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Placenta and Placental Analogs in Reptiles and Amphibians

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I. Reproductive Modes and Embryonic Nutrition
II. Placentae in Viviparous Squamate Reptiles
III. Placentae and Placental Analogs in Amphibians
IV. Evolution of Placentae and Matrotrophy

GLOSSARY

chorioallantois	The vascularized respiratory membrane of the amniote egg, which contributes to placental formation in all viviparous squamates and eutherian mammals.
extraembryonic membranes	Specific tissues lying outside of the body of the embryo proper (such as the yolk sac, amnion, and chorioallantois) which can function in embryo protection, physiological exchange, and placental formation.
lecithotrophy	A developmental pattern in which the yolk of the ovum provides nutrients to the embryo.
matrotrophy	A developmental pattern in which the mother provides nutrients during gestation by a means other than the yolk of the ovum (e.g., oviductal secretions, sibling yolks, and placental tissues).
oviparity	A reproductive mode in which females lay eggs, whether they be developing or unfertilized; also known as "egg-laying" reproduction.
placenta	Any apposition or fusion of the fetal organs to the maternal (or paternal) tissues for physiological exchange.
placentotrophy	A type of matrotrophy in which nutrients for development are supplied by placental organs.
viviparity	A reproductive mode in which embryos develop inside the female reproductive tract and are born as viable offspring; also known as "live-bearing" reproduction.
yolk sac	Extraembryonic tissues that surround and digest the yolk and that contribute to several distinct types of placentation in viviparous reptiles and mammals.

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Placentae are organs formed from extraembryonic and parental tissues that help sustain embryos physiologically during their development. In viviparous squamate reptiles, in which the fetus develops to term inside the maternal oviduct, the placental membranes typically accomplish gas exchange and provide water and small quantities of nutrients to the embryo. In certain lizards, placental membranes supply virtually all the nutrients for embryonic development. Morphological attributes of squamate chorioallantoic placentae correlate with the degree of placentotrophy. Some viviparous species of amphibians exhibit specializations for maternal–fetal nutrient provision that are functionally analogous to placentae. Simple placenta-like structures that function in gas exchange are occasionally found among egg-laying amphibians.

I. REPRODUCTIVE MODES AND EMBRYONIC NUTRITION

In most species of animals, females reproduce by laying unfertilized or fertilized eggs, a reproductive pattern known as "oviparity." In contrast, in species with "viviparity" (e.g., most mammals, a few amphibians, and many lizards, snakes, and fishes), females retain their developing eggs to term in their reproductive tracts and eventually give birth to their offspring. Many viviparous species exhibit placentae or placental analogs by which embryos are sustained physiologically during their development in the female reproductive tract.

The structure, function, and evolution of placentae are matters of considerable empirical and theoretical interest. Although placentae supply oxygen and water to the developing embryo, they also can provide organic and inorganic nutrients. Maternal provision of nutrients in this fashion is known as "placentotrophy." This pattern contrasts with "lecithotrophy," in which nutrients are supplied by the yolk of the ovum. Placentotrophy is a special case of "matrotrophy," which also includes various analogous ways of providing extravitelline nutrients for embryonic development (Table 1).

Most reptiles and amphibians exhibit lecithotrophic oviparity. Viviparity occurs in about 20% of the squamates, most of which are relatively lecithotrophic; however, placentotrophy characterizes three or four lineages of viviparous lizards. Among amphibian species, viviparity is rare and placentotrophy (strictly speaking) is absent. However, some viviparous amphibians are matrotrophic, having evolved analogous means of providing nutrients to the developing embryos.

