Macroevolution of Organismal Modularity and Integration

Gunther J. Eble
Bioinformatik, Universität Leipzig

What is macroevolution?

- evolution at and above the species level

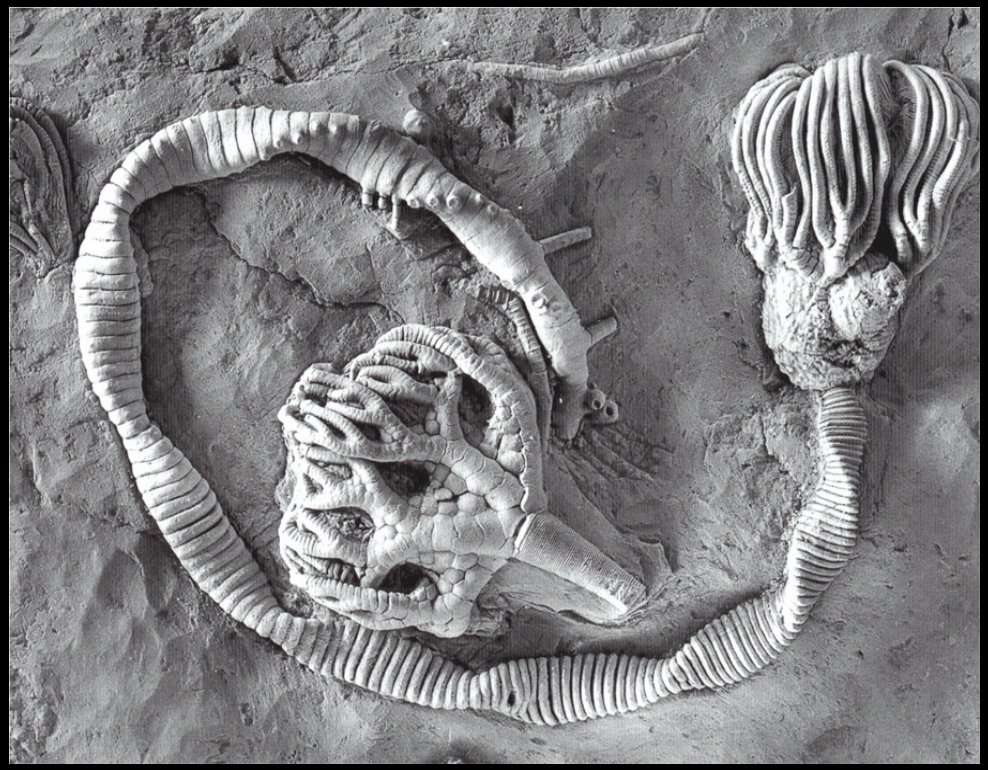
- large-scale phenotypic evolution

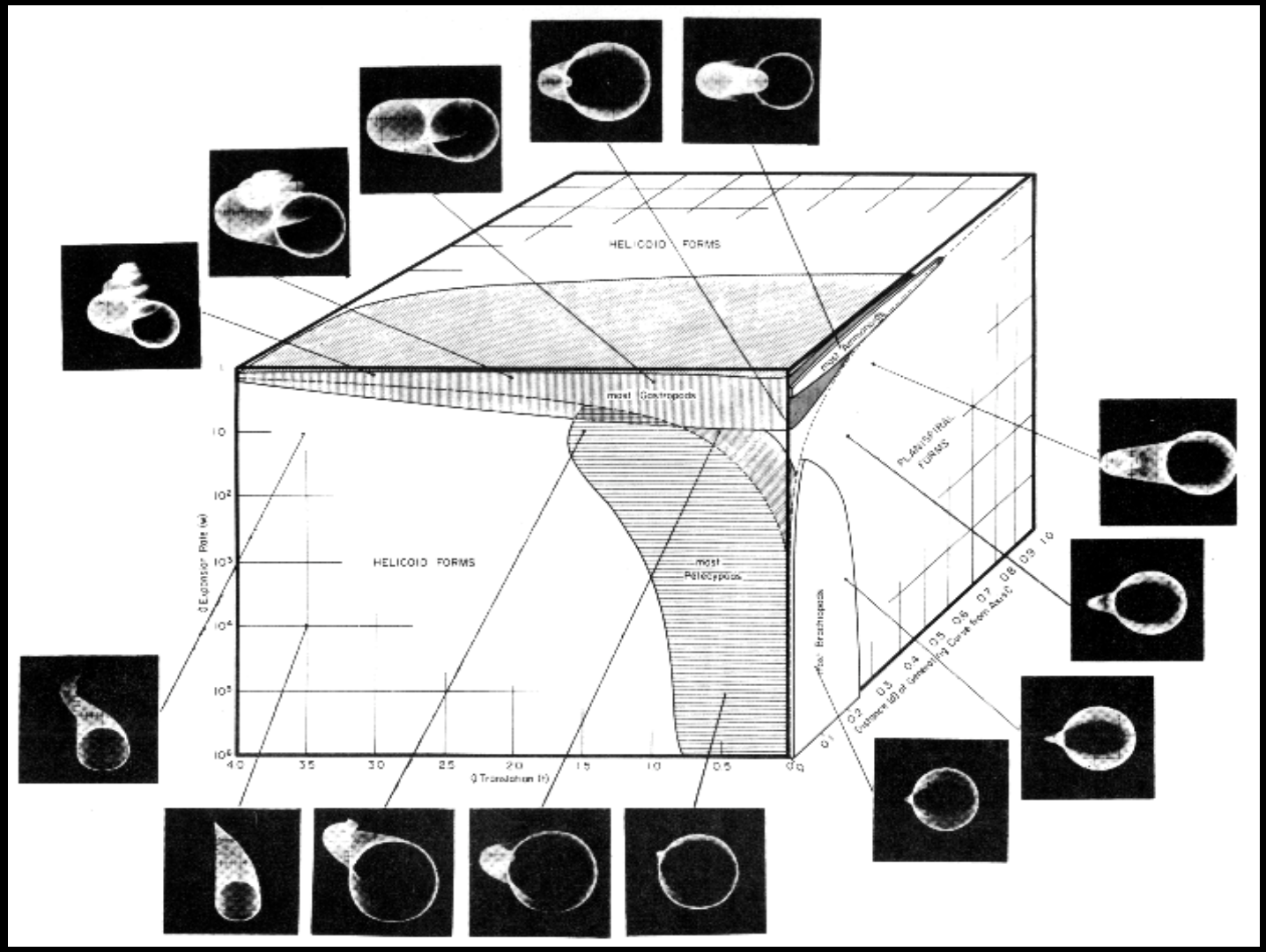
- among-species evolution

Macroevolutionary biology: the study of the origin and sorting of macroevolutionary variation

- *diversity, origination, and extinction*
- *evolutionary radiations*
- *innovations*
- *morphological disparity*
- *constraints on form and patterning of morphospace*
- *structure of the genotype-phenotype map*
- *selectivity of and recovery from extinction*
- *phylogenetic history and trends*
- *community structure*
- *size and allometry*
- *complexity*

Bits and Pieces: isolated yet integrated




HELICOID FORMS
most Gastropods
most Ammonoids
PLANISPIRAL FORMS
HELICOID FORMS
most Pelecypods
most Brachiopods
Log Ecological Rate (w)
Log Translation (T)
Distance (d) at Generating Curve from Axis (r)

Organismal Modularity: definition and theoretical justification

- Definition: Dissociability of phenotypic wholes into parts
- Justification: organizational and variational semi-independence of morphological organization; morphology itself is involved in the generation of new morphological elements late in ontogeny; morphostatic mechanisms (including physiological homeostasis, regeneration, and repair) rely on information conveyed by morphological states.

Organismal Modules: causal roles

- as raw material for combinatorial diversification
- as the substrate for changes in integration
- as units of hierarchical sorting and selection
- modularity as a property of clades

Needed: rigorous documentation of modules and of modularity in a macroevolutionary context.

Metrics of organismal modularity

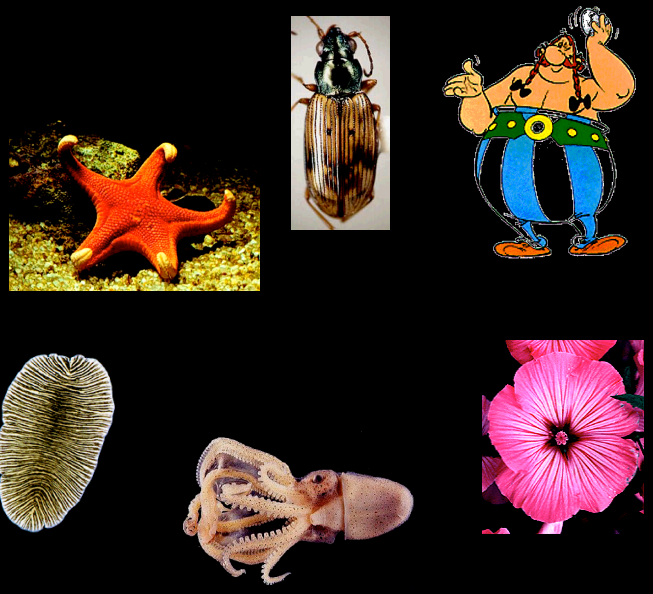
- Conceptually and statistically a number of explicit metrics can be advanced, but operationally some proxy metrics appear most useful:

  - number of parts, constructional elements, characters
  - within- and among-module integration
  - disparity

Disparity: the concept

Sample 1

Sample 2



Taxonomic diversity: sample 1 = sample 2 = 6 spp.

