Science B-16: The History of Life

Lab 4: Variation and Evolution

BRING TO SECTION: Calculator

OBJECTIVES

This exercise is designed to introduce you to the concept of **variation** in populations and its importance in evolution and natural selection. To accomplish this you will assess (by measurement and counting) the variation in two identifiable features of some fossil brachiopod shells and decide whether the samples likely represent one large population or two distinct, separate populations.

VARIATION

No two individuals of a species are identical. Variations may be due to **genetic** or **environmental** differences, or simply to chance. The presence of these differences dictates that the description of a single individual is not sufficient to describe an entire species' morphology, ecology, development, or anything else. Instead, the description of many individuals taken together defines a range of variation that encompasses the species.

Variation in morphology between individuals of the same species is the most obvious kind of variation. For example, domestic dogs (*Canis familiaris*) show a wide range of morphological variation from Chihuahuas to Great Danes. Most studies of evolution, especially those based on the study of fossils, rely exclusively on morphological variation. However, many aspects of organisms may vary, including behavior, ecology, genetic makeup, and growth patterns.

The standard unit of research concerning variation within and between species is the **population**. A population may be defined as a group of freely interbreeding individuals that share a common gene pool, *i.e.*, every individual can potentially mate with any other individual in the same population. Typically, species are comprised of several populations that may be partially or completely isolated from each other geographically. All individuals of the same species, however, are capable of interbreeding and producing fertile offspring given the opportunity. For example, two populations of elk may be separated by a mountain range across which only a few individuals typically travel, or two populations of Brazilian rain forest plants may be separated by the Amazon River, which its pollinators are seldom able to cross; however, they are still part of the same species.

Population variation is important to biologists because variation <u>within</u> a population of organisms is the cornerstone upon which natural selection, the mechanism that

Charles Darwin proposed to explain the fact of evolution, is based. As such, variation within and between populations forms the basis of investigations of the patterns, processes, and rates of evolution.

TYPES OF VARIATION

Variation within a population may be of four types: 1) age-group (ontogenetic) differences; 2) genetic differences; 3) environmental differences; and 4) chance.

1) **Age-group differences** are those differences produced by the presence of individuals of different ages in a population, *e.g.,* adults and children together at Disney World would vary widely in height, but adults or 6-year-olds taken as separate populations would vary much less than the group as a whole. Figure 1 below shows variation in the distribution of shell lengths of a population of blue mussels due to age differences. Note that the distribution of differences can change during the breeding cycle of the organism.

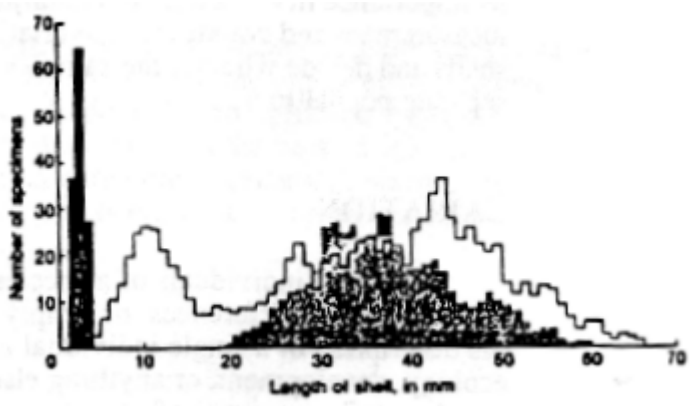


Figure 1. Relationship between age and size in a population of *Mytilus edulis* from Scotland. Shaded histogram is from April, outlined one is the same population in November.

At the least, age differences will appear as variation in size, but often they are manifested as differences in proportion. The proportions of a human infant's body are quite different from those of an adult, *e.g.,* compare the relative size of an adult's head to that of an infant's. Human adults are behaviorally different from human children, too.

2) Different individuals typically possess different sets of genes. [Identical siblings and clonal organisms (such as coral or grasses) are exceptions.] Some variation within a population is clearly the expression of these **genetic differences**. Hair color, eye color, and number of fingers are all human genetic traits that vary. (Some traits obviously vary more than others.) Another example of variation reflecting inherent genetic differences is *sexual dimorphism*, where males and females of a species look different from each other. Sexual dimorphism is often, but not always, expressed as a size difference. For example, female rabbits are typically larger than their male counterparts. Sexual dimorphism in fossils presents a particular problem because

some dimorphs are so extreme that what are probably females and males of the same species have been described as different species. One should be cautious, however, in assigning variation to sexual dimorphism, because in many species there are no recognizable morphological differences between sexes.

