0045597 "Positive regulation of cell differentiation"	^F <i>Phrynocephalus przewalskii</i>	^C <i>Chalcides ocellatus</i> (V)
<i>PTN</i>	GO:0022604 "Regulation of cell morphogenesis" & GO:0036120 "Cellular response to platelet-derived growth factor stimulus" & GO:0045597 "Positive regulation of cell differentiation"	^F <i>Phrynocephalus przewalskii</i>	^E <i>Pseudemoia entrecasteauxii</i> (V)
<i>RAB27A</i>	GO:0002065 "Columnar/cuboidal epithelial cell differentiation" & GO:0030133 "Transport vesicle"	^F <i>Phrynocephalus przewalskii</i>	^C <i>Chalcides ocellatus</i> (V)
<i>RASGRP1</i>	GO:0032252 "Secretory granule localization" & GO:0045597 "Positive regulation of cell differentiation"	^F <i>Phrynocephalus przewalskii</i>	^C <i>Chalcides ocellatus</i> (V); ^E <i>Pseudemoia entrecasteauxii</i> (V)
<i>SHROOM3</i>	GO:0022604 "Regulation of cell morphogenesis" & GO:0045176 "Apical protein localization"	^F <i>Phrynocephalus przewalskii</i>	^C <i>Chalcides ocellatus</i> (V); ^D <i>Saiphos equalis</i> (B); ^E <i>Pseudemoia entrecasteauxii</i> (V)
<i>SPDEF</i>	GO:0002065 "Columnar/cuboidal epithelial cell differentiation" & GO:0045597 "Positive regulation of cell differentiation"	^F <i>Phrynocephalus przewalskii</i>	
<i>SRF</i>	GO:0022604 "Regulation of cell morphogenesis" & GO:0045597 "Positive regulation of cell differentiation" & GO:0060562 "Epithelial tube morphogenesis"	^F <i>Phrynocephalus przewalskii</i>	^C <i>Chalcides ocellatus</i> (V)

Note: Letter in parentheses represents parity mode: V= viviparous, O= oviparous, B= reproductively bimodal. Superscript represents citations: A= Yang et al., (2020); B= Zhang et al., (2019); C= Brandley et al., (2012); D= Foster et al., (2020); E= Griffith et al., (2016); F= Gao et al., (2019); G= Alföldi et al., (2011).

Table 1.3. Differential Expression of Genes Associated with Water, Gas and Nutrient Transport During Gravidity & Gestation

	<i>Chalcides ocellatus</i> (V)	<i>Phrynocephalus vlangualii</i> (V)	<i>Pseudemoia entrecasteauxii</i> (V)	<i>Saiphos equalis</i> (B:V)	<i>Saiphos equalis</i> (B:O)	<i>Phrynocephalus przewalskii</i> (O)	<i>Lerista bougainvillii</i> (B:O)*	<i>Lampropholis guichenoti</i> (O)*
Water transport								
AQP1	↓			E↑; L↑				
AQP3				E↑; L↑	L↑		X	
AQP4								
AQP5	↑							
AQP6	↓							X
AQP8	↓		C↑					
AQP9	↑		C↑		E↑; L↑			
AQP11	↑						X	
AQP12B				E↑				
CFTR	↓						X	X
Gas Exchange								
HBA	↓							
HBB	↓							
HBM	↓						X	X
Vascularization/Vasodilation/Angiogenesis								
ADGRA2							X	X
ADGRB2								
ANGPTL1							X	
EPAS1	↑		C↑	L↑			X	X
EPHB4	↓							
HIF1A	↑		Y↑				X	
ISM1	↑		Y↓				X	X

Table 1.3 (Continued).