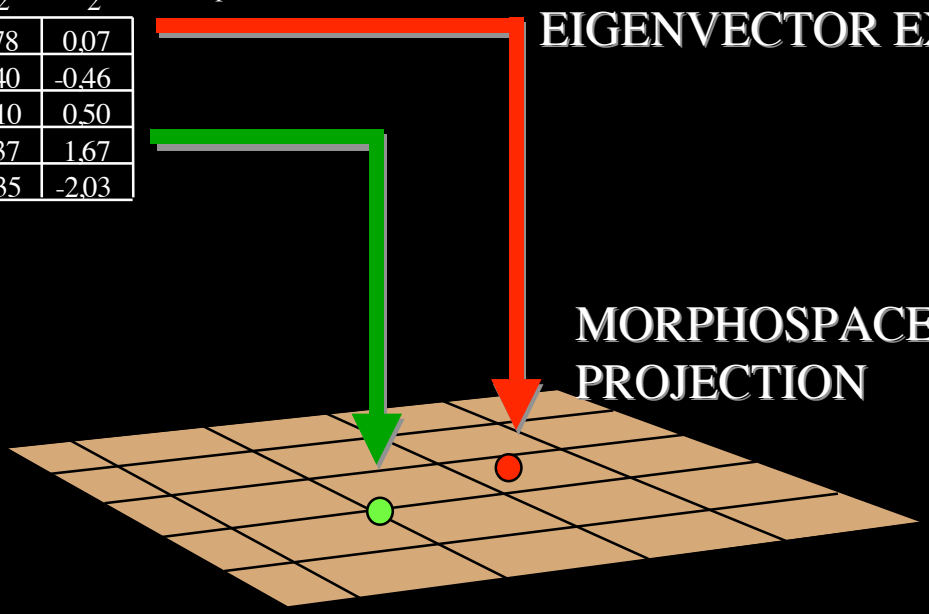
Morphological disparity: Δ sample 1 << Δ sample 2

Empirical morphospaces

DATA MATRIX:
n SPECIES x p VARIABLES

	X_1	Y_1	Z_1	X_2	Y_2	Z_2	... p
Species A	-0.28	-0.80	0.58	0.13	-0.78	0.07	
Species B	0.76	0.41	0.10	0.08	0.40	-0.46	
Species C	-0.73	-1.13	-0.56	-0.31	-1.10	0.50	
Species D	-1.71	4.45	1.07	-0.83	4.37	1.67	
Species E	1.56	-0.36	1.18	1.18	-0.35	-2.03	

:
:
n



Measures of disparity

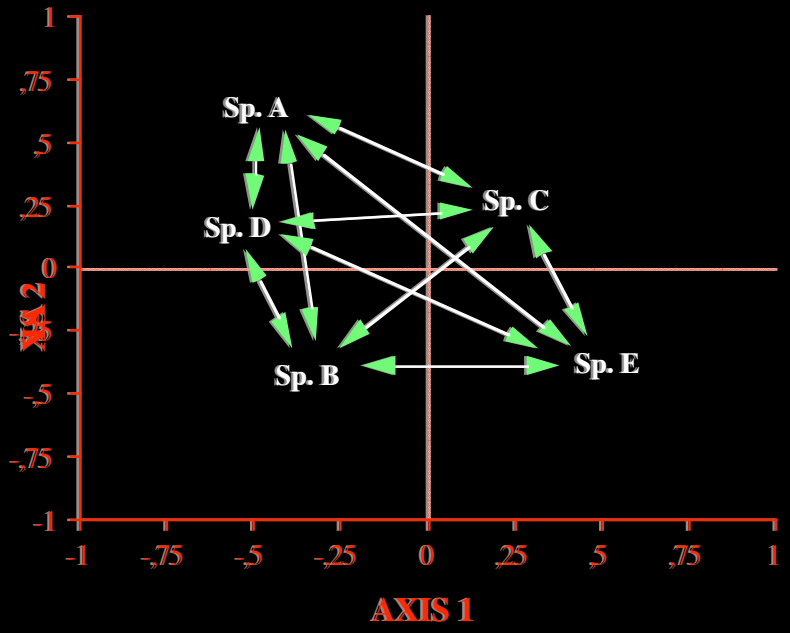
Disparity = dispersion in morphospace

- $\sum \sigma^2_n$ (sum of univariate variances)

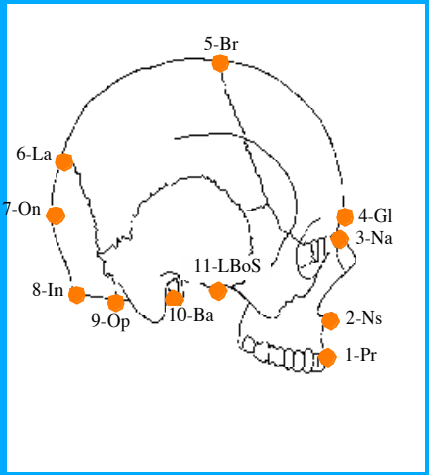
- $\sum \lambda_n$ (sum of eigenvalues)

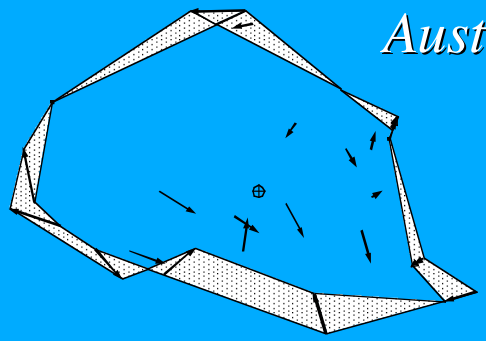
- mean Euclidean distance

- Procrustes distance



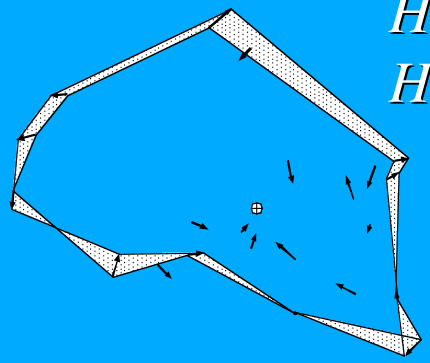
Modeling divergence between species and between genera





