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# Conflict and the evolution of viviparity in vertebrates

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26 *Abstract*

27 Viviparity has evolved from oviparity approximately 142 times among vertebrates. Different  
28 theories have been proposed to explain the evolution of each of its traits in the different  
29 taxa. None, however, is applicable to all the viviparous vertebrates, since the derived  
30 ecological advantages such as controlling incubating temperature or protecting eggs  
31 against predation differ amongst clades. Most theories have been developed under a co-  
32 adaptive perspective, whereas less attention has been paid to conflict. We developed a  
33 broad panorama of the gradual evolution, from oviparity to advanced forms of viviparity,  
34 that includes the different environmental and co-adaptive selective pressures that have  
35 been suggested to be at the root of the different instances of viviparity and of the diverse  
36 maternal-foetal adaptations for nutrient transfer seen amongst vertebrates. Furthermore,  
37 we highlight the importance of conflict as a crucial driver of the evolution of many of those  
38 traits, including the evolution of epigenetic control of maternal resources. We suggest that  
39 the different types of matrotrophic viviparity, and probably also some reversals to oviparity,  
40 have been the result of an antagonistic coevolution between mothers, fathers and  
41 offspring, and their genomes. We additionally suggest that the appearance of a trait that  
42 allowed or favoured the evolution of internal development and matrotrophy generates a  
43 new selective environment that promotes further adaptations or counteradaptations,  
44 leading to the observed diversity of forms of embryonic development, nourishment, and  
45 transfer of maternal nutrients, and ultimately to the diversity of extant viviparous taxa.

46

47 Keywords: lecithotrophy, maternal provisioning, matrotrophy, placenta, genomic imprinting.

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## 50        **1. Introduction**

51    Even in its simplest forms, reproduction is costly, since either self-dividing or producing  
52    and releasing gametes use resources (Stearns 1989; Blacher et al. 2017; Tarwater and  
53    Arcese 2017). These costs are referred to as reproductive investment because they are  
54    incurred in order to gain fitness. Investment in individual offspring can be made in one  
55    step, as when females produce yolk-provisioned eggs, or may be deferred through a  
56    gestation period via embryo-maternal (or paternal) interactions, and parental investment  
57    frequently continues after hatching or birth. However, although producing one descendant  
58    may convey the same benefit to both parents, the net fitness gain by each parent may  
59    differ if their respective parental contributions are not equal (Gross and Sargent 1985). For  
60    instance, withholding parental investment can be advantageous if the partner can provide  
61    enough resources for the offspring to reach independence, because the same fitness will  
62    be accrued with less investment. This is a type of sexual conflict, which more generally  
63    occurs when the evolutionary interest of males and females differ, or when their optima  
64    cannot simultaneously be realised (Trivers 1972). Sexual conflict can arise in relation to  
65    courtship, current or future mating decisions (Parker 1974; Smuts and Smuts 1993;  
66    Arnqvist and Rowe 2002; Magurran and Seghers 2008), as well as over parental  
67    investment (Trivers 1972), and it may lead to the evolution of traits (e. g. behaviours or  
68    protein production, which are determined by gene expression) that are beneficial to one  
69    sex, but that impose a cost to the other (Parker 1974). Such antagonistic coevolution  
70    resembles an evolutionary arms race, where adaptations to bring the interaction closer to  
71    the optimum value for one sex are met by counter-adaptations towards the optimum value  
72    for the other sex.

73            For a parent it is typically beneficial to make its partner to invest more than itself in  
74    their common offspring (McNamara et al. 2003; Osorno and Székely 2004), because it

75 enables a reduction in the amount of care it provides. Thus, sexually antagonistic  
76 coevolution is expected to give rise to attributes that induce partners to increase their  
77 reproductive investment, and of traits to resist such inducement (Chapman et al. 2003).  
78 Although demonstrations of antagonistic coevolution often deal with phenotypic traits such  
79 as those used to induce mating (Arnqvist and Rowe 2002; Buckling and Rainey 2002;  
80 Macías Garcia and Ramirez 2005), it has also been reported in relation to traits that  
81 influence provisioning to developing offspring, such as the augmented maternal  
82 investment by birds exposed to attractive male traits (Burley 1981; Gil et al. 1999). Sexual  
83 conflict can occur at the simpler but very transcendental level of the expression of genes in  
84 charge of regulating nutrient transfer during offspring development (Moore and Haig 1991)  
85 or it might also be related to signalling pathways that control resource allocation (Zwoinska  
86 et al. 2014)

87         We find that, although the potential role of parent-offspring and sexual conflict in  
88 driving the evolution of viviparity has been recognised by some authors (Crespi and  
89 Semeniuk 2004; Blackburn 2015a; Geist et al. 2019), in general, it has been undervalued.  
90 Conflict is in fact absent from most reviews regarding the evolution of viviparity and its  
91 traits in several viviparous taxa (Wake 1992; Murphy and Thompson 2011), and although  
92 some authors recognize the impact of epigenetic regulation on the evolution of viviparity,  
93 this is frequently associated to changes in the environment (Albergotti and Guillette 2011).  
94 Thus, we argue that conflict can, in fact, explain more attributes of the different modes of  
95 viviparity than has previously been contemplated. Additionally, we propose that once one  
96 trait related to viviparity and matrotrophy evolves, it sets up a new selective environment  
97 that promotes the evolution of other traits, leading to a diversity of forms of embryonic  
98 development and nutrition, and thus contributes to the current diversity of viviparous  
99 vertebrates.

## 100        **2. The evolution of viviparity**

101

102    In vertebrates, oviparity is the ancestral reproductive pattern, in which propagules  
103    enclosed within an egg envelope are fertilised -outside or inside the female body- and  
104    develop and hatch commonly in the external environment. Oviparous embryos are usually  
105    nourished exclusively from the vitellum (egg yolk). Viviparity, by contrast, is a mode of  
106    reproduction characterised by internal fertilization and egg retention, in which embryos  
107    fully develop within the female reproductive tract and are released to the external  
108    environment as free-living animals. The condition where embryos develop with minimal  
109    interaction to the maternal tissues, beyond some gas exchange, and hence embryonic  
110    nutrition depends on the yolk, is known as lecithotrophic viviparity, whereas the condition  
111    where embryonic nutrition is provided by the mother once the egg yolk is depleted is  
112    known as matrotrophic viviparity (Wourms et al. 1988).

113            Animal viviparity has evolved independently over 160 times, including 142  
114    instances of convergent evolution amongst vertebrates (Blackburn 1999, 2015b). Given  
115    the diversity of conditions currently experienced by viviparous taxa, it is not clear which  
116    selective force, or forces, promoted viviparity in the first place. This mode of reproduction  
117    confers a variety of demonstrated or suspected fitness benefits, several of which have  
118    been proposed as the primary forces driving its evolution (Blackburn 1999), yet each tends  
119    to be relevant only in some of the viviparous taxa, and thus, we lack a unifying theoretical  
120    framework for the evolution of animal viviparity and matrotrophy (embryonic nutrition via  
121    maternal resources other than yolk; Table 1, see Supplementary Information). Here we  
122    attempt to fill this gap in relation to vertebrate viviparity.

123            It is unlikely that all the viviparous clades followed precisely the same path in the  
124    evolution of viviparity and/or matrotrophy. Still, we argue that the underlying evolutionary

125 conflicts, which are common to- but played differently in the various viviparous clades,  
126 performed a key role in the evolution of traits related to viviparity and/or matrotrophy. We  
127 also argue that the diversity of reproductive patterns and their particular adaptations are  
128 the result of different combinations of conflict-driven selective pressures and the ecological  
129 context in which they take place.

