Genetics Primer

An introduction to guppy genetics for the absolute beginner.

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Genetics Primer

This primer is intended for the novice guppy breeder, or the longtime guppy breeder who is not really interested in advanced genetics. Perhaps you just want to know what will happen when you cross metallic guppies with snakeskin guppies. The fact is that even a simple cross like that requires at least a small amount of genetics knowledge to fully understand what is going on when you put the strains together. I know that you can just put the strains into the same tanks and wait to see how it turns out. But hopefully in reading and using the information in this primer you will understand there is a more efficient and more satisfying way to explore guppy crosses.

The primer was originally published on the IGEES (International Guppy Education and Exhibition Society) website. It has been expanded and revised for this publication.

Why Study Genetics

What is "genetics?" The word "genetics" means the study of "genes."

Here is the definition of a gene:

> "Genes are segments of DNA found on chromosomes. Chromosomes are located in the cell's nucleus. Genes store the body's blueprints. When a new part of the body needs to be built, the blueprint is read and the part is created from the blueprint. The gene passes this blueprint to the next generation."

So genes really the storage places for instructions on how to build the body and run its processes, including the color cells in the skin that give guppies color and pattern. They are tucked away on chromosomes and stored safely in the nucleus. Obviously the body wants to take special care of its instruction manual.

"Guppy genetics" is simply the knowledge we have accumulated about those blueprints for color cells and patterns. It is also knowledge about how those genes are passed on from one generation to the next. Most people are not interested in how the genes act as templates for body plans. They are more interested in what happens when you cross two guppies or how to preserve or enhance a trait like a long dorsal. But as any good mechanic will tell you, knowing how a car works when it is running is a big help when it breaks down.

A lot of people say they do not study guppy genetics. But as soon as they make a statement about how trait is inherited they fall into the realm of guppy genetics. For example, a guppy with the half-black or tuxedo pattern, when crossed to a guppy without the half-black pattern, will produce offspring with the half-black pattern. Anybody who has made this cross will confirm this outcome. Guppy genetics is just careful observation of the inheritance patterns of guppies.

The existence of a half-black gene is "just a theory."

At this point we are not entirely sure that there is a half-black gene. But there is a high probability that crossing a half-black guppy with a guppy without the half-black gene will produce sons or daughters (or both) that have the half-black pattern. So that is the second thing you need to know about "genetic theory." It involves a prediction. I predict that if you make this cross you will get half-black guppies, if not in the first generation of the cross, at least by the second generation of the cross. The fact that the half-black pattern's blueprint is stored in genes and those genes are passed on to sons and daughters is pretty amazing I think.

I have discovered a number of simple theories that explain why guppies look the way they do. For a long time I was puzzled by the weird colors and patterns on guppies that have the magenta gene. Then one day my friend José René Meléndez Berríos put a comparison chart between sibling guppies (brothers) on Guppy Designer.

The brother without the magenta gene is on the left, the magenta guppy is on the right.

I had done a lot of crosses involving the magenta gene and I have extensively studied both genetics and the color cells on the guppy. Previously I had proposed a theory about the effect of the magenta gene on the color cells of the guppy. But I was wrong. I was looking in all the wrong places. It took José René's picture to trigger a sudden insight. The magenta gene affects a type of metallic color cell called the "blue iridophore" and the red pigment color cell associated with it. I went to my fish room and examined my magentas. Wherever there were blue iridophores on the normal colored sibling, there was magenta red on the magenta sibling. My new theory: magenta is a gene that affects the distribution of iridophores and red color cells on the body.

Would I have noticed this without studying genetics and color cells? Perhaps. But the theory I had previously learned told me where to look and to properly interpret what I was looking it.

So why learn genetics theory and color cell biology? Well, you can come up with better (that is simpler and more elegant) theories about the expression of genes and the way they are passed on from one generation to the next. Better theories lead to better predictions. These predictions can save you a lot of time in the fish room. Years. Hundreds of gallons of water. Pounds of food. To test my magenta theory, I decided to select males that show a lot of blue metallic color. They should produce sons that show a lot more magenta color. See how that works? Instead of relying on trial and error, my continued research into the magenta gene is directed and focussed by theories.

If my theory proves to be correct, I will become a more deliberate designer of guppies. The magenta gene will become like a brush in my hand, a tool for coloring guppies. Instead of mixing two strains and hoping for the best, I am going to deliberately choose my strains. It's the difference between splashing paint on the canvas and hoping for the best versus deliberately applying paint to the canvas. Much more satisfying!

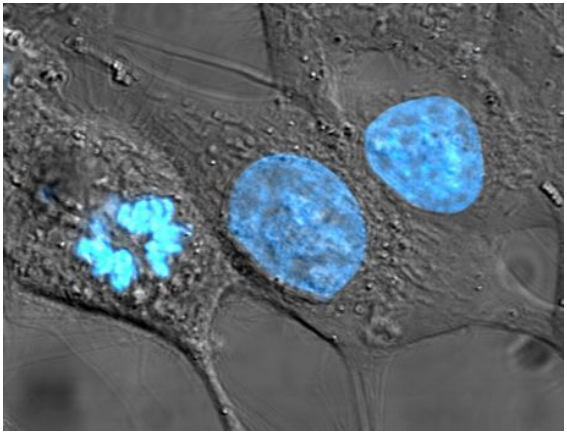
But there is an even better reason for studying genetics. The accumulated knowledge I have about color cells and how they are inherited makes my magenta guppies much, much more interesting to look at. It is what a chef experiences when she sits down for a meal. It is like what an astronomer sees

when he looks up to the sky at night. It is what a biologist sees when she goes for a walk in the forest. Guppy genetics is its own pleasure.

Hopefully you will see what I mean.

Genes as Blueprints

I provided a definition of a gene in the previous article as a "blue print" stored in the cell nucleus. I can actually show you a picture of this "blueprint." This photo from Wikipedia shows three cells and their nuclei.



The blue color you see in the picture is the genetic material (DNA) that has been stained with a blue dye. (No, I did not call the gene a "blueprint" because of the color of the dye. It is a happy coincident.) Seeing the genes in blue is visible proof of the existence of chromosomes, which store genes.

What do I mean by genes acting as blueprints for the structures and processes of the body?

Well, how are blueprints used? Did you have a grandmother who stored patterns for dresses in a cedar chest? She would take a pattern out of the drawer, packaged in an envelope. She would use the dress pattern as a kind of blueprint for the dress she wanted to make. The pattern would have different parts. She would take a part of the pattern from the envelope and lay it out over material and then cut out the material. She would cut out the other parts of the dress, using the different pieces of the pattern as templates. Then she would stitch the pieces together. After she had all the parts of the dress that she needed, she would fold up the pattern, tuck it back into the paper envelope, and put it away in the drawer of the cedar chest. Okay, I have a lot of metaphors going here: dress pattern, blueprint and template. The concept of template is the most accurate analogy, because the body uses the gene as a kind of template for the proteins that are made from genes. But I thought that the blueprint coupled with the picture would be easier for you to remember.

