Evolution and Biodiversity Laboratory
Systematics and Taxonomy

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Recent estimates of our planet's biological diversity suggest that the species number between 5 and 50 million, or even more. To effectively study the myriad organisms that inhabit the biosphere, we attempt to classify organisms into groups that reflect evolutionary relationships. The science of describing, classifying and naming organisms is known as **taxonomy**. The science of studying their diversity and evolutionary relationships is known as **biosystematics**, or simply **systematics**.

I. Taxonomy

Strictly speaking, **taxonomy** is the sorting of living organisms into various **taxonomic groups**, or **taxa** (sing. = taxon). Since most systematists are concerned not only with the ability to sort and identify organisms, but also with determining their evolutionary relationships, taxonomy is used as a tool within systematics .

Biological **nomenclature** is the application of names to organisms recognized to be part of a particular taxon. From most inclusive to least inclusive, the major taxonomic **ranks** are as follows:

- **DOMAIN** (e.g., Eukarya)
  - **KINGDOM** (e. g., Animalia)
    - **PHYLUM** (e. g., Chordata)
      - **CLASS** (e. g., Mammalia)
        - **ORDER** (e. g., Primates)
          - **FAMILY** (e. g., Pongidae)
            - **GENUS** (e. g., *Homo*)
              - **SPECIES** (e. g., *Homo sapiens*)

Each **Domain** contains related **Kingdoms**. The Kingdoms are made up of related **phyla**. Phyla, in turn, are composed of related **classes** of organisms, classes of related **orders**, orders of related **families**, families of related **genera** (singular: genus) and genera of related **species**. Within each of the major taxonomic ranks there may be larger and smaller taxa such as subkingdom, superphylum, subclass, subspecies, etc.

Living organisms were once classified into five Kingdoms (Monera, Protista, Fungi, Animalia and Plantae). More recent data indicate that Monera and Protista included organisms descended from more than a single common ancestor. In modern systematics, this is not acceptable, and so Monera and Protista were dismantled and their members assigned to taxa that more accurately reflect evolutionary relationships.

Every described, named organism is nested into a complete organizational hierarchy, from species through its domain, as shown above for our own species, *Homo sapiens*. Note that the scientific name of an organism (its genus and species) is *always* written with the genus capitalized and the **specific epithet** in lower case letters. Because the words are Latinized, they should be *italicized* (as is any text written in a language other than that of the main body of the writing, *n' c'est pas*)?. This standard form was devised by Swedish botanist Carl Linne (who Latinized his own name to Carolus Linnaeus, and who is best known by his last name, Linnaeus) in his seminal work, *Systema naturae* (1735).

A. The Aspects of a Taxon

A taxon is generally considered to have three aspects:

1. **The taxon's name.** For example, the name of the taxon containing all domestic dogs is *Canis familiaris*. The order to which all dogs belong (along with a host of other flesh-eating mammals with specialized cutting teeth called carnassials) is **Carnivora**.

The scientific name of a group of similar organisms has no more significance than any other convenient label used to describe a group of similar items. Taxonomic names such as "Bacteria," "Felidae" and "*Oryctolagus cuniculus*" are similar in function to descriptive names of similar objects, such as "shoes" or "machines."

Don't let names confuse or intimidate you. Often, once you know the Latin or Greek word roots, seemingly complicated names make perfect sense and become easier to remember. For example, the name of *Eleutherodactylus planirostris*, a frog naturalized in southern Florida gardens, can be broken down into its Greek roots: *eleuthero*, meaning "free," *dactyl*, meaning "toe," *plani*, meaning "flat" and *rostris*, meaning "nose." Our little pal is a flat-nosed frog with unwebbed toes!

2. **The taxon's rank.** For example, the taxon Mammalia is assigned the taxonomic rank of **Class**. Like the taxon's name, the taxon's rank has no true biological significance. It serves only to help the biologist locate the taxon within the hierarchy.

You may notice throughout this semester that a given taxon's rank may vary, depending upon the source you're reading. For example, some publications may list "Zygomycetes," "Ascomycetes" and "Basidiomycetes" as classes within Phylum Mycota, whereas others assign each of those three taxa the rank of phylum (Phylum Zygomycota, Phylum Ascomycota and Phylum Basidiomycota) within Kingdom Fungi. Classifications change as new data become available, and older publications are not changed to reflect the more recent classifications.

Confusing? We won't deny it. Just remember that as new data come to light, the ranks of familiar taxa may change with various authors' attempts to more accurately reflect evolutionary relationships. The *relative* rank of a given organism within its larger and smaller groupings is more relevant than the name of the rank itself, which is often subject to change.

For example, it's important to know that all members of *Felis* are classified within the larger taxon "Carnivora," and that all carnivores are classified within the still larger taxon "Mammalia." It's *less* important to struggle to recall that "Carnivora" is an order and "Mammalia," is a class (especially since those ranks could change in five minutes).

The confusion caused by constant updating is one reason that many institutions are moving towards a **rankless system**, in which taxa are described only by their name, and rank is tacitly understood, but not included in publications. An author using this system will write "Mammalia" rather than "Class Mammalia" to avoid confusion as the ranks shift and change along with new information.

3. **The taxon's content.** For example, all the students in your lab are (probably) members of the genus *Homo* and the species *Homo sapiens*. To the systematist, this is perhaps the most relevant aspect of the taxon. By grouping specific individuals within a single species, related species within a single genus, related genera within a single family and so on, the systematist tells us which organisms are believed to be most closely related to one another, in terms of common evolutionary ancestry.

Organisms are not randomly classified into the various taxa. The systematist uses morphological characters, DNA sequencing, protein analysis, developmental biology, karyology, ultrastructure and other information and techniques to determine evolutionary relationships to the best of his/her ability. It's an ongoing quest--and one in which you might some day participate. Let's start with some simple exercises right now.

B. The Taxonomic Key: A Tool for Identification

A biologist does not always receive materials neatly packaged with name and taxonomic information included. In many cases, the investigator must identify an unknown specimen, and one of the most common methods of doing so in biology is by using a **taxonomic key**.

A taxonomic key is constructed on the basis of similarities and differences between specimens, and constructed as a series of paired statements. Such a key, because it branches in two at each stage, is called a **dichotomous** (from the Greek *dicho* meaning "in two" or "split" and *tom*, meaning "cut") **key**.