3) **Environmental differences** are those attributable to outside influences on an organism. Flowering plants are especially plastic in their responses to the environment. For example, the shapes of pumpkins and cantaloupes are generally determined by the interaction of gravity with the materials of their construction. Under "normal" circumstances they form globular, sub-spherical forms. But, using molds provided by Vegi-Forms of Cincinnati, one may grow a squash with the likeness of Richard Nixon or Elvis Presley (True!). Regular echinoids (sea urchins) illustrate a more natural example of environmentally driven variation. Urchins living in shallow, turbulent water are typically somewhat flattened from top to bottom. When transplanted to deeper, quieter water, they will round out over time to become spherical. Some social insects (bees, ants, etc.) provide another example of environmental variation in that they are often **polymorphic**, that is, genetically identical individuals of the same colony may possess completely different adult morphologies. This type of variation is controlled by the local environment established inside the colony rather than by outside influences. Depending on how she is cared for, a female ant larva may develop into a worker, a soldier, or a queen.

4) **Chance** plays a role in each of the three types of variation listed above. Some variation is simply the result of random changes in the genetic code or chance exposure to certain events or environments. For example, identical twins, although they possess the same set of genes, have different fingerprints due to the random effects of cell division. Randomness is an integral part of all aspects of biological systems.

IMPORTANCE OF VARIATION IN EVOLUTION

In writing *On the Origin of Species*, Charles Darwin had two objectives: 1) to present an argument for the **fact** of evolution through an exhaustive catalogue of examples of change through time in modern and fossil organisms; and 2) to propose his **theory**, natural selection, as a mechanism for *how* evolution occurs.

Natural selection is based on three observations and a simple inference:

1. All organisms vary.

2. Some of this variation is heritable, *i.e.,* genetic, and therefore can be passed from parents to offspring.

3. All organisms produce more offspring than could possibly survive (what Darwin calls **superfecundity**).

Inference: Those organisms which survive to successfully reproduce will be those with features that happen to be better suited to local conditions at that time. Heritability ensures that at least some of these features will be passed on to the next generation.

Therefore, *individual variation is the raw material upon which natural selection acts*. Through differential birth or death of individuals, the mean of a population will tend to shift toward whatever variants are most adaptive for that particular time and place. This *is* natural selection.

VARIATION IN FOSSIL POPULATIONS

Fossils provide us with an important opportunity; they are our "window" into biological variation in the past. By comparing variation within and among fossil populations we can recognize and attempt to interpret the process of evolution. Unfortunately, problems inherent in the fossil record tend to smudge and obscure this window, distorting our view of the past by influencing what we see. These distortions can be attributed to three factors: 1) the incomplete nature of the fossil record; 2) the differential preservation of hard body parts; and 3) the physical distortion of fossil specimens.

The fossil record is complete neither in time nor in space. Unconformities caused by breaks in sediment accumulation and/or erosion of existing sediments leave gaps in the history of life as recorded in the earth's crust. Furthermore, some environments are much more likely to be preserved, which means that organisms in environments with high preservation potential are likely to be better represented in the fossil record. (Remember the marine bias discussed in Lab 1.)

Most of the fossil record is comprised of *parts* of organisms... those parts which, because of their composition, are amenable to preservation. For example, the hard, mineralized skeletal components of many marine mollusks (*e.g.,* clams and snails) are commonly preserved. Some plant compounds, *e.g.,* the material coating pollen grains, are equally hardy. Soft bodied organisms like worms are far less well represented in the fossil record. *Examination of variation in fossil populations is therefore often limited to the measurement of hard-part variation.* Keep in mind that what is preserved is only a part of the organism. There is also a bias against the preservation of small sized mineralized parts, resulting in the potential loss of juvenile individuals from a population during fossilization. This loss of information can result in lower variation in fossil populations when compared to the variation in modern, living populations.

