Mendelian speciation: part 3—fixation and reproductive isolation

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Mendel's law of exponential trait combinations reveals how pre-existing genetic information, both expressed and latent, can produce a large number of phenotypic variants. Heterozygous individuals freely mate among themselves, and highly variable species arise. This meiotic process of global genomic change, however, also leads to loss of heterozygosity, and gene fixation, and is an efficient mechanism of speciation. Reproductive isolation accompanies fixation, and progeny are constrained in groups of separated, less variable, individuals that produce unique species. Mendelian speciation gradually gives rise to genetic families of related species. It is clearly consistent with plants and animals being created after their kind.

Mendel's Law of Exponential Trait Combinations (he called it *das Gesetzt der Combinirung der differirenden Merkmale*[1]) reveals how the phenotypic diversity of species within a genetic family can arise within relatively few generations based on pre-existing genetic programs. Meiosis causes the profuse recombination. But how does reproductive isolation contribute to the emergence of species?

In the first two parts of this series[2,3] it was shown that living organisms have an enormous latent (hidden) reservoir of genetic information and that the processes created to produce variation can result in their expression within relatively few generations. This potential for variation provides for an exponentially large number of trait combinations within each genetic family (basic type/baramin), see figure 1. But how do new species arise from this diversity? How does reproductive isolation and thus speciation occur? Are there examples in nature that demonstrate dynamic speciation and reproductive isolation?

This third paper looks at the consequence of Mendelian speciation over a series of generations. It looks at the mathematics of heterozygosity loss and of homozygosity fixation. It examines the role of reproductive isolation and how this plays a crucial role both in the production of new species and in their persistence. The difference between genetic families and derivative species is discussed and how these natural processes can be understood in terms of the biblical claims about organisms and their kinds.

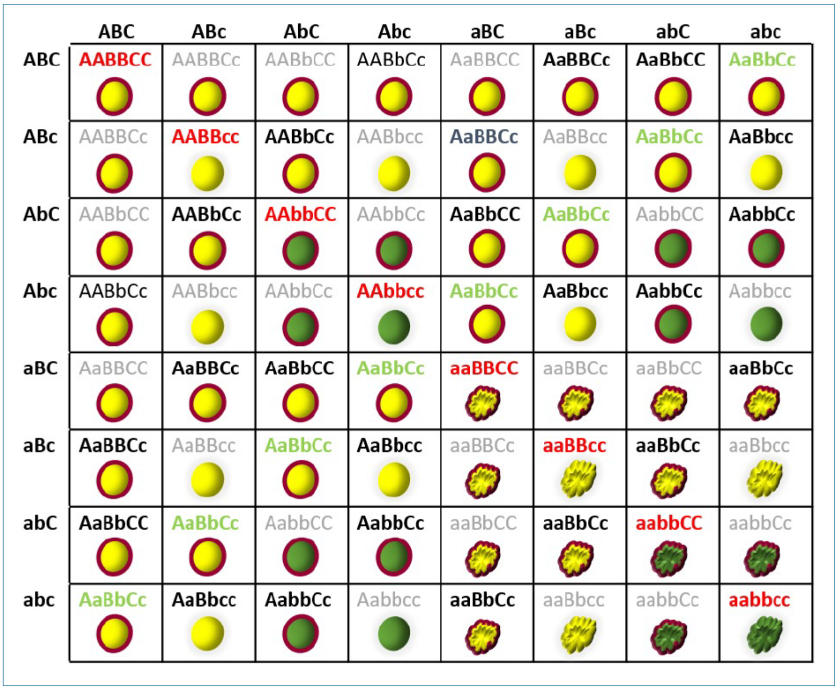
Fixation and global genotypic change

Figure 1 displays a Punnett square of a triple-heterozygous self-cross that obeys Mendelian rules. The lagging diagonal (top right to bottom left, green text) displays the genotype and phenotype of the triple heterozygote. As shown, this triple heterozygote can give rise to eight different phenotypes, all eight of which are displayed down the leading diagonal (top left to bottom right, red text) of the figure, together with all eight unique triple-homozygous genotypes. The other phenotypes have reduced variability: double-heterozygote genotypes (dark grey text) and single-heterozygote genotypes (light grey text). Self-crosses between triple heterozygotes give rise to any of the phenotypes and genotypes. Self-crosses between triple homozygotes, however, only give rise to the same triple homozygotes. Homozygosity permanently fixes genes. This fixing of homozygosity, or loss of heterozygosity (Mendel referred to the process as *das Entwicklungsgesetzt*, the law of population development) relentlessly drives populations to become entirely homozygous. However, which one of the various possible pan-homozygous alternatives arises is entirely arbitrary. The process, called 'random genetic drift', resulting in complete loss of heterozygosity, is central to the field of population genetics.[4]

