Poeciliid Research

From gonochoric fish to parthenogenetic poeciliids: maximum investments in females

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Abstract. Through this paper we aim to highlight the evolutionary strategy of fish, through which some species try to maximize their investments, directing them to the female sex, which produces offspring. In contrast to females, males only contribute to the production of offspring and can sometimes be dispensable. Among these strategies we mention the hybridogenesis model of the genus *Poeciliopsis*, the Prussian carp gynogenesis model, and the extreme gynogenetic model of the Amazon molly, a species that is formed almost exclusively from females.
Key words: *Poeciliopsis monacha, Poecilia mexicana*, parthenogenesis, hybridogenesis, gynogenesis.

Introduction. We know from literature that most teleosts have gonochoristic reproduction, with gametes that develop on organisms of different sexes (Petrescu-Mag 2007a,b,c; Petrescu-Mag 2008; Mag & Petrescu 2006). The biggest advantage of gonochoristic reproduction is genetic variability, without which, the theory says, the species would become extinct after 10-100 generations (Heubel 2004). The lack of genetic variability exposes the species to the risk of extinction due to the reduced opportunities to adapt to the permanent change of environmental factors (Petrescu-Mag 2009; Petrescu-Mag et al 2020). Another factor which makes asexuate reproduction less sustainable is an accumulation of deleterious mutations and gene combinations that cannot be purged in the absence of recombination (Muller 1932, 1964; Maynard Smith 1978; Quattro et al 1992).

Through this paper we aim to highlight the evolutionary strategy of fish, through which some species try to maximize their investments, directing them to the female sex, which produces offspring directly.

The Gynogenetic Prussian Carp. There are fish species that have developed, in addition to sexual reproduction, a reproduction based on gynogenesis. This means that the reproduction of females is performed asexually, without the participation of the genetic material from the male gamete (Zhou et al 2000). Gynogenesis is different from classical parthenogenesis. In the case of gynogenetic fish, the mating ritual of these females takes place by using and depleting the males of other related and competing species. These males and their sperm are used only to trigger the cell division of eggs and for nothing else (Iacob & Petrescu-Mag 2008).

This is the case for females of Prussian carp *Carassius gibelio* (Bloch, 1782) (Zhou et al 2000), which enter the breeding season before the females of other species, such as common carp (*Cyprinus carpio* Linnaeus, 1758), and deplete the number of mating partners of common carp females (Iacob & Petrescu-Mag 2008). The offspring of *C. gibelio* females will most likely be female and rarely or never of hybrid nature. Therefore, the common carp makes a waste of semen without any evolutionary advantage. In contrast, the Prussian carp (Figure 1) makes poor investments in males; most of the investment of the species is made in the female sex, which lays eggs (Zhou et al 2000). This reproductive strategy is one of the reasons why *C. gibelio* has become the dominant species of temperate inland waters in Europe (Bud et al 2006). Although natural populations of Prussian carp consist of a minor but significant proportion (about 20%) of males, the Prussian carp possesses two reproductive modes, i.e., gynogenetic and gonochoristic reproduction (Zhou et al 2000).

Hybridogenesis in Poeciliopsis. There are species that have abandoned classical gonochoric reproduction and are now mainly based on hybridogenesis. It is interesting for this type of reproduction that the resulting offspring are hybrid, but the genetic material of paternal origin is aborted after one generation and replaced with another paternal set of chromosomes, but also for a single generation. This type of reproduction is also called sexual parasitism, is present in the genus *Poeciliopsis* and is shown simplified in Figure 2.

Figure 1. The prussian carp, *C. gibellio* (source: original).

Poeciliopsis monacha-occidentalis is an all female (unisexual) hybridogenic lineage (Quattro et al 1992). It is a difficult task to classify this lineage taxonomically. It is an ancient clonal lineage of fish that appears to be older than 100,000 generations (Quattro et al 1992). Its origins was found to be inside of genus *Poeciliopsis*. The maternal ancestor was *Poeciliopsis monacha* Miller, 1960 and the paternal ancestor was *Poeciliopsis occidentalis* (Baird & Girard 1853) (Quattro et al 1992).

The case of *P. monacha-occidentalis* is not the only example of sexual parasitism within the genus. *P. monacha* created a network of parasitic lineages in river drainages of Sonora, Mexico (Quattro et al 1992; Figure 3). The phenomenon was first reported in the late 1950s by the scientists R. R. Miller and R. J. Schultz in a population of the genus *Poeciliopsis* from north-western Mexican streams (Lavanchy & Schwander 2019). This population became intriguing due to the fact entire population consisted only of females, with apparently no males. Because of the fact the conspecific males were absent, the females mated with males from a sympatric species (*P. lucida*) to reproduce.

