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REVIEW

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A review of the evolution of viviparity in lizards: structure, function and physiology of the placenta

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Abstract The aim of this review is to collate data relevant to understanding the evolution of viviparity in general, and complex placentae in particular. The wide range of reproductive modes exhibited by lizards provides a solid model system for investigating the evolution of viviparity. Within the lizards are oviparous species, viviparous species that have a very simple placenta and little nutrient uptake from the mother during pregnancy (lecithotrophic viviparity), through a range of species that have intermediate placental complexities and placental nutrient provision, to species that lay microlecithal eggs and most nutrients are provided across the placenta during development (obligate placentotrophy). In its commonest form, lecithotrophic viviparity, some uptake of water, inorganic ions and oxygen occurs from the mother to the embryo during pregnancy. In contrast, the evolution of complex placentae is rare, but has evolved at least five times. Where there is still predominantly a reliance on egg yolk, the omphaloplacenta seems to be paramount in the provision of nutrition to the embryo via histotrophy, whereas the chorioallantoic placenta is more likely involved in gas exchange. Reliance on provision of substantial organic nutrient is correlated with the regional specialisation of the chorioallantoic placenta to form a placentome for nutrient uptake, particularly lipids, and the further development of the gas exchange capabilities of the other parts of the chorioallantois.

Keywords Placentotrophy · Lecithotrophy · Embryo · Nutrition

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Introduction

The range of placental complexities represented in the squamate reptiles (lizards and snakes), which has resulted from multiple independent origins of viviparity (see Blackburn 2000), provides a solid model system to study the transitionary steps between oviparity and complex placentation. Although most squamates are oviparous, viviparity has evolved approximately 100 times in this clade (Blackburn 1982, 1985; Shine 1985), so that around 20% of extant species exhibit viviparity (or live-bearing) (Andrews 1997). Viviparity provides a major shift in life-history compared to oviparity, but its frequent evolution within squamates implies that common selective pressures are involved and the genetics of its evolution is relatively simple. Although the transition to viviparity has occurred often, the step from simple to complex placentation is relatively rare, having occurred only five (or six) times; four times in lizards and once in mammals (Blackburn 2000), with a possible extension to a fifth lineage of lizards (Flemming and Branch 2001; Flemming and Blackburn 2003). Species with simple placentae retain more or less shell-less eggs in utero, provide little nutrient across the placenta and have embryos sustained wholly or predominantly by nutrients in the yolk (the lecithotrophic condition). By contrast, species with complex placentae ovulate small eggs and transport nutrients to the developing embryos across the placenta (the placentotrophic condition). Within the Squamata, significant placentotrophy has evolved only in the lizard family Scincidae, and within this family there is a range of modes of nutrient provision from lecithotrophy (see Stewart and Thompson 2000) through to placentotrophy (e.g. *Mabuya heathi*, Blackburn et al. 1984; Blackburn and Vitt 1992), with several lineages showing intermediate conditions [e.g. *Pseudemoia spenceri* (Thompson et al. 1999a), *Niveoscincus metallicus* (Thompson et al. 1999b)]. Not surprisingly, therefore, skinks have been the major focus for research into the evolution of complex placentae.

Studies of viviparity in reptiles are of particular importance in understanding the evolution of reproduction in mammals, including humans, because of their shared derived embryology. Squamates and mammals are both amniotes, which means that their embryos develop the same range of extra-embryonic membranes, and the form of those membranes is highly conserved among the Amniota (reptiles, birds and mammals). The high degree of homology and conservative membrane development constrains the manner in which placentae can develop, which makes comparison among different amniote clades meaningful. In contrast, placental structures in anamniote lineages such as fish are not homologous, so, while they may be instructive in helping to interpret function, they are less instructive in interpreting evolutionary pathways.

Although the morphology and fine structure of placentae in lizards has been described for a long time, the history of study of the evolution of viviparity really began in the 1920s with the systematic surveying of placental structure in reptiles by Claire Weekes in a series of descriptions of the structure of embryonic membranes (Weekes 1927a, b, 1929, 1930, 1935). In later stage embryos of lizards, the embryonic pole of the egg has a well-vascularised placenta formed from the chorioallantoic membrane on the embryonic side. The abembryonic pole forms an omphaloplacenta, which consists of an un-vascularised bilaminar omphalopleure (Stewart and Thompson 2000). Because of the difference in the vascular support for each of the placentae, Weekes' work focussed on the chorioallantoic placenta, based on the assumption that little nutrient can be provided across a poorly vascularised, or avascular omphaloplacenta. Weekes' work culminated in an evolutionary hypothesis for the series of transitional steps required for more complex chorioallantoic placentae to evolve from simpler forms (Weekes 1935) and that hypothesis has formed the basis of many subsequent studies (e.g. Stewart and Thompson 1996).

