Laboratory #1:
EVOLUTION, SYSTEMATICS, AND CLADOGRAMS

OBJECTIVES FOR THIS LABORATORY

1. Understand the basics of evolution and systematics.
2. Understand the methods of constructing cladograms, which denote evolutionary history (phylogeny).
3. Learn the use of interactive computer programs for tracing phylogeny.

INTRODUCTION

This laboratory is an introduction to: 1) the basic theory and concepts of biological evolution and systematics, including an overview of taxonomy; 2) the methodology used in constructing cladograms, which denote the evolutionary history or phylogeny of life; and 3) the use of interactive computer applications that are used to trace the history of life. For the remainder of this course you will be studying individual groups of organisms in detail, including a summary of their phylogeny, major evolutionary novelties or apomorphies, and the adaptive significance of those apomorphies. Therefore, to understand future labs, it is essential that you understand the basic concepts and methods described here.

EVOLUTION

Evolution is the foundation of all biology and may be defined (as it was by Charles Darwin) as "descent with modification." It is essential to understand what "descent" means, how the "modification" occurs, and <u>what</u> is actually evolving. "**Descent**" refers to the transfer of genetic material, enclosed within a **cell** (the unit of life), from parent(s) to offspring. This is a simple concept, but one that is important to ponder and grasp thoroughly. Since the time that life first originated some 3-4 billion years ago, <u>all life has been derived from pre-existing life</u>. Organisms come to exist by the transfer of genetic material (plus a portion of a surrounding cell) from one or more parents. For all life today, the genetic material consists of DNA (deoxyribonucleic acid), which encodes all the information needed to form a new, fully functional individual. Descent may occur by simple clonal fission, such as a single bacterial cell "parent" dividing to form two "offspring" cells. It may also occur by complex sexual reproduction, in which each of two parents produce specialized cells called gametes (e.g., sperm and egg), which have half the original complement of genetic material (achieved by meiosis; see Laboratory #3) and which fuse together to form a new cell, the zygote, that constitutes or develops into a new individual. In either case, descent refers to this transfer of genetic material and cell from parent to offspring, ancestor to descendent, through time, generation after generation.

"**Modification**" refers to a <u>change</u> in the genetic material that is transferred from parent(s) to offspring, such that the genetic material of the offspring is different from that of the parent(s). This modification may occur either by mutation, a direct alteration of DNA, or genetic recombination, in which existing genes are re-shuffled in different combinations. An understanding of mutation and recombination requires a knowledge of the details of cell and molecular biology, which will not be covered in this laboratory manual.

Finally, it should be asked, <u>what</u> evolves? Although genetic modification may occur in offspring relative to their parents, <u>individual organisms do not evolve</u>. This is because the individual begins when it receives its complement of DNA from the parent(s); that DNA does not change during the lifetime of the individual. What does evolve are populations and species. **Species** may be defined as lineages (see below) that usually consist of intergrading, interbreeding groups of individuals that are usually reproductively isolated from other species. A **population** is a group of individuals of the same species, usually confined to a particular geographic region. With changes in the genetic makeup of offspring relative to parents, the genetic makeup of populations or species changes over time.

In summary, evolution is descent with modification occurring by a change in the genetic makeup of a population over time. How does evolution occur? Evolutionary change may come about by two major mechanisms: 1) genetic drift, in which genetic modification is random; or 2) natural selection, in which genetic change is directed and non-random. **Natural selection** is the differential contribution of genetic material from one generation to the next; i. e., those genetic combinations resulting in increased survival or reproduction are contributed to a greater degree. Natural selection results in an **adaptation**, a structure or feature that performs a particular function and which itself brings about increased survival or reproduction. As you learn the features of the major groups of biological diversity, it is important to consider the possible adaptive value of these features.

SYSTEMATICS

Systematics is defined here as that branch of biology that: 1) includes and encompasses **taxonomy**; and 2) has as its emphasis the reconstruction of **phylogeny**, the evolutionary history of a group of organisms. Systematics is founded in evolutionary theory. Its major premise is that there is one phylogeny of life; the goal of systematists is to infer that history. Systematic studies may incorporate and synthesize information from all branches of biology, including morphology, anatomy, biochemistry, ultrastructure, development, and molecular biology.

Taxonomy

Taxonomy is a component of systematics that includes four basic aspects: **D**escription, **I**dentification, **N**omenclature, and **C**lassification. (Remember the mnemonic device: **DINC**.) One interesting thing to note is that the four components of taxonomy are basic not only to the study of biological organisms, but comprise the basis for studying any field.

Description is simply listing the features or attributes of an organism. These features are commonly called **characters**. Two or more forms of a character are **character states**. One example of a character might be "cell organization," for which the two major character states are "unicellular" and "multicellular." Another simple character might be "flower color," for which two character states might be "blue" and "yellow." As you will see later, it is important to learn to discern organisms in terms of their characters and corresponding character states. An accurate listing of these features for organisms is one of the major objectives and contributions of taxonomy.

Identification is the association of an unknown taxonomic group (e.g., a species) with a known one. One generally identifies an unknown by first noting its characteristics, i.e., by describing it. These features are then compared with those of other taxa to see if they conform. Taxa can be identified in many ways: by reading descriptions to see if they match the unknown specimen, by comparing an unknown with photos and illustrations or other specimens, or, ideally, by simply asking an expert of that particular group of organisms. However, the most common way of identifying taxa is by using a taxonomic key, in which choosing between a series of contrasting statements ultimately leads to a correct identification. (See Figure 1.1 for an example of a simple, dichotomous key.)