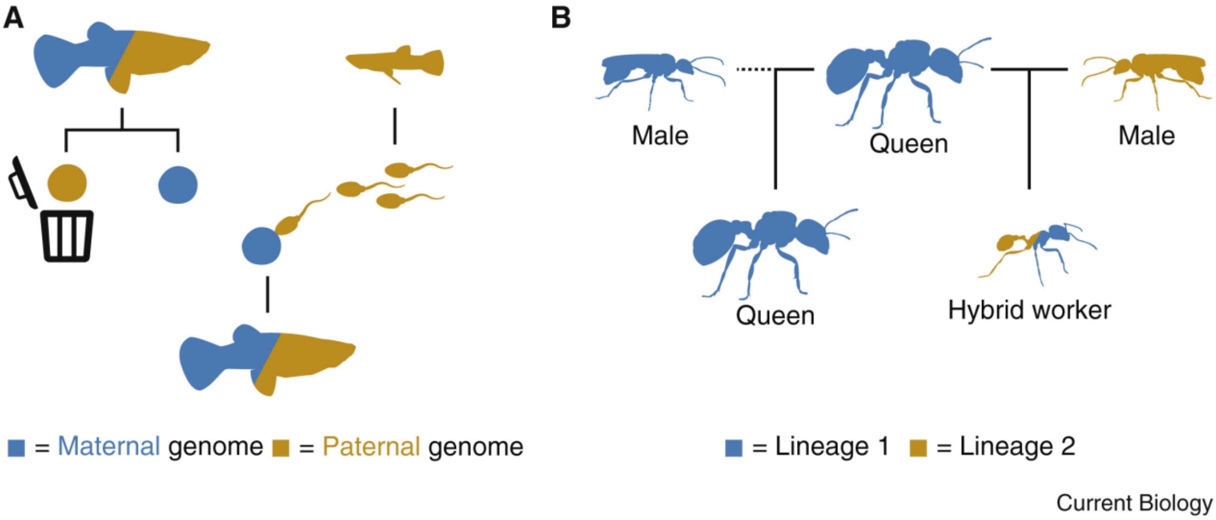

Figure 2. Two cases of sexual parasitism. (A) Classic hybridogenesis described in genus *Poeciliopsis*. The hybridogens are F1 hybrid females. They mate with males from their paternal ancestor and clonally transmit the genome of their maternal ancestor while discarding all paternally inherited chromosomes. (B) Social hybridogenesis observed in Hymenoptera. Queens are produced either by sexuate or asexuate reproduction, more exactly: via parthenogenesis (e.g. genus *Cataglyphis*) or from intra-lineage matings (e.g. genus *Pogonomyrmex,* see dotted line). Workers are always produced from hybrid crosses between genetically diverged lineages (Source: Lavanchy & Schwander 2019).

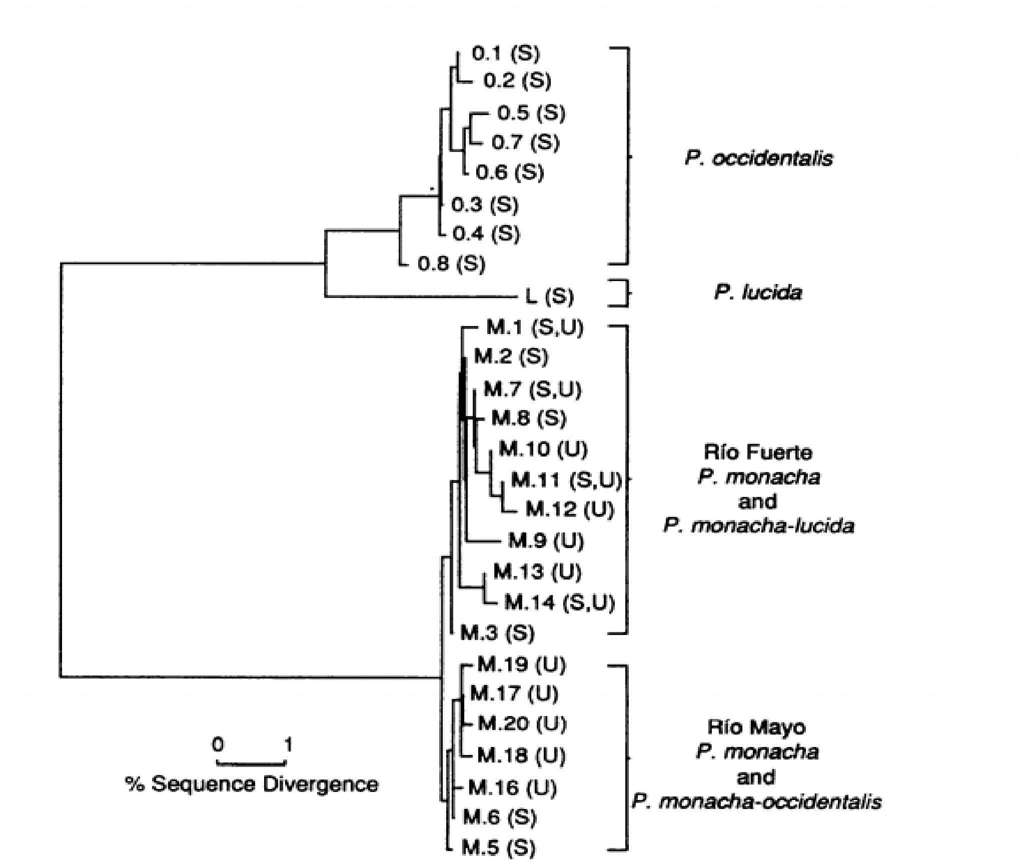

Figure 3. An unrooted phylogeny based on pairwise distances among haplotypes (Quattro et al 1991).

