Updated to say what can be learned if species IV in Figure 25.15 is known to be an outgroup

- **10 Phylogenetic systematics.**

- **The Linnaean system of classification is hierarchical**
  - Higher categories
    - The major categories are domain, kingdom, phylum, class, order, family, genus, species.
    - Intermediate categories exist, such as subphylum and superfamily.

- **Phylogenetic tree (phylogeny)**
  - *Darwin and classification*
    - In the *Origin*, Darwin said that descent from a common ancestral species could explain why the Linnaean system is hierarchical. Species in the same genus had a common ancestor more recently than species in different genera in the same family. The only figure in the *Origin* illustrated his idea. He introduced the idea of a phylogenetic tree.
  - A phylogenetic tree represents the history of most groups of species
    - For a phylogenetic tree to be a good description of the history of a group, the time it takes for new species to form (represented by the splitting of lineages) has to be very short compared to how long each species was present. The phylogeny of humans, chimps, gorillas and bonobos is typical and thought to be roughly accurate.
    - A few groups of plants, such as those in the genus *Clarkia*, do not have a tree-like history because many species are allopolyploids. The history of *Clarkia* and other such groups is reticulate (net-like) in which some species have two ancestors.
  - Information in a phylogenetic tree
    - The pattern of branching indicates ancestry.
    - The branch lengths indicate times.
  - Cladogram
    - A cladogram summarizes the branching pattern but contains no information about times.
    - Be sure to understand the difference between a phylogenetic tree and a cladogram.
  - A phylogenetic tree represents the pattern of evolution
    - A tree is a convenient summary of what actually happened. If you could replay the webcast of life, you could discover the tree that describes the true history of a group of species.

- **Phylogenetic trees and classification**
  - *Darwin and taxonomy.*
    - Darwin did not address the practical problem of how to use evolutionary history to classify species into higher groups. The problem was then and is still that, although
there is a phylogenetic tree that describes the history of most groups, it is difficult to know what the correct tree is.

- With the advent of DNA sequencing, much effort is going into inferring the phylogenies of all major groups. The Tree of Life project (www.tolweb.org) is an international effort to join phylogenetic trees of different groups into a single tree that describes the overall pattern of evolution.

### Terminology

- A monophyletic group is one that contains an ancestral species and all of its descendants. Mammals are a monophyletic group.
- A paraphyletic group is one that contains an ancestral species and some but not all its descendants. The family Pongidae (orangutans, chimpanzees, bonobos and gorillas) is paraphyletic. It does not include modern and extinct humans which are descended from a pongid ancestor.
- A polyphyletic group is one that contains descendants of two or more different ancestral species that are not in the group. All prokaryotes used to be classified in a single kingdom, which was later discovered to be polyphyletic. Now, the Bacteria and the Archaea are distinct monophyletic domains (p. 540).

### Phylogenetic systematics

- The overall goal is to make higher categories reflect evolutionary history by requiring that all taxa be monophyletic.
- In a phylogenetic classification, species in the same genus had a most recent common ancestor more recently than species in different genera in the same family, and so on.
- Phylogenetic systematics is based on the cladogram, not on the phylogenetic tree.

### Finding the right cladogram

- The problem is to determine the cladogram that describes the ancestry of a group.
- A simple method and one that is easy to apply is parsimony, which is the only one discussed in this course. Other methods, including maximum likelihood, rely on statistical models that make it possible to infer branch lengths as well the branching pattern.

### Parsimony

- Parsimony assumes that changes in characters or the appearance of new characters occur very rarely. The underlying idea is to choose the tree that requires the fewest changes.
- Counting evolutionary transitions requires that homologous characters be distinguished from analogous characters. Wings in different species of bats are homologous. Wings in bats and wings in birds are analogous.
- A shared derived character is a character that is shared by every species in a group but is not shared with any species outside the group. The assumption of parsimony is that a shared derived character arose once in the ancestor of the group. Monophyletic groups can be distinguished by identifying shared derived characters. An example is given in Fig. 25.11.
- In order to distinguish between shared primitive characters and shared derived characters, one or more outgroups are needed. Wings are a shared derived character of bats; fur is a shared primitive character.
lecture 10