These Punnett squares are very simplified examples. Characters and traits are typically encoded by a number of genes, each of which is regulated by a variety of genetic processes. The proteins and protein interactions that eventually give rise to the traits can be complex. This all enhances the potential for genetic variation. However, such extensive details detract from the simple take-home message.

We use the generic term *gene* to refer to a unit of heredity which gives rise to the alternative traits of a character. A gene in this sense can be composed of multiple genetic elements. Mendel referred to these units of heredity, A, a, B, b, *etc.* as elements[4]. He did not know their material composition but deduced that they came in pairs, one from each parent. We refer to each variant gene as an *allele* (each located on a different homologous chromosome).

The differences between the alleles can be caused by a plethora of possible sequence differences in the protein coding regions of the gene, or the regulatory regions of the gene, or differences in regulatory RNAs (e.g., miRNA and lncRNA), or differences in regulatory proteins (e.g.,



	ABC	ABc	AbC	Abc	aBC	aBc	abC	abc
ABC	AABBCC	AABBCc	AABbCC	AABbCc	AaBBCC	AaBBCc	AaBbCC	AaBbCc
ABc	AABBCc	AABBcc	AABbCc	AABbcc	AaBBCc	AaBBcc	AaBbCc	AaBbcc
AbC	AABbCC	AABbCc	AAbbCC	AAbbCc	AaBbCC	AaBbCc	AabbCC	AabbCc
Abc	AABbCc	AABbcc	AAbbCc	AAbbcc	AaBbCc	AaBbcc	AabbCc	Aabbcc
aBC	AaBBCC	AaBBCc	AaBbCC	AaBbCc	aaBBCC	aaBBCc	aaBbCC	aaBbCc
aBc	AaBBCc	AaBBcc	AaBbCc	AaBbcc	aaBBCc	aaBBcc	aaBbCc	aaBbcc
abC	AaBbCC	AaBbCc	AabbCC	AabbCc	aaBbCC	aaBbCc	aabbCC	aabbCc
abc	AaBbCc	AaBbcc	AabbCc	Aabbcc	aaBbCc	aaBbcc	aabbCc	aabbcc

Figure 1. A Mendelian triple-heterozygous self-cross displaying the phenotypic ratio 27:9:9:3:9:3:3:1. All eight phenotypes are displayed along the Punnett square's leading diagonal. Mendel conducted most of his experiments on garden peas, *Pisum sativum* (now *Lathyrum oleraceus*[5]). Three characters are displayed: A, seed shape; B, seed (endosperm) colour; and C, seed-coat colour (also causes purple and white flowers). Smooth, yellow seeds with purple seed-coats are dominant traits; wrinkled, green seeds with white coats are recessive traits. Mendel also studied three characters in hybrids of the Common Bean, *Phaseolus vulgaris*, with corresponding results.

transcription factors). They can be caused by transposons, or regions of DNA possessing alternative epigenetic regulatory methylation patterns. Each phenotypic character comprises a minimum number of molecular parts and is irreducibly complex. Many of their parts, however, can be modified and so give rise to alternative traits. Such characters would require far too many beneficial mutations to simply have arisen by chance. Such irreducible complexity can only realistically be explained as the product of design. Furthermore, only intensive research will eventually reveal how all the many parts and their interactions give rise to each of the various characters.

If four genes had been included in the Punnett square, it would be four times larger and display 16 different phenotypes. The number of possible phenotypes increases exponentially with the number of genes. Mendel described meiosis. He studied seven characters representing seven genes, and he observed all 128 different phenotypes.[1] Meiosis automatically gives rise to a great number of fixed phenotype alternatives (because of the homologous chromosome disjunction that occurs during anaphase I), resulting in a great number of potential species. Of fundamental significance to speciation is the fact that the resulting phenotypes vary in numerous different characters, from numerous different genes (because of the recombination that occurs during both prophase I and metaphase I). Meiosis is a genomically global mechanism; it is a polygenic process.

As discussed in part 2 of this series, Mendel recognized that well-defined species differ in many characters.[3] Mendelian speciation inexorably gives rise to a plethora of multi-character species. It is important to understand that although mechanisms of genetic change, such as mutation, transposition, and epigenetics, give rise to new traits (phenotypes), by modifying pre-existing characters, these are only very rarely granted the status of new species. This fact is most readily appreciated in humans, *Homo sapiens*, where many heritable diseases and phenotypic differences resulting from such genetic change have been observed, but never any species other than human, *Homo sapiens*.

Reproductive isolation

Mendelian speciation requires latent phenotypic information, loss of heterozygosity, but also reproductive isolation. The latter prevents mating between select individuals, which would otherwise result in hybridization, re-establishing heterozygosity and disappearance of recessive phenotypes.

For multiple species to arise through loss of heterozygosity, reproductive isolation must be a stable process. *Allopatric (geographic) speciation*, caused by spatial separation on islands or due to mountain ranges, is a single event that separates two subpopulations and which maintains isolation. As a result, two distinct phenotypes (or species) can arise due to random loss of heterozygosity, giving rise to alternative combinations of homozygous dominant and recessive traits.

Figure 2 illustrates how initially genetically heterozygous populations, which become reproductively isolated, can become more homozygous, leading to new species (smaller circles in figure 2. Hybridization can reverse the trend towards loss of heterozygosity. If natural selection (vertical arrows) occurs (in the third and fourth generations), the populations with the most favourable constellation of traits (darker shading in figure 2) are best adapted, fittest, and survive best.

The importance of reproductive isolation is easily overlooked, despite being fundamental to speciation. Mendel included a table describing how it works.[1,6] He illustrated the single two-trait character (or gene) situation. Organisms are typically diploid, their traits encoded twice, once in the paternally derived chromosomes, and once in the maternally derived chromosomes. Therefore, single-character organisms possess one of three possible genotypes: AA, Aa, or aa (which Mendel wrote as A, Aa, and a).

To begin with (generation P), all his plants were heterozygous; Aa. Table 1 shows what happens at each subsequent generation, F1–F4, (assuming each plant produces 4 viable seeds). Homozygous organisms have all homozygous traits. Here, there are two possible types: AA or aa. Heterozygous organisms have non-identical traits; i.e., Aa. If they self-cross, which Mendel's peas did, homozygous organisms will give rise to 4/4 offspring with identical homozygous genotypes; heterozygous organisms will give rise to all three genotypes in a 1:2:1 ratio. *With each successive generation, the homozygous organisms (highlighted in bold) overwhelm the growing population at an exponential rate. If reproductive isolation is maintained, the two homozygous phenotypes become two unique, separate species.*

The two gene, or double two-trait character situation gets quickly (exponentially) more complex. Such double-character organisms possess one of nine possible genotypes: AABB, AABb, AAbb, AaBB, AaBb, Aabb, aaBB, aaBb, or aabb. Table 2 shows what happens at each generation. Doubly homozygous organisms have two homozygous traits. There are four here: AABB, AAbb, aaBB, and aabb. Heterozygous organisms can be singly or doubly heterozygous: AABb, AaBB, Aabb, aaBb, or AaBb. If they can self-fertilize (which Mendel's peas could) doubly homozygous organisms will give rise to offspring with identical homozygous genotypes. Singly heterozygous organisms give rise to three genotypes in a 1:2:1 ratio, and doubly heterozygous organisms give rise to all nine genotypes in a 1:2:1:2:4:2:1:2:1 ratio.