Apart from the work of Weekes and a number of isolated studies (e.g. Kasturirangan 1951; Parameswaran 1962; Hoffman 1970; Thompson 1977a, 1981, 1982), no systematic analyses of the physiology of live-bearing in reptiles occurred until the 1990s. Recent studies have been aimed at describing the ontogeny of extra-embryonic membrane development (Stewart 1990; Stewart and Thompson 1994, 1996, 1998, 2004; Blackburn and Callard 1997; Flemming and Blackburn 2003; Jerez and Ramírez-Pinilla 2003), quantifying the major classes of nutrients that are transported across the placentae of lizards and how they correlate with egg size and placental complexity (Stewart and Thompson 1993; Thompson et al. 1999a, b, c, 2004), uterine preparation for pregnancy (Murphy et al. 2000; Hosie et al. 2003; Adams et al. 2004), describing changes to eggshell structures (Heulin 1990; Heulin et al. 1992; Qualls 1996), and aspects of metabolism and gas exchange (Grigg and Harlow 1981; Holland et al. 1990; Ingermann et al. 1991; Robert and Thompson 2000; Andrews 2002) and endocrinology (Girling et al. 2002; Girling and Jones 2003).

The aim of this review is to summarise the data available on placental structures and nutrient transport across the placentae of viviparous squamates and infer something about placental function in an attempt to identify hypotheses that will advance our understanding of how complex placentae evolve from oviparous ancestors.

For the purposes of this review, we will consider five categories of lizards (Table 1) that represent different reproductive modes (oviparous and viviparous) and placental complexities (predominantly lecithotrophic, species in the genera *Niveoscincus* and *Pseudemoia* that vary in placental complexity and degree of placentotrophy, and species in the genus *Mabuya* that produce microlecithal eggs). Predominantly, lecithotrophic species correspond to the chorioallantoic placental classification type I (Weekes 1935) and those that produce microlecithal eggs to type IV (Blackburn et al. 1984). *Niveoscincus ocellatus, N. metallicus* and *N. pretiosus* were considered type II (Weekes 1930, 1935), although recent analyses of their placental morphologies (Stewart and Thompson 1994, 2004) and net nutrient transport (Thompson et al. 1999b, 2001b) reveal a heterogeneous placental situation in the genus. Species of *Pseudemoia* were ascribed to type III (Weekes 1935; Stewart and Thompson 1998), and there is great uniformity in their placental morphologies (Stewart and Thompson 1996, 1998), but a quantitative range in net placental transport (Stewart and Thompson 1993; Thompson et al. 1999a, c). Detailed comparison of placentation in species of *Niveoscincus* and *Pseudemoia*, therefore, is likely to be insightful in our understanding of the evolution of complex placentae.

Extra-embryonic membrane development

As exchanges between embryonic lizards and their incubation environment rely on mediation through the extra-embryonic membranes, a brief description of the membranes, their ontogeny and how they vary with parity mode is warranted. It is important to remember that the extra-embryonic membranes grow and change through the development of the embryo, presumably in response to the differing needs of the embryo as it grows, as well as due to developmental constraints (Stewart and Blackburn 1988; Stewart and Thompson 2003). There are three categories of placentation in reptiles, one transient and uncommon (chorioplacenta), one at the abembryonic pole (yolk sac placenta), and one at the embryonic pole (allantoplacenta or chorioallontoic placenta) (reviewed by Stewart and Thompson 2000). The chorioplacenta is a close association of the chorion and uterine epithelium that appears transiently during the limb bud stage of embryogenesis, but has only been observed in the skinks *Chalcides chalcides* (Blackburn

Table 1 Dry mass of freshly ovulated egg yolks and neonates and ash contents of yolks and neonates, together with the neonate/egg ratios for each for species in the lizard family Scincidae

