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Viviparity and Oviparity: Evolution and Reproductive Strategies

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- I. Reproductive Modes of Animals
- II. Oviparity and Viviparity Compared
- III. Evolution of Viviparity
- IV. Evolutionary Aspects of Embryo Maintenance in Viviparous Species
- V. Oviparous Analogs to Viviparity and Matrotrophy

GLOSSARY

chorioallantois The vascularized respiratory membrane of the amniote egg which contributes to placental formation in viviparous squamates, eutherian mammals, and the marsupial bandicoot.

extraembryonic membranes Tissues that lie external to the embryo and that function in embryo protection, physiological exchange, and placentation; among them are the yolk sac, amnion, chorion, and chorioallantois.

lecithotrophy A developmental pattern in which the yolk of the ovum provides nutrients for embryonic development.

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 and placental tissues).

oviparity A reproductive mode in which females lay unfertilized or developing eggs that complete their development and hatch in the external environment; also known as "egg-laying" reproduction.

oviparous egg retention A form of oviparity in which the fertilized eggs are retained and begin to develop inside the maternal reproductive tract, are oviposited, and complete their development in the external environment; sometimes termed "extended oviparity."

ovoviviparity An archaic term, now seldom used, that was applied in the past to a wide variety of reproductive patterns including some that are mutually exclusive; these patterns include lecithotrophic viviparity, oviparous egg retention, and pseudoviviparity.

ovuliparity Reproduction by the laying of unfertilized eggs; a form of oviparity.

partition Expulsion by a female of the reproductive product, be it an egg or a neonate; this term subsumes oviposition and parturition.

placenta An organ formed through apposition of embryonic and parental tissues that functions in physiological exchange; mainly found in viviparous species.

pseudoviviparity An unusual form of oviparity in which the eggs are fertilized externally and are brooded in some parental structure such as the stomach, vocal sacs, skin pouches, branchial chambers, or gastrovascular cavity; found in a few anurans, teleosts, and invertebrates.

viviparity A reproductive mode in which females retain developing eggs inside their reproductive tracts and give birth to their offspring; also known as "live-bearing" reproduction.

yolk sac Extraembryonic tissues that surround and digest the yolk and that contribute to placental organs in certain viviparous fishes, most therian mammals, and all viviparous reptiles.

zygoparity Reproduction by the laying of fertilized eggs; zygoparity grades into oviparous egg retention.

Viviparity is a reproductive pattern in which females retain developing eggs inside their reproductive tracts or body cavity and give birth to offspring capable of a free-living existence. Oviparity, in contrast, is a pattern in which females deposit eggs that develop and hatch in the external environment. These patterns can be viewed as "reproductive strategies," patterns that have advantages as well as disadvantages that affect their evolution. An advantage of viviparity, for example, is that embryos are protected and physiologically maintained by the pregnant female. In many viviparous species, the mother provides nutrients to the embryo during gestation, a pattern known as "matrotrophy." Viviparity has originated over 160 times among animals and is found among bony fishes, cartilaginous fishes, amphibians, mammals, and squamate reptiles, as well as in several invertebrate groups. Viviparity and matrotrophy are phenomena of considerable biological interest. They have been studied from the standpoints of morphology, physiology, endocrinology, ecology, and evolution.

I. REPRODUCTIVE MODES OF ANIMALS

A. Oviparity and Viviparity

In the great majority of animal species, females reproduce by laying eggs that develop and hatch in the external environment. However, in some species, females retain fertilized eggs inside their bodies and

TABLE I
Phylogenetic Distribution of Viviparity among Major Groups of Vertebrates

Taxon	Frequency (%)	Examples of viviparous species
Agnathans	0	—
Chondrichthyans	65	Mackerel sharks, frilled sharks, whale sharks, butterfly rays, torpedo rays
Osteichthyans	2.8	Coelacanth, surf perch, poeciliids, half-beaks, four-eyed fish
Amphibians	3	<i>Salamandra atra</i> , East African frogs (<i>Nectophrynoides</i>), various caecilians
Mammals	99	Marsupials, eutherians
Chelonians	0	—
Squamate reptiles	20	Lizards and snakes of numerous families
Crocodylians	0	—
Birds	0	—

Note. Nonviviparous species are classified as oviparous.

give birth to their young. These reproductive patterns are known respectively as "oviparity" (egg-laying reproduction) and "viviparity" (live-bearing reproduction). Although viviparity is sometimes viewed as a mammalian phenomenon, many other groups of vertebrates also contain live-bearing species, including sharks, batoids, teleosts, caecilians, anurans (frogs and toads), salamanders, snakes, and lizards (Table 1). In some major taxa oviparity is predominant (frogs and teleosts) or universal (birds and turtles), whereas in others (chondrichthyans and mammals) viviparity is widespread. Several major invertebrate groups contain both oviparous and viviparous species, including insects, arachnids, crustaceans, tunicates, onychophorans, scorpions, sea cucumbers, and molluscs.

The existence of viviparity in so many unrelated animal groups raises a multitude of functional and evolutionary questions. What advantages and disadvantages accrue to viviparous and oviparous reproduction? What selective pressures have led some lin-

TABLE 2
Phylogenetic Distribution of Reproductive Modes and Embryonic Nutritional Patterns among Vertebrates^a

	Oviparity	Viviparity
Lecithotrophy	Crocodylians, chelonians, birds; most squamates and anamniotes	Many squamates, very few amphibians; some chondrichthyans and osteichthyans
Matrotrophy ^b	Monotreme mammals	A few squamates; some caecilians, frogs, and salamanders; some chondrichthyans and osteichthyans; therian mammals

^aLecithotrophy and matrotrophy represent extremes of a continuum. Except for therian mammals, viviparous species lie between these extremes and are classified by the predominant source of nutrients for development.

^b"Matrotrophy" refers to substantial provision of extravitelline nutrients to the embryo prior to birth or hatching. Provision of nutrients after birth or hatching is universal among birds and mammals.

eages to evolve viviparity and what factors have constrained its development in others? By what sequence of evolutionary steps has viviparity evolved from oviparity? How are oxygen and nutrients for development provided in viviparity and oviparity, and how can we account for the diversity in evolutionary terms? Such questions have intrigued reproductive and evolutionary biologists for the greater part of this century. Only in recent decades have we begun to answer such questions with confidence.

B. Embryonic Nutritional Patterns

Not only can we distinguish between species according to whether they lay eggs or give birth to their offspring but also we can characterize them according to how nutrients are provided to the embryos. In most animals, nutrients for development are contained within the yolk of the egg. This embryonic nutritional pattern is termed "lecithotrophy": The word *lecithos* is Greek for "yolk." This pattern contrasts with "matrotrophy," in which the female provides nutrients for embryonic development by means of a placenta ("placentotrophy") or by some analogous arrangement. Lecithotrophy and matrotrophy are extremes of a continuum. In many viviparous species, for example, nutrients for early development are derived from the yolk and later are supplemented by placental sources.

Reproductive mode and embryonic nutritional pattern can be used in combination to characterize animal species (Table 2). Most animals exhibit lecitho-

trophic oviparity; upon deposition by the female the egg is nutritionally autonomous. Excluding mammals, most viviparous vertebrates are also lecithotrophic; although the egg is retained to term in the female reproductive tract, nutrients are still supplied via the ovulated yolk. In animals with matrotrophic viviparity, nutrients are supplied by the mother during the course of gestation via a placenta or products of the reproductive tract (e.g., uterine or ovarian secretions and sibling yolks). Matrotrophic oviparity is rare but occurs in the monotreme mammals; the eggs absorb large quantities of oviductal secretions before being deposited. The confusing and archaic word "ovoviviparity" has been applied in the past to both oviparous and viviparous lecithotrophy but is now avoided by most reproductive biologists in favor of the bipartite classification system shown in Table 2.

C. Other Reproductive Distinctions

Just as fundamental as the distinction between oviparity and viviparity is a distinction based on the site of fertilization. In external fertilization, the male fertilizes the eggs after the female lays them. In contrast, internal fertilization occurs when males introduce sperm into the female reproductive tract. Accordingly, we can distinguish the oviposition of unfertilized eggs (ovuliparity) from the laying of fertilized eggs (zygoparity). In sexually reproducing animals internal fertilization is a prerequisite for viviparity.

In some oviparous species, females retain their fertilized eggs for some period before laying them; thus, the embryos can be in an advanced stage of development at oviposition. This pattern is termed "oviparous egg retention." Although in theory this pattern grades into viviparity, oviparous amniotic species with prolonged egg retention are rare. We reserve the term viviparity for species in which the embryos are retained to term by the female and in which hatching (if it occurs) precedes or accompanies emergence of the offspring from the mother. In contrast, in oviparous egg retention, the female typically deposits an intact egg that continues to develop in the external environment before it finally hatches.

In some oviparous invertebrates (e.g., certain molluscs and anemones) externally fertilized eggs are taken into the body (i.e., gastrovascular cavity and branchial chambers) of one of the parents. This pattern is best viewed as a type of egg tending. It is analogous to a pattern called "pseudoviviparity" in anamniote vertebrates and can be referred to by this same term.

II. OVIPARITY AND VIVIPARITY COMPARED

A. Site of Development

In oviparous species, egg development occurs in the external environment after oviposition. Fish eggs can be buoyant (most marine osteichthyans), non-buoyant (freshwater fishes), attached to marine plants via their egg casings (various sharks and skates), buried in gravel (salmonids), or deposited in nests (lampreys and sticklebacks). Eggs of amniotes are terrestrial and can be deposited in protected environments, buried, or laid in nests. Amphibian eggs usually develop in breeding ponds or streams, although in some oviparous anurans, eggs are deposited on terrestrial plants, laid in bubble nests, or carried by one of the parents.

In all viviparous animals, eggs develop inside the body of the maternal parent. However, the site of development varies. In most live-bearing vertebrates embryonic development occurs in the oviduct or its mammalian homolog, the uterus. This situation char-

acterizes the viviparous chondrichthyans, coelacanths, amphibians, squamates, and therian mammals. Thus, an organ that primitively provided a site of fertilization and deposited the egg encasements (e.g., eggshell or jelly coat) has been recruited evolutionarily for accommodation of the egg during development. Teleosts lack a homolog to the oviduct and gestation commonly occurs in the lumen of the hollow ovary. Moreover, in some teleost species (e.g., viviparous poeciliids and labriosomids), gestation occurs within the ovarian follicle; fertilization and hatching therefore precede ovulation. In others (embiotocids and goodeids), early development begins in the ovarian follicle and the embryo is then ovulated into the ovarian lumen where it completes its development. In the absence of a true oviduct, teleost viviparity seemingly evolved through recruitment of the only available reproductive structure capable of developing features to maintain the embryos—the ovary.

B. Extent and Duration of Development Inside the Female

In oviparous animals, most or all of embryonic development typically occurs in the external environment; thus, the eggs at oviposition are entirely undeveloped (ovuliparous species) or laid in an early stage of development. In birds, for example, females lay their eggs within a day or two of ovulation, at the preprimitive streak stage. Female turtles and crocodilians deposit eggs at the gastrula stage, and monotremes do so at the 18-somite stage. As a rule, the duration of gestation in the maternal reproductive tract is much shorter in oviparous species than in related viviparous forms.

Nevertheless, viviparous species vary widely in length of gestation and degree of development of the neonates. In eutherian mammals, for example, gestation lengths range from 20 days [shrews (*Sorex*)] to 660 days [the African elephant (*Loxodonta africana*)] and birth weight ranges from 7 to 91,000 g. The newborns range from very altricial (most rodents and bats) to precocial (ungulates). Gestation length bears an approximate relationship to birth weight in these matrotrophic species. Marsupials give birth to very tiny, altricial neonates (5 mg–0.5 g) after a

pregnancy of 12–38 days, depending on the species. Viviparous squamates universally give rise to precocial offspring; pregnancy commonly is 2–4 months, but gestation periods of more than a year are well documented in some lizards. Chondrichthyans also give birth to well-developed neonates and gestation lengths range from 2 or 3 months (some rays) to about 4 years (the soupfin shark *Galeorhinus*). In teleosts and amphibians, offspring commonly are born at a larval stage after a period of pregnancy that is relatively short by chondrichthyan standards. A notable exception is the Eurasian urodele *Salamandra atra*, in which neonates undergo metamorphosis in the oviduct, where they develop for a period of 2–5 years. Among viviparous invertebrates, offspring can be released at larval, pupal, or more advanced developmental stages.

C. Viviparity and Oviparity as Reproductive Strategies

Traditionally, viviparity has been assumed to be inherently superior to reproduction by laying eggs. This assumption reflects a bias toward therian mammals and fails to consider the biological significance of reproductive diversity. A more sophisticated approach considers oviparity and viviparity as reproductive “strategies” that entail both advantages and disadvantages, each of which may differ in their applicability to particular species.

Clearly, oviparity can entail disadvantages not found in viviparity. Oviposited eggs may be subject to a variety of predators as well as microbial attack, flooding, dehydration, ultraviolet light, and temperature extremes. A viviparous female can protect her developing eggs from many sources of mortality, both biotic and abiotic, while buffering her eggs from environmental fluctuations and maintaining them physiologically.

However, viviparity can entail significant disadvantages as well. During pregnancy, the ability of a female to locomote and feed may be affected, with consequent effects on maternal and offspring survival. Space constraints may limit litter size in viviparous forms more than in oviparous relatives because wet mass and volume of a neonate exceeds that of the ovulated yolk. Furthermore, pregnancy may pre-

vent a female from starting her next litter of offspring, with corresponding effects on reproductive output.

Therefore, from the standpoint of life history theory we would expect viviparity to evolve only when the benefits of stages that are evolutionarily intermediate outweigh the costs. Furthermore, viviparity is but one way in which developing eggs can be protected and should not be thought of as the best way to achieve that end in all circumstances. Birds are notable by having alternative ways of achieving the benefits that accrue to viviparity. Avian eggs are cared for and thermoregulated by one or both parents; protected from dehydration and microbial attack by the albumen, eggshell, and shell membranes; and can be protected from predators by parental care, camouflaged shells, and oviposition into constructed nests that are located in arboreal or inaccessible environments. The Antarctic emperor penguin, *Aptenodytes forsteri*, offers a case in point. Paternal care is critical in this species; following oviposition the male incubates the egg for 2 months while the female is away feeding. Egg retention could be severely disadvantageous to the female by requiring her to take on the entire burden of care for the developing egg, with corresponding effects on her own survivorship and reproductive output. The highly specialized nature of avian oviparity may help explain why oviparous egg retention and viviparity have not evolved among birds.

III. EVOLUTION OF VIVIPARITY

A. Reconstructing the Evolution of Viviparity

Questions about how and why viviparity has evolved traditionally have been approached by examining habitats of extant live-bearing species. Unfortunately, simply to consider the ecological conditions under which living viviparous species are found does not allow us to infer the circumstances or selective pressures under which that pattern originated. After all, we need look no further than mammals to see that viviparous vertebrates have radiated into virtually every conceivable habitat.

However, if we could identify and define each of

the independent origins of viviparity that have occurred among animals, we might be able to reconstruct the environmental circumstances in which this pattern evolved each time it originated. From such information we could assess hypothetical selective pressures and constraints. We could also test scenarios for the evolution of viviparity against information on actual lineages. The tools of cladistic analysis have allowed exactly this sort of analysis. Outgroup analysis indicates that oviparity is ancestral for each of the major vertebrate groups (including the traditional vertebrate classes). By superimposing data on reproductive modes over established phylogenies, we have been able to define the independent origins of viviparity. We can also reconstruct stages in the evolutionary transition to viviparity and infer habitats in which this pattern has originated.

B. Origins of Vertebrate Viviparity

Phylogenetic analyses have revealed that viviparity has evolved convergently on at least 142 separate occasions in vertebrate history (Table 3), far more frequently than previously suspected. At least 26 additional origins of viviparity are identifiable among invertebrates. The majority (<100) of these independent origins have occurred among lizards and snakes. In squamates, viviparity often has evolved at subfamilial and subgeneric levels and, in some cases, at the subspecific level. One of the latter origins (represented by the lizard *Lacerta vivipara*) is thought to have occurred during the Pleistocene. At the other extreme, the earliest origin of viviparity among reptiles is represented by the Mesozoic ichthyosaurs; pregnant females with developing fetuses have been found as fossils that date back 180 million years.

The other vertebrate origins of the live-bearing mode are distributed as follows. Viviparity has evolved at least 5 times in living amphibians—once among urodeles, twice among anurans, and at least twice among caecilians. In the osteichthyan fishes, viviparity has evolved at least 15 times. One of these origins is represented by the coelacanth, *Latimeria*, whose viviparity was discovered by dissection of a pregnant female at the American Museum of Natural History. Other origins are represented by poeciliids (e.g., swordtail guppies) and anablepid fishes, as well

TABLE 3
Evolutionary Origins of Viviparity and Matrotrophy among the Vertebrates

Taxon	Minimum number of origins ^a	
	Viviparity	Matrotrophy
Osteichthyans ^b	15	12
Chondrichthyans	20 ^c	5
Lissamphibia	5	4
Mammals	1	1
Ichthyosaurs	1	
Squamate reptiles	>100	3
Total	>142	25

Note. All data represent conservative estimates based on phylogenetic analyses. The analysis is based on the assumption that viviparity evolves irreversibly from oviparity.

^a From Blackburn (1992; unpublished data).

^b Represented by the clades Teleostei and Actinistia and some extinct basal chondrostei.

^c Chondrichthyans can be interpreted as exhibiting 11 origins if it is assumed that skates (Rajidae) have reverted to oviparity.

as goodeids, surf perches, half-beaks, and scorpae-nids. Among chondrichthyans, viviparity appears to have evolved on 20 separate occasions. Independent origins of viviparity are represented by the mackerel sharks, carpet sharks and their allies, frilled sharks, angel sharks, torpedo rays, butterfly rays, and a Paleozoic holocephalan.

The origins of viviparity that are now recognized (Table 3) are based on minimum estimates; actual numbers are probably higher. Mammals offer a case in point. Marsupial and placental mammals are conservatively interpreted as derivatives of a single Mesozoic origin of viviparity. However, viviparity may well have originated independently in the two groups, which differ in their placental membranes, reproductive physiology, early development, and the uterine sites at which the embryos undergo gestation.

C. Why Has Viviparity Evolved?

Because viviparity in squamate reptiles has evolved so frequently and at such low taxonomic levels, in many cases we can reconstruct the environmental circumstances in which it originated. A recurring

correlate of its origin among squamates is cold climate. Squamate viviparity frequently has evolved at high altitudes and high latitudes. Several lines of evidence—circumstantial, descriptive, and experimental—support the hypothesis that viviparity is adaptive under such conditions due to its thermoregulatory benefits. Because development rate is affected by temperature, eggs laid in cold environments may develop too slowly to hatch before the onset of winter or may succumb to low temperatures. As ectotherms, viviparous squamates can act as mobile incubation chambers, regulating their eggs at optimal temperatures for development. Perhaps thermoregulatory benefits also help account for viviparity in the high-altitude *S. atra*. However, cold climate cannot explain the origins of viviparity in tropical and subtropical caecilians and squamates, where its evolution presumably conferred other benefits. In therian mammals, the origin of viviparity may be associated with the pattern of nutrient provision, if it was preceded evolutionarily by altriciality and matrotrophy.

The selective pressures that led to viviparity in fishes are uncertain. Given that predation can take an enormous toll on aquatic eggs, perhaps retention of the eggs inside the female enhances egg survival. Why does such a minuscule proportion of amphibians and osteichthyans give birth to their young? The answer partly lies in the fact that most species in these groups have external fertilization. For viviparity to evolve requires that the eggs be fertilized inside the female reproductive tract. Internal fertilization is probably more than a prerequisite; it may also predispose lineages toward the evolution of live-bearing habits. Evidence for this supposition derives from the fact that most of the lineages of bony fishes that have evolved internal fertilization also include viviparous representatives. In addition, chondrichthyans (in which internal fertilization is universal) exhibit a high number of origins of viviparity and are second only to mammals in the percentage of viviparous species (Tables 1 and 2).

D. How Has Viviparity Evolved?

Viviparity is widely viewed as a result of a progressive, gradualistic, and unidirectional increase in the proportion of egg development that takes place inside

the female. Accordingly, over evolutionary time oviparous females would retain their eggs for progressively longer periods, laying them in more advanced stages of development. The culmination of this evolutionary trend would be viviparity, in which embryos are retained to term inside the female. Two main lines of evidence have been invoked to support this scenario in squamates: (i) the existence of oviparous species that lay eggs in early, middle, and advanced stages of development, and (ii) the existence of viviparous species that retain shelled eggs to term that hatch at the time of birth. As applied to particular taxa, other features have been added to this scenario, notably that both matrotrophy and simple placentae that function in gas exchange only evolve subsequent to viviparity.

However, consideration of the transition to viviparity in actual lineages has challenged aspects of the traditional scenario. Evidence from mammals indicates that matrotrophy can evolve prior to viviparity. Studies of squamates suggest that functional placentation as well as incipient matrotrophy can evolve simultaneously with viviparity. Thus, the chronological sequence by which viviparity has evolved differs between taxa (Fig. 1).

In addition, contrary to common belief, the eggs of oviparous squamates do not exhibit a full contin-

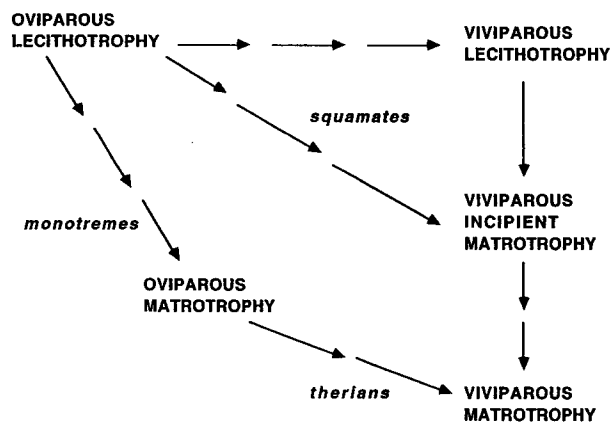


FIGURE 1 Multiple scenarios for reproductive evolution. Traditionally, matrotrophy was thought to have originated after viviparity. However, recent analysis suggests that in mammals matrotrophy evolved prior to viviparity and in squamates incipient matrotrophy commonly has evolved simultaneously with viviparity.

uum of developmental stages at the time of oviposition. Instead, most squamates either deposit their eggs at the limb bud stage of development (typical oviparity) or retain them to term (viviparity). On this basis, viviparity and placentation in squamates have been suggested to evolve in accord with a punctuated equilibrium model, in which intermediate evolutionary stages either never occur (aplacental viviparity) or are evolutionarily unstable and transient (i.e., oviparous egg retention). This model has been proposed recently and its implications and validity are under investigation. Application of the punctuated equilibrium model to anamniotes seems less likely; a broad spectrum of possible evolutionary stages is represented among living species. Due to differences in the tertiary egg membranes and the fact that aquatic offspring can be born at a larval stage of development, perhaps oviductal gestation of teleost and amphibian eggs does not involve the same physiological limitations that affect squamates.

IV. EVOLUTIONARY ASPECTS OF EMBRYO MAINTENANCE IN VIVIPAROUS SPECIES

A. Evolution of Matrotrophy

The origins of matrotrophy can be analyzed by using the same approach used for the evolution of viviparity. Phylogenetic analysis reveals that matrotrophy has evolved on 25 or more occasions among the vertebrates (Table 3). Most of these origins have occurred among the bony fishes, and only 4 have occurred among the amniotes, with mammals representing 1 such origin.

Given the multiple evolutionary origins of matrotrophy, this nutritional pattern presumably can have significant advantages over lecithotrophy. Although we do not fully understand the selective pressures that have led to its evolution, some plausible advantages of this pattern can be identified. In lecithotrophy, females have invested their nutrients into reproduction by the time of fertilization. In contrast, matrotrophy may permit females to control the provision of nutrients during gestation according to environmental circumstances and nutrient availability.

In addition, when circumstances warrant, in some matrotrophic species females can terminate reproduction early in gestation (via spontaneous abortion or embryo resorption) with relatively little energetic loss. Termination of reproduction in lecithotrophic species can result in loss of the energy invested into the yolk. Furthermore, matrotrophy minimizes the weight of the conceptus during much of gestation since its mass will not approach that of the newborn until late in development. Consequently, females may be able to circumvent a major cost of viviparity—the detrimental effects of pregnancy on maternal mobility.

B. Evolution of Specializations for Gas Exchange

In viviparous vertebrates with lecithotrophy, the immediate need of an embryo retained within the maternal reproductive tract is respiratory gas exchange. Structures that function in gas exchange under oviparous conditions commonly have been recruited to perform analogous functions in embryos of live-bearing forms. One example of such a structure is the chorioallantois, a vascularized extraembryonic membrane that is responsible for gas exchange in the eggs of all oviparous reptiles, birds, and mammals. This same structure forms an intimate placental relationship with the uterine tissues in each of the many lineages of viviparous squamates as well as in the eutherian mammals. Other respiratory structures shared by oviparous and viviparous embryos include the yolk sac of squamates, gills of fishes and caecilians, the "belly sac" (pericardial somatopleure) of cyprinodont fishes, and possibly the skin of larval amphibians. In various teleosts with ovarian gestation, the ovarian epithelium is vascularized and hypertrophied to provide for gas exchange with the embryos.

C. Evolution of Specializations for Nutrient Provision

Convergent evolution not only characterizes viviparity, matrotrophy, and specializations for embryonic gas exchange but also the specific structures by which nutrients are provided to developing embryos.

For example, in three unrelated genera of lizards, the chorioallantois has been recruited evolutionarily for placentotrophic nutrient provision. Chorioallantoic placentae also provide nutrients for development in eutherians and some marsupials, whereas a yolk placenta provides nutrients in most eutherians and all marsupials.

Like the chorioallantois, embryonic structures that function in gas exchange often have taken on a role in matrotrophy. Among these structures are the yolk sacs of certain sharks and poeciliids (which form yolk sac placentae), the belly sac of cyprinodonts (which also contributes to placentae), and gills of typhlonectid caecilians. Multiple lineages of teleost fishes have evolved trophotaeniae, outgrowths of the embryonic hindgut that absorb maternal secretions. Several viviparous lineages (*S. atra*, lamniform sharks, and multiple clades of osteichthyans) have evolved a pattern in which developing fetuses feed on siblings or ovulated yolks. Some lineages, including the viviparous caecilians and the frog *Nectophrynoides occidentalis*, have evolved a form of matrotrophy in which embryos ingest maternal tissues or secretions. These are but some of the adaptations for matrotrophy that have evolved among vertebrates. Diverse invertebrate specializations also abound.

V. OVIPAROUS ANALOGS TO VIVIPARITY AND MATROTROPHY

A. Parental Care, Egg Brooding, and Pseudoviviparity

As noted previously, viviparity is but one way for a parent to protect eggs from the vicissitudes of the environment. Parental care of eggs has evolved many times in oviparous animals. It is found in birds, monotreme mammals; crocodilians; various lizards, snakes, and salamanders; numerous lineages of frogs; and some teleost fishes. Care of eggs can range from simple proximity of the mother (as in crocodilians) to thermoregulatory incubation (birds, monotremes, pythons, and some scincid lizards). Care of eggs is sometimes labeled "brooding" and "egg tending."

In some anamniote vertebrates, the association of the eggs and parent is physiologically intimate.

Among teleosts, for example, externally fertilized eggs can be brooded in the mouth (e.g., certain cichlids and catfish) or carried in an integumentary pouch (male seahorses and pipefish). In anurans, eggs can be brooded in the stomach, vocal sacs, or depressions in the dorsal integument, or they can be carried on the back or legs by one of the parents. These patterns are types of egg brooding and it would be inappropriate to refer to them as viviparity. However, the term pseudoviviparity can be applied to such situations in recognition of their superficial similarity to cases in which the eggs develop to term in the female reproductive tract. Pseudoviviparity also can be applied to molluscs, in which externally fertilized eggs are taken into the branchial chamber of one of the parents, and cnidarians, which take hatched larvae into their gastrovascular cavities.

B. Lactation and Other Means of Nutrient Provision

Just as viviparity has its analogs among egg-laying species, matrotrophic nutrient provision has equivalents among oviparous forms. In a broad sense, matrotrophy could be applied to all cases in which females provide extravitelline nutrients to their offspring. Therefore, it can be useful to distinguish matrotrophy that precedes partition (oviposition or parturition) from that which follows it. Perhaps the most striking case of preparitive matrotrophy to have evolved among oviparous vertebrates is that of monotremes, in which the eggs absorb large quantities of nutritious oviductal fluids prior to their oviposition.

The most elaborate manifestation of postpartive matrotrophy is lactation, a phenomenon whose extraordinary nature tends to be taken for granted because it is so familiar. From the time of birth or hatching until weaning, a mammalian mother provides for the nutritional needs of her offspring by her own glandular secretions. The lactating female converts her own dietary nutrients and fat reserves into a secretion that is rich in lipids, carbohydrates, protein, and antimicrobial agents and that can offer immunological protection to the suckling young. Lactation reaches a pinnacle of complexity in marsupials; not only does the milk provide most of the nutrients for development but also female kangaroos

simultaneously can produce milks of markedly different composition to sucklings of different ages. Lactation in marsupials performs some of the same functions as does placentation in eutherian mammals, which commonly give birth to more advanced offspring.

Analogs to lactation have rarely evolved. They include the glandular secretions of the crop with which pigeons feed their young and the integumentary mucus which some teleosts secrete for ingestion by their hatchlings. Pipefish may offer another example because evidence indicates that the male parent provides nutrients to the eggs while carrying them in his brood pouch. This pattern and analogous cases in pseudoviviparous frogs can be called "patrotrophy." Parental feeding of the young by birds and mammals serves the same general function.

See Also the Following Article

PLACENTA AND PLACENTA ANALOGS IN REPTILES AND AMPHIBIANS

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Voles

see Cricetidae