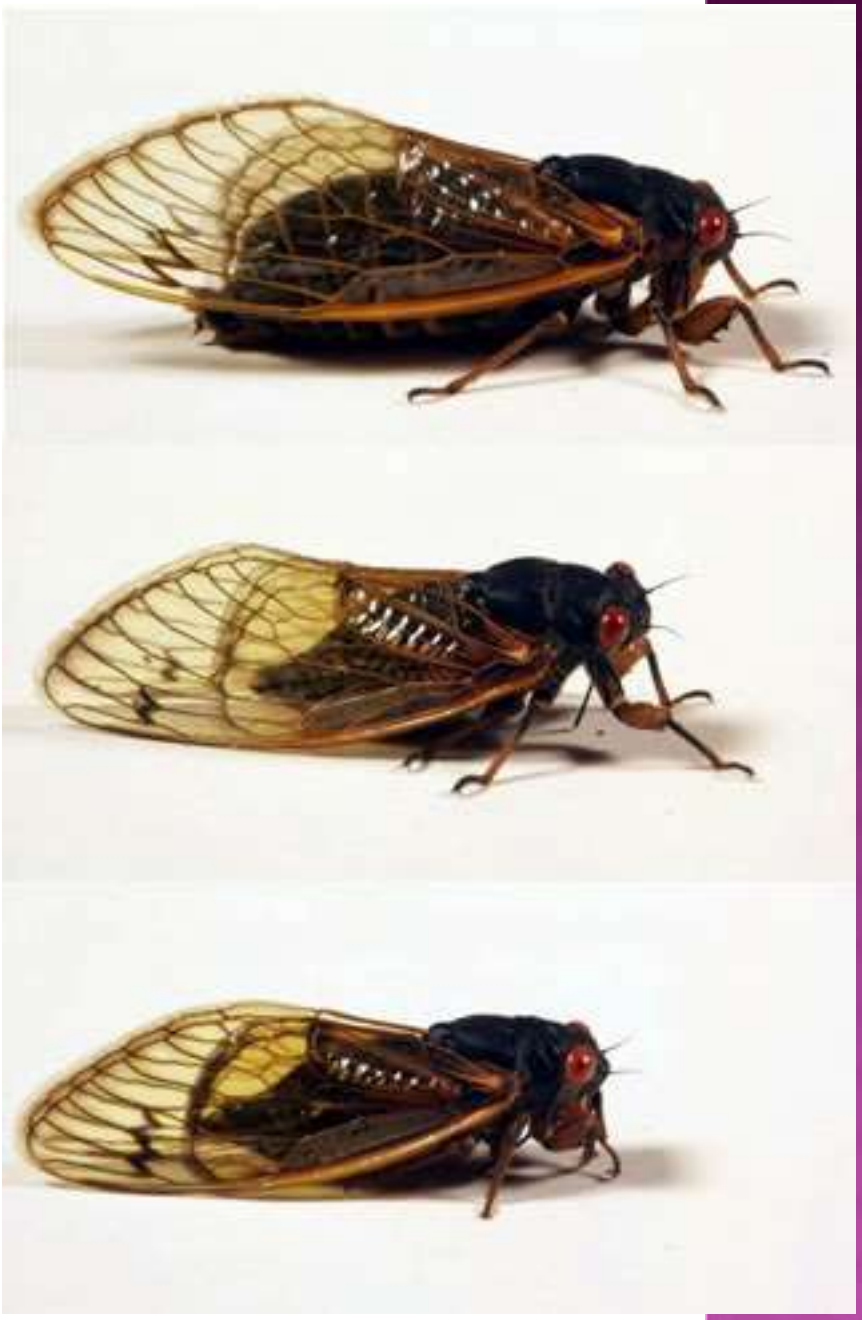
SPECIES, CONCEPTS

WHAT IS A SPECIES?

- **species** - basic unit of classification or taxonomy.
  - Species: “Kind of living thing”
  - Word “species” is both plural and singular
  - relatively easy to define for sexual organisms, hard for asexual organisms and extinct species.