130 Both gradualist (Blackburn 1992; Whittington et al. 2022) and saltationist models  
131 (Blackburn 1995) have been proposed to explain the evolution of viviparity and  
132 placentation. Yet neither gradual nor rapid transition from oviparity to matrotrophic  
133 viviparity would have been possible without the evolution of 1) the initial acquisition of  
134 internal fertilization and egg retention, which seem to be a pre-requisite for the evolution of  
135 viviparity *sensu stricto* (Blackburn 1999), followed by 2) internal embryonic development  
136 within typically the female reproductive tract, where embryos are nourished only with  
137 nutrients contained in the vitellum (yolk) of the ovum (Blackburn 2000). Subsequently, 3) a  
138 lengthening of developing time (extended uterine gestation) matched by an increasing  
139 supplementation of nutrients released by the mother into her reproductive tract (incipient  
140 matrotrophic viviparity), and culminating, in some cases, in what we know as 4)  
141 matrotrophic viviparity (Blackburn 2000), where instead of yolk, nutrients are gradually  
142 provided by the mother in the form of oviductal secretions or through placental organs (see  
143 Supplementary Information). Thus, from an egg-laying ancestor whose egg may already  
144 have had genetic and physiological attributes to enable a primitive form of matrotrophy  
145 (Wourms 1981), females would have become able to give birth to fully developed,  
146 independent, and particularly, as increasingly effective adaptations for embryonic nutrition  
147 evolved, bigger offspring than their oviparous counterparts (Sibly et al. 2018). The above  
148 route, however, has not been followed by all viviparous taxa (Blackburn 1992), and  
149 species are often in intermediate states, as in the case of caecilians that evolved

150 dermatotrophy, a type of oviparity where oviparous new-borns ingest some modified and  
151 nutritious maternal skin (San Mauro et al. 2014; Kupfer et al. 2016). Indeed, lecithotrophy  
152 and matrotrophy are not absolute conditions, but rather are extremes of a continuum of  
153 female investment (Wourms et al. 1988; Stewart and Thompson 1996; Blackburn 1998;  
154 Riesch et al. 2014). Several species regarded as lecithotrophic, also present some form of  
155 matrotrophy (e. g. histotrophy, which is a type of embryonic nutrition based on maternal  
156 nutrients that are absorbed by the embryo through specialised structures, such as the skin  
157 or gill epithelium) at the end of the embryonic development, after hatching and before birth,  
158 such as the stingrays (Hamlett et al. 2005) or have a very simple placenta, as in some  
159 reptiles (Stewart 1992). This highlights the need for a theoretical framework that may  
160 accommodate also more divergent paths towards matrotrophic viviparity.

### 161 **3. Conflict and the evolution of viviparity**

#### 162 *3.1. Conflict during the evolution of viviparity and matrotrophy: proposed pathway*

163 Theories proposed to explain the evolution of viviparity, matrotrophy and placentation are  
164 diverse and often contradictory, and it is unlikely that a single explanation holds for the  
165 whole of the complex, multi-stage transition from oviparity to matrotrophic viviparity among  
166 vertebrates. More probably, it must have been shaped by a variety of selective pressures  
167 that interacted simultaneously or sequentially, and even such interactions or sequences of  
168 events may have differed in the distinct lineages that became matrotrophic, thus promoting  
169 lineage diversification. Typically, reviews and theoretical papers have focussed on only  
170 one, or a few, of the evolutionary transitions that must have occurred between oviparity  
171 and matrotrophic viviparity. Here we present a possible scenario whereby natural selection  
172 and genetic conflicts of interests may have driven, through a diversity of particular  
173 pathways, the evolution of the several instances of vertebrate matrotrophy from an  
174 oviparous ancestral stage (Fig. 1).

175 3.1.1. Internal fertilisation

176 Following the idea that females are generally the limiting sex, as their reproductive output  
177 is normally set by the number of eggs they can produce, whereas that of the males is  
178 determined by how many female eggs they have the capacity to fertilise (Trivers 1985),  
179 there is a premium for males to gain access to fertile females before other males do. This  
180 leads to protandry, by which males emerge/arrive at the breeding ground before females  
181 (Wiklund and Fagerström 1977). This form of male-male competition that favours males to  
182 be prepared to mate before their rivals would, in externally fertilising species, promote a  
183 heightened readiness to ejaculate just as, or shortly before, spawning occurs (Fig. 1). In  
184 the extreme, any male feature that can allow males to deliver sperm directly into the  
185 female reproductive tract before egg laying would be favoured by intrasexual selection,  
186 even in the absence of any female adaptation for egg retention. Accordingly, it has been  
187 proposed that internal fertilisation initially evolved because: a) it can reduce the intensity of  
188 sperm competition (Parker 1970), or b) even in the absence of sperm competition, it can  
189 reduce the risk of sperm being lost, and hence increase the probability that eggs are  
190 fertilised (Parker 1984). If the original driving force was reducing the intensity of sperm  
191 competition, then internal fertilisation might have evolved through intra-sexual conflict, as  
192 male competition would determine paternity (in the absence of cryptic female choice). The  
193 ubiquity of external fertilisation in several taxa inhabiting all types of aquatic environments,  
194 such as many fish and amphibian species, suggests that sperm loss is not a very strong  
195 selective force against external fertilisation. Concurrently, the frequent evolution of male  
196 coercive means to ensure a successful copulation, such as the presence of claspers  
197 (Shibukawa et al. 2012), and a wide variety of male adaptations to deal with sperm  
198 competition in both oviparous and viviparous clades (Stockley et al. 1997) support our  
199 view that male-male conflict lies at the root of the evolution of internal fertilisation.



200 Hypotheses about the origin of internal insemination cannot be tested in amniotes,  
201 as they lack variation in the occurrence of this trait. It is even likely that, rather than being  
202 an adaptation to life outside water, internal insemination was a prerequisite to the  
203 independence from an aquatic medium for reproduction. Therefore, the following  
204 predictions pertain only anamniote vertebrates. If the attempts of males to monopolise  
205 females and fertilise their eggs favoured the evolution of internal fertilisation, then we  
206 expect that internal insemination has evolved more often in clades where multiple paternity  
207 amongst externally fertilising species is common. We also expect female adaptations to  
208 counter male monopolisation, such as sperm storage and superfetation, to be more  
209 common in clades where males have evolved more coercive means of securing internal  
210 insemination.

211 Alternatively, it has been suggested that external fertilisation predicts the  
212 occurrence of male parental care (Sutton and Wilson 2019), and that the transition from  
213 external to internal fertilisation is linked to the transition from paternal to maternal care  
214 among fishes and amphibians (Beck 1998; Mank et al. 2005; Kahn et al. 2013), two  
215 groups of viviparous vertebrates where paternal care is common.

216 Again, lack of variation in insemination mode, and the fact that in the overwhelming  
217 majority of mammals (Balshine 2012) and reptiles parental care is provided by females  
218 makes this prediction impossible to test in amniotes although we note that in the absence  
219 of conflict, we would expect that bi-parental and uniparental care to be equally likely to  
220 occur. Yet the proposal that the sex that releases the gametes first is the one that can  
221 desert parental care (Dawkins and Carlise 1976), can be tested in anamniotes, where we  
222 expect that any adaptation that allow males to release their gametes inside the female  
223 body and to fertilise her eggs, such as adaptations for sperm transfer and motility (Costa et  
224 al. 2016; Yokoe et al. 2016) would be a favoured outcome of intrasexual (male-male)

225 conflict over egg fertilisation. This suggest that conflict related to parental care could also  
226 have acted as a selective force in the evolution of male strategies that initially favoured  
227 internal fertilisation as a means to monopolise eggs, and subsequently allowed males to  
228 decrease their parental investment in the offspring.

229         As a third possibility, connected to the above argument, it has been suggested that  
230 external fertilisation evolved from internal fertilisation among the vertebrate ancestors  
231 (Long et al. 2014). This is also compatible with our proposal that sexual conflict underlies  
232 the evolution of fertilisation mode, since even if internal fertilisation evolved initially among  
233 gnathostomes, external fertilisation could have subsequently evolved as a female  
234 adaptation to desert parental care in aquatic environments (where sperm loss is not a  
235 major concern).

236

### 237         3.1.2. Egg retention

238         Egg retention is considered a result of adaptations to counteract the effect of harsh  
239 environmental factors and pre-hatching predation risks (natural selection pressures;  
240 Andrews and Rose 1994). According to this view, increased offspring survival would have  
241 followed from intrauterine development, hence in a more secure and stable environment  
242 that also accelerated their development or that allowed females to enhance offspring  
243 fitness by manipulating some of their phenotypic traits (Shine 2014). This may sometimes  
244 have been the case, but we note that harsh environments are just as likely to promote the  
245 production of resistant eggs that can survive hard environmental conditions, even if their  
246 parents themselves cannot. This, for instance, is the case of annual fishes  
247 (Cyprinodontiformes; Murphy et al. 1999), a diverse group of tropical minnows that inhabit  
248 ephemeral water bodies, which they re-populate each wet season from draught-resistant

249 eggs (Rodao et al. 2015). Hence while sometimes they may promote egg retention, harsh  
250 environments may in other cases lead to the production and laying of even more  
251 independent eggs. Thus, as with internal fertilisation, egg retention may have evolved in  
252 response to different selective pressures, some of which may be related to conflict (Fig. 1).  
253 (Motz and Callard 1988; Guillette et al. 1991a; Callard et al. 1992).