	<i>Chalcides ocellatus</i> (V)	<i>Phrynocephalus vlangalii</i> (V)	<i>Pseudemoia entrecasteauxii</i> (V)	<i>Saiphos equalis</i> (B:V)	<i>Saiphos equalis</i> (B:O)	<i>Phrynocephalus przewalskii</i> (O)	<i>Lerista bougainvillii</i> (B:O)*	<i>Lampropholis guichenoti</i> (O)*
NOS1	↑	↑blue						X
NOS2	↑		C↑				X	
NOS3	↓						X	
PDZRN3	↑						X	X
PGF	↓						X	
RHOJ	↓						X	X
TNMD								
VEGFA	↑		C↑		L↑		X	X
VEGFD	↓							
VEGFR1								
VEGFR2								
VEGFR3								
Nutrient Provisioning								
AP4S1	↑						X	X
APOA1	↑		C↑					X
APOA1BP			C↑;Y↑				X	X
APOA2	↑							
APOA4	↑		C↑;Y↑					
APOE	↑							
APOL6								
APOM	↑							
CTSL			C↑;Y↑					
CTSL1	↑							

Table 1.3 (Continued).

	<i>Chalcides ocellatus</i> (V)	<i>Phrynocephalus vlangalii</i> (V)	<i>Pseudemoia entrecasteauxii</i> (V)	<i>Saiphos equalis</i> (B:V)	<i>Saiphos equalis</i> (B:O)	<i>Phrynocephalus przewalskii</i> (O)	<i>Lerista bougainvillii</i> (B:O)*	<i>Lampropholis guichenoti</i> (O)*
CTSL2	↑							
GdA			C↑;Y↑					X
HYOU1	↑					↑S1		X
LIF								X
LPL	↓		C↑;Y↑				X	X
MUC-1	↑		Y↑				X	X
MUC-15			C↑;Y↑	↑	↑			
PLA2G10								X
SRPRA								
TGFB1	↑						X	X
TGFB1I1	↓						X	
TGFB2	↓							X
TGFB3	↓						X	X
TGFB1	↓		Y↓				X	X
TGFBR1	↓	blue					X	X
TGFBR2	↓						X	X
TGFBR3	↓	↑		L↓			X	
TGFBRAP1	↑						X	
VECG								
Generation of endometrial glands								
EGF								
AbdB								
cMet								

Table 1.3 (Continued).

	<i>Chalcides ocellatus</i> (V)	<i>Phrynocephalus vlangalii</i> (V)	<i>Pseudemoia entrecasteauxii</i> (V)	<i>Saiphos equalis</i> (B:V)	<i>Saiphos equalis</i> (B:O)	<i>Phrynocephalus przewalskii</i> (O)	<i>Lerista bougainvillii</i> (B:O)*	<i>Lampropholis guichenoti</i> (O)*
Emx2	↓						X	X
FGF10								
FGF7	↓						X	X
FGFR2IIIb								
HGF		↑	C↓				X	X
IGF1								
IGF2								
IGFBP5	↓							
Lhx1								
LIF	↑							X
Pax2	↓		Y↓				X	X
PRL								
VECG								
WNT10A	↑						X	X
WNT11	↓		C↓;Y↓					X
WNT16	↓		Y↓					
WNT2B	↓							
WNT3A	↑							
WNT4	↑							
WNT5A	↓							
WNT5B	↑							
WNT6	↑							
WNT7A	↓							

Table 1.3 (Continued).

	<i>Chalcides ocellatus</i> (V)	<i>Phrynocephalus vlangalii</i> (V)	<i>Pseudemoia entrecasteauxii</i> (V)	<i>Saiphos equalis</i> (B:V)	<i>Saiphos equalis</i> (B:O)	<i>Phrynocephalus przewalskii</i> (O)	<i>Lerista bougainvillii</i> (B:O)*	<i>Lampropholis guichenoti</i> (O)*
WNT7B	↑							
WNT9A	↓							
WNT9B	↑							

Note: In uterine tissue of gravid vs non-gravid uterine tissues only two genes and 0 zero gene are differentially expressed in *Lampropholis guichenoti* and *Lerista bougainvillii*, respectively (Griffith et al., 2016). Here, I marked X when a locus is expressed during gestation, indicating that it is expressed in utero during gestation but that the p-value of being differentially expressed compared to non-gestation was less than 0.05 (Brandley et al., 2012). Abbreviations: C= uterus of the chorioallantoic placenta; Y= uterus of the yolk sac placenta; L=late gestation/gravidity; E=early gestation/gravidity; ONG=oviparous non-gravid; VNG=viviparous non-gestational; blue=the locus is a member of the Blue Module from Gao et al. (2018) which is comprised of genes they suspect are involved with placentation; S1=the ovarian egg stage associated with eggshell deposition.

IX. References

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