About ten years later, the question mark of the reproductive strategy of these all-female fish was deciphered (Lavanchy & Schwander 2019). Researchers found that the strange females they studied were the result of an ancient hybridization event between *P. lucida* and a second, closely related species, *P. monacha* (Lavanchy & Schwander 2019). They observed that even though these females successively mate with *P. lucida* males, which should lead to a largely lucida-like genome over generations, the genome of the females looks like that of a first generation hybrid between the two species (Quattro et al 1991, 1992). The hybrid composition of the genome (Pereira et al 2017) is maintained due to a mechanism by which the females only transmit their maternal *P. monacha* genome to their offspring, discarding all *P. lucida* chromosomes in the process before any recombination between the chromosomes. In offspring, the genome of the F1 hybrid configuration is conserved over generations due to the fact the eggs are fertilized again with *P. lucida* males (see Figure 2A) (Lavanchy & Schwander 2019).

In hybridogenetic *P. monacha-occidentalis* reproduction is a hemiclonal mechanism whereby only the haploid maternal monacha genome is transmitted without recombination to ova; the paternal occidentalis genome is excluded during a premeiotic cell division, preventing synapsis and crossing-over (Schultz 1969; Cimino 1972).

How does *P. monacha* manage to maintain the existence and viability of the genome over hundreds of thousands of generations without classical sexual reproduction and genetic recombination? The answer is found in the permanent variability of the genome of the parasited species. As long as there are sympatric species related to *P. monacha* that reproduce sexually, they will ensure variability and adaptability for *P. monacha*. *P. monacha* will incorporate the new genomes of the parasitized species in real time, refreshing each generation's gene pool by complete replacement of the parasited genome.

Extreme Gynogenesis in Amazon Molly. Gynogenetic reproduction has been taken to the extreme by the Amazon molly*, Poecilia formosa* (Girard, 1859) (Zhu et al 2017; Gösser et al 2019). The species is a freshwater fish native to warm, fresh waters between Tuxpan River in northeastern Mexico and the Rio Grande and the Nueces River in the southern parts of the United States, Texas state (Froese & Pauly 2020).

P. formosa (Figure 4) reproduces through gynogenesis, which is sperm-dependent parthenogenesis (Schedina et al 2018; Costa & Schlupp 2020). As in the case of Prussian carp, the cell division of eggs is triggered only after contact with male gametes, and Amazon molly females use males of related species for this. The males are either *P. latipinna, P. mexicana, P. latipunctata*, or occasionally *P. sphenops* (Froese & Pauly 2020). This interspecific mating results in clones of the mother (Heubel 2004). This peculiar reproduction has led to the Amazon molly becoming an all-female species (Schlupp et al 2007).

A hypothetical male *P. formosa* may exist among female individuals in the wild. It would be rare, triploid and would induce the parthenogenesis of females, but would not be necessary for reproduction (Wikipedia.org 2020).

Since the parasited male will not transmit his genetic baggage to the offspring of the females of *P. formosa*, these matings are evolutionarily detrimental to him. However, females of parasited species have developed a strategy to counteract sexual parasitism. For instance, the Atlantic molly females (*Poecilia mexicana* Steindachner, 1863) give up personal preferences and accept mating with any male prone to mating with Amazon molly females (Balcombe 2017).

Like in the case of the hybridogenetic species *Poeciliopsis monacha*, the existence of the Amazon molly is strictly dependent on the existence of related sympatric species (Schlupp et al 2007).

The Amazon molly has been reproducing asexually for about 100,000-200,000 years (www.txstate.edu) or even more. This is about 500,000 generations of Amazon molly from the beginning until today. Asexual lineages theoretically go extinct after 10.0-100.0 generations (Heubel 2004). There is research being done to determine why this species has not gone extinct or developed a Muller's ratchet of mutations (Muller 1932, 1964). Unexpectedly, Warren et al (2018) found no widespread signs of genomic decay in *P. formosa*. However, more research is needed to explain the species survival in absence of genetic recombination.

Figure 4. *Poecilia formosa*, the Amazon molly (source: Froese & Pauly 2020; picture by Slaboch R.).

Conclusions. Pisces has developed strategies to maximize investment in females, which produce offspring. In contrast to females, males only contribute to the production of offspring and can sometimes be dispensable. Among these strategies we mention the hybridogenesis model of the genus *Poeciliopsis*, the Prussian carp gynogenesis model, and the extreme gynogenetic model of the Amazon molly, a species that is formed almost exclusively from females.

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