Why store a gene template in a nucleus? For the same reason your grandmom stored the dress pattern in her cedar chest: for safekeeping and to make it readily available. By keeping a copy of the genetic material, DNA, stored safely in the nucleus, the body can access it in the future to make more copies.

There is another value for storing the genetic material, neatly packaged in the nucleus as chromosomes. The pattern itself can be duplicated and widely distributed. This is what happens during growth. You can even pass the chromosome and its genes on to succeeding generations. That means that genes can act as the hereditary material.

We have got so accustomed to the idea of genes, that it comes as a surprise that it is a relatively modern idea. Through the thousands of years of animal and plant husbandry, breeders had no idea of a gene. Let me explain.

It was Gregor Mendel, the Austrian monk, who first discovered genes in the later part of the 19th century. He discovered them in his pea garden near his home in the monastery where he lived. His abbey had given him the task of helping farmers improve the yield of their crops. Mendel set about to discover the secrets of getting faster, more bountiful harvests. He decided to attempt to discover the laws of inheritance by crossing different strains of peas.

Mendel did not use a high resolution imaging device to discover genes. None existed. He used careful observation, scientific methodology and math. And simple gardening tools. In fact, Mendel had no clue about the physical structure of genes, calling them "factors" for a lack of a better term. So how did he discover "genes?"

Part of the answer is that he found a pattern in the inheritance of such visible traits in peas as wrinkled or smooth seeds. He would cross two different strains of seeds, noting that one of the two characteristics of the strain would disappear in the next generation. Then it would reappear in the subsequent generation. This led him to theorize that a gene is a unit of inheritance. It passes from one generation to the next unchanged. (The idea of a mutation would come much later.) That is a modern way of characterizing a gene, but it contains the central insight. When you cross two plants or animals, a gene is not altered, it remains intact and unchanged. It can reappear in subsequent generation unchanged. That was a huge insight, because previous to the theory of the gene, people thought that traits could be altered through crossing different strains. In fact there are still people who believe that genes can be physically altered by other genes!

But this is simply not the case. It's like the pattern for the dress. The master cannot be altered. The master can be damaged or a copy altered through some failure in the copying process, which we now call mutation. Damage to a gene very rarely happens, and when it does the offspring with a damaged copy of the gene often die. However in very rare cases a damaged copy will survive. It may confer some sort of advantage for the offspring. In this case the mutation can then become a new master gene.

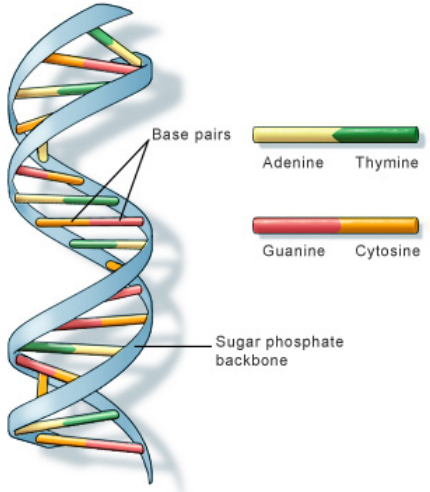
To illustrate the idea of the gene as the indivisible unit of inheritance, I'll use the classic example of the guppy albino. It is a fish that cannot express black color. It's eyes are red because there is no black color in the retina to absorb the light, and red blood shows through. The skin is a yellow color because the yellow color cells proliferate in the absence of black color cells. Red, white and other iridescent colors (silver, blue etc.) can appear, but no black color.

Albino Silverado above and his grey or wild type sister below. Notice the pink eyes of the albino. The albino male is also showing white and red colors, which are unaffected by the albino gene.

When you cross an albino guppy with a normal grey version of the same strain you get all grey offspring. But in the following generation you get about 25% albino offspring. The rest of the offspring are grey. If

you were Mendel, you would ask "What happened to the albino trait in the first generation of the cross?" Obviously it was hidden in the first generation, only to reappear in the second generation. But what does it mean to be "hidden?" Why is it not expressed? To a curious mind like Mendel's, saying that the gene was "hidden" would not be satisfactory. He would wonder what happened to it in the first generation of the cross. What makes the albino trait disappear in the first generation of a cross with a grey or normal colored guppy?

Genes as Genetic Code



U.S. National Library of Medicine

People have observed for thousands of years that visible traits, such as the shape of the eyes or nose, are transmitted between parents and child. Although the theory that traits are transmitted from one generation to the next seems somewhat obvious, it proved to be difficult to apply the theory. Farmers sought to improve their harvests and livestock by selecting the best individuals as the breeders for the next generation. But more often then not, selectively breeding the largest, most fertile male to the largest most fertile female led to the opposite outcome. Subsequent generations became smaller, less fertile and more fragile. Deformed individuals would appear.

You can say that to a large extent the guppy hobby finds itself in the same situation. The most common method for "improving" a strain is to select the best male and female according to some abstract standard and make them the new Adam and Eve for subsequent generations. Most people find it difficult to understand why selective breeding when practiced as inbreeding almost always results in the loss of a strain or its desirable attributes.

Such was the situation inherited by Gregor Mendel, the Austrian monk, more than a century and a half ago (around the year 1866). His task was to help local farms improve the yield of their crops through better breeding practices. The difference between Mendel and all the breeders before him was that he did exhaustive, carefully recorded and properly conducted experiments. Mendel analyzed nearly 21,000 hybrid plants! He used simple statistics to make sense of this massive amount of carefully gathered data. And he arrived at a conclusion that probably did little good for his local farmers (they listened politely but did not grasp the significance of his conclusion) but the concept would eventually revolutionize farming. He came up with the concept of the "factor," a single unit of inheritance, passed on unchanged from one generation to the next like a treasured family heirloom. We now call this factor a "gene" and consider it the irreducible single unit of inheritance.

It was not until many decades later that scientists traced the gene to a physical location, the chromosome in the nucleus of the cell. And not until the middle of the twentieth century that the chromosome was found to assume the shape of a double helix. You see it here looking like a spiral staircase. We now know its chemical structure. It can be fur-

ther broken down to smaller molecules called bases. These bases are of four types: adenine, thymine, guanine and cystosine. So a gene is a series of paired bases on a chromosome.

It is the order of these bases, abbreviated as A T G and C, that is important. If you look carefully at the illustration of the chromosome from the U.S. National Library of Medicine, you will see that it is composed of two strands of bases bound together. Wherever there is an adenine base, there is a thymine base bound to it. Wherever there is a guanine base, there is a cystosine base bound to it. In other words, each base along the length of the chromosome is duplicated. So a gene along a strand of DNA might look like this:

adenine - thymine

guanine - cytosine

cytosine - guanine

thymine - adenine

thymine - adenine

guanine - cytosine

etc.