The paired statements describe contrasting characteristics (the handiest taxonomic keys used for field identification usually rely on morphology—physical appearance—of the organisms) found in the organisms being classified. With the specimen at hand, the investigator chooses which of the paired statements best matches the organism in question. The statement selected may immediately identify the specimen, but more often it will direct the user to another set of paired statements. At the end, though, the item should be identified by name, if an appropriate key has been used. (You wouldn't use a book called *Key to the Flora of Southern California* to identify an unknown tree you've discovered in Guatemala.)

And there's the rub. Sometimes a key for identification of the specimen you have at hand simply doesn't exist, and you must go to the primary literature to see if any species descriptions match it. Identification of unknown species can be a very difficult and challenging enterprise. Fortunately, the specimens you're going to use in today's exercise are not only easily recognizable, but we have a taxonomic key for their easy identification.

Using a Taxonomic Key

Work in pairs for this exercise. At your station you will find a container containing several "species" of pasta native to the United States of Publix. As it turns out, these noodles do have an evolutionary relationship to one another (they all are members of the same Order, Semolina, which evolved from a common ancestor resembling a soda cracker). However, a taxonomic key may or may not reflect these relationships. It's simply a tool devised to allow identification of each pasta to genus and species.

Most taxonomic keys are arranged phylogenetically, largely because related organisms share morphological characters, and it makes sense to identify them on the basis of these characters. But some taxa show tremendous morphological variability even among closely related groups. These may be very difficult to sort and classify accurately. (Please don't ask us to key out anything from Family Chenopodiaceae, the "Goosefoot" family of flowering plants. They are %$^@# *impossible*.)

Let's **key out** (yes, this is the verb commonly used to describe the process of identifying things with a taxonomic key) some pasta! Select one individual from your container, and use the taxonomic key below to identify its species. Once you have done this, identify each different "species" of pasta in your container.

A TAXONOMIC KEY TO THE PASTA OF SOUTHERN FLORIDA

1a. Body tubular in shape …… 2
1b. Body not tubular …… 4

2a. Skin lined with small, symmetrical ridges …… 3
2b. Skin smooth …… *Ziti edulis*

3a. Anterior and posterior ends of organism slanted …… *Penna rigata*
3b. Anterior and posterior ends of organism perpendicular to body axis …… *Rigatonii deliciosus*

4a. Skin lined with small, symmetrical ridges …… *Conchus crispus*
4b. Skin not lined with ridges …… 5

5a. Body cylindrical in overall shape …… *Rotinii spiralis*
5b. Body dorsoventrally flattened in shape …… *Farfalla aurea*

Exercise II. Creating a Taxonomic Key

There's no single correct way to create a taxonomic key, and there are several other ways one could have been arranged for your pasta species. Though it's not required that a key reflect phylogenetic relationships, the most informative keys tend to do so.

Work in pairs for this exercise. Now that you have seen how simple it is to use a taxonomic key, you should be able to create one yourself. In another container at your station you will find several "species" of hardware. At this point, it's not important that you can tell their evolutionary relationships to one another. You are merely trying to create a tool that a field hardwareologist could use to identify them.

Create a dichotomous key to your hardware species, using the pasta key on the previous page as a guide for its construction. Use your paperback copy of "A Guide to Greek and Latin Word Roots" by Donald J. Borror to create a Latinized scientific name (consisting of genus and species) for each of your species, and try to be as descriptive as possible with the name. (Some of your individuals might be in the same genus. It's up to you to decide!) Use proper *Systema naturae* rules in writing the scientific name of your hardware species: Genus is capitalized, species is lower case, and the entire name is italicized.

A Key to the Hardware of Southern Florida

1a. ____

____…………..________

1b. ____

____…………..________

2a. ____

____…………..________

2b. ____

____…………..________

3a. ____

____…………..________

3b. ____

____…………..________

4a. ____

____…………..________

4b. ____

____…………..________

5a. ____

____…………..________

5b. ____

____…………..________

6a. ____

____…………..________

6b. ____

____…………..________

Once you have finished your key, including all species of hardware, trade keys with the partners across the table from you. Using each other's keys, try to identify all hardware species correctly, and check with your swap partners to see how well you did when you finish.

II. Systematics

Because new data constantly change our understanding of evolutionary relationships, classifications are constantly updated and changed. The goal of most modern systematists is to construct **monophyletic** taxa, which reflect true evolutionary relationships by including all descendants of a single common ancestor. Several different lines of evidence can be used to determine the degree of common ancestry between two taxa, including

1. Comparison of morphology
2. Comparison of biochemistry and physiology
3. Comparison of chromosomes
4. Comparison of cell ultrastructure
5. Comparison of cellular metabolism and pathways
6. Comparison of nucleic acid sequences and protein composition
7. Studies of geographical distribution (biogeography)
8. Comparison of behavioral patterns
9. Comparison of embryological development

…to name just a few. As new technologies arise, our ability to study evolutionary relationships will evolve.

A. Reconstructing Phylogenies

A **phylogeny** is a history of the evolutionary descent of **extant** (i.e., presently living) or **extinct** (i.e., no longer living) taxa from ancestral forms. To date, about 1.4 million species (including 750,000 insects, 250,000 plants and 41,000 vertebrates) of the 5 to 50 million on earth have been scientifically described and classified.

What is a **species**? Although biologists still debate the precise definition, we shall use the biological definition of a species as **a group of actually or potentially interbreeding natural populations which are reproductively isolated from other such groups.** More simply, two organisms can be considered members of the same species if they can breed and produce fertile offspring under natural conditions.

1. Primitive and Derived Characters

Ever since Darwin's publication of *On the Origin of Species by Means of Natural Selection*, the scientific community has labored to come to a consensus about how different species arose on earth. It is now generally accepted that extant species **evolved** by means of natural selection from previously existing **ancestral species**. A character that shows little or no change from the same character in an ancestor is said to be **primitive**, whereas one that has changed in appearance and/or function, relative to the ancestral form, is said to be **derived**.

A primitive character is also known as a **plesiomorphy**, and a primitive character shared between two or more taxa is known as a **symplesiomorphy** (literally "shared primitive character"). A derived character is also known as an **apomorphy**, and a derived character shared between two or more taxa is known as a **synapomorphy** (literally "shared derived character").

All living things share these most basic symplesiomorphies:

1. Organization of structure (anatomy)
2. Capacity to generate more organisms like themselves (reproduction)
3. Growth and development
4. Ability to utilize energy to do work (metabolism)
5. Response to environmental stimuli (reaction)
6. Regulatory mechanisms to keep the internal environment within tolerable limits (homeostasis)
7. Populations that change in gene composition over time (evolution)

To classify an unknown organism more precisely than just "a living thing," the systematist must consider characters that make that organism unique and different from members of other species. To this end, derived characters are the most informative characters to use. The next section explains why.