Nomenclature is a formal system of naming of taxa according to some standardized system. Currently, the rules and regulations for the naming of organisms are provided by the: 1) International Code of Botanical Nomenclature for plants, algae, and fungi; 2) International Code of Zoological Nomenclature for animals and "Protista;" and 3) International Bacteriological Code of Nomenclature for "procaryotes." These

1. Petals 4 or 5
Couplet: *Lead:* 2. Stamens yellow .... Species A
Lead: 2' Stamens purple .... Species B
1' Petals 3
3. Leaves linear .... Species C
3' Leaves ovate .... Species D

Figure 1.1 A simple dichotomous key, in which organisms are identified by sequentially choosing between two contrasting statements. Each pair of statements is called a couplet; the two members of a couplet are known as leads.

formal names are known as **scientific names**. (See Figure 1.2 for examples of scientific names at different ranks.)

One fundamental type of scientific name is the species name. A species name always consists of two parts: the genus name (always capitalized, e.g., "*Homo*") plus the specific epithet (e.g., "*sapiens*"), both of which are always either italicized or underlined. For this reason, species names are known as **binomials**, literally meaning "two names;" this type of nomenclature is called binomial nomenclature. The binomial system was first formalized in the mid-18th century by Carolus Linnaeus (Carl Linné), who is known in some quarters as the "father of taxonomy." (BEWARE: it is incorrect to say, e.g., that the species name for humans is "*sapiens*," as this is merely the specific epithet. The species name for humans is *Homo sapiens*; both parts of the binomial must be stated.)

Scientific names are, by convention, translated to Latin, which has an alphabet almost identical to that of English; thus, no matter what the language of the original person who describes and names a taxon, the name itself must be in Latin. Although they may seem difficult to learn at first, scientific names are much preferable to common names. First, only scientific names are universal, the same world-wide; common names may vary from region to region. Second, scientific names always refer to only one taxon, whereas common names are inconsistently applied. For example, more than one common name may be used for a single taxon (e.g., the bird species *Falco sparverius* is known both as a "Kestrel" and "Sparrow Hawk"); alternatively, a single common name may refer to more than one taxon (e.g., "Hemlock" may refer to two quite different plants, either a species of *Tsuga*, a tall coniferous tree, or *Conium maculatum*, an herb of the carrot family, the extract of which Socrates drank in execution). Third, scientific names may automatically denote the rank of classification (see below), whereas common names generally do not. Finally, many organisms may have no common name in any language. In summary, there is a rationale for putting you through the effort of learning Latinized scientific names. Once you lose your fear of them, they will become second nature.

Classification is the arrangement of objects into some type of order. The traditional way to classify life is by means of categories called **ranks**. (See Figure 1.2 for a list of the major taxonomic ranks.) These taxonomic ranks are hierarchical, meaning that each rank is inclusive of all other ranks beneath it. A **taxon** is a particular taxonomic group, which may be placed at a given rank; the plural of "taxon" is "**taxa**." For example, "Mammalia" is a specific taxon that is often placed at the rank of class (Figure 1.2). Some taxa at a given rank may have a standardized ending denoting that rank. For example, all plant family names end in "-aceae" (e.g., Rosaceae), whereas animal family names end in "-idae" (e.g., Hominidae). Recently, systematists have argued for the elimination of ranks altogether; see Phylogenetic Classification.

There are two major ways to classify living organisms: phenetic and phylogenetic. **Phenetic** classification is classification by overall similarities. Most of our everyday classifications are phenetic. For efficiency of organization (e.g., storing and retrieving objects, like nuts and bolts in a hardware store), it is common sense to group similar objects together and dissimilar objects apart. **Phylogenetic** classification is that which is based on evolutionary history, or pattern of descent, which may or may not correspond

Major Taxonomic Ranks*	**Example taxon**
Domain	Eucarya
Kingdom	Animalia
Phylum (“Division” also acceptable for plants, algae, & fungi)	Chordata
Class	Mammalia
Order	Primata
Family	Hominidae
Genus (plural: genera)	*Homo*
Species (plural: species)	*Homo sapiens*

Figure 1.2 The major, traditional taxonomic ranks, with an example of specific taxa at each rank. Only recently has “Phylum” been allowed for plants, algae, and fungi; for these taxa “Division” may be used interchangeably with “Phylum.” (Note: Any of the above ranks may have sub-ranks; e. g., Subkingdom, Subclass, etc.)

to overall similarity. A phylogenetic system of classification is inherently based on the concept of evolution. Thus, in general, only biological entities are grouped in a phylogenetic classification system; see Phylogenetic Classification.

Phylogeny

Phylogeny refers to the evolutionary history of a group of organisms. Phylogeny is commonly represented in the form of a **cladogram** or “phylogenetic tree,” a branching diagram that conceptually represents the best estimate of phylogeny (see Figure 1.3). The lines of a cladogram are known as **lineages** or **clades**. Lineages represent the sequence of ancestral-descendent populations through time, ultimately denoting **descent**, the transfer of genetic material from parents to offspring, generation after generation. Thus, cladograms have an implied time scale that is represented as relative, not absolute. Branching of the cladogram lineages denote **speciation**, the formation of two species from one **common ancestor**. Changes in the genetic makeup of populations, i.e., evolution, may occur in lineages over time. Evolution may be recognized as a change from a pre-existing, or **ancestral**, feature to a new, **derived** feature. The derived feature is an evolutionary novelty, also called an **apomorphy**. As seen in Figure 1.3, an apomorphy that unites two or more lineages is known as a **synapomorphy** (*syn*, together); one that occurs within a single lineage is called an **autapomorphy** (*aut*, self). In summary, cladograms represent the pattern of evolutionary history, both in terms of descent and in the distribution of derived or “apomorphic” character states, which represent unique evolutionary modifications.

