Taxonomic and Systematic Characters

A feature (attribute, observable part) of an organism. In practice, a character is a part or attribute of an organism that may be described, figured, measured, weighed, counted, scored, or otherwise communicated by one to another.

Multiple characters that are **homologous** in a series or other form are termed to be part of a **Transformation or Character series**.

For most systematic work, of course, for characters to be useful they must be divisible into two or more states or expressions.

- e.g. no. segments on tarsus of beetle (1,2,3,4)
- e.g. red spot on wing of bird, present or absent.

Mayr - any attribute of a member taxon by which it differs or may differ from a member of a different taxon. In other words, you need differences to detect taxonomic diversity.

<table>
<thead>
<tr>
<th><strong>Mayer</strong></th>
<th><strong>Wiley</strong></th>
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<tbody>
<tr>
<td>Character</td>
<td>Transformation Series</td>
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<td>Character State</td>
<td>Character</td>
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<th><strong>Signifer</strong></th>
<th><strong>Character</strong></th>
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<td>Signifer state</td>
<td>CS</td>
<td>Character</td>
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Some Possible Types of Characters Traditionally Used in Systematic Studies

**Morphological Characters** - structural attributes of organisms at the cellular level or above.

**Karyological Characters** - the structure of chromosomes

**Biochemical Characters** - the structure of or the physical attributes of molecules, including DNA and the products of DNA.

**Physiological Characters** - nonstructural metabolic or related activities which may be quantified.

**Behavioral Characters** - nonstructural, actions taken by organisms that may be described and/or quantified.

**Ecological Characters** - nonstructural, products of the interaction of the organism with its environment (including other organisms).

? **Biogeographic Characters** - geographic range data.
Taxonomic Characters have several functions:

1) They have a **diagnostic aspect** uniquely specifying a given taxon (used during an analytical phase to determine the units of classification).

2) Function as **indicators of relationship** (Synthetic phase of delimiting and ranking of higher taxa).

3) **Key Characters** - easily perceived, low variability, present in preserved materials.

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**Ontogenetic Display of Characters**

Individual organisms display a variety of possible characters in its life span. Juveniles to adult.

**Holomorphology** - The totality of an individuals' characteristics from fertilization to death or its "total form"

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**Semaphorant** - an organism at a particular stage in its life history. e.g. juvenile, lava, adult, medusa, polyp, etc.
Species have holomorphologies - This is the sum of holomorphologies of all individuals belonging to the species. In practice we estimate a species holomorphology by examining specimens representing various life stages, sexes, etc.

Most basic step in systematics involves comparing individual organisms to see if their characters are similar or different. Obviously, this comparison should involve comparable semaphorants.

Quantitative versus Qualitative Characters

Taxonomic and systematic characters may be either quantitative or qualitative.

1. **Quantitative** - those things counted, instrument values, distances, measurements, etc.

2. **Qualitative** - those things basically amenable to description, size, shape, color, etc.

Homologous Characters

Transformation Series: Character
Two characters are homologues if either of the following two conditions are met:

1. they are the same as the character that is found in the ancestor of the two taxa
2. they are different characters that have an ancestor/descendant relationship described as preexisting to novel.

Note: 3 or more characters are homologous if they meet criterion 2.

Relative Plesiomorphy and Apomorphy?

The preexisting character(s) is the **plesiomorphy** (relatively primitive character for the question at hand).

The novel character(s) is the **apomorphy** (relatively derived character for the question at hand).

Determining which of two or more homologues are plesiomorphic vs apomorphic is the process of phylogenetic systematics and is often referred to as *character polarization* or *character argumentation*.

Transformation or Character Series

**Definition:** A group of homologous characters. Below I have provided a series of examples of these types of series, along with relative apomorphy, and indications of homology (as per Criteria 1 and 2 above)
Unordered and Unpolarized Character Transformations

Partially ordered and Polarized Character Transformations

Ordered and Polarized Character Transformations
Criteria for Homology

Homology is an hypothesis to be tested through further experimentation and examination.

*A priori* assessment and hypothesis of Homology  **Followed by**  Phylogenetic Testing of Homology

1. There used to be a general problem with homology.
   a. Theoretical definition of homology was based on descent from a common ancestor.
   b. Actual recognition criteria were based on phenetic similarity.

SO, homology was defined in one way but was tested in another way.

2. Hennig (1966) solved this problem by pointing out the most critical test of homology was a consequence between homology (sensu apomorphy, synapomorphy) and phylogeny.

Thus, homologies are at some level synapomorphies (or autapomorphies) **AND** the phylogenies they are associated with as proper components are "self-illuminating systems!"