SPECIES

- Species is the smallest, most specific group in classification
- Organisms in the same species can reproduce together AND their offspring are fertile.



BIOLOGICAL SPECIES CONCEPT

biological species concept

(for sexual organisms) – one or more populations whose members are capable of interbreeding and producing fertile offspring, and whose members are reproductively isolated from other such groups.

not always clear-cut, because some can interbreed under “artificial” conditions but don’t appear to do so in nature

sometimes, “race” and “subspecies” designations are used, but often different specific epithets are used when there are clear morphological differences involved.

- asexual species – definition based on biochemical (think DNA sequence) and morphological differences; no solid rules
  - also includes use of “race,” “subspecies,” and “strain” designations
  - in asexual species, microevolution over time directly leads to macroevolution (speciation)

EVOLUTIONARY SPECIES CONCEPT

- **evolutionary species concept** – a single line of descent (lineage) that maintains its distinctive identity from other lineages; works for all species, but it can be hard to clearly define "distinctive identity"

- So how many species are there?
  - no one knows for sure, best guess is about 10 million, but only about 1.8 million have been described by humans
  - most are tropical

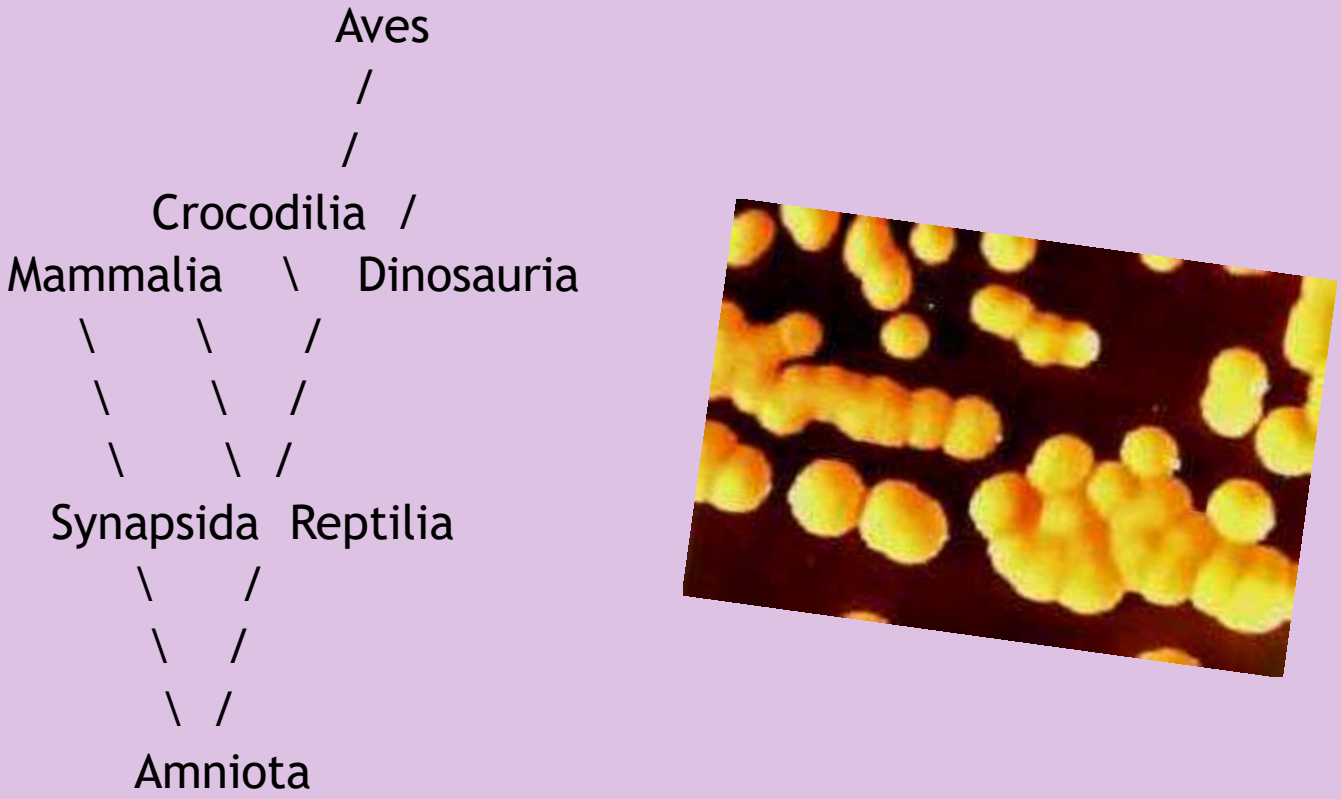
- human activities (particularly in the tropics) are certainly destroying many species before they can even be described; we are undergoing the sixth mass extinction event in the history of life on earth (and the first one driven by the activities of man.