Phylogenetic systematics, or **cladistics**, is a methodology that allows one to reconstruct the phylogeny of a group of organisms. The basic tenet of phylogenetic systematics is that shared derived character states constitute evidence that the taxa possessing those features share a common ancestry. These shared apomorphies represent unique evolutionary events that may be used to link two or more taxa in a common evolutionary history. Thus, by sequentially linking taxa together based on their common possession of apomorphies, the evolutionary history of those taxa can be inferred. The trick is to determine which features are derived and which are ancestral. If the ancestral condition or character state is established, then the direction of evolution, from ancestral to derived, can be inferred, and synapomorphies can be recognized. The methodology for determining the direction of evolutionary change is quite involved and beyond the scope of this laboratory manual. (See references listed in LITERATURE CITED AND ADDITIONAL READINGS for more detailed information.)

One concept critical to cladistics is that of **homology**. **Homology** can be defined as similarity resulting from common ancestry. Two or more features are homologous if their common ancestor possessed the same feature. For example, the wing of a pelican and the wing of an eagle are homologous as

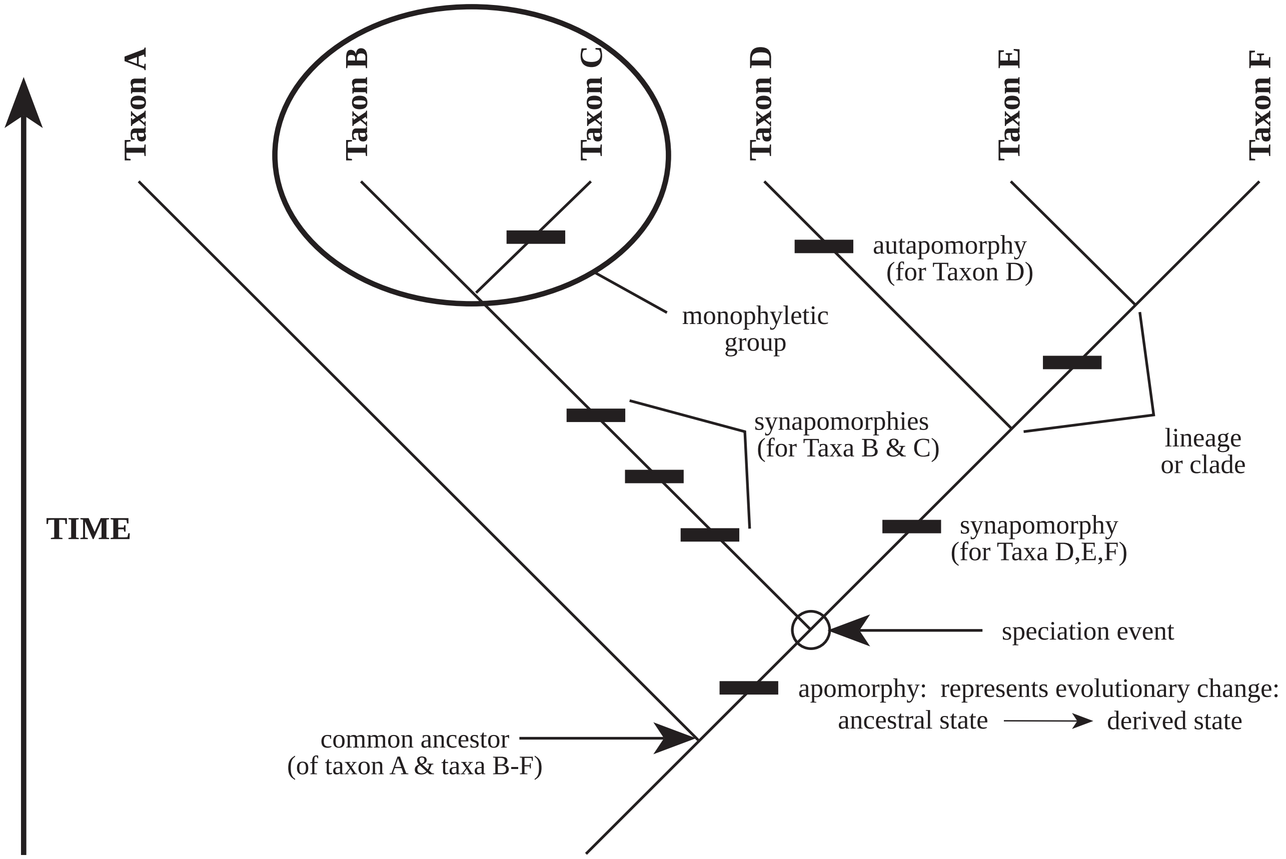

Figure 1.3 A cladogram, the conceptual representation of the evolutionary history (phylogeny) of a group of taxa.

wings because their common ancestor had wings. In contrast to homology, similar not due to homology is **homoplasy** (also called "analogy," though this term is not often used anymore). For example, the wing of a pelican and the wing of a bat are homoplasious as wings because their common ancestor lacked wings; in other words, wings in these two groups evolved independently. Homoplasy may arise in two ways: **convergence** (also called "parallelism") or **reversal**. **Convergence** is the independent evolution of a similar feature in two or more lineages. Thus, bird wings and bat wings evolved independently as flying appendages; their similarity is homoplasious, via convergent evolution. **Reversal** is the loss of a derived feature with the re-establishment of an ancestral feature. For example, relative to the Tetrapods (vertebrates with walking appendages), snakes underwent an evolutionary reversal, losing their legs and reverting to a condition resembling ancestors of Tetrapods.