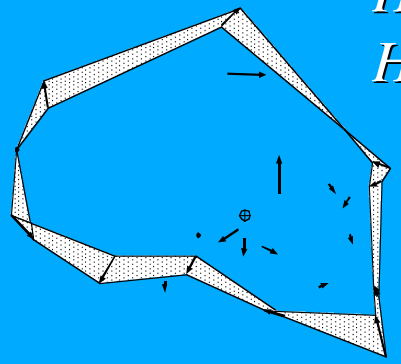
Australopithecus to Homo

$$\Sigma\Delta^2 = 1.08$$



Homo ergaster to Homo erectus

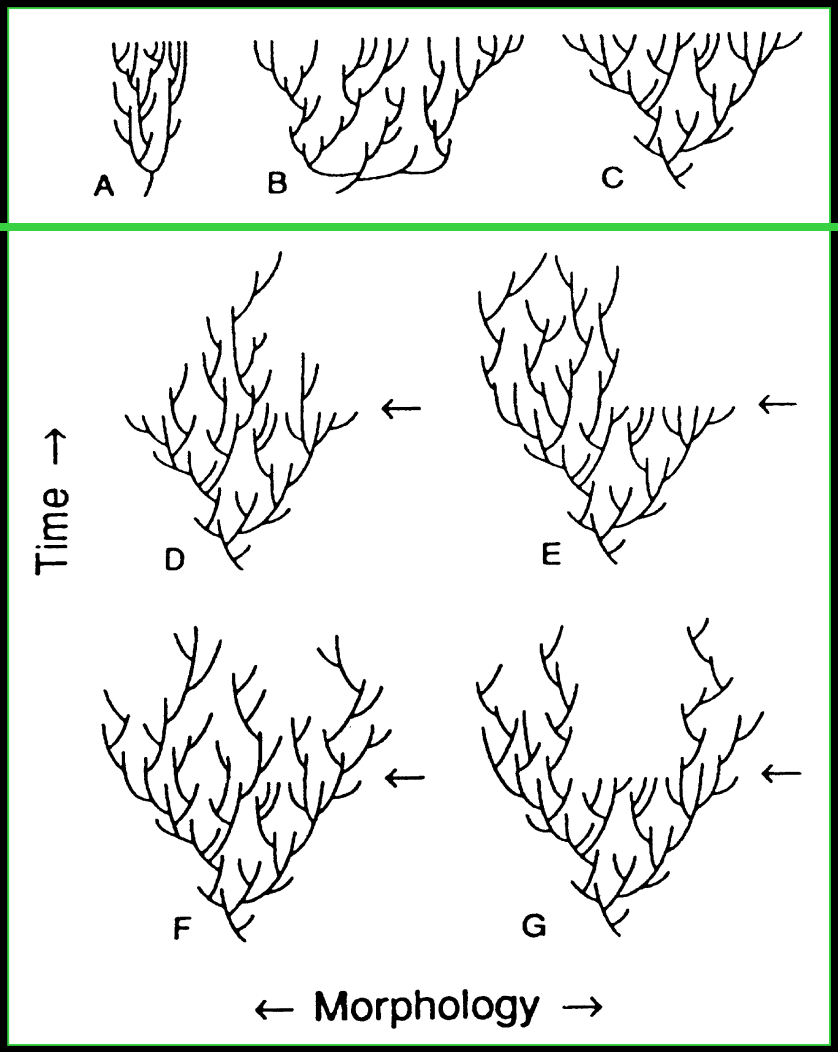
$$\Sigma\Delta^2 = 0.37$$



Homo erectus to Homo sapiens

$$\Sigma\Delta^2 = 0.58$$

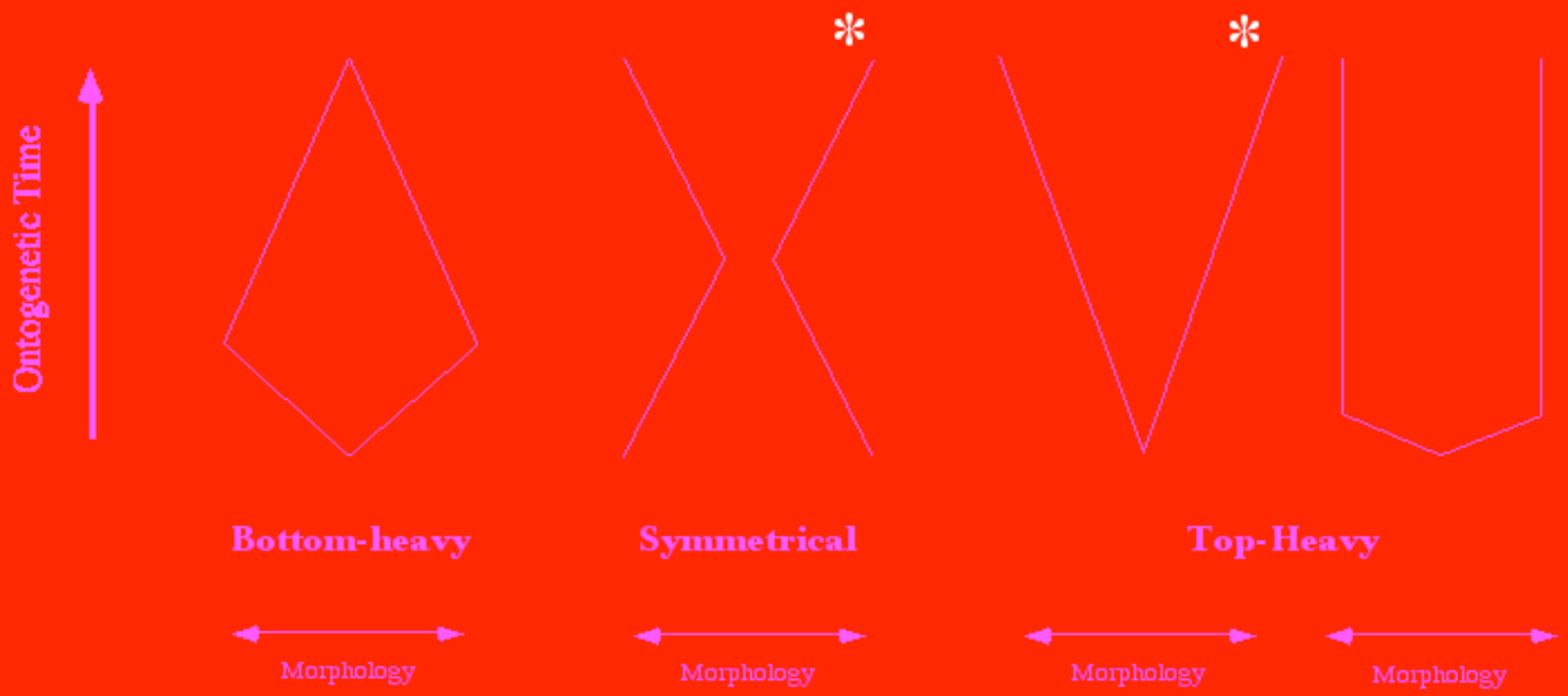
Disparity in Paleontology
- Alternative Clade Shapes in Geological Time -



