NJU Course

Principles of Paleobiology

Morphological Disparity

Morphological Disparity

Definition

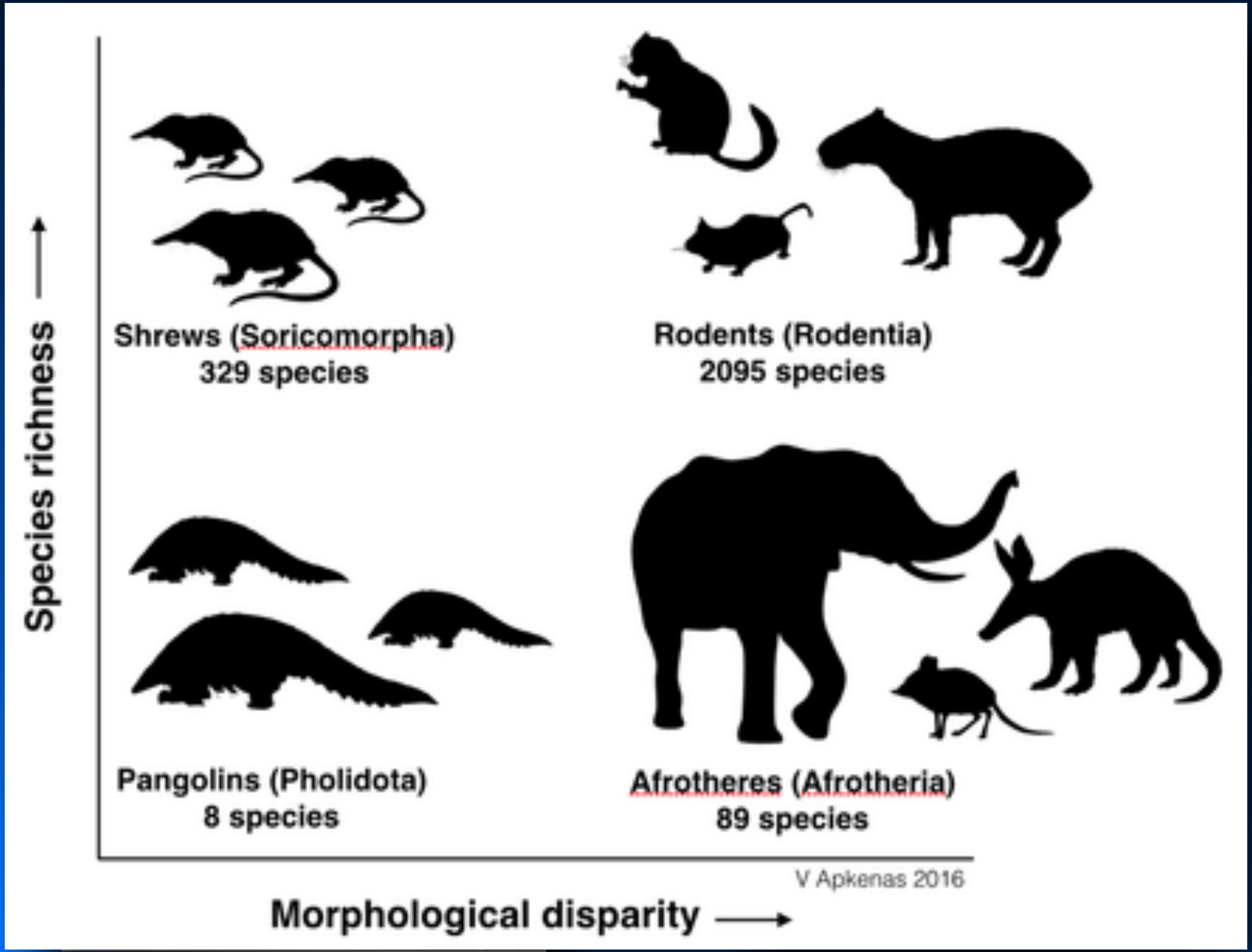
The measurement, representation, and analysis of morphological differences among species or higher-level taxa.

Morphological Disparity

Diversity versus Disparity

Shrews
(329 Species)

Pangolins
(8 Species)



Rodents
(2,095 Species)

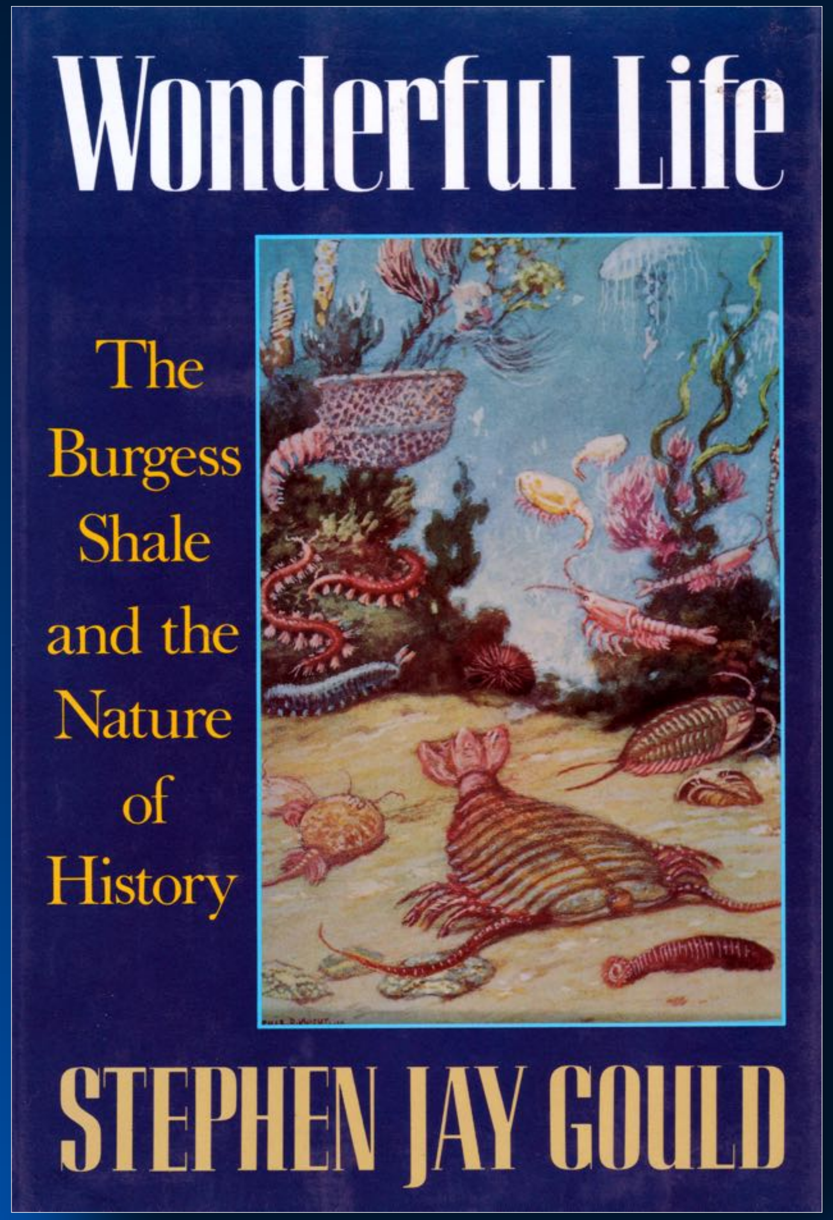
Afrotheria
(89 Species)

Morphological Disparity

Gould & The Burgess Shale Fauna

Stephen J. Gould
(1941 - 2002)

Burgess Shale Fauna
(Carel Brest van Kempen, 1989)



Wonderful Life
The Burgess Shale and the Nature of History
STEPHEN JAY GOULD

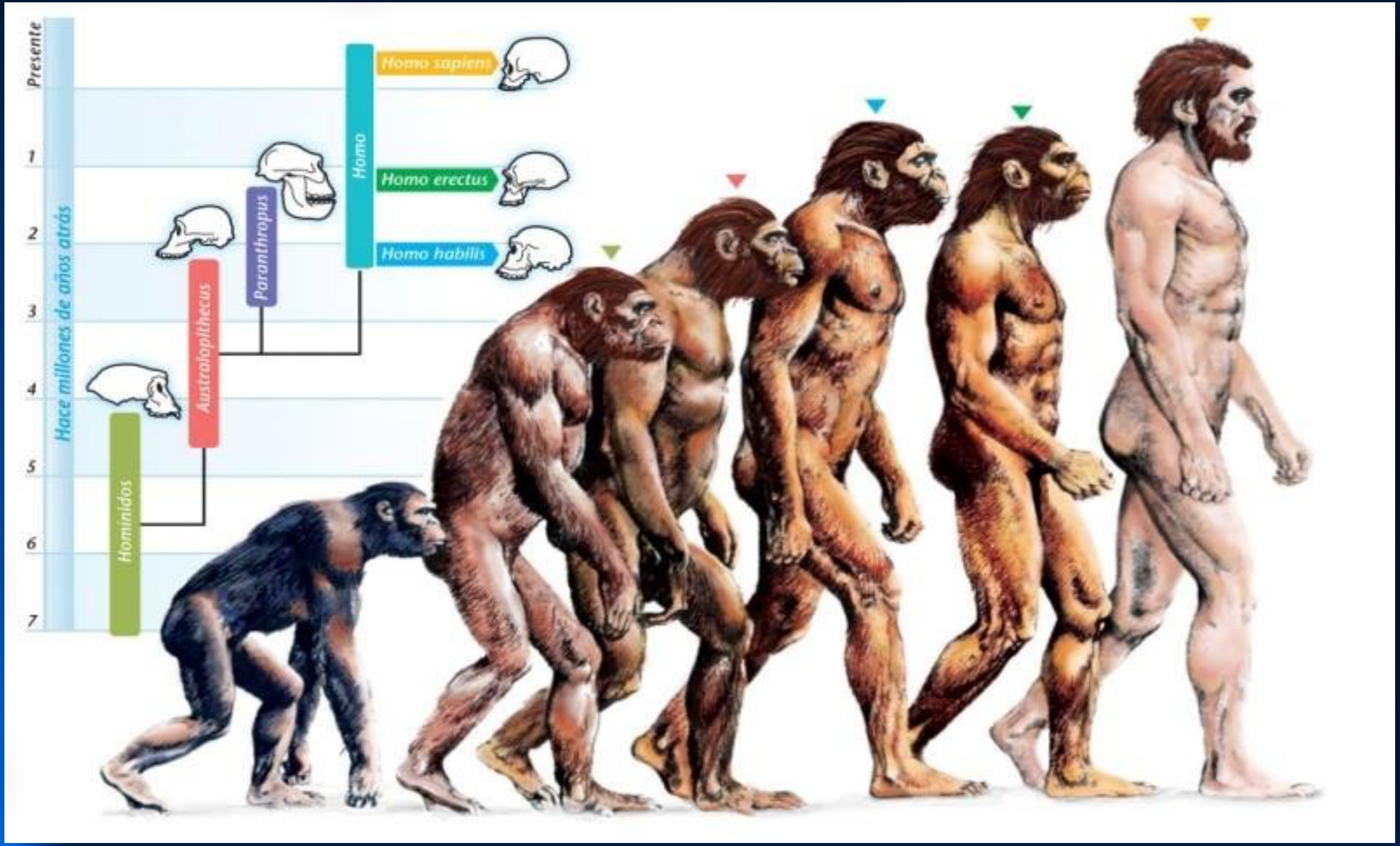
(1989)

Stephen J. Gould’s 1989 reinterpretation of the famous middle Cambrian Burgess Shale fauna was meant to provide support for, and extend, his theory of punctuated equilibrium. However, in responding to critics of his argument Gould inadvertently provided the intellectual underpinning and justification for the entire field of morphological disparity studies.

Morphological Disparity

Gould & The Burgess Shale Fauna

Typically we regard "evolution" as being a synonym for "progress". Indeed, many early phylogenies were organized in such a way as to underscore the impression the history of life was consistent with the idea of linear progress. Gould, and others, were at pains to point out that this represents a caricature of true evolutionary patterns in that, actually are full of false starts, premature terminations and branches that lead nowhere.