One strand is the mirror opposite of the other stand since thymine always bonds with adenine and guanine always bonds with cytosine. This structure creates an extremely stable molecule that cannot be easily disrupted by chemicals in the cells or stray radiation. Changing even one pair of bases is often lethal for the organism, so nature has gone to great length to protect the integrity of the DNA molecule. Genes can be thousands of base pairs long. In genetics a "single point mutation" occurs when one of the base pairs in this long chain of base pairs that makes up a gene changes. The string a g c t t g can become a g a t t g. So it is very important to the species that the exact order of the base pairs that make up the gene is preserved and passed on to the next generation. Let's say agcttg is the genetic code for coat color for a strain of mice. If the code changes through a copying error or physical damage (from radiation for example), the change in the code may produce a mouse with a black coat rather than a light grey coat. Potentially that would make such an individual more visible to carnivores. There is a strong bias against changes to the genetic code.

The order of bases on the chromosome is used as a template by the cell when it needs to make a new body part (usually a protein). This template is passed on from one generation to the next. Guppy breeders talk about the gene for a long dorsal (the elongated gene). What they are ultimately referring to is a unit of information that is passed on from one guppy generation to the next that provides instructions for determining the length of the dorsal.

Now we come to the most important discovery made by Mendel, a key to understanding genetics.

Mendel discovered something that people long suspected, that such visible traits as eye color or body shape were transmitted from generation to generation. But he also discovered something nobody had figured out. He discovered that genes came in pairs. This was perhaps even more significant than the discovery of genes. You should ponder on the significance of that discovery before reading on. It's one of the golden keys to guppy genetics.

Paired Chromosomes

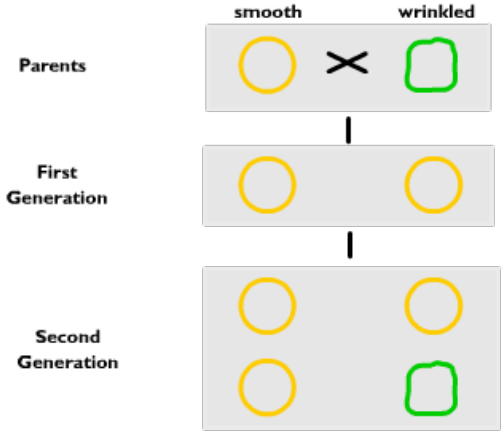
The story so far is that the traits we see in guppies, like the snakeskin pattern, are due to segments of DNA called genes, which are composed of a long series of paired bases. As it happens there are the same number of chromosomes in guppies as in humans, twenty-three. So all the instructions for building a guppy are spread out over 23 different chromosomes of different length.

There is a duplicate set of chromosomes. So the

grand total is 46 chromosomes or 23 pairs. On the diagram below I have represented one set of chromosomes. You can see that there is a red band on the chromosome. This represents a gene, perhaps one defining red color on a guppy.

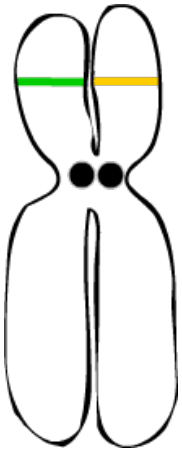
You can intuitively grasp the advantage of having genes in duplicates. It's the same reason why you make a second copy of keys to your safe, a second copy of your will or a backup copy of a computer file. If one copy is damaged or lost, the other copy can be used in its place.

It was Mendel who first discovered that genes are inherited in pairs. But he did not arrive at the conclusion that genes come in pairs by reasoning about gene security measures. He deduced the theory from his experiments with peas. What he noticed is that traits like smooth or wrinkled seeds seemed to be mutually exclusive. The seed was either wrinkled or smooth, there was no intermediate form like a "slightly wrinkled" but still smooth seed. When the smooth seed plant was crossed with the wrinkled seed plant, all the resulting progeny had smooth seeds. If he then crossed this first generation hybrid, and in the second generation he got a mixture of smooth and wrinkled seeds. This diagram shows what the results looked like:



As you can see, a smooth seed plant (yellow) is crossed with a wrinkled seed plant (green). The first generation produces all smooth seeds. The reappearance of the wrinkled seeds in the second generation of the cross must have puzzled Mendel for a long time. His solution to the problem echoes down to us almost a century and a half later. He deduced that the gene for the texture of the seed, wrinkled or smooth, came in pairs and one gene was dominant over the other.

We can visualize this through a modification of the chromosome graphic.



What you see is the green wrinkled trait paired with the yellow smooth trait. Both genes occupy the same relative position on their respective chromosomes. So they are said to "code for" the same trait, which means they provide the same information on how to texturize the seed. It is just that one codes is for a wrinkled texture and the other codes for a smooth texture. This is a chromosome that is giving conflicting information! So Mendel established a natural law. When two paired genes provide different genetic information on the same trait, one will be dominant over the other. The other is said to be recessive.

This is a law experienced by guppy breeders who have received trios from breeders and then found odd colored or strange fin shape guppies "suddenly" appearing in subsequent generations. Where did the strange guppy appear from?

Albino guppy. Picture by Philip Shaddock.

The example that is always given is the inheritance of the albino gene. An albino guppy is one with pink eyes and an overall yellow color. It has no black color. When you cross a truebreeding albino guppy to a truebreeding grey guppy, you get all grey guppies in the first generation of the cross. If you then take a male and female from that first generation and cross them, you will get a small percentage of guppies that are albino in the next generation.

The reason? The albino trait, where the guppy cannot manufacture black color, is said to be recessive to the normal or wild type trait.

This phenomenon can be explained on the biological level. Black color in guppies is due to a type of pigment called "melanin." One of the proteins that is used by the cell to manufacture melanin has become corrupted in the case of the albino guppy. Presumably one of the base pairs that makes up the gene that codes for the pigment protein has been changed. It is like messing up the instructions for baking a cake. In the case of the normal guppy, it has two good "recipes" for baking the cake. In the case of the albino guppy, there are two bad recipes for baking the cake. Since the albino guppy has no good instructions for making black melanin, it fails to get made. When you cross a normal guppy with an albino guppy, the offspring receive one good gene from the normal parent and one bad gene from the albino parent. So it has one good gene and one bad gene. The bad gene is useless for baking the cake. But the good gene is good.

So in the case of the albino X normal guppy cross, the one good gene was all that was necessary to color all the fry from the cross normal grey. It is not a case where the albino gene disappeared. It was there all along. Mendel called it "recessive." Defective is another term that comes to mind. As it turns out, the guppy only needs one good gene to make a grey guppy, not two. Now you see one reason why genes come in pairs. The other reason is even more intriguing. But I'll save that for later.

Mutation and Linkage

Gregor Mendel passed down to us an important concept which I will call provisionally, gene continuity. Nature goes to great length to prevent genes from changing. Genes are not physically changed by the presence of other genes or other external factors. A gene may be masked by a dominant gene. But it

is not destroyed or altered.

In fact, if a gene does change through a copying error or the exposure of the DNA to a chemical or radiation that alters the gene's physical structure, a new gene is born. The old gene continues on, unchanged. The new gene takes on a life of its own or dies. That is what I mean by continuity.