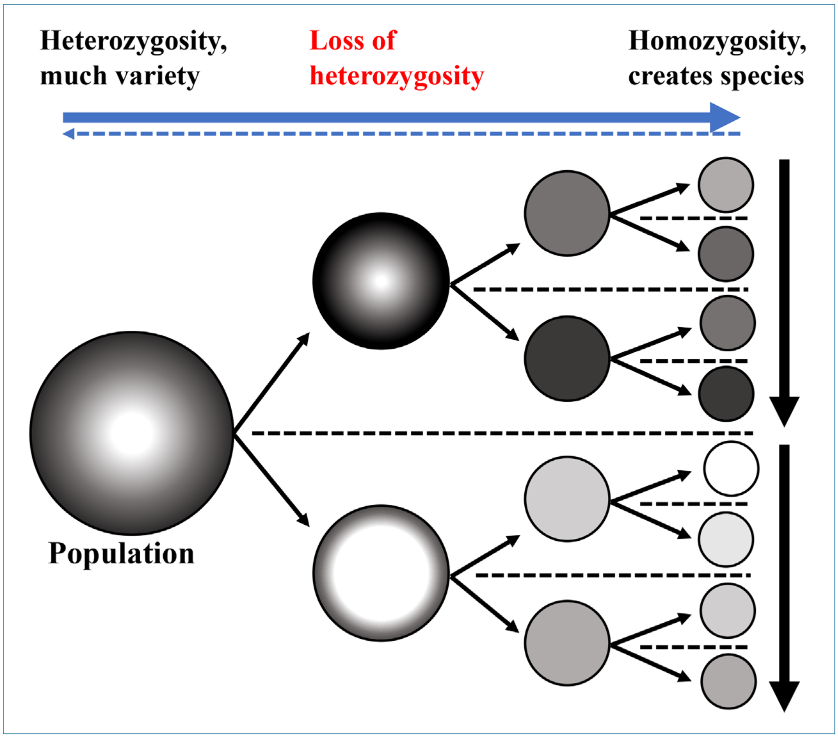


Figure 2. Loss of heterozygosity, reproductive isolation, and speciation. Populations are shown as circles. Each column of circles represents a consecutive generation. Over time, populations become reproductively isolated (dashed lines). Initially, the populations are genetically heterozygous (highly graded shading). However, with each successive generation they lose more and more heterozygosity, due to genetic drift, and eventually become homozygous, or fixed. At this point they form genetically distinct groups (uniform shading).

Table 1. Generational expectation of offspring number and genotype ratios for self-crossing (reproductively isolated) single-character organisms. The single character has two traits: one, A, is dominant; the other, a, is recessive. Offspring can be AA, Aa, or aa.

	Offspring number			Pop. size	Genotype ratios		
Generation	**AA**	**Aa**	**aa**		**AA**	**Aa**	**aa**
F1	**1**	2	**1**	4	**1**	2	**1**
F2	**6**	4	**6**	16	**3**	2	**3**
F3	**28**	8	**28**	64	**7**	2	**7**
F4	**120**	16	**120**	256	**15**	2	**15**
F(n)				4^n	$\mathbf{2^n-1}$	2	$\mathbf{2^n-1}$

Table 2. Generational expectation of genotype ratios for self-crossing (reproductively isolated) two-character organisms. Both characters display two traits: dominant A or B, recessive a or b.

Generation	**AABB**	AABb	**AAbb**	AaBB	AaBb	Aabb	**aaBB**	**aaBb**	**aabb**
F1	1	2	1	2	4	2	1	2	1
F2	9	6	9	6	4	6	9	6	9
F3	49	14	49	14	4	14	49	14	49
F4	225	30	225	30	4	30	225	30	225
F(n)	$(2^n-1)^2$				4	$2\cdot(2^n-1)$			

To find out what happens to a population of such plants over time, the simplifying assumption is made that each plant produces exactly 16 viable seeds. *With each successive generation the doubly homozygous organisms (highlighted in bold) overwhelm the growing population at an 'exponential-squared' rate. As long as reproductive isolation is maintained, the doubly homozygous offspring quickly become four unique, separate species.* (In table 2, for reasons of space and clarity, only offspring ratios are given; and general formulas for the genotype ratios (for the *double* and single homozygotes) are given only once).

Although the double-heterozygote ratios stay a constant four, *the doubly homozygote ratios* exponentially increase. (These ratios are conveniently simplified in this example; in reality, at each generation the fraction of double or pan-heterozygotes decreases at the rate $1/2^{ng}$; and *the total fraction of all pan-homozygotes increases at the rate* $[(2^n-1)/2^n]^g$, where n is the number of generations and g is the number of genes—here g is 2.)