Morphological Disparity

Gould & The Burgess Shale Fauna

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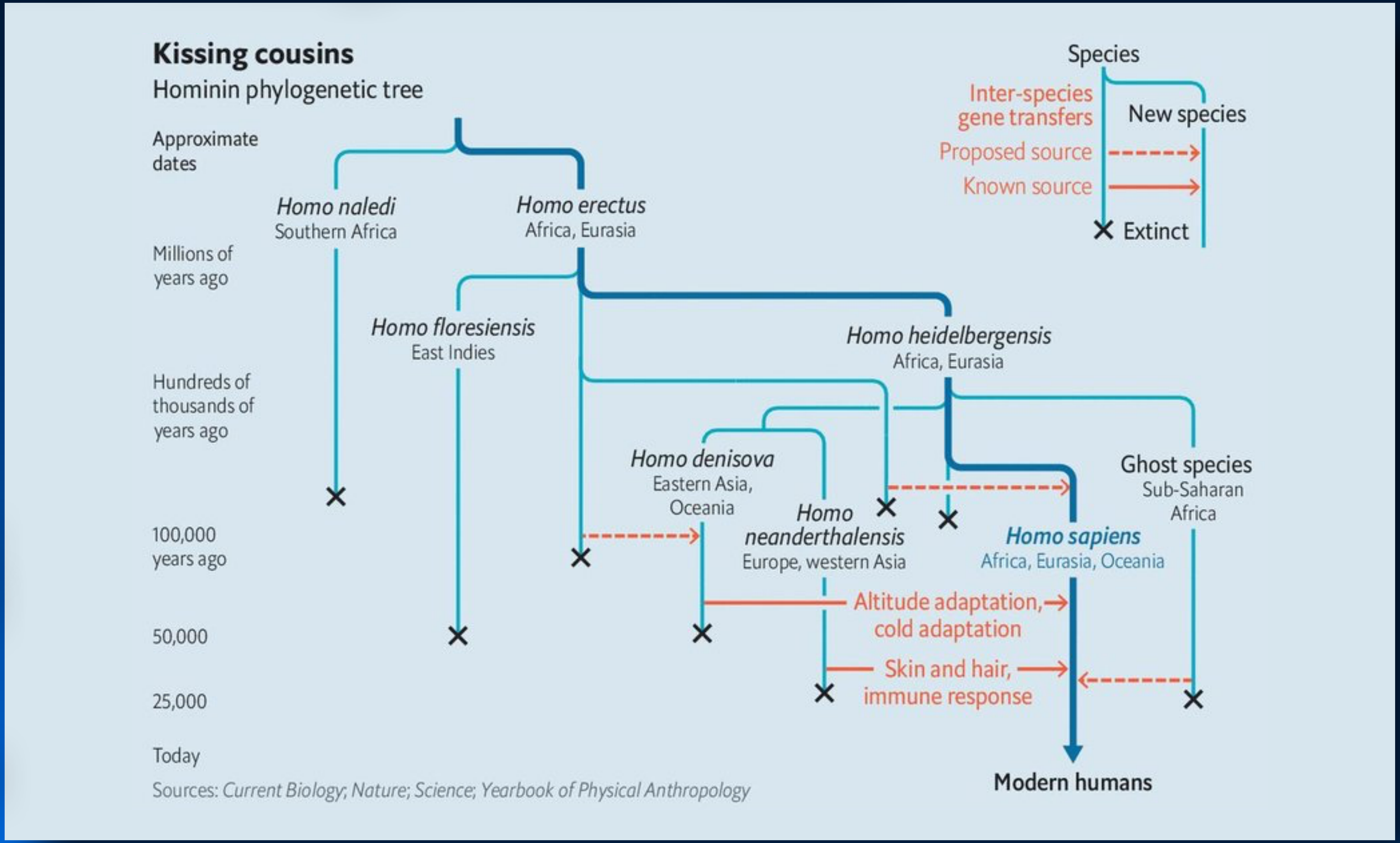


Kissing cousins

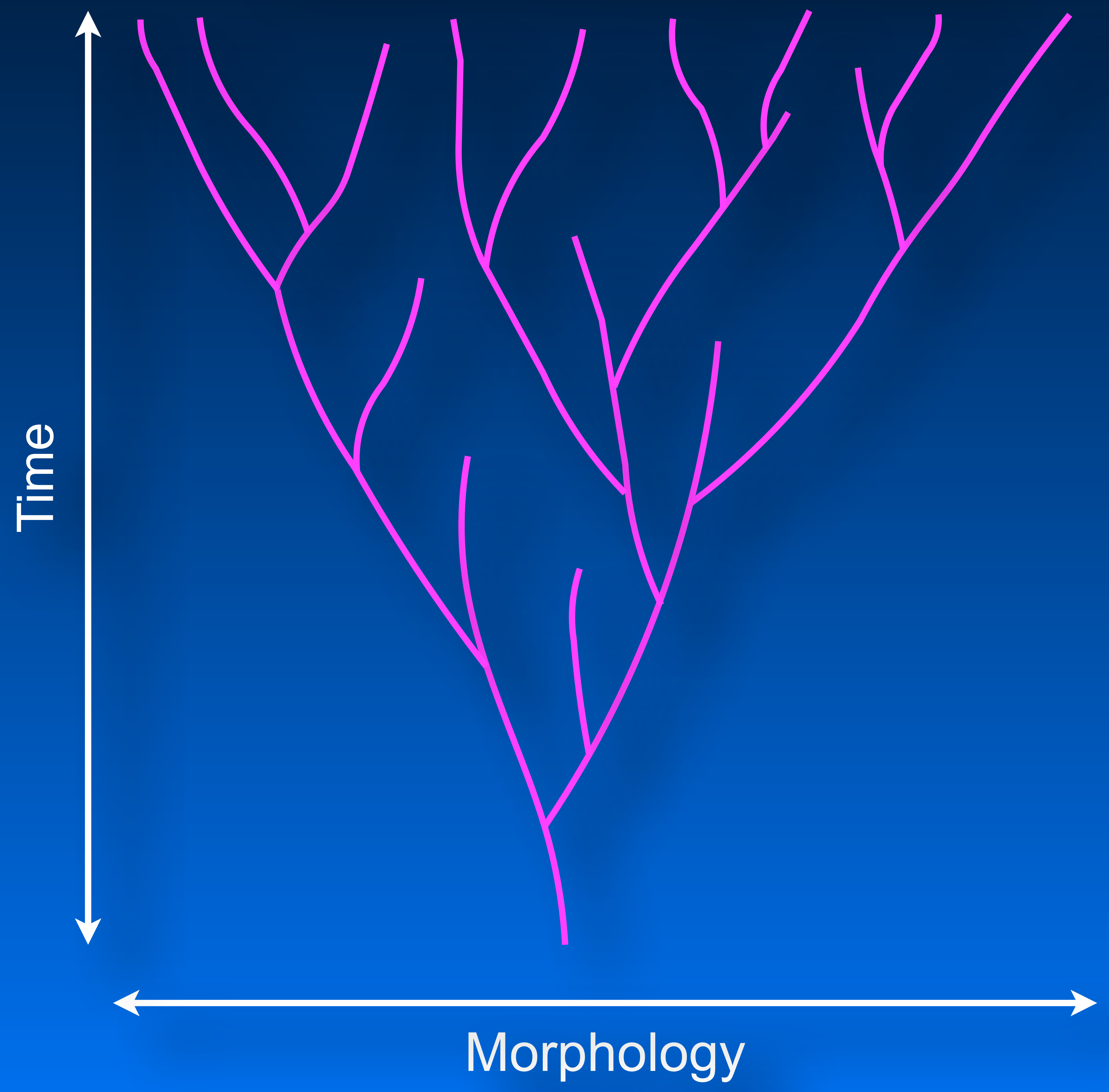
Hominin phylogenetic tree

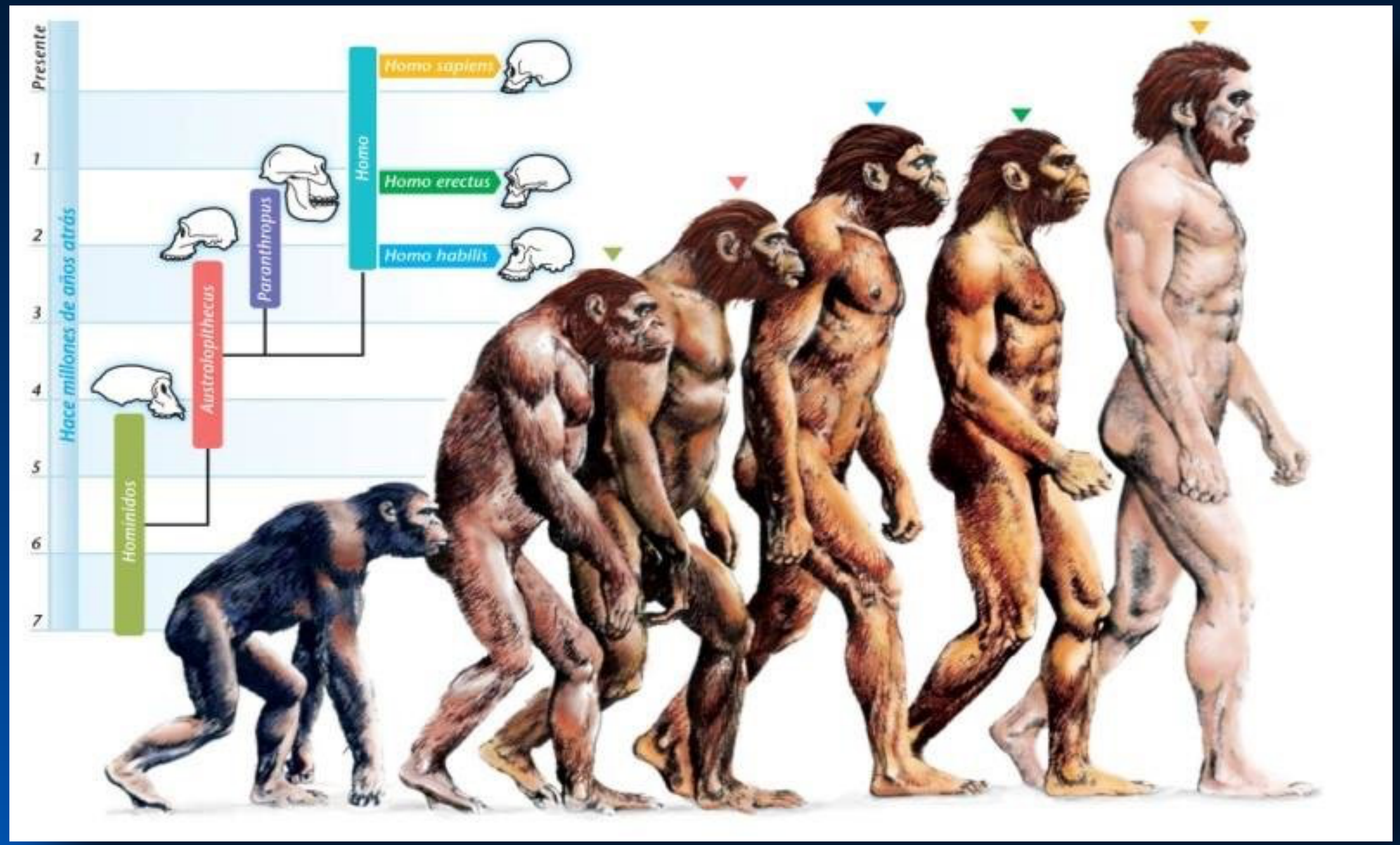
Sources: *Current Biology; Nature; Science; Yearbook of Physical Anthropology*

