Morphological data II -- ontogeny & structure of animals

Understanding ontogeny is important in systematics as it expand our source of characters
1. Ontogenetic intermediates are useful for suggesting otherwise unsuspected homologies because an origin from the same embryological precursors is strong evidence for primary homology recognition.
2. Diversity of semaphorants increases the chances that independent processes individuate features and so provide more independent evidence of history.
3. The explanation of homology requires understanding the mechanisms that constrain and individuate features during ontogeny and phylogeny. Sometimes all or part of development does recapitulate phylogeny, but there is no "biogenic law."
4. Wagner's (1994) "biological homology" (developmental similarity) and "historical homology" (synapomorphy or features shared due to common ancestry) was one way to separate these.

Constraint -- Supposed conservative nature of early developmental steps, internal selective environment or physical/chemical constraints. There is some tendency for development to have some conservative aspects. In its most extreme form it can be a kind of "Orthogenesis", i.e. biological variation results in new forms, always or usually along same path and natural selection is a weak force (Grehan & Ainsworth,1985).

Degeneracy -- developmental paths can be highly degenerate -- the same kind structure can be produced from a variety of different genetic and/or epigenetic events. Degeneracy relaxes the stringency of developmental constraints or at least points to different levels of constraint (or selection). The regulative aspects of development provides mechanism for evolutionary changes that would otherwise lead to lethal forms. Degenerate systems can still produce synapomorphies.

Atavisms -- Recurrence of ancient structures, throw-back of "bygone days" sometimes called "latent synapomorphies." What appear as multiple origins of structures within a clade in otherwise unrelated taxa that are proposed to be the result of a *propensity* to develop or lose a structure due to some underlying developmental mechanism. (How to turn ugly data into beautiful hypotheses (Platnick?)). But there is a logical polarity to what might be expected to be expressed during ontogeny, e.g. we would expect to find that some marsupials have embryonic "egg bursters" (and they do) but we would never expect a developing lizard to have nipples.

The origin or increasing complexity of ontogeny:
Early Eukaryotic Cells living independently –> Colonies of Cells –> Multicellular Organisms –> Sexual systems

Significant or complex ontogentic systems really only begin with multicellular organisms. Cell specialization and even the simple (passive) difference in the environment of inside vs. outside layers of cells creates a more complex development. Bilaterian body plan diversification has occurred primarily through changes in developmental regulatory networks rather than the genes themselves, which evolved much earlier (Erwin et al. 1997).

Heterotopy, Heterochrony and Sequence Heterochrony act to change ontogeny. Table from Schlichting & Pigliucci (1998).

	Ancestral ontogenetic sequence A→B→C→D		
	Descendant ontogenetic sequences		
Transformation	Initial	Middle	Terminal
Addition	X→A→B→C→D	A→B→X→C→D	A→B→C→D→X
Deletion	B→C→D	A→B ——→D	A→B→C
Novel substitution	X→B→C→D	A→X→C→D	A→B→C→X
Reciprocal substitution	B→A→C→D	A→C→B→D	A→B→D→C
Repatterning	W→X→Y→Z	A→B→X→Y→Z	

Example: (see K.K.Smith 2001). Relative to Eutherians, Marsupials have a very short interuterine period, short organogenisis and the postnatal individuals are clearly more altricial. However, the Marsupial neonate has disproportionally developed forelimbs and oral apparatus. Focusing on head structures and the central nervous system, various marsupials and placentals were studied for development and an acceleration of the head structures was found in Marsupials based on comparative methods looking at relative growth. A mosaic of developmental events was found but this is difficult to analyze given a time and size/shape based approach.

Phylogenetic method- Using event-based rather than size and shape, *per se*, multi state sequence pairs scored for events and taxa, e.g if event X occurred before event Y; character state 0, if X and Y occurred at the same time then state 1, and character state 2 if X occurred after Y. All pairs of relative occurrence can be scored as apposed to being relative to a single chosen point (i.e. n hours after event x).

	a	b	c	d			ab	ac	ad	bc	bd	cd
a	-	0	1	2		Taxon 1	0	1	2	1	1	0
b		-	1	1		Taxon 2						
c			-	0		Taxon 3						
d				-								

Some important differences between plants and animals

●Animals have specialized germline tissues, spermatogonia and oogonia, which diverge from somatic cells early in embryogenesis.

●Plant somatic cells remain more or less totipotent throughout the life of the plant. Animal cells tend to become terminally differentiated early in development, and can undergo genetic rearrangements which destroy totipotency..

●Animals have much more limited regenerative powers. Thus the interest in stem-cell research The totipotency of plant cells, less fixed cell fates during vegetative growth results in a more continuous program of differentiation throughout the lifetime of the plant. In animals, once an organ or tissue has formed it is more or less fixed.

