Morphological Data II – Ontogeny & Structure of Animals

All members of monophyletic taxa share a common ancestor whose developmental pathway has been modified to produce descendant morphologies.

But at what level or stage does morphology reveal patterns of relatedness?

1. Gametes - gastropod sperm - polyplacophoran eggs

2. Early cell division patterns - Spiral & Radial cleavage patterns, polar lobes, unequal vs. equal cleavage.

3. Larval forms - Planula, trochophore, Veligers, Instars, direct development

Hennig recognized the both the problems and advantages of ontogeny and coined term semaphoront - an organism at a particular stage in ontogeny. Also augmentation criteria.

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.), and that it is these processes that are important rather than their results.

Ontogeny enters into our consideration of phylogeny 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.

In addition to heterochrony, heterotopic or changes in spatial patterning of ontogenetic processes is also important. While heterochrony is of interest in part because it can produce novelties constrained along ancestral ontogenies, and hence result in parallelism between ontogeny and phylogeny, heterotopy can produce new morphologies along trajectories different from those that generated the forms of ancestors (Haeckel, 1866).
Modification of ontogenies involves both deletions and insertions. Nonterminal characters -- characters that occur in the ontogenetic sequence before a terminal character.

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.

*Xyloplax turnerae* is a deep-sea starfish with an enigmatic body plan. This beautiful and strange animal was once thought to be a newly discovered class of echinoderm but molecular and morphological cladistic analysis has shown that it evolved from the juveniles of its ancestors (Janies, 1999)
Fig. 5. Cleavage in *Limax* (A) and *Crepidula* (B) where the first and second polar bodies have formed at different sites. In both of these species a giant second polar body (2\textsuperscript{nd}PB) has formed. A\textsubscript{1}. Two-cell stage in which the furrow goes through the site where the second polar body was given off. A\textsubscript{2}. Four-cell stage in which the axis of both furrows goes through the site where the second polar body was given off. Both embryos are viewed from the side. The clear cytoplasm containing the nuclei is adjacent to the second polar body. B\textsubscript{1}. Two-cell stage in which the furrow goes through the first and second polar bodies. B\textsubscript{2}. Four-cell stage in which the axis of both furrows goes through the site where the first polar body was given off. Both embryos viewed looking down on the first polar body. The clear cytoplasm containing the nuclei is adjacent to the first polar body. A is adapted from Guerrier [1968]; B is adapted from Conklin [1917].
Fig. 1. Representations of cell lineages. (A) Node-based view of the strictly bifurcating cell lineage tree. The splitting, leading to cells of 2A and 1a, happen at the same node, the fourth. (B) Relative timing view of the strictly bifurcating cell lineage tree. The length of branches represents the length of time between splitting events. Thus, 2D splits when there are 14 cells in the embryo and 1d' at 18 cells. Numbering and lettering of cells is as described in the text. Abbreviations: First to fifth represent the number of nodes needed to follow to get back to the first cell; 2c to 18c represents number of cells comprising the embryo, from two to 18.
TABLE 14-1 Types of Postembryonic Development and Larvae in Decapods

<table>
<thead>
<tr>
<th>Group</th>
<th>Postembryonic Development</th>
<th>Larvae</th>
</tr>
</thead>
<tbody>
<tr>
<td>Suborder Dendrobranchiata Family Penaeidae</td>
<td>Slightly metamorphic Nauplius→protozoa→mysis→megalopon (zoea) (postlarva)</td>
<td></td>
</tr>
<tr>
<td>Family Sergestidae</td>
<td>Metamorphic Nauplius→elaphocaris→acanthosoma→megalopon (protozoa) (zoea) (postlarva)</td>
<td></td>
</tr>
<tr>
<td>Suborder Pleocyemata</td>
<td>Metamorphic Protozoa→zoea→parva (postlarva)</td>
<td></td>
</tr>
<tr>
<td>Infraorder Caridea</td>
<td>Metamorphic Protozoa→zoea→parva (postlarva)</td>
<td></td>
</tr>
<tr>
<td>Infraorder Stenopodidea</td>
<td>Metamorphic Phyllosoma→puerulus, nisto, or pseudobaccus (zoea) (postlarva)</td>
<td></td>
</tr>
<tr>
<td>Infraorder Palinura</td>
<td>Metamorphic Mysis→postlarva (zoea)</td>
<td></td>
</tr>
<tr>
<td>Infraorder Astacidea</td>
<td>Slightly metamorphic Zoas→glaucotoe in pagurids, grimothea (postlarva)</td>
<td></td>
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<tr>
<td>Infraorder Anomura</td>
<td>Metamorphic Zoas→megalopon (postlarva)</td>
<td></td>
</tr>
<tr>
<td>Infraorder Brachyura</td>
<td>Metamorphic Zoas→meagalopon (postlarva)</td>
<td></td>
</tr>
</tbody>
</table>

HETEROCHRONY

PAEDOMORPHOSIS
- Progenesis
- Neoteny
- Post-displacement
  (earlier offset)
  (reduced rate of morphological development)
  (delayed onset of growth)

PERAMORPHOSIS
- Hypermorphosis
- Acceleration
- Pre-displacement
  (delayed offset)
  (increased rate of morphological development)
  (earlier onset of growth)

Figure 2-3. The hierarchical classification of heterochrony. Modified from McNamara (1986a).

Figure 2-4. The six major types of heterochrony in terms of size versus age plots. From McKinney (1988a).
The ancestral trajectory would be located between $y$ and $x$. 