Some of these slides have been borrowed from Dr. Paul Lewis, Dr. Kirsten Jensen, Dr. Michael Engel, Dr. Derek Sikes, and Dr. Steve Ashe. Thanks to all!

Bos taurus is in Bovidae.
Moschus berezovskii and *Antilocapra americana* are in Ruminatia.

Is *Moschus berezovskii* more closely related to *Antilocapra americana* or *Bos taurus*?

Bos taurus is in Bovidae.
Alces alces and *Rangifer tarandus* are in Cervidae.

Is *Alces alces* more closely related to *Rangifer tarandus* or *Bos taurus*?

Principle of Priority

Each taxonomic group with a particular circumscription, position, and rank can bear only one valid (i.e., correct) name.

Synonyms: Two (or more) different names for the same taxon

The Principle of Priority:
Zoology: the **oldest available** name is the **valid** name for the taxon.

Botany: The oldest *legitimate* name is the *correct* name for the taxon.

Apis mellifera Linnaeus, 1758

Apis socialis Latreille, 1802

Later discovered that *Apis socialis* is just a dark variant of *Apis mellifera*, so the valid name for both forms is *Apis mellifera* Linnaeus, 1758.

Homonymy

Homonyms are identical names for two or more taxa.

Calliopsis hurdi Rozen, 1958 (a sand bee)
1966 Alvin Shinn described a new species from Mexico: *Calliopsis hurdi* Shinn, 1966. He was unaware of the species described by Rozen.

These names are homonyms, Rozen's name is the **senior homonym**, Shinn's name is the **junior homonym**.

Thus, the name established by Shinn had to be replaced to avoid confusion with an already existing, identical name.

Types

Each species name is "attached" to a type a specimen. The type of a species is a specimen.

- holotype - the single name-bearing specimen designated by the author as type of the species in the original publication.
- paratype - a specimens of the type series that were not designated as holotype (no special status in nomenclature).
- syntypes - any of two or more specimens used in the original description, when no holotype is designated (cotypes or types).
- lectotype - a syntypes promoted to name-bearing status after the original description
- neotype - a selected by a reviser to be the name-bearing specimen after destruction of the original material

Species and Speciation topics

- The species problem – are species "real"?
- Species concepts (and subspecies)
- Speciation

Much of the progress here came from the evolutionary systematists.

Species

- the fundamental unit in taxonomy
  - we'll see that the "subspecies" rank is controversial as a taxonomic rank.
  - all higher ranks are groups of species.
- a fundamental unit in evolutionary theory – there are theories of speciation, but not "generification," "familiation," "classation" ...

But for much of the history of systematics the status and definition of the species category has been unclear.

History of "Species"

- Before John Ray and Linnaeus, some viewed species as morphotypes and even believed that an organism could change species over the course of their life.
- the species class was seen as having an unchanging essence.
- Linnaeus promoted the fixed nature of species.
- Variation was thought to be the result of imperfection – failure to reflect the true, underlying, unchanging essence.
- **Typological** or Essentialist Species Concept
- In practice this meant the **Morphological** Species Concepts – a species was a group of organisms that were similar morphologically (the theoretical justification for the similarity was the fact that each individual of the same species shared the same essence).

History of "Species" – evolution

- Evolution implied that the theoretical underpinning of the Typological species was completely wrong.
  - species descend from a common ancestor,
  - the characteristics of species change through anagenesis.

- The opposite view was **nominalism**: only individuals are "real" – classes based on similarity were merely abstractions that might be useful for organizational purposes.

Bessey (1908) (quoted by Mayr and Ashlock, 1991): "Nature produces individual and nothing more ... species have no actual existence in nature. They are mental concepts and nothing more ... species have been invented in order that we may refer to great numbers of individuals collectively."