II. PLACENTAE IN VIVIPAROUS SQUAMATE REPTILES

A. Physiological Relationships in Oviparity and Viviparity

In oviparous squamates, as in other egg-laying amniotes, the eggs are fertilized inside the maternal reproductive tract, an eggshell is deposited by uterine glands, and the egg is laid on land. The oviposited eggs of lizards and snakes exchange gases with the surrounding air through the eggshell and absorb water from the substrate (Fig. 1). In fact, the eggs may

TABLE 1

Forms of Substantial Matrotrophy among Viviparous Reptiles and Amphibians

Type	*Nutrient source*	*Animal*
Placentotrophy	Placental membranes	A few viviparous lizards;[a] typhlonectid caecilians
Oophagy[b]	Sibling ova	*Salamandra atra* (Urodela)
Histotrophy, histophagy[c]	Oviductal secretions	*Nectophrynoides occidentalis* (Anura); viviparous caecilians

[a] Genera *Chalcides, Mabuya,* and *Pseudemoia* (family Scincidae); many (and perhaps all) viviparous squamates show incipient placentotrophy.

[b] Embryonic ingestion of sibling egg yolks.

[c] Absorption or ingestion of oviductal secretions and tissues.

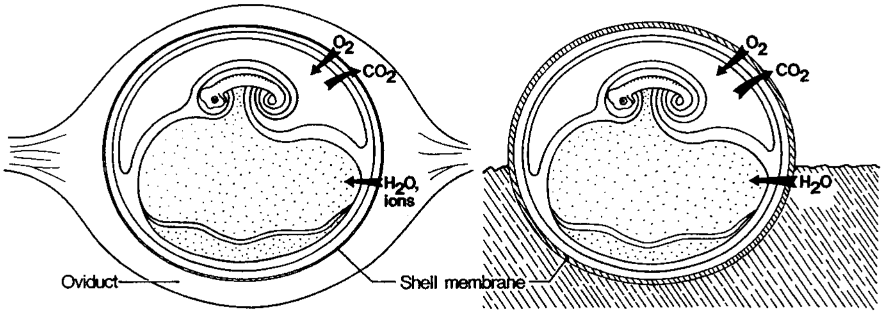

FIGURE 1 Physiological relationship between a squamate egg and its environment under conditions of viviparity (left) and oviparity (right). In the viviparous condition, exchange occurs with the uterine oviduct, and in the oviparous condition it occurs with the air and substrate. In each case, gas exchange occurs via the chorioallantois. The yolk sac is inferred to function in water uptake, although experimental evidence is not yet available (reproduced from Blackburn, 1993).

double or triple in wet mass after oviposition through water uptake while decreasing in dry mass (Table 2). Gas exchange is accomplished by the chorioallantois, a vascularized extraembryonic membrane that lines the inner surface of the eggshell at the dorsal (embryonic) hemisphere of the egg. Uptake of water from the substrate is probably accomplished by the yolk sac, although the mechanism is not well understood. Embryo nutrition is lecithotrophic; nutrients are supplied via the egg yolk. In many species, the eggshell supplies calcium to the embryo.

The physiological relationship between an egg and its environment in typical (lecithotrophic) viviparous squamates is similar to that in oviparous forms (Fig. 1). The developing egg increases in wet mass and decreases in dry mass approximately to the same extent as it does in oviparous squamates (Table 3). The main difference from the oviparous situation is that in the viviparous condition, oxygen and water are supplied (and carbon dioxide removed) by the uterine oviduct, where the egg resides during gestation. In addition, in viviparous squamates the eggshell is vestigial; in many species this remnant of the eggshell becomes progressively thinner during gestation. As a result, the maternal and extraembryonic tissues lie in close proximity, enhancing the potential for physiological exchange (Fig. 1). In viviparous, matrotrophic species of at least two lizard genera (*Chalcides* and *Mabuya*), the vestigial shell

TABLE 2
Developmental Changes in Mass of the Egg between Oviposition and Hatching in Various Oviparous Squamates

	Change in mass (%)	
Species	*Dry mass*	*Wet mass*
Anolis auratus	—	+82–204
Callisaurus draconoides	—	+53–100
Coluber constrictor	−14	+53
Crotaphytus collaris	—	+82
Eumeces fasciatus	−33	+14
Liolaemus tenuis	—	+125
Pogona barbata	−30	+66
Sceloporus undulatus	—	+106–170

TABLE 3
Developmental Changes in Mass of the Oviductal Conceptus in Selected Viviparous Squamates[a]

	Change in mass (%)	
Species	*Dry mass*	*Wet mass*
Elgaria coerulea	−18	+142
Eulamprus quoyii	−10	+96
Nerodia rhombifera	−22	+59
Notechis scutatus	−35	+96
Virginia striatula	−31	+48
Vipera berus	—	+51
Pseudemoia entrecasteauxii[b]	+68	+296
Chalcides chalcides[b]	—	+683
Mabuya heathi[b]	+38,400	+53,800

[a] In the relatively lecithotrophic species, dry mass of the conceptus decreases, as in oviparous forms.
[b] Species with substantial placentotrophy.

membrane ruptures and is shed early in development, with the result that extraembryonic and maternal tissues are in direct contact for most of gestation.