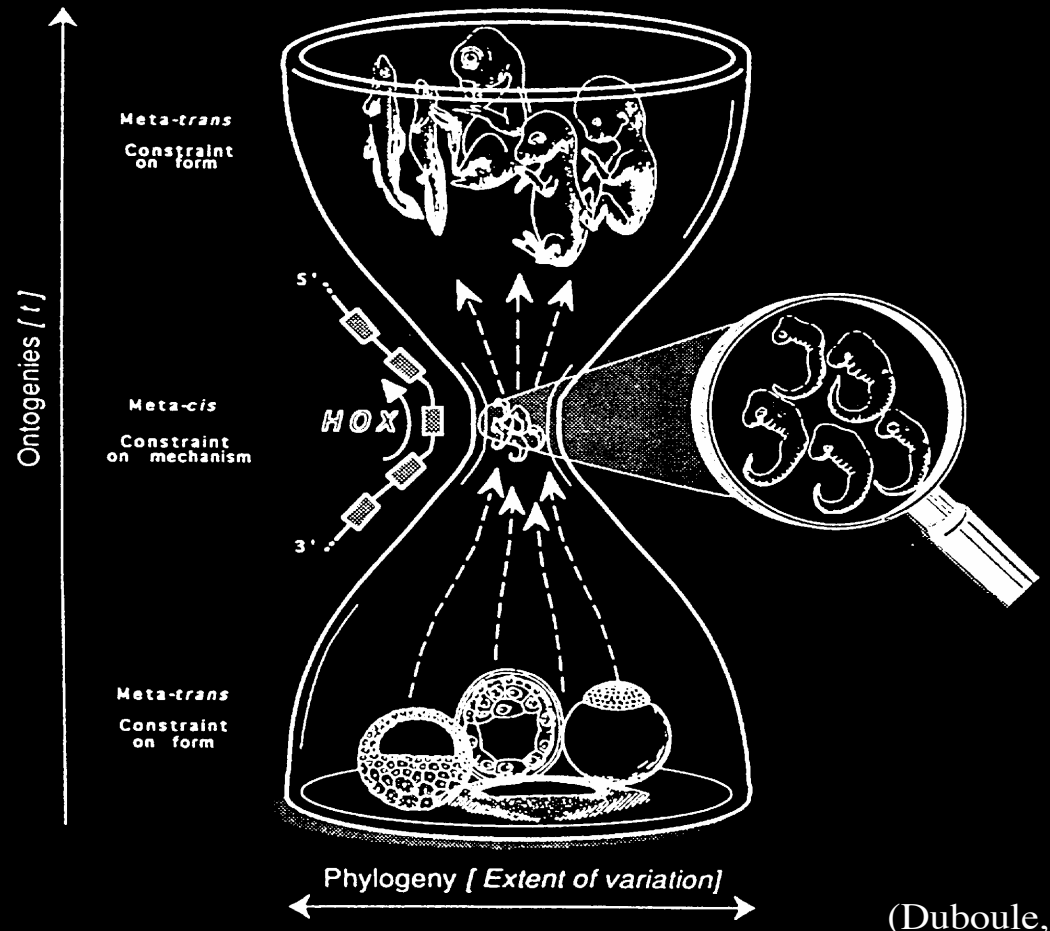
Morphological diversification

Morphological extinction

Disparity in Ontogeny
- Alternative Clade Shapes in Ontogenetic Time -



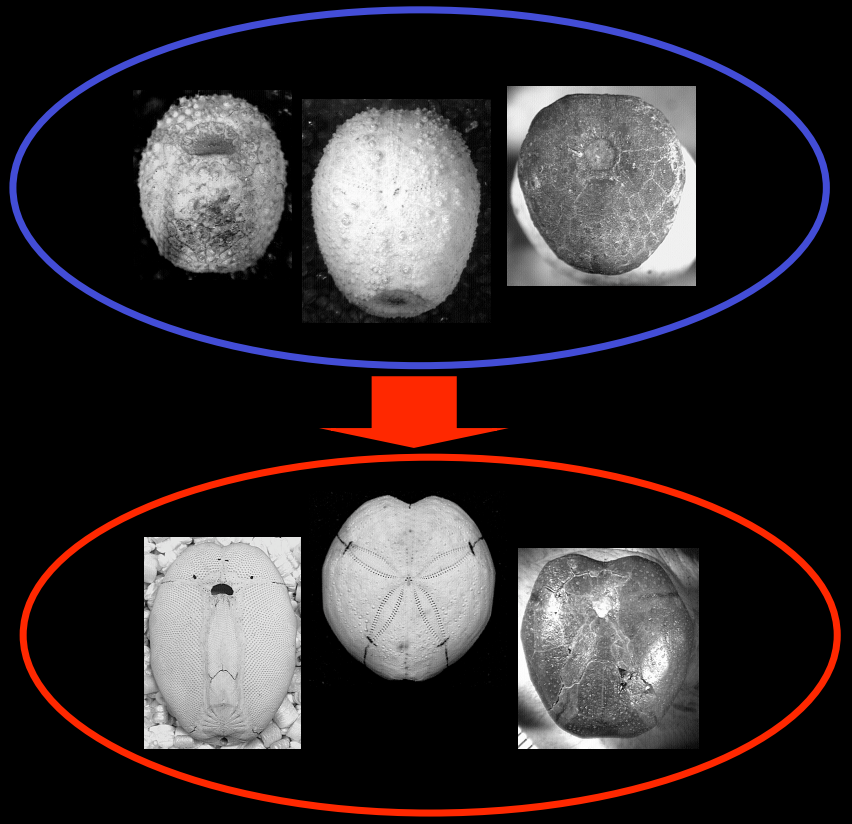
THE HOURGLASS MODEL

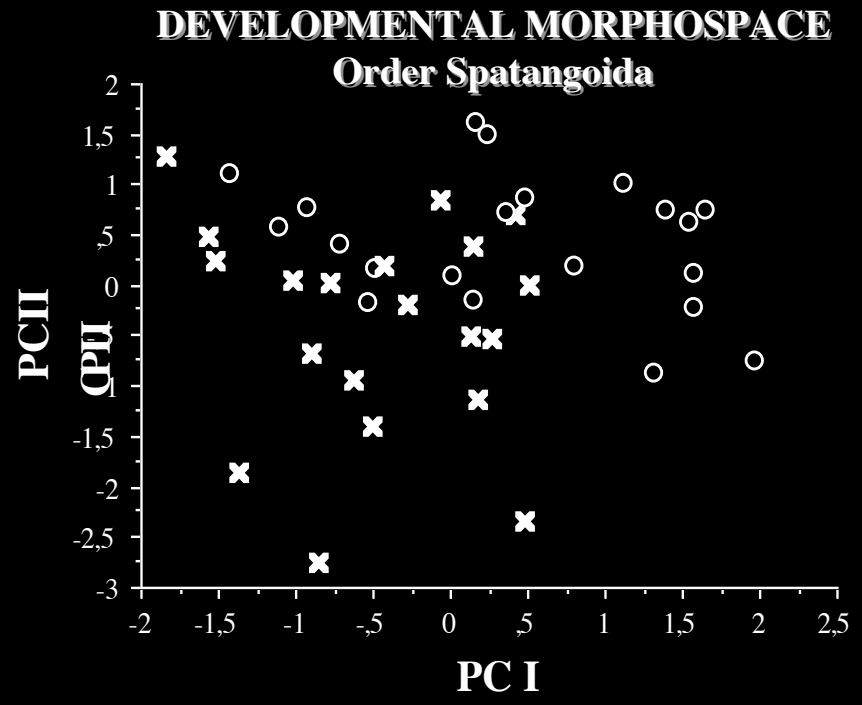


(Duboule, 1994)

Juvenile disparity

Adult disparity





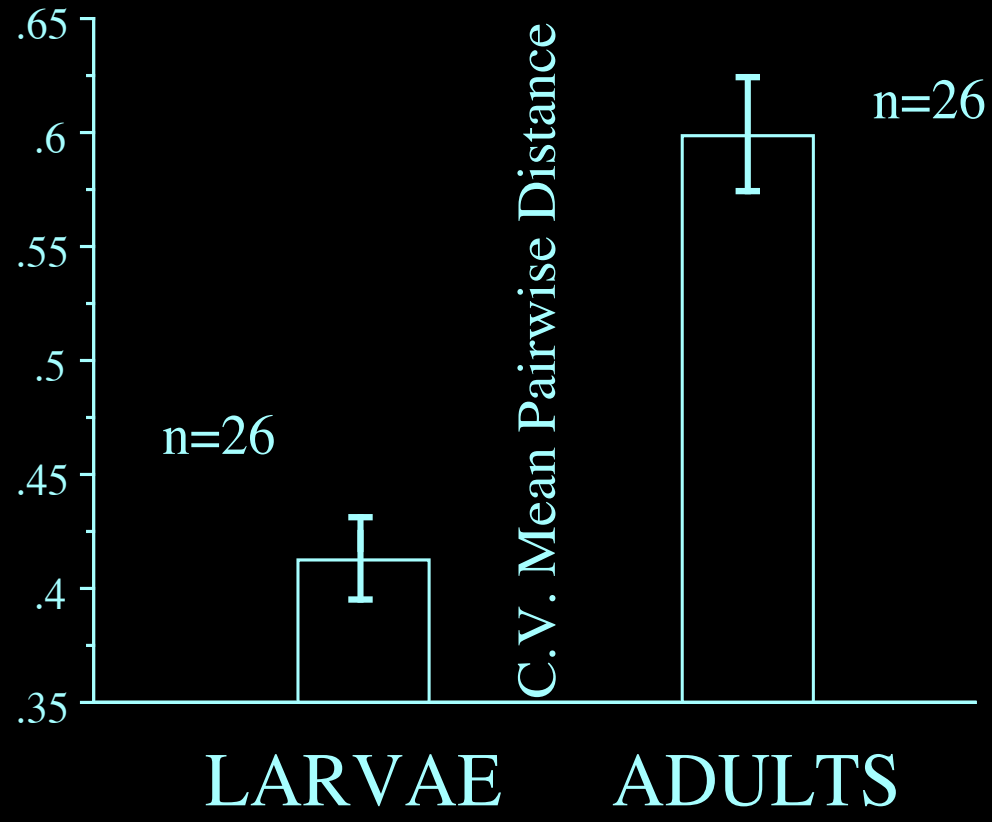
O	ADULT
X	JUVENILE

Variance

	PCI	PCII
O	1.06	0.43
X	0.54	1.15

$p<0.015$ $p<0.019$
(bootstrap z-test)

Disparity of Larvae X Disparity of Adults



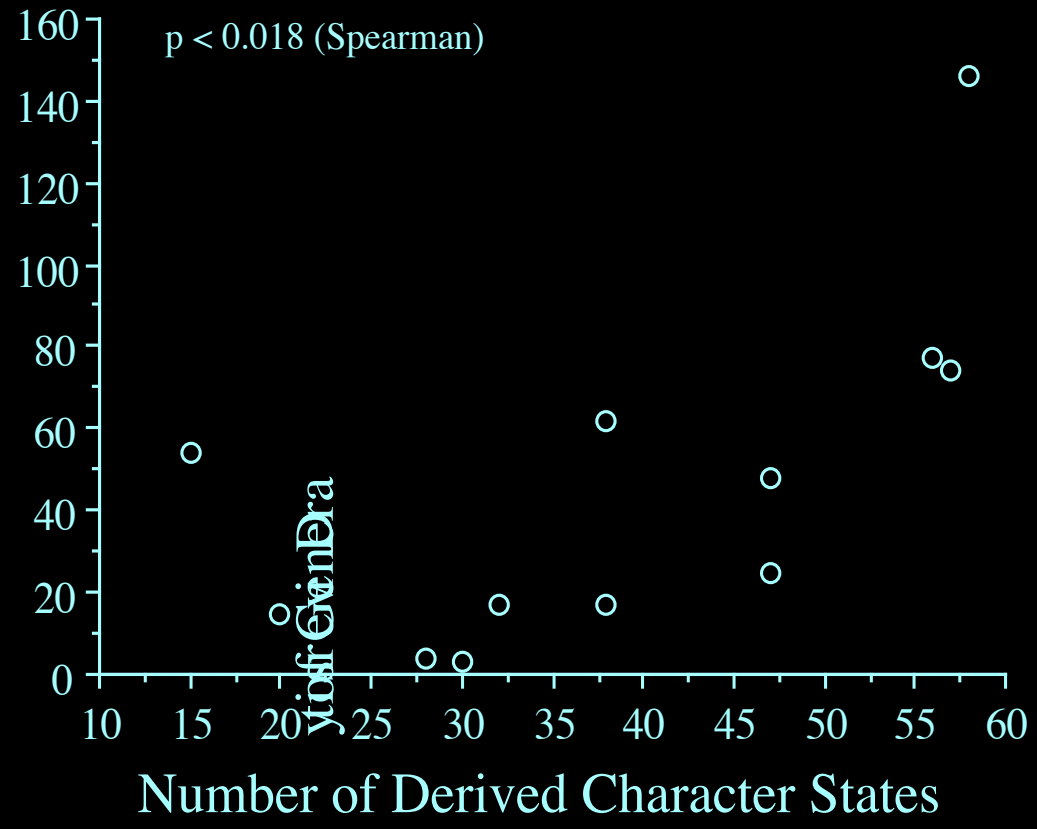
Error bars based on 1000 bootstrap replications