- classification is largely based on inferred evolutionary relationships between organisms; the two major approaches to this are **cladistics** and **traditional taxonomy**
  - **phylogeny** – evolutionary tree; explanation of evolutionary relationships among groups (what evolved from what, in what order, and when)
  - **systematics** – study and reconstruction of phylogenies
  - groups of organisms may be:

- **monophyletic** (includes most recent common ancestor and all descendants)
- **paraphyletic** (includes most recent common ancestor BUT not all descendants)
- **polyphyletic** (does not include most recent common ancestor)

- both cladistics and traditional taxonomy avoid polyphyletic groups; cladistics also avoids paraphyletic groups

- What do terms monophyletic, paraphyletic and polyphyletic mean?
- These terms are used to describe groupings of organisms, and indicate the extent to which they can be considered as ``natural groups". They are best explained using examples, so consider the following family-tree diagram:



- Here are examples of all three types of group:

- Consider the group consisting of all the animals in this diagram - that is, Amniota. This group is monophyletic because it consists of a single animal together with all of its descendants. The Dinosauria, including the modern birds, is another
- monophyletic group, sometimes defined as the most recent common ancestor of *Iguanodon* and *Megalosaurus* together with all its descendants.
- Monophyletic groups are also called *clades*, and are generally considered as the only ``natural" kind of group. They are very important in phylogenetic classification.

- Now consider the group consisting of the non-avian dinosaurs (which is what people usually mean by the informal term ``dinosaurs''). This is a paraphyletic group, because it can't be defined simply as ``this animal plus all its descendants'', but must be described as one clade minus another: in this case, Dinosauria minus Aves.

- **cladistics** groups organisms on the basis of unique shared characters inherited from common ancestor, or derived character
  - **clade** – group of organisms related by descent
  - **synapomorphy** – a derived character that is unique to and thus defines a particular clade
  - **cladogram** – branching diagram based on cladistic analysis that represents a phylogeny
    - cladograms are based on comparative analysis, so each cladogram must have an **outgroup** and **ingroup**
    - **outgroup** – organism that is different from all others in the cladogram (but not too different); it is expected to have split with the others from a common ancestor before any of the rest (the ingroup) split from each other

- often different cladograms can be produced for a given set of organisms depending on how the analysis is done; usually a choice has to be made for which cladogram is the most likely reflection of evolutionary history (usually the most **parsimonious** one, the one that requires the simplest explanation)
- cladograms are always open to refinement as more date become available
- naming based on cladograms only allows for monophyletic groups

- **The most widely accepted classification system today includes three domains and six kingdoms**
  - Two domains consist of **prokaryotes**, organisms with no internal membrane-bound organelles (and thus no true cellular nucleus)
    - Domain **Archaea** – Kingdom **Archaebacteria**

- Domain **Bacteria** – Kingdom **Eubacteria**
  - One domain, **Eukarya**, consists of **eukaryotes**, organisms with a discrete cellular nucleus (and other internal membrane-bound organelles); it is divided into four kingdoms
    - Kingdom **Protista** - protists
  - Kingdom **Fungi** - fungi
    - Kingdom **Plantae** – plants
  - Kingdom **Animalia** – animals

GLOSSARY

- **cladistic** A classification based entirely on monophyletic taxonomic groupings within a phylogeny; taxonomic units that are paraphyletic or polyphyletic are rejected.
- A **"cladist"** is one who practices "cladistics," usually in the sense of using parsimony to adjudicate between data from multiple characters in the construction of a "cladogram," which is an estimate of the true phylogeny.