As more information is gained through the application of many hypotheses of homology to phylogenetic hypotheses we gain a better understanding about character evolution.

3. Morphological Criteria of Homology

These are criteria for finding characters that are likely to be of interest in a phylogenetic analysis and not criteria for absolutely identifying homologues.

One strategy is to use various morphological criteria to see if characters in question fit these criteria of homology.

This method is not infallable. However, these methods do provide an array of evidence that can be brought to bear on the problem of evaluating characters.

Some cases single morphological observations may refute a hypothesis based on a mistaken observation.

Close inspection of morphology may provide evidence that a synapomorphy that seemingly refutes a phylogenetic hypothesis may actually be represented by two, non-homologous characters.

Remane (1956) provides the most detailed discussion of morphological criteria of homology.

**Criteria for any two or more characters of homology:**

1. Postion
2. Quality of resemblance (special similarity)
3. Continuance of similarity through intermediate species or forms.

**Position.**

There are three areas relative to postion a) topographic, b) geometric, c) relation to other parts of the body. These are self reinforcing and not so easily separated.
Topographic - relationship of one part to another (position of bones, cartesian coordinate system, etc.)

Geometric position - identifying corresponding parts in organisms whose body sizes differ considerably.

- different sizes - but parts correspond to similar geometry
- allometry - formula for this may allow one to recognize corresponding parts that may otherwise be considered as different and thus nonhomologous.

Quality of Resemblance/Special similarity.

This may either reinforce or falsify hypotheses based on positional criteria. However, one would expect that if it passes position criteria then finer structure inspection or outgroup comparisons would corroborate the hypothesis of homology.

Example: Gegenbaur (1873) proposed the endoskeletal shoulder girdle of gnathostomes was the
serial homologue of the gill arches.

Topological position - this seemed reasonable.

However, using the criterion of special similarity the shoulder girdles derived from lateral plate mesoderm and gill arches are derived from neural crest cells. Thus, the criterion here of special similarity (development, ontogeny) identified different embryological origins for these structures which falsified the initial hypothesis of homology.

Example: Vertebral centra of bowfin and teleost fishes. Similar topologically relative to other body parts but their origins are different. Non-homologous structures.
Continuance through intermediate forms

This method can also be used to corroborate or falsify homology.

Examples:

1. Inner ear bones

There are intermediate forms (taxa) known to exist that display the transformation of the second and third inner ear bones.

**Mammalian Inner Ear:** Three inner-ear ossicles

- 1. Stapes - hyomandibular
  
  **Change to Dentary** - squamosal jaw joint

- 2. Quadrate - incus

- 3. Articular - malleus

<table>
<thead>
<tr>
<th>Jaw Articulation</th>
<th>&quot;Reptiles&quot;</th>
<th>Mammals</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Articular/Quadrate</td>
<td>Dentary/Squamosal</td>
</tr>
<tr>
<td>Muscle Insertion</td>
<td>Angular</td>
<td>Dentary</td>
</tr>
<tr>
<td>Quadrat Bone</td>
<td>Part of Jaw Joint</td>
<td>Incus of inner ear</td>
</tr>
</tbody>
</table>
Articular | Part of Jaw Joint | Malleus of inner ear
---|---|---
Angular | Tympanic support / Muscle Attachment | Tympanic Support

2. Scales of bowfin and teleosts.

Both of these groups of fishes have Recent taxa with Cycloid scales. Thus, one may hypothesize that cycloid scales are homologous and represent a synapomorphy to unite bowfin and teleost fishes. However, by observing related but fossil taxa we find that basal members of both groups had rhomboid-type scales. Thus, in both groups a cycloid-type scale evolved independently. Thus, cycloid scales between these groups are not homologous. However, within teleosts cycloid scales are homologous.

Testing homology?

All of these hypotheses of homology are subject to testing through phylogenetic analysis of homology. While it is important to test by similarity, ontogeny, etc. the critical test is congruence or incongruence of a particular hypothesis of synapomorphy with other hypotheses of synapomorphy in an open system of the testing of competing phylogenetic hypotheses.

Phylogenetic Order of Homology

Because of the traditional "problem of homology" (incongruence between theoretical definition and its practical application) some have abandoned an evolutionary definition of homology.

Hanson quote

"Homology is direct (positional and compositional relationships) or derived (serial relationship) similarity of structural and/or functional aspects of different organisms, especially as they are members of different species."

Those who do not abandon the theoretical definition often are led to admit that the theoretical definition has low resolving power to separate homologues from nonhomologues.