Species	Mode	Dry mass			Lipid			Ash mass			References
		Yolk (mg)	Neonate (mg)	Neonate/ egg ratio	Yolk (mg)	Neonate (mg)	Neonate/ egg ratio	Yolk (mg)	Neonate (mg)	Neonate/ egg ratio	
Lampropholis guichenoti	O	34.9	26.2	0.75	13.4	7.1	0.53	3.8	2.3	0.61	Thompson et al. 2001c
Lampropholis delicata	O	27.1	24.1	0.89	9.4	3.9	0.41	2.1	2.1	1.00	Thompson et al. 2001c
Eumeces fasciatus	O	97.4	65.2	0.67	38.5	16.1	0.42	0.4	0.6	1.50	Florian 1990
Bassiana duperreyi	O	79.8	68.0	0.85	28.9	NA	NA	3.4	4.8	1.18	Stewart and Thompson 1993, Speake et al. 1999
Menetia greyii	O	21.4	16.0	0.75	NA	NA	NA	2.1	2.6	1.24	Thompson and Russell 1998
Morethia boulengeri	O	47.7	36.4	0.76	NA	NA	NA	1.9	2.4	1.26	Thompson and Russell 1999
Morethia adelaidensis	O	65.2	46.2	0.71	NA	NA	NA	3.1	3.5	1.13	Thompson and Russell 1999
Mean ± SD				0.76 ± 0.08			0.45 ± 0.07			1.13 ± 0.28	
Eulamprus quoyii	V I	286.0	240.0	0.84	76.0	42.0	0.55	19.0	23.0	1.21	Thompson 1977b
Eulamprus tympanum	V I	187.2	156.9	0.84	53.7	30.8	0.57	11.5	12.4	1.08	Thompson et al. 2001a
Mean ± SD				0.84			0.56			1.15	
Niveoscincus coventryi	V II	31.9	25.6	0.80	11.5	6.4	0.56	2.2	2.5	1.14	Thompson et al. 2001d
Niveoscincus ocellatus	V II	59.4	100	1.68	19.6	17.2	0.88	8.2	6.7	0.82	Thompson et al. 2001b
Niveoscincus metallicus	V II	45.7	34.5	0.75	12.7	6.2	0.49	2.1	2.9	1.38	Thompson et al. unpublished data
Niveoscincus metallicus	V II	41.8	37.9	0.91	10.2	5.6	0.55	2.4	2.5	1.04	Thompson et al. 1999b
Mean ± SD				1.04 ± 0.44			0.62 ± 0.18			1.10 ± 0.23	
Pseudemoia pagenstecheri	V III	19.0	41.1	2.16	5.4 (est.)	7.2	1.33	1.4	4.1	2.93	Thompson et al. 1999c
Pseudemoia entrecasteauxii	V III	32.5	54.0	1.66	6.8	8.2	1.21	1.9	5.3	2.79	Stewart and Thompson 1993
Pseudemoia spenceri	V III	55.5	71.5	1.29	14.3	17.5	1.22	3.0	5.3	1.77	Thompson et al. 1999a
Mean ± SD				1.70 ± 0.25			0.89			2.50 ± 0.37	
Mabuya heathi	V IV	0.40	154.0	385.00							Blackburn et al. 1984
Mabuya bistriata	V IV	0.47	222.4	473.19							Vitt and Blackburn 1991
Mabuya mabouya	VIV	0.40	155.9	389.75				0.33	2.32	7.03	18. Ramírez-Pinilla, unpublished data
Mean ± SD				415.98 ± 49.6						7.03	

Mode refers to the mode of reproduction*NA* not available, *O* oviparous, *V* viviparous, *VI* viviparous with type I chorioallantoic placenta, *VII* species of *Niveoscincus*, *VIII* species of *Pseudemoia* (type III chorioallantoic placenta), *VIV* viviparous with type IV chorioallantoic placenta and Callard 1997) and *Niveoscincus coventryi* (Stewart and Thompson 1998).

Ontogenetic development of yolk sac membranes of all Reptilia is fundamentally the same. The initial bilaminar omphalopleure of endoderm and ectoderm is transformed into a trilaminar omphalopleure by the invasion of non-vascularised mesoderm. The mesoderm provides the site for subsequent angiogenesis and hematopoiesis to form the choriovitelline membrane on the embryonic side of the choriovitelline placenta. The mesoderm of the choriovitelline membrane separates into the endoderm and vascularised mesoderm to form the yolk sac splanchnopleure and the ectoderm and non-vascular mesoderm to form the somatopleure (chorion) (Stewart and Thompson 2000). Unlike any other amniotes, however, the mesodermal invasion of the bilaminar omphalopleure in the Squamata does not proceed past the equator of the eggs, instead invading the yolk to become the intravitelline mesoderm, which isolates a section of yolk called the isolated yolk sac (Fig. 1). Thus, a trilaminar omphalopleure does not form over the abembryonic surface of the egg. The intravitelline mesoderm separates to form the yolk cleft, with the blood vessels forming in the mesoderm above the yolk cleft, but not on the other side, so the bilaminar omphalopleure and isolated yolk mass remain non-vascular (Stewart and Thompson 2000, 2003). The bilaminar omphalopleure of the isolated yolk mass and the apposing uterine epithelium together form the omphaloplacenta. Whether the evolution of intravitelline mesoderm and a yolk cleft has facilitated the evolution of viviparity is not known, but it is the only major embryological difference between the Squamata and the rest of the Amniota, and viviparity has evolved most commonly in the Squamata.

The chorioallantoic placenta results from the close association of the vascularised allantois and chorion, and the apposing uterine epithelium. The chorioallantois is the major gas exchange organ in amniote eggs, and it has a similar function in viviparous Squamata (Blackburn 1993a). Unlike other Reptilia, the chorioallantois of squamates does not ultimately encircle the entire circumference of the egg, as long as the bilaminar omphalopleure persists. Three patterns of development are known during later development (Stewart and Thompson 2000, 2003). In some, the isolated yolk mass regresses and the bilaminar omphalopleure is modified, resulting in the chorioallantois encompassing the abembryonic pole of the egg. In others, the bilaminar omphalopleure persists and the chorioallantois is confined to the embryonic hemisphere (Fig. 2). The third pattern involves the allantois invading the yolk cleft, and the bilaminar omphalopleure persists over the abembryonic pole, which remains avascular. This last pattern occurs in snakes and is absent in lizards (Stewart and Thompson 2003).