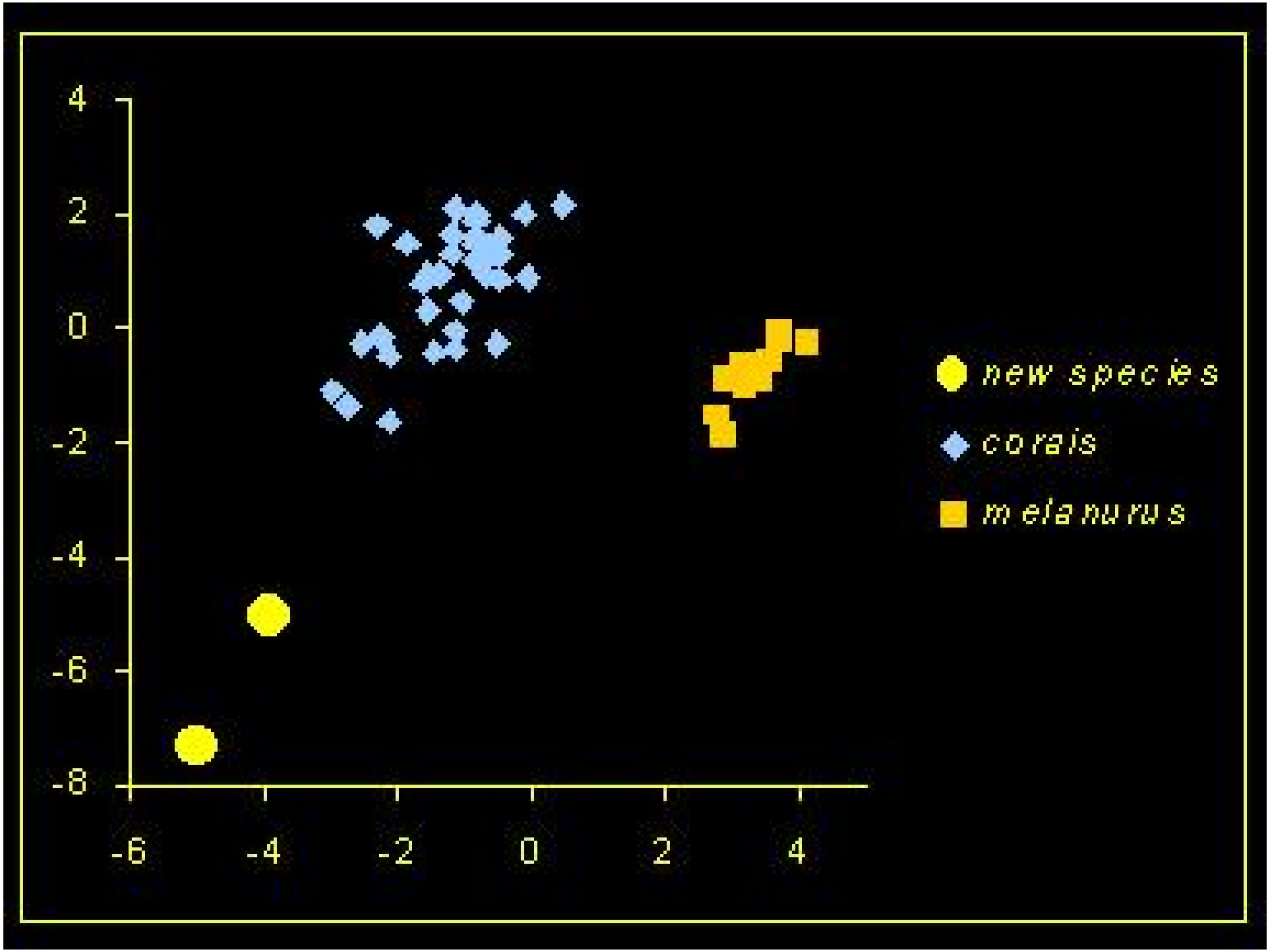
"In short, we shall have to treat species in the same manner as those naturalists treat genera, who admit that genera are merely artificial combinations made for convenience. This may not be a cheering prospect, but we shall at least be **freed from the vain search for the undiscovered and undiscoverable essence of the term species**." – Darwin 1859

Are mountains real?

mountain: a land mass that projects well above its surroundings; higher than a hill (wordnet.princeton.edu)

Clearly there is room for disagreement about whether a structure (e.g. "Mount" Oread) qualifies as a mountain rather than a hill.

Does that mean the concept is artificial?


4
2
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-2
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-4
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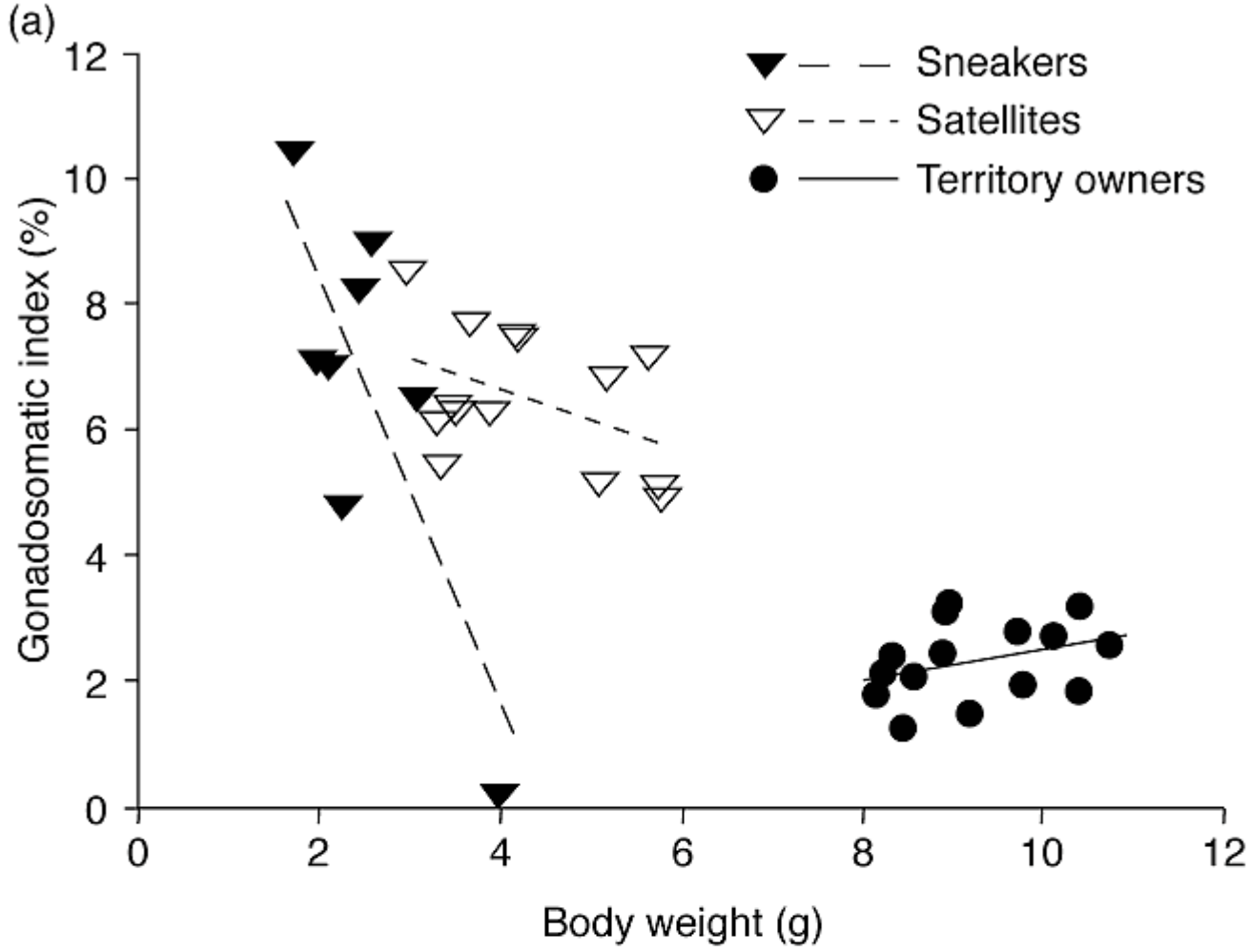
2
4
new species
corals
melanurus

