Poeciliid Research

Placenta and its implications in sexual selection - a minireview

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Abstract. Through this paper, the reproductive aspects of vertebrates that can significantly influence the evolution, speciation and diversification of the group is dicussed in the context of the current scientific literature. Poeciliid fish are an ideal group for sexual selection studies due to the fact that it contains all types of sexual selection: pre-copulatory sexual selection, post-copulatory pre-zygotic sexual selection and post-zygotic sexual selection. Many recent studies observed that the evolution of the placenta from a non-placental ancestor causes a shift of maternal investment from pre- to post- fertilization, making room for parent-offspring conflicts during the period of gestation. Investigations presented in literature show that the mother's supply of nutrients to the embryos through the placenta is correlated with the absence of elements like bright coloration of the skin or tegumentary productions, courtship behavior, and extreme ornamental display traits in males. In addition, researchers found that males of placental species have smaller bodies and more developed genitalia, which denotes a reproduction based on coercive or sneaky mating attempts and weak expression of female choice. They also pointed out that post-zygotic maternal provisioning is associated with a series of adaptations such as superfetation, polyandric females, and formation of temporally overlapping, mixed-paternity litters. We concluded that the type of reproduction of each species is a determining factor in a cascade of physiological, genetic and biochemical adaptations of vertebrate animals, and a decisive factor in the process of reproductive isolation and speciation. If interspecific hybridization is, in certain circumstances, considered an important factor for speciation, reproductive isolation is the most important factor contributing to speciation and vertebrate diversification.
Key Words: pre-zygotic, post-zygotic, polyandry, placental species, *Poeciliidae*.

Sexual Selection. Sexual selection is a particular case of natural selection (Bourne & Sammons 2008; Puts 2016). In this specific case, individuals of one biological sex choose mates of the other biological sex to mate with (intersexual selection), and compete with individuals of the same sex for access to individuals of the opposite sex (intrasexual selection) (Bourne & Watson 2009; Bolen 2019). These two subtypes of selection mean that some individuals have better reproductive success than others within a population, either due to the fact they are more attractive or developed a preference for more attractive mates to produce offspring with a better fitness (Miller et al 2010; Starr 2013; Vogt 2014).

Poeciliids and Sexual Selection. Poeciliid fish are an ideal group for sexual selection studies (Furness et al 2019; Lindholm & Breden 2002) due to the fact that within it we encounter all types of sexual selection. We find placental and non-placental species, both viviparous and ovoviviparous (Pollux et al 2014; Fleuren et al 2018; Jue et al 2018; Botha et al 2019; Olivera-Tlahuel et al 2019; Van Kruistum et al 2019).

Types of Sexual Selection. If we were to roughly divide the types of sexual selection by the time they appear, they would be: pre-copulatory sexual selection, post-copulatory pre-zygotic sexual selection, and post-zygotic sexual selection.

Pre-copulatory Sexual Selection. Pre-copulatory sexual selection has been observed in many vertebrate species that have elaborate courtship behavior (Cooney et al 2017; Cooney et al 2018). A well-known example is the guppy fish, *Poecilia reticulata* Peters, 1859 (Houde 1997; Lindholm & Breden 2002). In this species, in populations with medium or low predation risk, the female chooses its males for mating according to the intensity and pattern of the body ornamentation (Brooks & Endler 2001; Fitzpatrick & Servedio 2018). In species that present strong pre-copulatory sexual selection, the post-zygotic sexual selection is almost excluded (Pollux et al 2014).

Post-copulatory Pre-zygotic Sexual Selection. It can be also called Post-mating pre-zygotic. In the same species of guppy fish, it has been observed that the maternal organism favors male-producing sperm or female-producing sperm, according to the need of males or females in the population (Petrescu-Mag 2007). In a different study, the potential for ovarian fluid to act as a post-mating pre-zygotic barrier between two populations from different waters was observed in Trinidadian guppy (Devigili et al 2018).

Post-zygotic Sexual Selection. In the case of post-zygotic sexual selection, sexual selection expresses only after fertilization of female gametes. In species that present strong post-zygotic sexual selection, the pre-copulatory sexual selection is almost excluded (Pollux et al 2014).

Reproductive Isolation Allows for Speciation. Life diversity on Terra occurs because of several factors such as mutation, natural selection, and speciation, in one word, evolution (Xu & Shaw 2019). In order for species to evolve divergent into various lineages in the tree of life, populations of a taxon must be reproductively isolated from other taxa so that they are no longer able to create progeny in common (Uy et al 2018). Over time, mutations accumulate and new adaptations become visible, creating new species that come from a common ancestor (Scoville 2019).