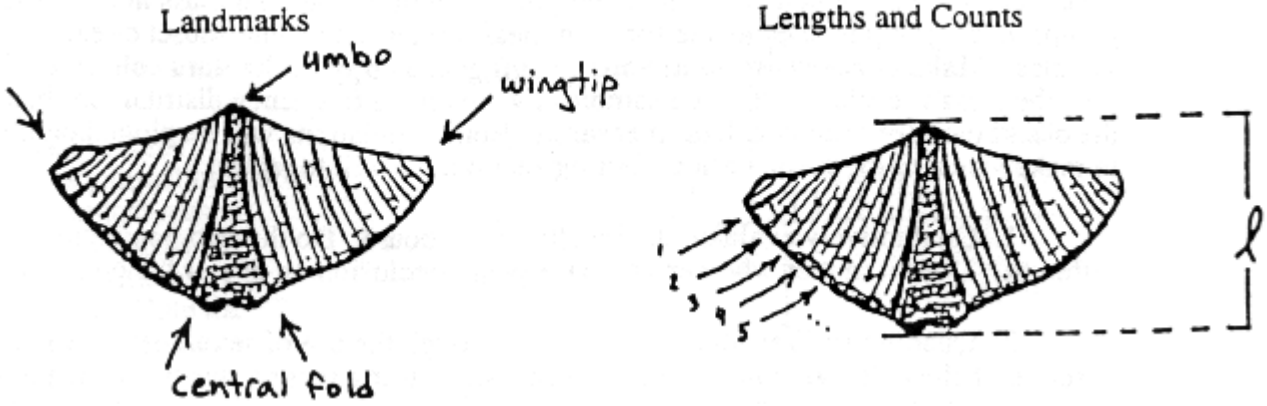
Finally, those organisms for which we do have a record may be physically distorted by compaction or crushing before, during, or after fossilization. Organisms with several distinct hard parts may be broken up and separated (disarticulated) prior to burial, and fossils may be stretched, bent, or smeared like soft plastic while they are buried in the earth's crust. Therefore, like preservational biases, distortion can alter the range of morphological variation originally present in a population.

HOW TO MEASURE VARIATION

If one were to use only words and pictures to describe and compare organisms, the task would be difficult and far too subjective. To make your study more rigorous, it is helpful to use a combination of numerical techniques that allow more objective comparisons of fossil specimens. These make an account of population variation quantitative, repeatable, and easier to communicate to others. Numerical methods, however, should not be used to the exclusion of careful, detailed description and illustration, for numerical methods can also be misleading if used or interpreted incorrectly. During this lab period you will gain experience with some of the most commonly used techniques for assessing variation. As mentioned before, paleontological studies rely almost exclusively on variation in shape (morphology) of hard parts of organisms, but biological studies can also include variation in the genetic code of individuals.

Morphological variation is measured and described by identifying **characters** on each individual in your sample population and evaluating the amount and nature of variation in each. A character is any feature of an organism that can be quantified, such as by linear measures, counts, or presence/absence. To save time and provide consistency for comparison in the following exercise, we will suggest characters for you to measure. If you were choosing characters for your own investigation, however, you would have to decide which characteristics are most appropriate. These are a few simple rules of thumb:

1) Look for easily and consistently recognizable landmarks that can be identified on all individuals to use for reference points in your measurements. *Mucrospirifer*, the beast you will be measuring, presents several good landmarks. Examples include the "wingtips" (far ends of the **hingeline**), the points where the edges of the central fold meet the shell edge, and the **umbo** or "beak" of the shell. See the figure below. The line along which the two halves of the shell come together is called the **commissure**; you will be using this as a landmark in the exercise to follow.



2) Length measurements are simple and easy to make. Returning to the landmarks described above, one could measure the length of the hinge line (wingtip to wingtip), the width of the fold at the far edge of the shell, or the distance from the umbo to commissure.

3) Counts of features may be used instead of linear measures when appropriate. For example, one could count the number of growth lines or the number of radial ribs on the shell of the brachiopod.

4) The presence or absence of distinguishing features can also be useful. Some brachiopods, for example, do not have a medial fold, while others do.