Development of the extra-embryonic membranes of viviparous lizards is fundamentally the same as in lecithotrophic oviparous species, with changes predominantly in the timing of development of features (Stewart and Thompson 1996, 2003; Stewart and Florian 2000). Not until complex placentae evolve does novel innovation occur. Placentotrophic species of the genera *Pseudemoia, Mabuya* and *Eumecia* have a structural

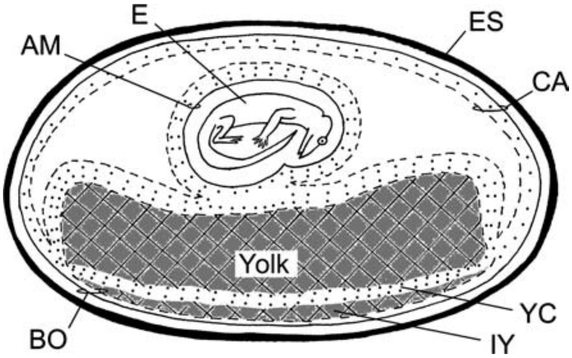

Fig. 1 Stylised arrangement of extra-embryonic membranes of an oviparous lizard after full development of the yolk cleft, but prior to the exhaustion of the isolated yolk mass (i.e. embryonic stages 35–38). In late development (after embryonic stage 38) of oviparous species, the isolated yolk mass is exhausted so that the endoderm of the bilaminar omphalopleure is replaced by the intravitelline mesoderm. The outer membrane of the expanding allantois fuses to this secondary chorion to form the chorioallantoic membrane of the abembryonic hemisphere. *E* embryo, *AM* amnion, *ES* eggshell, *CA* chorioallantois, *BO* bilaminar omphalopleure, *YC* yolk cleft, *IY* isolated yolk sac. Ectodermal tissue is represented by an *upbroken line*, endodermal tissue by a *broken line* and mesodermal tissue by a series of *dots*. Yolk is *cross-hatched* and shaped. Figure based on Florian (1990) and Stewart and Thompson (2000, 2003)

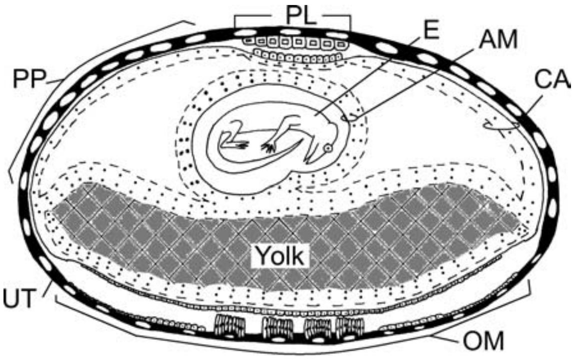

Fig. 2 Stylised arrangement of extra-embryonic membranes and placental cells in late stage embryo of *Pseudemoia* sp. The chorioallantoic placenta at the embryonic pole is differentiated into a placentoma (PL) of large cuboidal cells on both uterine and embryonic sides, and a paraplacentome (PP) consisting of squamous cells that form a cyto-epitheliochorial placenta. The isolated yolk mass has regressed so that the intravitelline mesodermal tissue, which contains blood vessels, lies adjacent to the bilaminar omphalopleure. Unlike oviparous species, the allantois of *Pseudemoia* does not invade the yolk cleft after exhaustion of the isolated yolk mass. *E* embryo, *AM* amnion, *UT* uterus, *CA* chorioallantois, *OM* omphaloplacenta. Ectodermal tissue is represented by an *upbroken line*, endodermal tissue by a *broken line* and mesodermal tissue by a series of *dots*. Yolk is *cross-hatched* and shaped. Figure based on Stewart and Thompson (2003), and descriptions in Stewart and Thompson (1996, 1998)

development of a specialised part of the chorioallantoic placenta, the placentome (Fig. 2; Stewart and Thompson 1996, 1998; Thompson et al. 2004; Adams et al. 2005; Flemming and Branch 2001; Flemming and Blackburn 2003), although it has arisen independently in each clade. The uterine epithelium of the placentome appears to be secretory (Thompson et al. 2004; Adams et al. 2005) and the chorionic epithelium is enlarged and absorptive (Blackburn 2000).

Details of the structure of the uterine components of the placenta in lecithotrophic viviparous species suggest that the epithelium apposing the chorioallantois is specialised for gas exchange (Thompson et al. 2004; Adams et al. 2005), whereas the uterine part of the omphaloplacenta, which contains hypertrophied cuboidal to columnar cells, is a secretory epithelium with histrotrophic uptake of nutrients by the embryo (e.g. Thompson et al. 2004). Histology of the embryonic sides of the placentae supports these conclusions (see Stewart and Thompson 2000). Differentiation of the chorioallantoic placenta into a placentome and paraplacentome (Fig. 2) has resulted in further specialization of the paraplacentome into a gas exchange organ, allowing the placentome to develop into a nutrient transport organ (Adams et al. 2005). Interestingly, the mechanism for secretion from the uterine epithelium of the placentome and omphaloplacenta are different, at least in *Pseudemoia entrecasteauxii* (Thompson et al. 2004; Adams et al. 2005). Different mechanisms for nutrient transport in the placentome and the omphaloplacenta suggests that different nutrients are transported, but to date no detailed transport studies have been conducted to establish what is transported by these organs, or how it changes with the demands of the embryo through pregnancy.