When a gene does have its physical structure altered by accident, we say it has mutated. The sequence of bases that used to define the gene,

adenine - thymine

guanine - cytosine

cytosine - guanine

thymine - adenine

thymine - adenine

guanine - cytosine

becomes something new (shown in green):

adenine - thymine

guanine - cytosine

cytosine - guanine

guanine - cytosine

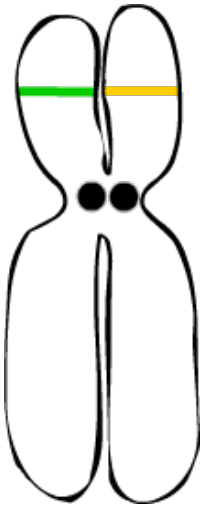
thymine - adenine

guanine - cytosine

That's because the gene blueprint has changed and the protein that is created from that blueprint is different. In the case of the albino guppy, the mutation causes a malfunction in the production of black pigment. In many cases a mutation results in the death of the guppy, although the more common occurrence is for the mutation not to matter at all. In others, a new version of the protein may produce a new and different version of the protein that is useful to the organism. I cited the case of a grey mouse that had become black. On a grey background a black mouse would be easy prey for a predator. But on black lava rocks a black mouse would have an advantage over its grey siblings. The black mouse would survive and multiply, passing on his or her new version of the gene to subsequent generations.

The population of mice will now have two different genes for coat color, gray and black. And the gray or wildtype color gene may be dominant over the black color gene. This would mean that the black gene would not be expressed when an individual had one grey and one black gene. It would allow grey mice who have one grey and one black gene to keep passing on the gene for black color to descendants. Eventually two recessive black genes would appear in an individual and it would either be targeted by predators or it would survive if it was born on ground blackened by a forest fire.

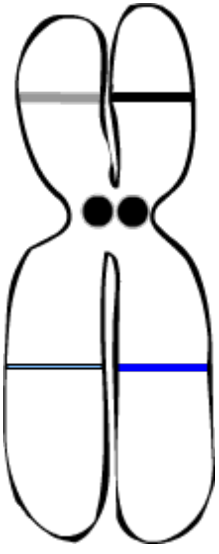
In order to talk about the two different genes, scientists refer to the old version of the gene as the wild type and the new gene as the mutant. They are said to be alleles of each other. So the grey mouse gene is an allele of the black mouse gene and vice versa. It is like saying they are brothers. Here is a graphical depiction of that relationship, an image you saw earlier:



Remember that genes are discreet sections of long strands of DNA. They are arranged in a row like beads on a string. The position of the gene on the DNA strand is very important. When the mechanism that reads (transcribes) the gene is ready to make a copy, it goes to that precise location along the length of the chromosome. If it is not there, the gene cannot be transcribed and the protein will not be made. This is usually lethal.

So a very important definition of a gene is that it occupies a specific position along the length of a chromosome and so do its alleles. An allele is a gene that is at the exact same locus (location) as another gene on a paired chromosome, just as you see in the picture.

Let's look at the case of two different genes on the same chromosome.

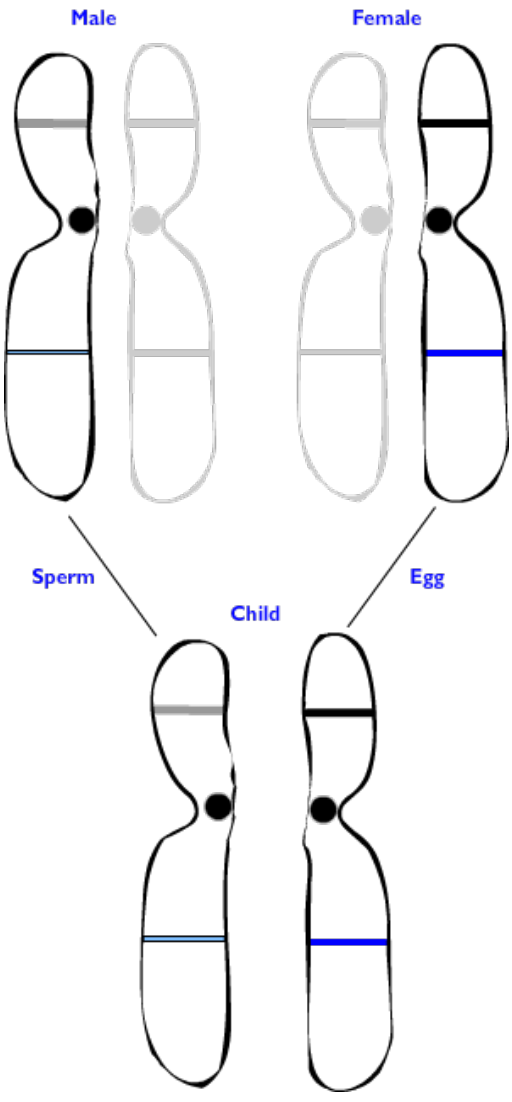


Two genes (black and blue)

Here we have two genes on the same chromosome, represented in blacks and blues. Let's say that the blue gene determines dorsal length and the black gene gives the guppy a half-black or tuxedo pattern. The blue and black genes are not alleles of each other. They are different genes, one determining dorsal length and the other color on the peduncle. I have made the black genes a slightly different color and I have also made the blue genes a slightly different color. Let's say that the dark black allele represents the half-black pattern and the grey allele represents the absence of the half-black pattern. Similarly, the dark blue gene represents a long dorsal and its light blue allele represents a short dorsal.

In other words, on one chromosome you have a short dorsal gene and no half-black pattern gene, and on the other chromosome you have a long dorsal gene and a half-black pattern gene. How do you think these will be inherited? This is something Mendel never found out, because he did not know about the physical structures that house genes. He thought in terms of genes as independently inherited units or factors. But long after his death, scientists discovered that genes existed on chromosomes. It is chromosomes that are passed on to the next generation. One of the pair of chromosomes of each parent goes to the child.

Let's look at a diagram of this. What I have shown here is the way individual chromosomes are passed on in the form of sperm and eggs. As you can see the pair of chromosomes break apart, and the individual member of the pair is passed on in the form of a sperm or an egg. I have greyed out the second member of the set to simply the diagram, but they also would be passed on this way:



How genes are inherited.

What you should take away from this diagram is that the chromosomes are inherited, and the genes go along for the ride. So it you have a long dorsal gene on the same chromosome as a half-black gene, they will be inherited as a unit, not separately. The two genes are said to be linked. Linkage is a very important concept in guppy genetics. In this case linkage means that the long dorsal gene and the half-black pattern are linked. Because they are both located on the same chromosome, they are passed on as a single unit. The breeder Doug Grey provides a good example of this in these pictures.

Here is an IFGA Blue Delta guppy without the half-black pattern and a short dorsal.

IFGA Blue Delta with no half-black pattern and a short dorsal

And here is a sibling of the IFGA Blue Delta, an IFGA Half-Black Blue.

IFGA Half-Black Blue with a long dorsal. From the same strain.