Morphological Disparity

Gould & The Burgess Shale Fauna

Cone of Increasing Diversity



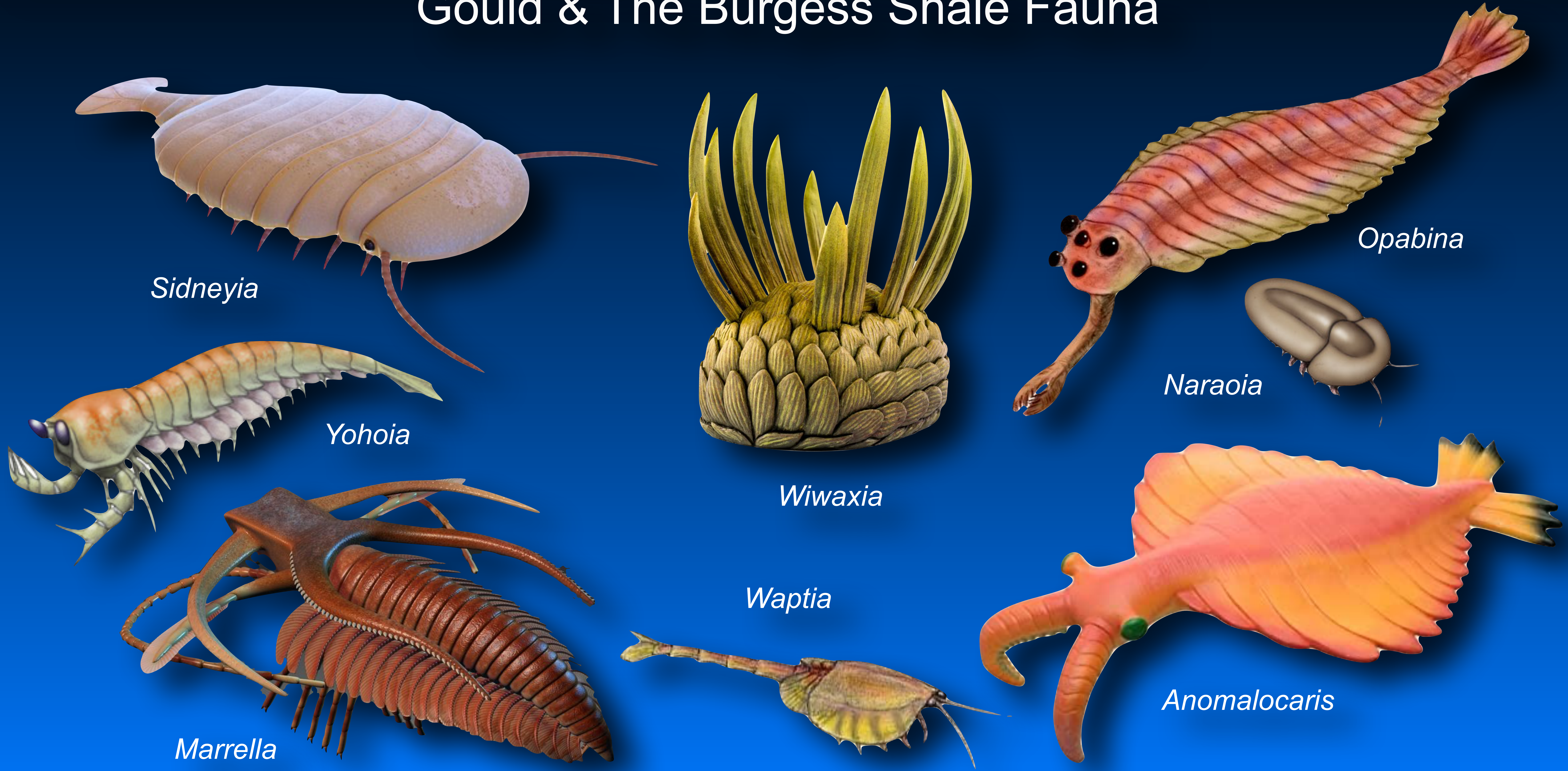


If evolution = progress the morphological variance should track increases in taxic richness. Barring the influence of extinction, younger members of a lineage should be more morphologically diverse.

Diagram redrawn from Gould (1989)

Morphological Disparity

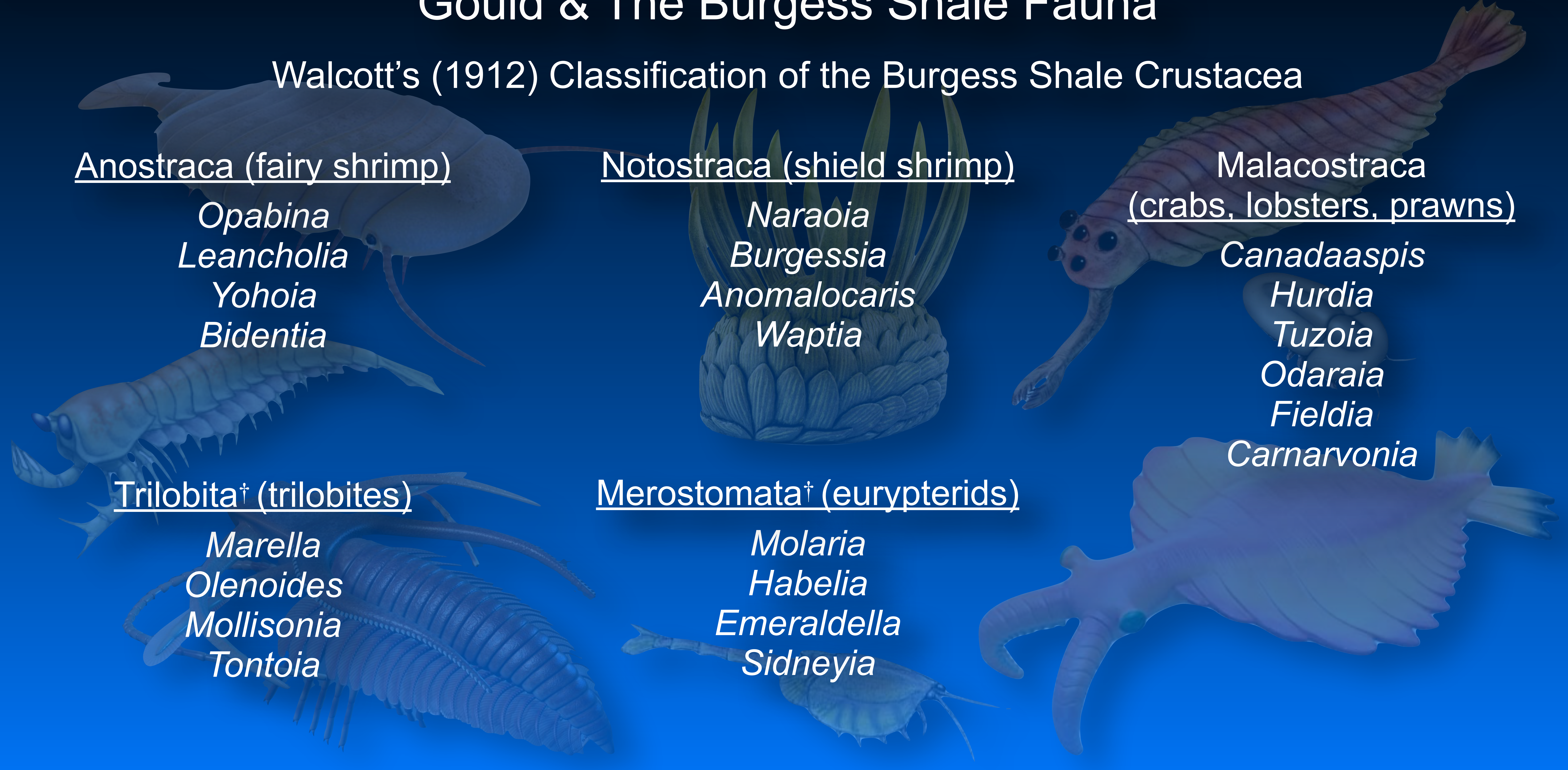
Gould & The Burgess Shale Fauna



Morphological Disparity

Gould & The Burgess Shale Fauna

Walcott's (1912) Classification of the Burgess Shale Crustacea



Anostraca (fairy shrimp)

Opabina
Leancholia
Yohoia
Bidentia

Trilobita† (trilobites)

Marella
Olenoides
Mollisonia
Tontoia

Notostraca (shield shrimp)

Naraoia
Burgessia
Anomalocaris
Waptia

Merostomata† (eurypterids)

Molaria
Habelia
Emeraldella
Sidneyia

Malacostraca
(crabs, lobsters, prawns)

Canadaaspis
Hurdia
Tuzoia
Odaraia
Fieldia
Carnarvonia

Morphological Disparity

Gould & The Burgess Shale Fauna

Current Classification of the Burgess Shale Crustacea

Genus	Classification	Genus	Classification
Opabina	Dinocardida (new class)	*Odaraia*	Malacostracan crustacean
Leancholia	New Phylum	*Fieldia*	Pirapulid
Yohoia	New Phylum	*Carnarvonia*	Dinocardida (new class)
Leanchoilia	New Phylum	*Marella*	New phylum
Naraoia	Trilobite	*Olenoides*	Trilobite
Burgessia	New Phylum	*Mollisonia*	Mollisonid Chelicerate
Anomalocaris	Dinocardida (new class)	*Tontoia*	Status unresolved
Waptia	Pancrustacea (?)	*Molaria*	New Phylum
Canadaspis	Malacostracan crustacean	*Habelia*	New Phylum
Hurdia	Dinocardida (new class)	*Emeraldella*	New Phylum
Tuzoia	Thylacocephalia† (?)	*Sidneyia*	New Phylum