Potential complications: Try to avoid measurements that may be too complex for consistent results. Measured dimensions that are so small that they approach the precision of the measuring instrument are also poor choices because they introduce too much noise to your analysis. Make sure your specimens are complete or as complete as necessary to accurately measure your dimensions, *e.g.,* don't guess at how long the hingeline would have been if the specimen hadn't been broken.

It is important to realize that the amount of variation recorded in any biometrical analysis is very sensitive to the *scale* of the objects being measured. The variation shown by some very large character may swamp the variation shown by some very small character. For example, when comparing the tails of elephants and mice, the absolute variation in elephants' tails is probably greater than the range of the lengths of whole mice; however, relative to body length, elephants' tails might vary less than mice tails.

TODAY'S EXERCISE

You will have before you two samples of brachiopods (Phylum Brachiopoda: Class Articulata: Order Spiriferida) collected from the Middle Devonian Hamilton Group, a related set of rock formations stretching across New York, Quebec, Ontario, Ohio, and Michigan. At the time these brachiopods were alive, shallow seas extended over much of this area, receiving sandy to muddy sediments from the newly forming Catskill Mountains in New York State. The resulting Hamilton Group strata are famous world-wide for their often exquisitely preserved fossils. Sample 1 is from Milan, in southeastern Michigan, and sample 2 is from Thedford, in southern Ontario, roughly 100 miles to the east-northeast. We do not know if the samples were collected from rocks precisely the same age or not. **Your job is to determine whether these two samples represent one large or two smaller, distinct populations.**

You will be recording data on two characters for each individual you measure: one linear measurement and one count. To that end your TF will divide your class into several small groups; each group is responsible for both measurements on some subset of each of the two samples. **Make sure everyone in your group gets a copy of the data collected!** We will then pool the class's results for the two samples by creating a frequency distribution (histogram) on

the blackboard for each character measured. Both populations will be plotted on the same graph to make visual comparison easier. During section, we will together:

1. Qualitatively evaluate the results on the board. Do the two populations "look" different? Does it matter whether you base your conclusion on one or the other character?

2. Quantitatively evaluate our results through the use of several simple statistics described below. To give more time to discussion during section, we have already measured the same brachiopods and calculated these statistics for you; our results should not differ much from section results. You will, however, have to calculate these values from your own subset of the class data for your assignment, so again, make sure everyone in your group has a copy of the data. Be sure to have a conceptual idea of what the following statistics mean *before* you come to section.

A FEW SIMPLE STATISTICS

Most biological variation is distributed such that the measurements for a given character cluster around some average value and become less and less frequent as you move away from that value. To characterize this pattern, we use two different types of descriptors: (1) measures of **central tendency**, to describe the point around which the measurements cluster; and (2) measures of **dispersion**, to describe how the measurements are distributed around this point.

The **arithmetic mean**, or simply the "average", of a sample is the most common way of describing central tendency. The mean of a sample, represented by the symbol X, is calculated by adding together all of the measurements for a given character and dividing the sum by the total number of measurements made (for example, the total number of brachiopods measured). In mathematical shorthand, this calculation is shown as:

$$\overline{X} = \frac{\Sigma X}{N}$$

where the symbol Σ (sigma) simply means add up all the values of X (your measurements), and N is the total number of measurements made for that sample.

Another useful measure of central tendency is the **mode**, the value of X in your histogram that describes the greatest number of individuals. If the mode (or peak in your distribution) is different from the mean, as in Figure 2c below, then you know that the distribution is "lop-sided", with more individuals on one side of the mean than the other. This can give you valuable information about your population: are there more young (small) individuals han old, suggesting perhaps a high juvenile mortality? Are there more large than small, suggesting that perhaps the small individuals were washed away by water currents leaving only the big, heavy ones behind? A distribution containing two distinct peaks ("bimodal") is reflective of the age-group differences discussed on page 2.