This rapid increase in pan-homozygous phenotypes, which represents the origin of four separate species, only takes place in the presence of reproductive isolation. If reproductive isolation is not in place, all plants can cross with all plants (the pan-cross situation) and the genotype ratios remain identical at each generation; e.g., with one two-trait character = 1:2:1; with two two-trait characters = 1:2:1:2:4:2:1:2:1. When no reproductive isolation is in place heterozygosity stays high [$= 1 - (0.5)^g$], and no speciation occurs. Theoretically, however, this would require a population of infinite size.

Actual populations are always finite in size, and the smaller the population, the faster it loses heterozygosity. This relentless fixation, a process called random genetic drift,[4] occurs quickly in Mendel's pea plants because they are self-fertilizing. It is more typical, however, for species to reproduce sexually. This requires at least two individuals, and under these circumstances heterozygosity is lost, but more slowly. In small groups of organisms (demes) heterozygosity is lost even more slowly, and in large populations heterozygosity is lost but can be maintained for numerous generations. Eventually, random genetic drift always leads to fixation, but this can take many generations. In large populations, considerable genetic variation can definitely be present. A fifth paper discussing random genetic drift as it relates to Mendelian speciation is currently in preparation.

The chronology of speciation and speciation exhaustion

It has been suggested that fixation would lead to an apparent paradox, because no further speciation should be possible: speciation exhaustion. When Mendelian speciation occurred in the past, at first there would have been rapid production of species, but gradually, as more and more heterozygosity was lost and species became fixed, speciation would have come to an end. Today, certainly, much speciation appears to have run its course, and many species are stable. Yet new species sometimes arise. How is this possible?

At least three mechanisms are known. First, speciation occurs as a result of interspecies hybridizations, when reproductive isolation is lifted and heterozygosity is partially restored, as discussed in part 1 of this series.[2] Second, speciation could be considered to have occurred if sufficient latent genetic variation were activated or traits were modified (e.g., by epistatic, epigenetic, or transpositional mechanisms, as discussed in part 2 of this series[4]). Third, speciation could also occur in the presence of reproductive isolation. In large populations with significant residual heterozygosity, if a deme (small group) undergoes a bottle-neck event, becoming reproductively isolated via physical isolation or expression of a veritable plethora of pre-zygotic and post-zygotic barriers,[7] loss of heterozygosity and speciation would proceed quickly and independently in the deme. This process has been observed on islands and in large lakes.[7]

When strict reproductive isolation is in place, as tables I and II confirm, at each generation heterozygosity decreases (is lost). Homozygosity, however, increases, and all the more so as the number of characters (genes) increases. *This is speciation in a nutshell. Reproductively isolated organisms with unique combinations of homozygous dominant and recessive traits (involving multiple genes) are typically considered separate species.*

A notable example of speciation is observed in the six abalone species found along the Pacific coast of California. They share the same marine environment, they freely release their gametes into the sea, and they are able to produce hybrids. Nevertheless, they remain reproductively isolated because of sympatric speciation.[8] This is a genetic process caused by gradual but progressive alteration of the interaction site between a ligand from the sperm cell and its receptor on the oocyte. In eukaryotes, sperm must locate, attach to, and fuse with the egg. The structures of the egg envelope are highly variable and taxon-specific, as shown in figure 3.[9] Egg–sperm interaction serves both for reproductive isolation and to assess the reproductive compatibility of the two parents. It is a major cause of sympatric speciation.

As in allopatric speciation, in sympatric speciation subpopulations are separated, and altered phenotypes (or species) emerge through the resulting loss of heterogeneity. The changes occur continuously and result in the continuous generation of subpopulations with unique phenotypes, which have the potential to become separate species.[10]

Buri demonstrated that loss of heterozygosity occurs randomly when subpopulations remain reproductively isolated.[11] A closer look at nature reveals a wealth of behavioural, morphological, or genetic mechanisms, which maintain reproductive isolation between species, thereby preserving their unique combinations of traits. If not, hybrids arise, and sometimes small species can even go extinct, merging into other species through hybridization.[12,13]

A species' current reproductive isolation may have been caused just once in the past by a single mechanism. However, the ancestors of an emerging species may have experienced the effects of various mechanisms of reproductive isolation. Some may have arisen through allopatric speciation, others through sympatric speciation.