Morphological Disparity

Gould & The Burgess Shale Fauna

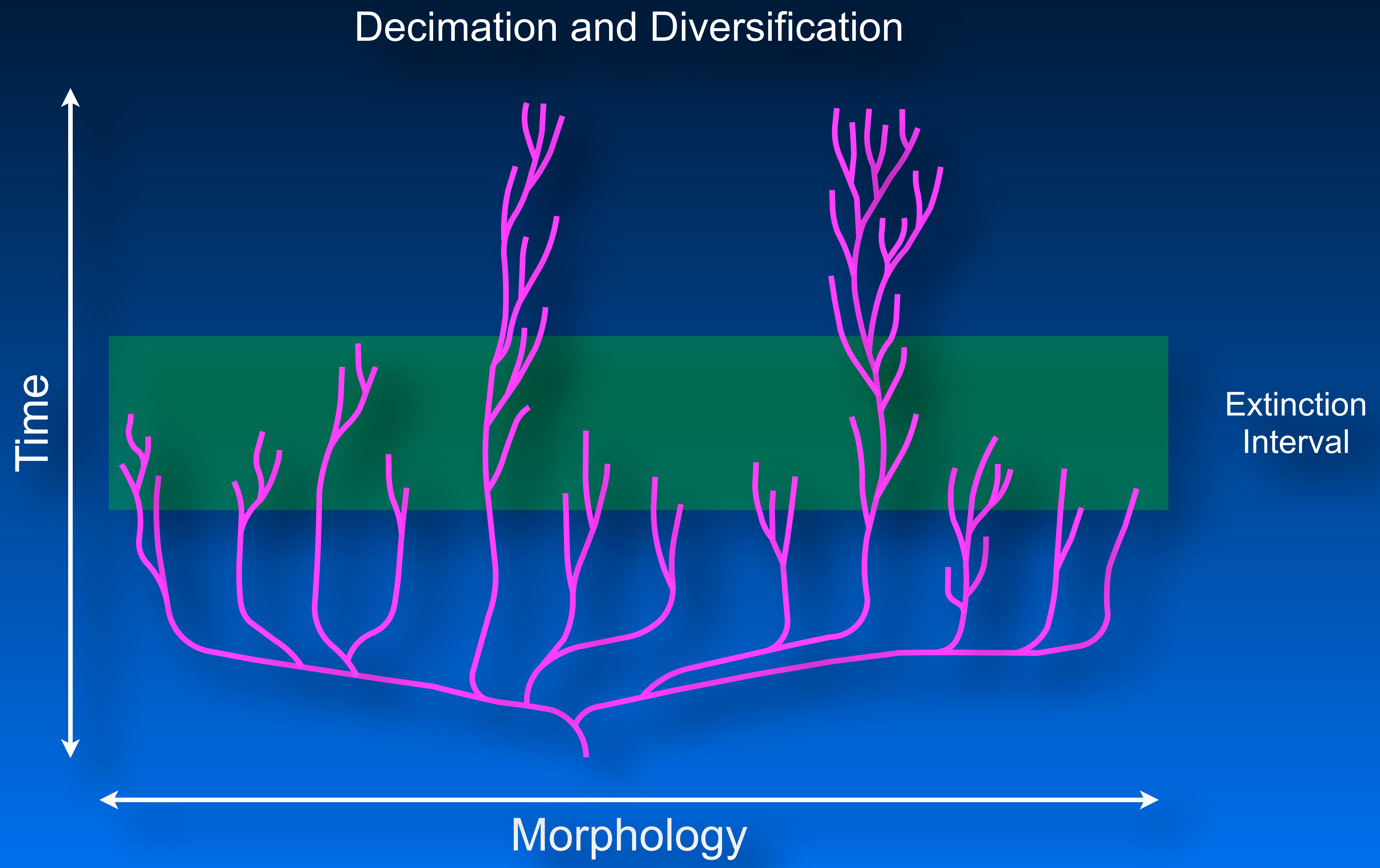
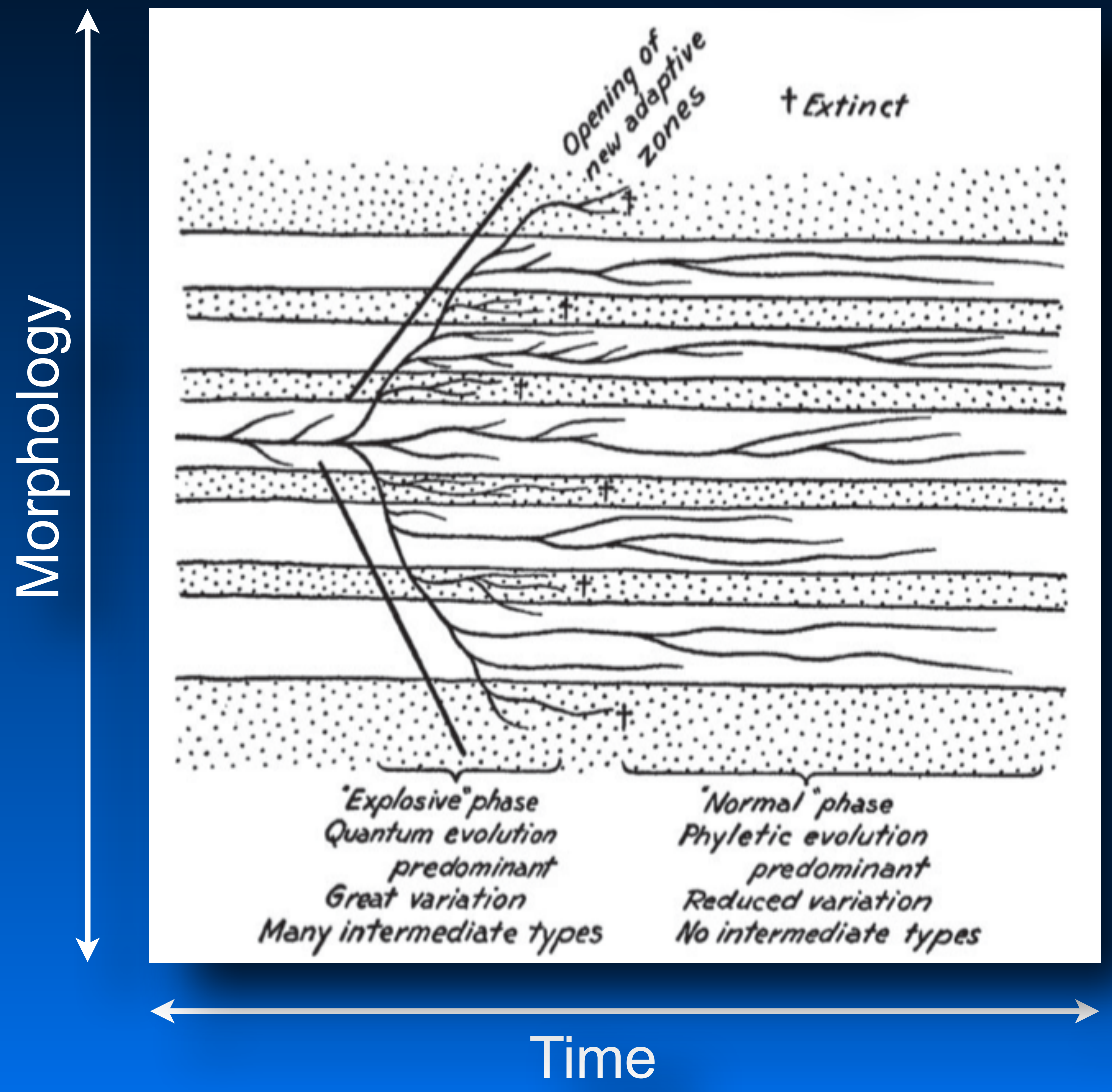
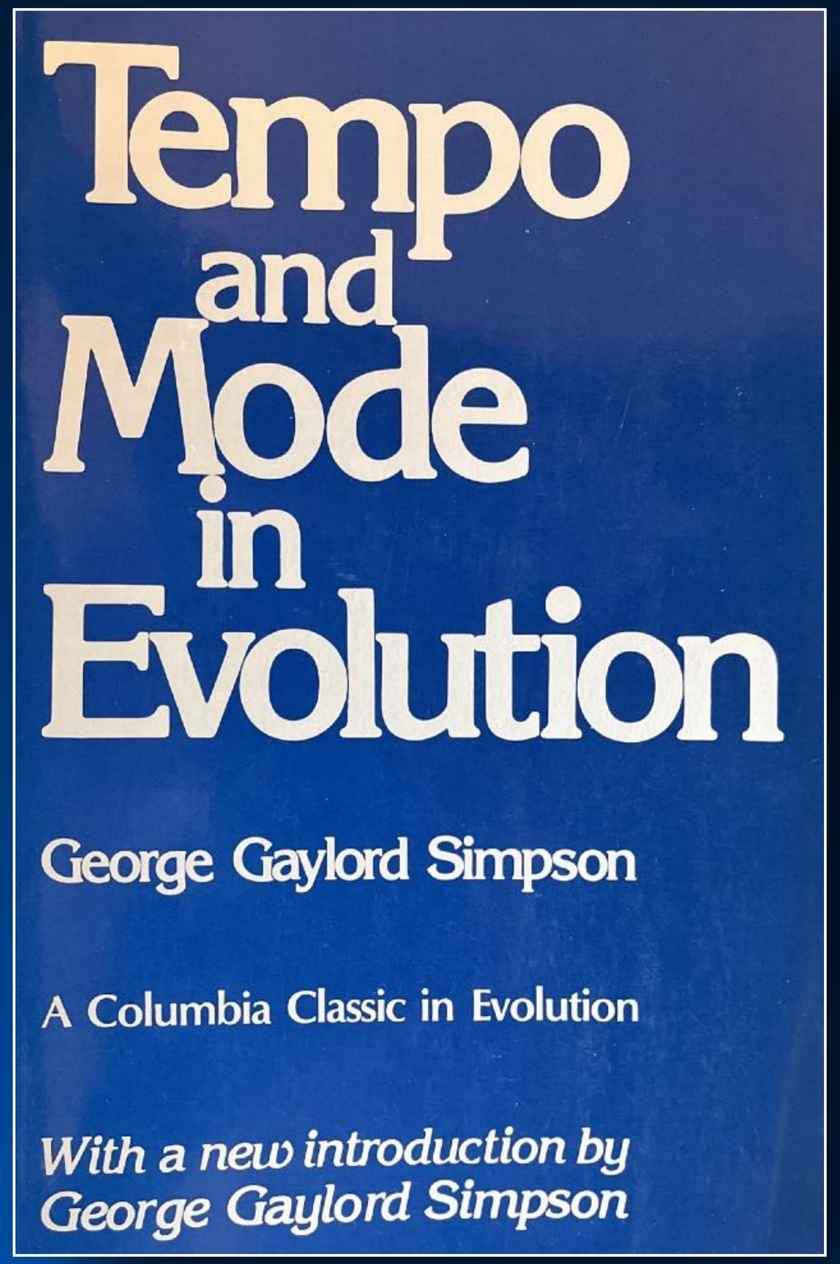


Diagram redrawn from Gould (1989)

Morphological Disparity

Simpson & Quantum Evolution

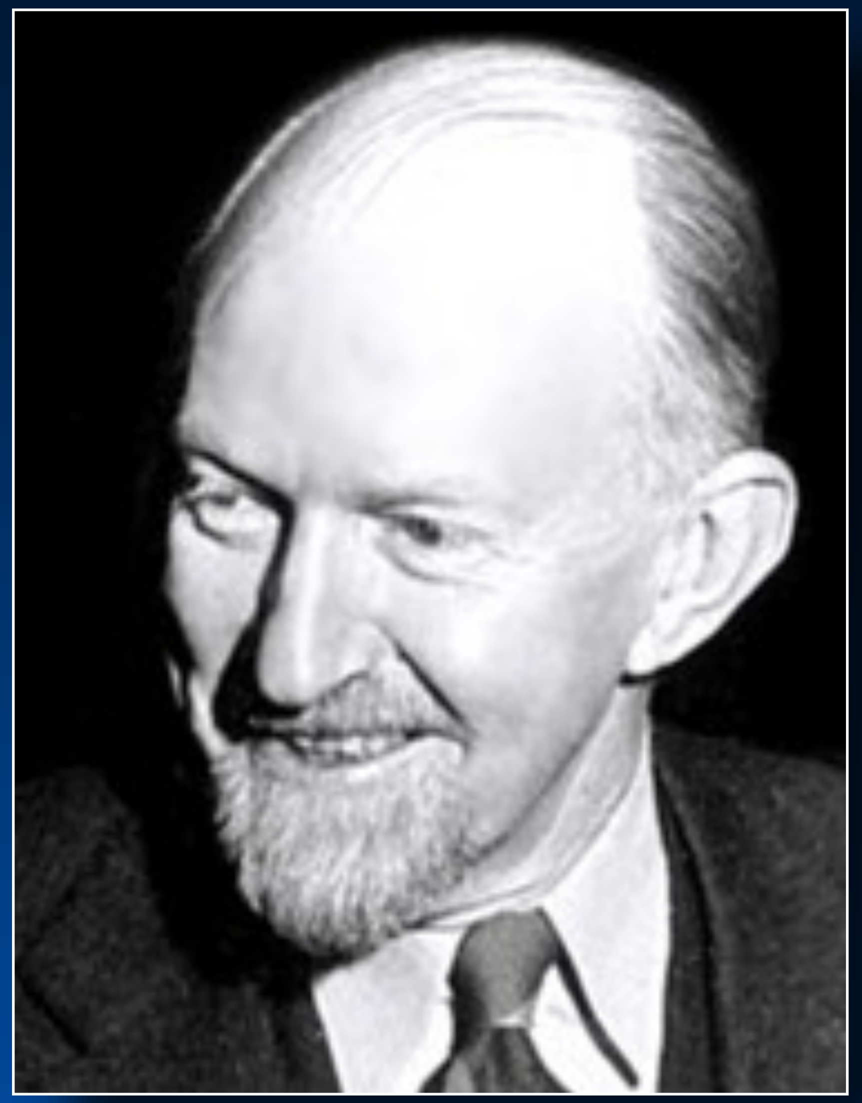



Tempo and Mode in Evolution

George Gaylord Simpson

A Columbia Classic in Evolution

With a new introduction by George Gaylord Simpson


George Gaylord Simpson
(1902 - 1984)

Gould's model was reminiscent of a Simpson's (1944) "quantum evolution" model which was proposed originally to explain the rapid appearance of higher taxonomic groups in the fossil record.

Diagram from Simpson (1944)

Morphological Disparity

Gould & The Burgess Shale Fauna

Paleobiology, 17(4), 1991, pp. 411–423

The disparity of the Burgess Shale arthropod fauna and the limits of cladistic analysis: why we must strive to quantify morphospace

Stephen Jay Gould

Abstract.—Three major arguments have been raised against the crucial claim, documented by Whittington and colleagues for the Burgess Shale fauna, and so contrary to traditional views, that disparity of anatomical design reached an early maximum in the history of multicellular life: (1) the presence of many early taxa with low membership and high rank is an artifact of naming; (2) cladistic analysis of Burgess arthropods negates the claim for greater early disparity; and (3) Whittington's argument is a retrospective fallacy based on assigning high rank to differentia only by virtue of their later capacity to define major branches. I show that all these arguments are either false or illogical, and that the claim for increased early disparity is justified: (1) Taxonomic rank is an artifact, but no one has ever based a claim for greater disparity on this false criterion. (2) Cladistics can only deal with branching order, whereas disparity is a phenetic issue. These two legitimate aspects of evolutionary "relationship" are logically distinct. The rooting of a cladogram only illustrates monophyletic ancestry (which no one doubts, as we are not creationists), and cannot measure disparity. (3) The active stabilization of the differentia of *Baupläne* (for genetic and developmental reasons only dimly understood) provides a powerful rationale for weighting these characters in considerations of disparity; nothing had so stabilized in the Burgess fauna. If these differentia were steadily changing contingencies, rather than actively stabilized features with "deep" architectural status, then the retrospective argument would be justified. Although the three arguments are wrong, the claim for greater early disparity cannot be confidently established until we develop quantitative techniques for the characterization of morphospace and its differential filling through time. This is a dauntingly difficult problem, much harder than cladistic ordering, but not intractable.

Stephen Jay Gould. Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts 02138

Accepted: May 7, 1991

Stephen J. Gould
(1941 - 2002)

Morphological Disparity

Gould & The Burgess Shale Fauna

Gould was supporting the interpretation of Harold Whittington and colleagues which supported a number of Gould’s long-standing views about evolutionary processes.

Criticisms:

- Apparent pattern is an artifact of naming taxa.
- Cladistic analysis negates claim for greater early morphological disparity.
- Apparent macroevolutionary pattern was manufactured by Whittington through his assignment of enigmatic Burgess Shale taxa to categories of high taxonomic rank.

Responses:

- Taxonomic rank is a human artifact and cannot be used to support arguments about structure of nature.
- Cladistic analysis can only document the order to evolutionary branching. It cannot be regarded as a reliable indicator of morphological divergence, which is a phonetic issue.
- The features that give the Burgess Fauna its unusual character were not segments of changing continua, but were stable aspects of these species Baupläne with deep architectural status.