Now you know why it is risky using a male from the pet store with a short dorsal. (Of course Doug did not get his guppies from the lfs!) It may be the

case that the pet store guppy short dorsal is linked to another desirable trait. So in trying to create the perfect combination of traits, you may find that they never appear together on the same guppy. The genes are linked.

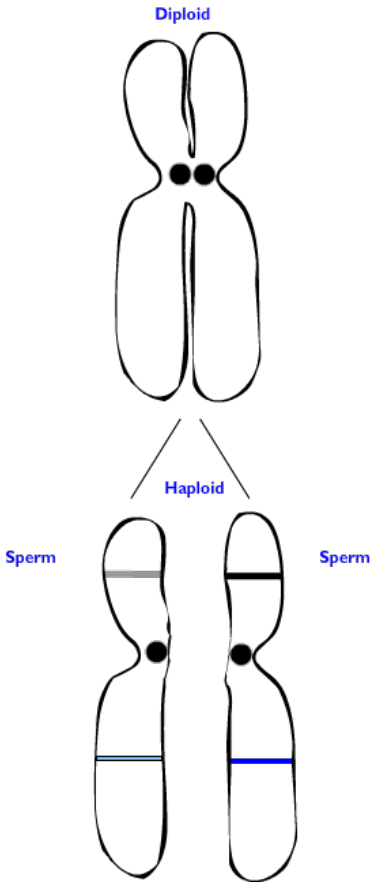
Is the task of creating the strain with a new combination of traits hopeless if the genes are linked? As it turns out nature has created a solution to this problem, which is called "crossover." I will describe this mechanism at length later. I will just say here that chromosomes actually break up and re-arrange themselves during sexual reproduction. So with patience, and time, and a lot of drops, you may some day come across a male where the linkage between the two traits has broken. You may come across a Blue Delta male with a long dorsal. It will probably be a single male in a drop of fifty or hundred. You may get lucky and find it in the next drop, or unlucky and not find it for two years. But chances are it will happen.

The farther apart the genes are on the chromosome, the more likely the break in the chromosome will occur between the two linked genes. So it is an odds game.

I have used the example of linkage of traits to get you thinking about how genes are inherited. Why don't you spend some time thinking about it before you turn to the next section?

The Punnett Square

As I showed in the last article, genes are passed on to the next generation on chromosomes. Like humans the guppy has 23 different chromosomes that are paired for a total of 46 chromosomes. When chromosomes are paired they are called diploid. When they are not paired, they are called **haploid**.



The paired diploid chromosomes are split into haploid gametes (eggs and sperm) during sexual reproduction.

The diploid set of chromosomes is broken up during sexual reproduction. Each set of 46 chromosomes is divided into two eggs or two sperm (the gametes), each gamete invested with 23 chromosomes. So briefly, during sexual reproduction, the chromosomes are haploid. When the haploid egg and haploid sperm are united, the new zygote is becomes diploid again.

Now here's the point that I have been leading up

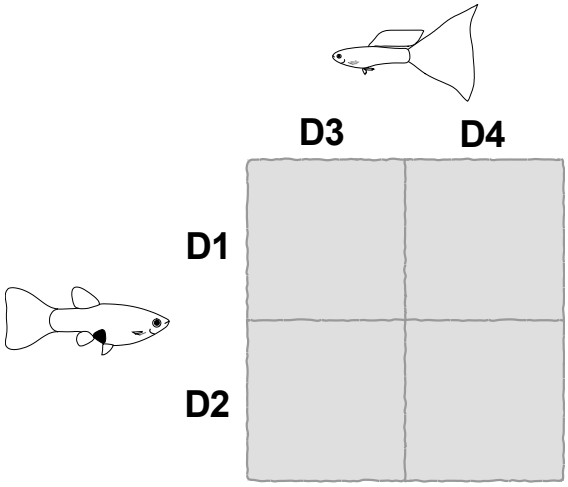
to. Notice that the chromosomes in the example I have chosen have different alleles. One might be for a half-black pattern and the wild type (no half-black pattern). Since sperm or eggs only carry one chromosome, any given sperm or egg can only carry one allele. Some may carry the gene for a short dorsal and the others for a long dorsal. The eggs the sperm fertilizes may have different genes as well. Which sperm fertilizes which egg is almost entirely a matter of chance.

The division of the diploid chromosomes into haploid gametes and their recombination is a kind of natural shuffling of the cards. You split the deck and mix the cards randomly. This genetic shuffling is a fundamental reason why nature invented sexual reproduction. By trying out new combinations of alleles, the different colors of mice can become better adapted to different colored environments.

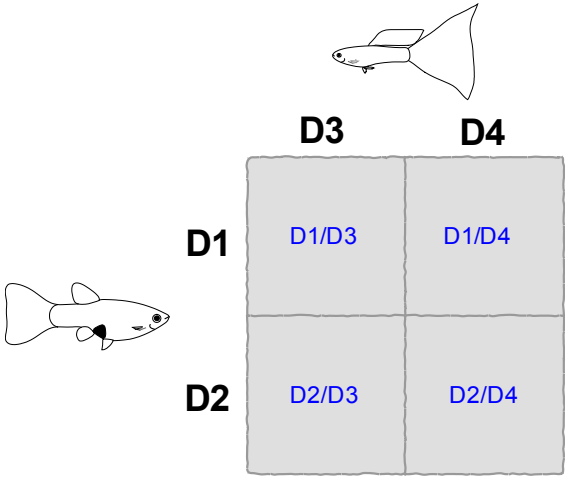
Potentially there can be four different versions of a gene, or alleles, in the children of a cross. The male could have two different alleles for dorsal length. The female can have two entirely different alleles for dorsal length, different from each other and different from the males. Because the egg and sperm match up randomly, you would have four different combination of alleles. Why only four and not sixteen? Because the there are two different sperm alleles and two different egg alleles, so 2 X 2 = 4.

Not following? Here is a way to work it out visually. For those of us who did poorly in math, this is a much better way to visualize the combinations.

Let's say you have four genes affecting the dorsal length, which we will call d1, d2, d3, d4. The female guppy has the allele combination d1, d2. The male has the allele combination d3, d4. So To figure out how the genes will combine in the fry, we use something called a Punnett Square. This is a very simple table:



The two sperm alleles are assigned to the rows and the two egg alleles are assigned to the columns. To determine how the sperm and egg genes match up, just fill in the squares where the columns and rows intersect.



It is a simple visual way of determining how the sperm and egg genes combine.

The Punnett Square is one of the most powerful tools you can use in guppy genetics. Just to make sure you understand it, I am going to employ it

again, using a real example.

Remember the albino guppy? It is a mutant that cannot manufacture black pigment. So the guppy is yellow with red eyes. It is a recessive trait, meaning that the albino gene cannot be expressed if it is partnered up with a normal or wildtype gene. Let's walk through a breeding experiment where we cross a truebreeding albino strain with a truebreeding grey or wildtype strain. What I mean by "truebreeding" is that each parent only has one version of the gene. The grey parent has two normal or wildtype genes and the albino parent has two mutant albino genes.