Isolation mechanisms can be genetic, encoded in the genome of a species. These can affect a species' phenotype, structure, behaviour, or other features. The nature of previous isolation mechanisms determines to what extent genetic variability is still present. Loss of heterozygosity can be minor or significant, as mentioned in part 2 of this series. Considerable potential for variation, and thereby adaptability to environmental factors, remains in the case of the grove snail, *Cepaea nemoralis*, shown in figure 4, and in the wood tiger moth, *Arctia plantaginis*.

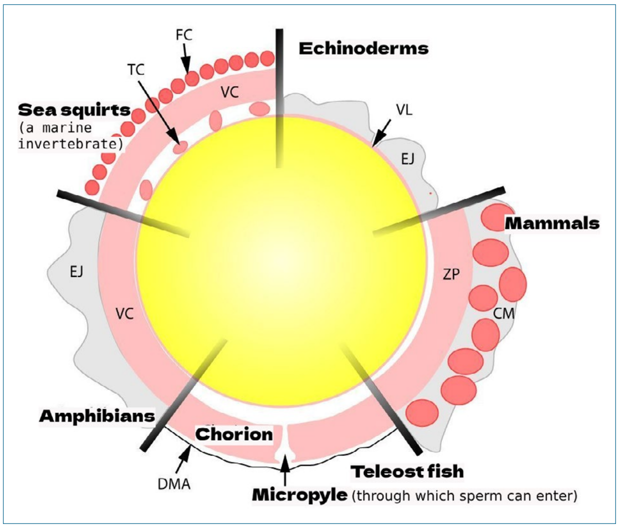


Figure 3. The structures of the outer layers of the egg complex in different groups of animals. The egg is displayed in yellow. Its outer extracellular layer, the egg envelope, shown in pink and grey, varies between animal taxa and forms one of various selective barriers preventing fertilization by incompatible sperm. Abbreviations: CM Cumulus protective layer (*corona radiata*); DMA aqueous slime zone; EJ egg jelly; FC follicular cells; TC test cells; VC vitelline shell; VL vitelline layer; ZP zona pellucida.[9]

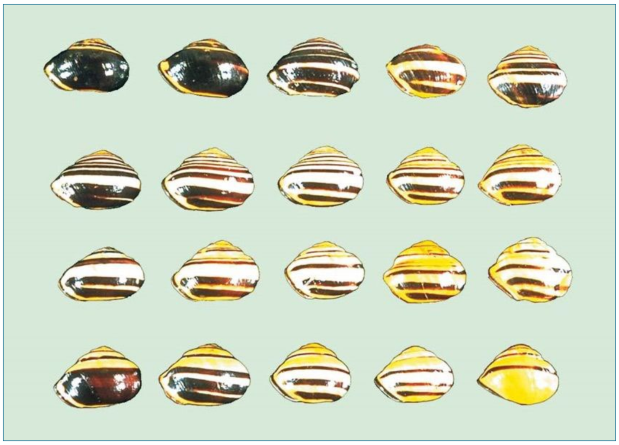


Figure 4. The grove snail, *Cepaea nemoralis*, is an example of a species which has retained much genetic potential for variability. (From Junker & Scherer 2013, with permission).[14]

Extreme reproductive isolation can lead to significant loss of heterozygosity, preventing the resulting genetically homogeneous species from being able to adapt to new, potentially challenging, environments. Examples of this are known in the cheetah, *Acinonyx jubatus*, and the northern elephant seal, *Mirounga angustirostris*.[15,16]

Difference between family and species

How do Mendel's experiments with plant hybrids help clarify what a species is, and what a family is? Let's assume that an ancestral species had 20 heterozygous genes. This