Morphological Disparity

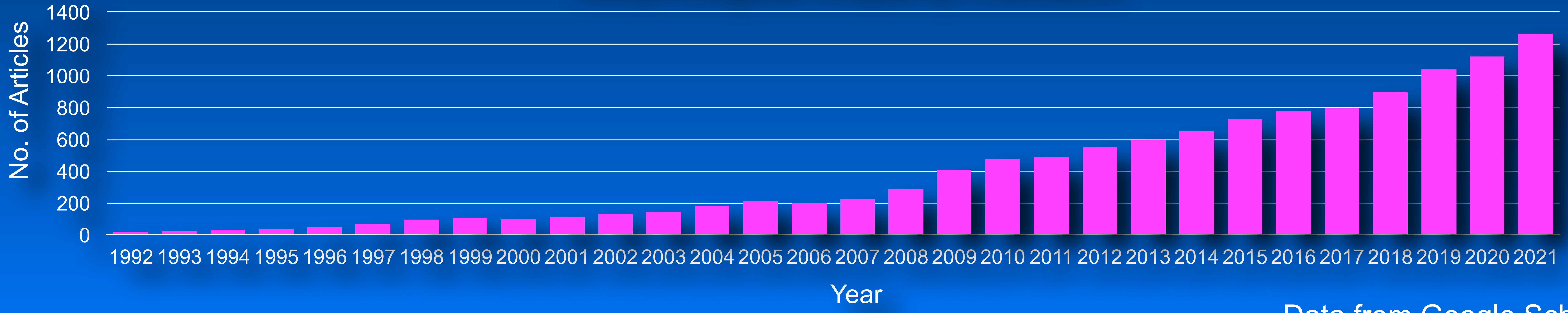
Gould & The Burgess Shale Fauna

However, Gould acknowledged that …

"… the claim for greater early [morphological] disparity cannot be confidently established until we [= paleontologists] develop quantitative techniques for the characterization of morphospace and its differential filling through time. … This is a dauntingly difficult problem, much harder than cladistic ordering, but not intractable."

Gould (1991, p. 411)

Morphological Disparity Literature



Data from Google Scholar

Morphological Disparity

Gould & The Burgess Shale Fauna

To accomplish this task Gould noted, “We need to …

- … define a full range of the abstract (and richly multivariate) space into which all organisms may fit (the morphospace).
- … be able to characterize individual organisms and plot them within this encompassing space.
- … measure density, range, clumping, and a host of other properties that determine differential filling of this totality.
- … be able to assess the variation in this differential filling through time.

But there are many challenges, including

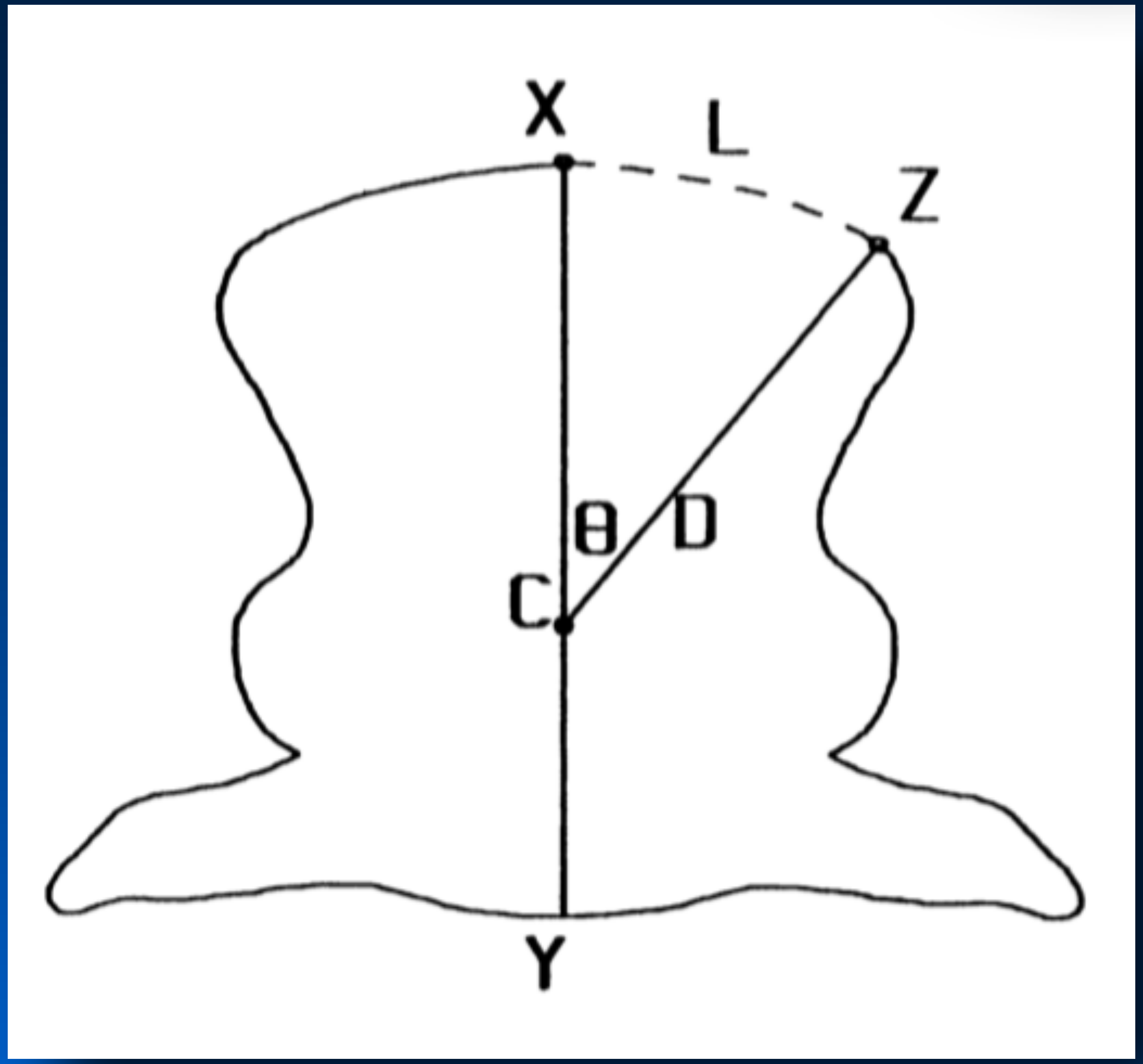
- If we define the morphospace empirically … how do we plot other creatures not of the original set and outside its bounds?
- How do we deal, theoretically, with the fact that potential measurements are infinite?
- How do we treat correlation, covariation, the simultaneous consideration of state, meristic, and metric variables?
- How do we express quantitatively the vague, but vital, concepts of relative importance or developmental depth?

Gould (1991, p. 420)

Morphological Disparity

Measuring Disparity

Fourier Analysis of Trilobite Cranidium



$$R(L) = \sum_{i=0}^{\infty} a_i\cos(iL) + b_i\sin(iL)$$

$$A(L) = \sum_{i=0}^{\infty} c_i\cos(iL) + d_i\sin(iL)$$

$$a_i = (2/n)\left(\sum_{j=1}^{n} R_j\cos(2\pi ij/n)\right)$$

$$b_i = (2/n)\left(\sum_{j=1}^{n} R_j\sin(2\pi ij/n)\right)$$

$$c_i = (2/n)\left(\sum_{j=1}^{n} A_j\cos(2\pi ij/n)\right)$$

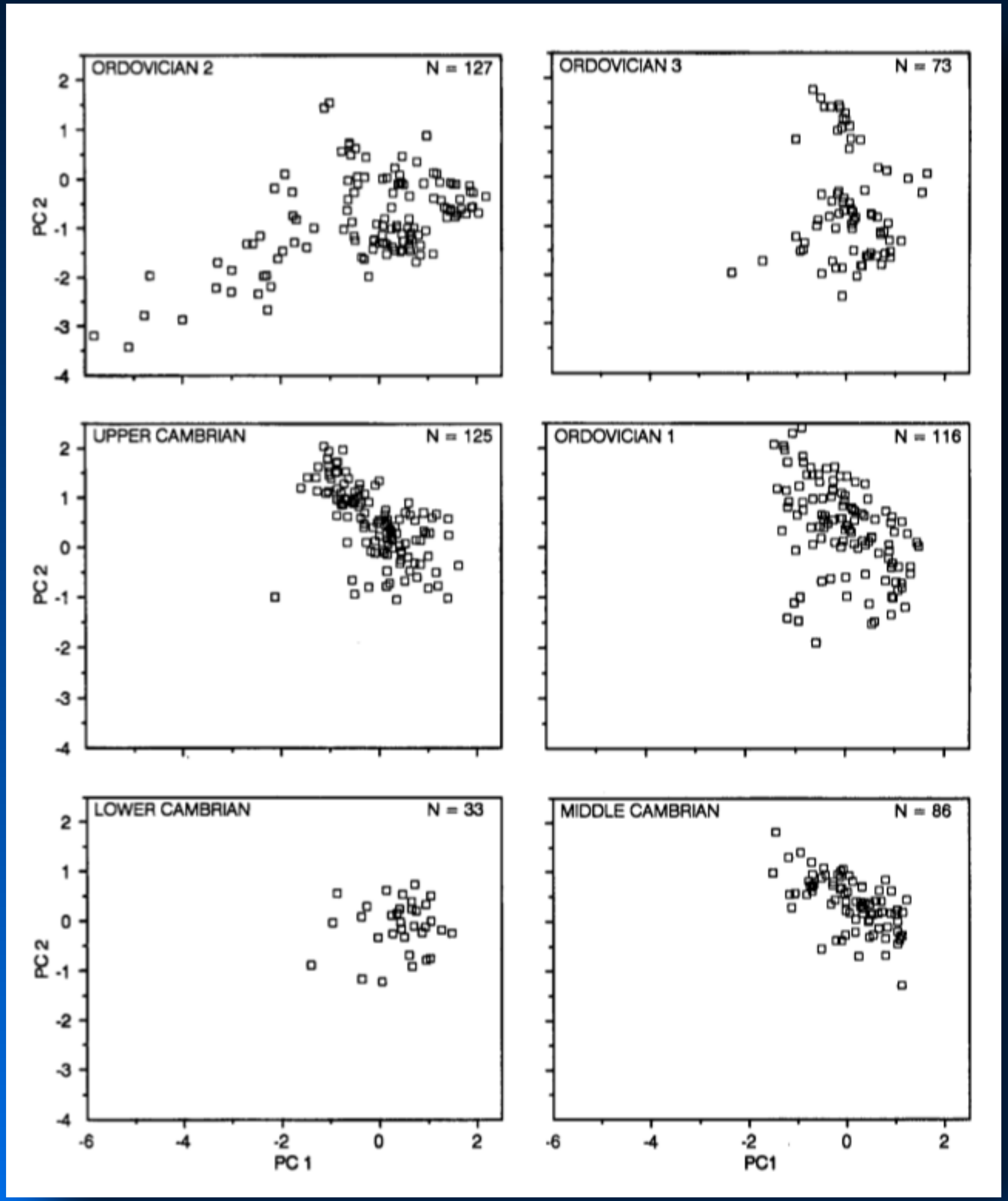
$$d_i = (2/n)\left(\sum_{j=1}^{n} A_j\sin(2\pi ij/n)\right)$$

However, use of standard radial Fourier analysis restricts analysis to the consideration of single-valued outlines.

Foote (1989)

Morphological Disparity

Measuring Disparity



Euclidean Distance

$$d_{i,j} = \sqrt[2]{\sum_{k=1}^{m} (x_{i,k} - x_{j,k})^2}$$

Where:

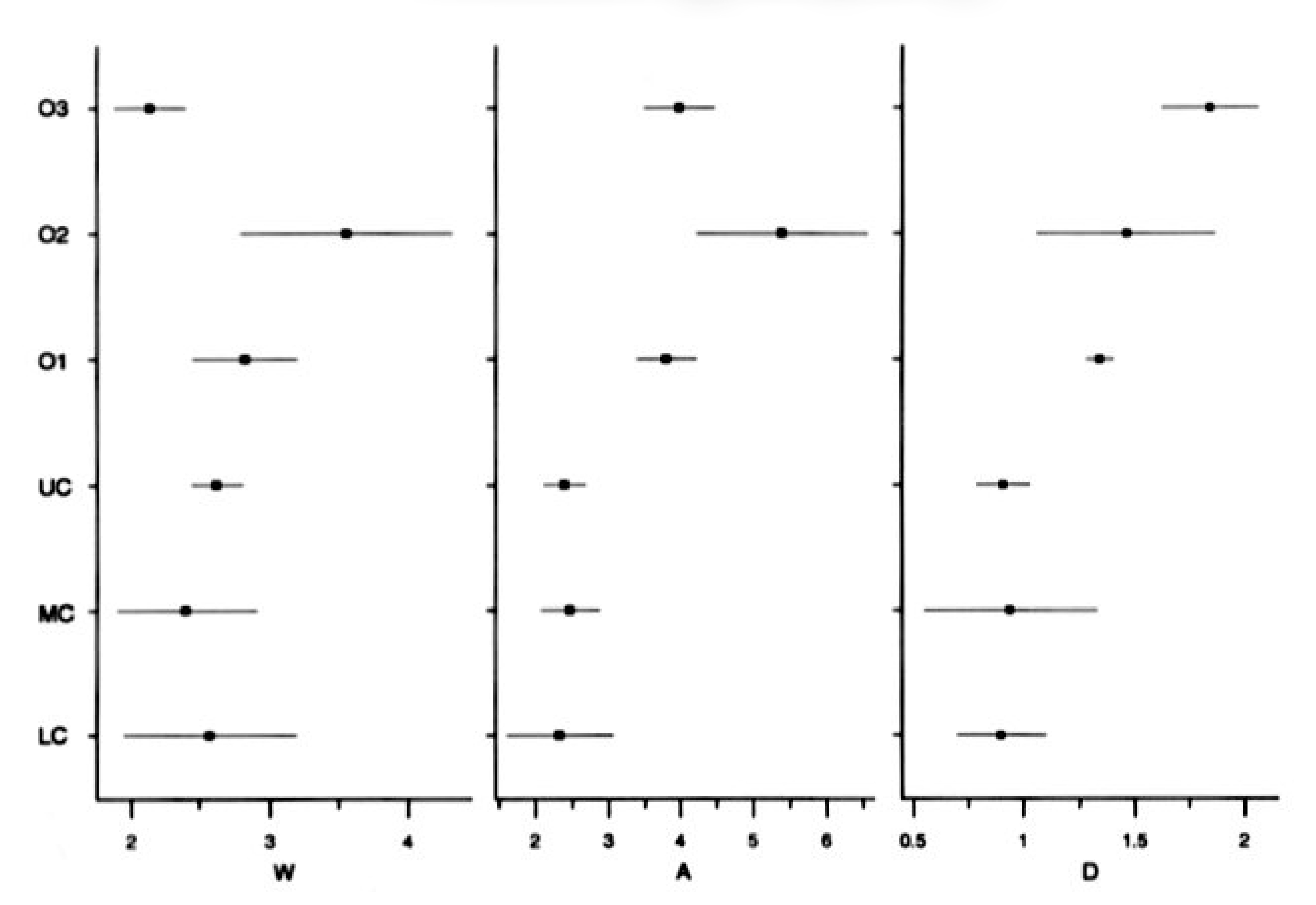
m = number of variables
i = specimen i
j = specimen j

A = weighted mean of distances among group centroids
W = weighted mean of within group distances
Discreteness (D) = A/W

Foote (1989)

Morphological Disparity

Measuring Disparity



Foote (1989)

Morphological Disparity

Measuring Disparity

Actual Range of Ordovician Trilobite Morphology

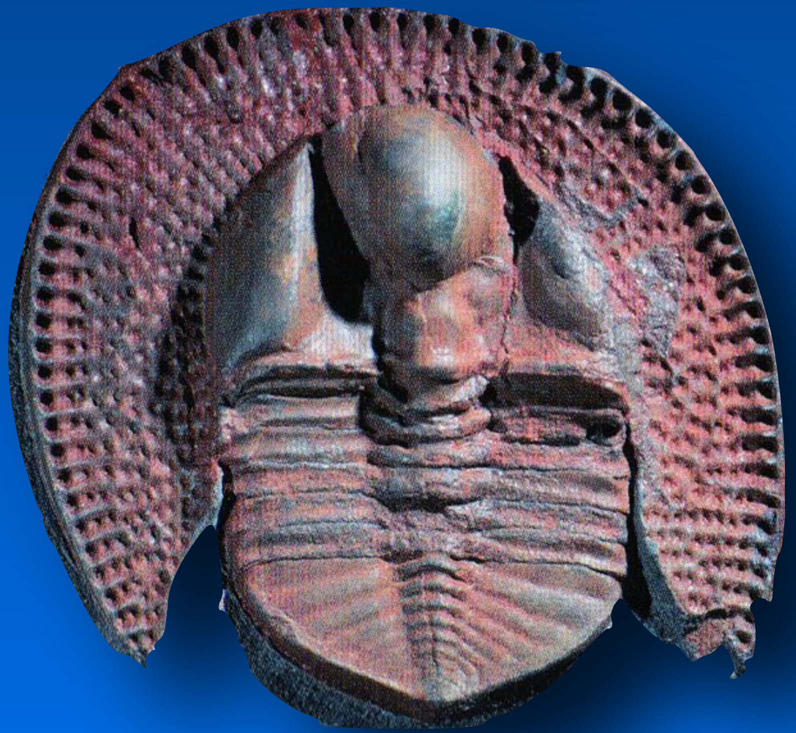
Ampyx

Asaphellus

Calynemella

Chlustina

Dicalymene



Delivolithus

Delivolithus

Megitaspis

Ogygiocaris

Selenopeltis

Lawrance & Stammers (2014)

Morphological Disparity

Measuring Disparity

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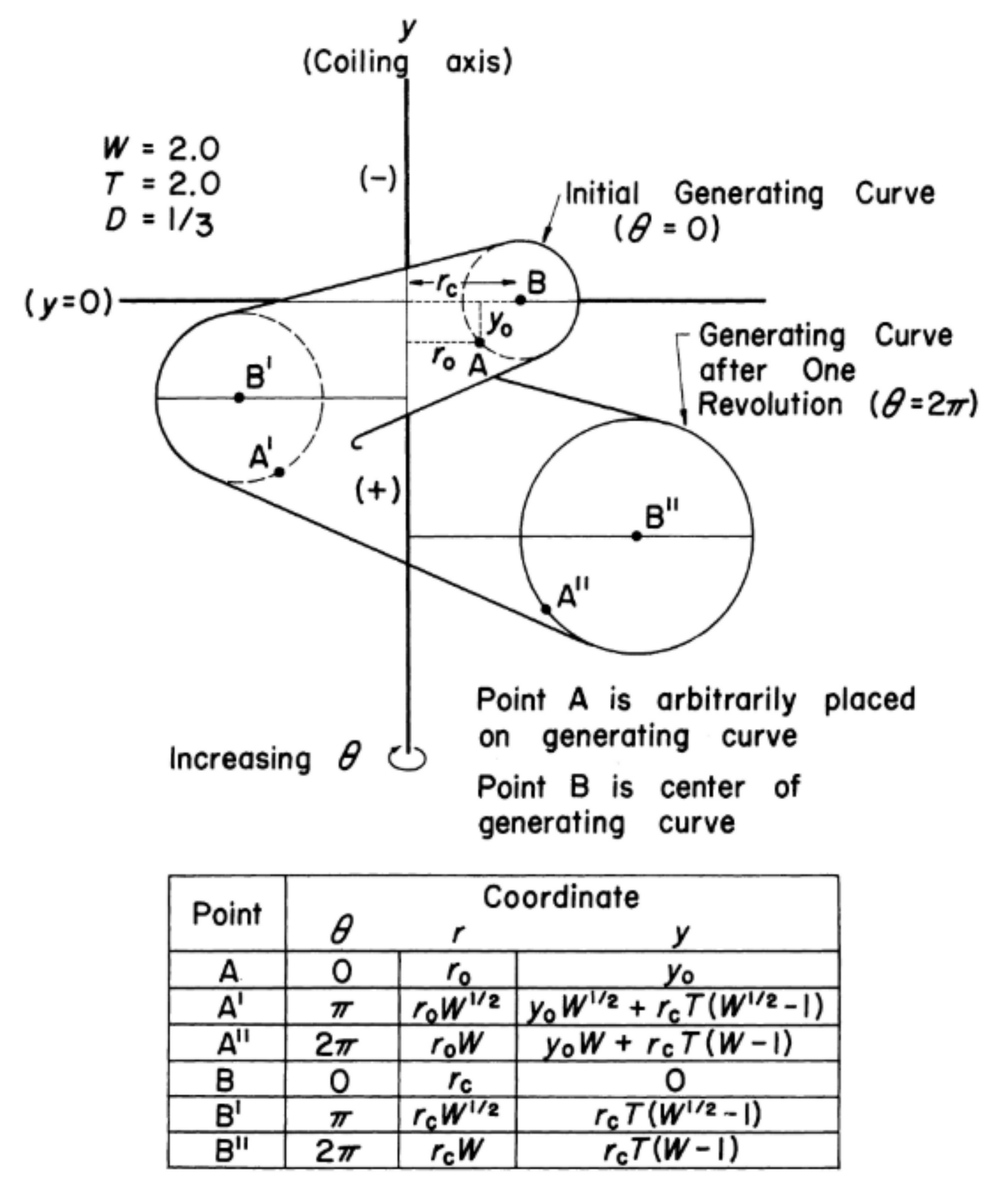
- ☑ …. be able to assess the variation in this differential filling through time.

Overall, not a bad first attempt. But the character of the “morphospace” is not even adequate to characterize trilobite cranidia adequately, much less trilobite morphology overall. Even if it was adequate, it would just represent the “morphospace” of trilobites.

Morphological Disparity

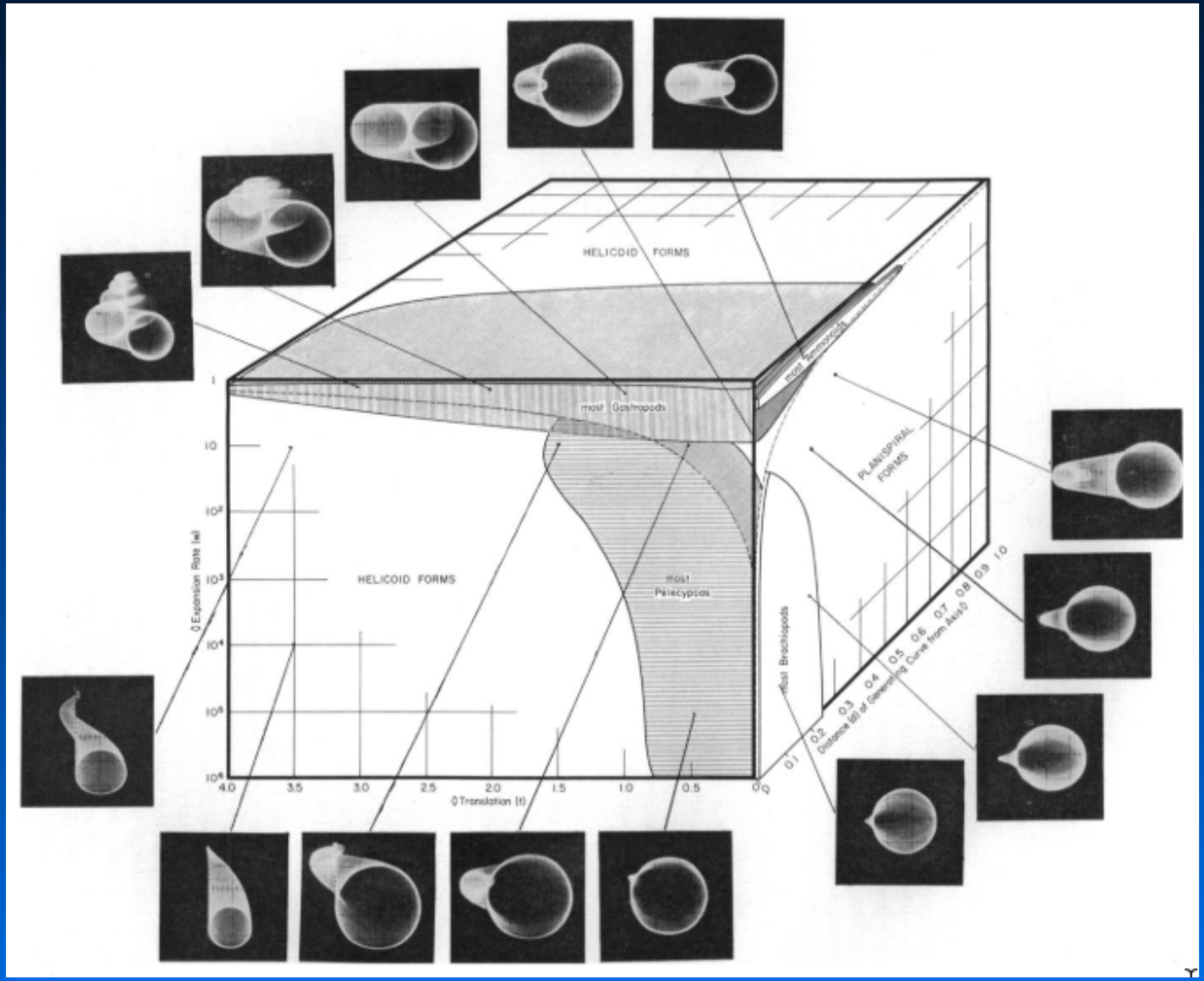
Measuring Disparity



Point A is arbitrarily placed on generating curve

Point B is center of generating curve

Point	Coordinate		
	θ	r	y
A	0	r_0	y_0
A'	π	$r_0 W^{1/2}$	$y_0 W^{1/2} + r_c T(W^{1/2} - 1)$
A''	2π	$r_0 W$	$y_0 W + r_c T(W - 1)$
B	0	r_c	0
B'	π	$r_c W^{1/2}$	$r_c T(W^{1/2} - 1)$
B''	2π	$r_c W$	$r_c T(W - 1)$