254         The presence and conserved function of some hormones that promote or delay  
255 oviposition is ubiquitous among vertebrates (e. g. luteinizing hormone (LH), arginine  
256 vasotocin (AVT); Pickford 1952; Bercu et al. 1980; Guillette and Jones 1982; Guillette et  
257 al. 1991b; Wang et al. 2008). Thus, it is likely that the production of hormones that induce  
258 egg retention -or the lack of hormones that induce oviposition- evolved first as a female  
259 mechanism to control oviposition depending on a variety of circumstances, such  
260 suboptimal places for oviposition, or to avoid predators or infanticide (Schneider 1999;  
261 Matsushima and Kawata 2005; Montserrat et al. 2007; Thiem 2020). Such mechanism  
262 was open to co-option by males or offspring to induce a longer egg retention, either i) via  
263 chemical suppression of female hormones that induce oviposition, such as AVT; ii) via  
264 embryonic production of hormones that induce egg retention, such as LH or hormones  
265 similar to progesterone and oestrogen (Motz and Callard 1988; Guillette et al. 1991a;  
266 Callard et al. 1992); or iii) if males or embryos could somehow promote embryonic  
267 development before eggs are laid, such as the embryonated eggs of caecilians by  
268 influencing their growth rate (see below; Motz and Callard 1988; Guillette et al. 1991a;  
269 Callard et al. 1992).

270         Testing this conflict hypotheses, however, is currently complicated due to the lack  
271 of information regarding the identity and regulation of hormones than induce oviposition,  
272 except for AVT, and egg retention in non-mammalian vertebrates. Nonetheless, if egg  
273 retention evolved as a female strategy to increase the embryos' survival or as a

274 consequence of conflict, this became a key precondition for the emergence of an  
275 antagonistic coevolution between the mother and the offspring and/or the father regarding  
276 the allocation of maternal resources. Once embryos were retained inside the female body,  
277 the eggshell became permeable and post-fertilisation mother-embryo communication was  
278 promoted, mothers became susceptible to embryonic physiological manipulation or to the  
279 embryos gaining control over nutrient consumption rate and amount (see section 3.2).  
280 Under this scenario, we then expect to find among oviparous species with different  
281 degrees of egg retention, correspondingly variable offspring adaptations that allow them to  
282 i) hatch inside the female body if certain development stage is reached and ii) increase  
283 their nutrient consumption (through large or efficient embryonic components of the egg  
284 membranes that favour a more effective nutrient acquisition or through teeth or structures  
285 to eat maternal tissues or siblings). We would also expect to find an ancestral version of  
286 those embryonic traits exclusively in oviparous clades with some degree of egg retention,  
287 but not in taxa with no egg retention, and a modified version (improved or vestigial) version  
288 of such adaptations in viviparous and closely related species, such as the case of the  
289 deciduous dentition of matrotrophic caecilians (Wake 1977b), and the specialised dentition  
290 of the oviparous taxa (Kupfer et al. 2006b).

291         At present, several examples among vertebrates of eggs that are laid with embryos  
292 in an advanced developmental have been documented. This is the case of the  
293 embryonated eggs of some caecilians (Kupfer et al. 2006a) and of sporadic accounts of  
294 developing fish embryos being laid by otherwise oviparous species (Hayakawa and  
295 Munehara 2001, 2003), something for which fish eggs may be regarded as pre-adapted  
296 (Wourms 1981). Among reptiles, there are frequent cases of eggs laid with embryos in  
297 stages 29-31 (Blackburn 1995). However, there is evidence that shows that a successful  
298 egg retention also depends on female's anatomy and embryonic factors specific to each

299 species (Andrews 1997). If egg retention is a consequence of internal fertilisation and a  
300 pre-requisite for viviparity, but its evolution is not equally successful in every taxon, then  
301 we expect the evolution of a more frequent and successful egg retention (which does not  
302 have a negative impact in embryo's developmental time compared to developmental  
303 status when born, or survival) in species with: 1) egg or embryonic primitive structures  
304 similar to placental analogues or equivalents, and 2) a relatively thin and at least partially  
305 permeable eggshell, and 3) small clutch sizes.

### 306 3.1.3. Staggered embryo provisioning

307 In internally-fertilising egg laying species insemination is often followed by a short-term  
308 egg retention during which the already yolked egg receives additional nutrients and, in  
309 some taxa, a hard, protective shell is added (Kupfer et al. 2006b). Long-term egg retention  
310 is incompatible with the presence of a hard shell that would impede gas exchange and  
311 could injure the female if accidentally broken. Mothers of strict lecithotrophic species face  
312 two constraints: 1) Their provisioning of resources cannot be modified over time if  
313 conditions improve, and 2) females are encumbered with the fully provisioned eggs  
314 through the gestation period, which compromises movement performance (Ghalambor et  
315 al. 2004). Those constraints place a premium on what we call here staggered embryo  
316 provisioning, i. e. the production of eggs with little yolk (with a subsequent  
317 supplementation of nutrients via oviductal secretions or the consumption of other  
318 siblings/eggs after hatching inside the female body), or with no yolk and a gradual supply  
319 through gestation.

320 The diversity of staggered embryo provisioning patterns in vertebrates is vast.  
321 Among therian mammals, which are highly matrotrophic, embryonic nutrition is possible  
322 thanks to the yolk sac and the chorioallantoic placenta (Smith 2015). Viviparous  
323 squamates, just like mammals, also evolved a placenta that results from the apposition of

324 the chorioallantois and a specialised derivative of the yolk sac, to the lining of the uterus of  
325 the mother (Stewart and Blackburn 1988). Although most viviparous squamates are  
326 relatively lecithotrophic, and mothers only transfer small amounts of nutrients to the  
327 developing embryos through the placenta, there are six clades with considerable embryo  
328 provisioning via placentotrophy (transfer of maternal nutrients via the placenta; see  
329 Supplementary Information), which in a few cases can be also supplemented with  
330 additional resources (reviewed in Blackburn 2015b).

331           Amphibians have evolved staggered embryo provisioning several times, but unlike  
332 mammals and reptiles, this has been accompanied by a diversity of embryonic and  
333 maternal adaptations for oophagy (ingestion of fertilised or unfertilised ova), embryophagy  
334 (ingestion of siblings), histophagy (ingestion of maternal secretions), matrophagy  
335 (ingestion of maternal tissues) or a combination according to each species (Table 1, see  
336 Supplementary Information; Wake 1977b; Guex and Chen 1986; Dopazo and Alberch  
337 1994; Buckley et al. 2007; Buckley 2012). Such adaptations are sometimes shared by  
338 several species but seem to be the result of multiple origins (reviewed in Blackburn  
339 2015b). Substantial matrotrophy has also evolved in the form of histotrophy, histophagy  
340 (ingestion of maternal secretion via specialised structures), placentotrophy, oophagy,  
341 embryophagy or a combination among teleosts (Turner 1936; Wourms et al. 1988;  
342 Hollenberg and Wourms 1994, 1995; Meisner and Burns 1997), and Chondrichthyans  
343 (Springer 1948; Gilmore et al. 1983; Wourms et al. 1988; Hamlett and Hysell 1998).  
344 Relatively lecithotropic chondrichthyans may also present some degree of staggered  
345 embryo provisioning, in the form of oophagy and histotrophy (Wourms 1977; Wourms et al.  
346 1988; Compagno 2001). Although different taxa seem to share the same patterns of  
347 embryonic provisioning, it is important to note that the same matrotrophy patterns can  
348 have notoriously different adaptations across taxa (reviewed in Blackburn 2015b).

349 In contrast to strict lecithotrophy, exclusive or predominant matrotrophic viviparity  
350 allows females to carry the full biomass of the clutch for only a fraction of the gestation  
351 period, hence reducing the energetic cost of mobility and the period of greater vulnerability  
352 to predation (Hagmayer et al. 2020), and to adjust the rate at which she delivers resources  
353 to the embryos in response to changes in ecological conditions (Pollux and Reznick 2011).  
354 Full maternal control of this process may not be adaptive to the embryos (Einum and  
355 Fleming 2000), or to all the embryos in a clutch, and this may lead to a departure from the  
356 honest signalling of embryonic needs (Godfray 1995; Haig 1996) and to the evolution of  
357 means that allow the embryos to control the flow of resources from the mother, such as  
358 the embryonic component(s) of the placentae (i. e. to changes in the pay-off matrix of  
359 mothers and embryos). Thus, although staggered provisioning might be beneficial for both  
360 the mother and the embryo, specific forms of matrotrophic viviparity may not be  
361 evolutionarily stable, as they can be open to invasion by manipulative strategies from  
362 either the embryos or the father(s) of the clutch (see section 3.2 for more details).

