

How Evolution Works

The word evolution means change. The ancient Greeks and Romans studied fossils, compared organisms, and philosophized about how plants and animals originated and survived. Through centuries of refinement, these ideas developed into the current biological definition of evolution as inherited change within a lineage. Over time, these inherited changes give rise to a new species.

By the 1800s, it was generally accepted among geologists and naturalists that the Earth was very old and that the vast **diversity** of species on Earth was the product of evolution. The big question, however, was how species evolve. There are now two widely accepted mechanisms for how species evolve: natural selection and genetic drift. Both of these processes are dependent upon variation, both genetic and morphological.



Diversity in a living population of the Bittersweet Clam (*Tucetona pectinata*) from Marathon, in the Middle Florida Keys.

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diversity • The variety of species in a sample, community, or area.

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heridity (adj. **heritable**) • The biological similarity of offspring and parents.

mutation • A change in the nucleotide sequence of genetic material whether by substitution, duplication, insertion, deletion, or inversion.

polychromism (adj. **polychromic**) • Polymorphism expressed as existing in several different colors.

variation • The differences among individuals in a population.

Variation

Variations are inheritable differences among the individuals of a single species. Often, with a quick glance, most individuals within a species look very similar, however, upon closer examination, many variations can be noted. Many can be easily observed, such as size, shape, color, texture, speed, etc. Others might be more difficult to observe but can be very important in terms of evolution. For example, there are often variations in the ability to produce offspring, hunting or hiding skills, and the ability to resist heat, cold, stress, drought, disease, etc. For variations to be acted upon by natural selection, they must be **heritable**; they are often the results of genetic **mutation**.



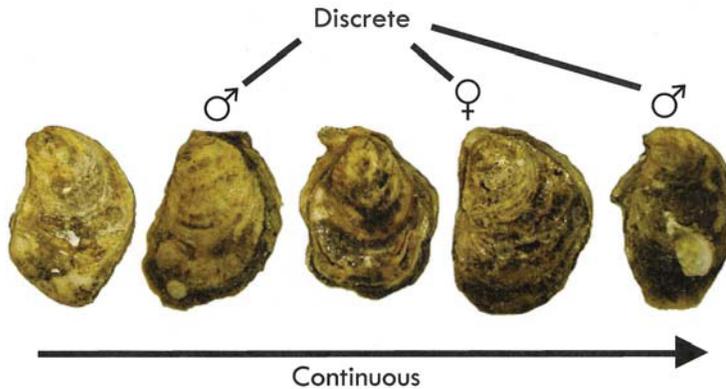
Polychromism (many color forms in a single species) is shown by these Florida Coquina Clams (*Donax variabilis*). Predatory shore birds recognize a coquina as food by its appearance, forming a "search image." If some Coquinas look different, they might not match the search image of the bird, and thus might be passed over as "not food," providing a survival advantage. In such cases, polychromism is maintained in a population.



Variation in size, shape, and color of the Eastern Oyster (*Crassostrea virginica*).

There are two main types of variation: continuous and discrete.

- **Continuous variation** results in a spectrum of variety (for example, in shell color, from light to dark) without clear-cut, separate categories; there are not only light and dark varieties but also a range of hues (potentially every hue) in between.
- **Discrete variation** exists in a limited number of clearly separable varieties; a good example of this is gender – most species exist in only two varieties - male and female.



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continuous variation • Variation measured on a continuum rather than in discrete units or categories (e.g., height in human beings, shell length in bivalves).

discrete variation • Variation within a limited number of categories (e.g., gender – male or female).

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genotype • The genetic makeup of an organism or group of organisms with reference to a single trait, set of traits, or an entire complex of traits.

natural selection • The process by which living forms with traits that better enable them to adapt to specific environmental pressures, e.g., predators, changes in climate, or competition for food or mates, will tend to survive and reproduce in greater numbers than others of their kind, thus ensuring the perpetuation of those favorable traits in succeeding generations.

phenotype (adj. phenotypic) • The observable physical or biochemical characteristics of an organism, as determined by both genetic makeup and environmental influences; what an organism “looks like.”

Natural Selection

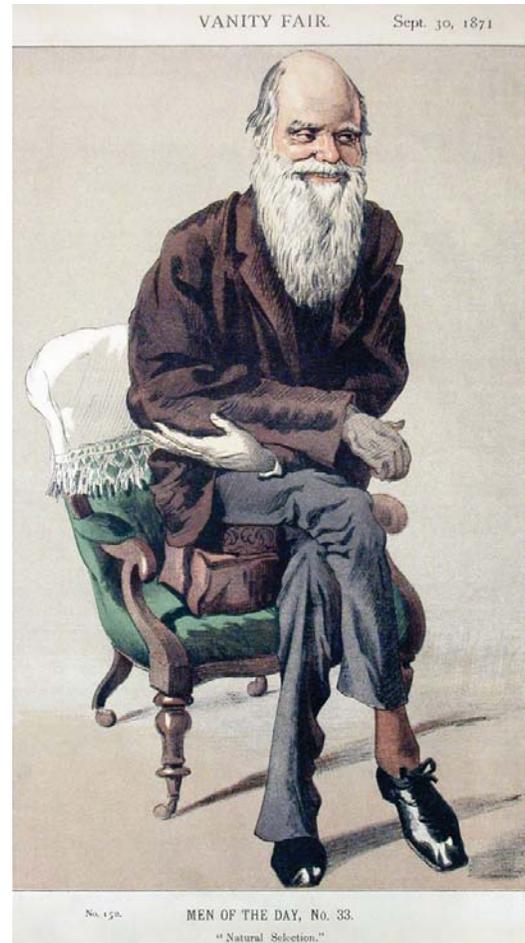
Charles Darwin is best known for his 1859 publication *On the Origin of Species by Means of Natural Selection* in which he proposed the first credible mechanism for evolutionary change: **natural selection**, sometimes also called “Darwinism.”

Natural selection includes six main principles:

1. **Variation:** All individuals within a species are unique, with **phenotypic** variations in body, chemistry, and/or behavior.
2. **Heredity:** Some of these variations will be inherited by offspring.
3. **Overproduction:** More offspring are produced than can survive.
4. **Limited resources:** Survival and reproduction are determined by competition for limited resources such as food, habitat, or mates.
5. **Fitness:** Some individuals (sometimes called “the fittest”) have variations (traits or features) that give them an advantage within their environment; these individuals will survive to reproduce and pass on those traits to their offspring.
6. **Genetic composition:** In subsequent generations, there will be a higher percentage of individuals that possess advantageous traits.

Therefore, the advantageous traits (that help certain individuals survive and reproduce) are said to be “selected” or favored by natural selection and are thus perpetuated through later generations. Over time, unsuccessful traits will disappear, advantageous traits will become more common, and, if and when the differences are great enough, new species will evolve.

Natural selection acts upon **phenotype**, not **genotype**. Although there can be a large number of genetic variations (genotypes) within a population, natural selection is only able to occur if the genetic variations result in physical, chemical, or behavioral expressions (phenotypes) in individuals.



This caricature of Charles Darwin by James Joseph Jacques Tissot (1836-1902), entitled “Natural Selection,” was published by Vanity Fair magazine in September 1871.

Some common misconceptions about natural selection are:

- 1. Natural selection has an inevitable result - *False*.** An important basis of natural selection is that variation is random and selection is natural, without intervention or predetermination. Natural selection has no direction. It is simply the process by which random variations that give an individual a favorable adaptation to its environment survive to be passed on to offspring.
- 2. Natural selection selects against unfavorable variations - *False*.** Natural selection is a positive, creative force of evolutionary change, not an executioner of the unfit. In other words, no feature or individual is "selected against." If a particular variation is "selected," an individual survives and produces offspring. If that variation is not selected, (a) the individual leaves fewer offspring, or (b) the individual is sterile and leaves no offspring, or (c) the individual dies before reproducing.
- 3. Traits that are advantageous remain advantageous - *False*.** The traits that are advantageous depend entirely upon the current environmental context. So, traits that are successful in one environment might be very detrimental in another setting or if the environment changes. Of particular concern is when the environment dramatically changes quickly (as we are seeing today as part of climate change or "global warming"). The advantageous traits of the previous generation can thus become the less advantageous traits among the offspring. Dramatic environmental changes often lead to mass extinctions, in part for this reason.
- 4. Variations make organisms better - *False*.** Most variations generated by random mutation are actually detrimental and are eventually lost through natural selection.
- 5. Survival of the fittest means that only the best survive - *False*.** "Survival of the fittest" is an often misinterpreted and misused phrase, especially in political or social terms. Fitness in the Darwinian sense does not necessarily mean long life, a hot car, and a million-dollar house. Evolutionarily, an underpaid waiter who dies at age 35 leaving five surviving children is more "fit" than an 80-year-old millionaire with one spoiled heir. Fitness in the Darwinian sense is defined as the relative genetic contribution to the next generation.
- 6. Natural selection of advantageous traits makes the species more complex - *False*.** Clams and humans are both equally suited to their environment. Although the human body is in many respects much more complex than the body of a clam, modern clams and humans are similarly "evolved." In fact, clams have been on Earth much, much longer than humans.

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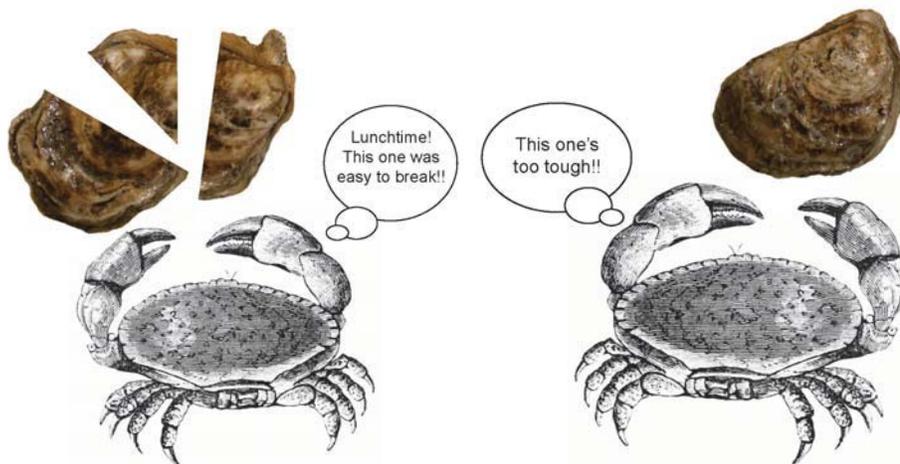
Natural selection can occur with or without environmental change.

1. In a constant environment, natural selection will keep a population stable and essentially maintain the status quo.
2. In a constant environment, if a new variation arises that is more advantageous, the new trait will be perpetuated and the species will evolve.
3. In a changing environment, natural selection will favor variations that result in a better fitness in the new environment, resulting in adaptation and evolution.

Directional Selection

Directional selection occurs when natural selection favors one extreme of continuous variation. Over time, the favored extreme will become more common and the other extreme will be less common or lost.

If thicker-shelled oysters are more resistant to breakage than thinner-shelled oysters, crabs will be less able to prey upon them, and thicker-shelled oysters will be more likely to survive to reproduce.



Stabilizing Selection

Stabilizing selection occurs when natural selection favors the intermediate states of continuous variation. Over time, the intermediate states become more common and each extreme variation will become less common or lost.

Continuing our oyster example, very light-colored or very dark-colored oysters might be more frequently preyed upon by shore birds, simply because they are more obvious on the oyster bar; as a result, the intermediate hues become more common.



directional selection • A type of natural selection that removes individuals from one end of a phenotypic distribution and thus causes a shift in the distribution.

stabilizing selection • A type of natural selection that removes individuals from both ends of a phenotypic distribution, thus maintaining the same distribution mean.

Disruptive or Diversifying Selection

Disruptive selection occurs when natural selection favors both extremes of continuous variation. Over time, the two extreme variations will become more common and the intermediate states will be less common or lost. Disruptive selection can lead to two new species.

This might happen in shallow water among rocks. Light-colored oysters are more cryptic (less easy for a predator to see) because they match the rock color. Dark-colored oysters blend into the shadows cast by the rocks. In this case, intermediate-colored oysters would be most heavily preyed upon by the crabs, and very light and very dark oysters would survive to reproduce.



Kin Selection

Kin selection occurs when natural selection favors a trait that benefits related members of a group. Altruistic behaviors are a result of kin selection, and are best illustrated by animals with complex social behaviors. Worker bees exhibit altruistic behavior by spending their lives serving the hive while never having an opportunity to reproduce on their own. In terms of simple fitness, the worker bee does not reproduce and therefore the traits that allow it to be a worker should be selected against. However, because all of the bees in the hive are close relatives, a worker bee's genes will be passed to the next generation indirectly through the queen. The queen is able to produce many more related offspring than the worker alone. As a result, servicing the queen to allow her to reproduce a larger number of offspring results in a higher fitness for the worker bee even though it never reproduces directly.