The problem with such an admission is that unless some other criterion is brought to bear, the whole question of the ability of an investigator to reconstruct phylogenies becomes open. If homologues must be identified before they can be used to reconstruct phylogenies, and if identity is dependent on criteria of low resolving process, then how can the resultant analysis be anything but very weak?

Wiley (1981) argues that this dilemma is a direct result of exclusive use of induction in framing hypotheses of homology and hypotheses of phylogeny.

Bock (1974) clearly expresses the dilemma of induction - similarities are recorded and via induction, identified as homologues. These inductions of homology can then induce hypotheses of relationships. Thus, the fact of homology is needed to induce phylogenetic relationships.

However, the "problem of homology" does not exist, if, as Hennig identified - *we admit that phylogenetic relationships based on multiple hypotheses of homology serves as a major criterion in the hypothetical-deductive mode of hypotheses testing.*
Hennig even clearly stated that any similarity criterion is secondary to the major criterion of phylogenetic position (ancestor shared with same character).

The truth will never be known for these natural historical systems and our hypotheses of homology because the true tree will never be known.

But, the problem of homology is broken by simply realizing that homologies can be treated as hypotheses which are testable and are tested by other hypotheses of homology and their associated phylogenetic hypotheses.

This reflects the idea that "truth" is approached asymptotically, that is, by testing and retesting in a system of reciprocal illumination. This is a direct appeal to the evolutionary process.

**Types of Characters**

There are many subdivisions that one may imagine as to the types of characters available for taxonomic and systematic studies. Some favor some and not others, some are less biased. Furthermore, sometimes the distinctions between the "types of characters" outlined below is somewhat arbitrary.

However, you must always keep in mind that all characters represent are markers that we believe are heritable and will provide clues for us as to the diversity that exist in nature and the phylogenetic relationships of this diversity!

**Morphological Characters**

- structural attributes of organisms at the cellular level or above.

  Characters of most groups, the traditional characters employed in systematics.

  Usually comprise a series of morphological complexes.

  = array of autogenetically linked morphological characters. In some cases this complex is composed of a number of more-or-less interrelated characters.

  Utility of a particular morphological character varies from group to group and different levels of universality.

To be useful they must be:

1. not subject to wide variation among specimens
2. not readily modified by the environment (ecophenotypic)
3. consistently expressed
4. available in specimens you are using
5. effectively recorded.

Characters that do not vary or vary randomly between groups are of no use to unraveling phylogenetic relationships at that particular level of analysis. However, a character that is invariant
may well have a homologue at another level of universality. It is advisable that someone interested in a particular group should examine previous work done by other investigators to evaluate the usefulness of characters used by previous researchers and 2) look for previously underutilized character.

**External Morphology**

Most characters, useful in keys, etc. may be single or complex

- shape
- size
- color
- color pattern
- counts of various repeated or comparable structures. Flower parts, setae or bristle, scales, fin rays, etc.

**Examples of Color and Color Pattern Characters in Fishes**

Images Copyrighted by Joseph R. Tomelleri and from [http://www.americanfishes.com](http://www.americanfishes.com)
Homologous landmarks for measurements.
Table 2. Variation in lateral scale rows, transverse scale rows, and caudal peduncle scale rows in *Elasmia alabamiae* (N=70) and select samples of *Elasmia zonata* (N=70) from Alabama. Holotype is indicated with asterisk.

<table>
<thead>
<tr>
<th></th>
<th>Lateral Scale Rows</th>
<th>Transverse Scale Rows</th>
<th>Caudal Peduncle Scale Rows</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>27  28  29  30  31 32 33 34 35 36 37 38 39  %  SD</td>
<td>10  11  12  13  14  15  %  SD</td>
<td>15  16  17  18  19  20  21  22  23  24  25  26  27  %  SD</td>
</tr>
<tr>
<td><em>Elasmia alabamiae</em></td>
<td>8  23  21* 10  7  4</td>
<td>5  29  31* 3</td>
<td>4  10  29* 12  8  7</td>
</tr>
<tr>
<td><em>Elasmia zonata</em></td>
<td>2  7  11  15  17 14 6  3  1</td>
<td>11  35  29 1</td>
<td>1  10  15  28 16 5  1</td>
</tr>
</tbody>
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<thead>
<tr>
<th></th>
<th>28.9 1.29</th>
<th>11.5 0.73</th>
<th>17.4 1.81</th>
</tr>
</thead>
</table>

<table>
<thead>
<tr>
<th></th>
<th>34.6 1.73</th>
<th>18.6 0.72</th>
<th>22.9 1.84</th>
</tr>
</thead>
</table>
Principle Component Analysis (PCA, SPCA)
A. Meristics

B. Shape – Males

C. Shape – Females
Internal Morphology

Various techniques used to provide examination of body parts (clean & stain, skeletal preps, sectioning, etc.). Frequent external characters have little information useful to evaluate systematic relationship and you must test internal traits.