- cohesion The sum total of forces or systems that hold a species together. The term is used especially in the interbreeding and cohesion species concepts. Cohesion mechanisms include isolating mecha- nisms in sexual species as well as "stabilizing" ecological selection, which may cause cohesion even within asexual lineages.

- **disruptive selection** Selection acting to preserve extreme phenotypes in a population. Speciation usually involves disruptive selection, because intermediates (hybrids between incipient species) are disfavored (see also stabilizing selection).

- DNA bar coding A means of delimiting species via DNA sequence clustering, usually from mi- tochondrial DNA.
- gene flow Movement of genes between populations, usually via immigration and mating of whole geno- types, but sometimes single genes may undergo horizontal gene transfer via transfection by micro- organisms.
- gene pool The sum total of the genetic variation within a reproductively isolated species population; this term is mostly used by supporters of the interbreeding species concept.

- **genomic cluster** A synonym for genotypic cluster.
- **genotypic cluster** In a local area, a single genotypic cluster (or species) is recognized if there is a single group of individuals recognizable on the basis of multiple, unlinked inherited characters or genetic markers. A pair of such genotypic clusters (or spe- cies) is recognizable if the frequency distribution of genotypes is bimodal.

- Within each genotypic cluster in a local region, allele frequencies will conform to Hardy-Weinberg equilibrium, and the different unlinked loci will be in approximate linkage equilibrium. The presence of more than one species or genotypic cluster can then be inferred if the distribution of genotypes is bimodal or multimodal, and strong heterozygote deficits and linkage dis-equilibria are evident between the clusters.

- **isolating mechanisms** The sum total of all types of factors that prevent gene flow between species, including premating mechanisms (mate choice), and postmating mechanisms (hybrid sterility and inviability).
- Modern authors deny that these "mech-anisms" have necessarily evolved to preserve the species' integrity as originally assumed, though this may sometimes be the case in reinforcement of

- premating isolation. العزلة المبكرةIsolating mechanisms are a sub- set of the factors that cause cohesion تماسك of species under the interbreeding and cohesion species concepts.
- monophyletic A grouping that contains all, of the descendants احفاد of a particular node in a phylogeny. Monophyly is the state of such groupings. Compare paraphyletic polyphyletic. Butterflies (Rhopalocera) and birds (Aves) are examples of two groups thought to be monophyletic.

- paraphyletic A grouping that contains some, but not all, of the descendants of a particular node in a phylogeny. Paraphyly is the state of such groupings. Compare monophyletic, polyphyletic. Moths (Le- pidoptera, excluding butterflies) and reptiles (am- niotes, excluding birds and mammals) are examples of two groups thought to be paraphyletic.

- phenetic A classification or grouping based purely on overall similarity. Pheneticists use matrices of overall similarity rather than parsimony to con- struct a "phenogram" as an estimate of the phylo- geny.
- Examples of phenetic methods of estimation include unweighted pair group analysis (UPGMA) and neighbor joining. "Cladists" reject phenetic classifications on the grounds that they may result in paraphyletic or polyphyletic groupings.

- polyphyletic Groupings contain taxa with more than one ancestor. “Polyphyly” is the state of such grou-pings. Compare paraphyletic and monophyletic.
- “Winged vertebrates” (including birds and bats)
- give an example of a polyphyletic group

- **sibling species** A pair of closely related, morphologically similar species (usually sister species).

speciation The evolutionary process of the origin of a new species.

- **taxonomic inflation** The process whereby the numbers of species in the checklist of a group increases due to a change in species concept rather than due to new discoveries of previously unkown taxa.