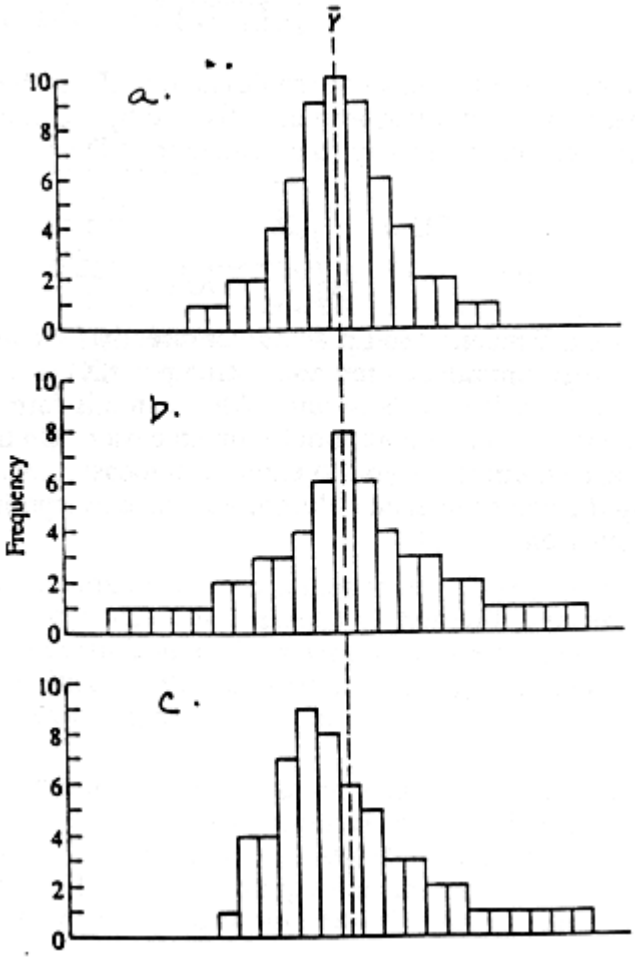
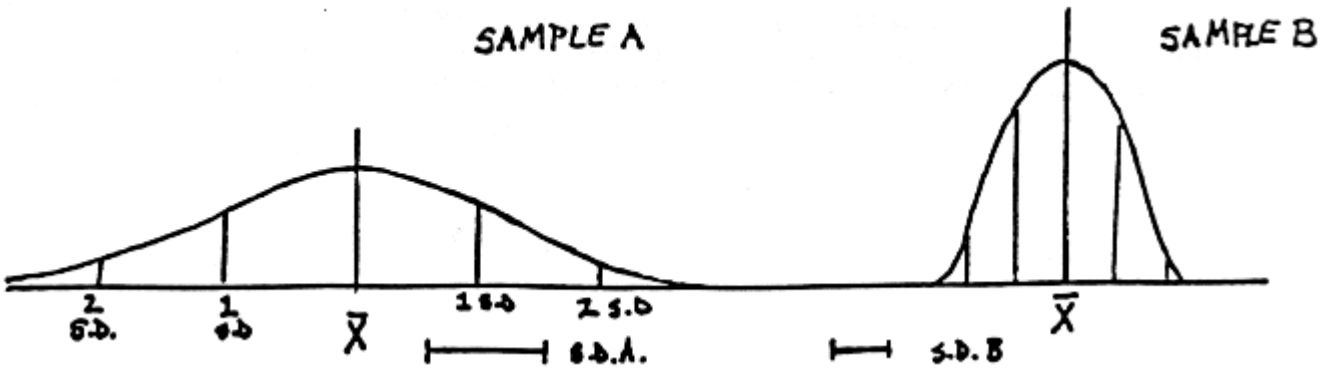


Figure 2. Three frequency distributions with identical means and sample sizes but differing patterns of dispersion. Note the position of the mean vs. the mode on each.

Knowing the mean value is important, but to fully describe the variation in your sample you must also address the issue of dispersion, or how observations "pile up" or "fall away" from the mean. Measuring dispersion about the mean is important because two different samples may have the same mean value for some feature but still be very different in the way the measurements are distributed around it, as shown in Figure 2 on the preceding page. The **standard deviation**, abbreviated here as **SD**, describes the average deviation from the mean of the values measured in a population. The larger the SD, the more spread out a sample is around its mean. Compare the two distributions shown below, both for the same number of individuals. Sample A has a greater range of values about the mean than does sample B; sample A's standard deviation is correspondingly greater than sample B's.



