NJU Course

Principles of Paleobiology

Species: Definitions & Concepts

Species: Definitions & Concepts

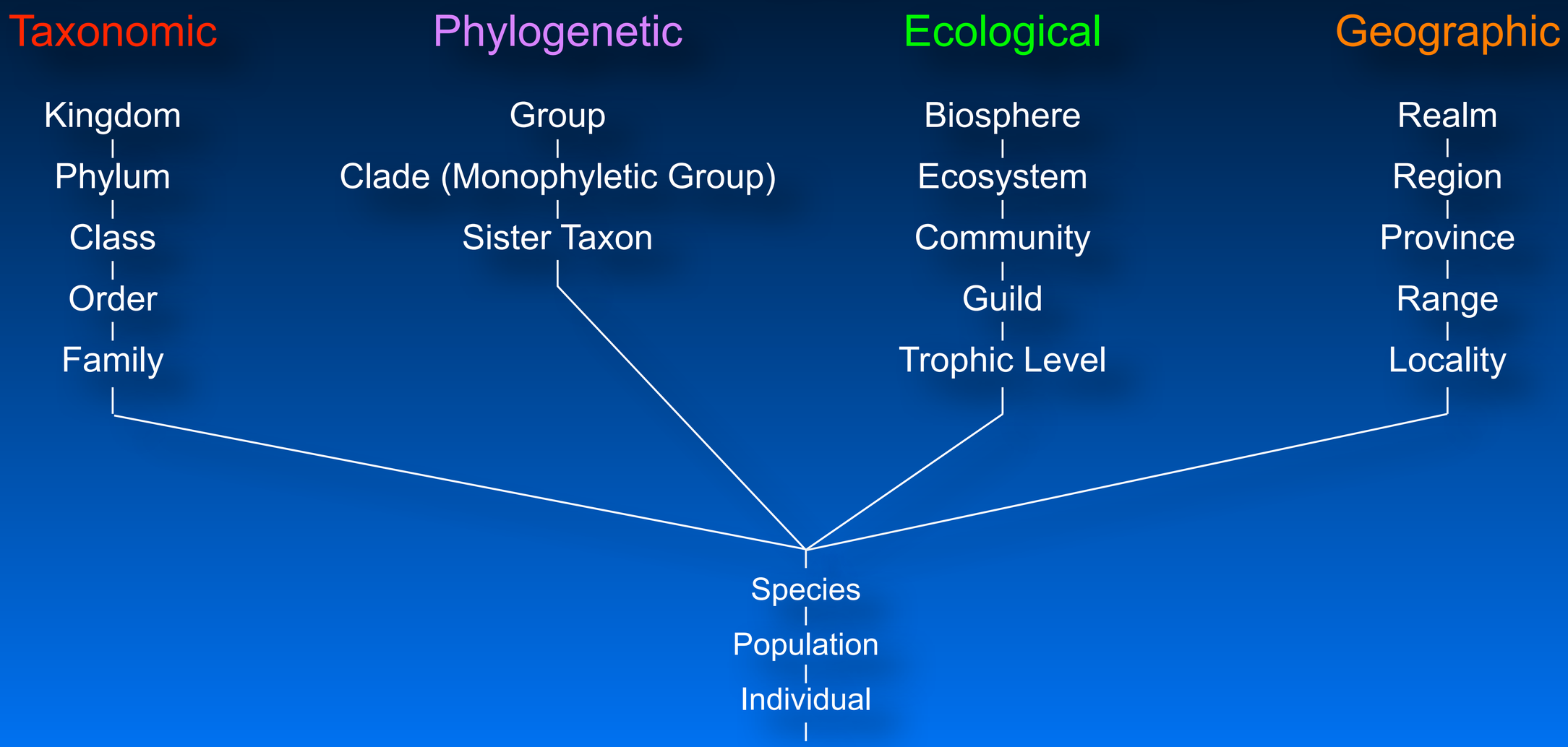
The term “species” has a complex history and remains controversial in almost all areas of biology, including paleobiology. At present there is little agreement along specialists regarding any of the following.

- What a species is.
- How a species should be defined.
- How a species should be recognized.
- How species originate.
- The extinction status of some Recent species.

Accordingly, paleobiologists need to be aware of these controversies and disagreements so that they can understand biological, taxonomic and philosophical contributions to this literature, even though they can do little to resolve any of the outstanding debates at the process level.

Species: Definitions & Concepts

Species represent a common category in several biological hierarchies.



Species: Definitions & Concepts

The Individual

In biology, an individual is regarded as being synonymous with the concept of an organism, which is any living system that is an assembly of molecules, exhibits the properties of life, and functions as a single entity.

Under the synthetic (Neo-Darwinian) theory of evolution the individual is regarded as the unit of selection, though subsequent developments in biology have suggested that units of natural selection other than individuals do exist (e.g., genes, genomes, groups).

Philosophically, individuals are regarded as having a definite and unitary beginning (birth, speciation) and a definite and unitary ending (death, extinction). These bounding conditions, along with the presence of structured (non-random) variation is what makes each individual unique. The same cannot be said (necessarily) of taxonomic categories.

Species: Definitions & Concepts

The Population

In biology, a population is any number of individuals of the same species that occupy an area and reproduce from generation to generation largely or wholly within its geographic confines.

In sexually reproducing species a population is usually composed of family units and is, on average more closely related to other members of the same population than members of different populations.

This genetic reinforcement makes some populations diverge phenotypically from other populations of the same species, usually driven (at least in part) by local environmental factors.

If divergence continues to the point at which interbreeding is prevented for a sufficient interval a new species can be created.

Species: Definitions & Concepts

The Species: Historical Perspective

Aristotle
(384–322 BC)

Aristotle recognized two levels of biological organization. He used the term génos (γενοσ) to refer to different kinds of organisms (e.g., birds, lizards, mammals) that were distinguished by common attributes (e.g., feathers, scales, hair). At a lower level, eidos (ειδοσ) was used to refer to different forms, or variants, within the kind (e.g., cranes, crows, sparrows) that were distinguished by the forms inherited from their parents.

Aristotle's terms are the etymological basis for the modern terms "genus" and "species".

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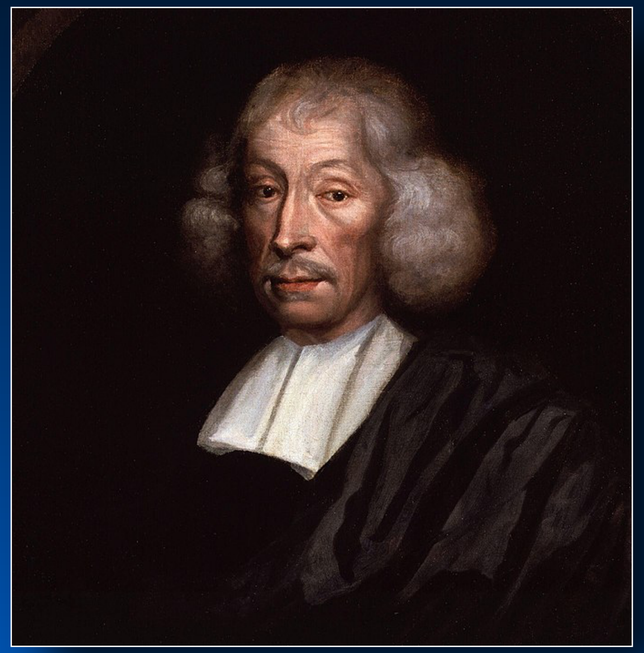
The Species: Historical Perspective



John Ray
(1627 – 1705)

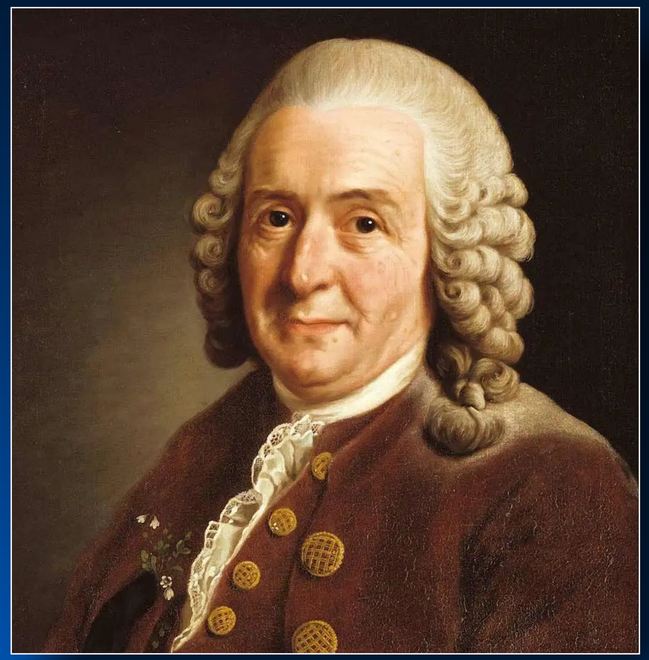
English naturalist-theologian who published important early modern works on plants and animals.

Ray rejected Aristotle's dichotomous subdivision, preferring a hierarchical system based on observed similarities and differences.

Ray was also among the first to attempt a modern concept of the category "species" which he regarded as being a group of morphologically similar organisms arising from a common archetype (or ancestor).

Species: Definitions & Concepts

The Species: Historical Perspective



Carolus Linnaeus
(1707 – 1778)

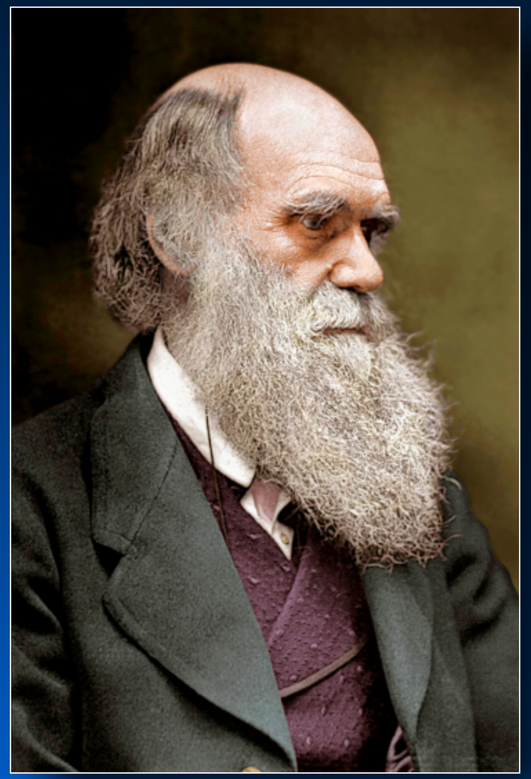
Widely acclaimed as the “father of taxonomy”, Linnaeus was a Swedish naturalist-physician who formalized the modern system by which species are named and set into a hierarch-ical classification.

Species – the lowest level of Linnaeus’ classification were recognized by shared physical characteristics (= positive evidence) rather than common differences (= negative evidence).

Linnaeus accepted that species could change through hybridization and acclimatization, but rejected the concepts of speciation and extinction.