Although interspecific hybridization is considered to have a critical role in evolution and speciation in certain situations (Oroian 2015; Vallejo-Marín & Hiscock 2016; Petrescu-Mag 2018), reproductive isolation contributes much more to species diversification and evolution (Devigili et al 2018). There are many different isolating mechanisms, some of them behavioral, others physiological, called pre-zygotic isolations, which prevent taxa from interbreeding with each other (Scoville 2019). If some different taxa do manage to produce interspecific hybrids, there are additional isolating mechanisms in place, called post-zygotic isolations, that ensure the hybrid offspring are not selected for by natural selection (Petrescu-Mag et al 2018; Scoville 2019).

Pre-zygotic Isolations. Since there are so many subtypes of pre-zygotic isolations, such as mechanical, gametic, ethological, habitat, and temporal isolations, it stands to reason that nature prefers these hybrids to not even form in the first place (Scoville 2019). Therefore, pre-zygotic isolation prevents, first of all, the occurrence of hybridization.

Post-zygotic Isolations. In cases when pre-zygotic isolation mechanisms fail to separate taxa, the post-zygotic isolations will take over and ensure that speciation is the preferred solution for evolution and this way diversity among species will continue to increase as natural selection acts (Petrescu-Mag et al 2018; Scoville 2019). In most cases of post-zygotic isolation, the hybrid progeny is produced, but it tends not to be viable, nor fertile (Petrescu-Mag et al 2018).

Both pre-zygotic isolations and post-zygotic isolations are necessary to keep taxa separate and on divergent paths of evolution. These types of reproductive isolations increase biological diversity on Earth and help drive evolution (Scoville 2019).

Placenta and its Implications in Sexual Selection. In animal groups like Batrachians and Aves, species pairs keep their ability to produce viable interspecific hybrids for tens of millions of years, longer than the mammalian group (Zeh & Zeh 2000). This is due to their reproductive mode. Both frogs and birds are species that lay eggs. In the case of viviparous species, the situation becomes more complicated.

Viviparity creates a post-fertilization arena for all sorts of conflicts, including genomic conflicts, which are missing in egg-laying species (Zeh & Zeh 2000). In viviparous taxa, conflict and competition can arise between sibling embryos in the womb, mother and embryos, and maternal and paternal genomes within individual embryos (Zeh & Zeh 2000). Cannibalism among shark species in the phase of embryo is widely known (Buddle et al 2019). Such kind of intra- and inter- genomic conflicts result in continual and long-term antagonistic coevolution, thereby accelerating interpopulation post-zygotic isolation (Zeh & Zeh 2000). Moreover, by creating intrapopulation genetic incompatibility, viviparity-driven conflict favors polyandry and reduces the potential for pre-copulatory divergence (Zeh & Zeh 2000; Pollux et al 2014).

For instance, mammalian diversification is known to be characterized by rapid evolution of incompatible feto-maternal interactions, asymmetrical post-zygotic isolation, F_2 hybrid enhancement, and disproportionate effects of genomically-imprinted genes (Zeh & Zeh 2000).

The evolution of the placenta from a non-placental ancestor causes a shift of maternal investment from pre- to post- fertilization, making room for parent-offspring conflicts during the period of gestation (Haig 1993; Zeh & Zeh 2000; Wilkins & Haig 2003; Crespi & Semeniuk 2004; Pollux et al 2014).

In fish species, specifically in the group of poeciliids, placentas have repeatedly evolved or been lost, producing diversity among closely related lineages in the presence or absence of placentation (Reznick et al 2002; Pollux et al 2009; Pollux et al 2014) (Figure 1).

In the same animal group, Poeciliidae, Pollux et al (2014) showed that the mother's supply of nutrients to the embryos through the placenta is correlated with the absence of elements like the bright coloration from the skin or tegumentary productions, courtship behavior, and extreme ornamental display traits in males. In addition, they found that males of placental species have smaller bodies and more developed genitalia, which favor sneak or coercive mating and, hence, avoids female choice (Matthews & Magurran 2000; Magellan & Kaiser 2010). They also pointed out that post-zygotic maternal provisioning is associated with a series of adaptations such as superfetation, polyandric females, and formation of temporally overlapping, mixed-paternity litters (Pollux et al 2014).

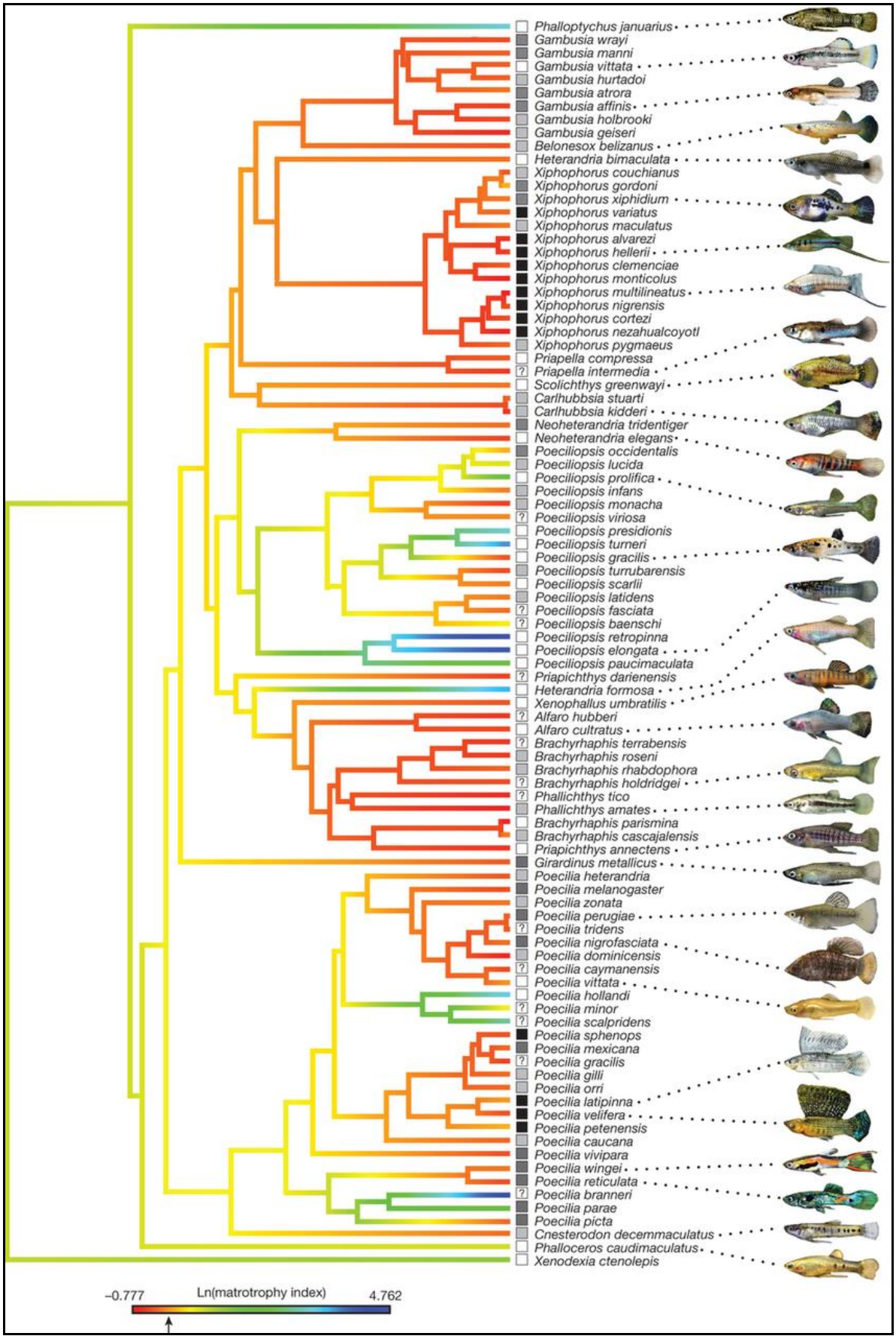

Figure 1. Phylogenetic tree showing relationships among 94 species of the fish family Poeciliidae (Reznick D. N., for details see the original source: Pollux et al 2014).

Conclusions. In order for species to divergently evolve into various lineages in the tree of life, populations of a taxon must be reproductively isolated from other taxa, so that they are no longer able to create progeny in common. There are various isolating mechanisms, some of them behavioral, others physiological, called pre-zygotic isolations, that prevent taxa from hybridization. If some different taxa do manage to produce interspecific hybrids, there are additional isolating mechanisms in place, called post-zygotic isolations, which ensure that the hybrid offspring are not obtained by natural selection. Poeciliid fish are an ideal group for sexual selection studies due to the fact that within it we encounter all types of sexual selection, namely: pre-copulatory sexual selection, post-copulatory pre-zygotic sexual selection, and post-zygotic sexual selection.

Many recent studies anticipated or observed that the evolution of the placenta from a non-placental ancestor causes a shift of maternal investment from pre- to post-fertilization, making room for parent-offspring conflicts during the period of gestation. In fish species, specifically in the group of poeciliids, placentas have repeatedly evolved or been lost, producing diversity among closely related lineages in the presence or absence of placentation. Investigations presented in literature showed that the mother's supply of nutrients to the embryos through the placenta is correlated with the absence of elements like: bright coloration of the skin or tegumentary productions, courtship behavior, and extreme ornamental display traits in males. In addition, researchers found that males of placental species have smaller bodies and more developed genitalia, which denotes a reproduction based on coercive or sneaky mating attempts and weak expression of female choice. They also pointed out that post-zygotic maternal provisioning is associated with a series of adaptations such as superfetation, polyandric females, and formation of temporally overlapping, mixed-paternity litters.

We can conclude that the type of reproduction of each species is a determining factor in a cascade of physiological, genetic and biochemical adaptations of vertebrate animals, and a decisive factor in the process of reproductive isolation and speciation. If interspecific hybridization is, in certain circumstances, considered an important factor for speciation, reproductive isolation is the most important contributing factor to speciation and vertebrate diversification.

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