Another important concept of phylogenetic systematics is that of monophyletic groups. A **monophyletic** group or taxon is one that consists of a common ancestor and all descendants of that ancestor. For example, in Figure 1.3 the circled region is a monophyletic group that includes taxon B, taxon C, and the common ancestor of B and C. Any two monophyletic taxa that share an immediate common ancestor are called **sister groups** or **sister taxa**. For example, sister group pairs in Figure 1.3 are: 1) A and BCDEF; 2) B and C; 3) BC and DEF; 4) D and EF; and 5) E and F. In contrast to a monophyletic group, a **paraphyletic group** is one that includes a common ancestor and some, but not all, known descendants of that ancestor. For example, in Figure 1.3 the group consisting of taxa B, C, D, and F is paraphyletic because it does not include taxon E, one of the descendants of the common ancestor of B-F. A real example of a paraphyletic group are the traditionally defined "Reptiles," which omitted birds. Because most systematists believe that the nearest relatives of birds are Crocodiles, the Reptiles must now include birds. Paraphyletic groups are

- taxon ABCDEF (monophyletic group)
  - •taxon A
  - •taxon BCDEF (new monophyletic group)
    - taxon BC (new monophyletic group)
      - taxon B
      - taxon C
    - taxon DEF (new monophyletic group)
      - taxon D
      - taxon EF (new monophyletic group)
        - taxon E
        - taxon F

A

- taxon ABCDEF (monophyletic group)
  - •taxon A
  - •taxon BC (new monophyletic group)
    - taxon B
    - taxon C
  - •taxon D
  - •taxon EF (new monophyletic group)
    - taxon E
    - taxon F

B

Figure 1.4 Two different classification schemes for the cladogram of Figure 1.3. A. Dichotomous, in which sister group pairs receive the same level of indentation and sister group pairs within a given group are further indented. B. Annotated, in which taxa within a group are listed in sequence from the base to the top of the cladogram.

to be avoided because they are not complete evolutionary units; their usage in comparative studies of, e.g., evolutionary process, ecology, or biogeography will only distort the truth. In addition, paraphyletic groups cannot be used to reconstruct the true evolutionary history. Although some paraphyletic groups will still be seen in the literature, these will be abandoned as more evidence accumulates. They are only used in the system of this manual when their relationships have yet to be refined. **Note:** if a group is known to be paraphyletic, it is placed in quotation marks.

Why study phylogeny? Knowing the evolutionary history in the form of a cladogram can be viewed as an important end in itself. However, the cladogram can be used as a tool for addressing several interesting biological questions. It may be used to trace character state evolution and better assess the adaptive significance of a given feature. It may be used to study processes of speciation, such as the mechanism and rate of speciation events. It may be used to infer the geologic, geographic, or ecological history of a group by correlating the evolutionary history with geographic distributions. Finally, the cladogram may be used to directly devise a classification system, one of the goals of taxonomy (below).

Phylogenetic Classification

As stated earlier, classification refers to placing objects in some type of order. In practice, classification entails listing taxa in such a way that they are grouped together in some orderly fashion. A phylogenetic classification is a listing of taxa which represents the evolutionary relationships of those taxa and which may be used to reconstruct the cladogram. There are two general ways to construct a phylogenetic classification. First, in a so-called **dichotomous classification**, every monophyletic group is named, and the two sister groups within each monophyletic group are listed at the same indentation; within any one taxon, additional sister groups are further indented. For example, for Figure 1.3, the dichotomous classification system of Figure 1.4A could be used. Note that in a dichotomous system, within a given monophyletic group there are always only two taxa listed at the same level of indentation, these being sister groups. In a standard taxonomic scheme, each member of a sister group would receive the same rank, which would be at a higher level than the groups contained within it (see Figure 1.5A-C). A second method of ordering taxa based on their phylogeny is an **annotated classification**, in which taxa are simply listed in sequence from the base of the cladogram to the top (e.g., Figure 1.4B). In an annotated classification, within a given monophyletic group there may be more than two taxa at the same level of indentation; e.g., taxa A, BC, D, and EF have the same indentation in Figure 1.4B. If only two taxa occur in a group, the dichotomous and

A

- Phylum ABCDEF
  - Class A
  - Class BCDEF
    - Order BC
      - Family B
      - Family C
    - Order DEF
      - Family D
      - Family EF
        - Genus E
        - Genus F

B

- Class ABCDEF
  - Order A
  - Order BCDEF
    - Family BC
      - Genus B
      - Genus C
    - Family DEF
      - Genus D
      - Genus EF
        - Species E
        - Species F

C

- Order ABCDEF
  - Suborder A
  - Suborder BCDEF
    - Family BC
      - Subfamily B
      - Subfamily C
    - Family DEF
      - Subfamily D
      - Subfamily EF
        - Genus E
        - Genus F

D

- Phylum Embryophyta
  - Subphylum Hepaticae
  - Subphylum Anthocerotae
  - Subphylum Musci - Mosses
  - Subphylum Tracheophytina
    - Class Lycopsida
    - Class Sphenopsida
    - Class Psilopsida
    - Class Pteridopsida
    - Class Spermatopsida