Here is the picture of the male albino platinum magenta and his grey wildtype sister.

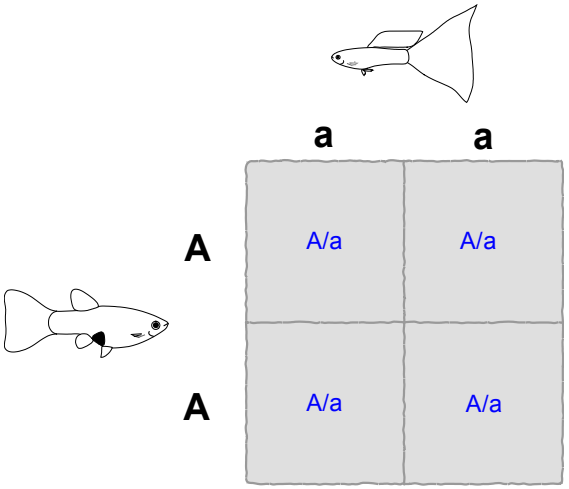
Albino above and grey female sibling below. Photo by Philip Shaddock.

Scientists have a shorthand notation for genes. For the albino gene it is the letter "a" (a for albino). Because the albino trait is recessive, the "a" is lowercase. By convention the normal or wildtype allele is given the same letter, only it is capitalized. So the wildtype allele of the albino gene is "A." Since potentially a gene can have many variations, the original form of the gene, the one found most commonly in nature, is called the wildtype allele. When you are comparing alleles you always have to remember this. The gene that colors the guppy black is called "albino" and it is designated with a capital "A." Its mutant allele is designated with a lowercase "a." Since there are two chromosomes, and the genes can be different alleles, you use two symbols (AA).

So here is how we designate a truebreeding grey or wildtype guppy: AA

And here is how we designate a truebreeding albino guppy: aa.

Now let's see what kind of combination we get if we breed these two guppies.



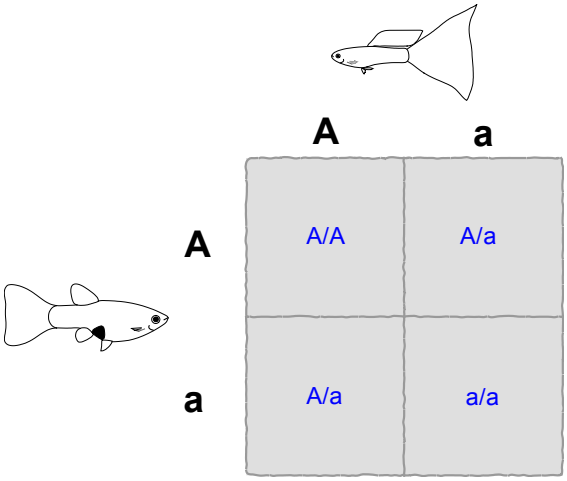
Cross between an albino male and grey female.

The male had only one type of allele (a) and the female had only one type of allele (A), so when you combined them, all the fry got one type of allele combination: aA. Since the combination of the recessive allele a with the dominant allele A means only the dominant allele will be expressed, all the fry will be wild type grey.

This actually happens a lot when you cross one truebreeding strain to another truebreeding strain. The

first generation of the cross looks fairly similar to each other. If there is not a lot of allele variation in the parental strains, then the fry will show relatively little variation.

This is an important reason why you should wait until the second generation before rendering judgement on the value of a cross. I'll show you what I mean. Let's take a male and female from the first generation of the cross we just did and mate them. To see how the genes segregate out, we'll once more do a Punnett Square.



The second generation of the cross.

In the second generation of the cross we get three different combinations:

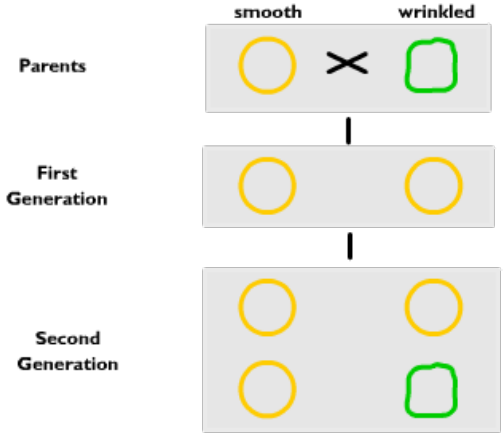
aa (like the male parent)

aA (like the first generation)

AA (like the female parent)

Both the aA and AA individuals will be grey (aA has the dominant A allele). The aa individuals will albino. In other words 3 of 4 of the fry will be grey and 1 of 4 fry will be albino. Remember that the combination of alleles will be random, so when we say that the albino individuals will be in a 1:4 ratio, and the grey individuals will be in a 3:4 ratio, we mean on average. Your results may vary.

Long before the guppy was domesticated and long before the Punnett Square was invented by somebody with the surname Punnett, somebody had already figured out the ratio of recessive individuals in the second generation of a cross. It was Gregor Mendel. He noticed a statistical regularity in the results of his crossing. Remember his experiments with wrinkled and round pea seeds?



Mendel formed his theory by working backward from statistical analysis of his results. That was his genius. As you will see as you get further into guppy genetics, you can follow in his footsteps. By carefully noting the ratios of traits in your drops you can work backwards to the probable gene makeup of your strain. This makes the Punnett Square an extremely powerful tool for exploring the genetics of your strain. For example, if in the second generation of a cross 25% of your drop is of one type and 75% is of another type, you know that the trait is possibly a recessive trait.

Mendel had better terms for what I have been calling genetic "shuffling." He called it independent assortment and segregation. What he meant was

that genes are inherited independently of each other and form new combinations in subsequent generations of crosses. In guppy genetics discussions you will hear his term "segregation" used quite often. A person will talk about how a strain reappeared in subsequent generations to a cross. Or a certain hybrid strain will constantly produce certain visual variations, like blue and red versions. This phenomenon is due to Mendelian segregation. I have given you the Punnett Square as a tool for working out how genes segregate.

Why learn how to use a Punnett Square? Well it allows you to work out on paper the future outcome of crosses. Instead of just tossing some guppies together and hoping for the best, you now have a tool for predicting the combination of genes that will result from a cross. This can save you a lot of time and effort pursuing crosses that eventually take you down blind alleys.

I will come back to the Punnett Square and give you more examples of its use. You should take some time to play with it until you understand its relationship to genes and the way they are inherited.