363 Placentae can be considered, in general, as the most advanced form of  
364 matrotrophy because of their capacity for nutrient transfer and gas exchange (Ostrovsky et  
365 al. 2016). If placental diversity is due to divergent adaptations to a variety of ecological  
366 conditions calling for special requirements in the transport of nutrients (as it has been  
367 suggested in adaptive theories for the evolution of placenta: see above), then we would  
368 expect the same type of adaptations and placentae in closely related species that live in  
369 similar environments. However, the environment experienced by, say, zebras and gazelles  
370 is essentially the same, whereas their placentae are widely different (Roberts et al. 2016).  
371 Considerations such as these led some authors to emphasize the importance of intense  
372 selective pressures, such as conflict, as important factors that shaped changes in the  
373 anatomy and function of the mammalian placenta during mammalian cladogenesis

374 (Wildman et al. 2006; Roberts et al. 2016). It also led Crespi and Semeniuk (2004; see  
375 also Klisch and Mess 2007) to propose that antagonistic parent-offspring coevolution might  
376 explain the differentiation of placental types within and across taxa (Uribe and García  
377 Alarcón 2005; Mess and Carter 2007). However, this type of conflict may only influence  
378 the evolution of viviparity and its traits once internal embryonic development and  
379 matrotrophy emerged. Parent-offspring conflict has been implicated in the differentiation of  
380 placental types (a form of matrotrophy), however, there are also other forms of  
381 matrotrophy whose evolution may also have been linked to conflict. If this is true, then we  
382 expect to see across phylogenetic evidence of antagonistic coevolution between mothers  
383 and embryos (or fathers) in the form of i) gradual increases of invasiveness of embryonic  
384 component of the placentae, ii) a continuum in the degree of nutrient ingestion in the form  
385 of ova, siblings or maternal tissues within clades or families. Also, since the outcome of  
386 conflict over embryo provisioning is likely to be context-dependent, we may also expect iii)  
387 occasional polymorphisms in the degree of matrotrophy (matrotrophy index, MI= dry mass  
388 of the offspring at birth divided by the dry mass of the egg at fertilization) within species,  
389 which can be coupled with polymorphisms in the mode of nutrient transfer. We also expect  
390 to see maternal adaptations to regulate the embryonic consumption of resources, such as  
391 reversals to oviparity (or via gene expression) in clades which also include highly  
392 developed placental systems (see section 3.4).

393

### 394           3.2.   *Mother offspring conflict and the evolution of matrotrophic* 395                           *viviparity*

396 We have argued ways in which sexual conflict could have influenced or been the main  
397 driver of the evolution of most of the salient traits associated with viviparity. In this last  
398 section, we will develop the proposal that mother-offspring conflict has played a crucial



399 role in the evolution of matrotrophy. Crespy and Semeniuk (2004) advanced a very well  
400 supported proposal showing that mother-offspring conflict is present in many forms of  
401 vertebrate viviparity, and that it is the main leading force behind the evolutionary  
402 diversification of mammalian placentae. Here, we extend that proposal and suggest that  
403 the offspring drive to extract as much nutrients as possible from the mother lies at the root  
404 of the mother-offspring conflict, the main selective force that led to the evolution and  
405 diversification of the extant forms of vertebrate matrotrophy and their particularities (Fig.  
406 1).

407

### 408 3.2.1. Pre-adaptations for the evolution of matrotrophy in the 409 different vertebrate groups

410 It is likely that certain pre-existing adaptations, such as a semi-permeable eggshell and/or  
411 egg membranes that allowed some small nutrients to enter the egg, or the appearance of  
412 new characteristics such as new embryonic adaptations to ingest dissolved nutrients,  
413 maternal tissues, or other eggs or siblings, facilitated the evolution of the diverse  
414 matrotrophic systems.

415 In the case of fish, for example, Morrison and co-workers (2017) found evidence  
416 suggesting that their eggs are preadapted for the evolution of matrotrophy (small  
417 molecules from the surrounding environment can traverse the egg membranes using  
418 mechanisms of active transport) and proposed that this is likely the main reason why  
419 matrotrophy has evolved considerably more times among fishes (Blackburn 2015b) than in  
420 reptiles and mammals (Blackburn 2015b).

421 Among mammals and reptiles, however, matrotrophy evolved in the form of  
422 placentotrophy, in which the chorioallantoic membrane and other pre-existing tissues of

423 the amniote egg have been recruited for the formation of the placenta to enhance the  
424 maternal-embryonic communication and nutrient transfer (Griffith and Wagner 2017; Kent  
425 2018). Additionally, this type of placenta co-opted the endocrine function of the egg's  
426 chorioallantoic membrane and shows expression of genes that are important for resource  
427 uptake during pregnancy (Griffith et al. 2017).

428         Finally, amphibian embryos evolved adaptations to feed on maternal nutrients,  
429 tissues, siblings, or other eggs, such as the modification of gills or skin (ectotrophoblast),  
430 foetal dentition, precocial development of the jaws, teeth, jaw musculature, and of the  
431 digestive tract (Wake 2015). In fish, similar as well as different traits have emerged to  
432 facilitate histophagy, histotrophy, placentotrophy, oophagy and embryophagy (Blackburn  
433 2015b).

434         Although all these new traits and specialisations were influential in the evolution of  
435 the different forms of matrotrophy, the ability of the embryos to hatch inside the female  
436 body, probably associated to the need to seek more nutrients (Wake and Hanken 1982;  
437 Buckley et al. 2007), was probably the key feature that allowed and favoured increased  
438 and diverse mother-embryo and embryo-embryo interactions, which subsequently could  
439 have favoured the other mentioned adaptations. Given that the evolutionary interests of  
440 the several actors are seldom completely coincident during reproduction (Trivers 1974;  
441 Arnqvist and Rowe 2005; Royle et al. 2012), this would have led to different levels of  
442 conflict among the members of the family (mother and embryos, or among siblings), and  
443 thus probably been responsible for the diversification within the different types of  
444 matrotrophy.

445

446         3.2.2. Internal hatching and the evolution of mother-offspring conflict

447           The release of embryos from any type of eggshell or hard, impermeable membrane  
448 inside the female body, and the permanence there of embryos for at least part of their  
449 development is a trait shared by all viviparous matrotrophic taxa. The removal of barriers  
450 between embryonic and maternal tissues allowed embryos to have access to new-, or to  
451 increase their access to sources of food. Once offspring are able to reach the maternal  
452 tissues, they can get into closer contact with her physiology, or other eggs or developing  
453 siblings, potentially gaining some control over their own nutrient intake to a level that may  
454 be sub-optimal for the mother.

455           In species that evolved matrophagy, for example, embryos consume maternal  
456 tissues, which is a form of maternal cannibalism and is likely to be costly for the mother,  
457 since embryos can ingest more tissue than what may be ideal for her to transfer to them.  
458 The interests of mother and offspring can also clash under oophagy and embryophagy,  
459 since the developing embryos ingest unfertilised eggs -potential siblings- and siblings in  
460 advanced stages of embryonic development (Gilmore et al. 2005). Among these species,  
461 although the embryo or embryos that are born develop faster and/or are better fed and  
462 with a greater chance of survival, eating potential siblings in the form of ova or developing  
463 siblings in which the mother already invested, may negatively impact her fitness.

464           Placentae can be another tool used by offspring to increase their nutrient intake.  
465 Reptilian and mammalian placentae can be very invasive (Blackburn and Flemming 2009;  
466 Kent 2018) and produce hormones able to manipulate and increase the maternal nutrient  
467 supply (Haig 1996). Even in the cases of non-invasive placentae, such as those of horses,  
468 embryos can influence the placental supply of nutrients by producing hormones, such as  
469 insulin like growth factor 2, that increases maternal resource allocation (Allen et al. 2002).

470           Although there is little evidence of hormonal manipulation in histotrophic and  
471 histophagic matrotrophy, as a rule, hormones are implicated in maternal-embryonic

472 communication across taxa (Bowman et al. 2021). Thus, even where mothers seem to be  
473 in total control of nutrient supply, embryos may have the physiological tools to send  
474 deceiving signals of nutritional state, or can develop other traits, such as organs or tissues  
475 that favour a continuous and a more effective intake of maternal secretions (Hamlett 1999;  
476 Blackburn 2015a).

477         The different means available to embryos for increasing the acquisition of maternal  
478 resources are not always mutually exclusive, and there are species where more than one  
479 form of matrotrophy co-occur. For example, among goodeid fish, embryos of *G.*  
480 *multiradiatus* and *A. splendens*, apart from receiving nutrients constantly through the  
481 trophotaenial placenta, also may ingest other eggs or viable siblings (Greven and  
482 Grossherr 1992). As mentioned above, embryos of *S. salamandra* start to ingest sibling  
483 eggs, and in some cases also less developed sibling embryos once they have consumed  
484 their own yolk (Buckley et al. 2007).