Other biological causes of clusters of individuals in morphospace

- gender (sexual dimorphism),
- stage of ontogeny (think caterpillar vs butterfly),
- caste (some ant castes have been described as different species),
- genetic polymorphism,
- lifestyle strategy – think reproductive strategies in many fish e.g. *Xiphophorus* and wrasses
- parasite load (e.g. *Andrena* parasitized by *Stylops* wasps)
- plastic response to environment (locust raised in crowded environment).
- seasonal effects,
- ...



From http://cas.bellarmine.edu/tietjen/Ecology/sperm_competition_in_fish.htm

(b)

Pattern and Process

Pattern: the state of natural objects. Pattern is observable.

Evolutionary processes: the set of mechanisms that drive evolution. The cause of the pattern.

Modern (post 1900) work on species bears this pattern vs process distinction in mind.
It stimulates research into species as a pattern:

- Process question: Why do organisms seem to be groupable into distinct clusters? What processes lead to the clusters that we call "species"?

and species role in process theory:

- Species as a unit of selection.

Viewing species as entities in theories of biological processes contrasts with the (previous) view that species was simply another grouping category:

"... the term 'species,' as one arbitrarily given for the sake of convenience to a set of individuals closely resembling each other, ... it does not essentially differ from the term 'variety,' which is given to less distinct and more fluctuating forms" and "the grades of acquired differences [between taxonomic groups are] marked by the terms varieties, species, genera, families, orders, and classes"
– Darwin (1859) quoted by (de Queiroz, 2005)

"New Systematics" or "Modern Synthesis" view of species

A species is

- a reproductive community – reproduction occurs among individuals in a species. Species are populations or groups of populations.
- an ecological unit
- a species is a genetic unit (a "gene pool")

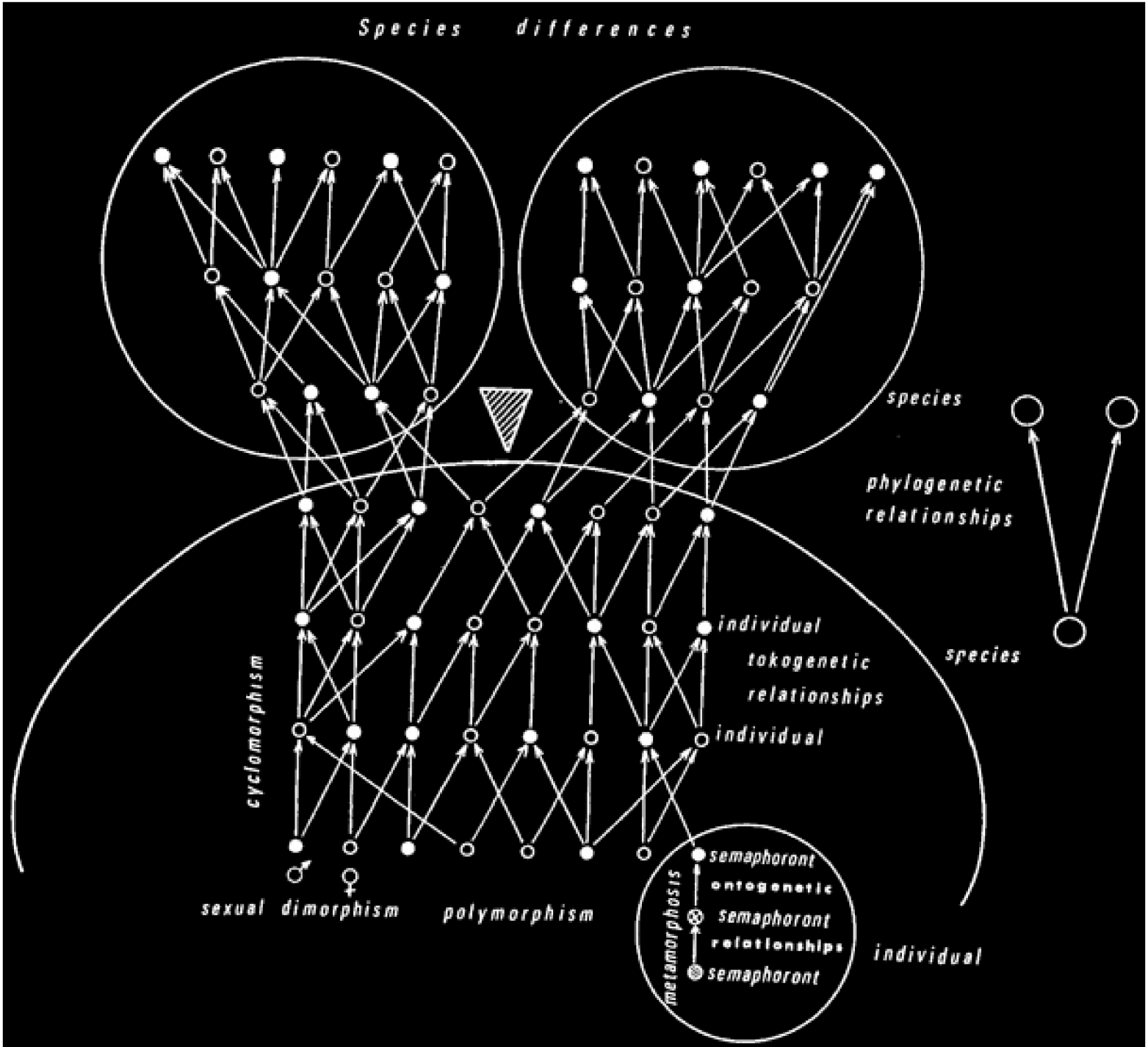


Figure 6. The total structure of hologenetic relationships and the differences in form associated with its

a Biological Species Concept

Mayr in "Systematics and the Origin of Species" (1942) stated: "species are groups of actually or potentially interbreeding natural populations, which are reproductively isolated from other such groups"

He referred to this as a *biological* species concept, to emphasize that it was not just a taxonomic device that could be used to classify anything.

"Species" is Latin for "kind," but "biological species" has more meaning than simply a kind.

Benefits of the BSC

- Helped the field move away from the essentialist, morphological, and nominalist species concepts;
- Closely tied into evolutionary theory – very similar to population geneticist's view of species (e.g. Sewall Wright's);
- Emphasizes one of the important the biological force that lead to cohesive lineages through time;
- Defines speciation theory clearly – the study of the development of reproductive barriers;
- Has stimulated great interest in more inclusive species definitions – (at least 24 named species concepts).

Weaknesses of the BSC

Theoretical:

- Interbreeding is not the only force that leads to evolving lineages (more on this later).

Applicability. The BSC requires:

- contemporaneous populations – what do paleontologists do?
- sexual organisms – what about bacterial species? allopatry

sympatric overlapping ranges
allopatric having geographic ranges that do *not* overlap

Naive interpretation of the BSC

Perform a cross of member of group A $\times$ member of group B

	sympatry	allopatry
hybrids	1 species	1 species
no hybrids	2 species	2 species

BSC in the real world

A = allopatry, S = sympatry
D = divergent morphology, Sim = very similar morphology
C = close in range, F = ranges are far apart
How many species?

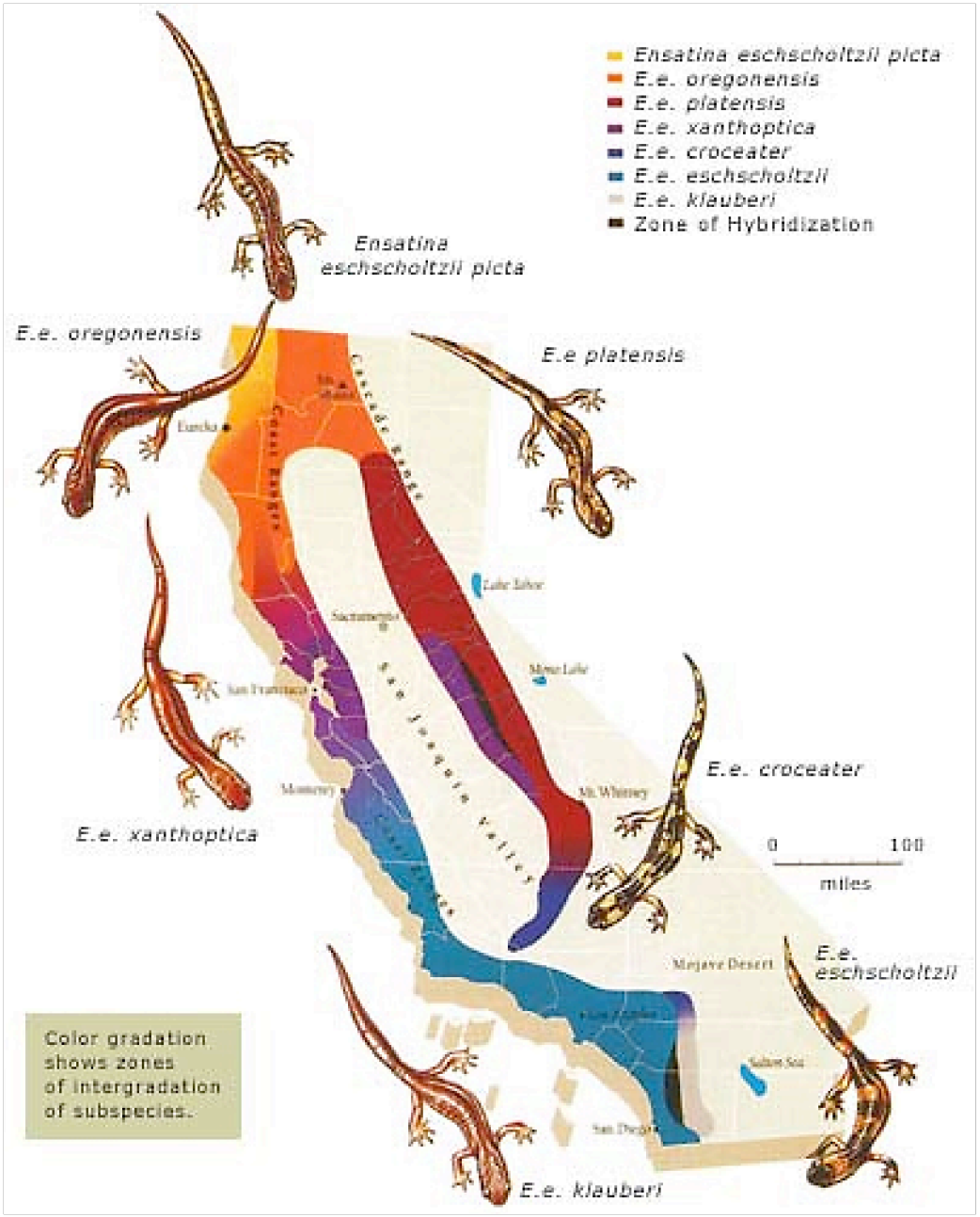
hybrids	S D -	S Sim -	A D C	A Sim C	A D F	A Sim F
many, fit	?	1	?	1	?	?
few, unfit	2?	?	2?	?	2?	?
sterile	2?	2?	2?	2?	2?	2?
?	2?	1?	2?	1?	2?	?
none	2	2	2	2	2	2

Weaknesses of the BSC (continued)

Difficult cases:

1. in allopatry tends to fall back to a morphological species definition
2. vague "potentially interbreeding natural populations" phrase
3. interbreeding is very hard to observe
4. is species status transitive? – problem of ring species.

The BSC works for sympatric populations that do not interbreed – but any (modern) species concept works in this case.


Ensatina eschscholtzii picta
E.e. oregonensis
E.e. platensis
E.e. xanthoptica
E.e. croceater
E.e. eschscholtzii
E.e. klauberi
Zone of Hybridization
Ensatina eschscholtzii picta
E.e. oregonensis
E.e platensis
E.e. xanthoptica
E.e. croceater
E.e. eschscholtzii
E.e. klauberi
Cascade Range
Coast Ranges
San Joaquin Valley
Mojave Desert
Eureka
Lake Tahoe
Mono Lake
Mt. Whitney
Salton Sea
0
100
miles
Color gradation shows zones of intergradation of subspecies.

"Many taxonomists have ignored it for practical reasons." Sokal and Crovello (1970) (speaking about the BSC).

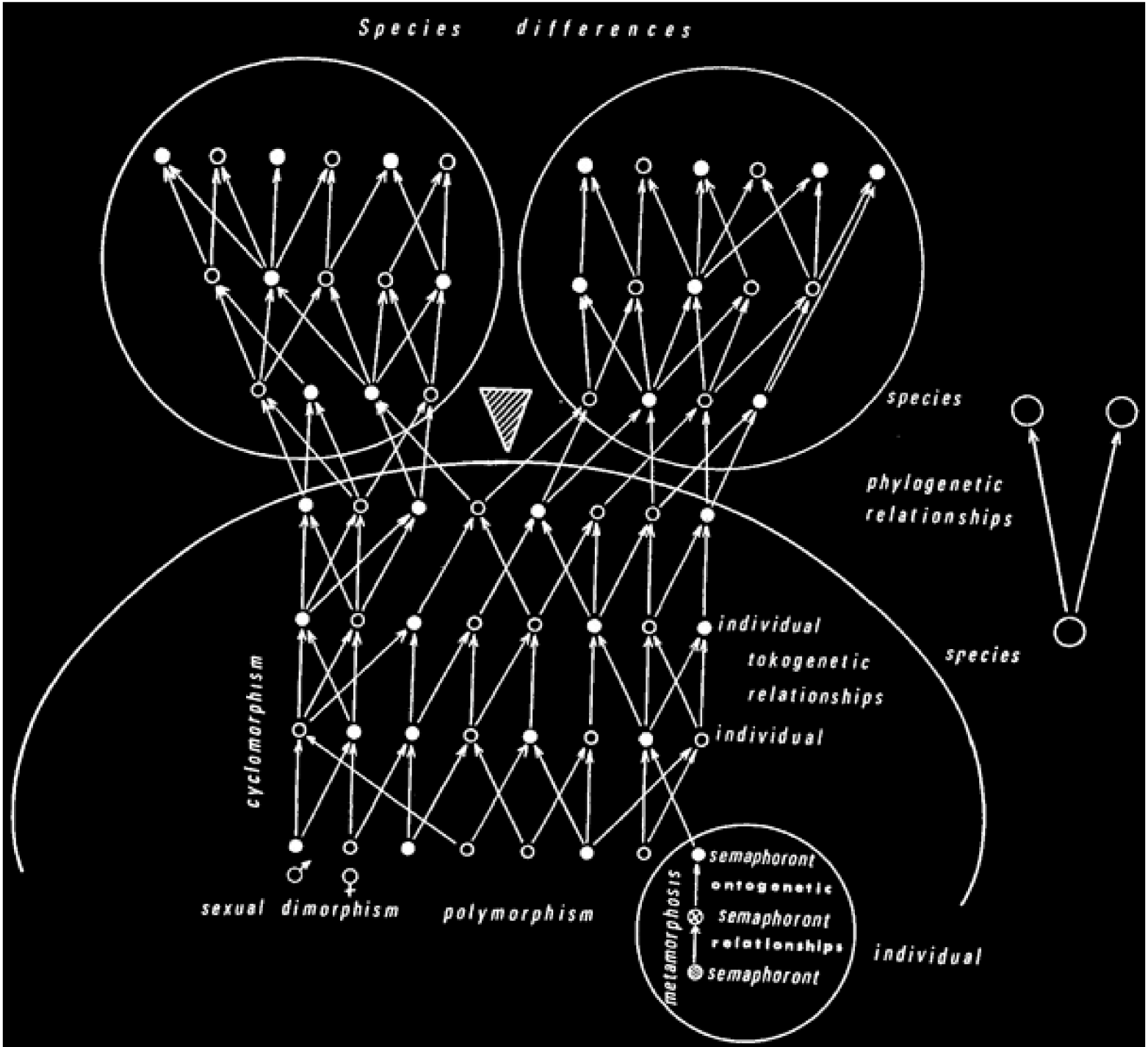


Figure 6. The total structure of hologenetic relationships and the differences in form associated with its

Evolutionary Species Concept

Simpson, 1961:
"an evolutionary species is a lineage (ancestor-descendant sequence of populations) evolving separately from others and with its own evolutionary role and tendencies.

Wiley, 1978:
"A species is a single lineage of ancestral-descendent populations of organisms which maintains its identity from other such lineages and which has its own evolutionary tendencies and historical fate."

ESC

Advantages over B.S.C. -

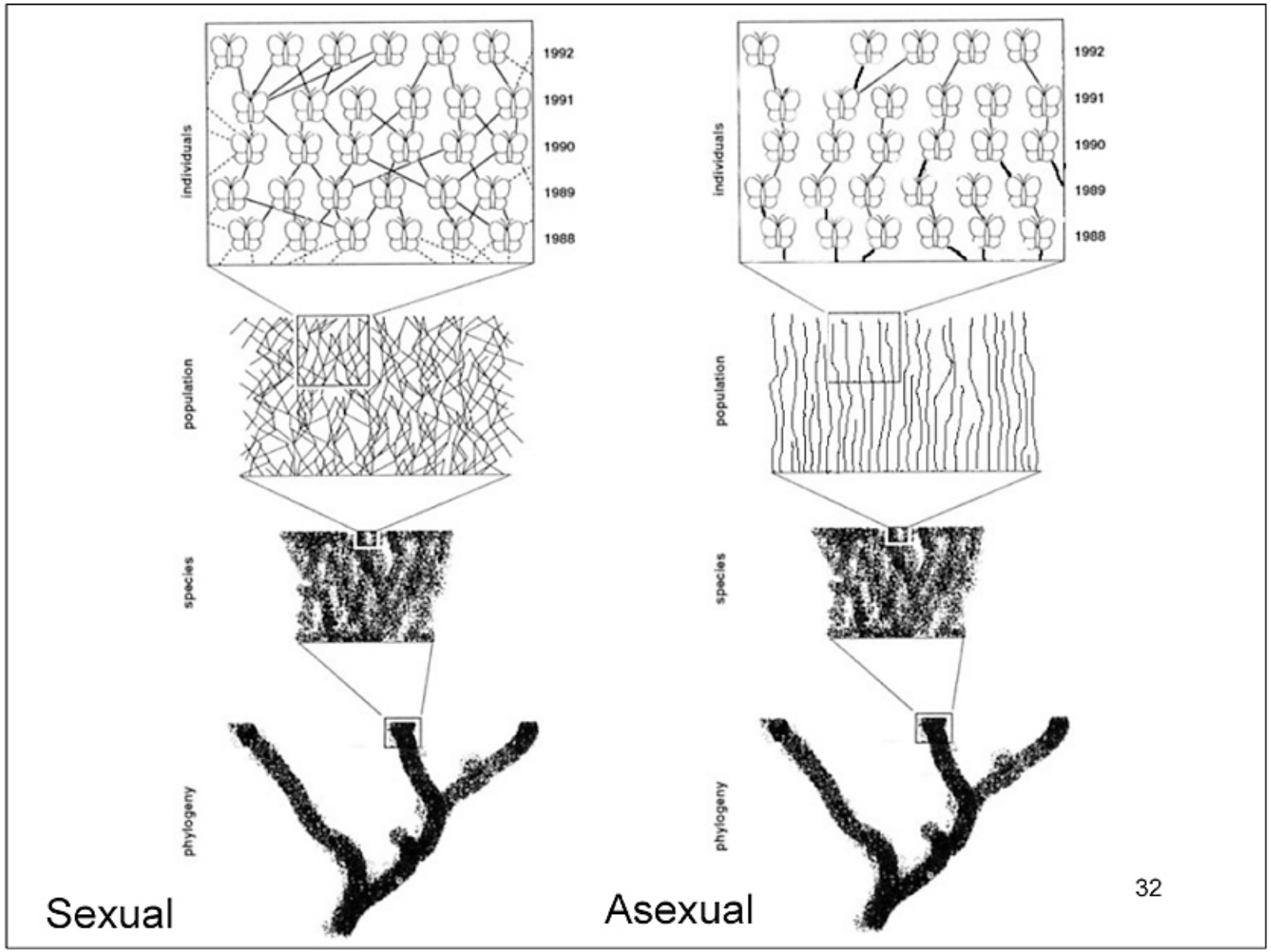
- explicitly reflects the fact that species are evolving entities
- geographically isolation is not a problem
- not tied to one mechanism of lineage maintenance

Disadvantages

- not tied as closely with the mechanisms of evolution – or is this an advantage?
- "lineage" and "independence" can be hard to diagnose – so not all methodological problems disappear.

Cohesion Species Concept (Templeton)

- Similarity with ESC: recognizes an evolving lineage as a key property.
- Similarity with BSC: tries to recognize the mechanisms of lineage cohesion through time.
- Difference from BSC: recognizes "demographic exchangeability" as a mechanism.


individuals
1992
1991
1990
1989
1988
population
species
phylogeny
Sexual
individuals
1992
1991
1990
1989
1988
population
species
phylogeny
Asexual

Cohesion Species Concept (Templeton) continued

Genetic exchangeability

- limits of gene flow's ability to keep a lineage cohesive
- factors that affect mating between individuals and gene flow between populations

Demographic exchangeability

- limits of natural selection and drift to keep a lineage cohesive.
- connected to the fundamental niche of the species
- if the descendants of two individuals are competing for the same "niche" then (eventually) one of the two lineages will replace the other.

Subspecies: "An aggregate of phenotypically similar populations of a species inhabiting a geographic subdivision of the range of that species and differing taxonomically from other populations of that species" –Mayr and Ashlock (1991)

polytypic species: is one that is made up of two or more subspecies

monotypic species: a species that is not divided into subspecies.