WHAT ARE SPECIES CONCEPTS FOR?

- Individual organisms can usually be recognized, but the larger units we use to describe the diversity of life, such as populations, subspecies, or species, are not so easily identifiable.
- Taxonomists further group species into genera, families, orders, and kingdoms, while ecologists group species into higher structures such as communities and ecosystems.

- The justification for these group terms is utility, rather than intrinsic naturalness, but as far as possible we attempt to delimit groups of organisms along natural fault lines,
- so that approximately the same groupings can be recovered by independent observers. However, there will be a virtually infinite number of different, albeit nested, ways of classifying the same organisms, given that life has evolved hierarchically.

- Species concepts originate in taxonomy, where the species is “the basic rank of classification” according to the International Commission of Zoological Nomen-clature.
- The main use of species in taxonomy and derivative sciences is to order and retrieve information on individual specimens in collections or data banks.
- In evolution, we would like to delimit a particular kind of evolution, “speciation,” which produces a result qualitatively different from within-population evolution, although it may of course involve the same processes

- In ecology, the species is a group of individuals within which variation can often begin red for the purposes of studying local populations or communities, so that species can compete, for example, while subspecies or genera are not usually considered in this light. In biodiversity and conservation studies, and in environmental legislation, species are important as units, which we would like to be able to count both regionally and globally.

- III. DARWINIAN SPECIES CRITERIA
- A. Darwin's Morphological Species Criterion
- Before Darwin, it was often assumed that each species had an Aristotelian "form" or "essence," and that variation within a species was due to imperfections in the actualization of this form.

- Each individual species was defined by its essence, which itself was unvarying and inherently different from all other species essences. This mode of thought of course precluded transformation of one species into another, and was

- associated with belief that each form was separately created by God. Darwin's extensive travels and knowledge of taxonomy led to a realization that the distinction between intraspecific and interspecific variation was false.
- His abandonment of the essentialist philosophy and its species concept went hand in hand with his appreciation that variation itself was among the most important characteristics of living organisms, because it was this variation which allowed species to evolve.

- B. Polytypic Species

- A major revolution in zoological taxonomy occurred around 1900. As the great museum collections became more complete, it became obvious that apparently distinct species found in different areas frequently in- tergraded where they overlapped. These replacement species were usually combined as subspecies within a

- “polytypic’’ species, an idea suggested for ‘‘geograp- hical varieties’’ by early systematists and Darwinists such as Wallace (1865). The taxonomic clarification that followed, which allowed identifiable geographic varieties to be named below the species level as sub- species, was conceptually more or less complete by the
- 1920s and 1930s. At the same time, other infraspecific animal taxa such as local varieties or forms were deemed unnameable in the Linnaean taxonomy. These changes are now incorporated into the International Code of Zoological Nomenclature.

IV. THE PHILOSOPHIZATION OF SPECIES, THE "INTERBREEDING" CONCEPT

- Poulton proposed "syngamy" (i.e., interbreeding) as the true meaning of species. Poulton and Wallace were both particularly knowledgeable about swallowtail butter- flies (Papilionidae). In swallowtails, there were strong sexual dimorphisms: the female color pattern often mimicks unrelated unpalatable butterflies while the male is nonmimetic.

- The females themselves are often polymorphic, each female form mimicking a different distasteful model. Under a morphological criterion each form could be designated as a different species, whereas mating observations in the wild showed that the forms were part of the same interbreeding group.

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V. ALTERNATIVE SPECIES CONCEPTS

- A. Ecological Species Concept
- Asexual organisms such as the bdelloid rotifers can clearly be clustered into groups recognizable as

- taxonomic species, very likely because competition made intermediates extinct (Hutchinson, 1968). On the other hand, distinct forms such as oaks (Quercus), between which there are high rates of hybridization, can remain recognizably distinct even where they co- occur. This suggested to van Valen (1976) and others that the true meaning of species was occupancy of an ecological niche rather than interbreeding. This ecological idea became known as the “ecological spe- cies concept.” It became clear to Mayr during the

- 1970s also (see Mayr, 1982) that gene flow could not unite every population in a polytypic, biological spe- cies' range, and that stabilization of phenotype might be effected by ecologically mediated "stabilizing selec- tion" (see also Sections VII.B and VIII.B) rather than purely because of gene flow.