Species: Definitions & Concepts

The Species: Historical Perspective



Charles Darwin
(1808 - 1882)

Darwin regarded the “problem” of species largely to be a non-issue. To him variation was the important aspect of biology and the cause of evolution. Accordingly, “species” were simply convenient labels biologists attached to bits of natural variation that enable them to talk about the natural world.

“... varieties have the same general characters as species, for they cannot be distinguished from species, -- except, firstly, by the discovery of intermediate linking forms ... ; and except, secondly, by a certain amount of difference, for two forms, if differing very little, are generally ranked as varieties ...”

“Independently of blending from intercrossing, the complete absence, in a well-investigated region, of varieties linking together any two closely-allied forms, is probably the most important of all the criterions of their specific distinctness”.

Darwin (1859)

Species: Definitions & Concepts

Species Concepts: Overview

- Biological Species Concept (Mayr, 1942)
- Evolutionary Species Concept (Simpson, 1961)
- Hennig's Species Concept (Hennig, 1966)
- Phenetic Species Concept (Michener, 1970)
- Ecological Species Concept (Van Valen, 1976)
- Phylogenetic Species Concept (Rosen, 1979)
- Genotypic Species Concept (Mallet, 1995)

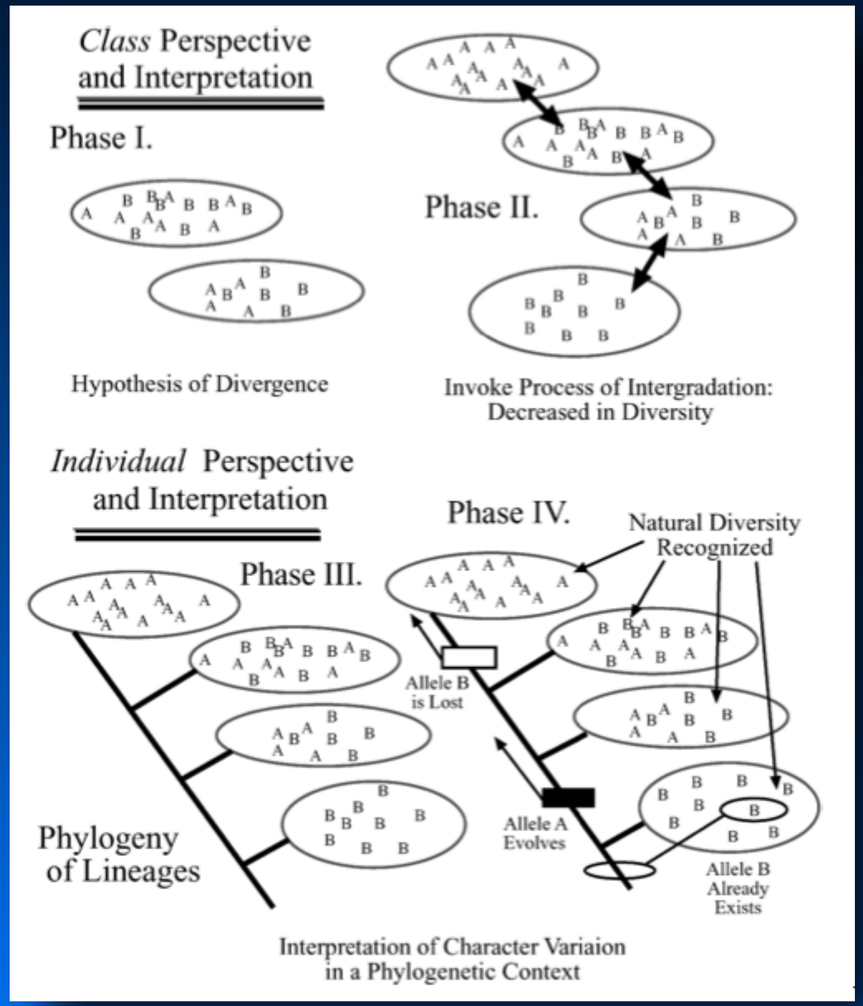


Diagram from Mayden (2002)

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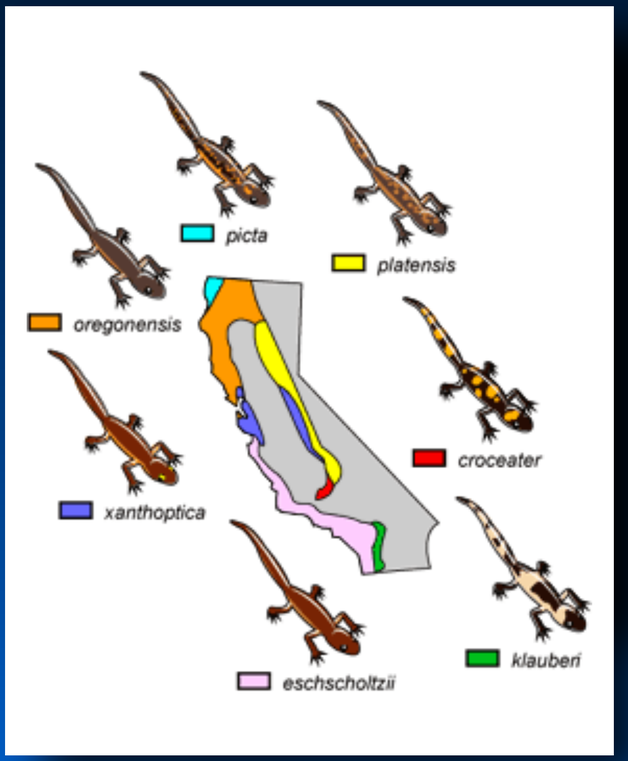
Biological Species Concept (BSC)

- Formulated by Buffon (1753), but promoted and popularized by Ernst Mayr (1942)
- Species are populations that can produce offspring and are reproductively isolated from other such populations.
- Emphasizes the process of reproductive isolation as being critical to the creation of new species, but is agnostic with regard to the mechanisms by which this isolation might come about.

- Has difficulty accounting for hybridization, asexual reproduction, horizontal gene transfer and, most recently, speciation by epigenesis.
- In a sense is based on negative evidence (= failure to reproduce) which might arise in different parts of a population for different reasons.



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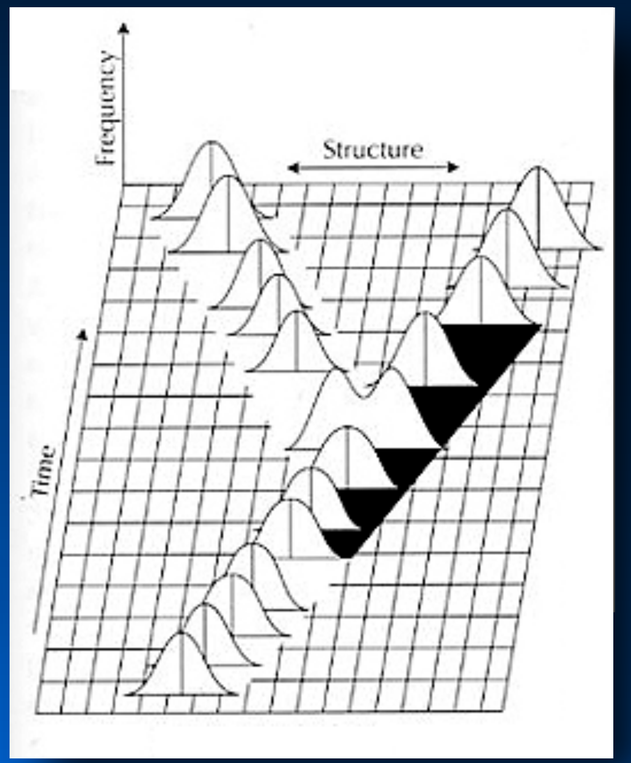
Evolutionary Species Concept (ESC)

- Formulated by G. G. Simpson (1961).
- A single lineage of ancestral descendant populations which maintains its identity from other such lineages and has its own evolutionary tendencies.
- Implies species are individual entities rather than taxonomic categories.
- As individuals species have historical, temporal and spatial attributes.
- Is agnostic regarding the mechanisms by which species identity is maintained.



- Under this definition all individuals within a lineage must be regarded as constituting the same “species”.
- Has difficulty accounting for hybridization, asexual reproduction, horizontal gene transfer and speciation by epigenesis.

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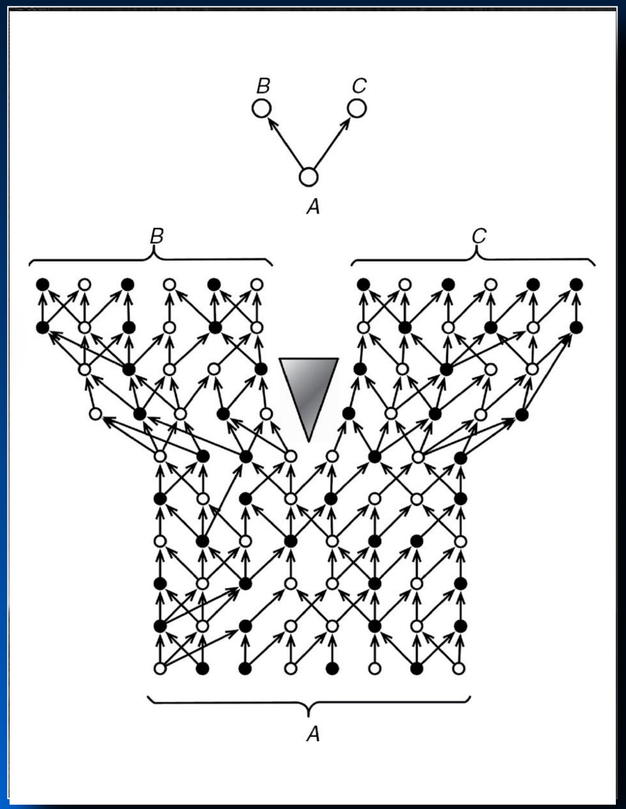
Hennig's Species Concept (HSC)

- Formulated by Willi Hennig (1966).
- Specifies that, whenever reproductive isolation occurs within a formerly contiguous population two new species are formed and the parent species becomes extinct.
- Represents an effort to use the speciation event to delimit species' ranges in time.
- Was the first species concept to take phylogenetic data and inferences into consideration explicitly.

- Extinction of the ancestral species at each cladogenetic event seems arbitrary and has not proved popular.
- Difficult to apply to uniparental species (agamotaxa).



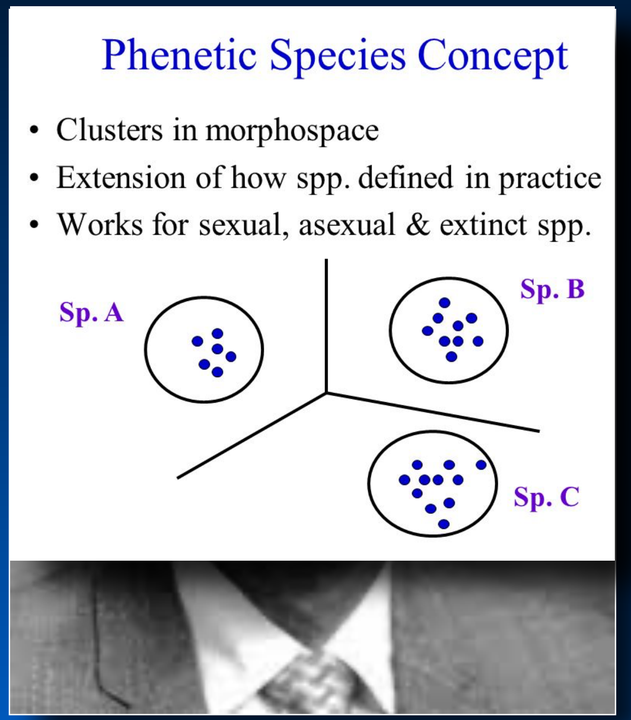
Willi Hennig
(1913 – 1976)

Species: Definitions & Concepts

Phenetic Species Concept (PheSC)

- Proposed by Michener (1970).
- A set of organisms that are phenotypically similar to one another and phenotypically different from members of other species.
- This is the species concept applied by (most) paleontologists and, indeed, the only concept that can be applied to (most) fossils.
- One of the few species concepts that can be subjected to testing and verification by statistical methods.

- Numerous examples of modern taxa exist in which interbreeding (= gene flow) exists between phenotypically different populations and vice versa.
- This concept has difficulty subdividing a continuously varying lineage through time.



Charles Michener
(1918 – 2015)

Species: Definitions & Concepts

Ecological Species Concept (EcSC)

- Proposed by Leigh Van Valen (1976).
- A species represents a set of organisms adapted to a particular set of resources, called a niche, in the environment.
- Represents an attempt to recognize the importance of ecology in the species concept.

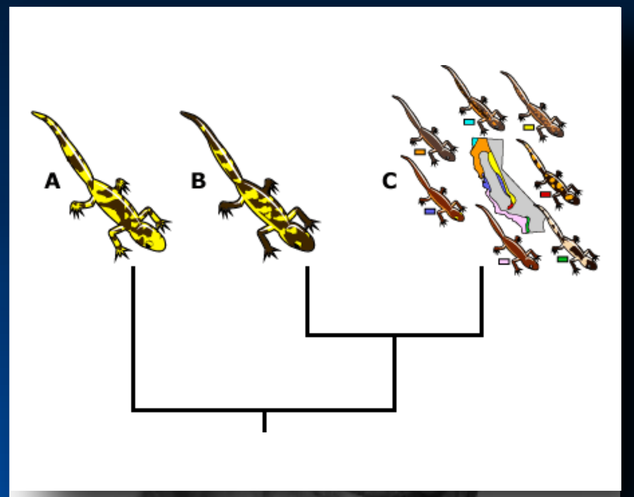
- In almost all widespread species populations exhibit slight differences in their niche occupation. Under these conditions such populations would need to be regarded as different species.
- In some species (e.g., cichlid fish) offspring of the same parents can occupy different niches.
- In other cases sympatric species may occupy the same (apparent) niche.

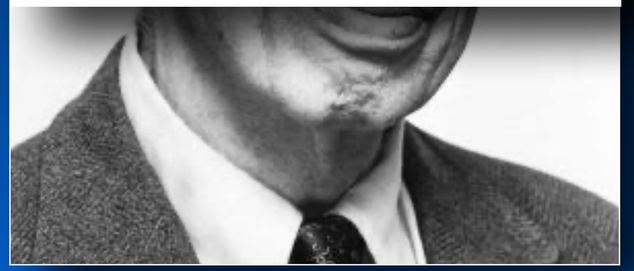
Species: Definitions & Concepts

Phylogenetic Species Concept (PhySC)

- Proposed by Dan Rosen (1979) but many variants exist.
- The smallest aggregation of populations (sexual) or lineages (asexual) diagnosable by a unique combination of character states in comparable individuals.
- Based on phenotypic data, but differs from the PheSC in that only unique, derived character states may be used for species diagnosis.

- Suffers from same flaws as PheSC.
- Fails to distinguish between phyletic and cladogenetic speciation.
- Strictly speaking cannot be applied to asexual lineages as these would be defined by non-unique or ancestral character states.



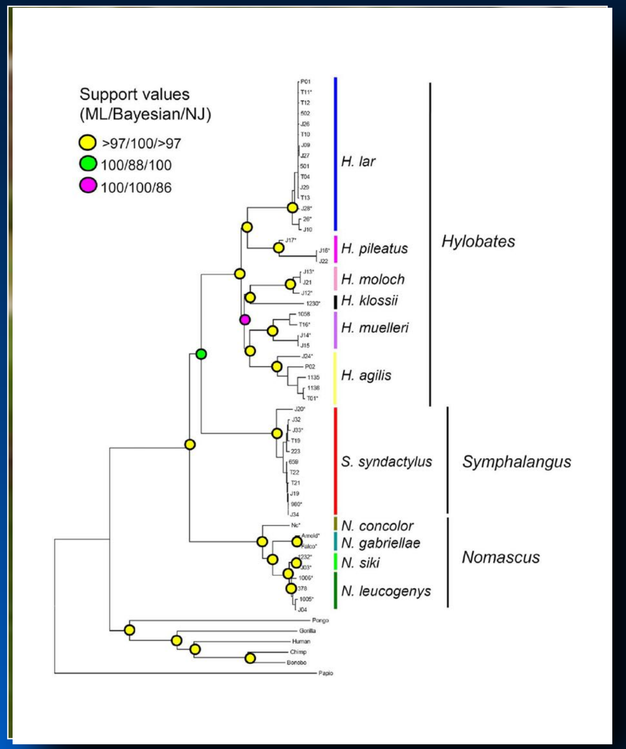


Donn E. Rosen
(1928 – 1986)

Species: Definitions & Concepts

Genotypic Species Concept (GtySC)

- Proposed by James Mallet (1995) but many variants exist.
- Species constitute, and are defined by, identifiable genetic clusters – either at single or multiple loci – with no or few intermediates.
- Essentially at updating of Darwin's definition of species that incorporates new discoveries in genetic and genotypic data.
- This definition may be extended to morphological data with the provision that discontinuities in genotypic variation may not be reflected accurately by morphological variation.
- Vague regarding what constitutes an "identifiable genetic cluster".



James Mallet
(b. 1955)

Species: Definitions & Concepts

Summary

- The basic problem with species “concepts” since Darwin is that they have mixed the qualities of a theory-neutral definition of the discontinuities in variation we call species with ideas about how those discontinuities arise and are maintained.
- The fact is that morphological and genotypic discontinuities among populations can arise for a large number of process and mechanistic reasons. There is little need to, and no justification for, preferring one reason over another as representing to “true” distinction between species.
- In addition, confusion has arisen with respect to whether species constitute (somewhat arbitrary) taxonomic categories or ontological individuals with their own evolutionary characteristics, spatial and temporal limits, and historical fates.
- This second controversy has largely been resolved in favor of the latter concept which, in turn, begs the question of whether supra-specific individuals also exist.

Species: Definitions & Concepts

What is a Paleontological Species?

- A set of organisms that are phenotypically similar to one another and phenotypically different from members of other species. (Phenetic Species Concept).
- An aggregation of populations diagnosable by a unique combination of character states in comparable individuals (cf. Phylogenetic Species Concept).
- An identifiable morphological cluster – either in single or multiple attributes – with no or few intermediates (cf. Darwinian Species Concept).

- Paleontological species may be consistent with other species concepts, but cannot be demonstrated to conform to their requirements, definitions, mechanisms, or attributes.

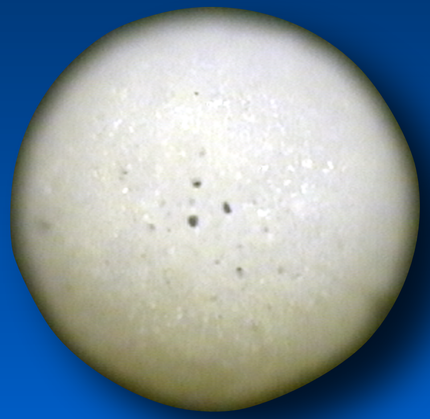
Species: Definitions & Concepts

Species Identification in Paleobiology

Species: Definitions & Concepts

Qualitative Species Identification

In some cases a fossil species morphology is so distinctive there is little question the forms in question differ from any closely related species with no or few intermediates ever being observed.



Orbulina universa
(Planktonic Foraminifer)

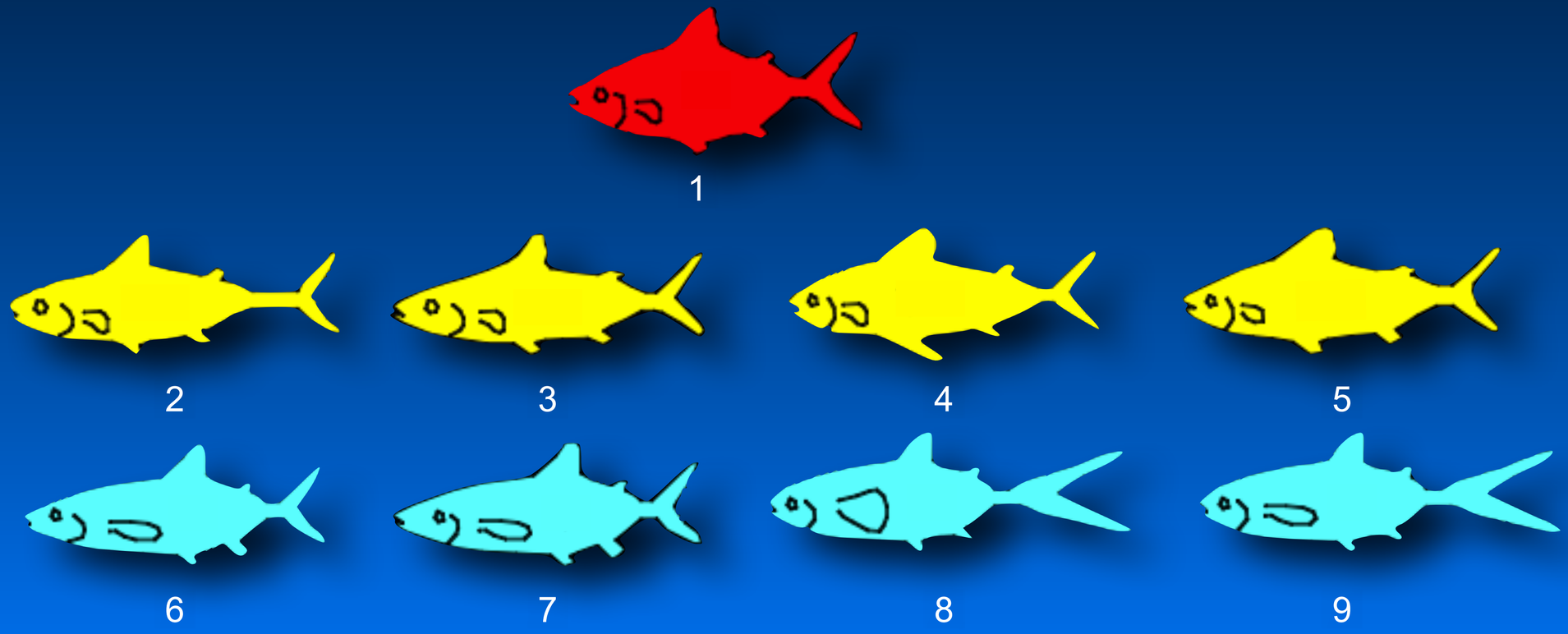
Megaloceros giganteus
(Deer)

Phacops rana
(Trilobite)

Species: Definitions & Concepts

Species Identification

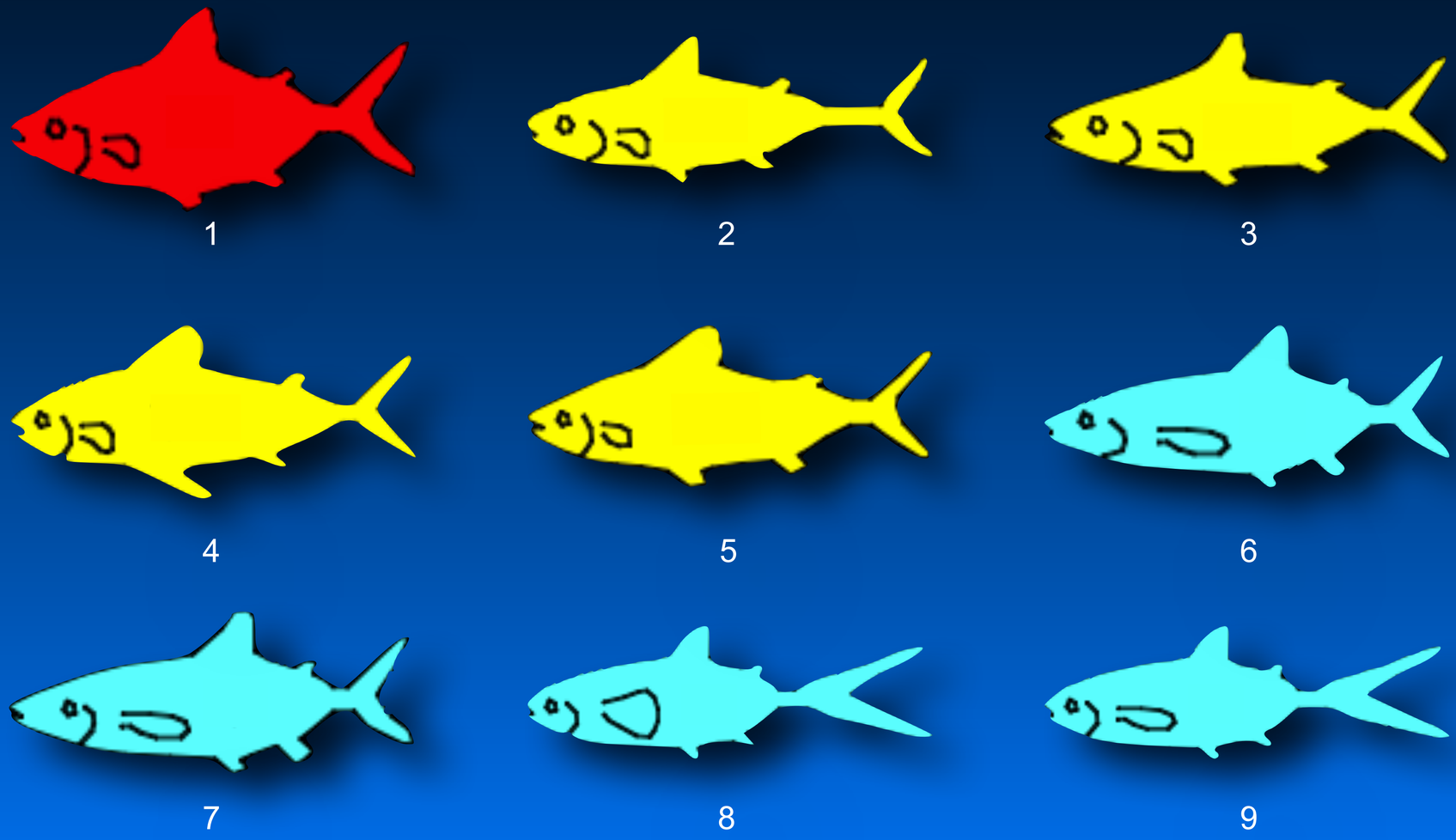
In order to demonstrate a paleontological species exists it is always necessary to undertake comparative analyses, and usually necessary to undertake quantitative analyses, of its morphology, either as a whole or on a character-by-character basis.



Fish drawings after Naylor (1996)

Species: Definitions & Concepts

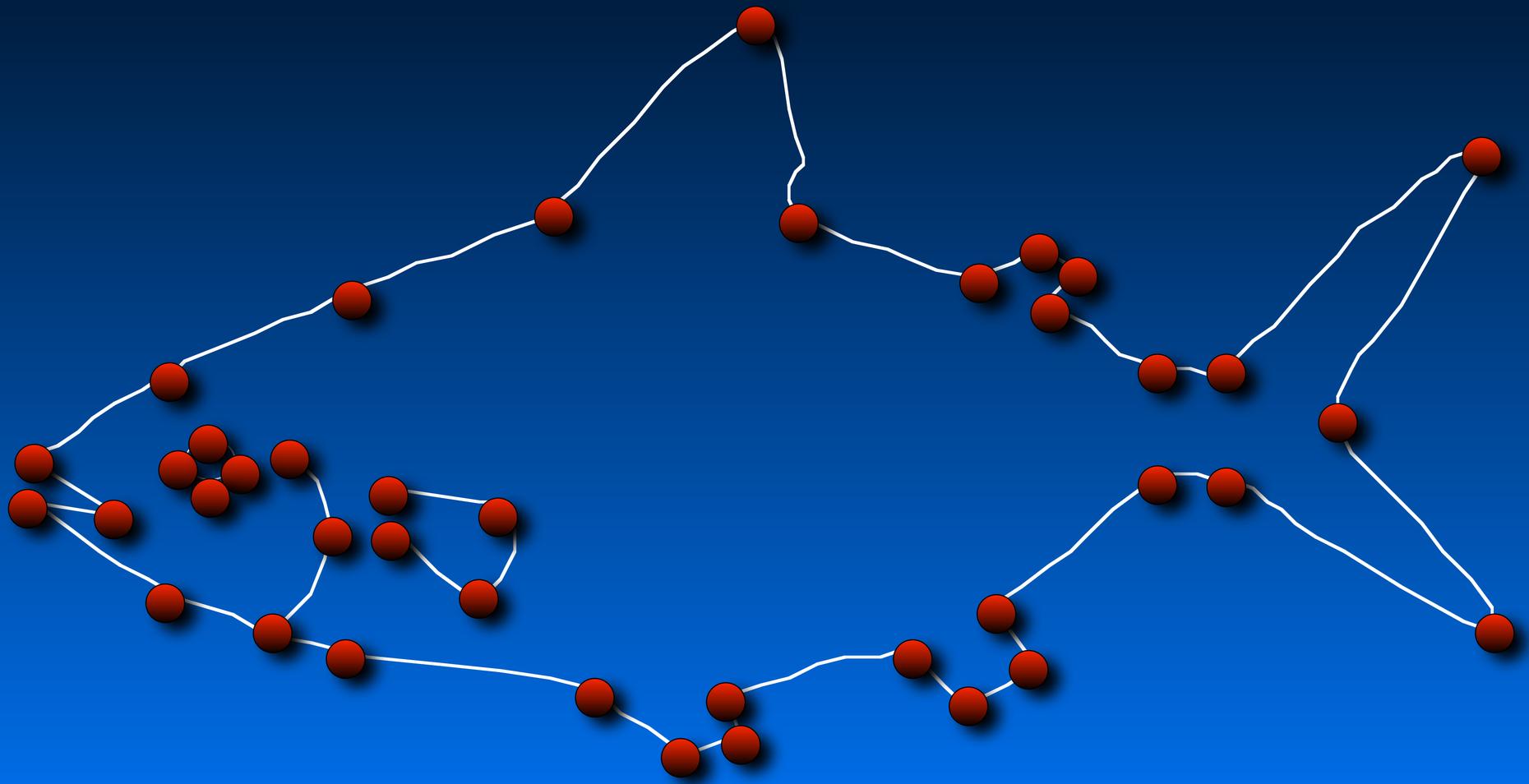
Qualitative Species Identification



Fish drawings after Naylor (1996)

Species: Definitions & Concepts

Quantitative Species Identification



MacLeod (2002)

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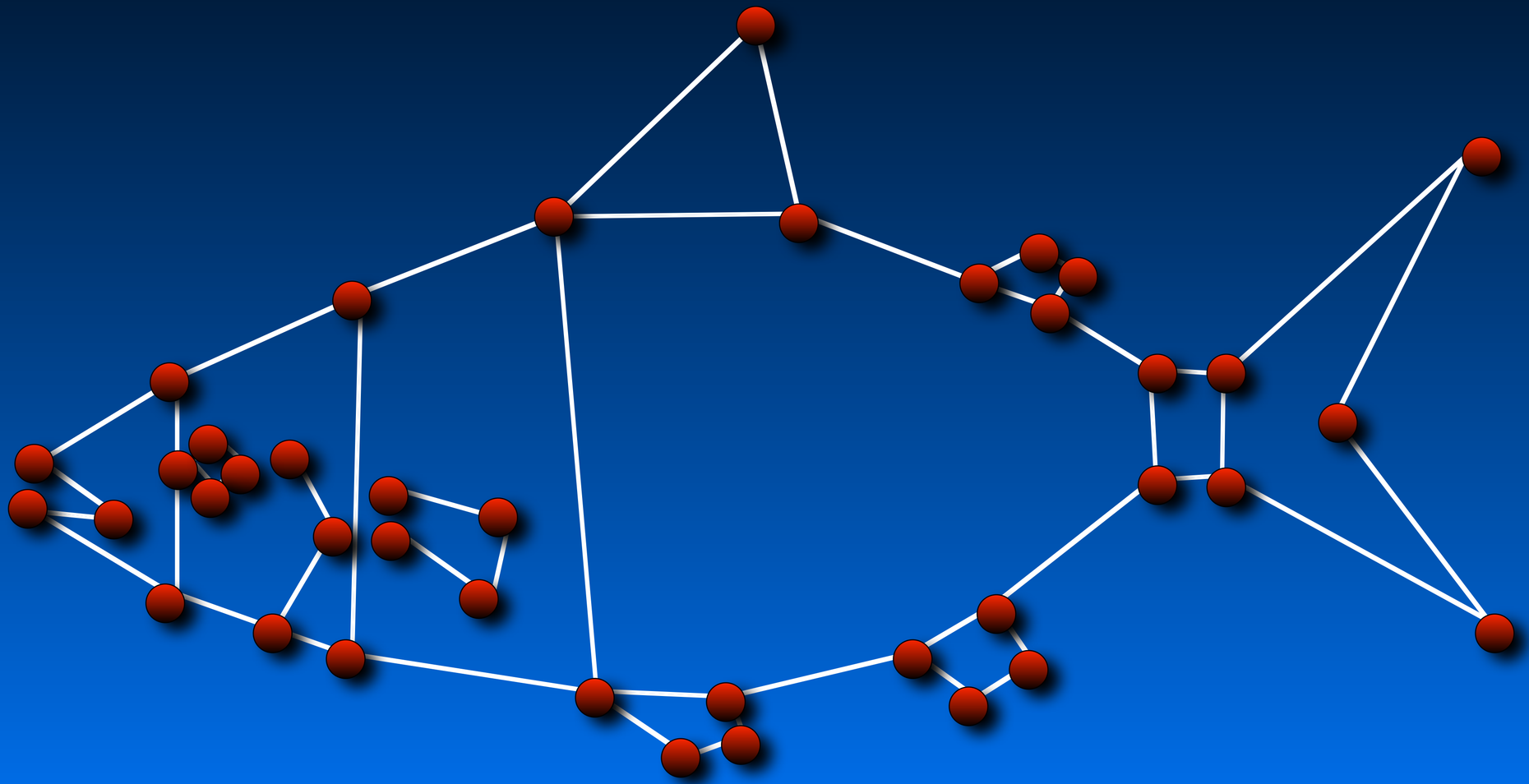
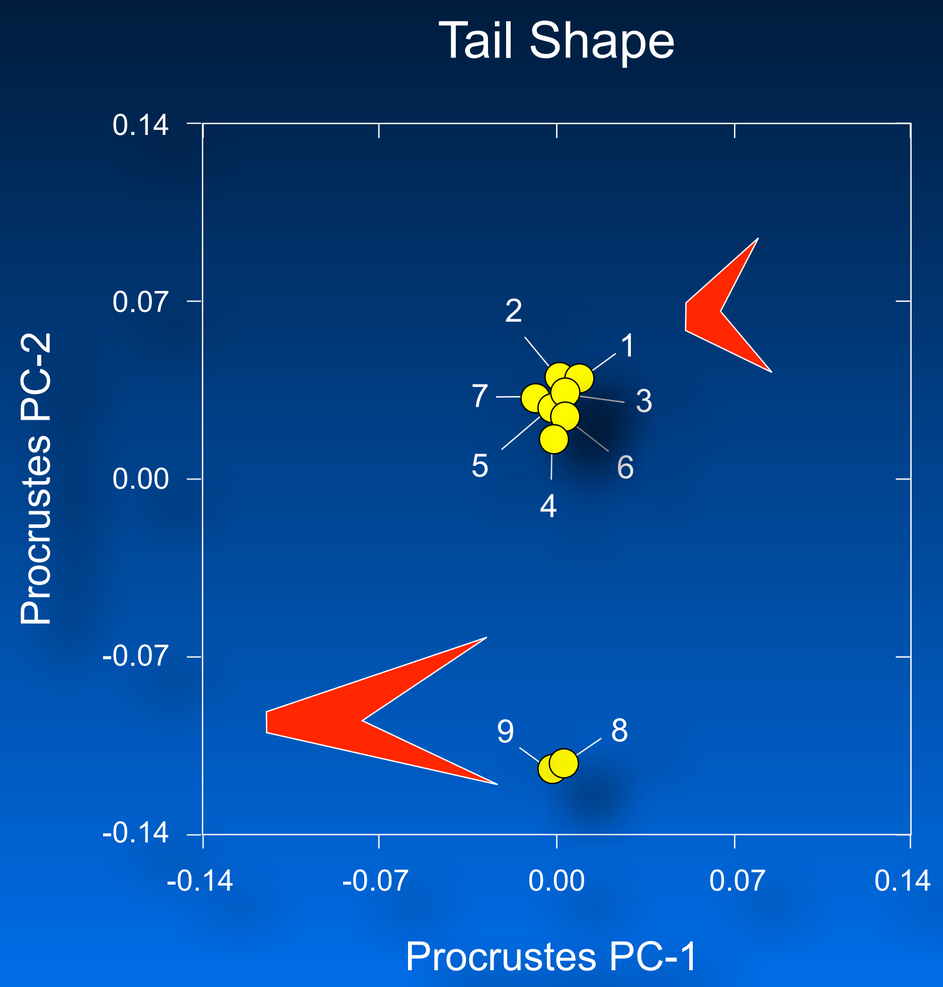
Quantitative Species Identification

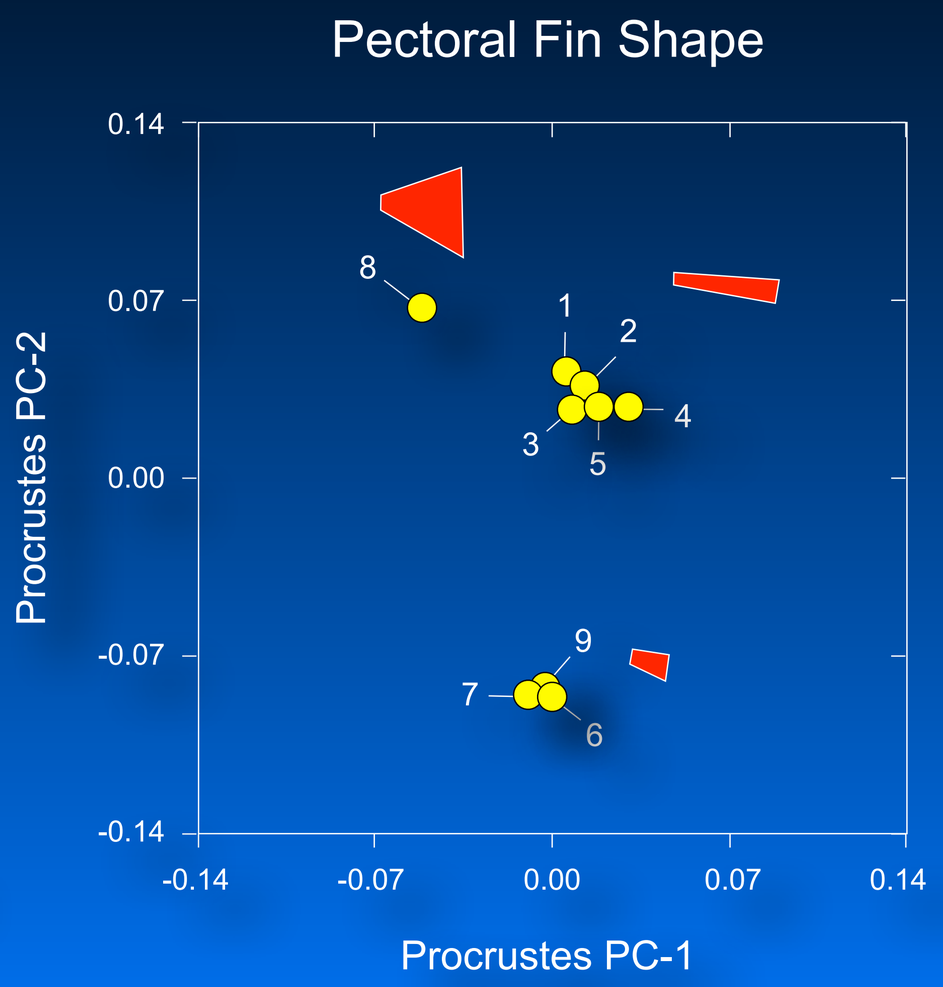


MacLeod (2002)

Species: Definitions & Concepts

Quantitative Species Identification





MacLeod (2002)

Species: Definitions & Concepts

Species Identification

Patient and systematic evaluation reveals each form has a unique and diagnosable combination of character states

	Species								
	1	2	3	4	5	6	7	8	9
Head Shape	0	0	0	0	0	1	1	0	0
Orbital-Branchial Region Shape	0	1	1	0	0	1	0	0	0
Pectoral Region Shape	0	0	0	0	0	1	1	1	1
Abdomen Shape	0	1	1	1	1	0	0	0	0
Caudal Peduncle Shape	0	1	0	0	0	0	0	0	0
Tail Shape	0	0	0	0	0	0	0	1	1
Dorsal Fin Shape	0	0	0	1	1	0	0	0	0
Adipose Fin Shape	0	0	0	0	0	1	1	1	1
Pelvic Fin Shape	0	1	1	1	1	0	0	0	0
Anal Fin Shape	0	0	0	1	0	0	0	0	0
Eye Shape	0	2	2	0	0	1	1	0	0
Gill Slit Shape	0	0	0	0	0	1	0	0	0
Pectoral Fin Shape	0	0	0	0	0	2	1	0	1

MacLeod (2002)

Species: Definitions & Concepts

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Caudal Peduncle Shape	0	1	0	0	0	0	0	0	0
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MacLeod (2002)

Species: Definitions & Concepts

Species Identification

Patient and systematic evaluation reveals each form has a unique and diagnosable combination of character states

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Gill Slit Shape	0	0	0	0	0	1	0	0	0
Head Shape	0	0	0	0	0	1	1	0	0
Pectoral Fin Shape	0	0	0	0	0	2	1	0	1
Adipose Fin Shape	0	0	0	0	0	1	1	1	1
Pectoral Region Shape	0	0	0	0	0	1	1	1	1
Tail Shape	0	0	0	0	0	0	0	1	1

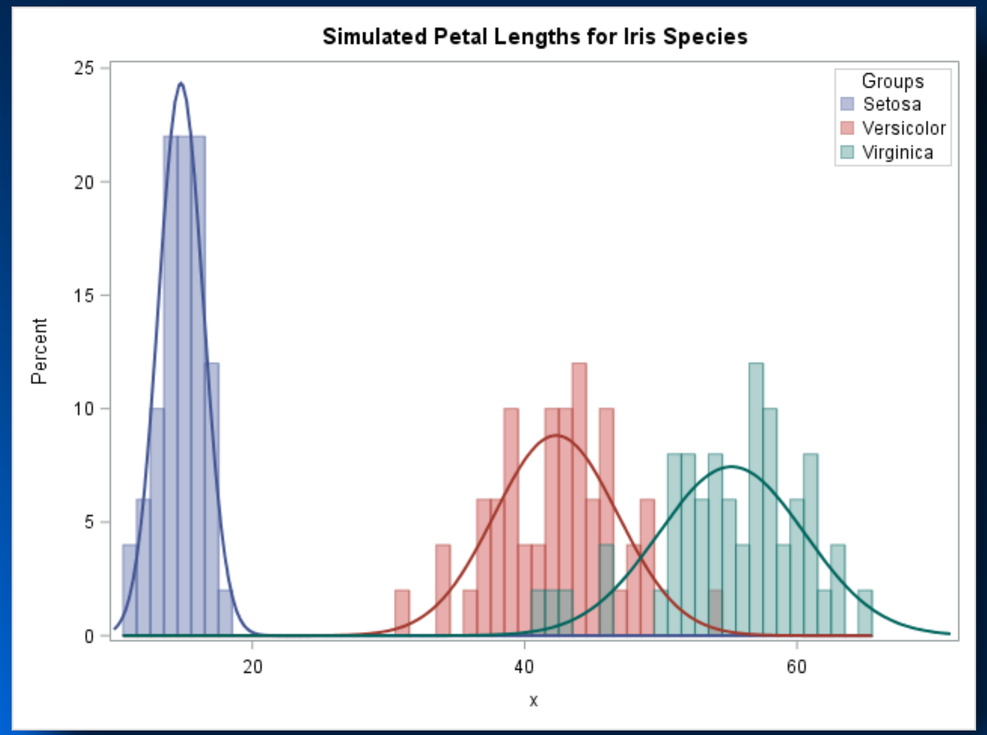
MacLeod (2002)

Species: Definitions & Concepts

Quantitative Species Identification

Simulated Data

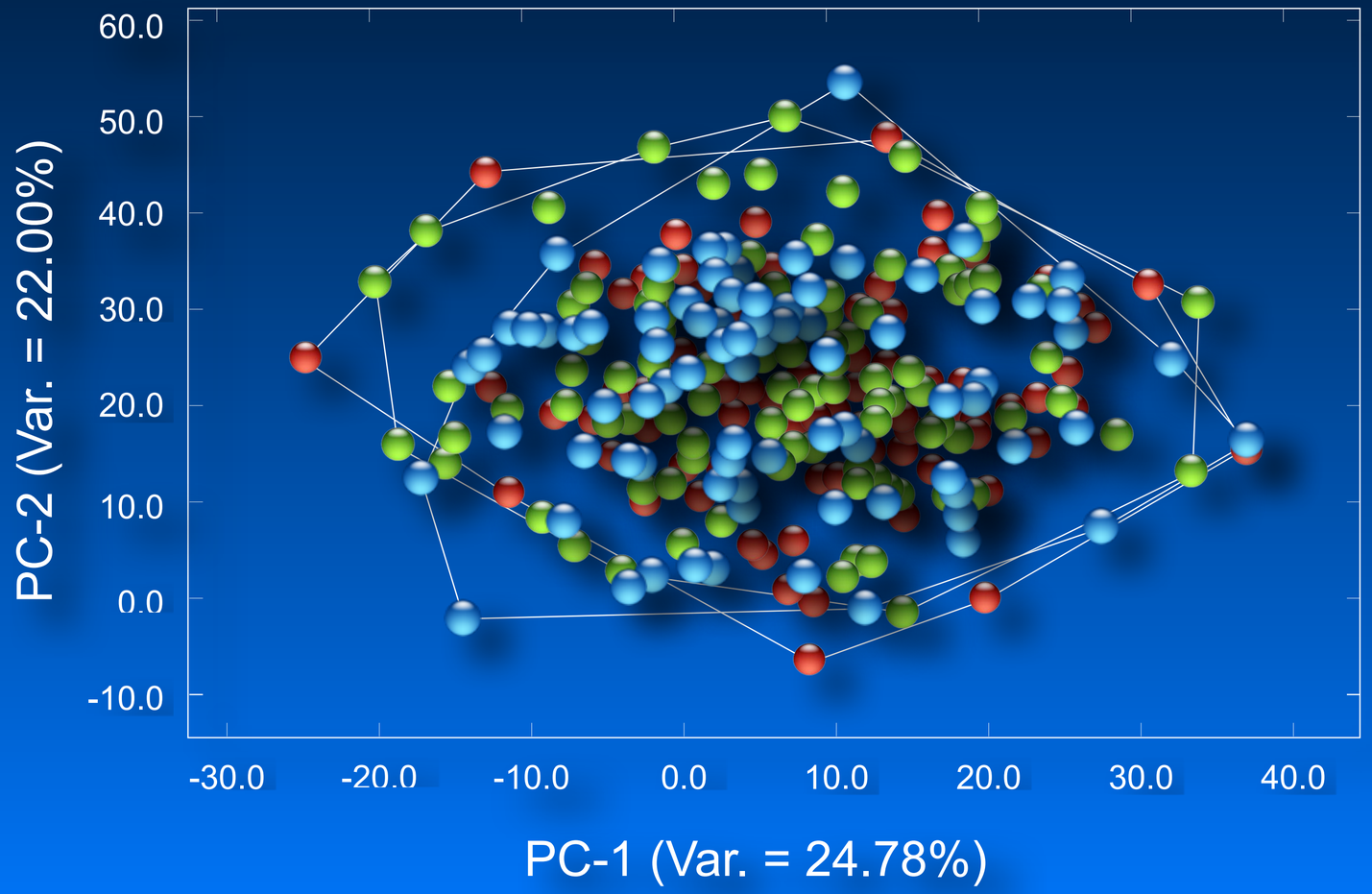
- Three (3) groups
- 50 specimens per group
- 10 variables
- Monotonically declining amount of variance for each variable
- Random variation in first none (9) variables
- Discontinuous partitioning of variation in the last (10th) variable (= variable exhibiting the least variance)



Species: Definitions & Concepts

Quantitative Species Identification

Simulated Data Analyzed via Principal Component Analysis (PCA)



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Species: Definitions & Concepts

Principal Components Analysis

Vector sets used to characterize a data set in multiple dimensions.

X = Data Matrix

X^TX = (Pooled) Covariance Matrix of X

$$X^TX = W\Lambda W^T$$

Λ = Eigenvalue Matrix

W = Eigenvector Matrix

$T = XW$ Projects new data into eigenvector space

$X = TW^{-1}$ Projects position in eigenvector space back into space of original variables

Species: Definitions & Concepts

Principal Components Analysis

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Species: Definitions & Concepts

Linear Discriminant Analysis

Ronald Fisher
(1892- 1962)

Iris setosa

Iris versicolor

Iris virginica

$$DM = W^{-1}B$$

Where:

DM = Discriminant Function Matrix

W = Within-Groups Covariance Matrix

B = Between-Groups Covariance Matrix

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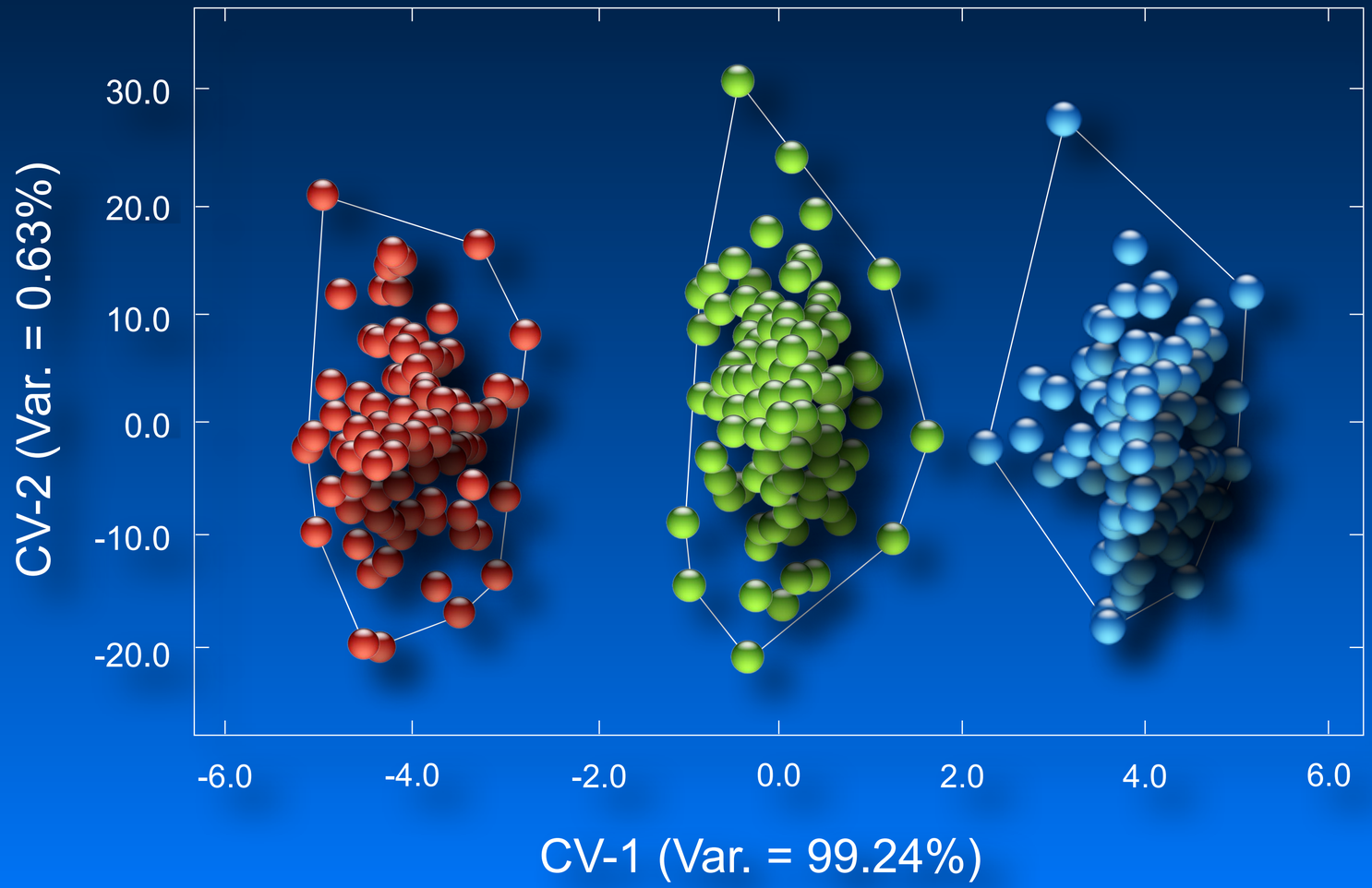
Quantitative Species Identification

Simulated Data Analyzed via Canonical Variates Analysis (CVA)



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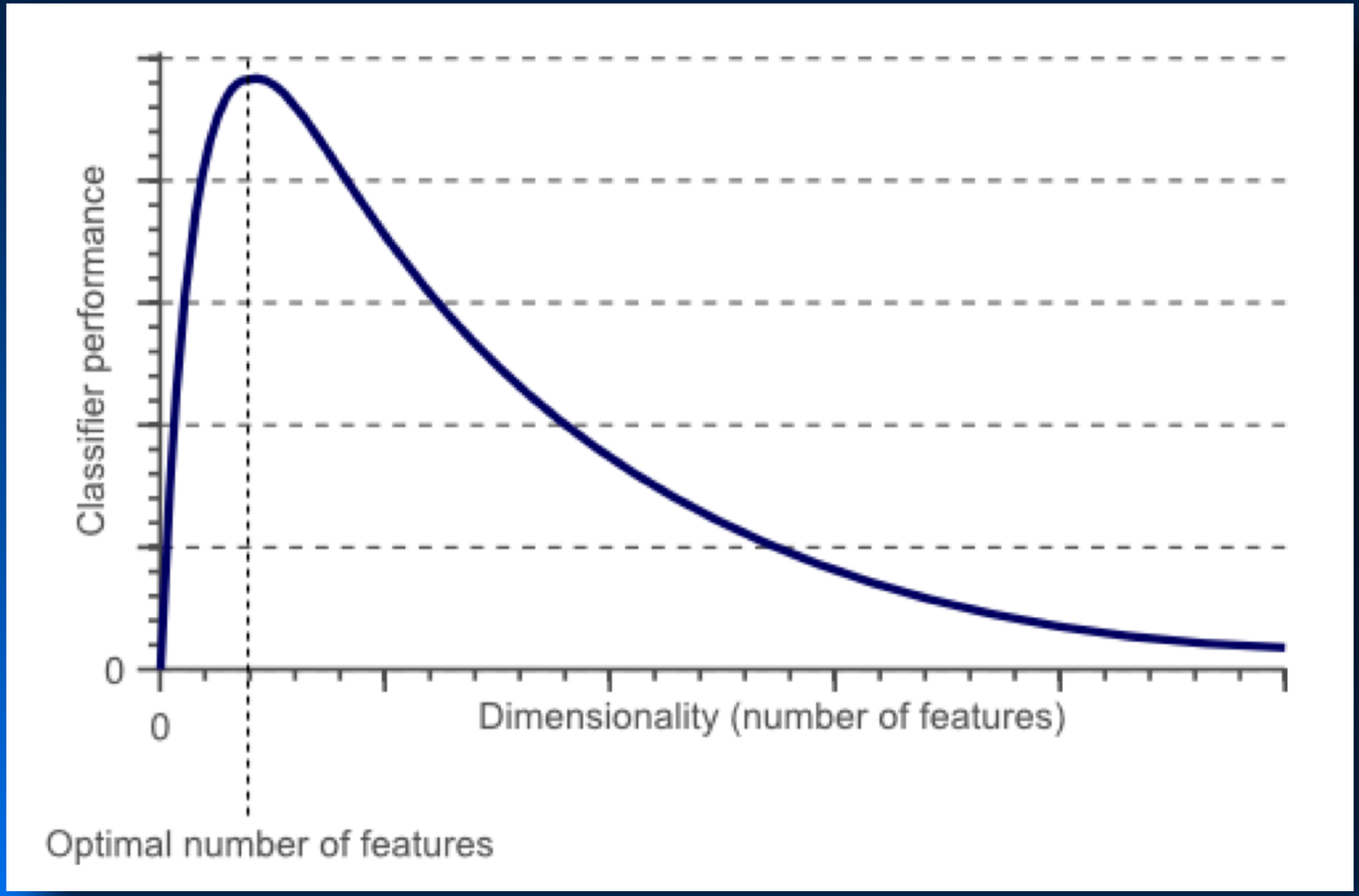
Quantitative Species Identification

Curse of Dimensionality

Species: Definitions & Concepts

Quantitative Species Identification

Performance of Linear Classifiers



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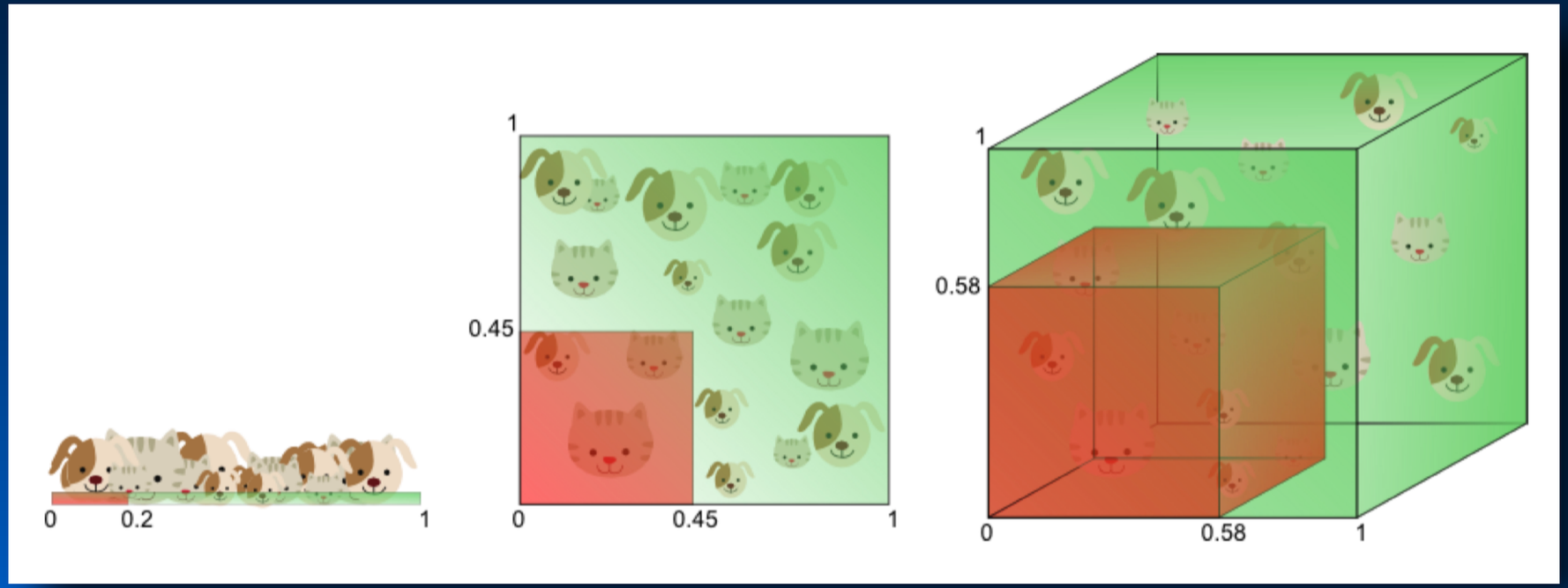
Quantitative Species Identification

Performance of Linear Classifiers



As the number of dimensions increases the number of samples required to provide reasonable coverage of any given proportion of the feature space increases exponentially with the volume of the feature space.

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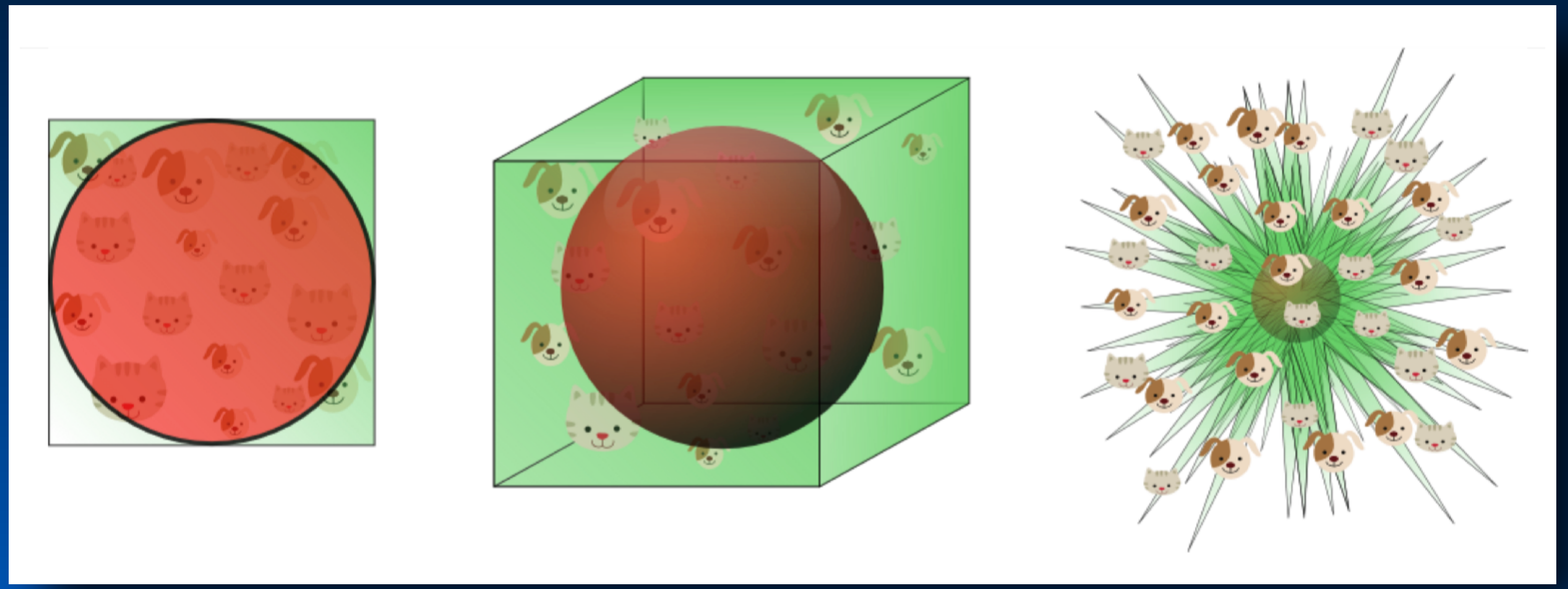
Quantitative Species Identification

Performance of Linear Classifiers



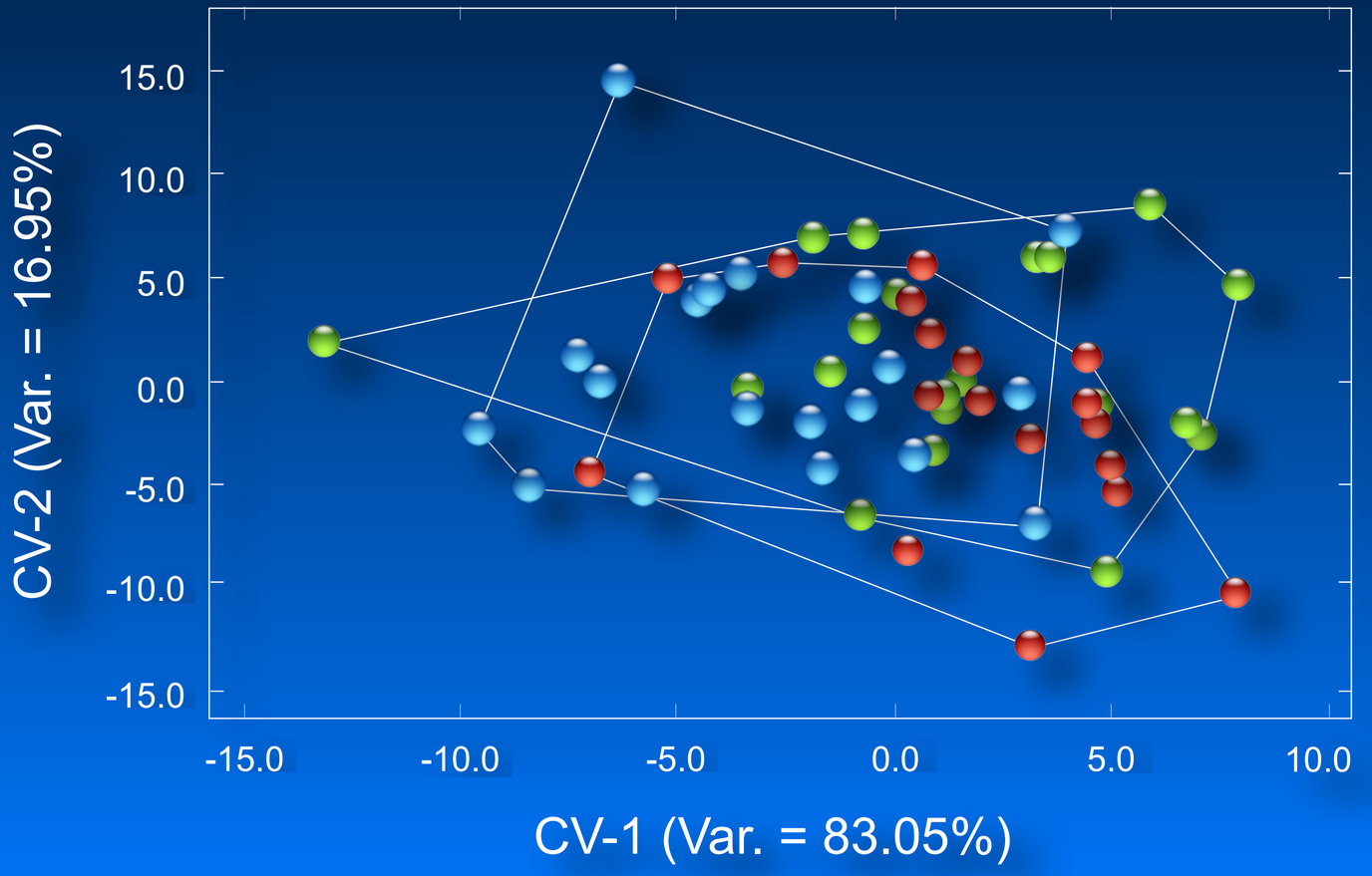
Moreover, as dimensionality increases a greater proportion of the data resides in the corners of the feature hyperspace rather than in its common center. Linear classifiers are poor at creating models of variation that include data points are that margins of the distribution accurately.

Species: Definitions & Concepts

Quantitative Species Identification

Canonical Variates Analysis

Random Data: 20 Objects/Group, 10 Variables



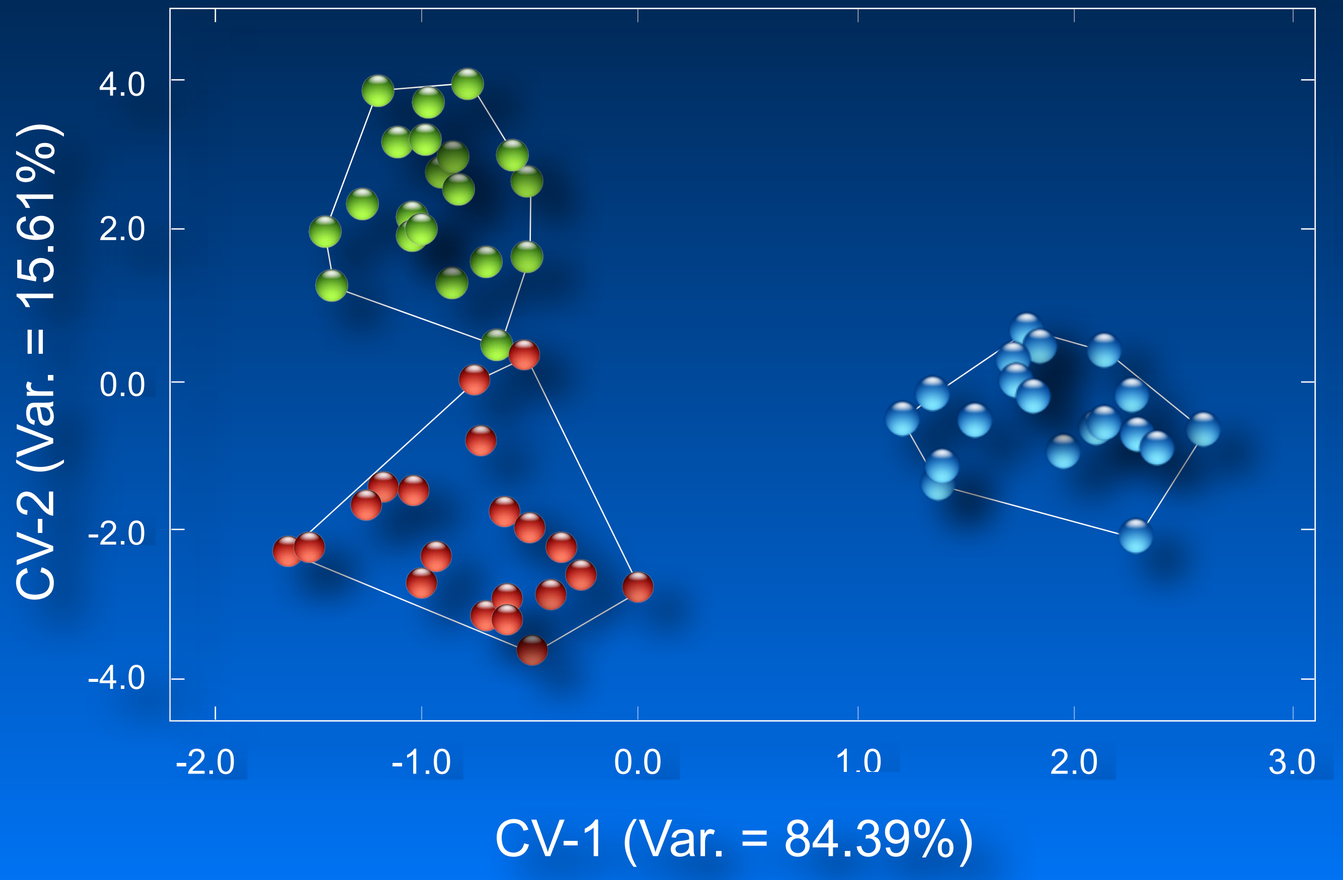
MacLeod (2018)

Species: Definitions & Concepts

Quantitative Species Identification

Canonical Variates Analysis

Random Data: 20 Objects/Group, 50 Variables



MacLeod (2018)

Species: Definitions & Concepts

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Random Data: 20 Objects/Group, 10 Variables

Parametric

Statistic	Test	Observed Value	α-Probability (%)
Wilks λ	*F*-ratio	0.990	48.121
Log Likelihood ϕ	X^2	19.690	47.752

Random Data: 20 Objects/Group, 50 Variables

Parametric

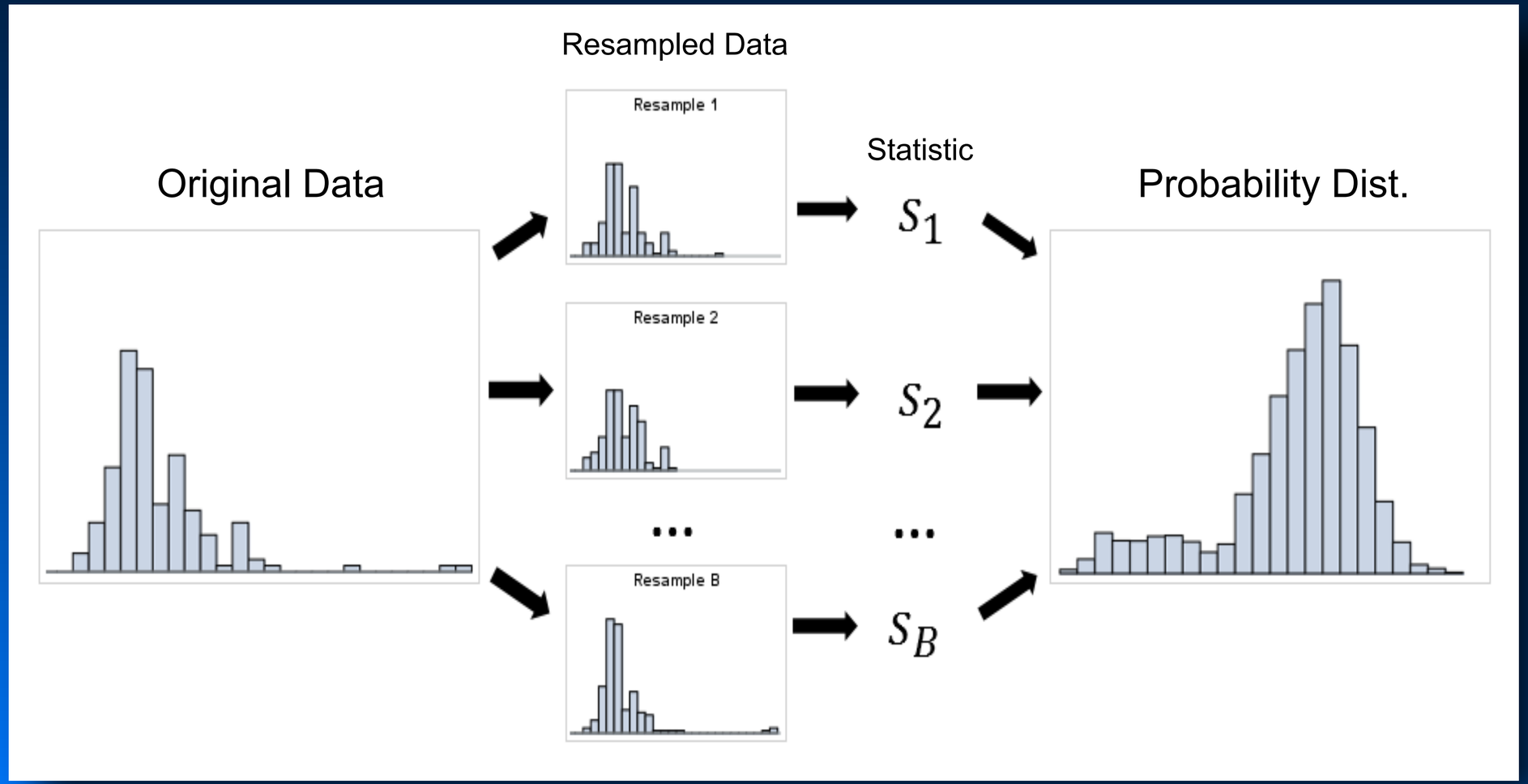
Statistic	Test	Observed Value	α-Probability (%)
Wilks λ	*F*-ratio	0.003	3.055
Log Likelihood ϕ	X^2	183.900	0.000

MacLeod (2018)

Species: Definitions & Concepts

Quantitative Species Identification

The Statistical Bootstrap



Species: Definitions & Concepts

Quantitative Species Identification

Canonical Variates Analysis

Random Data: 20 Objects/Group, 10 Variables

Bootstrap

Statistic	Test	Observed Value	α-Probability (%)
Wilks λ	*F*-ratio	0.990	46.90
Log Likelihood ϕ	X^2	19.690	46.90

Random Data: 20 Objects/Group, 50 Variables

Bootstrap

Statistic	Test	Observed Value	α-Probability (%)
Wilks λ	*F*-ratio	0.003	13.900
Log Likelihood ϕ	X^2	183.900	13.900

MacLeod (2018)

Species: Definitions & Concepts

Quantitative Species Identification

Summary

- Paleontological species are sets of morphologically similar individuals at comparable life stages that exhibit no or few intermediates with other species.
- Paleontological species can be recognized on the basis of simple inspection, but should be erected only after detailed comparative, and often quantitative, analysis.
- In order to facilitate comparison complex morphological should be subdivided into simpler characters and character states.
- The lack of obvious clustering of taxa or morphologies in an ordination space formed by the analysis of a pooled similarity of distance matrix does not provide sufficient evidence that no clustering exists.
- If possible morphological discontinuities should be tested using robust statistical procedures.

NJU Course

Principles of Paleobiology

Species: Definitions & Concepts