The uterine epithelium of the omphaloplacenta of lecithotrophic viviparous species is secretory (e.g. *Eulamprus tympanum*, Lui 2004), providing nutrients to the embryo via histotrophic transfer. There is no net uptake of nutrients across the placenta of *E. tympanum* (Thompson et al. 2001a), so the question remains, what is being transported across the omphaloplacenta? In *E. tympanum*, like all viviparous species, there is a net uptake of inorganic ions, but there may also be important uptakes of quantitatively minor, but nonetheless important, organic chemicals that have not yet been investigated. Such groups of substances may include hormones and immunoglobulins, but probably some major classes of nutrients are also transported. The use of labelled molecules reveals the potential for the transport of amino acids (Thompson 1977a; Swain and Jones 1997), even if the amounts are quantitatively unimportant.

Species with intermediate complex placentae (*Niveoscincus* sp., *Pseudemoia* sp.) have egg yolks that contain the same major nutrient classes as those of lecithotrophic oviparous and viviparous species (Thompson et al. 2002), so the mechanisms for transport across the placentae must include all of the classes of nutrients that are in the egg yolk of an oviparous species. Differences in the cell structure and apparent transport mechanisms in the omphaloplacenta and placentome of species with complex placentae suggest that the reduction in egg size (and hence transport of all nutrient classes) depends on the evolution of the mechanism in the placenta to do so. That mechanism probably is associated with the chorioallantoic placenta and further developed in the placentome. Species in the genus *Niveoscincus* will be useful in testing these ideas because they show the greatest range of degrees of placentotrophy, which is correlated with their placental complexities, of any single lineage with complex placentation. Interestingly, *N. ocellatus* exhibits considerable placentotrophy (Thompson et al. 2001b), being equivalent to that in *P. entrecasteauxii* (Table 1), but unlike *P. entrecasteauxii*, *N. ocellatus* lacks a placentome.

The development and function of the omphaloplacenta differs in species with microlecithal eggs (*Mabuya* sp., *Eumecia* sp.) compared to other viviparous squamates. In *Eumecia anchietae*, the ompahaloplacenta is well developed and holocrine secretion from the uterine epithelium provides nutrients taken up by the embryonic omphaloplacenta. There is no isolated yolk sac from mid-gestation, and late in gestation all placentotrophic activity in the omphaloplacenta has stopped (Flemming and Blackburn 2003), so the well-developed placentome must provide all the nutrition for the embryos for the latter part of gestation. The microlecithal *Mabuya* species also have no isolated yolk mass from mid-gestation (Blackburn and Vitt 2002; Jerez and Ramírez-Pinilla 2003; Flemming and Blackburn 2003).

Nutrient transport

Lipid

Lipids and protein make up the bulk of the egg yolk of lizards, with varying proportions around a 1:2 ratio (Thompson and Speake 2004). The lipid content and composition of lizard eggs is much better studied than proteins (Thompson and Speake 2004), partly because lipids are the predominant source of the organic energy during embryogenesis. Lipids also provide a major structural component to the developing embryo, especially in the form of phospholipids (PL) that make up the cell membranes. In predominantly lecithotrophic species, including oviparous species, there is approximately half as much lipid in the neonate as was present in the egg yolk at the time of ovulation or oviposition (Table 1).

Species in the genus *Pseudemoia* are particularly instructive in assessing the impact of placentotrophy on the relative transport of lipids compared to other classes of nutrients. The placentae of different species of *Pseudemoia* are all morphologically very similar (Stewart and Thompson 1996, 1998), so we can expect the transport mechanisms to be similar, but they display a range of degrees of placentotrophy. *Pseudemoia spenceri* is the least placentotrophic and *P. pagenstecheri* is the most placentotrophic (Table 1, Stewart and Thompson 1993; Thompson et al. 1999a, c). *Pseudemoia spenceri* has neonates only 1.3 times as large as the fresh egg yolk, whereas neonatal *P. pagenstecheri* are 2.2 times as large (Table 1), implying that more than twice as much nutrient is transported across the placenta in *P. pagenstecheri* as *P. spenceri*. *Pseudemoia entrecasteauxii* lies somewhere between the other two (Table 1). It is interesting, therefore, that the proportional uptake of lipids varies little among these species, which means that the differences in dry matter uptake must be due mostly to other nutrients, only a small proportion of which are inorganic ions (Table 1). Explaining this observation is not possible without detailed functional studies, but it may reflect the ultimate uses of lipid compared to other nutrients by the embryo during development (Speake and Thompson 2000).

