All members of a monophyletic taxon share a common ancestor whose developmental pathway was modified to produce descendant morphologies.

Haeckel, E. 1899 - originally a physician became professor of comparative anatomy, later professor of zoology, a chair established for him at Jena. Haeckel was deeply influenced by Darwin's "Origin...", and became "the apostle of Darwinism in Germany." Also coined term "Ecology."

"I established the opposite view, that this history of the embryo (ontogeny) must be completed by a second, equally valuable, and closely connected branch of thought - the history of race (phylogeny). Both of these branches of evolutionary science are, in my opinion, in the closest causal connection; this arises from the reciprocal action of the laws of heredity and adaptation... 'ontogenesis is a brief and rapid recapitulation of phylogenesis, determined by the physiological functions of heredity (generation) and adaptation (maintenance)."

Rejection of recapitulationist ideas in the early part of this century, however, the study of links between development and evolution was relatively neglected until Ontogeny and Phylogeny was published by Gould in 1977. Gould presented his own ideas on heterochrony (evolutionary changes in the timing of development), presenting a unified view of neoteny, recapitulation, paedogenesis, retardation, progenesis, etc. Basic idea is that all heterochrony is a result of acceleration or retardation of different developmental processes (growth, sexual maturation, morphological changes, etc.).

Heterochrony involves three kinds of evolutionary changes in the timing of development: changes in rate, changes in onset time, and changes in offset time. Each change can either be an increase or a decrease, thus six kinds of pure heterochrony can be defined: neoteny (slower rate), acceleration (faster rate), post-displacement (late onset), pre-displacement (early onset), progenesis (early offset) and hypermorphosis (late offset). Paedomorphosis (underdevelopment in descendant adults) is caused by the first of each preceding pair. Peramorphosis is the opposite pattern with opposite processes. (McKinney & McNamara, 1991).
Ontogeny enters into our consideration of phylogenetics at three levels:

(1) Polarization of character state transformations (augmentation or primary).

(2) Assessment of homology.

(3) The recognition and exploration of heterochronic (and heterotopic) patterns in the ingroup.

Heterotopy - change in spatial patterning of ontogenetic processes (another Haeckel term).

Heterochrony is of interest because produces novelties constrained along ancestral ontogenies, giving rise to parallelisms between ontogeny and phylogeny. Heterotopy can produce new morphologies along trajectories different from those of the ancestors. As discussed above, heterochrony has an analytical formalism that virtually precludes the recognition of heterotopy (Zelditch & Fink 1996).

Hennig recognized both the problems and advantages of ontogeny and coined term semaphoront - an organism at a particular stage in ontogeny. Also considered it another augmentation to sister taxon in determining polarity.

The quantification of these patterns usually involves constructing ontogenetic trajectories; vectors or curves that describe shape and size change through development. Although differences in these trajectories have been equated with developmental processes (i.e. progenesis, neoteny, acceleration, hypermorphosis, etc., trajectories confound the mechanisms that create morphology with the results of those processes (i.e., shape or size change at different times in ontogeny). Thus, heterochronic and heterotopic shifts cannot be considered processes or causal in producing novel morphologies, but rather the outcomes of changes in mechanisms that do. Although heterochrony and heterotopy do not necessarily produce novel morphologies, the construction of ontogenetic trajectories serves as a starting point for examination of generative mechanisms.

Lindberg & Guralnick (2003)
Homology of structures  (Ponder & Lindberg, in prep)
Smith (2001)

Table 1. The terminology of growth heterochrony as presented by Gould (1977) and Alberch et al. (1979). Paedomorphosis refers to cases in which the outcome is less relative growth; peramorphosis to cases in which the outcome is more relative growth; cases of gigantism and dwarfism do not include relative growth. See also Figure 1 for examples of graphic representation of these phenomena. Note the explicit characterization of all types of heterochrony as either recapitulatory or reverse recapitulatory phenomena, a concept that arose with Gould, and was included in the characterization of Alberch et al. (1973). Note also that only limited types of changes are characterized by growth heterochrony approaches. The terms used to describe growth heterochrony (e.g. neoteny, hypermorphosis, etc.) are by and large global terms, not particularly useful for the kinds of issues discussed in sequence analysis. These terms are not discussed in this paper.

<table>
<thead>
<tr>
<th>Heterochronic phenomenon</th>
<th>Gould (1977) characterization</th>
<th>Alberch et al. (1979) control parameter</th>
<th>Relative size change</th>
<th>Phylogenetic effect</th>
</tr>
</thead>
<tbody>
<tr>
<td>Progenesis</td>
<td>Size/shape relation constant, early maturation</td>
<td>Early growth offset</td>
<td>Paedomorphosis</td>
<td>Reverse recapitulation</td>
</tr>
<tr>
<td>Neoteny</td>
<td>Shape slowed relative to size and maturation</td>
<td>Decrease shape growth rate</td>
<td>Paedomorphosis</td>
<td>Reverse recapitulation</td>
</tr>
<tr>
<td>Postdisplacement</td>
<td>Later growth onset</td>
<td>Paedomorphosis</td>
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<tr>
<td>Proportional dwarfism</td>
<td>Size slowed relative to shape and maturation</td>
<td>Decrease size growth rate</td>
<td>Paedomorphosis</td>
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</tr>
<tr>
<td>Hypermorphosis</td>
<td>Size/shape relation constant, late maturation</td>
<td>Later offset growth</td>
<td>Peramorphosis</td>
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</tr>
<tr>
<td>Acceleration</td>
<td>Shape increased relative to size and maturation</td>
<td>Increases shape growth rate</td>
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<td>Predisplacement</td>
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<tr>
<td>Proportionate gigantism</td>
<td>Size increased relative to shape and maturation</td>
<td>Increase size growth rate</td>
<td>Peramorphosis</td>
<td>Recapitulation</td>
</tr>
</tbody>
</table>

Organisms are not "heterochronic." Dissociation of developmental pathways.
32 Cells
Lindberg & Guralnick (2003) – Developmental characters

Characters 7-9 — this cell lineage produces prototroch and posttrochal ectoderm; the first stomatoblast contributes to the formation of the foot and shell gland (Dictus and Damen 1997).

- **7** — median number of cells present at formation of 2q cell lineage (4th division): 16=0 and 12=1.
- **8** — median number of cells present at formation of 2q' cell lineage (5th division): 32=0, 24=1.
- **9** — median number of cells present at formation of 2q" cell lineage (6th division): 60=0, 52=1, 44=2, 41=3, 37-38=4 and 32=5.

Characters 10-11 — this cell lineage produces ectomesoderm and posttrochal ectoderm (Dictus and Damen 1997).

- **10** — median number of cells present at formation of 3q cell lineage (5th division): 20=0, 23-24=1, and 32=2.
- **11** — median number of cells present at formation of 3q' cell lineage (6th division): 54=0, 60=1, 48=2, 40-41=3, and 36=4.