Sexual Dimorphism

Frequently species differ sexually in characters so that the mature epiphenotypes appear different. May occur only during breeding season.

Embryonic Character

Characters have an ontogeny and this may be continuous or discontinuous where there are discrete body forms which undergo metamorphosis. Because of these changes we must use equivalent semophorants. Some ontogenetic characters are useful in establishing relationships. Particular ontogenetic pathways may be useful for relationships. However, there can be problems with these types of characters if one assumes terminal addition.

<table>
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<tbody>
<tr>
<td>Taxon 2: A --&gt; B</td>
<td>Taxon 5: A --&gt; B --&gt; C</td>
<td>Taxon 8: A --&gt; C --&gt; D</td>
</tr>
</tbody>
</table>

Chromosomes

Chromosomal changes may accompany or provide speciation reduced fecundity, invisible hybrids, sterile.

Three levels are analyzed commonly for chromosomes:
**Alpha Karyology** - Number and size of chromosomes

**Beta Karyology** - Number and location of centromere (where spindle fibers attach) to allow for comparison of chromosomes between species.

**Gamma Karyology** - Number, centromere & stains for various regions of chromosomes to identify homologous parts of chromosome

Chromosome number expressed as haploid or diploid

Morphology - pair homologous pairs in illustrations (photos)

compare number of metacentrics, telocentrics, acrocentrics

Bandaging - particular stains identify particular regions of DNA. These bands allow you to determine homologous areas of a chromosome.
Biochemical and Molecular Characters  
(should be treated equally with other traits)

**Two types of gene homologies:**

**Orthologous genes** - homologous genes that are the result of speciation. Changes in genes reflect the history of the group. (alpha hemoglobin)

**Paralogous genes** - Homologous genes that are the result of gene duplication. They evolve independently during history of speciation. They both may reflect the history of a group. (alpha & beta hemoglobin)
Isoenzyme data

1. Allozyme characters

Evaluates variation in proteins on the basis of molecular weight or change. Presumptive mutations or changes of genes (producing proteins) will alter the protein. Underestimates variation two-three times. Some enzymes are less variable than others. Had its origin with population genetics.

Restrictions - Two different alleles may code for the same protein. Electromorphs may not
be homologous.

Electrophoresis detects only those amino acid substitutions which affect electrohoretic
mobility. Under estimates differences between species.

Restricted to water soluble proteins encoded by structural genes.

Electrophoretic data frequently used to evaluate degree of divergence with similarity and
divergence (distance) indices (S) (D). Some have used these distance or similarity values to
determine whether something is a species. Must assume equal rates of evolution.

Many populations vary = .71 à 1.0

Between populations = .37 à .79

Electrophoretic data also can be decoupled from other characters. May have divergence in one and
not the other. In general, there is asymmetry in data. Low values of electromorph similarity may
corroborate decisions that two things are distinct while high values do not necessarily indicate same
species.

Electrophorh data are treated like other data. Locus is the transformation series (character), alleles at
a locus = character (or character state).
Table 1. Allele Frequencies at the Gpi-A and Gpi-B Loci. Locality abbreviations are those listed in the Materials and Methods section.