While there are few data for lipid (or other nutrient) transport across the placenta of species with very complex placentae (*Mabuya* sp., Table 1), such data are of little value in interpreting what nutrients are transported and what their use is by the embryo because virtually all nutrients must be transported. On the other hand, data for *N. ocellatus* are revealing. *Niveoscincus ocellatus* represents a separate origin of viviparity from the *Pseudemoia* species, yet it has substantial placentotrophy, being little different from that for *P. entrecasteauxii*, which is in the mid-range for *Pseudemoia* species (Table 1). In *N. ocellatus*, there is much less net uptake of lipid (Thompson et al. 2001b) than in any of the *Pseudemoia* species (e.g. Speake et al. 2004), supporting the suggestion that there is a differential increase in the transport of lipids compared to other nutrients in species that rely on both lecithotrophy and placentotrophy. Particularly instructive is the lack of a placentome in *N. ocellatus* (Stewart and Thompson 2004), which suggests that the placentome may facilitate the increased transport of lipids across the placenta.

Most of the lipid component of egg yolk in lizards consists of triacylglycerides (TAG) and PL (Jones et al. 1998; Speake and Thompson 2000). TAG provides the main energy source for embryological development, whereas PL contributes substantially to the development of cell membranes (Speake and Thompson 1999). The proportions of TAG and PL are very similar in egg yolks of species with no significant uptake of nutrients by the embryo during development (oviparous and lecithotrophic viviparous species), with 83 ± 3% of the lipid being TAG and 11 ± 2% being PL ($n=5$ species, calculated from data in Speake and Thompson 2000). Lipid of eggs of species of *Niveoscincus* and *Pseudemoia* consists of 68 ± 3% TAG and 20 ± 2% PL ($n=5$, Speake and Thompson 2000). The interpretation of the difference between these two groups is that less TAG is provided to the eggs of placentotrophic species than to lecithotrophic species because energy, presumably in the form of free fatty acids, can be provided across the placenta during development, whereas all of the lipid requirement for lecithotrophic species must be contained in the egg yolk at the time of ovulation (Speake and Thompson 2000). The explanation is plausible, and reflects the difference in the proportions of TAG and PL in eggs of precocial and altricial birds (Speake and Thompson 2000), where the precocial birds use relatively more energy during development than do altricial birds (Hoyt 1987).

If the explanation is correct, it means that a significant proportion of the lipid provided to placentotrophic species during development may be maternally derived free fatty acids that compensate for the relatively lower provision of TAG from the yolk. Mammalian placentae transfer lipid to the foetus in the form of free fatty acids, which are derived either directly from the maternal plasma free fatty acid pool or from fatty acids released from the TAG of plasma lipoproteins by the action of placental lipoprotein lipase (Dutta-Roy 2000; Bonet et al. 1992). A portion of the transferred free fatty acids will then be consumed for energy during development and thus not reflected in the net comparisons that have been made to date for lizards. It is possible that the amino acids transported across the placenta are primarily used for foetal protein synthesis as opposed to oxidation for energy, which could explain the discrepancy in the relative net uptakes of lipid compared to total dry matter in placentotrophic species (Table 1).

Although the carbohydrate content of the yolk of lizards is negligible, it is not known whether glucose transferred across the placenta is used as an additional energy source by the foetus. Carbohydrate is transported across the specialised chorionic areolae of the chorioallantoic placenta of the microlecithal viviparous *M. heathi*, but the form of that carbohydrate is not known (Flemming and Blackburn 2003). We have no data on the relative consumption of lipid and protein for energy during development of placentotrophic lizards, but oviparous species consume approximately equal amounts of lipid and protein (e.g. Thompson and Russell 1999a), which reflects the relative composition of yolks of lizards (Thompson et al. 2001c). That composition in turn reflects the transport of lipids as a lipoprotein complex in the form of vitellogin and very low density lipoprotein (VLDL) to the yolking follicles in the ovary (Thompson and Speake 2004) (Table 1).

An intermediate step in the evolution of placentotrophy may be facultative placentotrophy (Stewart and Castillo 1984; Stewart 1989), where the provision of nutrients to the embryo varies flexibly with the nutrient available to the mother during pregnancy. Facultative placentotrophy has been identified in many viviparous species that have quantitatively important yolks, or are even predominantly lecithotrophic (Stewart 1989; Swain and Jones 2000). Interestingly, although facultative placentotrophy is well known, there have been few experimental attempts to study the effect of maternal nutrition during pregnancy, or indeed make measures in different natural populations of a single species or a single population in different seasons. The sole experimental study (Swain and Jones 2000) showed that, although facultative placentotrophy occurs in *N. metallicus*, it does not make up for poor yolk provision during vitellogenesis. Complete understanding of the role of facultative placentotrophy in the evolution of complex placentae awaits further empirical study.