485         While the various forms of matrotrophy and their diverse features may constitute  
486 maternal strategies to provide additional resources to the developing embryos, the  
487 evidence mentioned above supports the idea that, at least in several cases, embryos have  
488 made use of those features to increase their nutrient uptake to levels that are probably  
489 sub-optimal for the mother. This suggests that the conflict that results from the offspring  
490 measures to increase their nutrient ingestion could have prompted the evolution of the  
491 different embryonic and maternal adaptations and counter-adaptations to gain control over  
492 the amount and pace of embryonic nutrient intake (see section 4 for more details on  
493 maternal adaptations and counter-adaptations), and that such antagonistic coevolution  
494 would be responsible for the diversity of forms of matrotrophic viviparity seen in  
495 vertebrates. If so, we expect to see among highly matrotrophic groups with considerable  
496 embryonic control over nutrient ingestion rate or maternal allocation (i. e. placentotrophy,



522 would have been an outcome of the way intra-family genetic conflict over the allocation of  
523 maternal resources evolves in different taxa -and may have promoted lineage divergence  
524 (Helmstetter et al. 2016; Zeh and Zeh 2000). Indeed, while the basic set of hormones  
525 involved in the regulation of reproductive processes is highly conserved among  
526 vertebrates, their sources, functions, and targets differ among taxa, therefore, Crespi and  
527 Semeniuk (2004) proposed that such variation may reflect a long evolutionary history of  
528 maternal–foetal antagonistic coevolution.

529         The increased and prolonged maternal provisioning during embryonic development  
530 takes place in several animal groups through the placenta or placenta-like structures,  
531 (Blackburn et al. 1985). This probably evolved from pre-existing tissues that acquired new  
532 functional attributes, modified their developmental programs, and evolved novel cell types  
533 (Griffith and Wagner 2017), allowing a close association between mother and offspring  
534 tissues, and an efficient exchange of nutrients, gases and excretions (Mossman 1991;  
535 Wooding and Burton 2008). Mammalian placentation has been described and studied in  
536 great detail, yet it evolved first in fish (Wourms and Lombardi 1992), and several other  
537 groups (reptiles, amphibians, invertebrates and plants) have also independently evolved  
538 placenta-like structures (Kaye et al. 1972; Haig and Westoby 1991; Blackburn 1999;  
539 Reznick et al. 2002) that are responsible for increasing of embryonic dry weight from  
540 zygote to birth of up to 38,700 % (Goodeid fish; Lombardi and Wourms 1979).

541         Although the primary function of placentae is shared among taxa (Faber et al.  
542 1992), it is one of the most morphologically and physiologically diverse vertebrate organs  
543 (Mossman 1991). This organ constitutes a key functional link in the transition from  
544 lecithotrophy to matrotrophy, providing the physiological scenario in which conflict can be  
545 expressed. In fact, some authors beyond Crespi and Semeniuk (2004) have proposed and  
546 found evidence that suggests that the divergent interests between mother and offspring,

547 followed by a rapid antagonistic coevolution, were the main causes of the diversifying  
548 evolution of the mammalian placenta (Klisch and Mess 2007), and that the proteins that  
549 that mediate in this organ the mother-embryo interactions may often be targets of  
550 evolutionary conflict (Chuong et al. 2010). Furthermore, there is evidence that most  
551 imprinted genes -those that are expressed in a parent-of-origin manner- are expressed in  
552 the placenta (Kaneko-Ishino et al. 2003), and some of them are essential for placental  
553 development and growth (Baker et al. 1993; Renfree et al. 2013). Among these, the genes  
554 that increase embryonic growth are usually paternally expressed whereas those that tend  
555 to restrict growth are maternally expressed (Renfree et al. 2013), thus, additional types of  
556 conflict, such as conflict between males and females, the parental alleles in the offspring  
557 or between half-siblings in the womb, are likely playing a role in the evolution of the  
558 placenta and its physiology (Burt and Trivers 1998; Parker 2006; Moore 2012).

#### 559           3.4.   *Genetic conflict and the evolution of genomic imprinting*

560

561 Genomic imprinting is a widespread phenomenon, in which certain genes are expressed in  
562 a parent-of-origin manner, usually as a result of DNA methylation or histone modifications  
563 (Tilghman 1999).

564           Trivers (1974) was the first to mention the possibility of a conflict between parents  
565 and offspring related to differing genetic interests, which could drive offspring to employ  
566 physiological weapons to manipulate maternal investment. During pregnancy, different  
567 sources of genetic conflict may arise: i) between genes expressed in the mother and in the  
568 foetus/placenta, or ii) between maternally derived and paternally derived genes within the  
569 embryonic genome (Haig 1996). Whenever there are mother-offspring interactions, four  
570 sources of genes can be recognisable: a) genes expressed in the mother, b) genes

571 expressed in the offspring, c) maternally inherited genes expressed in the offspring, and d)  
572 paternally inherited genes expressed in the offspring (Crespi and Semeniuk 2004).

573         The evolution of the gene expression type (a) and (b) may be shaped by a process  
574 of antagonistic coevolution between mother and embryo. Under this scenario a genetic  
575 conflict may arise between maternal and foetal genes, where expression of the latter will  
576 be selected to increase the transport of maternal nutrients, and maternal genes will be  
577 selected to be expressed so that nutrient transport takes place at a level that is optimal for  
578 the mother (Haig 1993). Indeed, in mammals, hormones produced by the embryonic  
579 placenta may be interpreted as foetal attempts to manipulate maternal metabolism for the  
580 offspring's benefit (Haig 1996). Gene expression type (c) and (d), on the contrary, may  
581 reflect a conflict between parental alleles expressed in the offspring, where paternally  
582 derived alleles will be selected to favour a more efficient nutrient acquisition and  
583 maternally derived alleles will be selected to favour an even distribution of maternal  
584 resources among broods (Haig and Westoby 1989). This kind of conflict has been  
585 interpreted as the force that drove the evolution of genomic imprinting.

586         The Kinship Theory of genomic imprinting mainly proposes the parent-of-origin  
587 gene expression evolved as a consequence of a conflict between the interest of the  
588 paternally inherited alleles (paternal alleles or patrigenes) and maternally inherited  
589 alleles (maternal alleles or matrigenes) over maternal investment during offspring  
590 development (Moore and Haig 1991; Haig 2000). According to the Kinship theory, because  
591 the conflict is associated to maternal allocation of resources, it is predicted that the genes  
592 that increase nutrient demand from the mother will be paternally expressed and the genes  
593 that restrict embryo growth will be maternally expressed (Haig 1996, 2000; Renfree et al.  
594 2013). This is more likely to evolve when: 1) offspring are sired by more than one father,  
595 either among litters or in the same litter, 2) provisioning of offspring during development is



596 largely performed by the mothers, and 3) there are genes expressed on the offspring that  
597 can manipulate the amount of resources that the mother provides (Wilkins and Haig 2003).

598           A classic example of genomic imprinting that is consistent with kinship theory is  
599 the expression pattern of the Insulin-like Growth Factor 2 (*igf2*) and its receptor *igf2r* (Haig  
600 2004). IGF2 is a protein that, among other functions, promotes growth and cellular  
601 differentiation during development (Cohick and Clemmons 1993). It also regulates the  
602 placental supply of nutrients, and the genetic demand for nutrients by the foetus  
603 (Constância et al. 2002; Fowden et al. 2006). On the other hand, *igf2r* encodes a  
604 membrane protein (cation independent mannose-6-phosphate receptor or IGF2R) that  
605 captures and transports the excess the of mannose-6-phosphate and IGF2 to the  
606 lysosomes for posterior degradation (Kornfeld and Mellman 1989), and thus it is essential  
607 for regulating normal foetal growth, circulating level of IGF2, and heart development  
608 (DeChiara et al. 1991; Lau et al. 1994). In therian mammals, the paternal allele of *igf2* is  
609 expressed and the maternal allele is silent (DeChiara et al. 1990) while *igf2r* is maternally  
610 active and paternally silent (Barlow et al. 1991). This accords to the proposal by Moore  
611 and Haig (Moore and Haig 1991).

#### 612           3.4.1. A new perspective of conflict and genomic imprinting

613           Haig (2000) proposed that the conflict between parental alleles drove the evolution  
614 of genomic imprinting. More generally, this form of control of gene expression may have  
615 evolved in the context of sexual conflict. For example, in the case of *igf2*, a protein that  
616 controls the demands for nutrients by the embryo, and the nutrients delivery by the  
617 placenta, the cost of an increase in maternal investment (imposed by a paternally induced  
618 excess of the embryonic protein) is only faced by females. This makes the interest of both  
619 sexes diverge and clash, especially if fathers do not sire subsequent litters that the female

620 may produce, leading to an evolutionary arms race between sexes that takes place at a  
621 genomic level and reflects allele conflict, as Haig (2000) suggested. However, it is difficult  
622 to establish whether the alleles are in conflict directly with each other, or if their evolution is  
623 directed by the conflict between sexes. In other words, the conflict that we see in  
624 viviparous polyandrous systems between parental alleles is part of the conflict between  
625 males and females.