- **Theory and practice**
  - In theory, it should be possible to always find the correct cladogram by identifying the right set of shared derived characters, as in Fig. 25.11. In practice, that is almost never possible because, for a given set of characters and species, there is no cladogram that perfectly fits in the sense that only one change is needed for each character.
  - Shared derived characters are homologous. Characters that arose independently in different groups are analogous. The problem is that without knowing the cladogram, it may be difficult to know which characters are homologous and which are analogous. That is true whether the characters are morphological characters or differences in DNA sequence. Figure 25.15 works through an example in which the most parsimonious cladogram of four species is found.
  - In Figure 25.15, if species IV is known to be an outgroup, then the history of the other three species can be inferred. In the best-fitting cladogram, a group containing species I and II is monophyletic; a group containing species II and III (but not I) is paraphyletic.

- **The goal of phylogenetic systematics cannot always be achieved.**
  - There are a limited number of taxonomic levels: genus, family, order, etc. Even if they are subdivided, as they sometimes are, into subfamilies, subgenera etc. you will run out of reasonable names.
  - For many groups, the cladogram is unknown or poorly known because there has not been enough effort devoted to studying that group.
  - There is inertia. In the traditional classification of mammals, Pongidae is a paraphyletic family. To ensure that all families are monophyletic, you would have to either put humans in the Pongidae or create a new family containing the chimps, bonobos and humans (and possibly gorillas and possibly orangutans). Similarly, mammals and birds are monophyletic, but reptiles are not. Reptiles, birds, and mammals together are monophyletic. Some taxonomists want to make these changes but some do not.
  - Using monophyly as the only criterion for deciding on a taxonomic level ignores the importance of major adaptive changes. Some people argue that the major adaptive changes in the history of humans (bipedalism, large brains, speech etc.) justifies their being put into a separate family even if it leaves Pongidae as a paraphyletic group, and that the major adaptive changes in the history of mammals and birds justifies their being put separate classes.

- **DNA sequences provide many characters**
  - There is increasing use of DNA sequences of gene from different species to infer phylogenetic trees.
    - **Molecular clocks.**
      - Population genetics tells us that neutral sites evolve at a roughly constant rate.
      - Even genes that are affected by purifying selection evolve at approximately constant rates but those rates are lower than the neutral rate.
      - Different genes evolve at different rates, which makes them useful for analyzing species that diverged at different times in the past.
- Ribosomal RNA evolves very slowly. The recognition that Archaea and Bacteria were quite different first came from the analysis of ribosomal RNA sequences. Once the groups were distinguished, phenotypic differences between them were then found. Table 27.2 summarizes the differences, but it will not be necessary to know those differences in this course.
- Mitochondria in animals contain small circular DNA molecules (about 16,000 bases in length) that are inherited maternally. Animal mtDNA evolves more rapidly than nuclear DNA, so it is useful for examining variation within species and between species that diverged recently. Mitochondrial DNA of mammoths was sequenced recently. A comparison with the mtDNA of African and Asian elephants shows that the mammoth is slightly more closely related to the Asian elephant than to the African elephant.

Sample questions (correct answer is underlined)

- What statement provides the best definition of a monophyletic group?
  - a. A group of species in the same genus.
  - b. A group containing an ancestral species and all of its descendants.
  - c. A group containing an ancestral species and some of its descendants.
  - d. A group containing an ancestral species and none of its descendants.
  - e. A group containing descendants of two ancestral species that are in different taxonomic groups.

- What statement provides the best definition of a phylogenetic classification system?
  - a. Taxonomic groups are all polyphyletic.
  - b. Taxonomic groups are all paraphyletic.
  - c. Taxonomic groups are all monophyletic.
  - d. Taxonomic groups are all homologous.
  - e. Members of taxonomic groups are all found in the same geographic area.

- The table below contains the nucleotides found at 7 sites in the sequences from four different species. Using the principle of parsimony to choose the best cladogram for these four species. In the cladogram you inferred, which one of the following groups is a monophyletic?

<table>
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<th>2</th>
<th>3</th>
<th>4</th>
<th>5</th>
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</table>

- a. I & III
- b. I & IV
- c. II & IV
- d. II & III
- e. None of the above