Inorganic ions

Embryos of oviparous lizards take up inorganic ions during development (Table 1), and even species such as *Lampropholis delicata* and *L. guichenoti* that sustain a net loss of inorganic ions (Table 1) take up some ions, especially calcium (Thompson et al. 2001c). Of particular importance to the discussion on the evolution of viviparity is the potential uptake of ions into eggs of oviparous species from the environment during incubation (Thompson et al. 2001c; Oftedal 2002). Both lecithotrophic and placentotrophic viviparous species take up inorganic ions during incubation (Table 1) and, presumably, the same mechanisms involved in uptake by oviparous species are involved in the process. The way in which ions are supplied by the mother may change, but studies to date have focused on net uptake of calcium and easily measured monovalent ions that diffuse readily, rather than on transport mechanisms.

Calcium is a key element, because yolks of lizards contain insufficient calcium to sustain embryonic development (e.g. Thompson et al. 2001c), and calcium makes up a proportion of eggshells (Packard et al. 1985; Packard and Hirsch 1986). The uterus of oviparous species has an extensive mechanism for the provision of calcium for the egg-shelling process (Thompson et al. 2004), so the basic machinery for supply of calcium is already present in the uterus. The timing and rate of that provision must change from a short, intense period during egg-shelling in oviparous species to a potentially extended and less intense period later in development, but there is no need for new structures to take over the process. To date, studies of calcium have focused on the total net uptake (reviewed by Stewart and Thompson 2000), so studies of where and when calcium (and other ions) are transported are now required. Preliminary work suggests that Ca^{2+} ATPase channels in shell glands and/or the uterine epithelium may be important (Thompson et al. 2004).

Protein

The protein and amino acid composition of lizard egg yolk has never been investigated. To date, measures of total nitrogen, and from that an inference of the total protein composition, of eggs and neonates provide the main information of proteins in lizard eggs (Thompson et al. 2000). Nevertheless, vitellogenin has been purified and characterised from yolks of the lizards *Anolis pulchellus* (De Morale et al. 1987, 1996) and *Podarcis sicula* (Romano et al. 2002) and VLDL has been isolated from the snake *Bothrops jararaca* (Janeiro-Cinquini et al. 1995). The characterisation of VLDL in *B. jararaca* suggests a similar transport mechanism for lipids (VLDL*y*) to birds (Thompson and Speake 2004). None of these studies is comparative and the data are insufficient to draw any conclusions about evolution of viviparity from them.

More detailed analyses of the non-lipid and non-inorganic ion component of egg yolks of oviparous and viviparous lizards are needed before any comment about changes that accompany the evolution of complex placentae can be made. The surprising result of little change in net lipid uptake during development by different species of *Pseudemoia* with different degrees of placentotrophy suggests that there will be a concomitant increase in the transport of proteins in these species, but it is not possible to predict which proteins might be represented.

Function of placentae

Functional studies that show where and how nutrients are transported across the placenta are so far scarce. A number of studies show the uptake of radio-labelled amino acids into embryonic compartments in squamates, including skinks (Thompson 1977a; Swain and Jones 1997), and inorganic ions in lizards and snakes (reviewed by Stewart and Thompson 2000). Although none of these studies show where or how the nutrients are transported, at least in *N. metallicus*, there is more uptake in the middle to later stages of pregnancy when the embryos are most rapidly growing than early in development and just before parturition (Swain and Jones 1997). To date, the best indications of where and how nutrients are provided across the placenta come from interpretations of morphological studies, particularly using light and electron microscopy (e.g. Adams et al. 2004).

The focus on chorioallantoic placentae by Weekes (1935) provided a long-lasting framework for future studies, but probably led to a delay in potentially informative studies of the omphaloplacenta. More recent analyses strongly suggest that the chorioallantois is a specialised gas exchange organ and that nutrient transport is more likely in the omphaloplacenta (Adams et al. 2005). What is interesting, however, is that species with complex placentae and substantial placentotrophy (e.g. *Pseudemoia* sp., some *Mabuya* sp. and *Eumecia* sp.) (Stewart and Thompson 1996, 1998; Flemming and Blackburn 2003) all have a specialised region of the chorioallantois called a placentome that is implicated in transport of nutrients to the embryo, but is morphologically and histologically separated from the specialised gas exchange regions (Thompson et al. 2004; Adams et al. 2005).

Molecular approaches

Viviparity has evolved independently many times in squamate reptiles (Blackburn 2000), which implies that it must be a relatively simple thing to achieve. Its simplest form, lecithotrophic viviparity, involves the retention of eggs that have reduced shells (Heulin 1990; Qualls 1996) in the oviducts until the embryo is fully developed. Few steps are involved in this transition: (1) the change in timing of expulsion of the conceptus, (2) a reduction in the thickness of the eggshell to allow uptake of oxygen, (3) possibly an increase in the vascular support of the uterus, also to allow oxygen uptake by the embryo, and (4) the provision of water to the egg. None of these steps involves new structures or processes, but merely an upregulation (increased vascularity), downregulation (reduced eggshell), or a change in the timing (expulsion of conceptus) of existing processes. To date, none of these processes have been investigated from a molecular perspective, despite their apparent simplicity.