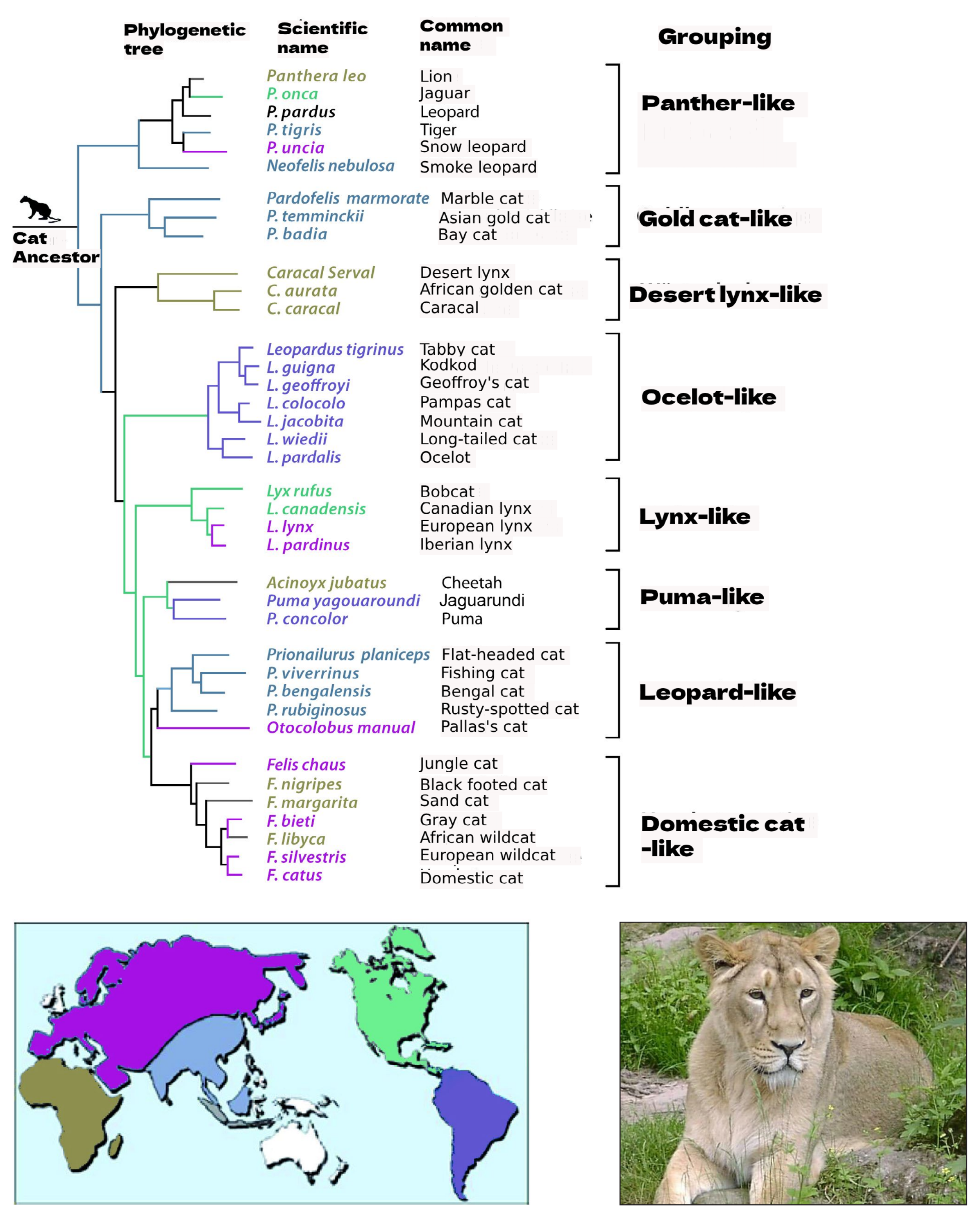


Figure 5. Dendrogram of the cat groups. The end points correspond to a species. The colours link them to the continent(s) they live on. Of all cats, the leopard has the widest geographic distribution, from Africa through southern Eurasia to East Asia. Redrawn from Johnson *et al.*[18] (where additional information such as genetic distance etc. is also available). Inset picture: Female Asiatic lion (*Panthera leo perisca*). (Photo: Edradour, CC BY-SA 3.0; translated and modified by R. Truman using Photopea; photopea.com).

species could theoretically produce more than a million (2^{20} = 1,048,576) unique homozygous trait combinations (phenotypes). Many of these descendants would be assigned to separate species, and even separate genera, because of extensive phenotypic differences.