Sexual Selection

The evolutionary fitness of an organism not only depends upon its ability to survive but also its ability to reproduce. To reproduce, an individual must obtain a mate and produce viable offspring. Natural selection favors traits that maximize the ability of an individual to compete for and attract mates, and/or the ability to produce offspring – this is called **sexual selection**.

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disruptive selection • A type of natural selection that removes individuals from the center of a phenotypic distribution and thus causes the distribution to become bimodal.

kin selection • A type of natural selection that involves altruistic behavior, e.g., the protection of offspring, in which a parent acts to preserve the gene pool of offspring at the expense of itself.

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sexual selection • A type of natural selection in which the forces determined by mate choice act to cause one genotype to mate more frequently than another genotype.

- **Sexual dimorphism.** Sexual dimorphism is when males look different than females of the species. Some of the most obvious examples involve animals that attract mates by virtue of their appearance, such as peacocks with larger, more flamboyant tail fans. The male that is most attractive will win the right to mate with the female. Over time, the features that most attracted the females will become more common.

Some freshwater pearl mussels also exhibit sexual dimorphism, but obviously not to visually attract a mate. The endangered Cumberlandian Combshell (*Epioblasma brevidens*) of the American midwest is a medium-sized (to 2 inches) mussel with an oval to quadrate shell. Female shells have a low bulge along the edge of the shell that accommodates the enlarged gills in which it broods its larvae; males lack this bulge and are more streamlined. In this example, females that have a larger bulge (= larger gills) might produce more offspring, ultimately leading to a population with females that have larger bulges and larger gills.



Females of the Cumberlandian Combshell have a low bulge along the edge of the shell that accommodates enlarged gills for brooding larvae; males have more streamlined shells.

- **Mating rituals and other complex behaviors.** As with appearance, males that have the most attractive mating ritual potentially win the right to mate with the female. Birds provide the best examples of complex mating rituals, often involving dances, vocalizations, and fluffed up feathers. Over time, the rituals most preferred by the females will become more common.

There are no good examples of mating rituals among bivalves, but we can look to their relative, the octopus. The Day Octopus (*Octopus cyanea*), found in the South Pacific and Indian Oceans, has an elaborate mating ritual that signals his mating intent to the female. The ritual involves arm waving and skin darkening as the male approaches the female. If the male is positively received, the female is inseminated by the placement of spermatophores into her oviduct through the use of his modified arm. The female then lays thousands of eggs inside her lair. In this way, successful male rituals are passed down to offspring; males whose displays fail to attract a mate do not produce offspring.



Octopus cyanea on a reef in Kona, Hawaii.

Freshwater pearl mussels have an interesting behavior of another sort related to reproduction. Female mussels brood their larvae, called **glochidia**, in their gills. But these glochidia depend on an intermediate host to complete their life cycle – they must attach to the gills or fins of a fish for a period of time before they can settle and metamorphose into baby mussels. Some female freshwater mussels have modified flaps of tissue near their



The Wavy-Rayed Lampmussel (*Lampsilis fasciola*), of the American Midwest, has an elaborate lure display.

siphons – called a “lure” – that flutters in the water to attract a fish. When the fish draws near the lure (thinking that it might be something to eat), the mussel releases a cloud of glochidia, which then attach to the fish. Conceivably, females with lures that are more effective in attracting fish will produce more offspring. See more about this specialized reproductive mode under *Life Cycles* in the section **The Evidence for Evolution: Developmental Biology.**

- **Male-male competition.** In species with males that battle over rights to mate with females, such as elephants and deer, the male that wins a fight because he is the strongest, most dominant, or most intelligent will win the right to mate with the female. Over time, the features that allow the males to win (larger tusks, larger antlers, larger body size) will become more common.

We again look to the octopus for a molluscan example. Octopus males are very aggressive when fighting over females. They are seen wrestling and rolling around on the sea floor. In some cases, they have been observed strangling an opponent by cutting off the flow of water to its gills.



The Common Octopus, *Octopus vulgaris*, is found worldwide in tropical and semitropical waters from nearshore shallows to as deep as 200 meters (over 650 feet). It is one of the most studied invertebrate animals.

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glochidium (pl. **glochidia**) • The specialized larval form of freshwater pearl mussels that usually has hooks that enable it to attach itself to a host (e.g., to the gills of a fish) for a period of time before it detaches and falls to the bottom and takes on the typical form of a juvenile mussel.

siphons • Posterior extensions (usually two) of the mantle through which water is directed in and out of the body, along with waste products and gametes of bivalves.

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allele • An alternative form of a gene; one of the different forms of a gene that can exist at a single locus.

effective population size (N_e) • The number of individuals in a population that can actively contribute to the gene pool of the next generation.

gene frequency • The number of occurrences of an allele in a gene pool.

gene pool • The complete set of unique alleles in a species or population.

Hardy-Weinberg Equilibrium (or Principle or Law) • The principle that states that when $N_e = N$, in the absence of selection or mutation, gene frequencies will achieve equilibrium after one generation.

population • A group of interbreeding individuals and their offspring.

population size (N) • The number of individuals sharing a gene pool; a complete set of alleles.

Hardy-Weinberg Equilibrium

Evolution can be defined simply as inherited change within a lineage, however, various mechanisms within a lineage can affect the genetic variation in a natural population.

Populations

A **population** (a group of interbreeding individuals and their offspring) fluctuates in **population size (N)** over time. The genetic variation within that population is expressed by the frequencies of the various **alleles** (gene variants); these frequencies vary over time and are affected by changes in population size. Because not all individuals in a population contribute equally to reproduction, **effective population size (N_e)** is usually less than the actual population size (N), so that $N_e < N$.

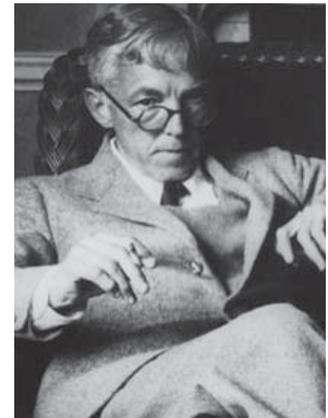
Four factors typically regulate effective population size (N_e):

1. **Breeding sex ratio** – If one sex is rarer than the other in the population, it is likely that all members of that rarer sex will mate and reproduce. Therefore, the rarer sex will dominate the gene pool and it is more likely that genes of the rarer sex will be passed on to the next generation.
2. **Population size** – If the population size (N) fluctuates, effective population size (N_e) will be dominated by the smallest gene pool.
3. **Breeding groups** – If the population forms small groups for breeding (e.g., prides of lions), $N_e = N_g$ (population size of a group). N_e is influenced by how long small groups last and by the amount of migration between groups.
4. **Fertility** – Individuals within population often vary in fertility; more fertile individuals will have a greater influence on the gene pool.

In practice, N_e is difficult to measure. $N_e = N$ when none of the four factors listed above apply to a population. In this case, the sex ratio is 1:1, the population is of a constant large size, mating is random (no groups exist), and fertility is approximately equal among individuals. Under these ideal conditions (when $N_e = N$), after one generation (and assuming that there is no selection or mutation), the population's **gene frequencies** will attain equilibrium.

The Hardy-Weinberg Equation

The above mentioned equilibrium, known as the **Hardy-Weinberg Equilibrium (or Principle or Law)**, states that when $N_e = N$, in the absence of selection or mutation, gene frequencies will achieve equilibrium after one generation. The term was named after English mathematician Godfrey Harold Hardy (1877-1947) and German physician Wilhelm Weinberg (1862-1937), who independently and nearly simultaneously published on the principle in 1908. [It was called Hardy's Law for a brief time, because Weinberg had published his results in an obscure German journal.]



Godfrey Harold Hardy

These equilibrium values are expressed as simple functions of gene frequencies, where the frequency of the dominant allele (A) = p, the frequency of the recessive allele (a) = q, and $p + q = 100\%$.

Hardy-Weinberg Equilibrium

After one generation, gene frequencies will achieve equilibrium:

p = frequency of dominant allele (A)

q = frequency of recessive allele (a)

$$p + q = 100\%$$

	A	a
A	AA	Aa
a	Aa	aa

$$p^2 + 2pq + q^2 = (p + q)^2$$

	A (p)	a (q)
A (p)	AA (p^2)	Aa (pq)
a (q)	Aa (pq)	aa (q^2)

p^2 = frequency of dominant homozygote (AA)

$2pq$ = frequency of heterozygote (Aa)

q^2 = frequency of recessive homozygote (aa)

Although the Hardy-Weinberg Equation in its simplest form (above) is calculated for two alleles, it is easily expanded for three or more alleles.

- Expansion for three alleles: $(p + q + r)^2 = p^2 + r^2 + q^2 + 2pq + 2pr + 2qr$
- Expansion for **polyploidy** = $(p + q)^c$, where c = **ploidy**
e.g., tetraploidy, c = 4: $(p + q)^4 = p^4 + q^4 + 4p^3q + 6p^2q^2 + 4pq^3$

	AA (p^2)	Aa (pq)	aA (pq)	aa (q^2)
AA (p^2)	AAAA (p^4)	AAAa (p^3q)	AAAa (p^3q)	AAaa (p^2q^2)
Aa (pq)	AAAa (p^3q)	AAaa (p^2q^2)	AAaa (p^2q^2)	Aaaa (pq^3)
aA (pq)	AAAa (p^3q)	AAaa (p^2q^2)	AAaa (p^2q^2)	Aaaa (pq^3)
aa (q^2)	AAaa (p^2q^2)	Aaaa (pq^3)	Aaaa (pq^3)	aaaa (q^4)

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ploidy • The number of sets of chromosomes in a cell or organism.

polyploidy (adj. polyploid) • More than two sets of chromosomes in a cell or organism.

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polychromism (adj. *polychromic*)
• Polymorphism expressed as existing in several different colors.

Using the Hardy-Weinberg Equation

The Hardy-Weinberg equation can be used to calculate gene frequencies (under Hardy-Weinberg conditions) from any one of its components.

Example 1: In one hypothetical Zebra Mussel (*Dreissena polymorpha*) population, most of the individuals have dark, zebra-striped shells (below left). However, solid light-colored shells (below right, caused by a homozygous recessive gene, aa) occur in 1 of every 10,000 individuals.



Problem: Calculate gene frequencies and numbers of dominant homozygotes (AA, at left) and recessive homozygotes (aa, at right) in a population of 10,000 individuals.

Solution:

- frequency of aa = $q^2 = 1/10,000 = 0.0001$, so $q = 0.01$
- number of aa = $0.0001 \times 10,000 = 1$ individual
- $p + q = 1$, so $p = 0.99$
- frequency of AA = $p^2 = 0.9801$
- number of AA = $0.9801 \times 10,000 = 9,801$ individuals
- For extra credit: frequency of Aa = $2pq = 2 \times 0.9801 \times 0.01 = 0.0198$ or 198 individuals

Example 2: The Coquina Clam (*Donax variabilis*) is highly **polychromic** (with shells of many different colors). In a population of 2,000 clams, 1,920 are solid colored, whereas the remainder has radiating color bands. Solid color occurs in homozygous dominant (BB) and heterozygotes (Bb); color banding only occurs in homozygous recessive individuals (bb).



Problem: Calculate gene frequencies and numbers of BB and Bb.

Solution:

- 1,920 are solid (BB and Bb), so 80 banded are recessive (bb)
- frequency of bb = $q^2 = 80/2000 = 0.04$, so $q = 0.20$
- $p + q = 1$, so $p = 0.80$
- number of BB: $p^2 = 0.64$, so BB in population of 2,000 = $0.64 \times 2,000 = 1,280$ individuals
- number of Bb: $2pq$ [frequency of Bb] = $2 \times 0.2 \times 0.8 = 0.32$, so Bb = $0.32 \times 2,000 = 640$ individuals

Deviation from the Hardy-Weinberg Equilibrium

The Hardy-Weinberg Equilibrium can be used as a null hypothesis, compared to values from a real population, to describe statistically significant deviations from the Equilibrium. If the deviation is significant, then the gene frequencies are changing and thus, *evolution is occurring*.

Example 3: In a population of Zebra Mussels (*Dreissena polymorpha*), 1,469 individuals have the CC form of the enzyme phosphoglucose isomerase (PGI), an enzyme critical in the second step of glycolysis. Another 138 have the Cc form of PGI, and another 5 individuals have the form cc of the enzyme. All of these forms of the enzyme are fully functional.

Problem: Is this population in Hardy-Weinberg Equilibrium?? [In other words, the null hypothesis is that the population is at H-W equilibrium.]

Solution:

- p = frequency of dominant allele (C) = $2(CC) + 1(Cc) / 2n$
 $= 2 \times 1,469 + 138 / 2 (1,469 + 138 + 5) = 3,076 / 3,224 = 0.954$
- $q = 1 - p = 0.046$
- For this example, HW expectations are:
 - $Exp(CC) = p^2n = 0.9542 \times 1,612 = 1,467.4$
 - $Exp(Cc) = 2pqn = 2 \times 0.954 \times 0.046 \times 1,612 = 141.2$
 - $Exp(cc) = q^2n = 0.0462 \times 1,612 = 3.4$
- determine deviation of actual from HW expectations:

	CC	Cc	cc
O (actual)	1,469	138	5
E (H-W)	1,467.4	141.2	3.4
Deviation	1.6	-3.2	1.6

- Is the deviation significant? Use Pearson's Chi-square (χ^2) test for significance:

$$\chi^2 = \sum \frac{(O - E)^2 \text{ (square of deviation)}}{E} \text{ for each genotype}$$

$$= \frac{(1469 - 1467.4)^2}{1467.4} + \frac{(138 - 141.2)^2}{141.2} + \frac{(5 - 3.4)^2}{3.4}$$

$$= 0.001 + 0.073 + 0.756 = 0.823$$

- Look up 5% significance level for 1 degree of freedom = 3.84 [look up in a table or use a significance calculator]
- Because the calculated χ^2 (0.823) < 3.84, the actual and expected values are not significantly different, the null hypothesis is not rejected, and we conclude that the population is (currently) at Hardy-Weinberg Equilibrium.

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How to find significance levels: Search your web browser for "Table of Chi-square statistics."

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genetic drift • Change in the gene pool that occurs when the frequency of an allele changes over generations due to random chance.

phenotype (adj. **phenotypic**) • The observable physical or biochemical characteristics of an organism, as determined by both genetic makeup and environmental influences; what an organism “looks like.”

Genetic Drift

Real populations rarely exist under the rigid conditions of the Hardy-Weinberg Equilibrium. Instead, gene frequencies in real populations change randomly with time through **genetic drift**.

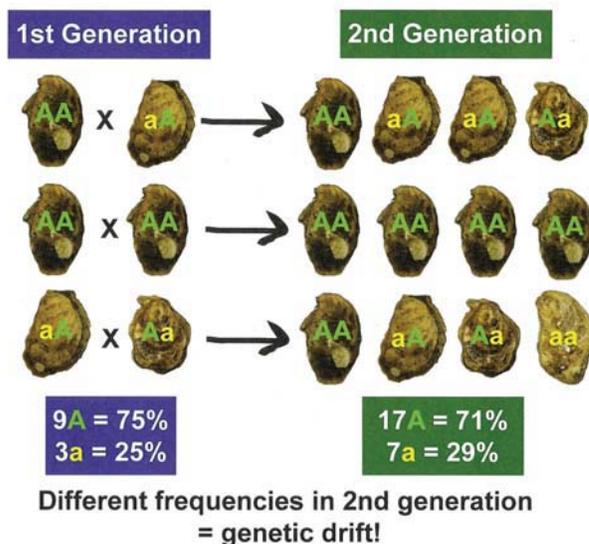
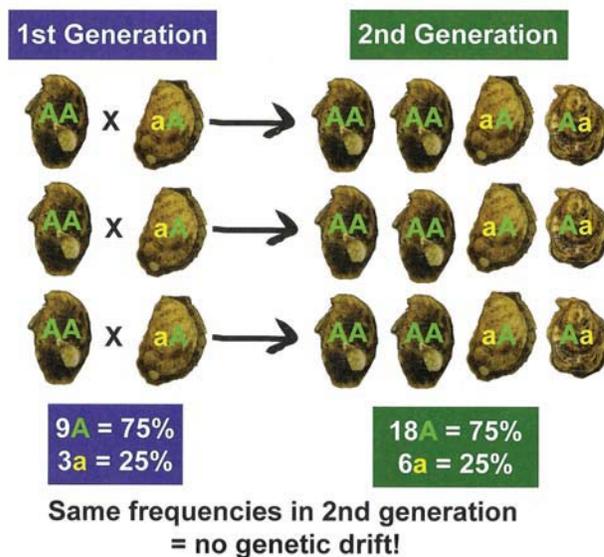
There are two main mechanisms of evolution, natural selection and genetic drift. Genetic drift occurs when the frequency of an allele changes over generations due to random chance. Evolution due to genetic drift is not caused by environmental or other kinds of stresses on individuals, and the resulting random changes can be detrimental, neutral, or beneficial to the reproductive success of the following generation.

The effects of genetic drift are much easier to see in small populations. Whereas the effects of genetic drift on large populations are minor compared to the entire gene pool and are often overshadowed by natural selection, genetic drift working in small populations can quickly result in big changes.

Suppose you have 6 oysters, 3 dark-colored (AA genotype) and 3 medium-colored (Aa genotype). In this population, you have a total of 9 A alleles and 3 a alleles, or 75% A and 25% a.

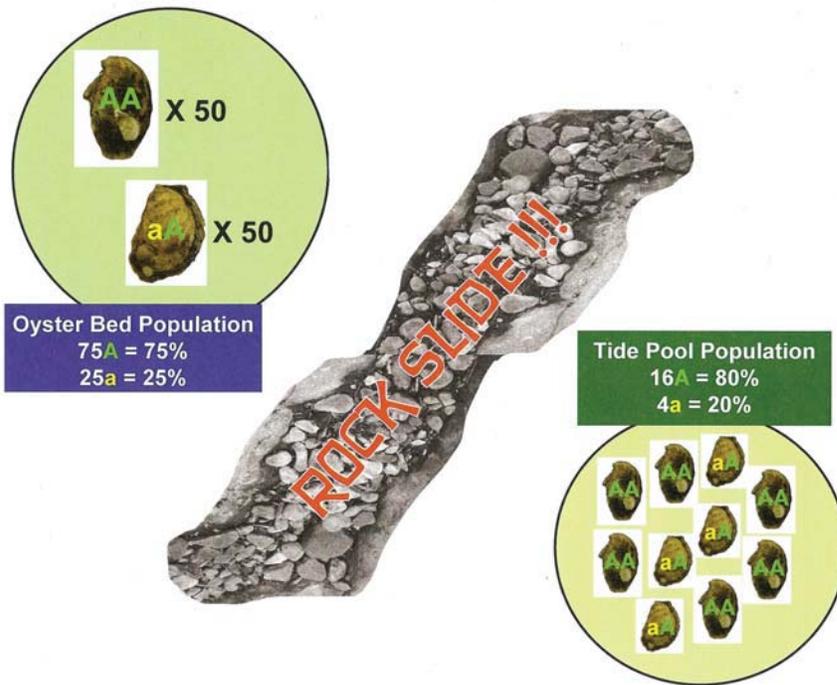
If all of these oysters mate equally, the second generation will have the same proportions of each allele - 75% A and 25% a. (In this example, what the offspring oysters look like - their **phenotype** - doesn't matter.) No “evolution” (change to the gene pool frequencies) has occurred.

However, if the oysters mate unequally, due to random chance, it is very easy to end up with different proportions, such as 17 A alleles and 7 a alleles (or any other combination). Random chance thus can result in an inherited change (of allele frequency) within the lineage, thus we say that evolution has occurred through genetic drift.



One common example of the results of genetic drift is the **Founder Effect** (or “bottleneck effect”). When a small part of a large population is removed from the main population, this “founder population” might have a very different allele frequency than that of the original. As the founder population reproduces in isolation, the gene pool of the population will continue to diverge from that of the original population.

If you have a large oyster bed of 100 oysters, composed of 50 dark-colored (AA) and 50 medium-colored (aA) oysters, that population has 75 A alleles (75%) and 25 a alleles (25%). Let’s suppose that a rock slide isolates a small group of 10 oysters in a tide pool (thus separated from the main population) and that this group has only 6 dark-colored (AA) and 4 medium-colored (aA) oysters. In this tide pool population, there are 16 A alleles (80%) and 4 a alleles (20%) – the new gene pool is different from that of the original population as a result of the random rock slide. As the population in the tide pool reproduces over time, genetic drift can further change the allele frequencies, becoming more and more different from the proportions in the original oyster bed.



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Founder Effect • Genetic drift observed in a population that was founded by a small non-representative sample of a larger population.

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genotype (*adj. genotypic*) • The genetic makeup of an organism or group of organisms with reference to a single trait, set of traits, or an entire complex of traits.

gradualism • The process of gradual evolutionary change over time.

macroevolution • Evolution happening on a large scale, i.e., at or above the level of species, over geologic time resulting in the formation of new taxa.

microevolution • Small-scale evolution that results in minor changes to the gene pool of a population.

phenotype (*adj. phenotypic*) • The observable physical or biochemical characteristics of an organism, as determined by both genetic makeup and environmental influences; what an organism “looks like.”

punctuated equilibrium • The evolutionary process involving long periods without change (*stasis*) punctuated by short periods of rapid speciation.

Evolutionary Results

Although we rarely see evolution “happening,” we see its effects every day. Scientists can study these effects to learn how evolution works and how evolution has occurred in specific cases.

Microevolution & Macroevolution

Microevolution produces minor changes to the gene pool of a population. These changes are caused by mutation and genetic recombination, which generates variation. These genetic variations result in different **genotypes** within the population that appear as different **phenotypes** among the individuals. Genetic drift acts upon the genotype, whereas natural selection is only able to act upon the phenotype.

Over time, natural selection and genetic drift result in macroevolution. **Macroevolution** results in large changes to a gene pool often resulting in the evolution of a new species. Macroevolution can occur very gradually over a long period of time, called **gradualism**, or very quickly after a long period of stability, called **punctuated equilibrium**.

During the Early Paleozoic Era, certain bivalve species developed long siphons and a muscular foot that gave them the ability to bury themselves within the sediment, providing them with a strong advantage against predators on the surface of the seafloor. The minor genetic mutation that resulted in longer siphons is an example of microevolution. Over thousands of generations, and many additional favorable mutations, burrowing bivalves diversified through the process of macroevolution. You can find more information about the early evolution of bivalves on the University of Bristol’s Fossil Record of Bivalves webpage (<http://palaeo.gly.bris.ac.uk/Palaeofiles/Fossilgroups/Bivalvia/Fossilrecord.html>).



Short and long siphons of living bivalves. Short siphons (left column, top to bottom) are found in the Heart Cockle (*Fragum unedo*), the Galeommatid Clam (*Scintillona cryptozoica*; the excurrent siphon is between the orange-tipped tentacles at left), and the Coquina Clam (*Donax veruinus*). Long siphons (right column, top to bottom) are found in the Pipi Clam (*Donax deltoides*), Razor Clam (*Solen vaginoides*), and Dipper Clam (*Cuspidaria latesulcata*; the long siphons are encased in the shelly "rostrum"). All of these species live in or near Moreton Bay, Queensland, Australia.

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camouflage • Structural adaptation that enables an individual to blend with its surroundings, and that allows an individual to avoid detection by predators.

epibiont • An organism that lives on the surface of another living organism.

fitness • The relative probability of survival and reproduction for a genotype.

fouling community • Community of organisms found attached to hard substrata, most usually human-made, e.g., on the sides of docks, marinas, harbors, or vessels.

mimicry • A phenomenon in which an individual gains some sort of survival advantage by looking like an individual of another (often more harmful) species.

species • A group of organisms formally recognized as distinct from other groups; the taxon rank in the hierarchy of biological classification below genus; the basic unit of biological classification, defined by the reproductive isolation of the group from all other groups of organisms.

Adaptation, Speciation, & Diversity

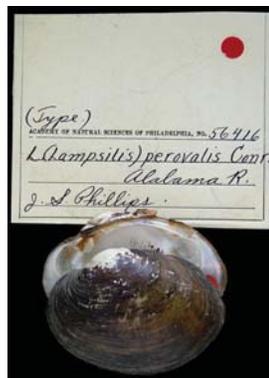
A **species** is the basic unit in the classification of life. For a species to be successful (that is, able to survive and reproduce), it must be well adapted to its environment. Adaptation occurs over time by natural selection favoring variations that improve the species' **fitness**. These adaptations can be physical, chemical, or behavioral.

Camouflage and mimicry are two forms of physical adaptation. **Camouflage** occurs when an individual “blends” into the environment in the eyes of a potential predator. **Mimicry** is present when one species has evolved to look like another species in a way that will provide some advantage. The best-known examples of mimicry are those in which a species mimics another that is toxic or harmful to a potential predator, such as the nonvenomous Scarlet Kingsnake that closely resembles the venomous Coral Snake in the color bands on its body. Camouflage and mimicry are both adaptations because they increase the likelihood of an individual evading predation long enough to reproduce.

Bivalves also provide good examples of camouflage and mimicry. The spines on the shells of Spiny Oysters (family Spondylidae) provide crevices in which algae, sponges, and other **epibionts** can settle and grow to cover and camouflage the shell. With time, this growth helps the Spiny Oyster to “disappear” on the surface of the reef, lowering the threat of predation from top-level predators such as fish. Octopuses and squid (both cephalopods, and close relatives of bivalves) are the “camouflage champions” of the mollusk world, able to change the color and texture of their soft bodies to blend into their surroundings.



A living Thorny Oyster (*Spondylus varians*, left) shows a thick cover of epibionts – mainly sponges and algae – that help it blend into its surroundings to avoid predation. When closed, this oyster is barely noticeable on the rock. The Thorny Oyster shell at right (*Spondylus regius*) probably looked much like the encrusted *Spondylus varians* before it was cleaned (a laborious process, as many shell collectors know). The spines are an adaptation that provides added surface for the attachment of a **fouling community**.



The Orange-Nacre Mucket

Females of the freshwater pearl mussel called the Orange-Nacre Mucket (*Hamiota perovalis*) have evolved a marvelous example of mimicry that works to their reproductive advantage. Freshwater pearl mussel larvae, called **glochidia**, must attach to the gills or fins of a fish to successfully metamorphose. The female Orange-Nacre Mucket produces a discrete mass of larvae, called a superconglutinate, that resembles a small fish in shape and coloration. After release from the female mussel, the mass of larvae looks just like a small fish darting about in the current of the stream (very similar to the complex behavior of mantle lures of other freshwater mussels). The fish-like supercon-

glutinate attracts a predatory fish that is interested in eating the “small fish.” When the predatory fish attacks, the mass disintegrates, releasing the larvae to attach to the fish.

Scientists at Missouri State University have produced a video of the *Hamio-ta* superconglutinate in action, which can be viewed online at http://unionid.missouristate.edu/gallery/L_perovalis/lampsilis_perovalis_movie.htm.

Over a long period of time, natural selection is able to utilize many variations and evolve new species in the process of **speciation**. All species have evolved from earlier forms of life. Earth’s great diversity of life is the result of 3.8 billion years of natural selection favoring advantageous variations, some of which ultimately lead to new species. Genetic drift also plays a part in speciation, but due to its randomness, it is very difficult to identify specific instances.

There are four broad categories of speciation:

1. Allopatric speciation occurs when a population is split into two geographically isolated populations. Each population is then exposed to different selective pressures that result in genotypic and phenotypic changes. Over time, the populations develop into two different species and if they ever come into contact again, they would be unable to reproduce.

Allopatric speciation could occur if a population of freshwater mussels is cut in half by the construction of a dam. The mussels upstream would be isolated in the newly formed lake and the mussels downstream would be isolated in the remaining river. Assuming that both populations could survive the new living conditions, the populations will evolve separately and eventually become two distinct species. The mussels in the lake would adapt to the slower moving, deeper water. The mussels in the river would remain adapted to the faster moving, shallow water, more similar to the original conditions of the population.



Hoover Dam, on the Arizona-Nevada border in the southwestern United States, impounded the Colorado River to create Lake Mead. The average depth of the Colorado River is 20 feet (6 meters), whereas Lake Mead is at its greatest 500 feet (> 150 meters) deep. Such a change in water depth and conditions, inflicted on a split population of freshwater mussels, could be a powerful force for adaptation leading to speciation.

2. Peripatric speciation occurs when a single population is physically split into two isolated populations (= allopatric speciation), but the term peripatric speciation is used when one population is much smaller than the other.

Peripatric speciation could occur if a few members of a clam population get swept ashore during a hurricane and become isolated in a brackish lake. Assuming that the clams in the lake can survive the brackish-water conditions, the population in the ocean and the new population in the lake will then evolve separately and eventually become two distinct species.

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glochidium (pl. **glochidia**) • A specialized larval form of freshwater pearl mussels that usually has hooks that enable it to attach itself to a host (e.g., to the gills of a fish) for a period of time before it detaches and falls to the bottom and takes on the typical form of a juvenile mussel.

speciation • The process in which one species evolves over time into a different species (anagenesis) or in which one species diverges to become two or more species (cladogenesis); see also allopatric speciation, parapatric speciation, peripatric speciation, sympatric speciation.

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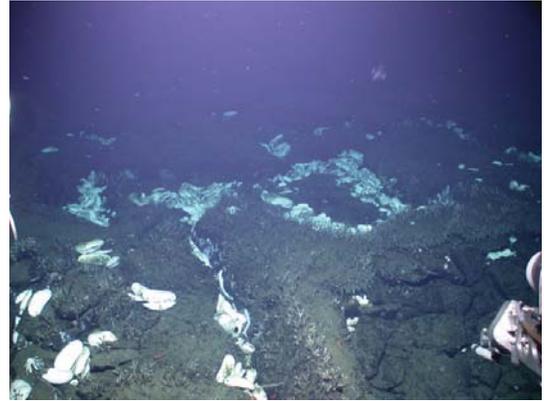
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3. Parapatric speciation occurs when a population is in the process of splitting, due to some non-physical factor (such as a change in physiology or ecology), but continue to overlap. Each part of the population has its own ecological niche. The diverging members might occasionally come into contact but their offspring are not well suited for either niche. Over time, the populations develop into two different species, each suited for their own niche, and eventually they will lose the ability to reproduce with each other.

Vesicomyid clams (family Vesicomyidae) are dominant organisms in chemo-synthetic-based deep-sea communities, such as methane or cold seeps and hydrothermal vents. In a recent study involving molecular and morphometric analyses[1], five lineages (including three undescribed species) were identified. All five species are broadcast spawners (adults release eggs and sperm freely into the water where fertilization occurs), but are nevertheless now segregated by depth, suggesting that the species diverged and are maintained by bathymetric (depth) and substratum factors exerted on the larvae rather than on the adults. This might be an example of perapatric speciation - the gametes of the five species can commingle in the water column, but “hybrid” larvae might not be as well adapted to the niches of the “pure” larvae.



Vesicomyid clams on the Bucky Hydrothermal Vent Field, East Pacific Rise, 2,493 meters depth (> 14,000 feet), ALVIN submersible dive 3934. Each of these impressive clams is 20-30 centimeters (8-12 inches) in length.

4. Sympatric speciation occurs when a single population diverges into two while inhabiting the same physical space. This usually occurs as a result of sexual selection.



Sympatric speciation might occur if, within one population of octopuses, some females favor large aggressive males whereas other females favor smaller more colorful males. Over a very long time, the two preferences could result in divergence and two new species – one large and aggressive, the other small and colorful.

The small colorful octopus, Octopus rubescens, from off of Washington State, USA.

[1] Goffredi, S. K., L. A. Hurtado, S. Hallam, & R. C. Vrijenhoek. 2003. Evolutionary relationships of deep-sea vent and cold seep clams (Mollusca: Vesicomyidae) of the “*pacifica/lepta*” species complex. *Marine Biology*, 142: 311-320.

Coevolution

Coevolution occurs when two species evolve together, that is, when variations in one species lead to change in another species with which it interacts.

- **Symbiosis** is a close and long-term interaction between two different species.

(a) **Mutualism** occurs when both species benefit from the interaction.

In the Red Sea, Date Mussels (*Lithophaga simplex*) are bivalves that live inside the Porous Star Coral (*Astreopora myriophthalma*) [1]. The mussels are completely encased by the skeleton of the coral with only the ends of their siphons reaching the surrounding seawater through a small hole. Researchers have discovered that the relationship is mutualistic with the bivalve gaining protection against predators and the coral receiving the ammonium produced as a by-product of the mussel's metabolism. Ammonium is a rich source of nitrogen that is important for the survival of the coral colony.



The Date Mussel, *Lithophaga*.

(b) **Commensalism** occurs when one species benefits and the other is unaffected.

Yoyo clams (family Galeommatidae) are tiny bivalves that live in the mud burrows of mantis shrimps on sand flats in eastern Florida [2]. The clams benefit from the protection offered by the burrow, and have evolved very fragile, often internal, shells presumably because they no longer need robust shells to ward off predators. They also benefit from the feeding activities of the predatory shrimp, filtering small bits of fish and other food scraps from the water inside the burrow. The mantis shrimp is not affected by the presence of the small bivalves, and does not feed on them.



Yoyo clams (family Galeommatidae).

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coevolution • Two or more unrelated species with a close ecological relationship that evolve together, such that one species adapts to the changes of the other, thereby affecting each other's evolution.

commensalism • A type of symbiosis in which two (or more) individuals of unrelated species live in close proximity to one another, in which one member is unaffected by the relationship and the other benefits from it.

mutualism • An interaction between members of two species which benefits both; in strict terms, obligatory mutualism occurs when neither species can survive under natural conditions without the other.

symbiosis • A long relationship between two different species; see also mutualism, commensalism, parasitism.

[1] Mokady, O., Y. Loya, & B. Lazar. 1998. Ammonium contribution from boring bivalves to their coral host — a mutualistic symbiosis? *Marine Ecology Progress Series*, 169: 295-301.

[2] Mikkelsen, P. M., & R. Bieler. 1989. Biology and comparative anatomy of *Divariscintilla yoyo* and *D. troglodytes*, two new species of Galeommatidae (Bivalvia) from stomatopod burrows in eastern Florida. *Malacologia*, 31(1): 175-195.

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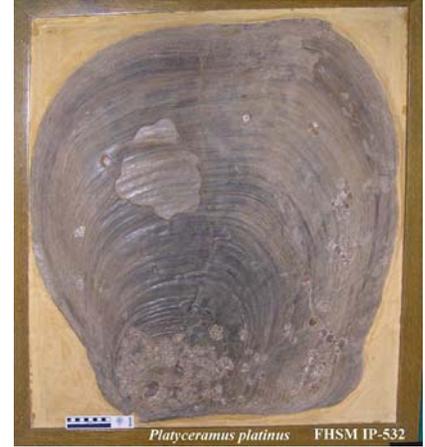
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parasitism • A form of symbiosis in which one organism (the parasite) benefits at the expense of another organism of different species (the host). The association can also lead to the injury of the host.

(c) **Parasitism** occurs when one species benefits and the other is harmed in some way.

Inoceramids are an ancient family of extinct bivalves similar to living pearl oysters. They were massive organisms and are often called the “the pearl oysters of the Age of Dinosaurs.” What caused their extinction at the end of the Mesozoic probably involves many factors, but researchers have found evidence of shell deformities becoming very common just before the group disappeared from the fossil record [1]. Some of the shell deformities look like small bubbles inside the shell and could have been formed if the oyster was releasing calcium carbonate to battle parasitic worms. The worms would have received nutrients from feeding on the inoceramid’s waste but the inoceramid would have died and as a result the whole group became extinct.



This huge specimen of *Platyceramus platinus* is on display at the Denver Museum of Nature and Science in Denver, Colorado.

- **Competition** occurs when two species are coevolving in the same territory or needing the same resources. Competition of this kind can lead to extinction of the lesser-competitive species.

Invasive species, such as Zebra Mussels (*Dreissena polymorpha*), are perhaps the best examples of bivalve competitors. Zebra Mussels (native to southeastern Russia, and introduced into the American Great Lakes in 1988 from the discharge of ballast water from cargo ships) compete with native freshwater pearl mussels for food (organic particles filtered from the water) and living space. Zebra Mussels can also smother freshwater pearl mussels by attaching to their shells, preventing them from opening properly to feed and reproduce.



Introduced Zebra Mussels crowd onto the exposed end of a native freshwater pearl mussel, preventing it from opening to feed and respire, and ultimately smothering it.

[1] Ozanne, C. R., & P. J. Harries. 2002. Role of predation and parasitism in the extinction of the inoceramid bivalves: an evaluation. *Lethaia*, 35(1): 1–19.

A predator-prey “arms race” results from co-evolution between a predator and its prey. As the prey species evolves more sophisticated adaptations to evade its predator, the predator in turn has to evolve more sophisticated adaptations to capture the prey.

Early in their evolutionary history, bivalves were **epibenthic**, living on the surface or only shallowly buried in the seafloor. With the appearance of more predators in the Mesozoic Era, bivalves evolved **siphons**, which allowed them to bury deeper in the sand or mud, using their siphons as a “snorkel” to the food- and oxygen-laden water. As predators later evolved the ability to burrow, bivalves developed longer siphons to bury deeper in the mud.



The Soft-Shelled Clam (*Mya arenaria*, at left) with its long, extended siphons. Only the tips of the siphons show at the mud surface - like those shown above of the Caribbean Reef Clam (*Periglypta listeri*).

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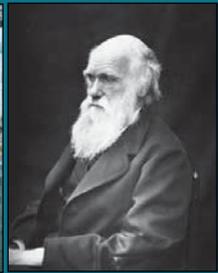
epibenthic • Living on the surface of the sediment, most usually at the bottom of a body of water.

siphons (adj. siphonal) • Posterior extensions (usually two) of the mantle through which water is directed in and out of the body, along with waste products and gametes of bivalves.

The Teacher-Friendly Guide to Evolution

Using Bivalves as a Model Organism

By Paula M. Mikkelsen & Robin Henne



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