The formula for the standard deviation is as follows:

$$SD = \sqrt{\frac{\Sigma\left(X - \overline{X}\right)^2}{N-1}}$$

In other words, the standard deviation, SD, is the square root of the summed deviations from the mean for every measurement, divided by the number of measurements made minus one. In practice, an easier way to calculate the SD is:

$$SD = \sqrt{\frac{\Sigma X^2 - \frac{\left(\Sigma X\right)^2}{N}}{N-1}}$$

Again, Σ means add up whatever directly follows it. Thus, ΣX^2 means take the squares of all the measurements, then add them up. (ΣX) is simply the sum of the unaltered measurements, and $(\Sigma X)^2$ is this value's square. Although this formula looks more complicated than the first version, it is computationally much easier. On the data sheets at the back of this lab, we have made columns for you to enter each measurement and that measurement's square. Once you add up the values in each column, you have everything you need to calculate the mean and standard deviation.

SOME THINGS TO THINK ABOUT... TOPICS FOR GROUP DISCUSSION

1. a) Compare the mean of sample 1 with the mean of sample 2 for rib number. Is there difference?

b) Compare the mean of sample 1 with the mean of sample 2 for umbo-to-commissure length. Is there a difference?

c) Compare the standard deviations of the two characters for sample 1, and repeat for sample 2. Is this a valid comparison? Why or why not?

2. Why might one feature be more variable than the other, both within and between populations? Which is more likely to be genetically controlled, and which environmentally? Why might this be?

Technically, one should perform a statistical test called a "t-test" to determine whether the sample means are truly distinct from each other and therefore represent two separate populations. The formula to calculate the t-test is included here for those who are interested; your TF will help. However, to paraphrase Jack Sepkoski, a noted paleontologist and statistician, "if two things look different, they probably are". Beware of researchers that report "statistically significant differences" between populations even when the graphs they include show only fuzzy distinctions at best!

t =

3. What benefit do you get from using umbo-to-commissure length for your measurements rather than length of the hingeline? Which do you think could be more variable and why?

4. a) Would you say that these two samples represent one population or two distinct ones? Why?

b) Would you say that these two samples represent one *species* or two distinct ones? Why?

c) What are the problems associated with making decisions like these?

Assessment of population variation through time is done in exactly the same way as assessment of population variation in space. If mean values for a population shift through time, that indicates that evolution has occurred. Tracking the changes in fossil populations through time is a way of "watching" evolution occur.

5. Suppose new information has become available stating that sample 2 was collected from a horizon above sample 1, and is thus estimated to be roughly 1 million years younger. Plot the sample means for rib number against time. Put time on the vertical axis increasing downward. Do the same for umbo to commissure. (We will do these plots on the board.)

Do these two points suggest any apparent trends in the brachiopod's morphology during this time interval? (*i.e.,* do either of the characters seem to be changing consistently in one direction?) Is it valid to conclude that such trends exist from only two data points? Why or why not?

6. To test your hypothesis, you return to the area and collect samples 3, 4, and 5, each from successively higher (and hence younger) beds in the Hamilton Group. The means for rib number and umbo to commissure are the following:

Sample	**Rib Number**	**Umbo to Comm.**
3	12	23
4	10	24.5
5	11	29

Add to the plot on the blackboard the means for these additional samples. Separate them by 1-million-year intervals.

a) Describe what has happened through time for each character. Do you see any apparent trends now?

b) What is the nature of change through time? (constant, unidirectional, reversing, gradual, episodic, etc.) Can you really say anything about this issue given the data available?

7. How would you distinguish true speciation events from morphological change within a single species? What makes this a difficult task?

DATA SHEETS **Name_____**

SAMPLE _____

N = _____ (sample size)

	Umbo To Commissure Width		Rib Number	
	X (mm)	**X^2**	**X**	**X^2**
TOTALS	**ΣX**	**ΣX^2**	**ΣX**	**ΣX^2**

MEAN = _____ **MEAN = _____**

SD = _____ **SD = _____**

DATA SHEETS **Name_____**

SAMPLE _____

N = _____ (sample size)

Umbo To Commissure Width Rib Number

X (mm)	**X^2**	**X**	**X^2**

TOTALS	ΣX	ΣX^2	ΣX	ΣX^2

MEAN = _____ **MEAN = _____**

SD = _____ **SD = _____**