The close association of extraembryonic membranes with the uterine lining that exists in viviparous squamates meets Harland Mossman's (1937) criteria for recognition of a placenta: "Any intimate apposition or fusion of the fetal organs to the maternal (or paternal) tissues for physiological exchange." Given that biologists in past decades have applied the concept of placentation to reptiles in discrepant ways, three points should be noted. First, organs need not transfer organic nutrients to be recognized as placental; even oxygen provision qualifies as physiological exchange. Second, placentae are not necessarily vascularized. As mammalian studies have shown, some placentae transfer nutrients from mother to offspring through secretion and absorption rather than between bloodstreams. Third, the presence of a remnant of the eggshell between extraembryonic and maternal tissues does not disqualify the arrangement as placental. After all, acellular layers lying between fetal and maternal tissues are a common feature of mammalian placentae.

B. Types of Placentae

Squamate placentae are defined anatomically according to the particular extraembryonic membrane that contributes to them. For example, apposition of the chorioallantois to the uterine lining forms the chorioallantoic placenta (Fig. 2). Similarly, the avascular chorion (formed from ectoderm and mesoderm) can contribute to the chorionic placenta, a transitory structure of early development. Both placental types have equivalents among mammals. Squamates differ from other amniotes in the variety of extraembryonic tissues that develop from the yolk sac, a fact that is overlooked in embryology textbooks and all but a handful of reviews. Each of these membranes contributes to a distinct type of yolk sac placenta. Thus, viviparous squamates can exhibit a choriovitelline placenta, a bilaminar yolk sac placenta, an omphaloplacenta (formed from the avascular omphalopleure and isolated yolk mass), and an omphalallantoic placenta (the omphalopleure as vascularized internally by the allantois).

Of these six placental types, the chorioallantoic placenta is the only one that invariably persists until the end of gestation in all species. Either an omphaloplacenta or an omphalallantoic placenta also persists to the end of development. Although the remaining placental types have been described only occasionally, they may well be universal among viviparous squamates, having been overlooked due to their transitory nature. Our definition of the concept "placenta" has both a structural and a functional component. Unfortunately, because information on placental function is limited, we do not know whether all the placental types recognized on morphological grounds function in physiological exchange. We do have excellent reason to believe that the chorioallantoic placenta functions in gas exchange and nutrient transfer, as discussed later. We also know that yolk sac placentae can be sites of striking cellular specializations. Clarification of the particular roles of the various placental arrangements is one of the most important and difficult tasks facing placentologists who study reptiles.

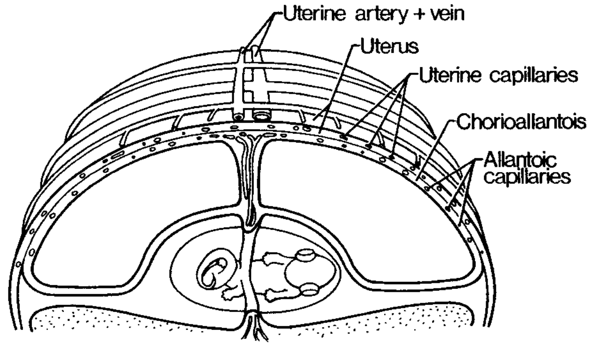

FIGURE 2 Apposition of the chorioallantois to the uterine lining, forming the squamate chorioallantoic placenta. The vestigial shell membrane is not illustrated (reproduced from Blackburn, 1993).