Echinoderms as model organisms for the study of modularity and integration

- Many plates and other skeletal elements
- Many types of plates
- Distinct body regions and growth fields

Issues to be addressed: relationship with diversity, size, evolvability, trends, and context-dependence

Modularity and Taxonomic Diversity



Discordances between diversity and disparity

DIVERSITY

DISPARITY

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XXXXXXXXX

XXXX

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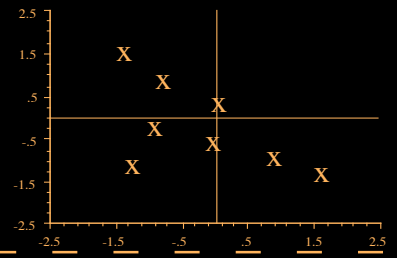
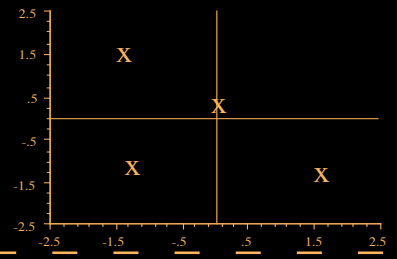
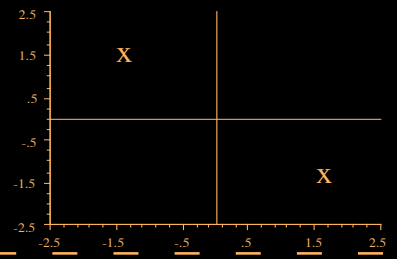
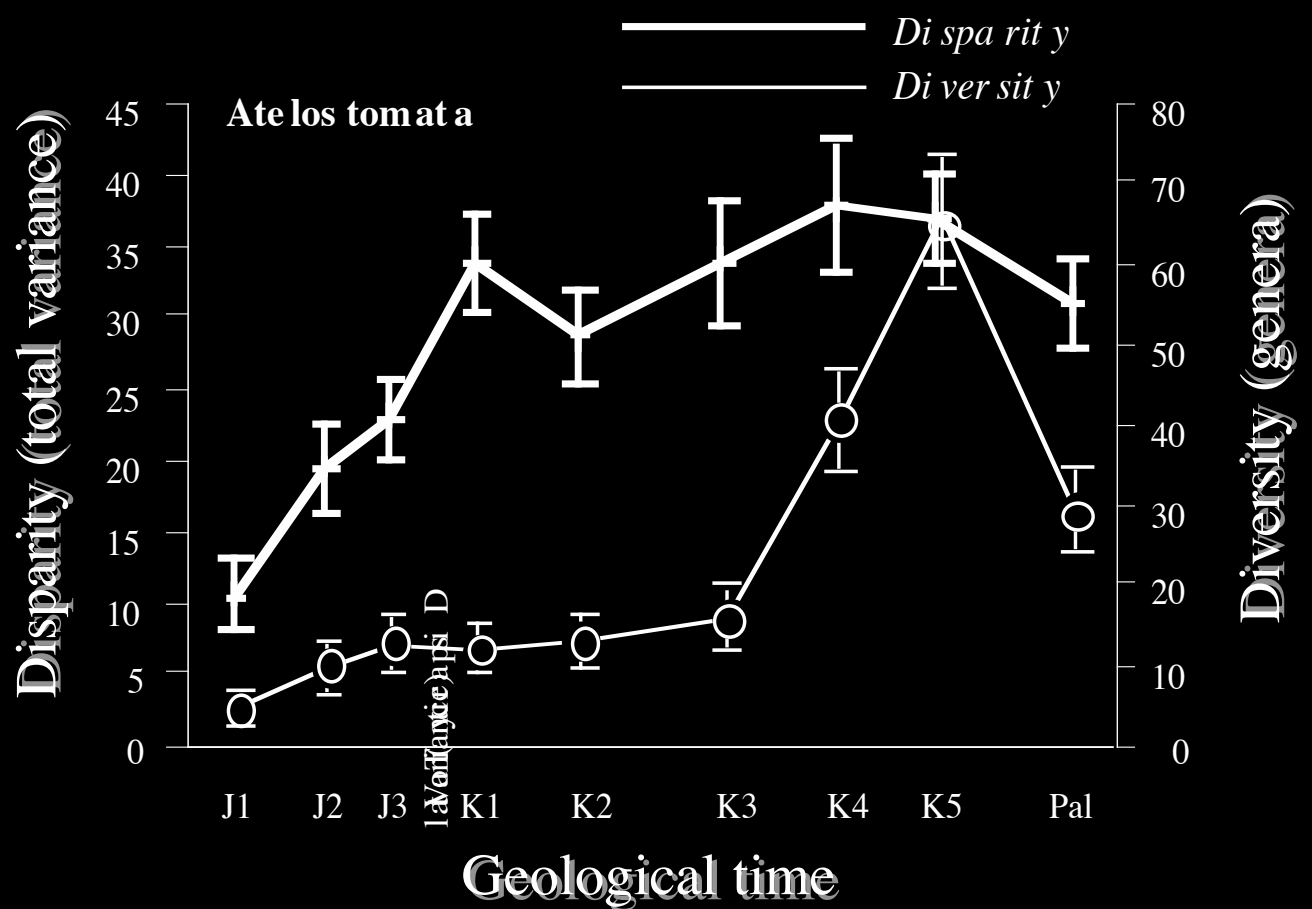