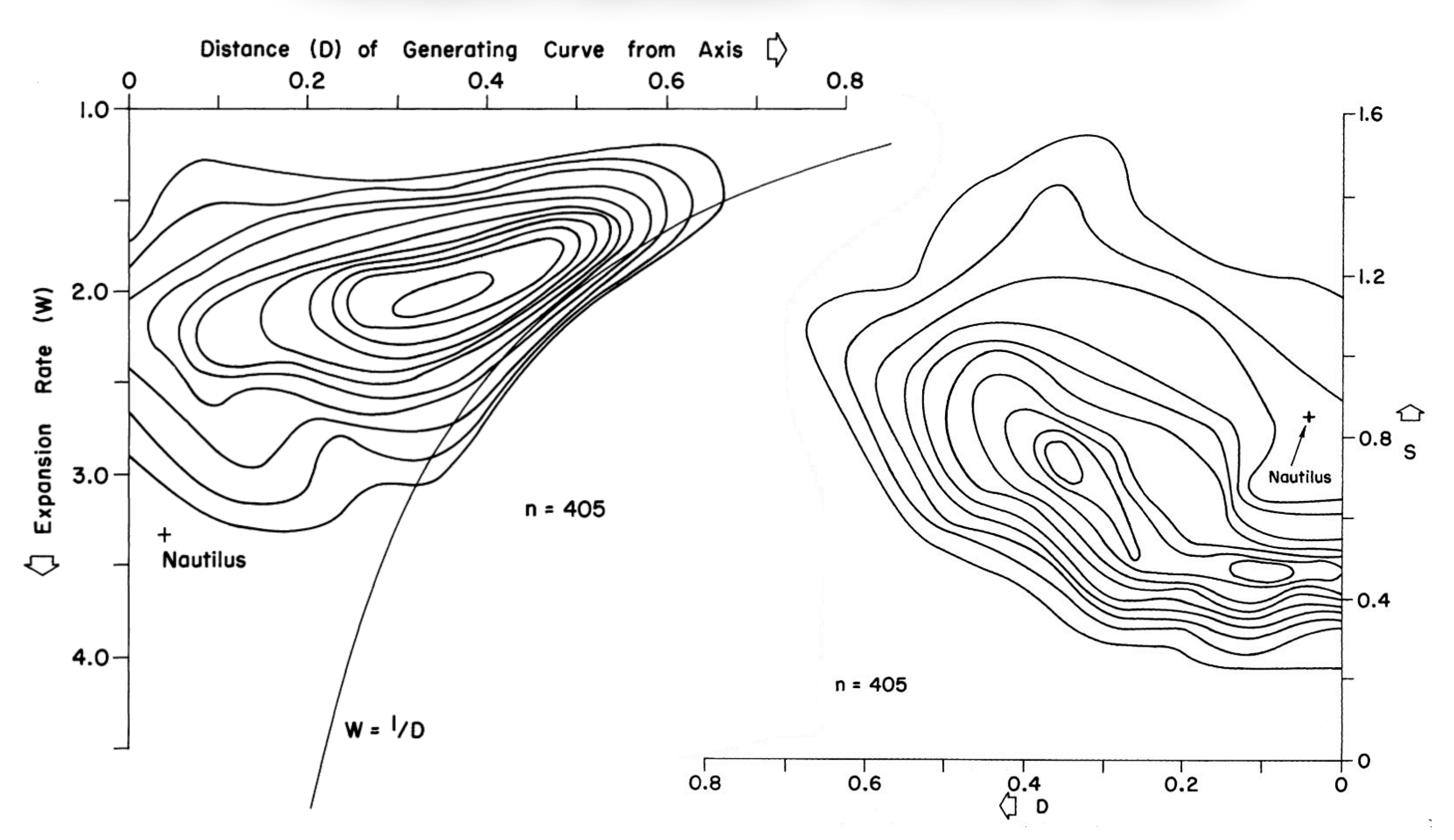


From Raup (1966)

Morphological Disparity

Measuring Disparity

Planispiral Cephalopod Theoretical Space



From Raup (1967)

Morphological Disparity

Measuring Disparity

Actual Range of Ammonite Morphology

Morphological Disparity

Measuring Disparity

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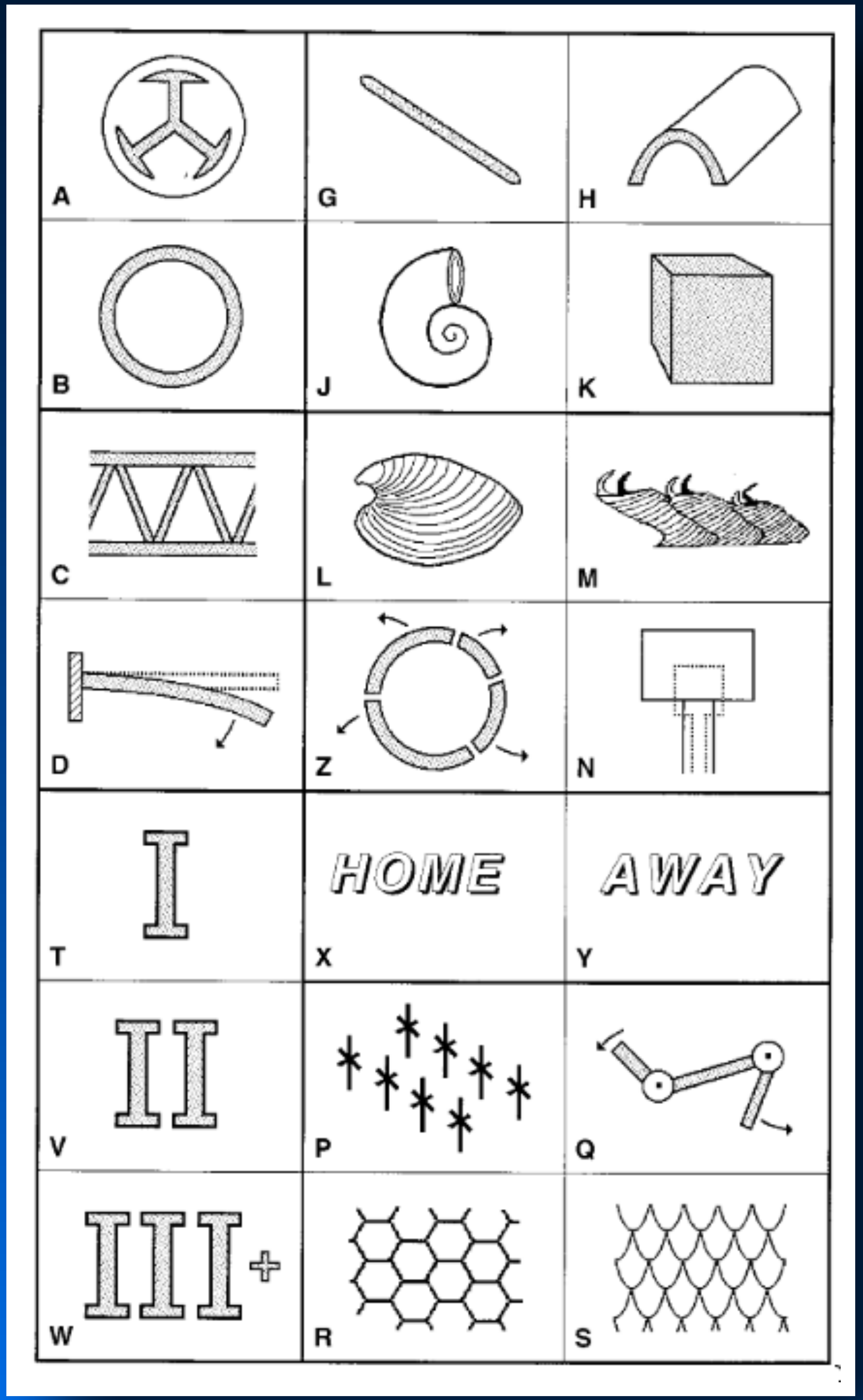
Again, not a bad attempt. But while the “morphospace” of molluscs is more generalized than that of Foote’s trilobites, it’s still not generalized enough to include all molluscs. And even if it was adequate, it would just represent the “morphospace” of molluscs.

Morphological Disparity

Measuring Disparity



Skeleton Location
A. Internal
B. External

Material
C. Rigid
D. Flexible

Number
T. One element
V. Two elements
W. > Two elements

Shape
G. Rods
H. Plates
J. Cones
K. Solid

Growth
L. Accretionary
M. Serial Units + branching
Z. Replacement / molting
N. Remodeling

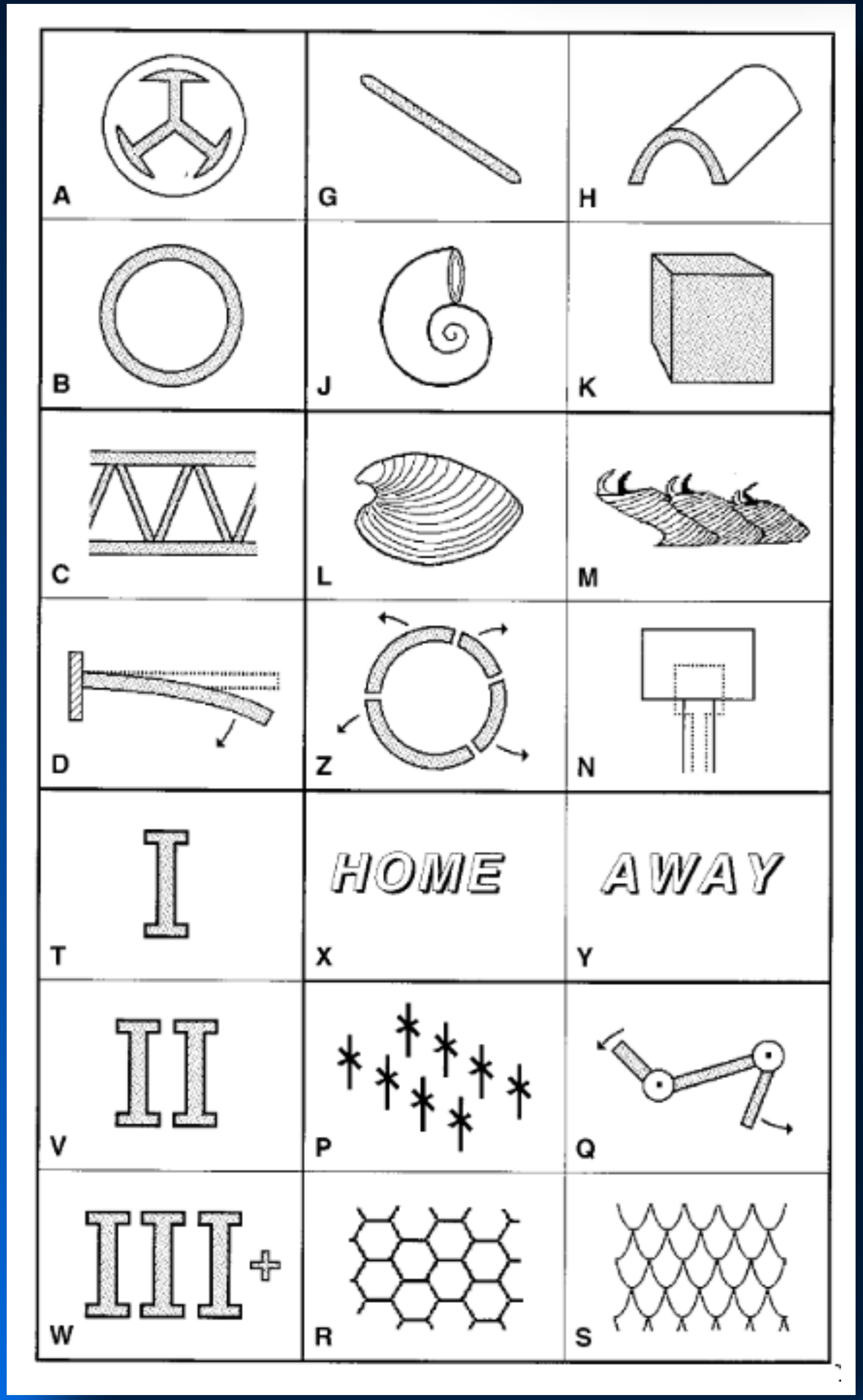
Assembly
X. Growth in place
Y. Prefabrication