C. Placentae in Lecithotrophic Squamates

1. *Gas Exchange and the Chorioallantoic Placenta*

Because the lumen of the oviduct is a relatively hypoxic environment, a major problem facing an egg retained in the uterus is that of gas exchange. Embryonic needs for oxygen progressively increase during development and accelerate in the postembryogenic growth phase. In the oviparous condition, gas exchange is accomplished by the chorioallantois. Because it is the only vascularized extraembryonic membrane that invariably persists until the end of gestation, this membrane probably accomplishes this same function in all viviparous squamates.

Examination of the chorioallantoic placenta reveals an organ with considerable potential for gas exchange. The entire dorsal hemisphere of the egg is devoted to chorioallantoic placentation (Fig. 2), and in some squamates this placenta continually expands at the expense of the yolk sac during later development. Both the uterus and the chorioallantois are vascularized via an extensive network of capillaries. Capillary density increases during development. In addition, the uterine and chorionic epithelia become progressively thinner as capillaries migrate toward the luminal surfaces. As a consequence, by late development a very thin layer of epithelium separates the uterine and allantoic capillaries, presenting a narrow barrier to gas diffusion (Fig. 3). Although previous studies inferred that the uterine epithelium erodes to expose the underlying capillaries, recent work has not confirmed such erosion. Nevertheless, the diffusion distance between allantoic and uterine capillaries can be $<0.5\ \mu m$. In a peculiar (and largely unappreciated) feature of squamate development, the allantois vascularizes the inner face of the omphalopleure in many species, forming an omphalallantoic membrane. The extent to which the omphalallantoic placenta contributes to gas exchange is not known.

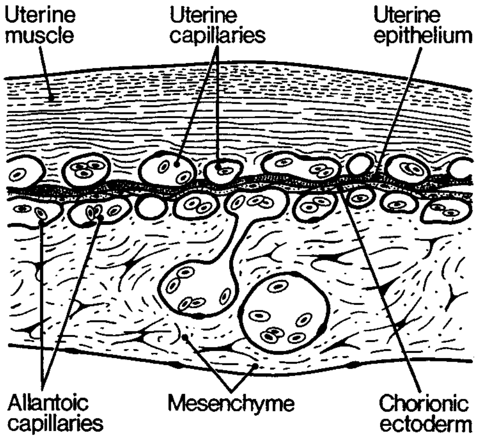

FIGURE 3 Interface of uterine and chorioallantoic tissues in the generalized chorioallantoic placenta of lizards and snakes. This placental type is characteristic of relatively lecithotrophic, viviparous squamates, in which it functions as a respiratory organ. Only thin layers of uterine and chorionic epithelia separate the fetal and maternal vascular systems (reproduced from Blackburn, 1993).

2. *Water and Nutrient Provision*

Although the yolk provides most of the nutrients for development in lecithotrophic viviparous squamates, radiotracer studies have revealed that amino acids and inorganic ions are transferred from maternal to embryonic tissues in several species. Quantitative analyses have shown that placental provision can account for considerable amounts of sodium and calcium, among other ions. Thus, even lecithotrophic viviparous species exhibit an incipient form of placentotrophy. In addition, the developing viviparous egg absorbs water from maternal tissues.

The precise site of placental transfer of water, ions, and organic molecules in lecithotrophic squamates has not been determined. However, a few physiological studies have implicated yolk sac placentae in nutrient transfer in these species. In addition, anatomical studies have revealed cellular specializations suggestive of secretion and absorption across the yolk sac placenta in some viviparous lizards and snakes.

D. Specializations for Placentotrophy

In at least three lineages of viviparous lizards, placental membranes transfer substantial quantities of organic nutrients. For example, in South American *Mabuya* as well as the Mediterranean skink *Chalcides chalcides*, the ovulated egg is very small and virtually all of the nutrients for development are supplied by placental means. In these lizards, the dry mass of the conceptus between ovulation and birth increases markedly, in contrast to the decrease in mass that characterizes lecithotrophic forms (Table 3).

The chorioallantoic placentae in such species are correspondingly specialized. Each exhibits a "placentome"—a region of interdigitation between hypertrophied uterine and chorionic tissues. At this site, the chorionic epithelial cells are enlarged and bear mi-

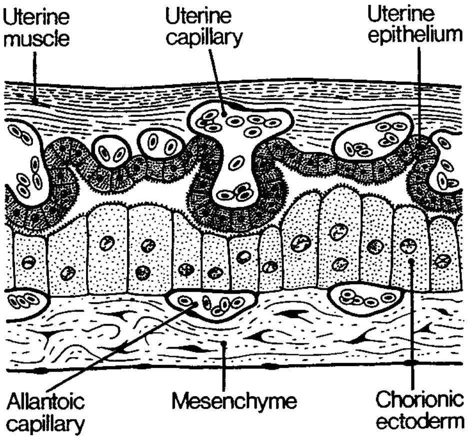

FIGURE 4 Interface of uterine and chorioallantoic tissues in the placentome *Chalcides chalcides*. The uterine epithelium is secretory, and the chorionic epithelium bears microvilli. Outside the placentome, the placenta looks like that shown in Fig. 3 (reproduced from Blackburn, 1993).

crovilli, a morphology typical of absorptive cells (Fig. 4). The apposed uterine epithelium consists of large secretory cells. Similar specializations are found in some unrelated Australian lizards of the genus *Pseudemoia*. In *Mabuya*, the uterus contains enlarged glands whose secretions appear to be absorbed by the chorionic cells. Outside of the placentome, the chorioallantoic placenta in these lizards appears much like that of generalized (lecithotrophic) species. Thus, the chorioallantoic placenta shows regional differentiation in placentotrophic forms, with one region being specialized for nutrient transfer and the other for gas exchange.

III. PLACENTAE AND PLACENTAL ANALOGS IN AMPHIBIANS

The vast majority of amphibians reproduce by laying eggs, which are either fertilized externally [most frogs and toads (anurans)] or internally (caecilians and most salamanders). However, viviparity occurs in one genus of salamanders, two lineages of frogs, and among the caecilians. Representatives of each of these amphibian groups have placental analogs (i.e., mechanisms by which matrotrophys is accomplished), as do a few oviparous anurans.

A. Specializations for Gas Exchange

In the viviparous amphibians, the eggs are fertilized internally and the larvae develop within the maternal oviduct. Respiration via the skin and gills may suffice for the small larvae of some of these species. However, some developing caecilians exhibit enormously elongated gills during development that function in gas exchange with the oviduct. In the viviparous frog *Eleutherodactylus jasperi*, a lecithotropic species, the tail of the developing tadpole may accomplish respiratory exchange; it is broad and highly vascularized and adpressed to the oviductal epithelium. Analogous situations occur in various oviparous anurans. For example, in certain *Gastrotheca*, after fertilization the eggs are carried in integumentary pouches on the back of the mother frog, and the enlarged gills of the developing tadpole closely appose the pouch lining. Although the term "placenta" has not traditionally been applied to such specializations, they do lie within the bounds of the definition.

B. Specializations for Nutrient Provision

Although few amphibians exhibit matrotrophic viviparity, their mechanisms of nutrient provision are diverse and unusual compared to those of squamate reptiles (Table 1). In the East African frog *Nectophrynoides occidentalis*, females produce tiny (0.6-mm) eggs and nourish their fetuses by oviductal secretions. The fetuses have specialized oral papillae that may aid in ingestion of the secretions. In the urodele *Salamandra atra*, the gestation period lasts from 2 to 5 years, during which time the embryos consume sibling yolks as well as uterine secretions. A specialized region of the pregnant oviduct sheds epithelial cells that are ingested by the embryos.

About 50% of those caecilians whose reproductive modes are known are both viviparous and matrotrophic. The developing fetuses ingest nutritious oviductal secretions as well as epithelial cells, which they scrape away with specialized teeth. Abrasion of the oviduct lining is said to stimulate release of the secretions. Embryos of typhlonectid caecilians exhibit highly unusual sac-like gills that are thought to function not only in gas exchange but also in absorption of oviductal nutrients.