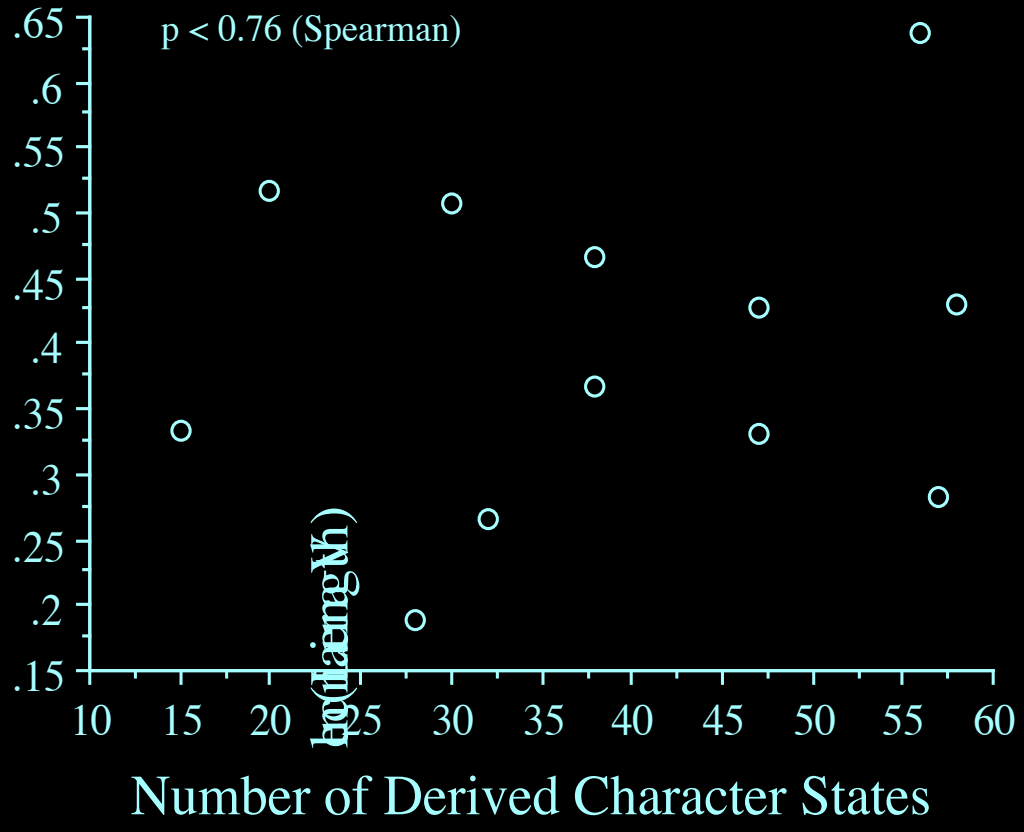




Sea urchin disparity and diversity



Modularity and Body Size Variance



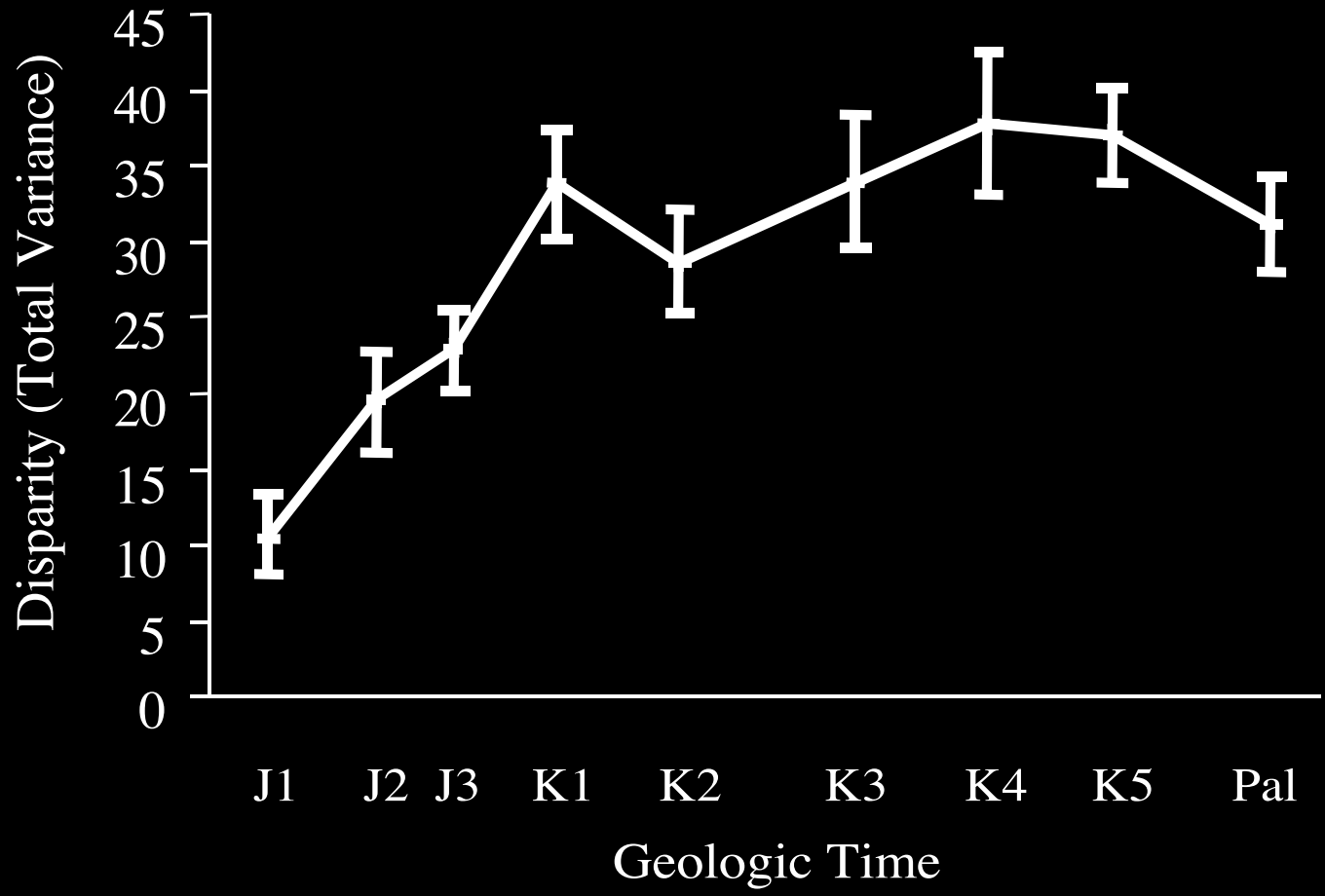
Modularity and Evolvability

In microevolution: “ability to sometimes produce improvement (Wagner and Altenberg 1996)

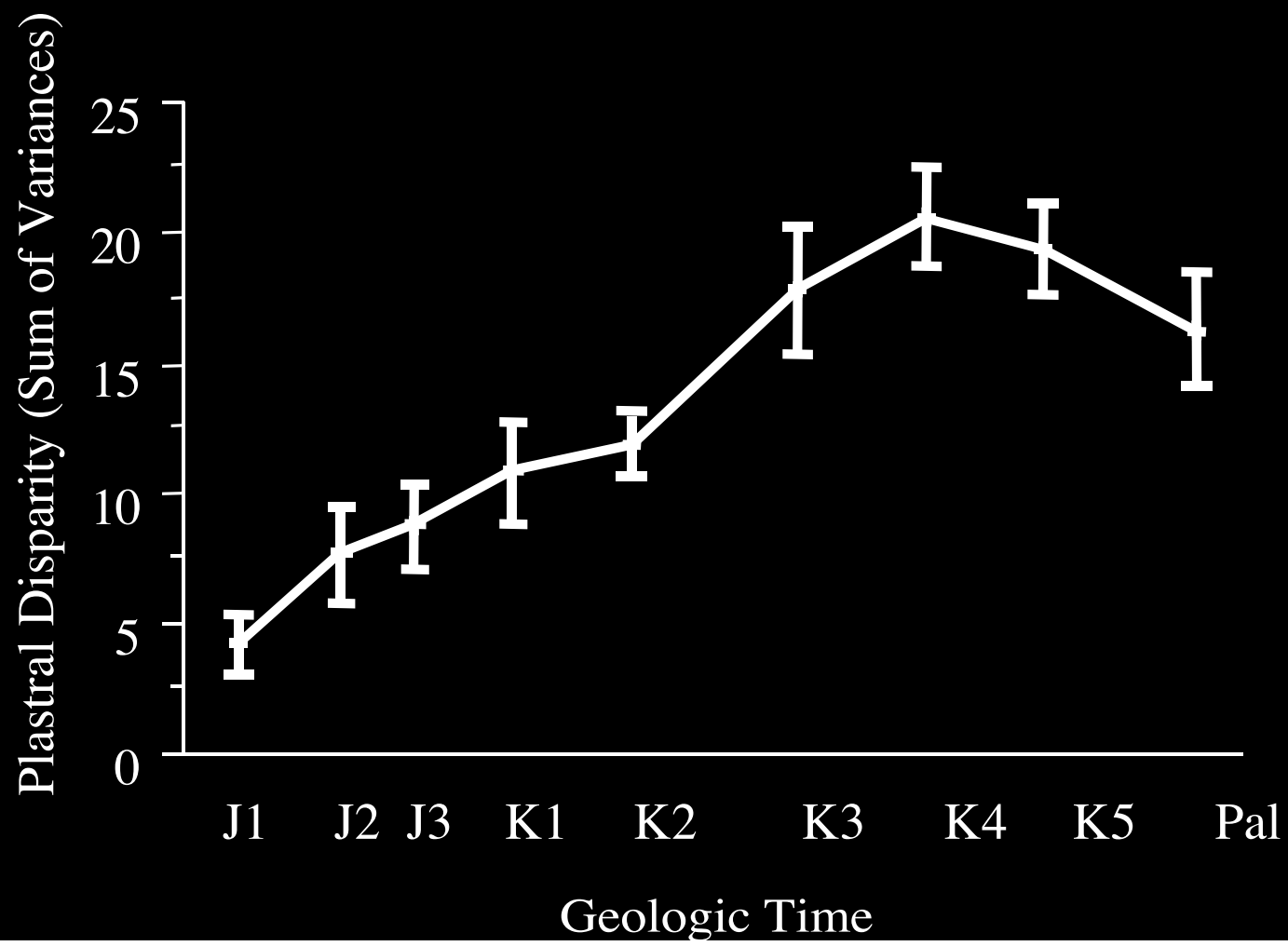
In macroevolution: “ability to sometimes produce substantial morphological change”