2. Symplesiomorphies and Synapomorphies

Because of the shared evolutionary history of all living things, each species shares certain very ancient (i.e., **primitive**, or **plesiomorphic**) characters with other species, whereas other more recently evolved (i.e., **derived**, or **apomorphic**) characters set them apart from other species. The more synapomorphies two taxa have in common, the more recent their common ancestry.

For example, we humans share certain primitive characters with *all* members of Kingdom Animalia. List six primitive characters all humans share with all other animals, *but not with any other living things*:

1. ____________________
2. ____________________
3. ____________________
4. ____________________
5. ____________________
6. ____________________

Note: the characters you have listed above--if they are exhibited only by animals and by no other living organisms--are considered *symplesiomorphies only with respect to Animalia*. But if you are considering all living things, then the very same animal characteristics on your list are considered *synapomorphies that set animals apart from all other living organisms*. This means that any given character cannot be "primitive" or "derived" on its own. It can be described as "primitive" or "derived" only in relation to characters in other taxa.

With this in mind, now list three derived characters that set mammals (Mammalia, of which you are a member) apart from all other animals (you should already know two!):

1. ____________________
2. ____________________
3. ____________________

Do you exhibit all three of the characters listed? (Good! You're a mammal!) Since you share those characters with all your mammalian relatives, the characters are said to be **primitive with respect to all mammals**, even though they **are derived with respect to all other animals**.

You can see where this is going. Because you share those three characters with all mammals, they don't help you determine how closely related you are to any other mammal groups. To determine this, we must consider synapomorphies at an even higher resolution.

List three derived characteristics shared by all primates (Primates, of which you are a member), but not shared by other mammals. (You might have to do some searching!)

1. ____________________
2. ____________________
3. ____________________

What you have listed are three synapomorphies shared by Primates that set them apart from all other mammals. But because all primates share these three characters, they must be considered symplesiomorphies with respect to primates alone. In other words, these three characters do not help you to determine which primates are your closest relatives. To do that, we must find more unique characters.

List two derived characteristics shared by all great apes (Pongidae, of which you are a member), but not shared by other primates. (Again, you might have to do some searching. Notice that it gets more and more difficult to find synapomorphies linking a particular taxon as that taxon becomes less inclusive.)

1. ____________________
2. ____________________

Finally, list as many derived characters as possible that make *Homo sapiens* different from all other great apes. Be sure to restrict your list to truly BIOLOGICAL characters--not cultural ones. (This is where it gets really challenging, and sometimes there is simply not a clear line to draw, especially where cultural influences ("nurture") interact with a truly genetic and heritable ("nature") character.)

1. ____________________
2. ____________________
3. ____________________
4. ____________________
5. ____________________
6. ____________________

As you can see, it is not a simple task to find biological characteristics that truly separate *Homo sapiens* from other species of great apes. In fact, we share more than 99% of our DNA with our closest ape relatives, the Common Chimpanzees (*Pan troglodytes*) and Pygmy Chimpanzees (*Pan paniscus*).

Take a look back at the several lists you have drawn, and note how synapomorphies identified at higher and higher resolutions help us to determine most recent common ancestry among the various taxa. You've done this with primates, but this is what biosystematists do with all taxa. This method is used to construct and revise complex phylogenies as new data (e.g., DNA sequences, cell ultrastructure) become available.

3. Homologous and Analogous characters

If the similarity between two characters in two separate taxa can be attributed to their presence in a common ancestor of those taxa, then those two characters are said to be **homologous**. For example, the forelimb bones of all tetrapod (four-legged) vertebrates are homologous to one another, because they all evolved from the same bones in a common tetrapod ancestor. Although the bones may be of very different sizes and shapes, and may be present in limbs with very different functions (the fluke of a whale versus the wing of an egret), they all developed from the same embryonic sources and have evolved from the same ancestral tetrapod limb bones.

List five homologous characters you share with all other vertebrates that perform the same function in you as they do in all other vertebrates:

1. ____________________
2. ____________________
3. ____________________
4. ____________________
5. ____________________

Now list five homologous characters you share with other vertebrates that have evolved to serve a different function in you than they serve in some other vertebrates:

1. ____________________
2. ____________________
3. ____________________
4. ____________________
5. ____________________

Of the five characters you just listed, which are unique to *Homo sapiens*, and which are shared with at least some other vertebrates? What does this say about the recency of your common ancestry with those other vertebrates?

Not all physical similarities are homologous. In many cases, unrelated taxa have evolved superficially similar morphologies in response to similar pressure from natural selection. For example, a shark and a dolphin both share a streamlined, fusiform shape well adapted for swift swimming. However, while the shark's body evolved from a fishlike ancestor with a somewhat fusiform shape, the dolphin's fishlike form is secondarily derived from that of a terrestrial, four-legged mammalian ancestor.

The superficial similarity of shark and dolphin is a result of **convergent evolution.** Specifically, what is meant by the term "<u>convergent</u>" evolution?

____
____
____

Characters that have evolved similar form and function from disparate ancestral sources are said to be **analogous.** In some sources, analogous characters are called **"homoplasies"** or **"homoplastic characters."** Before you allow the similarity of the two terms "homoplastic" and "homologous" confuse you, look up their root derivations in your Dictionary of Word Roots and Combining Forms. Write their exact meanings here:

homo (Greek) = ____________________
analog (Greek) = ____________________
plas (Greek) = ____________________

List five characters <u>*you*</u> have that are analogous to characters with the same function but of different ancestral origin in any other species. Discuss the evolutionary significance of each of these in your group.

1. ____________________
2. ____________________
3. ____________________
4. ____________________
5. ____________________

B. Schools of thought in Systematics

Not everyone agrees on a single correct way to classify organisms. Although the cladistic system is the most widely accepted school of thought in today's institutions of higher learning, there are still some holdovers teaching more outdated methods. Take note of the tenets of each system.

1. Phenetic System (also known as Numerical Taxonomy)

Systematists who use the **Phenetic System** group organisms on the basis of phenotypic (physical) similarity. Pheneticists do not try to reconstruct evolutionary relationships, claiming that these relationships cannot ever be truly known.

To devise a classification, the pheneticist chooses a number of phenotypic traits and determines whether they are present (+) or absent (-) in the organisms being studied. Groups having the most traits in common are said to be the most closely related. Such classification schemes usually identify symplesiomorphies, and do not use derived characters to construct phylogenies

A purely phenetic analysis often does not allow the investigator to distinguish homologous characters from homoplasies. This can result in the creation of taxa that fail to reflect evolutionary relationships (which the hard-core pheneticist would claim are irrelevant, anyway).