626           It has been suggested that among vertebrates, genomic imprinting is a  
627 characteristic exclusive of viviparous mammals that appeared before the marsupials and  
628 eutherian split, and that evolved differentially in both groups, resulting in a larger number  
629 of imprinted genes in eutherians compared to marsupials (Renfree et al. 2013; Fig. 2).  
630 Thus, the evolution of genomic imprinting as a result of conflict between parental alleles, or  
631 between the sexes, over maternal allocation of resources has been extensively studied in  
632 mammals (Tycko and Morison 2002; Haig 2004). However, viviparity and maternal  
633 provisioning of resources during pregnancy (the main enhancers of this type of conflict),  
634 have been also documented in many vertebrate taxa, including fish. Although signs of  
635 genomic imprinting have not been found in reptiles, birds and marsupials so far (e.g.  
636 O'Neill et al. 2000; Griffith et al. 2016; Schwartz and Bronikowski 2016), the evolutionary  
637 foundation of genomic imprinting has been demonstrated in oviparous fish (Xie et al.  
638 2009); reprogramming of DNA methylation similar to that of mammals has been  
639 demonstrated in zebra fish (MacKay et al. 2007; Daneshfozouna et al. 2015), and there is  
640 evidence that insulin-like growth factor 2 is under positive selection, which coincides with  
641 the evolution of placentation in fishes (O'Neill et al. 2007). Moreover, spontaneous  
642 abortion rate in crosses between populations of poeciliid fish with a different level of  
643 polyandry has been related to the postzygotic reproductive isolation as a product of  
644 parent-offspring conflict (Schrader and Travis 2008), and there is already evidence

645 suggesting that *igf2* is imprinted in a family of highly matrotrophic viviparous fish (Saldivar  
646 Lemus et al. 2017).

647         The above suggests that the same type of conflict and antagonistic coevolution that  
648 has been documented in mammals may be occurring in other organisms with similarly  
649 strong conflict over maternal allocation of resources and with similar mating systems.  
650 Therefore, although some attempts to find evidence of genomic imprinting in vertebrate  
651 taxa other than mammals have been conducted, we suggest that more research is needed  
652 in viviparous vertebrates, especially in fish, in relation to genomic imprinting on genes in  
653 charge of embryo-maternal communication and nutrient transfer. In line with the genomic  
654 imprinting conflict theory, we expect to see in other groups that the paternally expressed  
655 alleles promote growth while maternal alleles restrain it, and that such balance as may be  
656 observed today would have arisen by coevolution, being facilitated by clustering of genes  
657 with antagonistic effects (Reik et al. 2003). While *igf2* seems to be the most studied and  
658 best described example of genomic imprinting and conflict in mammals, there are many  
659 other genes that enhance or restrict growth during development in mammals (Table 2).  
660 Thus, we expect that further research will reveal even more genes involved, both in  
661 mammals and in other viviparous vertebrates. Additionally, although 1) genomic imprinting  
662 has not evolved in the same way even among organisms of the same group (Kalscheuer  
663 et al. 1993; Pearsall et al. 1996; Okamura et al. 2000), and 2) genomic imprinting of  
664 important genes, such as *igf2*, does not occur in all the matrotrophic groups, this does not  
665 necessarily mean that imprinting as a result of sexual conflict over maternal allocation of  
666 resources has not evolved in some other growth-related genes. And we note that almost  
667 none of those genes have so far been tested in other viviparous and more matrotrophic  
668 organisms than mammals.

669

670           **4. Further evidence supporting the role of conflict during the**  
671           **evolution of viviparity and matrotrophy among vertebrates**

672   An extended mode of amphibian reproduction involves the occurrence of a larval stage,  
673   which in several cases can undergo metamorphosis before hatching. Larvae may ingest  
674   unfertilised eggs provided by the mother (Buckley 2012), while in oviparous caecilians,  
675   females may exhibit extended egg retention, and thus lay embryonated eggs (Kupfer et al.  
676   2006a). These allow the mother to control a staggered delivery of resources to the  
677   developing young, and there is little opportunity for the latter (or the father) to control the  
678   female investment in their own benefit. The embryos of viviparous salamanders and  
679   caecilians sometimes have specialised teeth that scrap the maternal tissues (Buckley  
680   2012) and may have evolved because they promote the interests of the father (i. e. being  
681   the result of sexual conflict), unless its expression was a function of the embryos'  
682   nutritional state, a condition that would suggest mother-offspring conflict. This form of  
683   embryotrophy (known as matrophagy, Table 1, see Supplementary Information) may  
684   preclude the evolution of an embryonic placenta, and in some salamander species is  
685   preceded by an oophagous phase. Oophagy (Table 1, see Supplementary Information)  
686   may allow the female to determine the maximum investment she is willing to make in a  
687   given reproductive effort, while the embryos regulate the tempo at which the resources are  
688   consumed. Embryophagy (Table 1, Supplementary Information), on the other hand, limits  
689   the control that can be exerted by the female on the rate at which resources are passed  
690   from the mother to the offspring, since embryos can ingest their viable siblings to which  
691   females have allocated nutrients during gestation. Although this form of amphibian  
692   embryotrophy is exclusive of the fire salamander *Salamandra salamandra* (Linnaeus,  
693   1758) (Buckley et al. 2007; Buckley 2012) and little is known about its mating system, we  
694   predict a stronger selective pressure for the evolution of embryophagy in polygamous

695 mating systems with multiple paternity. This is because the payoff of half-sibling ingestion  
696 is greater than that of ingesting full sibs, and because the cost of embryophagy is  
697 unequally shared between mother and fathers. We further predict that once embryophagy  
698 evolves, females have very few alternatives to prevent it, short of reverting to oviparity (as  
699 in Chondrichthyes; see Supplementary Information, Fig. 8.

700 Both histophagy (Table 1, Supplementary Information), occurring in some  
701 salamandrids (Blackburn 2015b) and bufonids (Xavier 1973; Wake 1980), and histotrophy  
702 (Table 1, Supplementary Information) found among the hemiphractid anurans (Savage  
703 2002; Roberts et al. 2016) should allow females to control the nutrient delivery; yet in  
704 some caecilians and salamandrids, embryos can induce maternal secretions by abrading  
705 the uterine lining with their prenatal teeth (Wake 1977a; Guex and Chen 1986). If the  
706 extent of the secretion-inducing damage was against the interests of the mother, we would  
707 expect to see mechanisms like maternally induced epigenetic inhibition of transcription  
708 factors associated with teeth formation (e. g. AmeloD; Chiba et al 2019) in embryos, and  
709 such maternal resistance should be a derived, and the expression of the embryonic teeth  
710 an ancestral condition within salamandrid clades.

711 Most viviparous squamates are relatively lecithotrophic and transfer small  
712 quantities of nutrients through the placenta via histotrophy (Blackburn 1994; Stewart and  
713 Thompson 2000; Thompson and Speake 2006); nevertheless, substantial matrotrophy has  
714 evolved in six clades of scincid lizards (Blackburn 1992; Stewart and Blackburn 2014). All  
715 squamate placentae have maternal (uterine epithelium) and embryonic components  
716 (chorioallantois or specialised derivatives of the yolk sac), and in the genera *Pseudemoia*,  
717 *Mabuaya* and *Eumecia*, they have the placentome (an absorptive embryonic structure with  
718 maternal secretory elements; (Thompson et al. 2004; Adams et al. 2005; Blackburn  
719 2000a).

720 Social monogamy is uncommon among reptiles (Harrison 2013) and multiple  
721 paternity, which can involve as many as 50% of all litters, has been documented in all  
722 lizard and snake species investigated so far (Uller and Olsson 2008). Thus, if maternal-  
723 foetal communication in squamate reptiles is regulated chemically, and offspring signal  
724 their necessities via hormones synthesised in / released by the placentome, then both the  
725 embryo and (or) the father may influence maternal resource allocation.

726 Fish are characterised by a continuous progression of viviparous species, from  
727 cases where mothers do little more than merely protecting the ova inside them, to true  
728 viviparous species, where the nutritional, respiratory and excretory demands of the  
729 embryos are satisfied by the mother (Amoroso 1960; Wourms and Lombardi 1992)  
730 through structures such as placentae or ovarian nipples (Turner 1940; Lombardi and  
731 Wourms 1979; Blackburn 2015b), or via oophagy, embryophagy, histotrophy and  
732 histophagy (see Supplementary Information). Substantial matrotrophy has evolved in at  
733 least nine of the 12 clades of viviparous teleosts, and in four of the eight clades of  
734 viviparous elasmobranchs (Blackburn 2015b). Embryos can absorb or ingest nutrients  
735 deposited in the ovarian lumen or the ovarian follicle across permeable surfaces (Wourms  
736 1981; Kunz 2004). Although oophagy is widely distributed among viviparous fishes  
737 (Blackburn 2015b), and the mother can control the maximum quantity of nutrients she  
738 provides, allocation mediated by placentae, histotrophy and histophagy, may still be  
739 influenced by the embryos or the father (see section on genomic imprinting above).