E

- Subkingdom Embryophyta
  - Phylum Hepaticae
  - Phylum Anthocerotae
  - Phylum Musci - Mosses
  - Phylum Tracheophyta
    - Subphylum Lycophytina
    - Subphylum Sphenophytina
    - Subphylum Psilophytina
    - Subphylum Pteridophytina
    - Subphylum Spermatophytina

F

- Class Reptilia
  - Subclass Chelonia
  - Subclass Lepidosauria
    - Order *Sphenodon*
    - Order Squamata
  - Subclass Archosauria
    - Order Crocodylia
    - •Class Aves

Figure 1.5 A-C. Three possible ranked classification systems for the dichotomous classification of Figure 1.4A. D-E. Two alternative ranked classification schemes for the Land Plants. F. Illustration of non-correspondence of ranks in the Reptilia. Note that "Class" Aves is incorrectly included within a taxon of lower rank (Subclass Archosauria).

annotated systems are identical. The great advantage of an annotated system is that every monophyletic group need not be named, which is of value if the number of monophyletic groups is large or if no formal names have been proposed for every monophyletic group. Both the dichotomous and annotated classification systems, however, recognize and name only taxa that are monophyletic. Both systems directly reflect the entire group's phylogeny and can be used to reconstruct the cladogram. Both systems are used in this laboratory manual, sometimes in combination. Refer to Laboratory #7 for a good example of an annotated system and to Laboratory #13 for one of a dichotomous system.

Recently, systematists have argued for the elimination of ranks altogether. One reason for this is that the assignment of a taxon to any particular rank is ultimately arbitrary. For example, Figure 1.5A-C illustrates three different ranked classifications for the dichotomous classification scheme of Figure 1.4A. Note that, as long as taxa of lower rank are indented beneath those of higher rank, any one of these could be used. The result of this arbitrariness is that particular ranks assigned to taxa may vary from one reference to the next. For example, compare Figures 1.5D & E, two ranked classification schemes from the literature; treating the "Vascular Plants" as a phylum or subphylum (or some other rank) is arbitrary, as long as the subsidiary taxa retain the same, relative position. Another argument against a ranked classification is that traditionally accepted ranks often do not correspond with new ideas about phylogenetic classification. For example, it has for some time been known that birds (Aves) are actually members of the Reptilia, their closest living relatives being crocodylians. However, if both Aves and Reptilia are kept at their traditional ranks of Class, then an unacceptably confusing result would be the classification of Class Aves contained within taxa of lower rank (Figure 1.5F). A third argument against a ranked classification is that ranks of different groups are not at all comparable. For example, it makes little sense to compare or equate a family of molluscs with a family of brown algae. Thus, in general, elimination of the rank names with retention of the taxa names solves the above problems.

We largely concur with the view that ranks have disadvantages or are unnecessary. This approach has not been officially adopted and by no means universally accepted, but it probably will be in time. Thus, we have omitted or de-emphasized the rank names for taxa, but have retained the binomial structure of species names. In practice, the names of specific taxa remain the same; taxa names are simply stated without reference to a rank. For example, we refer to the group "Vertebrata" without reference to whether it is a phylum, class, subclass, order, or any other rank. This is a somewhat novel approach. Most textbooks will still refer to rank names, but the names and characteristics of the groups will be largely unaltered, regardless of rank. In any case, we urge that the beginning student learn the scientific names of taxa without emphasis on its rank in any particular classification system.

CLADOGRAMS: RECONSTRUCTING THE HISTORY OF LIFE

Constructing the cladogram for a group of organisms is the best means for inferring their evolutionary history. Cladograms are constructed via the following steps:

1) Select a group to be analyzed. Name and define all the taxa of that group.

2) Select and define characters and character states for each taxon.

3) Arrange the characters and their states in a data matrix (see example in Figure 1.6A)

4) For each character, determine which state is ancestral (also called "primitive") and which is derived or more recently evolved. A hypothetical ancestor may be added to the data set to represent all ancestral character states (Figure 1.6A).

5) Construct the cladogram by grouping taxa based on shared apomorphies (which are shared derived character states or "synapomorphies"). First, place all taxa radiating from the ANCESTOR, as in Figure 1.6B. Next, sequentially group sets of taxa based on their common possession of one or more shared derived character states (Figure 1.6C-D). Note in Figure 1.6D that the derived state ("herb") for character #2 ("Plant habit") is restricted to the taxon *Lutea* and is therefore an autapomorphy. The derived states of characters #1, #3, #4, and #5 group together two or more taxa and are therefore synapomorphies. Finally, note that the derived state ("spiny") for character #6 ("Pollen surface") evolves twice, independently in species *Alba* and *Purpurea*. This represents **convergent evolution** or "parallelism."

6) Create a hypothetical classification system by naming all monophyletic groups and arranging these sequentially and hierarchically. For example, for the cladogram of Figure 1.6D, all of the monophyletic groups are circled in Figure 1.6E. A possible dichotomous classification is shown below on the left; an annotated classification is shown on the right.