●Animal cells migrate through the embryo during development. Plant cells are constrained by their cell walls to stay where they are. Differentiation must be carried out without migration.

●Animals go through a single iteration of the developmental program while plants can go through many iterations, often responding to the environmental. -vegetative propagation without a gametophyte stage.

●Post embryonic development in vertebrates essentially means size increase, functional change or initiation, but relatively little new developments. Allometric growth (unequal growth in part of an organism in relation to its whole) and heterochrony both explain the phenotypic changes.

●Discrete states of characters and/or semaphorants can be very difficult to delimit. When is an adult an adult? Quantity of mature sperm/eggs; development of genitalia; initiation of breeding?

Many invertebrates have a distinct series of stages often involving major metamorphosis defined by ecdysis. This often involves forms that are primarily suited for feeding and growth (thus an emphasis on mouth and head structures and rather generalized bodies) in immatures and with an emphasis on dispersal and mating (leading to an emphasis on genitalia and locomotory structures). In parasitic adult forms and sessile marine animals this may be reversed for locomotory structures. These various forces acting on different semaphoronts should help to provide more independent characters for phylogenetic analysis.

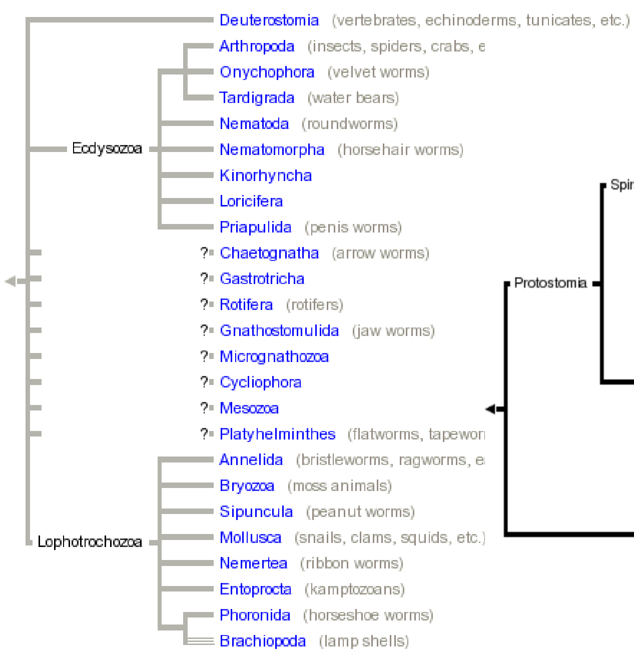
Larval forms may be generalized. For many beetles groups distinctive as a clade in the adult form
(~genera in most cases) have virtually identical larvae, distinguished by number an position of a few hairs or pores.

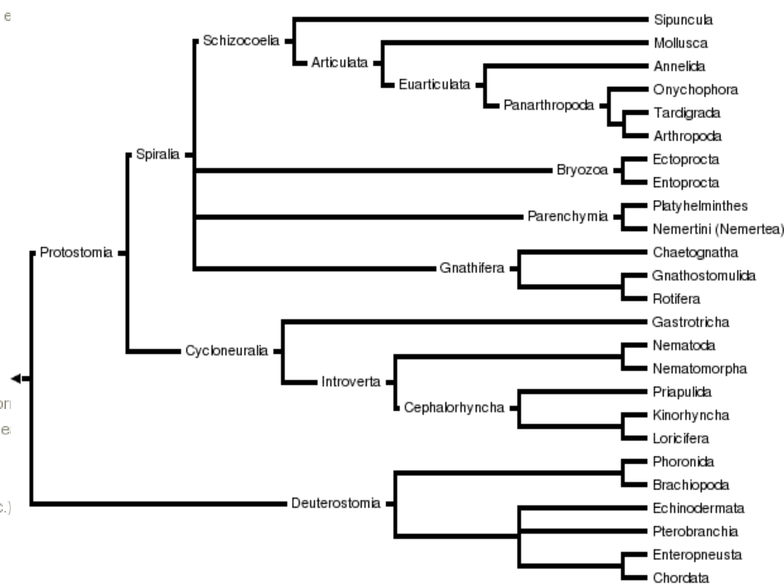
●Subtle shifts in regulatory gene expression, cell fate specification and cell migration all act to establish distinct developmental pathways. e.g. in echinoderms planktotrophic larvae and yolk-feeding larvae switch about 20 times with significant differences in eggs and patterns of early cell cleavage (A.B. Smith 1997).

Single or multiple origins of the coelom? Most ideas on coelomic origins are from early studies in embryology and all share the premise that there was a single origin.

Protostomes (Annelida, Mollusca, Arthropoda) -spiral cleavage, blastopore becomes mouth...

Deuterostomes (Chordates, Echinoderms)- radial cleavage, blastopore becomes anus...
Ecdysozoa - Lophotrochozoa - Deuterostomia





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