2. Classical Evolutionary System

The **Evolutionary Classification System** is the one most commonly encountered by the student new to biology. Like the phenetic system, this classification groups organisms according to basic similarity, but unlike the phenetic system, it demands an evolutionary explanation for these similarities. Evolutionary taxonomists regard phenotypic specialization and degree of change *after divergence from a common ancestor* as important components of classification. This is perhaps the system's greatest weakness.

Traditionally, classical evolutionary taxonomists have considered a taxon worthy of separate status if its members show a high degree of specialization relative to those of a closely related taxon. The problem arises in the subjectivity of this judgment.

Let us consider birds and reptiles as an example. Genetic and ontogenetic data indicate that birds share a most recent common ancestor with crocodilians. However, because birds have feathers, are "warm blooded", and are superficially very different from crocodilians, the classical evolutionary biologist places them in Class Aves, and the crocodilians in Class Reptilia. This means that Class Reptilia does not include all the species that descended from the original ancestral reptile that gave rise to lizards, snakes, crocodilians, and birds. Such an artificial taxon, which does not include all descendants of a single ancestor, is said to be **paraphyletic**

Similarly, *Homo sapiens* has traditionally been assigned to its own family (Hominidae), although there is no objective reason to taxonomically separae it from the great apes (Pongidae). Like Reptilia, Pongidae not including *Homo sapiens* is paraphyletic. As you can see, placement of organisms subjectively judged to be "more derived" can be misleading, and can cloud true evolutionary relationships.

3. The Cladistic System

The **Cladistic System** was first published by German zoologist **Willi Hennig** in 1950. Systematists who use this system classify organisms exclusively on the basis of the recency of their descent from a common ancestor. Such relationships are determined by identification of synapomorphies. Taxa that share many derived characters are considered to be closely related to one another.

Cladists believe that differences in evolutionary rate of change among branches of organisms are irrelevant to their classification. For example, the cladist recognizes that birds--despite their plumage (modified scales homologous to reptile scales) and "warm-bloodedness"--share a most recent common ancestor with the crocodiles (Reptilia), and so would place birds in Reptilia, along with the other reptilian descendants of the common ancestor.

Although some systematists feel that the cladistic system's weakness is its failure to consider unequal rates of evolution, the cladist would argue that this is one of cladism's greatest strengths. The cladistic system is the most objective and quantitative of modern classification systems, and it is to its tenets that we will adhere this semester.

C. Phylogenetic Trees

By considering synapomorphies and symplesiomorphies and by identifying homoplasies, the systematist attempts to construct a phylogeny reflecting true evolutionary relationships. Often, phylogenies are represented in treelike diagrams showing how various extant taxa "branched off" from common ancestors and from each other. Such a diagram is called a **phylogenetic tree.**

In Figure ST-1a, the terms at the right of the diagram represent nine **extant** (i.e., currently existing) lineages of primates. Located beneath (to the left of) them on the "tree" are their hypothetical ancestors. For example

The **Ancestral Primate** gave rise to all primates.

Ancestor A is gave rise to Tarsiers and Anthropoids, but not Lemurs and their kin.

Ancestor E is the most recent common ancestor of all Great Apes, but not Gibbons.

Ancestor G gave only rise to humans, chimpanzees and bonobos.

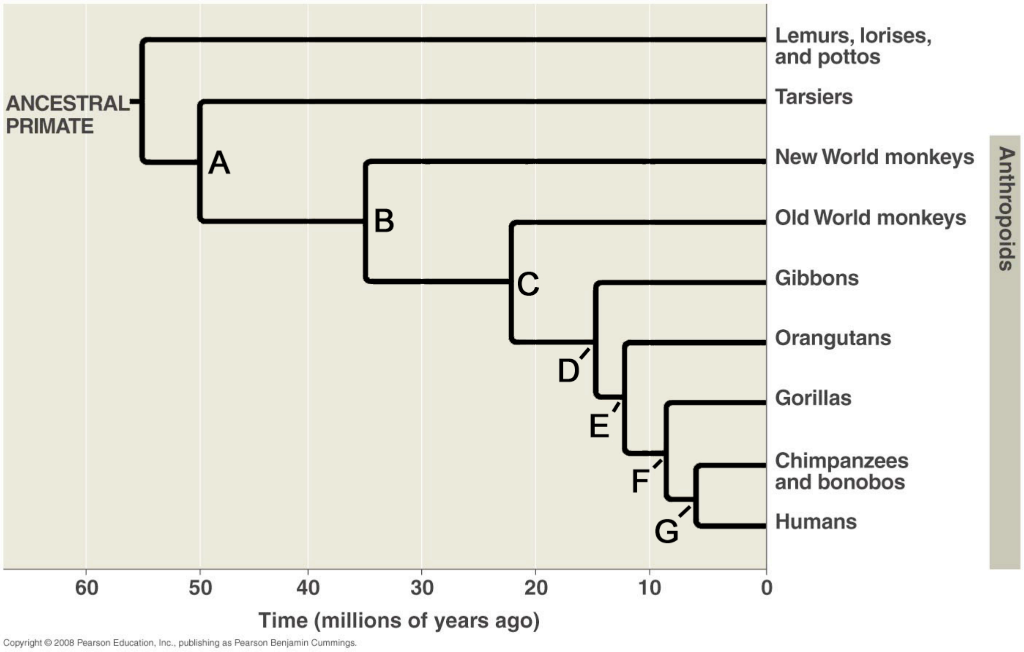
…and so on.

Note that this phylogenetic tree shows only *recency of common descent*. It does not indicate which species might be (subjectively) described as "primitive" or "derived" (Those terms are meaningless when applied to an entire species.)