- *Hypothetica* (including all 5 original taxa)
  - *Luteoalba*
    - *Alba*
    - *Lutea*
  - *Rubnigropurpurea*
    - *Rubens*
    - *Nigropurpurea*
      - *Nigra*
      - *Purpurea*

- *Hypothetica* (including all 5 original taxa)
  - *Luteoalba*
    - *Alba*
    - *Lutea*
  - *Rubens*
  - *Nigra*
  - *Purpurea*

CHARACTERS / CHARACTER STATES

A

	1	2	3	4	5	6
TAXA	Leaf shape	Plant habit	Petal number	Flower color	Stamen number	Pollen surface
Alba	elliptic	shrub	five	red	four	spiny
Lutea	elliptic	herb	five	red	four	smooth
Nigra	linear	shrub	four	yellow	two	smooth
Purpurea	linear	shrub	four	yellow	two	spiny
Rubens	linear	shrub	four	yellow	four	smooth
ANCESTOR	elliptic	shrub	five	yellow	five	smooth

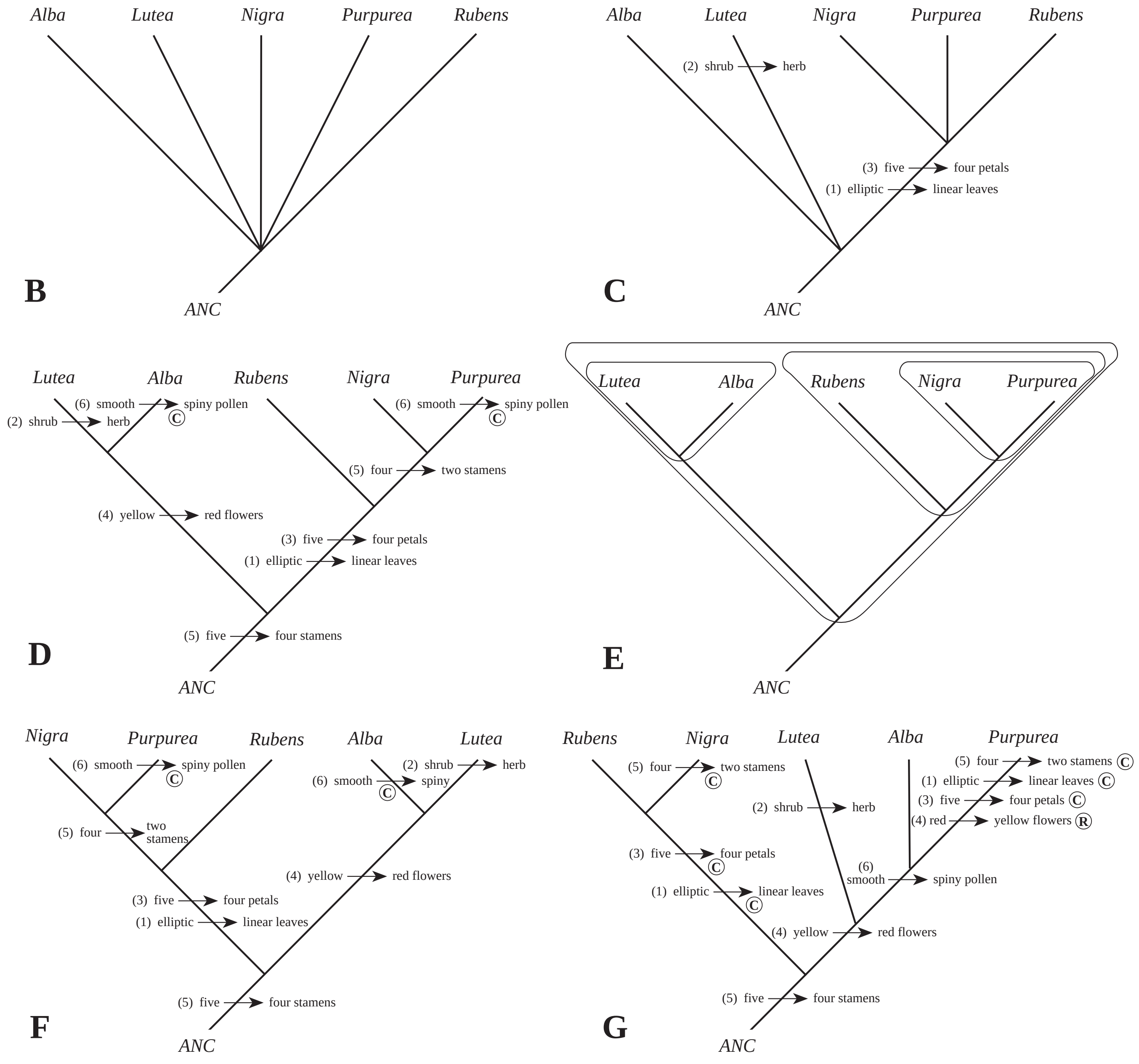

Figure 1.6 Data matrix 5 species of a hypothetical group plus a ancestral taxon, showing 6 characters and their character states for each of the listed taxa. B. Unresolved cladogram. C. Addition of characters #1 - #3. D. Most parsimonious cladogram, with addition of characters #4 - #6. E. Cladogram at Fig. 1.6D, with all monophyletic groups circled. F. Most parsimonious cladogram of Fig. 1.6D & 1.6E. Note that clades are rotated, but that the cladogram structure ("topology") is identical. G. Alternative cladogram for the data set of "A," showing a different relationship among the five species, requiring 11 character state changes, three more that the most parsimonious cladogram at "D-F." Convergent and reversal homoplasies are denoted by circled "**C**" and "**R**" respectively.

Exercise: can you think of a second annotated classification system for the cladogram of Figure 1.6D,E?