B. RECOGNITION CONCEPT OF SPECIES

- An important attack on the biological species concept came from H. E. H. Paterson in the early 1980s. His claims were twofold: first, that the Dobzhansky/Mayr term isolating mechanisms implied that reproductive isolation was adaptive, which Paterson felt was un- likely; second, that the true reality underlying species was prezygotic compatibility, consisting of mating signals and fertilization signals.

- According to Paterson (1985), this compatibility is strongly conserved by stabilizing selection, whereas isolating mechanisms such as hybrid sterility or inviability are nonadaptive and can be argued to be a result rather than a cause of species separateness. To Paterson, the true reality of species must be adaptive.

- He termed his idea of species the “recognition concept” versus Mayr’s “isolation con- cept,” and its important characteristics “specific mate recognition systems” (SMRSs) instead of isolating mechanisms. Species were defined as “that most incl- usive population of individual biparental organisms which share a common fertilization system” (Paterson,
- 1985).

- VI. SPECIES CONCEPTS BASED ON HISTORY
- A. Monophyly
- The rise of "cladistic" methods revolutionized systematics by proposing that all classification should be based on the idea of "monophyly."
- This new system formalized the principle that "paraphyletic" and "polyphyletic" taxa were unnatural groupings, which should not be used in taxonomy.

- It was natural to attempt to apply this idea throughout systematics, all the way down to the species level, leading to a monophyly criterion of species, a type of "phylogenetic species concept".
- Species were seen as forming when a single interbreeding population split into two branches or lineages that did not exchange genetic material.

- In a somewhat different formulation, the "cladistic species concept," species are branch segments in the "phylogeny," with every branching event leading to a new pair of species (Ridley, 1996).
- Otherwise, if only one of the two branches were recognized as new, the other branch would become paraphyletic.

- B. Genealogy
- Another problem with a monophyly concept is that a single, true phylogeny of taxa may rarely exist: an organismal phylogeny is in fact an abstraction of the actual genetic history, consisting of multiple gene genealogies, some of which may undergo genetic exchange with other taxa. There is now good evidence that occasional horizontal gene transfer and hybridization

- may selectively cause genetic material to flow between unrelated forms. Furthermore, there are multiple gene lineages within any population, so that, if such a population were to become geographically or genetically split into two distinct forms, it would be some time before each branch became fixed for different, reciprocally monophyletic gene lineages at any single gene.

- The idea of monophyly for whole genomes then becomes hard to define, especially near the species boundary. However annoying, phylogenetic methods and evolutionary theory must face up to these facts.
- It has therefore been suggested that species should be defined when a consensus between multiple gene genealogies indicates reciprocal monophyly. This is called the ‘‘genealogical species concept’’.

- C. Diagnostic Species Concept
- The motivation for the diagnostic concept, usually called the "phylogenetic species concept" by its adherents, was again to incorporate phylogenetic thinking into species-level taxonomy.
- There are many cases of hybridization between taxa on very different branches of species-level phylogenies, which suggests that interbreeding and "phylogenetic realities" conflict.

Cracraft (1989) also noted that many bird taxa, normally thought of as subspecies, were far more recognizable and stable nomenclaturally than the polytypic species to which they supposedly belonged.

- Cracraft therefore argued that the polytypic/interbreeding species concept should be rejected, and, in its place, we should use a diagnostic criterion in the form of fixed differences at one or more inherited characters. “A phylogenetic species is an irreducible (basal) cluster of organisms, diagnosably distinct from other such clusters, and within which there is a parental pattern of ancestry and descent”

- According to Cracraft, species defined in this way are the proper basal, real taxa suitable for phylogenetic analysis and evolutionary studies.

Questions