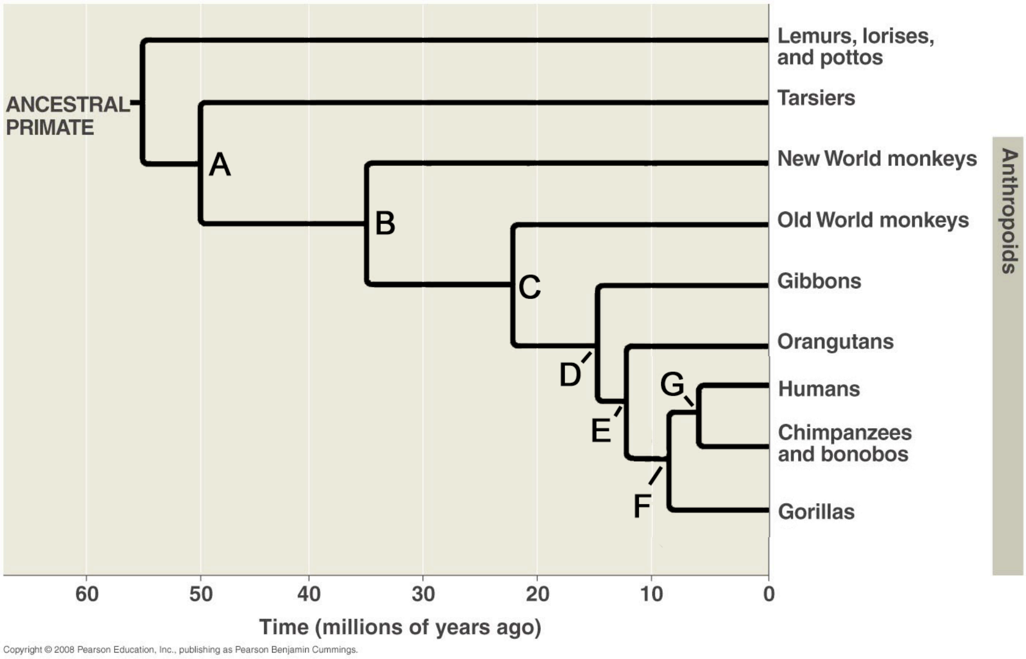
Note also that two lineages branching from the same ancestor arose at the same geological time. Many people have the misconception that *Homo sapiens* is the “most highly evolved” species, or even the most recently evolved. Neither is true. Always remember…

Rule #1: The branches coming from every node can be rotated. The branches do not imply any sort of order; they indicate only recency of common descent. For example, the node at Ancestor F could be rotated so that the tree looked like the one shown in Figure ST-1b, and the information given would be exactly the same. Any node on the tree can be rotated in a similar fashion.

Rule #2: Two lineages branching from a single ancestral node are known as sister taxa. Further specialization after a branch point is irrelevant to the systematist using cladistic analysis (which we do). Therefore, it would be incorrect to say that humans evolved more recently than chimpanzees, or that Humans should be placed in their own family (“Hominidae”) simply because they seem so different from chimpanzees. Taxonomic groupings are based on common ancestry only, not subjective perceptions of specialization.



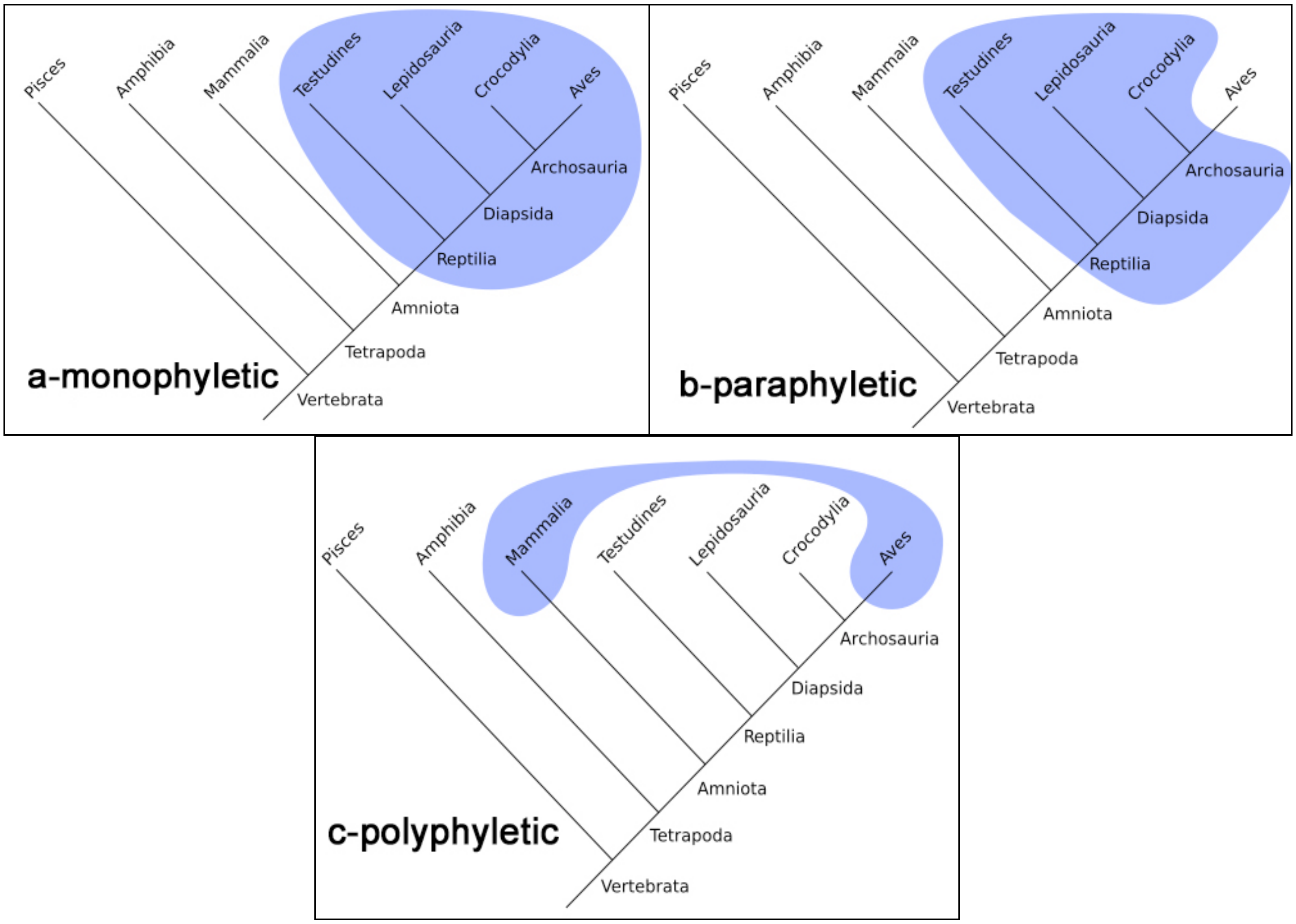
<u>Figure ST-1a.</u> **Phylogeny of primates. The nodes from which branches emerge represent the hypothetical common ancestor of all taxa above that node on the tree. The endpoints of the branches represent the descendants of that ancestor. Some phylogenetic trees include both extinct and extant (still living) taxa. In modern systematics, extinct taxa (represented by fossils) are treated the same way as extant taxa, and are *not considered ancestral* to extant taxa.**



<u>Figure ST-1b.</u> **Phylogeny of primates demonstrating a rotation of the node at Ancestor G, relative to the original drawing shown in Figure ST-1a. Rotating the node in this manner does not change the phylogenetic information.**

Rule #3: There is no such thing as a "most highly evolved species". All extant species are descended from successful ancestors, and are evolved to survive and reproduce in the context of their specific environment. Evolution is a process. It has neither a goal nor a subjective value system.