Evolvability Modularity Integration Disparity

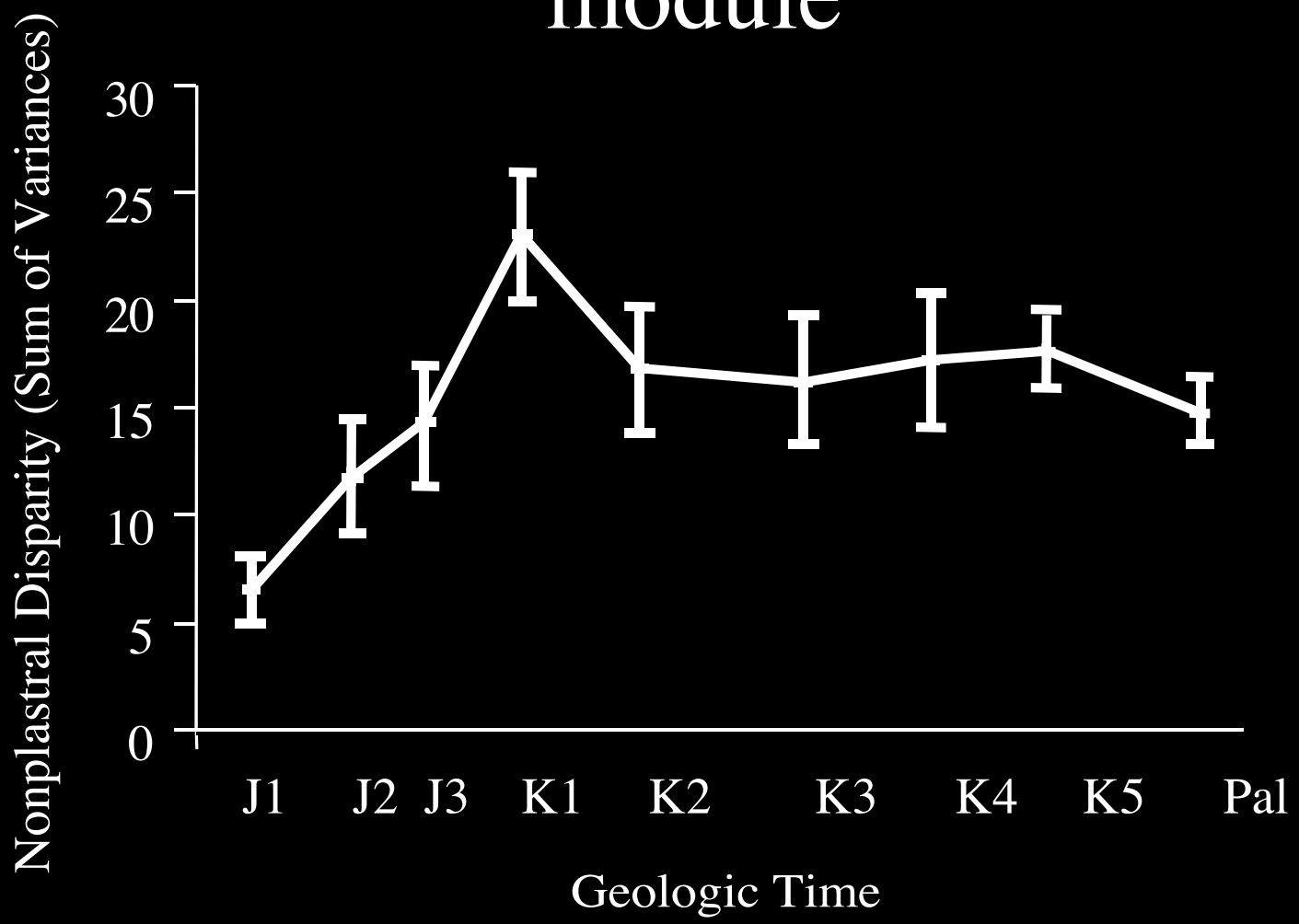
Integration among plastral and nonplastral modules



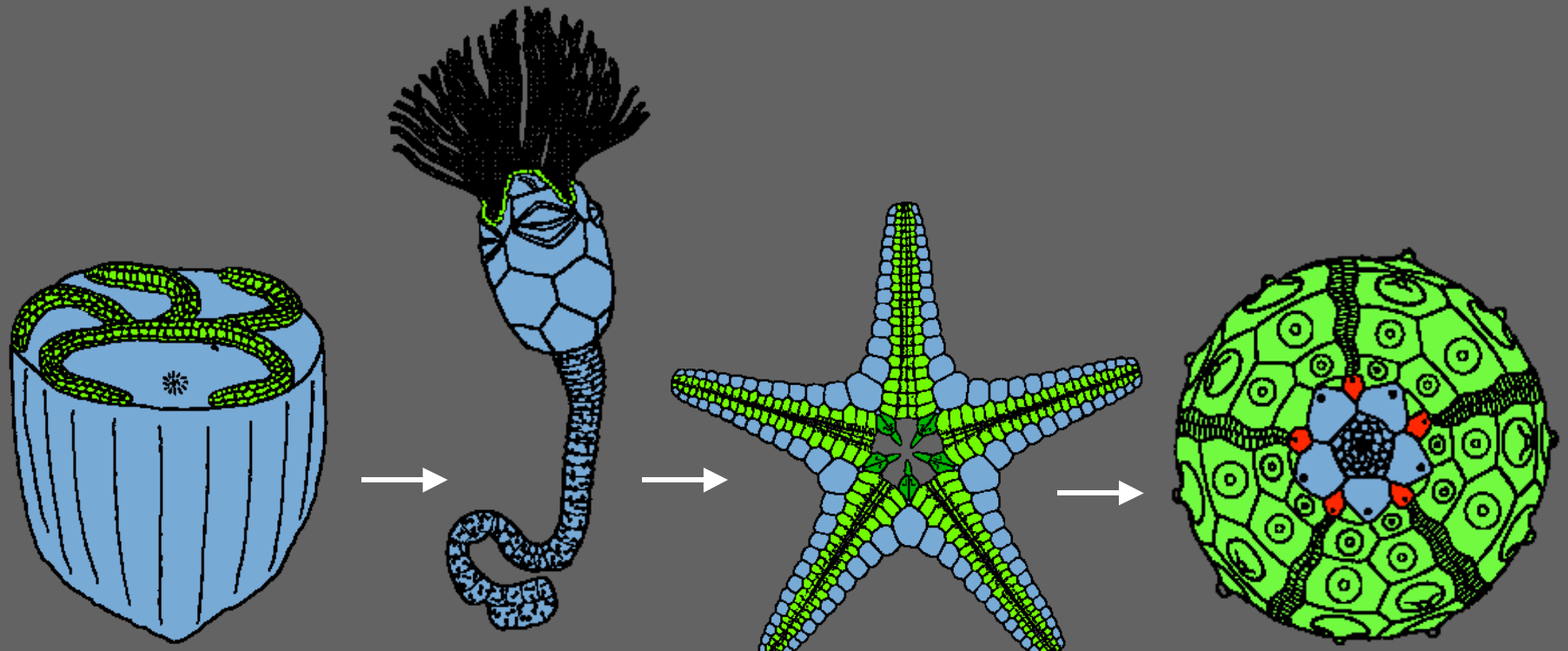
Integration within plastral module



Integration within nonplastral module



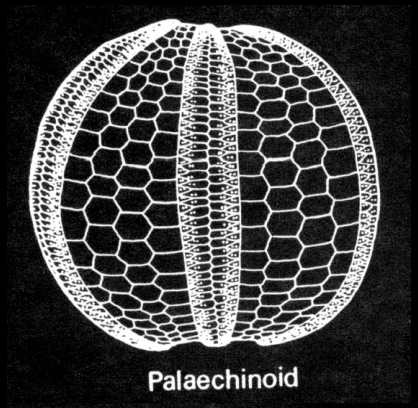
Modularity and major trends in echinoderm evolution -EAT Theory