740 The bewildering diversity of adaptations surrounding viviparity in vertebrates may  
741 obscure any underlying evolutionary pattern. Still, as mentioned earlier, we propose that 1)  
742 certain sequential transitions are more likely to have occurred than others (e. g.  
743 lecithotrophic viviparity – matrotrophic viviparity; unchecked embryonic control of nutrients  
744 transfer – reversion to oviparity), and 2) that conflict of interests between the participants

745 (mother, father, embryos) would have promoted diversity, as the processes and outcomes  
746 would vary from one instance to other (see Fig. 3 and 4). We used two families of teleost  
747 fish that include oviparous and viviparous species, Goodeidae and Zenarchopteridae, and  
748 traced the features related to mode of reproduction and control over maternal nutrient  
749 transfer. Oviparity was the ancestral state in both families, and it apparently was followed  
750 by lecithotrophic viviparity, sometimes complemented by some mode of matrotrophic  
751 viviparity (Zenarchopteridae), or by matrotrophic viviparity in the form of placental viviparity  
752 (Goodeidae). Although placental viviparity is not present among zenarchopterids, some  
753 species that belong to the genera *Dermogenys* have evolved some structures that allow a  
754 maternal-embryonic connection (Meisner and Burns 1997) and that could be considered  
755 as very primitive placentae. The embryonic nourishment of the different lecithotrophic and  
756 some matrotrophic species of this family is characterised mainly by histotrophy/histophagy,  
757 where the mothers can control the amount of resources they transmit to their embryos, or  
758 by oophagy and embryophagy, which allow embryos to gain control over the amount of  
759 resources they ingest (Meisner and Burns 1997; Reznick et al. 2007; Fig. 3). The evolution  
760 of an incipient placental viviparity among *Dermogenys* species and the reversion to  
761 oviparity by *Hemirhamphodon tengah* (Tan and Lim 2013) may reflect the conflict among  
762 mother and siblings for controlling the maternal allocation of resources within this family.  
763 There is evidence of a similar conflict being at play in the Goodeidae (Fig. 4). For instance,  
764 the placenta is almost completely absent in a non-basal species: the striped goodeid  
765 *Ataeniobius toweri* (Meek, 1904) which may have allowed females to regain control over  
766 the nutrient allocation via some type of histotrophy or histophagy. The opposite case,  
767 where embryos ingest their siblings, evolved in species such as the butterfly splitfin *Amecca*  
768 *splendens* (Miller and Fitzsimons, 1971) (Greven and Grossherr 1992) and the Amarillo  
769 fish *Girardinichthys multiradiatus* (Meek, 1904) (YSL and CMG pers. obs.). This suggests  
770 that conflict for controlling maternal allocation of resources is continuously shaping the

771 evolution of patterns of matrotrophy among vertebrates. Both sets of predictions  
772 (sequence of events and conflict-linked diversity) require comparative analyses. We are,  
773 however, still ignorant of the ways in which internal gestation works in most of the taxa  
774 where it occurs, and appropriate phylogenies at the family or sub-family level are often  
775 lacking. Nonetheless, there are studies that suggest that viviparity has led to lineage  
776 diversification in Cyprinodontiformes (Helmstetter et al. 2016) and squamates (Recknagel  
777 et al. 2021a), although not in all taxa (Zúñiga-Vega et al. 2016). Even though lineage  
778 diversification in reptiles has been linked to the evolution of viviparity resulting from  
779 environmental conditions and of each species' genetic background (Recknagel et al.  
780 2021b), sexual- and mother-offspring conflict can also be tested as the main driver for the  
781 evolution of this reproductive pattern that is producing such diversification of lineages  
782 among vertebrates. We conducted a preliminary exercise of tracing several features of  
783 viviparity on the phylogenies of vertebrates (see Supplementary Information) to try to infer  
784 whether forms of viviparity and matrotrophy that resulted from an antagonistic coevolution  
785 between mothers or offspring/fathers for the control of the maternal allocation of  
786 resources, could have led to more complex forms of maternal-foetal interactions, and  
787 potentially, to the resolution of conflict. While some works have advocated a role of  
788 viviparity-linked conflict on evolutionary diversification (e. g. Helmstetter et al. 2016;  
789 Recknagel et al. 2021a), the relatively crude descriptions of the modes of viviparity in  
790 several taxa, and the resolution at which information can be traced in the phylogenies  
791 preclude at this point the evaluation of those hypothesis for many families or orders.

792

## 793 **5. Predictions and future directions**

794



795 Our exploration of the modes of reproduction and the diverse types of embryonic nutrition  
796 among vertebrates allow some preliminary conclusions and some predictions:

797 a) We suggest that the evolution of internal fertilisation, which is a pre-requisite for  
798 the evolution of viviparity, was led by intra-sexual conflict, where the first copulating males  
799 can fertilise more eggs or where males that inseminate females can desert parental care.  
800 This is consistent with the fact that whenever claspers or other coercive means of internal  
801 fertilisation evolved, these are invariably present in males, and not in females. In the case  
802 of matrotrophic species lacking precopulatory female mate choice, b) we predict either the  
803 evolution of a strong cryptic female choice to select the sperm of the preferred male, or the  
804 evolution of a type of matrotrophic viviparity where females can control the amount of  
805 nutrients that are transferred to the developing embryos (i. e. histotrophy, histophagy,  
806 dermatotrophy or some forms of oophagy where females provide unfertilised eggs  
807 specifically as a source of nutrients). In these species with maternal control of the nutrient  
808 transfer, however, we also expect c) counter adaptations in the offspring to gain control  
809 over maternal allocation, as in the case of placentotrophy -partial physiological control-, or  
810 via embryophagy and oophagy of potential siblings. Further, d) we expect the evolution of  
811 these forms of matrotrophy more commonly occurring after the appearance of histotrophy,  
812 histophagy or dermatotrophy and not the other way around. Once evolved, some forms of  
813 embryonic control of maternal resources cannot be checked by the mother except by  
814 reverting to oviparity, which e) we predict would be more common in lineages where  
815 oophagy, embryophagy or very invasive placentotrophy first evolved.

816 Several imprinted genes related to growth have been described to come to play  
817 during embryonic development in mammals, (Table 2). We predict f) the evolution of  
818 genomic imprinting, or allele-specific DNA methylation patterns (seen as a primitive state  
819 of genomic imprinting), in genes related to growth in highly matrotrophic species with

820 strong sexual conflict related to mating (e. g. polygamous species with highly dimorphic  
821 and/or courting males). In the specific case of placental species, as a result of the mother-  
822 offspring and sexual conflict, we expect g) more parent-of-origin expressed genes in  
823 placenta (as a whole) than in the developing embryo, with opposite expression patterns  
824 between the maternal and embryonic components of the placenta, or at least opposite  
825 DNA methylation levels in those genes in both components of the placenta. Under this  
826 scenario, h) the evolutionary rate of such genes should be asynchronous between  
827 components. Matrotrophic viviparity is very diverse among vertebrates, and we have  
828 argued that this is in part the evolutionary consequence of the different types of conflict  
829 among all the interacting parts. Most research has been devoted to the mother-offspring  
830 conflict and the evolution of placental matrotrophy in mammals. However, viviparity has  
831 evolved also in fish, amphibians and reptiles, and the diversity of the matrotrophic forms is  
832 greater and also likely the result of the conflicting interests of mothers, fathers, and  
833 offspring. To test these predictions, more research should be conducted on sequence  
834 evolution and DNA methylation patterns of key genes, Bayesian analyses to infer the order  
835 in which adaptations related to viviparity evolved, and phylogenetic analyses to infer the  
836 most likely sequence of events that led to the diverse forms of viviparity and matrotrophy  
837 that we see today.

## 838 **6. Conclusions**

839 (1) Reproduction is costly, and selection has rewarded those organisms that can  
840 manipulate their partner to invest more than their fair share in raising their  
841 common offspring. The evolution of matrotrophic viviparity, and especially  
842 placentation, allowed offspring and fathers (via the expression of their alleles in  
843 the offspring) to influence the maternal allocation of resources.

844 (2) Among reptiles, since there is conflicting evidence, it is impossible to determine if  
845 the evolution from oviparity to matrotrophic viviparity, including all the  
846 intermediate steps, and the subsequent appearance of a great diversity of  
847 forms of matrotrophy and placentae among vertebrates, has been gradual and  
848 shaped by several forces of natural and sexual selection or not. In other taxa,  
849 however, a higher diversity and complexity of matrotrophy forms can lead to  
850 different conclusions.