Rule #4. No extant taxon is ancestral to any other extant taxon. When an ancestral lineage diverges to become two separate taxa, the ancestral lineage is considered extinct. This should be remembered when one hears the oft-repeated, but incorrect statement "humans evolved from monkeys". They did not. Humans and monkeys share a common ancestor. That's not the same thing.



<u>Figure ST-2.</u> Representative vertebrate taxa are grouped in monophletic (a), paraphyletic (b) and polyphyletic (c) assemblages, shown by blue shading. Note that the paraphyletic tree (b) shows the traditional, evolutionary system for classifying Reptilia (turtles, crocodilians, snakes, and lizards), which does not reflect actual evolutionary relationships. Reptilia can be made monophyletic by including Aves (birds). The polyphyletic tree (c) illustrates what can happen when organisms are classified on the basis of superficial similarity, such as "warm bloodedness" or "four-chambered heart". These characters most likely evolved independently in mammals and in birds.

A phylogenetic tree is not constructed randomly. The systematist uses data on morphology, homology of nucleic acids, congruence of similar proteins, etc. to determine recency of common descent.

A **clade** is a group of species that includes an ancestral species and all of its descendants. Such a group is said to be **monophyletic**. The systematist uses cladistic techniques to construct monophyletic phylogenies that reflect true common ancestries. However, this is not always easy. When new data become available, it is sometimes discovered that a taxon under study is not monophyletic.

A **paraphyletic** taxon fails to include all descendants of a particular common ancestor. A **polyphyletic taxon** includes members that have descended from more than one different ancestor, but the common ancestor of those has not been included. These are illustrated in Figure ST-2.

Using some of the characteristics of the pasta you met earlier in this exercise, we have constructed a hypothetical phylogenetic tree showing their possible evolutionary relationships. (Figure ST-3) This may not be the only possible tree, and the more different data sets used to construct a tree that show congruency between them, the more likely it is that the tree reflects actual evolutionary relationships.

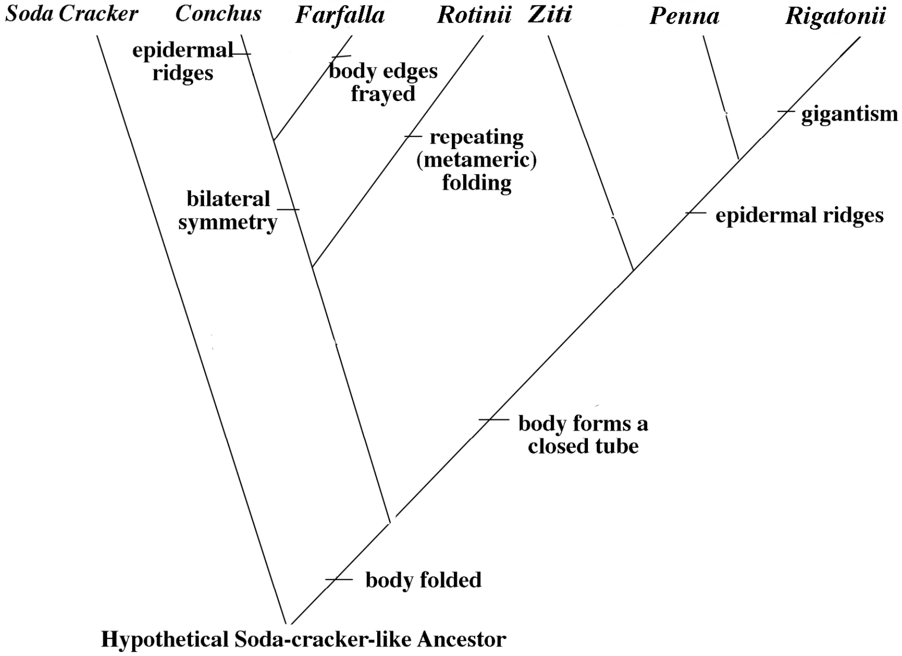


Figure ST-3. A hypothetical phylogeny of the pasta of the United States. The hash-marks along the tree indicate the appearance of synapomorphies found only in the taxa above that character on the tree.

Exercise IV. Constructing Phylogenetic Trees

Most biologists agree that our classifications should be "natural" so that to the extent possible they reflect evolutionary relationships. We do not, for example, place slime molds and whales in the same family. Biosystematics, then, is a two-part endeavor. First, one must erect an hypothesis of evolutionary relationship among the organisms under study. Second, one must devise a classificatory scheme that faithfully reflects the hypothesized relationship. We will use a series of imaginary animals to introduce you to two rather different methods that attempt to do this.

The hypothetical animals used in this exercise are called **Caminalcules** and were created and "evolved" by **J. H. Camin**, Professor of Biology at the University of Kansas in the 1960's. They have served as test material for a number of experiments concerning systematics, its theory and practice. Use of imaginary organisms for such studies offers a distinct advantage over using real groups, because preconceived notions and biases about classifications and evolutionary relationships can be eliminated.