The XY Sex System

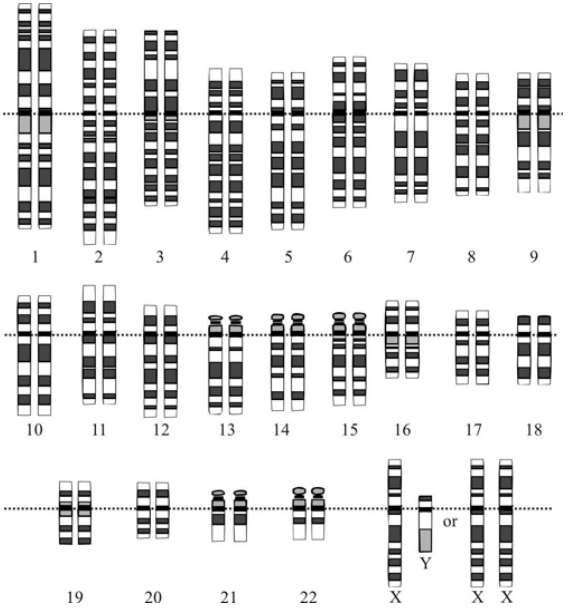
The similarity between guppy and human genetics goes beyond the fact they both have 23 chromosomes that are diploid. They also share the XY sex system.

There are two very special chromosomes in the set of 23. These are the sex chromosomes, designated as X and Y. The Y chromosome has a gene or genes that determine whether the fertilized egg develops as a male or female. The female lacks the Y chromosome.

male = XY
female = XX

So the male has all the chromosomes that the female has, plus the Y chromosome. The female lacks the Y chromosome.

This diagram shows a graphic representation of the different sized chromosomes of humans.



Notice that all the chromosomes except the X and Y chromosome are homologous, meaning each member of the pair is of the same size and has the exact same complement of genes. The exception is the X and Y chromosomes (no. 16 in the diagram). The male Y chromosome is substantially smaller than that of the female. The Y chromosome has virtually no genes. In fact he is downright puny. About the only thing he is good for is to signal the fertilized egg to develop the secondary sexual characteristics of males.

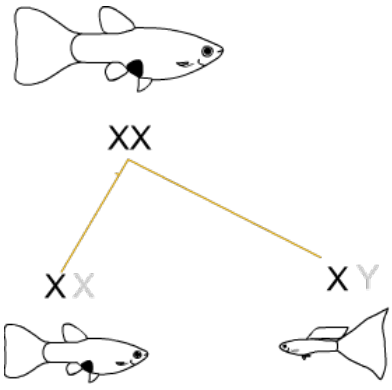
Here is where the guppy sex system differs significantly from the human sex system. In the case of the guppy X and Y chromosomes, they are not distinguishable from each other when in the condensed state. It is widely believed they are an example of the earliest stage of development of the XY sex system.

In fact sex determination in guppies is less stable than that in humans. Most people in the hobby are unaware that many of the males in their drops were born female and vice versa. Occasionally sharp-eyed breeders will notice a female guppy suddenly change into a male relatively late in development.

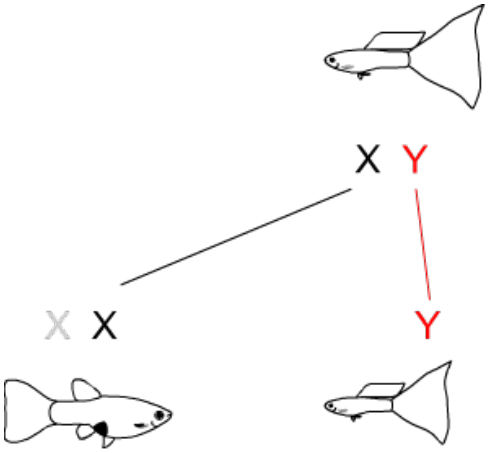
Now comes perhaps the most important fact about guppy genetics. Both the X and Y chromosomes carry the majority of color and fin shape genes. Remember how I said guppy body blueprints in the form of genes are spread among the 23 chromosomes? The genes that are of most interest to guppy breeders, the genes associated with color, pattern, and fin shape and length are mostly located on the X and Y chromosomes. In other words, they are sex-linked. What that means is that they are traits that are linked to the X and Y chromosomes.

There are exceptions, like the vertical bar gene, the golden and blond genes, the full body black genes, metal genes, albino and other genes. But patterns and colors like the snakeskin pattern, the color dots, many red genes, the half-black pattern and such fin shapes as the long dorsal are located on the X and Y chromosome.

When you hear somebody say that the snakeskin gene is X-linked, they are saying that the gene on their strain is located on the X chromosome. Let's see what happens when that gene is inherited:



The female's two X chromosomes are inherited by both daughters and sons. But look at the case of Y-linked inheritance:



The male guppy passes on his X chromosome to his daughters. But he passes on the Y chromosome only to his sons. All the genes on the male's Y chromosome are inherited only by sons.

What is the significance of this fact? In wild guppies the males use their color and pattern to advertise their fitness to potential mates. But this puts them at risk by being easy targets for predators. Drab females have a much better chance at survival. In fact it is precisely because male guppies are so colorful, and females so colorless, that guppies were an early wet lab "rat" favorite among geneticists. The pioneering scientist was Johann Schmidt from the Carlsberg Laboratory in Denmark who was particularly struck by the fact guppies tended to segregate into strains. He had a strain of wild guppies in his lab as early as 1916. But some years later he visited a fish exhibition and discovered guppies with quite different patterns than found on his guppies back in the lab. He crossed them with his strain and found that the males passed on their patterns

to their sons, even when outcrossed to a female of a different strain. This led him to the conclusion that the guppy used the XY sex system and that there was something called "male only inheritance." That is, sons inherited their pattern from the father and not the mother. Schmidt had discovered Y-linked inheritance of genes.

This may seem contrary to your breeding experience. After all you have crossed two strains and found that the female indeed did influence the patterns on the sons. But Schmidt conducted his experiments with wild guppies or guppies taken recently from the wild. And if you acquire a female from the wild today, you will see that the females completely lack color, with the exception of their gray background color.

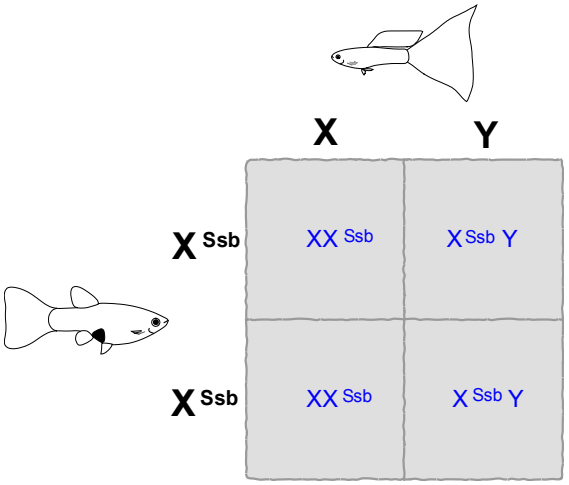
Now you know why it is so important to know where the genes are located on your strain. You cannot cross a male with a Y-linked color pattern to another female and expect the offspring to inherit the father's color. An example is the Moscow. The typical metal head of Moscows is strictly Y-linked.

Hawaiian Blue Moscow. Guppy and photo by Philip Shaddock

The fact that the blue head and some other body color and areas are strictly Y-linked on the Moscow means that you can create new strains by crossing females to Moscow males, but female Moscows will not carry the key Moscow traits to another strain.