Because life is thought to have arisen only once, any two species you can name have had at some point in the past a **common ancestor**. Thus, an important principle of systematics is that phylogenetic "relationship" between taxa is measured by **recency of common ancestry**. Recency of common ancestry is the rationale for grouping taxa into monophyletic groups. For example, from the cladogram of Figure 1.6D and the above classification, it is evident that *Nigra* and *Purpurea* are more closely related to one another than either is to *Rubens*. This is because the former two taxa together share a common ancestor that is more recent in time than the common ancestor that they share with *Rubens*. The fact that they are classified as separate groups reflects this. Similarly *Rubens* is more closely related to *Nigra* and *Purpurea* than it is to either *Lutea* or *Alba* because the former three taxa share a common ancestor that is more recent in time than that shared by all five taxa.

Also note that, because descent is measured by means of recency of common ancestry, the lineages of a given cladogram may be visually rotated around their junction point at the common ancestor with no change in phylogenetic relationships. For example, the cladogram portrayed in Figure 1.6F is the same one as that of Figure 1.6D, differing only in that the lineages have been rotated about their common ancestors.

Finally, an important aspect of reconstructing phylogenetic relationships is known as the **principle of parsimony**. The basic tenet of the **principle of parsimony** is that the cladogram having the fewest number of evolutionary steps is accepted as being the best estimate of phylogeny. The principle of parsimony actually represents a major tenet of science in general, known as Ockam's Razor: of two competing hypotheses, each of which explain the facts, the simplest one is accepted. The principle of parsimony can be illustrated as follows. For the data set in Figure 1.6A, which includes five taxa plus a hypothetical ancestor, there are actually many possible cladograms that could be imagined. For example, Figure 1.6G shows an alternative cladistic hypothesis. Note, however, that for this cladogram, there are a total of 11 character state changes, including 4 pairs of convergent evolutionary events. Thus, of all the possible cladograms for the data set of Figure 1.6A, the one illustrated in Figure 1.6D-F is the shortest, containing the fewest number of evolutionary steps (a total of 8).

LABORATORY EXERCISES

CLADOGRAM RECONSTRUCTION

1. Study Figure 1.7, which illustrates eight species (A-H) of a hypothetical group of organisms. In addition, Figure 1.7 shows a presumed extinct ancestor ("Anc"), which contains all ancestral characteristics. Your job is to infer relationships of the eight species of this taxon.

a) Working with a partner, name and record as many characters with associated character states as possible. Arrange these in the form of a data matrix, with "Taxa" in a column (at left) and "Characters" in a row at the top. Name and record the character states of each character for each taxon.

b) For each character, circle those character states that are derived. Those shared by two or more taxa are synapomorphies and can be used to link together all taxa that possess them.

c) Draw the cladogram for the hypothetical organisms, after the example of Figure 1.6A-D. Circle all monophyletic groups, as in Figure 1.6E.

d) From the cladogram devise an indented classification scheme, both dichotomous and annotated. Make up new names for monophyletic groups as needed. Experiment with placing these new monophyletic groups into ranks. What are the advantages and disadvantages of having ranks?

2. Computer phylogeny applications. If a computer is available, you may wish to explore one of the available phylogeny software applications. Two common programs for visualizing cladograms are: a) MacClade (Maddison and Maddison, 1993), written for computers using the Macintosh operating system; or b) Clados (Nixon, 1993), written for computers using DOS or Windows. Either of these programs allow the user to input data, including taxa names and their characters and charater states. Both enable both the phylogenetic relationships of taxa and specific character state changes to be visualized.

With the help of your instructor, set up a data file using MacClade, Clados, or some other phylogeny application for a given taxonomic group. Engage the function that displays characters and visualize several, noting the distribution of their states. You may also "swap branches" on the cladogram, exploring alternative evolutionary hypotheses.

3. TREE OF LIFE. If you have available a computer with a web browser internet connection, log onto the "Tree of Life" (http://phylogeny.arizona.edu/tree/phylogeny.html). This web page contains up to date information on the relationships of organismal groups. Browse through the "Tree of Life" by simply clicking (with the computer mouse) on various highlighted words or images. Note that cladograms of many more taxonomic groups are illustrated than are covered in this laboratory manual. Also note that these phylogenetic relationships may be different than those portrayed here, indicating that workers in the field may disagree and that systematic studies have not yet unambiguously resolved all the details of phylogenetic relationships.

PREPARATION FOR LABORATORY'S #2:

1. Bacterial culures. For next week's laboratory, each student should take home one petri dish with a taped lid: a nutrient agar petri dish that is neutral pH and low nutrient, encouraging environmental bacteria. Five days before your next lab (Laboratory #2), open the plate to the air for one hour in the environment of your choice (inside or outside). Tape the lid back on and leave at room temperature (do not open). Label the plate with your name and the type and date of exposure. Be sure to bring this to next week's lab!

> **WARNING:** If you have an allergy to molds or are immune compromised, please speak to your instructor before doing the above preparation for Labs #2!