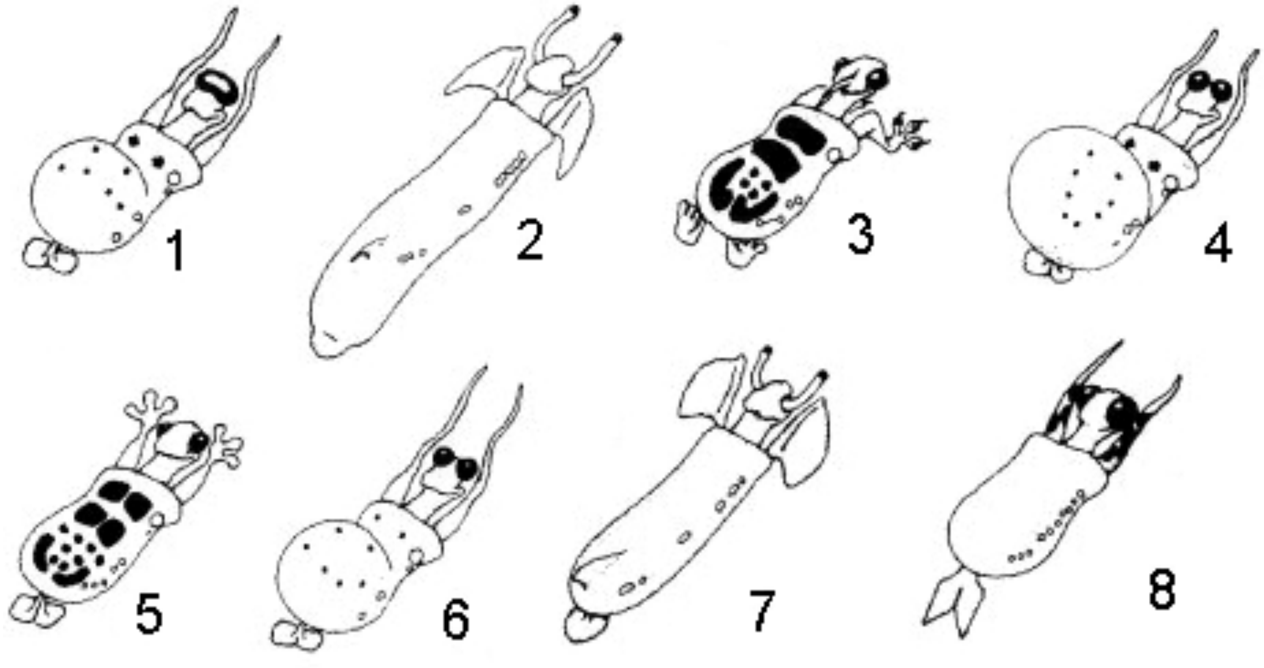


Figure ST-4. A variety of Caminalcules, arranged in no particular order.

Cladistics: Synapomorphies and Cladograms

Carefully examine the eight Caminalcules illustrated in Figure ST-4. These will be your Operational Taxonomic Units (OTUs)--a name we use to avoid assigning them to any particular taxonomic rank (such as “species”). You may think of them as biological species, and refer to them by number.

Cladistic methods provide an objective and suitable way of inferring evolutionary relationships. Cladistics is sometimes known as **quantitative phyletics**. Rather than grouping organisms on the basis of overall similarity, as in numerical taxonomy, the investigator using this method groups OTUs together on the basis of shared, derived characters (**synapomorphies**)--characters whose presence or absence in two or more OTUs is inferred to be the result of inheritance from their common ancestor.

Results of a cladistic analysis are usually summarized in a phylogenetic tree called a **cladogram** (from the Greek *clad* meaning "branch"), an explicit hypothesis of evolutionary relationships.

In the cladogram shown (Figure ST-7), A and B are considered most closely related if they share characters in common that are not found in C. C is considered most closely related to A and B if it shares characters common to all three OTUs, but absent from other OTUs outside this three-OTU group.

As we already have mentioned, a taxonomic group descended from a single common ancestor is said to be **monophyletic** if it includes all the descendants of that common ancestor, and none of the taxa descended from a different common ancestor. For example, A and B would comprise a monophyletic group, but a group made up of only A and C would not.

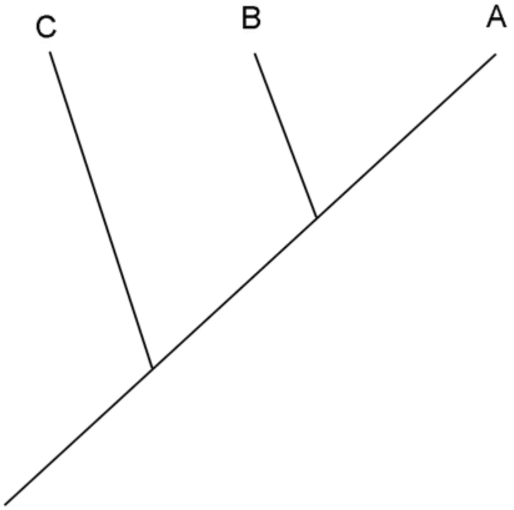


Figure ST-7. **A cladogram**

A Sample Procedure

We will examine the eight Caminalcules in Figure ST-4, this time in an attempt to infer the evolutionary relationships among them, as follows.

Step One. Select a series of characters that can be expressed as binary (i.e., two-state). For example:

Character a:	"eyes present" (+) versus "eyes absent" (-)
Character b:	"body mantle present" (+) versus "body mantle absent" (-)
Character c:	"paired, anterior non-jointed appendages present" (+) versus "paired, anterior non-jointed appendages not present" (-)
Character d:	"anterior appendages flipperlike" (+) versus "anterior appendages not flipperlike" (-)
Character e:	"eyes stalked" (+) versus "eyes not stalked" (-)
Character f:	"body mantle posterior bulbous" (+) versus "body mantle posterior not bulbous" (-)
Character g:	"eyes fused into one" (+) versus "eyes separate" (-)
Character h.	"forelimbs with digits" (+) versus "forelimbs without digits" (-)

Step Two. Examine all your organisms and determine which character state it exhibits. Enter the data in a matrix like the one shown in Table ST-4.

Note that in this example, character a (presence or absence of eyes) and character b (presence or absence of a body mantle) is the same in all eight OTUs. Hence, this (primitive) character is not useful to us if we are trying to determine differences between the OTUs.

Note also that only OTUs 2 and 7 share character e (stalked eyes), which is absent from all other OTUs. This suggests that OTUs 2 and 7 both inherited this character from a common ancestor. Likewise, OTUs 1, 4, and 6 share character f (bulbous mantle posterior) which is absent from all others. This supports the hypothesis of common ancestry among these three OTUs.. The same reasoning argues for common ancestry among OTUs 1, 4, and 6 (character f), and for OTUs 3 and 5 (character h), and so on.

Table ST-4. Character states of characters a - h in Caminalcules in Figure ST-4.

character	1	2	3	4	5	6	7	8
a	+	+	+	+	+	+	+	+
b	+	+	+	+	+	+	+	+
c	+	+	-	+	-	+	+	+
d	-	+	-	-	-	-	+	-
e	-	+	-	-	-	-	+	-
f	+	-	-	+	-	+	-	-
g	+	-	-	-	-	-	-	-
h	-	-	+	-	+	-	-	-

A cladogram consistent with the distribution of these eight characters among the eight OTUs is shown in Figure ST-8.