Subspecies designation has been used to mean

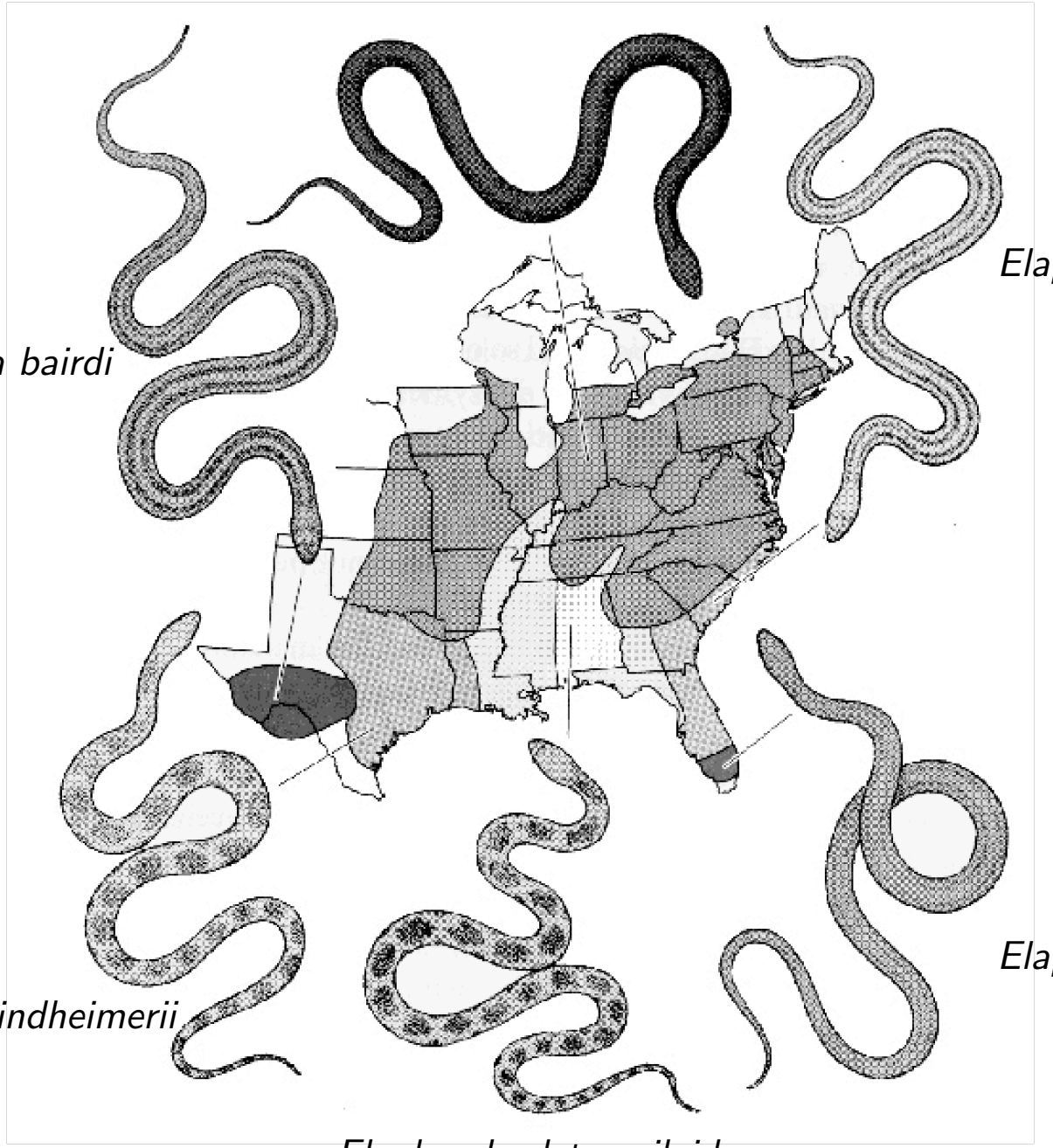
- incipient species, OR
- population of a widespread species that have adapted to regional differences in environment.

Elaphe obsoleta obsoleta

Elaphe bairdi

previously:

Elaphe obsoleta bairdi



Elaphe obsoleta quadrivittata

Elaphe obsoleta rossalleni

Elaphe obsoleta lindheimerii

Elaphe obsoleta spiloides

Subspecies bonanza

- Multiple definitions for "subspecies" exist
- In the early 1900's it was very popular to reclassify a set of similar allopatric species as a polytypic species.
- 315 of the 607 North American bird species were "demoted" to subspecies (Mayr, 1982) – without regard to reproductive connectivity. Later widespread acceptance of the BSC resulted in the promotion of these taxa back to species rank.
- Mayr (1982) argued that the subspecies was not fundamental (as the species category was), because subspecies are not closely tied to evolutionary theory.

Phylogenetic Species Concept

1983, Joel Cracraft
"A species (phylogenetic) is the smallest diagnosable cluster of individual organisms within which there is a parental pattern of ancestry and descent."

He claims:

1. origin of reproductive isolation is not the proper focus for the study of biological diversity.
2. the systematic status of taxa depends, above all else, on that differentiation.
3. the fundamental unit of evolution should be a population that has evolved one or more distinctive features.

Applications of phylogenetic species concept

1. Smallest diagnosable cluster of individuals
2. Diagnosable feature has to be fixed within the population.
3. The species must be a lineage (parental pattern of ancestry and descent) – not morphs or individuals.

Most subspecies would be considered to be phylogenetic species.

Phylogenetic Species Concept

Pros:

1. Obviously compatible with the rest of phylogenetics,
2. Species status determined strictly on the basis of species data (characters).

Cons:

1. plesiomorphies and apomorphies alike may define species.
2. species are not recognized if apomorphies have not appeared.
3. no clear tie with a speciation theory – fails to identify importance of changes.

Scrub jays

- prior to 1990 - 3 species
- allozyme analysis - paraphyly of 1 species (Peterson, 1992)
- protein study - 10 genetically distinct units (parapartic/allopatric) (Peterson, 1992)
- corroborated by mitochondrial gene sequences (Rice et al., 2003)
- plumage alone not enough to distinguish the 10 taxa, but can be combined with range and behavior

Currently:

- 5 species
- bears little resemblance to our understanding of actual diversity

Recently proposed species diagnosis methods

- DNA barcodes – species demarcations (and future identifications) based on sequence data in a 648 base-pair region of the COI gene.
  - A cutoff of 10x (mean of within-species variation) is used to mark the within-species vs. among-species split
- Model comparison using coalescent theory (Rannala and Yang [2011]; Leaché, Rannala, Yang [2011])

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