The much rarer event, evolution of placentotrophy, has occurred rarely and involves much more complex changes than the retention of eggs. By its nature, placentotrophy involves the reduction in nutrient provision to eggs in the ovary in favour of transport across the placenta, which invariably involves new processes (transport of nutrients across the uterine epithelium where no transport has occurred previously) and structures (transport organs, such as a placentome), or the loss of structures (isolated yolk mass degenerates part way through development in *Mabuya* or *Eumecia*, Flemming and Blackburn 2003). The molecular basis of the evolution of placentotrophy is likely to be much more difficult to identify, and is really predicated on the identification of the processes involved in the first step of the process—the evolution of lecithotrophic viviparity. Our results imply that the evolution of placentotrophy in the *Pseudemoia* lineage has required the transfer of lipids or their fatty acid components across the anatomically complex placenta, which presumably has a molecular basis. The transfer of free fatty acids from the maternal to the foetal circulation of mammals is achieved by the action of a range of fatty acid transport proteins located in the plasma membranes of the placental cells (Dutta-Roy 2000). In addition, the placental expression of lipoprotein lipase activity results in the hydrolysis of lipoprotein TAG in the maternal plasma, releasing free fatty acids for transfer across the placenta (Bonet et al. 1992). It would be of interest to investigate the possible expression of fatty acid transfer proteins and lipoprotein lipase in the *Pseudemoia* placenta.

Conclusion

Among the amniote vertebrates, viviparity is known to have evolved once in mammals, once in the Ichthyosauria and over 100 times in the Squamata, but not in the Archosauria or turtles (Blackburn 1982, 1985, 1999). Only the Squamata contains species with independent origins of viviparity and with a range of placental complexities, so only in the Squamata can hypotheses to explain the evolution of viviparity from oviparity be tested. The Squamata and mammals share the basic complement of extra-embryonic membranes of amniotes, and these membranes provide the embryonic elements of placental structures. The unique feature in Squamata is the occurrence of intravitelline mesoderm and the formation of an isolated yolk sac.

Perhaps it is something about the isolated yolk sac complex that facilitates the evolution of viviparity. The uterine epithelium of the associated omphaloplacenta is secretory (Adams et al. 2005), even in lecithotrophic species (Stewart 1990), and the embryonic omphaloplacenta is preadapted as an uptake epithelium because the bilaminar omphalopleure of oviparous species takes up water and presumably calcium and perhaps inorganic ions from outside the egg. In contrast to lecithotrophic viviparity, placentotrophy has evolved much less commonly and involves elaboration of the chorioallantoic and omphaloplacentae and the apposing uterine epithelia. There is a general correlation between placental complexity and net uptake of nutrients by the embryo, although details of what is being transported, and by which structures are lacking. The correlation between an elaborate chorioallantoic placenta and substantial placentotrophy implies that the omphaloplacenta is unable to provide all of the needs of a developing embryo, strengthening the conclusion that the chorioallantoic placenta is involved in dry matter transport.

A number of observations suggest fertile areas for future investigation. The proportion of TAG and PL in the yolks of lecithotrophic and placentotrophic species are quite different, and suggest that energy is provided to the embryos of placentotrophic species later in development, but the form of that energy supply has not been characterised. Presumably that supply is across the chorioallantoic placenta, also. Indeed, although the assumption has been that lipid would be the form of energy supply, the possibility of carbohydrate has not been discounted. The observation that the proportional net uptake of lipid during development in species of *Pseudemoia* that vary considerably in the total net uptake of dry matter suggests either that most of the lipid taken up is consumed, or that lipid uptake becomes relatively less important as placentae become more complex and total placentotrophy increases. In addition, we conclude that specialisation of the chorioallantois to form a placentome is associated with an increase in the capacity for transport of lipids generally. A test of this hypothesis would be an analysis of lipid transport in a species such as *Chalicides chalicides* that has a placentome (Blackburn and Callard 1997), but is unrelated to the *Eugongylus* group skinks studied to date.

The evolution of complex placentae then suggests a scenario where the step from oviparity to lecithotrophic viviparity involves the co-opting of existing function. The chorioallantoic placenta continues the gas exchange function of an oviparous species and the omphaloplacenta takes over the uptake of aqueous materials (water and inorganic ions) of the bilaminar ompalopleure of oviparous species. Maintenance of pregnancy presumably involves chemical communication between the embryo and mother, and it seems that the most likely place for that, together with limited uptake of other nutrients (e.g. hormones), is the omphaloplacenta. The evolution of placentotrophy is highly correlated with embellishment of the chorioallantoic placenta and the regional differentiation of the chorioallantois to form a placentome (and chorionic areolae in species with microlecithal eggs). Currently, detailed comparisons of placentomes that are independently derived in different clades are lacking, so it is possible that they function differently in different groups. The important point is that structurally complex organs form, and these organs are involved in nutrient transport from the mother to the embryo by mechanisms different from those in the omphaloplacenta. Consequently, different nutrients are probably also transported. Functional studies of different placental structures are now required to test these hypotheses.

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