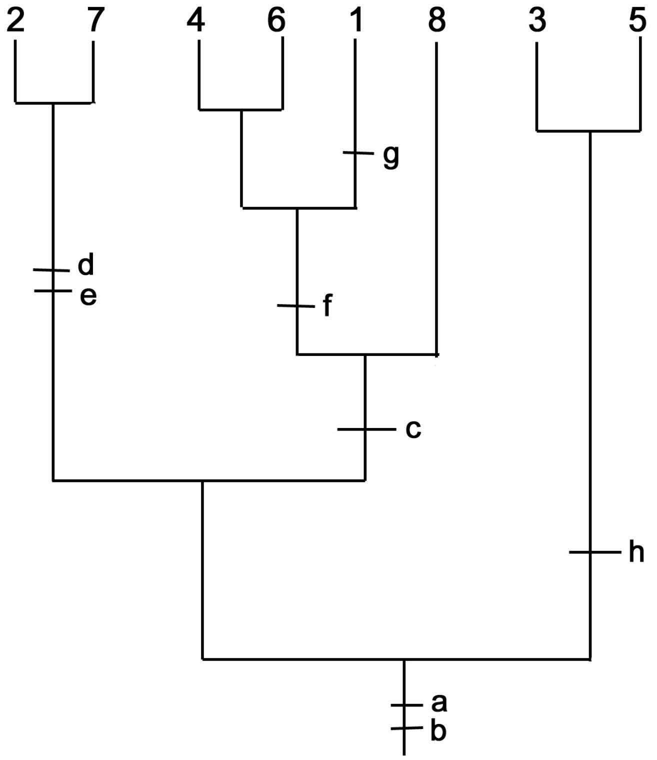


Figure ST-8. A cladogram based on synapomorphies in Caminalcules 1 - 8.

This is not the only possible phylogeny consistent with the character distribution among the OTUs. In practice, there are often several, or even many, cladograms that can be constructed, all of which are consistent with the data. In such cases, systematist generally applies a **parsimony** criterion for selecting the "best" cladogram. The rule of parsimony states that when two or more competing hypotheses are equally consistent with the data, we provisionally accept the simplest hypothesis. This is not to say that evolution is always parsimonious, only that our hypotheses should be.

In the case of competing cladograms, the rule of parsimony would require that we accept the simplest cladogram, the one with the fewest "steps" to each of the taxa on the tree. In our example, we could hypothesize that OTU 6 is actually more closely related to OTU 1 than to OTU 4. However, this would require that character g (fused eyes) had been evolved once, and then secondarily lost in both OTUs 4 and 6. This is less parsimonious than stating fused eyes evolved only once, in OTU 1.

Cladistics and Linnaean Classification

Given an hypothesis of evolutionary relationships, the second step in biosystematic endeavor is to erect a classification that faithfully reflects those relationships. Because the results of a cladistic analysis (i.e., the cladogram) are heirarchical, they can easily be incorporated into the Linnaean hierarchy, as shown in Figure ST-9.

In cladistic analysis, all taxa must be **monophyletic**, meaning that they must include the common ancestor (almost always hypothetical) and all descendants of that common ancestor. Thus, in the cladogram above, OTUs 2 and 7 together with their common ancestor (at the branch point just below them) constitute a monophyletic genus, as do OTUs 1,4,6 and 8 and their common ancestor (at the branch point just above the appearance of character d).

A Family consisting of only OTUs 2 and 7 would not be monophyletic, because it does not include all the descendants of the common ancestor (at the branch point just below character d). Such a group would be considered **paraphyletic** (containing some, but not all, of a particular ancestor's descendants).

A Family consisting of OTUs 2 and 7 plus OTUs 3 and 5 would be considered **polyphyletic** (consisting of species derived from more than one most recent common ancestor). This is because such a taxon would be made up of groups descended from both the ancestor just below the appearance of character h, and the one just below the appearance of characters c and e.

Order Caminalcula:
- **Family 1**
  - **Genus 1**
    - **Species 2**
    - **Species 7**
  - **Genus 2**
    - **Species 1**
    - **Species 4**
    - **Species 6**
    - **Species 8**
- **Family 2**
  - **Genus 3**
    - **Species 3**
    - **Species 5**

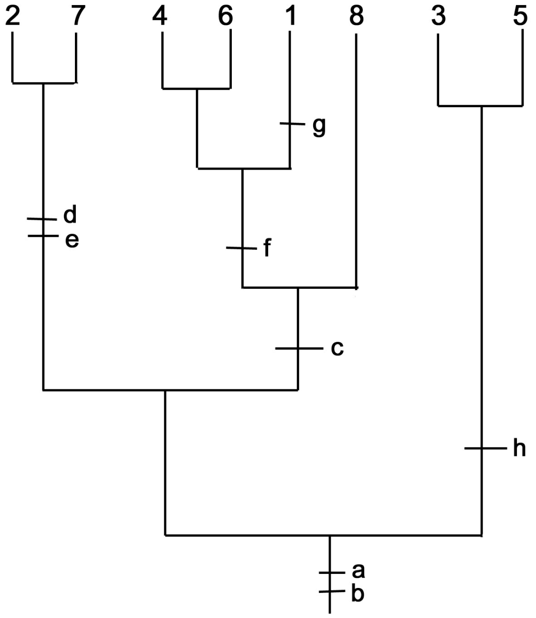


Figure ST-9. Incorporated results of a cladistic analysis showing Linnaean relationships among the OTUs.

Exercise: Constructing a Cladogram Based on Synapomorphies

Using the Caminalcules in the packet at your lab station, go through the steps of sample cladistic analysis we did for the Caminalcules in Figure ST-4. Use the spaces and matrix provided to choose shared, derived characters that help you group the OTUs into taxa that reflect their hypothetical evolutionary relationships. Finally, in the space provided, draw a cladogram of your Caminalcules, showing the appearance of each character, as we did in Figure ST-9.

character	state of character if (+)	state of character if (-)
a		
b		
c		
d		
e		
f		
g		
h		

OTUs

character								
a								
b								
c								
d								
e								
f								
g								
h								

Questions

1. The results of phenetic and cladistic analysies are inherently hierarchical, as is the branching sequence of the evolution of organisms. So, too, is the Linnaean classificatory system of ever more inclusive taxonomic categories from species, Genus, Family, Order, Class, Phylum, Kingdom and Domain. Can you name some other hierarchical classification systems (not necessarily biological)?

2. Taxonomists were erecting classifications of organisms long before Darwin convinced biologists of the reality of evolution. Some of these taxonomists believed in the fixity of species and in special creation. Nevertheless, in some respects, these pre-Darwinian classifications are rather similar to those produced later by evolutionary taxonomists. Why do you think this is so?

Use the following page to draw your cladogram. This page and your cladogram will be turned in to your TA for grading.

Name:

Lab section:

Draw your cladogram below.