851 (3) Although it is likely that egg retention and incipient matrotrophy would have been  
852 favoured at least partly because of the adaptive benefits that result from  
853 increasing offspring developmental stage at birth and their survival, while  
854 decreasing the mother predation risk and the possibility of losing the brood, we  
855 suggest that conflict also played a central role on its evolution. Additionally, we  
856 propose that the evolution of the variety of embryonic nourishment types in  
857 matrotrophic viviparous species and the enormous variety of mammalian  
858 placentae (and maybe of species among viviparous vertebrates) was probably  
859 due to the substantial conflict of interests between mother and offspring, and  
860 between mother and father -expressed in the genome of their offspring-  
861 regarding the optimal maternal allocation of resources during offspring  
862 development. This role of conflict seems to be constant and essential in the  
863 evolution of the different patterns of matrotrophy among vertebrates.

864 (4) Patterns of lecithotrophy and matrotrophy are very diverse among vertebrates, and  
865 so are their correlated traits. Although there are taxa that evolved one or the  
866 other, in most cases, species exhibit a type of viviparity that lies somewhere  
867 along that continuum. In many cases, once viviparity evolved, an evolutionary  
868 arms-race for the control of maternal resources seems to have ensued.

869 (5) Since viviparity has evolved in most of the vertebrate clades and the patterns of  
870 viviparity and mating systems vary enormously across taxa, we suggest that the  
871 evolution of parent-of-origin methylation patterns related to maternal control of  
872 nutrient allocation has evolved in other viviparous taxa apart from mammals,  
873 and that it should be investigated in amphibians, and reptiles, but especially in  
874 fish.

875 (6) We propose that sexual conflict was a main driver during the evolution of most of  
876 the traits related to viviparity seen only as internal gestation, but mother-  
877 offspring conflict played a key role in the evolution of the different forms of  
878 matrotrophy.

879

880

881 **Acknowledgments.** We thank Michael G. Ritchie for providing the parenthetical notation  
882 of the phylogeny of goodeids and for his comments on an earlier version of the  
883 manuscript, and Marcela Méndez-Janovitz and Nadia Neri-Vera for their guide during the  
884 construction of phylogenetic trees. YSL is grateful to the Doctorado en Ciencias  
885 Biomédicas (UNAM) and to CONACyT for providing a PhD scholarship (No. 46568). This  
886 manuscript was much improved thanks to the comments of two referees.

887

#### 888 **Statements and Declarations**

889 Funding.

890 CONACyT provided a PhD scholarship (No. 46568) for YS-L.

891

892 Conflicts of interest.

893 The authors declare that there is no conflict of interest.

894

895 Authors' contributions

896 Authors contributed equally to this work. YS-L conceived the review, conducted the  
897 literature search, and generated a first draft that was subsequently reworked jointly by  
898 both YS-L and CMG.

899

900 Ethical approval

901 This is not an empirical study, but a review, and no animals or humans were used to  
902 gather any data.

903

904 Consent for publication.

905 All authors declare their consent for publication of this review.

906

907 Data Availability

908 Data sharing not applicable to this article as no datasets were generated or analysed  
909 during the current study.

910

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1462 **Fig. 1** Possible pathway leading to the evolution of matrotrophic viviparity and placentae  
1463 from an ancestral oviparous condition. The evolution of matrotrophic viviparity and  
1464 placentotrophy from oviparity was probably the result of several selective pressures acting  
1465 together. Although the appearance of live-bearing reproduction had mutual benefits for  
1466 mothers and their offspring, different types of conflict also must have favoured the  
1467 evolution of internal fertilisation, the staggered delivery and intake of maternal resources,  
1468 and the diversity of forms of matrotrophy and placentae

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1470 **Fig. 2** Scheme of appearance of genomic imprinting. Genomic imprinting has been  
1471 documented in therian mammals, and it is known to be absent (N) in monotremes or birds.  
1472 There is evidence that suggest that it is also present in at least one species of the fish  
1473 family Goodeidae (Saldivar Lemus et al. 2017). The possibility of the evolution of a parent-  
1474 of-origin gene expression in reptiles, amphibians and fish has been poorly investigated  
1475 (O'Neill et al. 2000; Griffith et al. 2016; Schwartz and Bronikowski 2016) and deserves  
1476 further attention

1477 **Fig. 3** Phylogeny of Zenarchopteridae and the attributes of viviparity and control over  
1478 maternal allocation of resources. This is not an ancestral state reconstruction, but rather a  
1479 graphic representation of the traits across the family. The external group (family  
1480 Belonidae) and genus *Zenarchopterus* are oviparous. After the split of *Zenarchopterus*, it  
1481 seems that the ancestor of the other genera developed lecithotrophy. *Nomorhamphus* and  
1482 *Demogenys* are lecithotrophic, however, some species have evolved also matrotrophic  
1483 viviparity independently (Reznick et al. 2007) in the form of maternal and embryonic  
1484 control. In the specific case of the genus *Demogenys*, structures that could be considered  
1485 as a primitive placenta (embryonic-maternal control) evolved in some species.  
1486 *Hemirhamphodon* is a lecithotrophic genus except for one species that is oviparous.

1487 Information regarding embryonic in *Hemirhamphodon* is scarce, however, they appear to  
1488 be lecithotrophic (Reznick et al. 2007). Crossed-out icons indicate the loss of the character

1489 **Fig. 4** a) Phylogeny of Goodeidae and the attributes of viviparity and control over maternal  
1490 allocation of resources. All viviparous goodeids evolved viviparity from an oviparous  
1491 ancestor. Although trophotaenial placenta (E-M control) is characteristic of the subfamily  
1492 Goodeinae, which encompass the viviparous species, *Ataeniobiuos toweri* is characterised  
1493 by the lack of a placenta and the evolution of some kind of histotrophy/histophagy (M  
1494 control). Additionally, embryophagy (E embryonic control) has been reported in two  
1495 species. b) Photographs of males and females of selected goodeid species. Crossed-out  
1496 icons indicate the loss of the character

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1501 Table 1 Different modes of reproduction and matrotrophy among vertebrates. Embryos  
 1502 can develop within an egg outside the female body (oviparity) or inside the reproductive  
 1503 tract of the mother (viviparity). Embryonic development in viviparous species can take  
 1504 place within an egg where embryos are nourished by the egg yolk (lecithotrophy) or it can  
 1505 happen without any type of eggshell and embryos are nourished by sources of maternal  
 1506 origin, such as maternal tissues, unfertilised ova, maternal secretions or their own siblings  
 1507 (matrotrophy)  
 1508

<b>Reproduction type</b>	<b>Embryonic nourishment type</b>	<b>Matrotrophy type</b>	<b>Embryonic development</b>	<b>Source of nutrients</b>
Oviparity	Lecithotrophy	NA	External	Yolk of the egg
	Matrotrophy after birth	Dermatotrophy	External	Transformed and nutritious maternal skin
Viviparity	Lecithotrophy	NA	Internal	Yolk of the egg
	Matrotrophy	Oophagy	Internal	Unfertilised eggs
	Matrotrophy	Embyophagy/ Adelphopagy	Internal	Cannibalised Siblings
	Matrotrophy	Matrophagy	Internal	Maternal internal tissue
	Matrotrophy	Histophagy	Internal	Maternal secretions
	Matrotrophy	Histotrophy	Internal	Maternal secretions
	Matrotrophy	Placentotrophy	Internal	Maternal nutrients transmitted via the placenta

1509



1510 Table 2 Imprinted genes that enhance or restrain growth

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<b>Gene</b>	<b>Expression</b>	<b>Effect on growth</b>	<b>Source</b>
<i>Igf2</i>	Paternal	+	(DeChiara et al. 1990)
<i>Ins1/Ins2</i>	Paternal	+	(Giddings et al. 1994; Duvillié et al. 1997, 1998)
<i>Mest/Peg1</i>	Paternal	+	(Lefebvre et al. 1998)
<i>Peg3/Pw1</i>	Paternal	+	(Li et al. 1999)
<i>Slc38a4</i>	Paternal	+	(Matoba et al. 2019)
<i>H19</i>	Maternal	-	(Gabory et al. 2009)
<i>Grb10</i>	Maternal	-	(Charalambous et al. 2003)
<i>p57Kip2</i>	Maternal	-	(Andrews et al. 2007)
<i>Igf2r</i>	Maternal	-	(Ludwig et al. 1996)
<i>Gnas</i>	Maternal	-	(Yu et al. 1998, 2000, 2001)
<i>Tssc3/lpl</i>	Maternal	-	(Frank et al. 2002)
<i>Esx1</i>	Maternal	-	(Li and Behringer 1998)

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