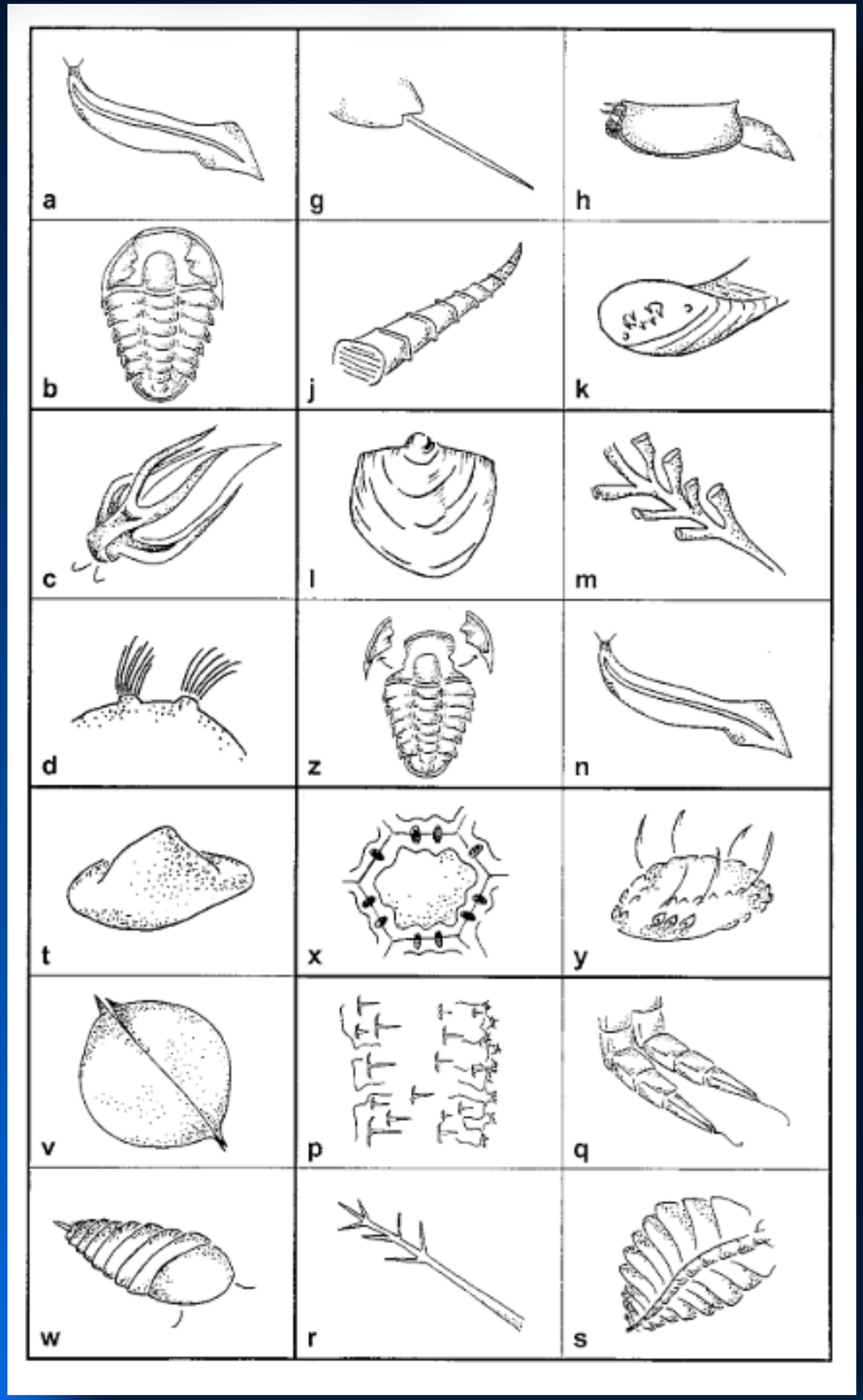
Element Interplay
P. Contact
Q. Jointed
R. Sutured / fused
S. Imbricate

From Thomas et al. (2000)

Morphological Disparity

Measuring Disparity





From Thomas et al. (2000)

Morphological Disparity

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Actual Range of Ordovician Trilobite Morphology


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Measuring Disparity

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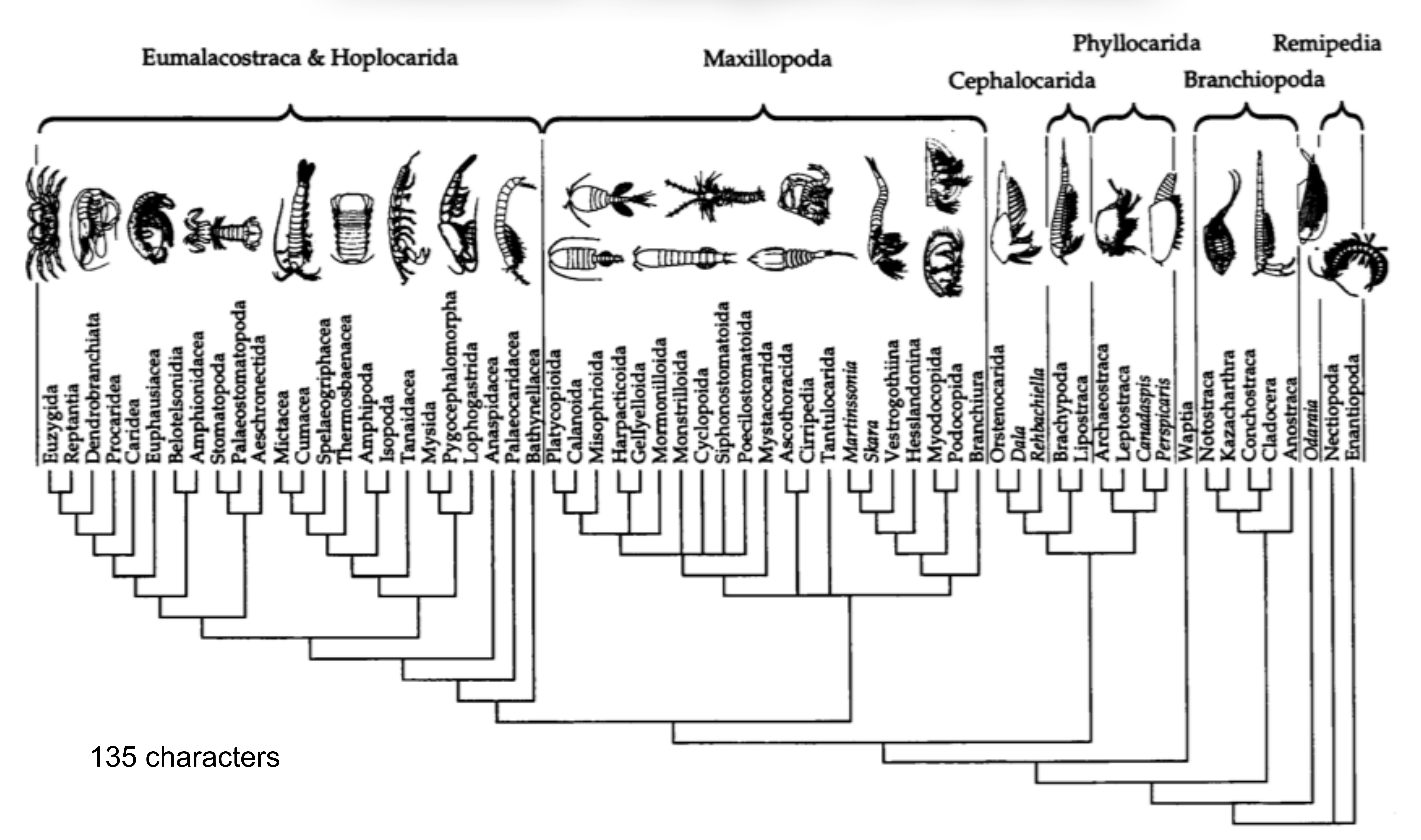
Problematic. Thomas’ skeleton design space is a bold attempt at devising a truly generalized “morphospace” that can, in principle, accommodate a very wide range of morphologies. But it’s a categorical space, not a metric space.

Morphological Disparity

Measuring Disparity

Crustacean Cladogram (Consensus)

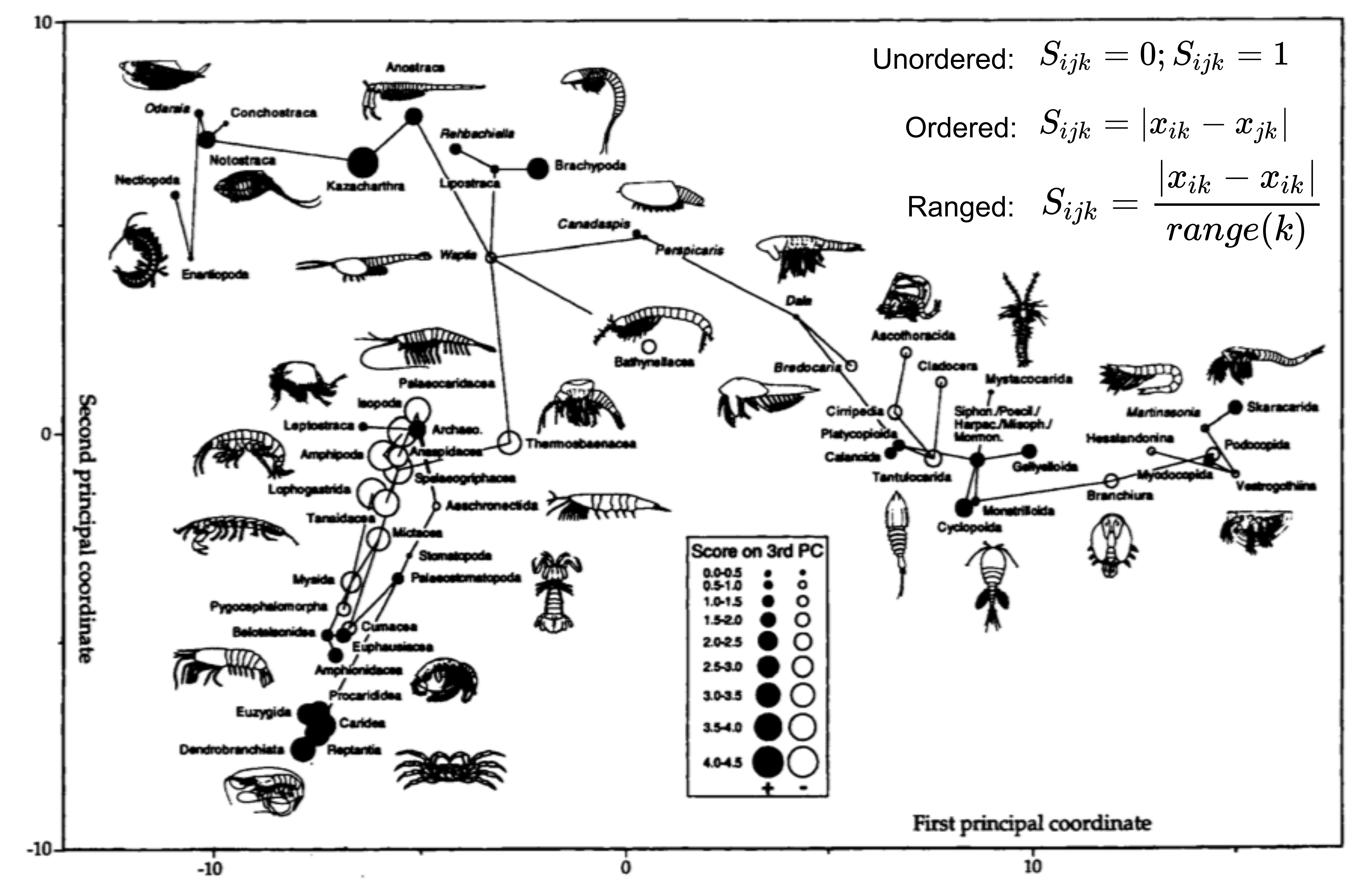


From Wills (1998)

Morphological Disparity

Measuring Disparity

Crustacean Cladogram (Consensus)



Unordered: $S_{ijk} = 0; S_{ijk} = 1$

Ordered: $S_{ijk} = |x_{ik} - x_{jk}|$

Ranged: $S_{ijk} = \frac{|x_{ik} - x_{ik}|}{range(k)}$

From Wills (1998)

Morphological Disparity

Measuring Disparity

A Plethora of Disparity Indices

Measure	Data	Index Type	Equation	Description
Morph. Variety	Any	Volume	$v = \sqrt[m]{\prod_{j=1}^{m} var(x_j)}$	Product of variances across variables
Morph. Variety	Any	Volume	$v = \sqrt[m]{\prod_{j=1}^{m} (max(x_j) - min(x_j))}$	Product of ranges across variables
Morph. Variety	Any	Volume	$v = \sqrt[m]{\sum_{j=1}^{m} (max(x_j) - min(x_j))}$	Hyper-ellipsoid volume
Morph. Variety	Any	Sum	$s = \sum_{j=1}^{m} var(x_j)$	Sum of variances across all variables
Morph. