Evolution of Placentas in the Fish Family Poeciliidae: An Empirical Study of Macroevolution

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Abstract

The placenta is a complex organ that mediates all physiological and endocrine interactions between mother and developing embryos. Placentas have evolved throughout the animal kingdom, but little is known about how or why the placenta evolved. We review hypotheses about the evolution of placentation and examine empirical evidence in support for these hypotheses by drawing on insights from the fish family Poeciliidae. The placenta evolved multiple times within this family, and there is a remarkable diversity in its form and function among closely related species, thus providing us with ideal material for studying its evolution. Current hypotheses fall into two categories: adaptive hypotheses, which propose that the placenta evolved as an adaptation to environmental pressures, and conflict hypotheses, which posit that the placenta evolved as a result of antagonistic coevolution. These hypotheses are not mutually exclusive. Each may have played a role at different stages of the evolutionary process.

1. INTRODUCTION

1.1 Darwin's Dilemma: What Good Is Half an Eye?

Placenta: an intimate apposition or fusion of maternal and fetal tissues for sustenance and physiological exchange

Darwin recognized that the evolution of "organs of extreme perfection and complication" posed a challenge to his theory. Such organs consist of many independent yet interacting elements, all of which need to be present for normal function. In Chapter 6 of *On the Origin of Species* ("Difficulties on Theory"), Darwin (1859) defined the dilemma posed by such complexity with the example of the eye:

> To suppose that the eye, with all its inimitable contrivances for adjusting the focus to different distances, for admitting different amounts of light, and for the correction of spherical and chromatic aberration, could have been formed by natural selection, seems, I freely confess, absurd in the highest possible degree. (p. 186—first edition)

Darwin's dilemma was that it seemed impossible for such complexity to arise in a gradual fashion if all parts had to be present and appropriately integrated for the organ to function. Here Darwin faced Archbishop Paley's argument that when we see such evidence of design, there must be a designer. It was this apparently irreducible complexity that inspired Darwin to propose the first mechanistic explanation for the evolution of complex organs by suggesting that complexity can indeed evolve by a gradual stepwise process leading to a succession of organs, each a bit more complex than its predecessor and each favored by natural selection. What we see in living organisms appears as irreducibly complex not because it arose at once in its current form, but because all of the intermediate steps in the evolution of the trait have been lost through extinction, leaving us with just the end product of what was otherwise a gradual process.

We accept that the many complex organs displayed by living organisms evolved in this stepwise evolutionary manner, but our acceptance is, of necessity, based upon indirect inferences because nature does not generally provide us with living evidence of the transition. For Darwin, these inferences were derived from the range of photosensitive organs that we see among species in the arthropod or gastropod phyla. In these lineages, photosensitive organs range from no more than a patch of cells that can only discriminate light versus dark to complex organs that have perceptual abilities comparable to vertebrates (Ekström & Meissl 2003, Fernald 2006, Salvini-Plawen & Mayr 1977). Between these two extremes lie other organisms with eyes of increasing complexity. It is this variation arrayed across entire phyla in the complexity of photosensitive organs that yields clues for how complexity can evolve. The existence of so many species with photosensitive organs less perfect than those of a vertebrate or octopus argues that a half of an eye serves perfectly well in many environments and for many lifestyles. However logical this argument may be, the presence of diversity that spans a phylum is of limited virtue if one wants to actually define how and why such complexity evolves because of the long intervals of time that separate those species with simple or complex eyes from their common ancestor.

Imagine how much more we could learn about the evolution of eyes if we could find a single genus of mammals in which there had been three independent origins of eyes, which also contained living species that had no eyes or eyes of intermediate complexity. Such opportunities are hard to imagine because we envision the requirement of immense spans of time for complexity to evolve, yet Nilsson & Pelger (1994) argue that it is feasible for an organ like an eye to evolve in as little as a few hundred thousand years. All that is required is for us to find a taxon for which the evidence of transition has not been erased by extinction. Here we present an argument for the existence of such a transition in the evolution of placentas in the fish family Poeciliidae.

1.2 The Placenta: A Complex Organ

The best-studied placentas are those of mammals. They are an ideal example of complexity because normal functioning depends on a wide range of intricate anatomical, physiological, genetic, and endocrine interactions, all of which appear to be essential to normal development between mother and offspring (Haig 1993, Simpson & MacDonald 1981, Wooding & Burton 2008). Placentas must fulfill the functions of all of the main organ systems of the body while accommodating the antigenic differences between the mother and developing young. If we adopt Mossman's (1937, 1987) definition of the placenta as an intimate apposition or fusion of maternal and fetal tissues for sustenance and physiological exchange, then we can argue that placentas have evolved throughout the animal kingdom. Mossman's definition encompasses the remarkable structural and developmental diversity of the placenta while recognizing the conservative nature of its primary function of physiological exchange. The placentas of all organisms must in some way deal with the same diversity of functions as the mammalian placenta. In spite of this diversity, little has been done to study the evolution of placentas as a feature of the life history. The comprehensive reviews of life-history evolution (Stearns 1992; Roff 1992, 2002) make no mention of placentation as a life-history strategy.

In this review we focus on the evolution of placentation by drawing on insights from a single fish family: the Poeciliidae (Hrbek et al. 2007, Rosen & Bailey 1963). The Poeciliidae represent a model system for studying the evolution of complexity, because the placenta evolved independently multiple times within the family. Moreover, this family contains closely related species that display remarkable variation in maternal provisioning ranging from species with no placenta to species with intermediate degrees of placentation to species with extreme postfertilization maternal provisioning. Such diversity greatly facilitates testing of hypotheses for the evolution of the Poeciliid placenta.

Oviparity: a reproductive mode in which organisms lay eggs

Viviparity: a reproductive mode in which organisms give birth to live young

Lecithotrophy: a form of maternal provisioning in which nutrients are provided by yolk allocated to the eggs prior to fertilization

Matrotrophy: a form of maternal provisioning in which nutrients are provided throughout embryonic development

Superfetation: a reproductive mode in which a female can carry multiple broods at different developmental stages

2. MODES OF MATERNAL PROVISIONING IN THE POECILIIDAE

The family Poeciliidae (Rosen & Bailey 1963) (subfamily Poeciliinae; Parenti 1981, Parenti & Rauchenberger 1989) is a widespread group of small Neotropical fish that consist of approximately 220 species in 28 genera (Lucinda & Reis 2005). The Poeciliidae is one of the most extensively studied fish families, and its representatives, which include the well-known guppy (*Poecilia reticulata*), mollies (*Mollienesia* spp.), swordtails (*Xiphophorus* spp.), and mosquito fish (*Gambusia* spp.), are often used as model systems in evolutionary biology theory. One of the reasons why Poeciliids are so appealing to evolutionary biologists is their short generation times and ease of culture, as well as the staggering diversity in reproductive adaptations found in this family, which include internal fertilization, oviparity, clonality, viviparity, lecithotrophy, matrotrophy, and superfetation (Meffe & Snelson 1989).

2.1 From Oviparity to Viviparity

Live-bearing is a taxonomically widespread phenomenon that has evolved independently many times in distantly related taxonomic groups, including plants (Elmqvist & Cox 1996), invertebrates [e.g., bivalves (Cooley & Foighil 2000), gastropods (Köhler et al. 2004), echinoderms (Hart et al. 1997), insects (Meier et al. 1999), onychophorans (Havel et al. 1989)] and virtually all classes of vertebrates (fish, amphibians, reptiles, marsupials, mammals) (Dulvy & Reynolds 1997, Blackburn 1992) except birds (Dunbrack & Ramsay 1989). Egg-laying is assumed to be the ancestral state from which live-bearing has evolved, though different lineages may have gone through (slightly) different evolutionary scenarios to arrive at the final reproductive stage of live-bearing (e.g.,

Matrotrophy index: a quantifiable measure of prenatal maternal provisioning, defined as the dry mass of an offspring at birth divided by the dry mass of the egg at fertilization

Blackburn 1992, 1995; Dunbrack & Ramsay 1989; Meier et al. 1999; Qualls et al. 1997; Reynolds et al. 2002; Wourms 1981). In fish, initial steps in the evolution of live-bearing from egg-laying are believed to have involved a shift from external to internal fertilization, followed by an increased retention of eggs and developing embryos within the female reproductive system (coinciding with morphological and physiological adaptations of the ovary or oviduct in order for it to function as a site of gestation) and a reduction in the thickness of the egg envelope to facilitate female-embryo interactions (Wourms & Lombardi 1992, Wourms et al. 1988).

2.2 From Lecithotrophy to Placentotrophy

The evolution of live-bearing was accompanied by several trophic adaptations to accommodate embryonic development within the female's reproductive tract. Lecithotrophy (that is, yolk-provisioning) is considered to be the primitive trophic mode of live-bearing in which all resources are allocated to the eggs during oogenesis prior to fertilization, essentially the way egg-layers provision their eggs. From this primitive mode of reproduction, live-bearing fish have independently evolved a reduction in prefertilization provisioning coinciding with an array of trophic specializations for the postfertilization transfer of nutrients from the mother to developing young (see Wourms 1981, Wourms et al. 1988). These latter modes of reproduction are collectively referred to as matrotrophy (that is, provisioned by the mother). In this review we focus on the evolution of the placenta, which is one mechanism of matrotrophy.

Within fishes, the first vertebrates to evolve a placenta (Long et al. 2008), there have been several independent origins of placentation, and whereas different lineages may have evolved placentas that are structurally very different from one another, they all fulfill similar functions and are derived from the same preexisting embryonic and maternal tissues (Hamlett 1989, Schindler & Hamlett 1993, Wourms et al. 1988). Today, placentas are found in several families of cartilaginous (e.g., Carcharhinidae, Sphyrnidae) and bony fish (e.g., Anablepidae, Clinidae, Embiotocidae, Goodeidae, Labrisomidae, Poeciliidae, Zenarchopteridae) (Hamlett 1989; Reznick et al. 2002, 2007b; Wourms 1981; Wourms et al. 1988).

Within the Poeciliidae, the fish family with the largest number of viviparous members, there is a near perfect continuum of pre- versus postfertilization maternal provisioning—following a left-skewed leptokurtic distribution—ranging from strict lecithotrophy to extreme matrotrophy (**Figure 1**; Pires 2007, Reznick et al. 2002). The matrotrophy index (MI), defined as the dry weight of neonates at birth divided by the dry weight of eggs at fertilization, has been invoked to assess a species' place in this trophic spectrum. The far left of this continuum (**Figure 1**) represents the lecithotrophic species, which allocate all maternal resources to their offspring prior to fertilization. These species typically display a considerable loss of dry weight (approximately 25–55%), associated with the metabolic costs of embryonic development ($MI < 0.75$; Reznick et al. 2002, Wourms 1981). As we move farther to the right through this continuum (**Figure 1**), species start to show a limited uptake of nutrients during embryo development. In some species, this uptake is so limited that it can only be studied by means of radioactively or fluorescently labeled tracers or amino acids (Demarias & Oldis 2005; Marsh-Matthews et al. 2001, 2005). This transitional zone between lecithotrophy and matrotrophy has been referred to as incipient matrotrophy (Blackburn 1992; Demarias & Oldis 2005; Marsh-Matthews et al. 2001, 2005). As the degree of postfertilization maternal provisioning increases, the loss of dry weight caused by metabolic activity during development is gradually compensated for, leading to matrotrophy indices >1. Some matrotrophic species have a very high degree of postfertilization maternal provisioning, such as *Micropoecilia branneri* ($MI = 63–99$; Pires 2007) and *Poeciliopsis retropinna* ($MI = 117$; Reznick et al. 2002).

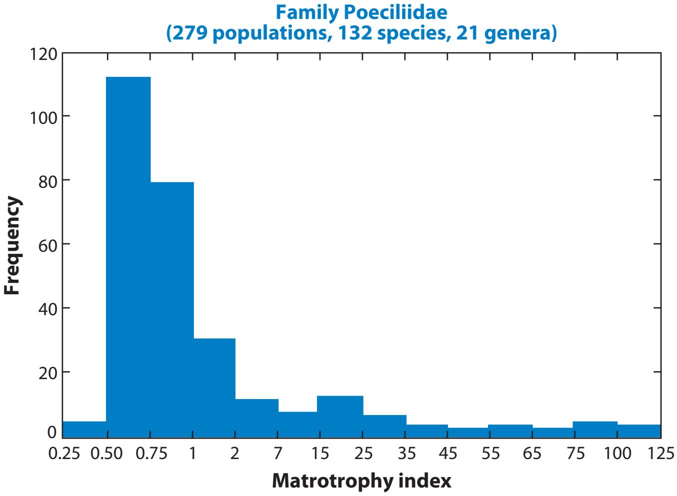

Figure 1

Frequency histogram of the matrotrophy index (MI) in the family Poeciliidae, showing a continuous, left-skewed distribution of the degree of pre- versus postfertilization maternal provisioning, ranging from strict lecithotrophy (*left* in the continuum) to extreme placentotrophy (*far right* of the continuum).

Surprisingly few studies have looked at the anatomical details of maternal-fetal interactions during embryonic development underlying these different modes of maternal provisioning (Grove & Wourms 1991, 1994; Jollie & Jollie 1964; Turner 1940a). Fertilization occurs within the ovarian follicle, and the embryos are retained within the follicle during development. Lecithotrophic poeciliids are nourished by a yolk reserve that surrounds the developing embryo (Turner 1940a). The external surfaces of the yolk sac are highly vascularized and function both as a respiratory organ and as a transportation system of nutrients from the yolk sac to the embryo. The unspecialized follicular wall of lecithotrophs is very thin and plays no role in maternal provisioning (Jollie & Jollie 1964, Turner 1940a).

Matrotrophic species, by contrast, have a number of anatomical adaptations to mediate postfertilization provisioning. The two genera studied so far (*Heterandria* and *Poeciliopsis*) show that maternal-embryo nutrient transfer in the Poeciliidae occurs via a structure referred to as a follicular placenta, which is formed by the close apposition of the embryonic absorptive tissues to the maternal follicular epithelium. Interestingly, detailed studies suggest the existence of distinctly different anatomical features associated with placentation in both of these lineages. The absorptive tissues of embryos of *Heterandria formosa* consist of the highly vascularized surfaces of the greatly enlarged pericardial and reduced yolk sacs, which cover the head of the embryo entirely in a hood-like manner (Turner 1940a). In addition, the surface epithelium of the embryo possesses features characteristic of absorptive epithelia (e.g., microvilli, complex system of vescicles, Golgi complexes, and an extensive rough endoplasmatic reticulum), suggesting that the entire embryonic surface may play a role in nutrient acquisition of *H. formosa* (Grove & Wourms 1991). By contrast, in placental *Poeciliopsis* spp. the ventral portion of the pericardial sac is greatly enlarged, whereas the lateral portions remain poorly developed, leading to the formation of a large, highly vascularized belly sac (Turner 1940a). Whether the embryos of *Poeciliopsis* spp. have an absorptive surface epithelium on their bodies, comparable to those found on *H. formosa*, remains to be investigated. The follicular epithelium, in both genera, features specialized adaptations that aid in the maternal-embryo nutrient transfer, such as a thick, vascularized inner follicle wall with dense microvilli and specialized cytoplasmic organelles (Grove & Wourms 1994, Turner 1940a).

Placentotrophy: a specialized form of matrotrophy in which nutrient transfer occurs via a placenta

Far too little work has been done on the functional morphology of the Poeciliid placenta. There is clearly a need for more detailed comparative studies that include members from throughout the family to determine the extent of anatomical variation of the placenta. Nevertheless, the work done so far at least shows (*a*) that the follicular placenta of the Poeciliidae satisfies Mossman's (1937, 1987) definition of a placenta, (*b*) that the extent of postfertilization maternal provisioning appears to be correlated with the elaborateness of the placenta (Turner 1940a), and (*c*) that the anatomical adaptations of placentation vary considerably among Poeciliid species (Grove & Wourms 1991, 1994; Turner 1940a).

2.3 Superfetation

The Poeciliidae display a second variation on the theme of live-bearing that may bear some relationship to the evolution of the placenta. Superfetation refers to the presence of multiple broods at different developmental stages in a single female (Turner 1937, 1940b). Species that have superfetation tend to produce smaller litters of young and do so more often. This phenomenon is widespread within the family Poeciliidae (Reznick & Miles 1989; Reznick et al. 2007a; Scrimshaw 1944b; Thibault & Schultz 1978; Turner 1937, 1940b) and has been observed in other families such as the Clinidae (Gunn & Thresher 1991) and Zenarchopteridae (Reznick et al. 2007b). This trait is of interest because there is a close association between superfetation and matrotrophy, which suggests that the origin of one of these traits may facilitate the evolution of the other (Reznick & Miles 1989, Reznick et al. 2007b, Thibault & Schultz 1978).

3. TAXONOMIC DISTRIBUTION OF REPRODUCTIVE MODES IN THE POECILIIDAE

All Poeciliid species, save for *Tomeurus gracilis*, are obligate live-bearers. Because the egg-laying *T. gracilis* possesses what is generally considered to be the more primitive life history, it was long considered to be the ancestral species in the family (Lucinda & Reis 2005, Parenti 1981, Rosen & Bailey 1963). Recently, however, Hrbek et al. (2007) published a well-resolved DNA-based phylogenetic tree of the Poecillidae, which instead suggests that *Xenodexia ctenolepis* is basal to the family (**Figure 2**). *X. ctenolepis* is live-bearing and has a moderate degree of matrotrophy (MI of 3.5–4) and superfetation (Reznick et al. 2007a). The remarkable conclusion that *X. ctenolepis* is the sister taxon to the remainder of the subfamily gives rise to two opposing hypotheses for the evolution of live-bearing in the basal branches of the phylogeny: One hypothesis is that live-bearing, superfetation, and placentotrophy were present in the common ancestor of the family and that some or all of these traits were lost in descendent lineages and later re-evolved in some lineages (Hrbek et al. 2007, Reznick et al. 2007a). An alternative hypothesis is that the common ancestor was an egg-layer, like *Tomeurus*. If so, then *X. ctenolepis* represents an independent origin of live-bearing, superfetation, and placentotrophy (Reznick et al. 2007a).

In cartilaginous fishes and reptiles, the evolutionary transition from live-bearing to egg-laying appears to occur far less frequently than the reverse (Dulvy & Reynolds 1997, Lee & Shine 1998), and in bony fishes there is no evidence for any such reversals (Goodwin et al. 2002, Mank & Avise 2005). Thus, live-bearing appears to be much more easily gained than lost (Lee & Shine 1998). Though certainly not conclusive, these findings argue in favor of the second hypothesis.

Matrotrophy is present in at least 11 lineages within the family (**Figure 2**; not all origins are shown here), including *H. formosa* (Scrimshaw 1944a), the genus *Poeciliopsis* [3 independent

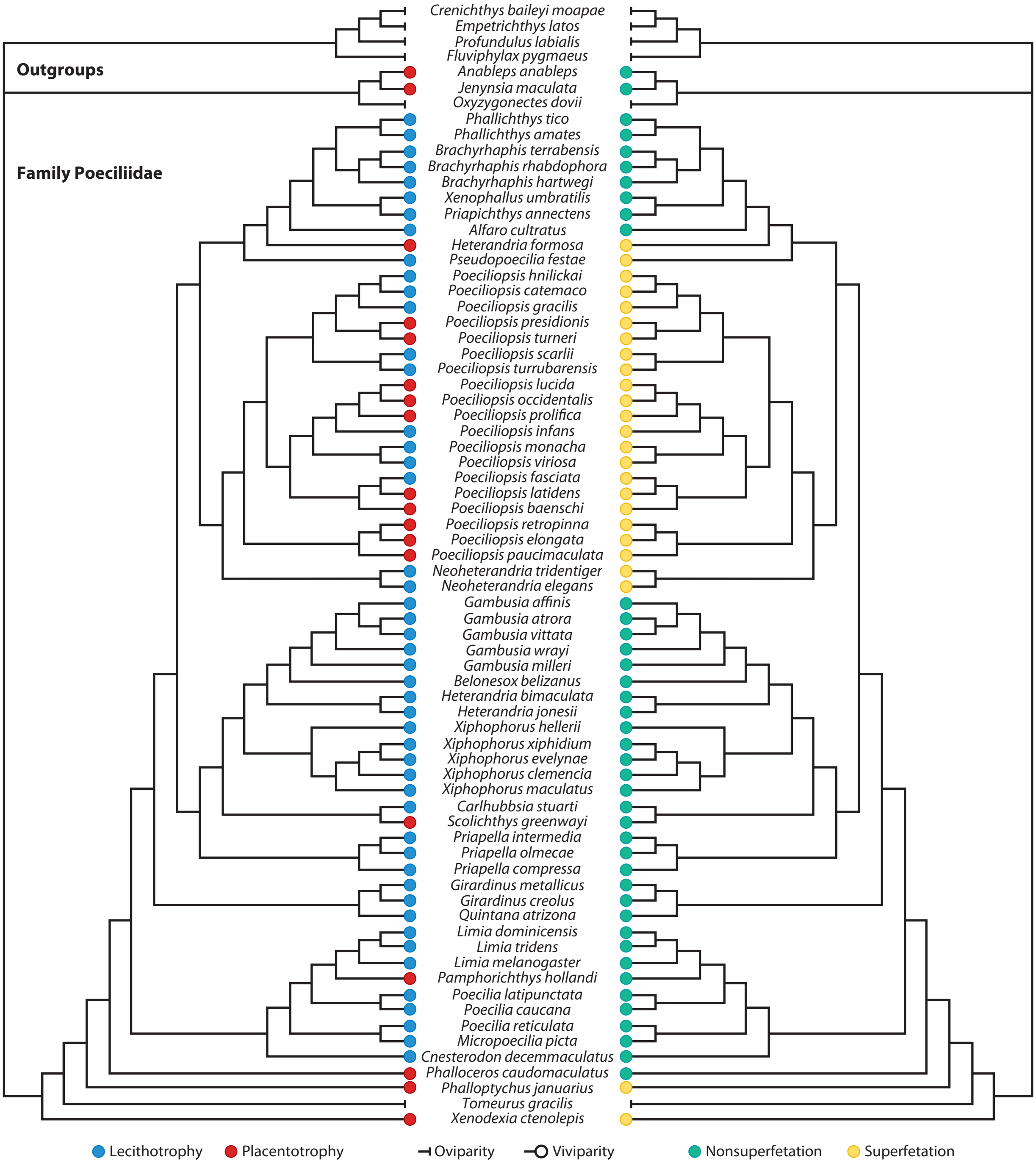

Figure 2

Phylogenetic tree showing the taxonomic distribution of reproductive modes in the family Poeciliidae (redrawn after Hrbek et al. 2007, Reznick et al. 2002).

origins (Reznick et al. 2002)], *Scolichthys*, *Poecilia* [3 apparently independent origins in the subgenera *Micropoecilia*, *Mollienesia*, and *Pamphorichthys*, respectively (Pires 2007, Reznick et al. unpublished)], *Girardinus* (Reznick et al. unpublished), *Phalloptychus*, and *Phalloceros* (Arias & Reznick 2000, Reznick et al. unpublished). It has been shown that the matrotrophy index is a stable feature of the life history that persists through multiple generations in a common laboratory environment, which argues that there is a genetic basis to this diversity (Pires 2007, Pires et al. 2007). In a few cases, lecithotrophic species may be capable of a small degree of facultative matrotrophy, so that MI can range between 0.6 and 1.0 (Demarias & Oldis 2005; Trexler 1985, 1997). This complexity lends itself to a diversity of evolutionary scenarios that we will soon address by combining our large life-history data set with an improved molecular phylogeny of the family that includes representatives from throughout the order Cyprinodontiformes. For now, these patterns at least argue that there is considerable evolutionary lability in maternal provisioning within this family and that we can often find closely related species that have very different patterns of maternal provisioning.

Superfetation also evolved more than once in the family Poeciliidae and appears to be closely linked to the evolution of the placenta, because most species are either matrotrophic with superfetation or lecithotrophic without superfetation. There are, however, notable exceptions to this rule, indicating that these two reproductive traits can evolve independently from one another. For example, *Girardinus denticulatus*, *Phalloceros caudiomaculatus*, and *Scolichthys greenwayi* are weakly matrotrophic ($MI = 1–2$), yet lack superfetation. *Priapichthys festae*, *Neoheterandria tridentiger*, *Neoheterandria elgans*, and several *Poeciliopsis* spp. are lecithotrophic with superfetation (Arias & Reznick 2000, Reznick & Miles 1989). Similar correlations between matrotrophy and superfetation are found in the Clinidae and Zenachopteridae (Reznick et al. 2007b).

4. HYPOTHESES ON THE EVOLUTION OF THE PLACENTA

There are two categories of hypotheses for why the placenta evolved: adaptive hypotheses, which propose that the placenta evolved as an adaptation to environmental or ecological pressures, and conflict hypotheses, which posit that the placenta evolved as a result of conflict, driving evolutionary change via antagonistic coevolution. Here we will discuss the two main adaptive hypotheses and the conflict hypothesis on the evolution of the placenta (**Figure 3**). Although we specifically focus on the evolution of placentation in fish, these hypotheses are likely to be applicable to other taxa as well.

4.1. Adaptive Hypotheses

4.1.1 Locomotor costs hypothesis. Live-bearing has been shown to impose severe locomotory costs to pregnant females in a variety of taxa, including invertebrates (Shaffer & Formanowicz 1996), fishes (Ghalambor et al. 2004, Plaut 2002), reptiles (Miles et al. 2000, Shine 1980), and mammals (Wu et al. 2004). During pregnancy, developing embryos show an increase in mass and volume, leading to an increase in female reproductive allocation, defined as the proportion of female wet mass that consists of developing embryos. The weight gain during pregnancy associated with an increase in reproductive allocation can lead to a decreased fast-start escape response as well as a decrease in sustained locomotory performance, because the same amount of muscular tissue has to accelerate and then maintain a steady velocity of a larger body mass. In addition, an increase in volume will lead to a less streamlined female body shape, both directly and indirectly affecting locomotory performance owing to reduced axial flexibility (and hence maneuverability) as well as increased drag forces on the female body as a result of an increased frontal area and surface-to-volume ratio (Ghalambor et al. 2004, Webb 1975).

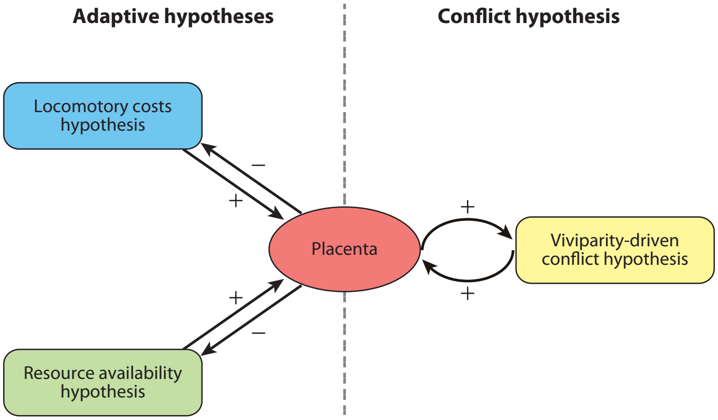

Figure 3

Overview of the main hypotheses on the evolution of the placenta in Poeciliid fish (see text for details). The primary distinction between the adaptive hypotheses (*left*) and the conflict hypothesis (*right*) is the underlying evolutionary mechanisms: In the two adaptive hypotheses, the evolution of the placenta (indicated by the + signs) is driven by specific types of selection, but as the placenta evolves, the strength of selection declines (indicated by the – signs). The conflict hypothesis, by contrast, proposes that the evolution of the placenta is the result of a self-reinforcing process of adaptation-counteradaptation between maternal and fetal tissues driven by the parent-offspring conflict (Crespi & Semeniuk 2004, Haig 1993, Rice & Holland 1997, Zeh & Zeh 2000). These three, nonmutually exclusive, hypotheses may play different roles during the evolution of the placenta; ecological selection may initiate the evolution of live-bearing and then the placenta, but once a rudimentary placenta evolves an intraspecific Red Queen process of perpetual antagonistic coevolution may accelerate evolution, leading to rapid diversification (Crespi & Semeniuk 2004, Haig 1993).

In fishes, pregnancy has been shown to detrimentally affect both escape response and sustained swimming (Ghalambor et al. 2004, Plaut 2002). A shift from lecithotrophy to matrotrophy should reduce reproductive allocation, because lecithotrophic females produce large eggs, committing all maternal resources prior to fertilization, whereas matrotrophic females start with relatively small eggs and provide resources throughout their pregnancy (**Figure 4*a***). Matrotrophic females are therefore likely to suffer less-impaired escape responses and hence a have higher survival rate and higher aerobic performances (e.g., prolonged swimming performance) compared to lecithotrophic females. This comparison assumes that female size, degree of superfetation, and offspring number, size, and precociousness at birth are the same for each of the two modes of reproduction. Because the difference in reproductive burden between matrotrophs and lecithotrophs is largest during the early gestational stages (**Figure 4*a***), this selective advantage in swimming performance should, in theory, be highest during the early stages of pregnancy and then diminish over the course of pregnancy. Superfetation can, either by itself or in concert with matrotrophy, reduce reproductive allocation (**Figure 4*b***), thereby providing an additional selective advantage in environments where fitness is linked to locomotion, such as high-predation environments or habitats with high water-flow velocity (Thibault & Schultz 1978, Reznick & Miles 1989).

4.1.2 Resource-availability hypothesis. Trexler (1997) suggested that another selective advantage of matrotrophy over lecithotrophy might be the ability to enhance fecundity when resources are abundant. Assuming that the total cost per neonate is comparable between the two modes of provisioning, Trexler (1997) argued that facultative matrotrophy allows females to increase brood size if sufficient resources are available to complete development of a brood. In lecithotrophic species, brood size is constrained at the time of egg fertilization by the requirement for all

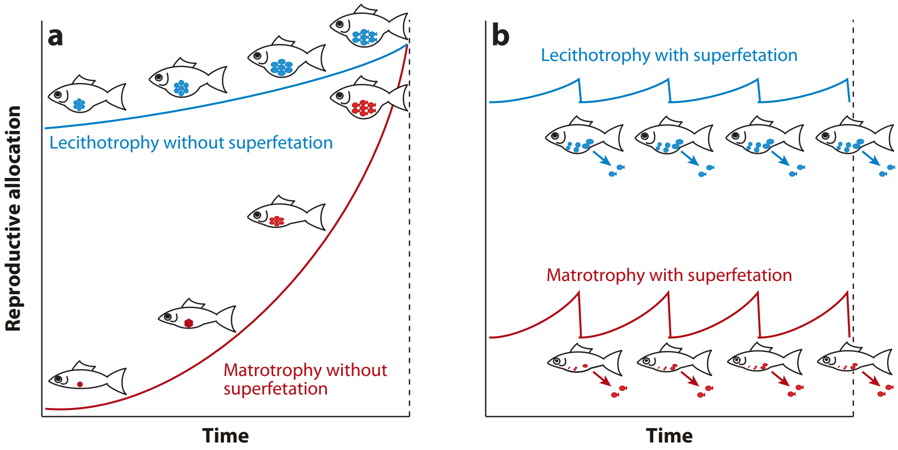

Figure 4

Predicted patterns of reproductive allocation (defined as the proportion of female wet mass allocated to reproduction) in live-bearing fishes with different modes of reproduction. (*a*) Lecithotrophic species produce large eggs, providing all maternal resources in the form of yolk prior to fertilization. The increase in reproductive burden during embryonic development is solely due to water uptake (*blue*). Matrotrophic species produce tiny eggs with little yolk and provide most resources during embryonic development. The sharp increase in reproductive allocation is due to both postfertilization maternal provisioning and water uptake (*red*). Note that matrotrophic species will have a lower reproductive burden during their entire pregnancy than lecithotrophic species if female size, offspring number, offspring size, and precociousness at birth are the same for both reproductive modes. (*b*) Superfetation increases the frequency of offspring production [often associated with a reduced litter size (Reznick & Miles 1989)] and reduces the amplitude around the mean reproductive allocation, ultimately reducing the maximum reproductive burden without affecting overall fecundity compared to nonsuperfetatious species (both in lecithotrophs and matrotrophs).

resources up front and the larger size of fully provisioned ova. With matrotrophy, more, smaller ova can be fertilized.

Trexler & DeAngelis (2003) developed the first theoretical model to address the questions of how and why matrotrophy evolved. If sufficient resources can be gleaned from the environment during their development, then a matrotrophic individual that initiated more, smaller offspring can produce a larger brood than a similar-sized lecithotrophic female. Matrotrophy could become a disadvantage if sufficient resources are not available to sustain developing offspring throughout development. Trexler & DeAngelis (2003) thus approached matrotrophy as a life-history adaptation and introduced a cost-benefit analysis that identified the set of conditions that favor a matrotrophic over a lecithotrophic strategy. Their models predict that matrotrophy is likely to be favored over lecithotrophy (*a*) when resource availability is predictable and high and (*b*) if the female has the ability to abort and resorb embryos and to reallocate their energy if insufficient resources are available to sustain all offspring.

4.2 Conflict Hypotheses

It has long been recognized that the placenta is one of the most morphologically diverse organs in the animal kingdom (Mossman 1937). This is true not only for mammals (Faber et al. 1992; Mossman 1937, 1987) and reptiles (Thompson & Speake 2006), but also for fishes (Wourms 1981, Wourms et al. 1988). Even within single fish families, such as the Poeciliidae and Zenarchopteridae, there is considerable variation among closely related species if one considers the degree of postfertilization maternal provisioning as a proxy for placental complexity (Pires 2007; Reznick et al. 2002, 2007b; Turner 1940a). This diversity of the animal placenta compared to other, more conserved, organs in the animal body plan argues for a very rapid evolutionary divergence in placental structure (Crespi & Semeniuk 2004), more rapid, in fact, than might be expected from a mere adaptive response to a particular agent of selection (Crespi & Semeniuk 2004, Rice & Holland 1997, Zeh & Zeh 2000). The conflict of interest between mother and developing embryos over the degree of maternal provisioning [parent-offspring conflict (Trivers 1974)] is thought to give rise to antagonistic coevolution at the site where maternal and fetal tissues meet, driving the evolution of ever more diverse and complex placentas (Crespi & Semeniuk 2004, Haig 1993).

Polyandry: a reproductive mode in which a female mates with multiple males

An underlying assumption of the parent-offspring conflict theory is that offspring are not merely passive recipients of parental resources, but that both parents and offspring can actively influence the transfer of resources (Trivers 1974). The theory posits that mothers, who have an equal degree of relatedness to any of their offspring ($r = 1/2$), will benefit most by providing as many offspring as possible with sufficient resources to ensure their survival. Offspring, on the other hand, will demand more than merely sufficient resources, because any given offspring is more closely related to itself ($r = 1$) than to its full siblings ($r = 1/2$) or half-siblings ($r = 1/4$). This ability of offspring to manipulate the transfer of resources is mediated by gene expression and can take place during the prenatal and/or postnatal period in an offspring's life. During these two periods, offspring employ strikingly different strategies to induce parents to increase their investment (Trivers 1974), using mainly chemical signals [e.g., hormones (Haig 1993)] during the prenatal period and behavioral signals (e.g., loud begging or crying) during the postnatal period.

The importance of parent-offspring conflict as an evolutionary force is largely determined by the reproductive mode of the species (Crespi & Semeniuk 2004, Zeh & Zeh 2000). If parental investment solely occurs prior to fertilization, such as in egg-laying (e.g., turtles) or strictly lecithotrophic live-bearing species that have no postnatal parental investment, then the parent-offspring conflict is unlikely to occur because offspring will have no opportunity to influence parental investment. If, however, parental investment continues after fertilization, coinciding with a period in which offspring are in the position to influence parental investment, then conflict may arise. This may occur either in egg-laying species with postnatal parental investment (potentially leading to postnatal conflict, e.g., birds), live-bearing, matrotrophic species without postnatal parental care [potentially leading to prenatal conflict, e.g., matrotrophic reptiles (Blackburn 1992, 1995)], or finally, live-bearing, matrotrophic species with postnatal care, which may have conflict during both the pre- and postnatal period [e.g., monotremes, marsupials and eutherian mammals (Haig 1993, Wilkins & Haig 2003)].

The potential for parent-offspring conflict is predicted to be most intense during the prenatal period in placental animals with a high degree of polyandry because (*a*) live-bearing offers longer contact between mother and developing embryos than egg-laying, (*b*) placentation allows for prolonged, intimate physiological interactions between mother and fetus, and (*c*) a high degree of polyandry promotes genomic conflict because of the reduced relatedness among littermates (Crespi & Semeniuk 2004, Haig 1993, Trivers 1974, Zeh & Zeh 2000). Here, the placenta acts as a battlefront where maternal and embryonic tissues meet and where the parent-offspring conflict comes to its full expression, because it is the frontier where mothers allocate and offspring acquire resources. The resulting evolutionary dynamics of perpetual adaptation and counter-adaptation between the fetus' trying to extract more resources than would be optimal for mothers to give and mother's regulation of the allocation of resources to embryos (Haig 1993) is hypothesized to be the driving force behind a continuous rapid divergence in the genomic, developmental, morphological, and physiological details of the placenta (Crespi & Semeniuk 2004, Haig 1993, Rice & Holland 1997, Zeh & Zeh 2000).

Crespi & Semeniuk (2004) carried this argument a step further. They argued that the first opportunity for conflict may arise early in the evolutionary shift from egg-laying to live-bearing because of the intimate contact between mother and embryo that is associated first with the retention of developing embryos before the egg is laid, then prolonged by the evolution of livebearing. The emergence of such conflict may, in turn, initiate an antagonistic coevolution between maternal and offspring traits associated with nutrient acquisition, ultimately leading to the accelerated evolution of the placenta. It is as if the evolution of placentation were like balancing a rock at the apex of a hill—once the rock is displaced, its acceleration downhill is inevitable. The evolution of an elaborate placenta is, thus, the product of the persistent conflict that began simply because egg retention created the opportunity for the embryo to make inroads on the mother's resources.

5. EMPIRICAL EVIDENCE FROM THE POECILIIDAE

5.1 Locomotor Costs Hypothesis

Several studies provide circumstantial evidence supporting the idea that matrotrophy among Poeciliids could have evolved as an adaptive response to ecological or environment pressures by reducing reproductive allocation and, consequently, enhancing swimming performance. Pregnant guppies (*Poecilia reticulata*) and mosquitofish (*Gambusia affinis*) are known to show a progressive increase in wet reproductive allotment over the course of gestation, leading to a reduction of their critical swimming speed and maximum velocity, mean rotational velocity, and distance traveled during a fast-start escape response (Ghalambor et al. 2004, Plaut 2002). A reduction in these swimming-performance variables increases predation risk in guppies exposed to a natural predator (Walker et al. 2005), suggesting that during pregnancy females may become increasingly vulnerable to predation. The finding that an increased reproductive allocation during pregnancy may have detrimental effects on swimming performance provides a compelling argument for the idea that matrotrophy, if associated with a smaller average reproductive investment, should confer a selective advantage to live-bearing fish, particularly during the early stages of pregnancy. What remains to be done is comparative experimental studies of the impact of pregnancy on performance in closely related lecithotrophic and matrotrophic species.

Superfetation is another reproductive mode that, in theory, could enhance swimming performance by reducing the reproductive burden of the female without decreasing overall fecundity (Reznick & Miles 1989, Thibault & Schultz 1978). Zúñiga-Vega et al. (2007) found that *Poeciliopsis turrubarensis* inhabiting inland drainages characterized by higher water-flow velocities had a higher degree of superfetation and a more fusiform body morphology compared to populations inhabiting slow-moving lowland rivers, suggesting that superfetation may help offset the extra costs associated with life in a faster-moving medium. Comparative studies on swimming performance, ideally using closely related sister species that differ in the mode of reproduction, will provide the most rigorous method for future tests of the hypothesis that locomotory costs during pregnancy act as a driving force responsible for an evolutionary shift from lecithotrophy to matrotrophy. Now that we have identified such closely related species, such comparisons are possible.

5.2 Resource Allocation Hypothesis

The key prediction of the Trexler-DeAngelis hypothesis, that matrotrophy is advantageous over lecithotrophy in predictable high-resource environments, has yet to be tested. However, in line with the Trexler-DeAngelis hypothesis, laboratory experiments clearly show that matrotrophy is disadvantageous in unpredictable low-resource environments. First, lecithotrophic species

(*P. reticulata*, *Priapichthys festae*) have been found to respond to low or fluctuating food levels by producing larger offspring (Banet & Reznick 2008, Bashey 2006, Reznick & Yang 1993, Reznick et al. 1996). There is evidence that this response is an adaptive maternal effect on offspring development, assuming that the mother's environment is a good predictor of the environment to be experienced by the offspring, because larger offspring have a growth and survival advantage over small offspring when food is scarce (Bashey 2002). Females from matrotrophic species (*H. formosa*, *Poeciliopsis prolifica*) have the opposite response to low or fluctuating food availability; they produce smaller offspring that suffer a much more substantial loss of fitness than large offspring when food availability is low (Bashey 2002, Reznick & Yang 1993 and references therein).

Second, females of lecithotrophic species (*Poeciliopsis monacha*, *Poeciliopsis gracilis*) respond to low food availability by maintaining their body condition (lipid levels) but reducing their allocation to sacrificing reproduction, whereas females from closely related matrotrophic species (*Poeciliopsis prolifica*, *P. turneri*) maintain reproduction at the expense of their body condition—a potentially costly strategy in fluctuating or low-resource environments (Banet & Reznick, unpublished). Finally, and most importantly, matrotrophic females do not appear to be able to abort and resorb developing offspring under low-resource conditions (Banet & Reznick, unpublished; Meffe & Vrijenhoek 1981), a critical assumption of the Trexler-DeAngelis hypothesis (Trexler & DeAngelis 2003). Experimental studies revealed no evidence of higher abortion rates in matrotrophic and facultatively matrotrophic species (*P. prolifica*, *G. geiseri*) exposed to low levels of food availability (Banet & Reznick 2008, Marsh-Matthews & Deaton 2006, Meffe & Vrijenhoek 1981), nor any differences in abortion rates between lecithotrophic (*P. monacha*, *P. gracilis*, *P. reticulata*) and matrotrophic (*P. prolifica*, *P. turneri*) species (Banet and Reznick, unpublished; Meffe & Vrijenhoek 1981). The notion that matrotrophic females are capable of recycling the energy from aborted embryos has been persistent in the literature (Blackburn et al. 2003, and references therein, Meffe & Vrijenhoek 1981), but studies on fishes and reptiles have consistently failed to support this idea (Banet & Reznick 2008, Blackburn et al. 2003, Meffe & Vrijenhoek 1981, Trexler 1997).

In conclusion, no direct evidence is available to support the hypothesis that matrotrophy is advantageous over lecithotrophy under high-food conditions. Many independent studies, conversely, point to a selective disadvantage of a matrotrophic strategy under low and unpredictable resource conditions, consistent with some of the predictions of the Trexler-DeAngelis hypothesis. Moreover, there is no support to the idea that matrotrophic females can reclaim resources from aborted embryos, one of the key assumptions of the Trexler-DeAngelis models. It thus seems clear that the hypothetical conditions under which matrotrophy is advantageous must be refined and that, under any new scenario, matrotrophy could only evolve under stable, high-food conditions.

5.3 Viviparity-Driven Conflict Hypothesis

An underlying assumption of Trexler & DeAngelis' (2003) resource availability hypothesis is that postfertilization resource transfer from mother to embryo is a one-way interaction that is unilaterally controlled by the mother. Empirical evidence, however, argues more for a two-way interaction, in which mother and offspring both have an influence over the degree of resource provisioning. When matrotrophic females experience low-food conditions, developing embryos continue to extract nutrients from the mother, apparently at her expense, given her deteriorating body condition. Moreover, the mother remains tethered to her offspring, unable to abort them at will and resorb some of their resources (Banet & Reznick 2008). On the other hand, food-deprived mothers are not entirely defenseless and are able to counter this unrelenting demand by reducing the total amount of transferred nutrients, leading to a smaller offspring size at birth (Banet & Reznick 2008, Pires et al. 2007, Reznick et al. 1996).

This dual influence over postfertilization resource provisioning during pregnancy may give rise to a prenatal parent-offspring conflict in live-bearing matrotrophic species (Crespi & Semeniuk 2004, Trivers 1974), a theory that has been coined the viviparity-driven conflict hypothesis (Zeh & Zeh 2000, 2008). Zeh & Zeh (2000) proposed a number of testable hypotheses to, albeit indirectly, assess the presence of parent-offspring conflict in species: The first is that the parent-offspring conflict should increase as the rate of multiple paternity within populations increases, selecting for a more aggressive gene expression related to resource transfer in both the developing offspring (which will try to increase resource transfer) and the mothers (who will aim to suppress a disproportionate demand). The second is that this perpetual antagonistic coevolution between mother and offspring, driven by the parent-offspring conflict, should accelerate the rate of postzygotic isolation between populations, particularly between populations that differ markedly in their level of polyandry (Zeh & Zeh 2000, 2008).

Schrader & Travis (2008) were the first to provide compelling evidence of a parent-offspring conflict in the Poeciliidae by testing the predictions of the viviparity-driven conflict hypothesis. They conducted laboratory crosses between *H. formosa*, a highly matrotrophic viviparous species, derived from two wild populations: Trout Pond, a predominantly monandrous population, and Wacissa River, a highly polyandrous population. Control crosses between males and females from the same population and the cross of a female from the polyandrous population with a male from the monandrous population all had low spontaneous abortion rates. In contrast, the cross between monandrous females from the Trout Pond population and polyandrous males from the Wacissa River had a fivefold higher abortion rate, indicating an asymmetric postzygotic isolation between populations. Schrader & Travis (2008) argued that the fast rate with which this asymmetrical hybrid inviability evolved between Trout Pond and Wacissa River populations of this viviparous species (which became separated 20,000–100,000 years ago), compared to the relatively slow rate with which it evolved in oviparous fish species (∼3.5–25 million years), supports the idea that prenatal parent-offspring conflict accelerates the evolution of postzygotic reproductive isolation in viviparous matrotrophic species.

The conflict hypothesis makes three other critical predictions (Crespi & Semeniuk 2004) that are supported by findings from the family Poeciliidae: First is the presence, and high interspecific diversity, of placental structures that reflect a conflict of interest between mother and embryo over nutrient acquisition. This prediction is supported by studies showing a rapid diversification of the anatomical (Grove & Wourms 1991, 1994; Turner 1940a) and functional (Reznick et al. 2002; see also **Figure 1**) details of the Poeciliid placenta. Whereas an extensive, family-wide, comparative anatomical study in the family Poeciliidae is as yet lacking, studies of eutherian and metatherian mammals support the idea that many features of the placenta have evolved as (counter)adaptations between maternal and fetal tissues struggling over resources (e.g., Crespi & Semeniuk 2004, Elliot & Crespi 2006, Haig 1993).

Second is a positive association between placental complexity and maternal investment. Evidence for this prediction was provided by Turner (1940a), who showed that, for the genus *Poeciliopsis*, a progressive reduction of the yolk sac (indicating an increased dependency on placental provisioning) was indeed correlated with a progressive increase in the complexity of the follicular placenta (e.g., enlargement of the belly sac and portal system, and an increase in number and size of microvilli and vascularity of the follicle wall).

Third is a rapid evolution and positive selection on placentally expressed genes driven by the parent-offspring conflict. Evidence for this last prediction comes from a comparative study of complete protein-coding sequences of the *insulin-like growth factor II* (*IGF2*) gene in several Cyprinodontiform species (O'Neill et al. 2007). The kinship theory of genomic imprinting states that the conflict between maternal and paternal genomes expressed in the offspring mediating the maternal provisioning to the offspring is the driving force behind the evolution of genomic imprinting of *IGF2* and other genes in placental mammals (Haig 2000, Wilkins & Haig 2003). The high expression of *IGF2* in the placenta of *H. formosa* and *P. prolifica* suggests that this gene also plays a central role in the regulation of embryonic growth in Poecillids (Lawton et al. 2005, O'Neill et al. 2007). Despite the fact that *IGF2* is bi-allelically expressed in these two species (Lawton et al. 2005), this gene appears to be subject to strong and ongoing positive Darwinian selection, as evident from the high ratio of nonsynonymous mutation to silent mutations at protein codon sites [ω (dN/dS) > 1; O'Neill et al. 2007]. O'Neill et al. also found accelerated nonsynonymous substitution rates in lecithotrophic live-bearers, suggesting that, even in the absence of extensive postfertilization maternal provisioning, the mere retention of eggs within the mother confers limited abilities to developing offspring to manipulate their growth via gene expression. O'Neill et al. (2007) argued that the relatively strong positive directional selection found in placental Poeciliids is the result of antagonistic coevolution driven by a genomic conflict between parental genomes, the rise of which presumably coincides with the evolution of placentation.

6. CONCLUSIONS

We proposed to develop the placenta as a model for studying the evolution of complexity. The fish family Poeciliidae represents a particularly suitable model system for studying the evolution of placentation because the placenta evolved multiple times within the family and there is a remarkable diversity in morphology and degree of maternal provisioning among closely related species. The three main hypotheses for the evolution of the placenta outlined in this review are not mutually exclusive; each may have played a role at different stages of the evolutionary process. Whereas its initial evolution might have been driven by environmental or ecological pressures, its subsequent rapid diversification may have been greatly accelerated by conflict-driven antagonistic coevolution. These hypotheses, and many of their derivative hypotheses, still need further validation by means of more experimental work, some of which might follow along the research lines suggested below.

FUTURE ISSUES

1. There is a need for a much larger phylogeny and more detailed life-history descriptions not only of other members of the family Poeciliidae, but also of its closest live-bearing sister families within the order Cyprinodontiformes, to allow inferences about the patterns of evolution (sequence of evolution, directionality, evolutionary lability, reversibility) of important reproductive modes such as live-bearing, superfetation, and placentation.
2. A phylogeny will also provide an important tool for identifying close relatives that differ dramatically in the extent of maternal provisioning. The identification of such closely related species pairs is paramount to the further testing of both adaptive and conflict hypotheses about the evolution of the placenta in a comparative experimental framework.
3. The potential of the Poeciliidae as a model system for the study of placentas must further be realized through the comparative evolutionary study of the genetic basis for the anatomical and physiological changes that underlie an evolutionary shift to placentation in live-bearing species.
4. Finally, similar studies could be performed on the distantly related family of halfbeak fish (Zenarchopteridae), which are found in southeast Asia and appear to have evolved the same array of life histories (live-bearing, superfetation, and placentation) as the Neotropical Poeciliidae.

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