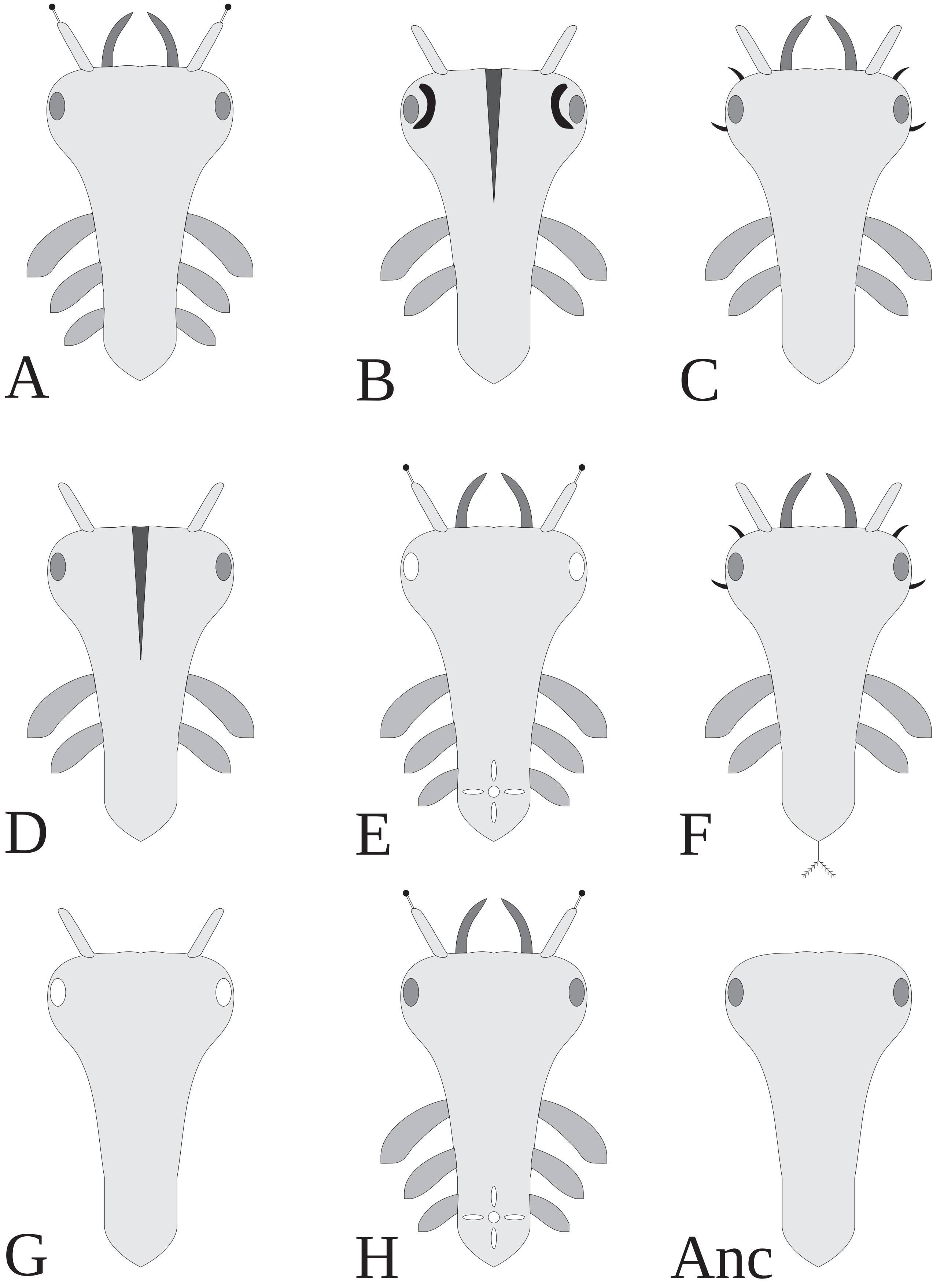

Figure 1.7 Hypothetical organisms for a phylogeny reconstruction exercise. A-H = taxa; Anc = Ancestor.

2. Microscope Use. If time is available, your T. A. will demonstrate the use of the compound microscope and have you practice with available prepared slides. Refer to the “Laboratory Exercises” of Laboratory #2.

LABORATORY QUESTIONS

1. Define evolution, describing what is meant both by descent and by modification.
2. What is a feature that results in increased survival or reproduction called?
3. What is systematics and what is its primary emphasis?
4. Name and define the four components of taxonomy.
5. Define and give an example of a character and character state.
6. Why are scientific names preferable to common names?
7. Define taxon and give the plural for this term.
8. Name the major ranks in the traditional, hierarchical classification.
9. What is a binomial and what is each part of the binomial called?
10. Name the two main ways to classify organisms and describe how they differ.
11. Define phylogeny and give the name of the branching diagram that represents phylogeny.
12. What is a lineage or clade?
13. What does a split from one lineage to two represent?
14. Name the term for both a pre-existing feature and a new feature.
15. What is an apomorphy? synapomorphy? autapomorphy?
16. Define homology and homoplasy and give an example of each.
17. Define and contrast monophyletic group and paraphyletic group.
18. Name two ways that a phylogenetic classification system can be devised from a cladogram.
19. What is meant by recency of common ancestry?
20. What is the principle of parsimony?

LITERATURE CITED AND ADDITIONAL READINGS

LIFEmap. 1992. California Academy of Sciences. Published by Warner New Media, 3500 West Olive Avenue, Burbank, CA.

Maddison, W. P. and D. R. Maddison. 1992. MacClade, version 3. Analysis of phylogeny and character evolution. Sinauer Press, Sunderland, MA.

Nixon, K. C. 1993. Clados Version 1.4. Published by the author, Trumansburg, New York.

Wiley, E. O., D. Siegel-Causey, D. R. Brooks, and V. A. Funk. 1991. The Compleat Cladist: A Primer of Phylogenetic Procedures. Univ. Kansas Museum Nat. History Sp. Publ. no. 19. [Note: "Compleat" is not misspelled.]