In the case of snakeskins, the gene (or genes) for the pattern do come in both forms. You can have X-linked or Y-linked snakeskin strains. In this case you can transfer the snakeskin pattern to another strain using an X-linked snakeskin female. See how that works?

The Punnett Square, which I introduced to you in the last article, is very useful for planning crosses that involve the sex chromosomes. Let's say you are crossing a snakeskin (which has the gene symbol for the body pattern of Ssb) with a non-snakeskin guppy. You can use the Punnett Square to see how the snakeskin gene is inherited. Do a Punnett Squares for the two possible scenarios (X-linked or Y-linked). Here is the scenario for an X-linked snakeskin line:

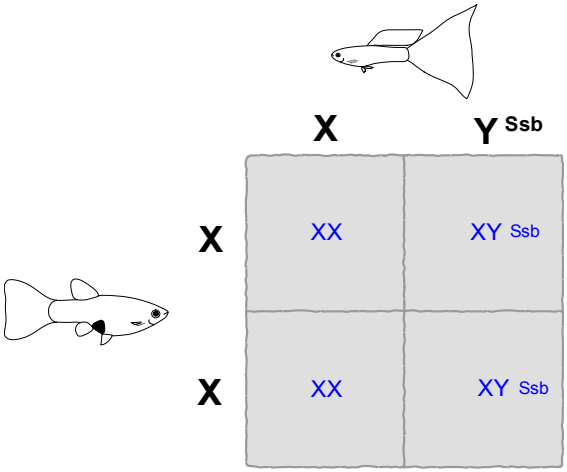


The X-linked scenario.

I have put the male's X and Y chromosome across the top of the square and the females along the left

side. Where the rows and columns intersect, you can see that all the offspring will get the female's X-linked snakeskin allele. (This assumes both X chromosomes on the female carry the gene.) So all males will show the snakeskin pattern.

And here is the scenario for the Y-linked scenario:



The Y-linked scenario.

In the Y-linked scenario, the snakeskin gene is inherited only by sons. If you practice with Punnett Squares, you will soon become a guppy geneticist rather than a guppy breeder staring into your tank with your fingers crossed.

I should note in passing that the notation for sex-linked genes is to show the dominant gene name capitalized and to associate the gene's symbol with the chromosome it is found on. It is also shown in superscript. This is an albino (aa) snakeskin guppy that is Y-linked. The wild type gene name is not shown by convention.

$$XY^{Ssb}\ aa$$

One other note. The genes that are found on the non-sex chromosomes are generically called the autosomal genes. For example, the albino gene is autosomal.

Some of you who have been reading this series closely will wonder how modern female guppies came to be so rich in X-linked color genes.

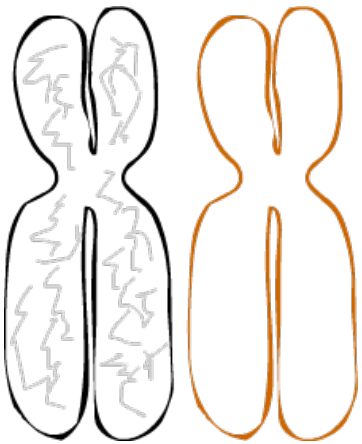
Breaking the Link: The Crossover

In the last article I noted that modern guppy females had a lot more color genes than their wild cousins. The reason for this is crossover. Crossover allows paired chromosomes to exchange genetic material. This breaks the link between two genes on the same chromosome, and allows the X and Y chromosomes to exchange genes. In nature, females that acquire color genes are selected against. But guppy breeders select for colorful females, if not directly, indirectly.

An example of a gene that quite readily crosses over is the gene for the snakeskin pattern. It can be found on either the X or Y chromosome because of this ability to crossover. Let's look at the physical mechanism involved.

Crossover occurs during sexual reproduction.

Here are two chromosomes.

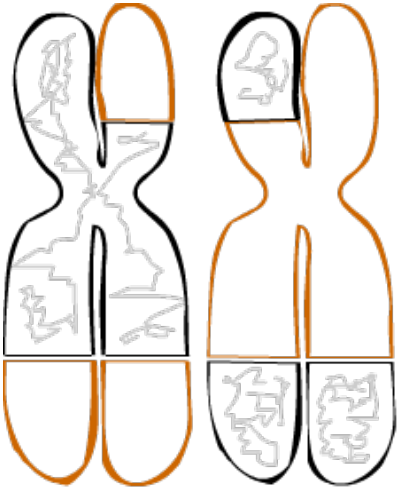


Before crossover

During the production of eggs and sperm the chromosomes literally cross over each other.

During crossover

The chromosomes break apart and re-assemble, exchanging one, sometimes two or three different segments.



After crossover

Crossover ensures that linked genes (genes on the same chromosome) are broken apart so that they can segregate and be passed on independently. In the case of the X and Y chromosomes, a gene that was on the Y chromosome and only passed to sons, will be shuffled to the X chromosome, where it can be passed on by the mother to daughters. And the daughters can carry it to males of a different strain. Crossover is the tool for change in the domestic guppy world.

There is at least one region on the Y-chromosome that does not cross over. That is the area around the sex-determination gene called the SDR or sex-determining region. If the sex-determining gene were allowed to cross over, the difference between the X and Y chromosome would be lost. The mechanism that prevents crossover of the SDR is not understood by science. But there are male guppy colors that never cross over, like the red spots on guppies and such genes as the Moscow supergene.

The frequency of crossover varies depending on how distant the gene is from the SDR. The closer genes are to the SDR, the more infrequently crossover occurs. For example, the Moscow gene has never been shown definitely to have crossed over. The snakeskin gene does so fairly frequently (perhaps as high in 1 in 50).

Sometimes a "sport" shows up in a drop, a male significantly different than his brothers or sisters. A lot of people will think that a mutation happened, when it was more likely a case of crossover. It's difficult to estimate the guppy mutation rate, but in general it is in the range of 10-4 to 10-6. In other words the rate of mutation is extremely rare. You should think "crossover" when you see an oddly colored or patterned guppy appear in a drop. Of course if the guppy is the result of a recent cross, that is within the last ten generations, than you cannot rule out the gene was there all the time, but masked or recessive.

This concludes the primer I have given you a bare bones introduction to guppy genetics. I have skipped

over or ignored the many exceptions to the theories and laws I have presented here. For example, genes can have more complicated relationships than "dominant - recessive." Genes can be co-dominant or partially dominant. Some genes can mask others (epistatic). Many genes are not simple point mutations as I have described earlier. They are composed of a network genes. For example, there is not a single Moscow gene, but a number of genes that act like they were a single gene. However the basic genetics that I have explained here should serve you well until you have reached the point where you need better explanations for what you witness in the fish room. That would be a good point to join Guppy Designer, where I do go beyond simple genetics. Meanwhile good luck in your fish room. And may your crosses eventually have less to do with luck and more to do with good planning based on good solid theory and understanding.