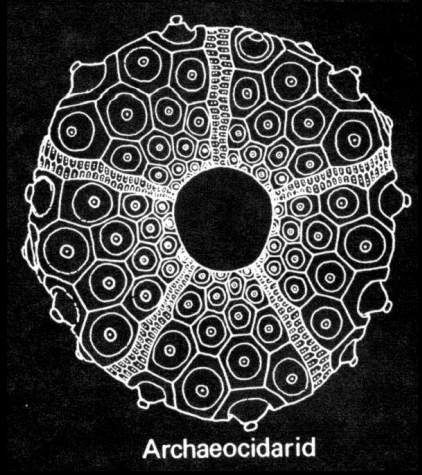


camptostromatoid cystoid asteroid echinoid

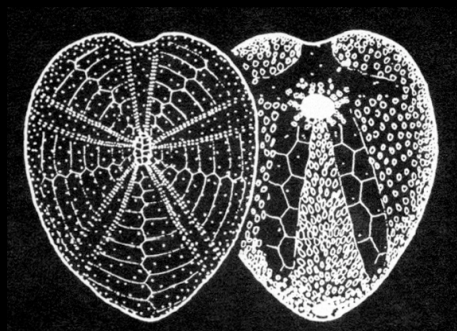
Context-dependence of modularity

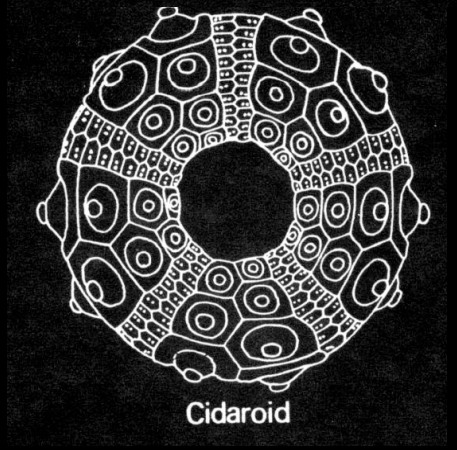
Modularity as number of plate columns





Pz > Post-Pz

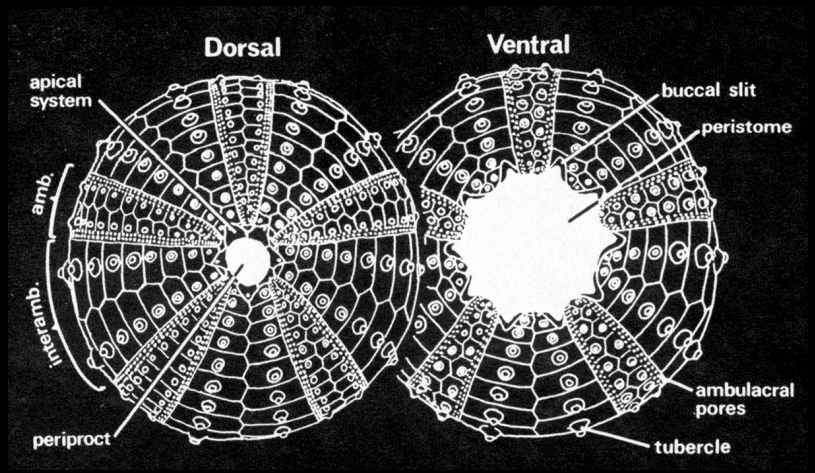




Context-dependence of modularity

Modularity as number of plates

Regular



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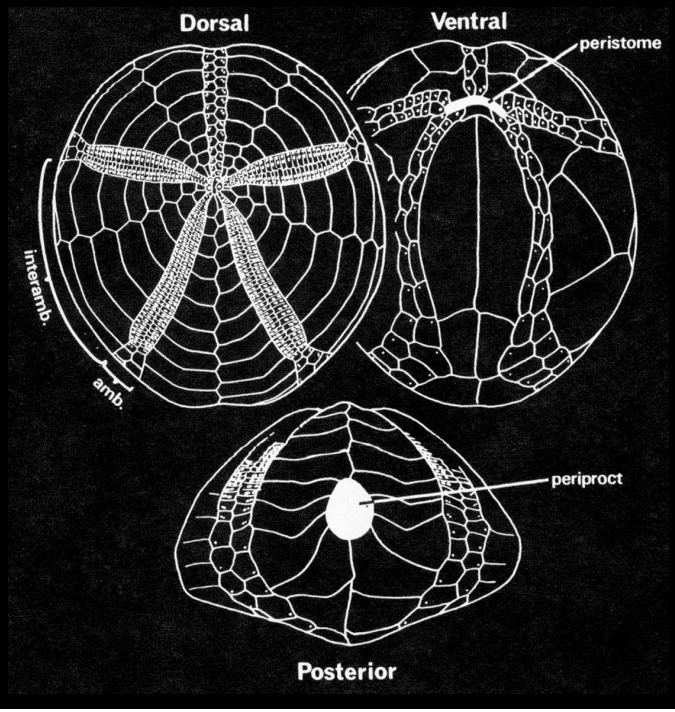
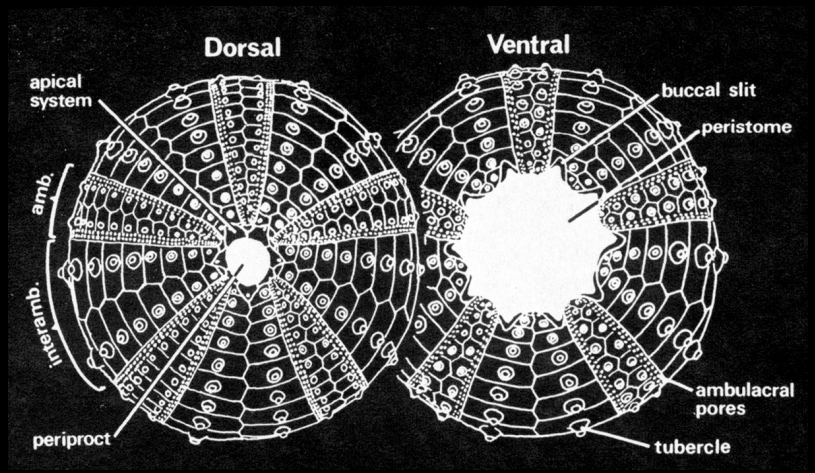
Irregular



Context-dependence of modularity

Modularity as number of plate types

Regular



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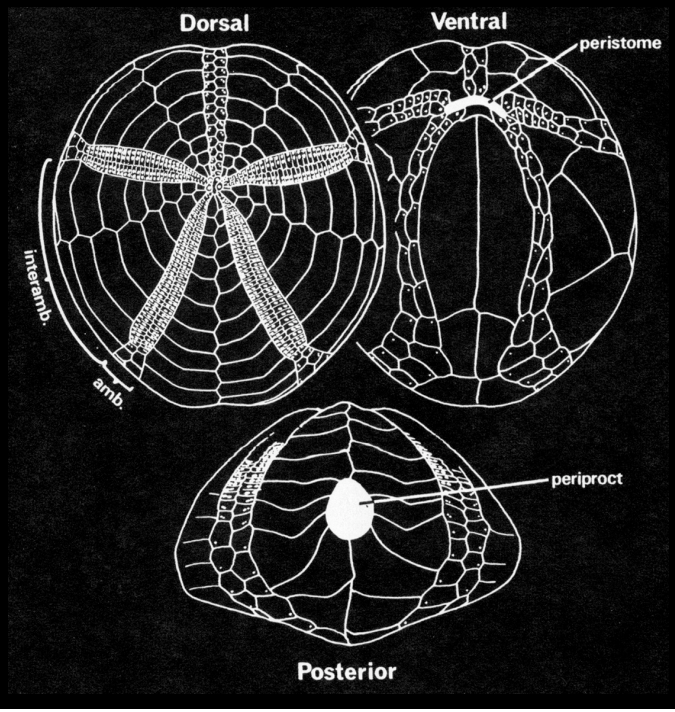
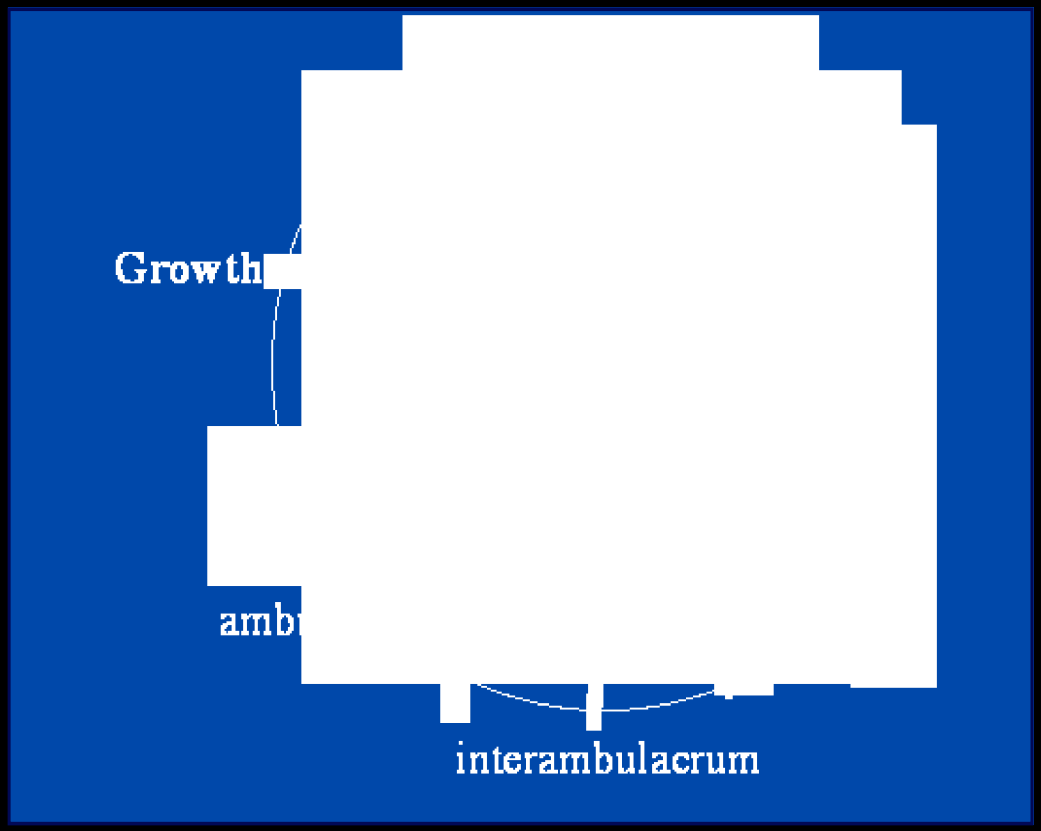
Irregular



Context-dependence of modularity

Modularity as number of growth zones



Constant across echinoids

Is integration the converse of modularity?

No,
"because the whole is more than the sum of the parts"

Yes,
"because, all other things being equal, integration and parcellation are logical opposites and are inversely correlated"

Is integration the converse of modularity?

Wait…

Yes and no: they are logical opposites and tend to be inversely correlated, **but** the opposition may not be symmetric and the correlation imperfect because of

1) The geometry of organisms
2) The topology of morphospace
3) Historical contingency

Is integration the converse of modularity?

1) The geometry of organisms

The size and shape of organismal parts affects connectivity and the strength of interactions among parts.

Ex. For homogeneous parts such as serial homologues, modularity may increase of decrease without change of integration

Is integration the converse of modularity?

2) The topology of morphospace

Heterogeneities in morphospace, imply asymmetric transition probabilities: in any particular evolutionary trajectory, changes in modularity or integration may not be reversible or else have a lower probability of reversal.

Is integration the converse of modularity?

3) Historical contingency

Modules have potentially different degrees of entrenchment, and chance may at times lead to loss of modularity as well as of integration (e.g., limb loss).

Future Challenges

- Are morphometric landmarks minimal modules? If so, in what sense?
- Can morphospaces themselves be differentially modular or integrated? In principle.
- How to address the relationships between modularity, integration, disparity, and complexity in a single framework? Or is more than one framework needed?