In this limiting case of just 20 heterozygous genes, these million different phenotypes represent a basic limit to the potential phenotypic diversity of the ancestral species. In theory, all the descendants belong to the same species, the pan-heterozygous ancestor. However, for practical reasons, due to their significant phenotypic differences and reproductive isolation, they are often classified into separate species and genera within a single overarching genetic family. When reference is made in the Bible to plants and animals being made "after their kind", it is reasonable to equate this reference with the ancestral pan-heterozygous organisms, which are capable of giving rise to a plethora of related descendant species; i.e., after their kind. These differ significantly, but still within genetically defined limits, from their ancestral origin. As such, the Genesis kinds (also called 'baramins') are considered to be these genetic families.

For example, lions, tigers, servals, cheetahs, lynxes, leopards, pumas, and domestic cats are all members of the Felidae family. They likely share a single common pan-hybrid ancestor. Based on the criterion of being able to interbreed, most cat species belong to a single basic type.[17] They share the same characters and the same genes, and form a genetic family as shown in figure 5.

The combinations of constant traits (combinations of homozygous dominant and recessive alleles) are the basis for their classification into unique species and genera.

Similarly, the Birds of Paradise display a spectacular array of amazing phenotypes. DNA sequence studies show that they are all members of the family Paradisaeidae. The ability of most species to hybridize confirms they belong to a single basic type.[19] The fact that the various intergeneric hybrids show similar phenotypes strongly indicates they all descend from a common pan-heterozygous ancestor.[20] The Birds of Paradise are a genetic family.

Conclusions

Mendelian speciation is based on his law of exponential trait combinations. It is an efficient genetic mechanism for the emergence of biological diversity. It is a meiotic process of global genomic change, and because of loss of heterozygosity it leads to polygenic fixation of unique phenotypes. It is a highly effective mechanism of speciation. It is accompanied by reproductive isolation, and the progeny are constrained in groups of separate, less variable, populations. Mendelian speciation eventually gives rise to whole genetic families of related species, completely consistent with plants and animals being created after their kind. Mendelian speciation readily occurs because the genetic information required for speciation is already present in the genomes of ancestral organisms, though usually unseen; i.e., present in a latent state.

A fourth accompanying paper[21] describes fascinating examples of rapid and extensive speciation episodes, 'microevolution on steroids', referred to as 'adaptive radiations'. It examines how Mendelian speciation readily accounts for these extraordinarily impressive examples of natural diversity; attended by, though certainly not requiring any, mutation events.

Glossary

Adaptive radiation: Emergence of many differently adapted species from one ancestral form.

Allele: Variant of the same gene, having a unique nucleotide sequence. When a gene is sequenced; what is almost always meant is that a single allele of the gene was sequenced.

Allopatric speciation: Speciation caused by physical (geographical) separation.

Epistasis: Gene interaction. The action of one gene, called 'epistatic', masks the effects otherwise caused by another gene, called 'hypostatic'.

Gene: The functional unit of heredity. Usually, restricted to a single site in the genome that may then be called its 'locus'. Its variants are referred to as 'alleles'. In his classic paper,[1] Mendel referred to these units of heredity as 'elements'.

Genetic family: A family whose species are characterized by common genetic ancestry. It is similar in concept to a Genesis kind or a baramin. It results from Mendelian speciation.

Genome: An organism's chromosome complement.

Heterozygous: When information for more than one trait of a gene is present in the genome; also, when a gene has two different alleles.

Homozygous: When information for only one trait of a gene is present in the genome; also, when a gene has two identical alleles.

Karyotype: The number and visual appearance of the chromosomes.

Meiosis: Formation of four (usually unique) genomes from a single parental genome when the sex cells develop.

Pan-heterozygous: When all genes are heterozygous.

Pan-homozygous: When all genes are homozygous.

Recessive allele: An allele, the expression of which is suppressed by the effect of a dominant allele.

Recombination: The mixing of portions of homologous chromosomes and the mixing of chromosome sets, during meiosis when the sperm and egg are formed.

Reproductive isolation: Separation of sub-populations, and suppression of gene exchange.

Speciation: When a species splits into two daughter species.

Sympatric speciation: Evolution of new species from an ancestral species when both continue to inhabit the same geographic location.

Translocation: Rearrangement of chromosome segments.

Zygote: A fertilized egg cell resulting from the fusion of a sperm and an egg cell.

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