Nutrient provision following hatching may occur in Darwin's frog, *Rhinoderma darwinii*, a species in which males carry their young in their vocal sacs though the period of metamorphosis. Experimental study indicates that labeled amino acids injected into the paternal circulation are transferred to the larvae—a pattern which legitimately could be labeled "patrotrophy."

IV. EVOLUTION OF PLACENTAE AND MATROTROPHY

A. Reptiles

Since the early 1900s, biologists have assumed that placentae evolve subsequent to viviparity in squamates. Much effort has been devoted toward estimating whether particular viviparous squamates have structures worthy of being called placentae. However, by modern criteria, functional placentae are universal among viviparous squamates. Placentae apparently evolve concomitantly with viviparity because thinning of the eggshell allows apposition of the extraembryonic membranes to the uterine lining.

The evolutionary implications are profound. Given that viviparity has evolved on over 100 separate occasions among squamates, placental organs must have also originated as frequently. No other animal organ is known to have originated on so many independent occasions. Squamate placentae therefore offer a powerful resource for studies of the interplay of structure and function in an evolutionary context.

From comparisons of oviparous and viviparous squamates, we can trace structural and functional changes through which placentation evolves. Retention of the viviparous egg inside the maternal oviduct and thinning of the eggshell places the chorioallantois in close proximity to the vascularized uterine mucosa (Fig. 1). Associated evolutionary modifications include diminution of uterine gland secretion (such that only a remnant of the eggshell is deposited) and, according to some studies, an increase in vascularity of the uterus. As noted previously, the epithelia of both the uterus and the chorioallantois are greatly thinned in viviparous forms, minimizing the diffusion distance between fetal and maternal bloodstreams (Fig. 3). Whether oviparous and viviparous squamates differ in this regard has not been determined.

In any case, the result is a chorioallantoic placenta that functions in gas exchange, as does the chorioallantois of oviparous species. If yolk sac placentae function in water uptake, as some biologists have speculated, the yolk sac of viviparous forms may also have retained its original oviparous function. Interestingly, intermediate evolutionary stages in the evolution of viviparity and placentation are exceedingly rare among extant species, perhaps because they are evolutionarily unstable. The great majority of squamates either lay fully shelled eggs at an early stage of development or retain eggs to term and form functional placentae.

Modification of the chorioallantoic placenta for nutrient transfer has occurred in three separate lineages of squamates, all members of the lizard family Scincidae. Specializations of the chorioallantoic placentae are similar in these three lineages, providing a striking example of evolutionary convergence at the cellular level.

B. Amphibians

Matrotrophy clearly has evolved independently in *Salamandra*, *Nectophrynoides*, and the caecilians. Because the embryos of these amphibians are not surrounded by extraembryonic membranes, ingestion and absorption of products of the maternal reproductive tract can occur. True placentotrophy appears to be confined to typhlonectid caecilians, in which it occurs via specialized gills of the embryo. Thus, although the anamniote condition has precluded forms of placentotrophy such as those of squamates, it has facilitated alternative mechanisms of maternal–fetal nutrient transfer.

Placentae also have evolved to serve respiratory functions in both oviparous and viviparous amphibians through the evolutionary recruitment of embryonic gills and tails. The integumentary placental structures found in some oviparous frogs have no equivalent among amniotes, and their evolution is made possible by the glandular skin and small unshelled eggs.

Our understanding of the structure and function of placentae and their analogs in reptiles and amphibians is based on incomplete information on a miscellaneous sampling of species. Without question, much more needs to be learned. Unfortunately, several key viviparous species are now threatened in large parts of their ranges (e.g., certain South American *Mabuya*), and at least one (the frog *E. jasperi*) recently appears to have gone extinct. Thus, studies of reproduction in viviparous reptiles and amphibians gain special urgency from the prospects that what we do not learn soon may be forever lost to science and humankind.

See Also the Following Articles

ALLANTOCHORION; AMPHIBIAN REPRODUCTION, OVERVIEW; PLACENTA AND PLACENTAL ANALOGS IN ELASMOBRANCHS; PLACENTAL GAS EXCHANGE; PLACENTAL NUTRIENT TRANSPORT; REPTILIAN REPRODUCTION, OVERVIEW; VIVIPARITY AND OVIPARITY

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