<table>
<thead>
<tr>
<th>Species (locality)</th>
<th>Gpi-A</th>
<th>Gpi-B</th>
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<tbody>
<tr>
<td></td>
<td>75</td>
<td>100</td>
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<tr>
<td><strong>N. pilibrasi</strong></td>
<td></td>
<td></td>
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<tr>
<td>Arkansas Dr.</td>
<td></td>
<td></td>
</tr>
<tr>
<td>P1</td>
<td>—</td>
<td>1.00</td>
</tr>
<tr>
<td>P2</td>
<td>0.05</td>
<td>0.95</td>
</tr>
<tr>
<td>P3</td>
<td>—</td>
<td>1.00</td>
</tr>
<tr>
<td>P4</td>
<td>—</td>
<td>1.00</td>
</tr>
<tr>
<td>P5</td>
<td>—</td>
<td>1.00</td>
</tr>
<tr>
<td>White Dr.</td>
<td></td>
<td></td>
</tr>
<tr>
<td>P6</td>
<td>—</td>
<td>0.97</td>
</tr>
<tr>
<td>P7</td>
<td>—</td>
<td>0.97</td>
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<tr>
<td>P8</td>
<td>—</td>
<td>1.00</td>
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<tr>
<td>P9</td>
<td>—</td>
<td>1.00</td>
</tr>
<tr>
<td>P10</td>
<td>—</td>
<td>1.00</td>
</tr>
<tr>
<td>P11</td>
<td>—</td>
<td>1.00</td>
</tr>
<tr>
<td>P12</td>
<td>—</td>
<td>1.00</td>
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<tr>
<td><strong>N. zonatus</strong></td>
<td></td>
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<tr>
<td>Missouri Dr.</td>
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<tr>
<td>Z1</td>
<td>—</td>
<td>—</td>
</tr>
<tr>
<td>Z2</td>
<td>—</td>
<td>0.03</td>
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<tr>
<td>Z3</td>
<td>—</td>
<td>—</td>
</tr>
<tr>
<td>Z4</td>
<td>—</td>
<td>—</td>
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<tr>
<td>Z5</td>
<td>—</td>
<td>—</td>
</tr>
<tr>
<td>Black Dr.</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Z6</td>
<td>—</td>
<td>—</td>
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<tr>
<td>Z7</td>
<td>—</td>
<td>—</td>
</tr>
<tr>
<td>Z8</td>
<td>—</td>
<td>—</td>
</tr>
<tr>
<td>St. Francis Dr.</td>
<td></td>
<td></td>
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<tr>
<td>Z9</td>
<td>—</td>
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</tbody>
</table>
2. Isozyme Characters
3. Tissue Specificity

Figure 13 Diagram of isozyme patterns expected in homozygotes and heterozygotes for enzymes of common subunit composition. Modified from Harris and Hopkinson (1976). Ratios of intensity of isozyme activity in heterozygotes are indicated. See Table 6.

Amino Acid Sequencing
Most direct method. Time consuming but provides information on actual changes at specific points that the DNA changed.

Break protein down with enzyme into fragments. Each fragment is then analyzed by a protein sequence.

Table 10.1 of Wiley shows what the position 9-20 of cytochrome C look like for a variety of mammals.

Problems

1. Proteins may vary in length between species ad you need to be comparing homologous positions.

2. Figure out minimum number of AA substitutions. Computer algorithms are available to do this.

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**DNA hybridization**

Technique used to measure similarities of two strands of DNA

Uses the double helix and similarity of the complimentary strands

1. Can separate by denaturing and heating

2. Parts will rebind (renature), depending upon similarity when you warm up again.

3. Amount is directly proportional to the amount of difference between the strands.

Problems

1. Cannot identify homologies.

2. Strictly a similarity-based method.

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**DNA Restriction**

Restriction endonucleases will cut a strand of DNA at a particular nucleotide sequence. Match up points of prescribed homology and the cleavage points are the characters.
Label 3' end with $^{32}$P

(A) RE digestion
Enzyme 1

(b) Electrophoresis
Detection

**Partial digests**

- $^{32}$P $\ a + b + c$
- $^{32}$P $\ a + b$
- $^{32}$P $\ a$

**Complete digest**

- $^{32}$P $\ a + b + c$
- $^{32}$P $\ a + b$
- $^{32}$P $\ a$

Electrophoresis
Detection

Lane S: Size standard, all fragments end-labeled

Increasing digestion (1–4)
DNA Sequencing

Actual sequencing of DNA (nuclear, mitochondrial, or chloroplast)

This is a relatively expensive process. The learning curve is quite steep for manual sequencing. New, automated sequences are available in some laboratories.

With the development of the polynuclease chain reaction (PCR) the cost has decreased significantly. This system uses 2 primer sequences bordering the sequence that you are interested in and allows for the generation of millions of copies of the target piece of DNA. This can also be done with DNA cloning methods and usually the DNA is much cleaner.

Manual DNA Sequencing
Denature DNA to produce single-stranded template (only one strand shown)

Add primer and anneal

Divide into four samples, each with dATP, dCTP, dGTP, dTTP (at least one dNTP radioactively labeled) and DNA polymerase

Separate fragments by electrophoresis and visualize by autoradiography

Sanger Sequencing Method
Figure 1  Synthesis of both strands of a DNA molecule proceeds by action of polymerases (shown as ovals), which add bases complementary to the template strand. Synthesis is always in the 5' → 3' direction. Polymerases will begin synthesis wherever they find a stretch of double-stranded DNA just "upstream" (meaning in the 5' direction) of a stretch of single-stranded DNA.

Manual DNA Sequencing Rig and Product

GATC GATC

Alignment of Sequences

Taxa  Cytochrome B sequences
Automated Sequencing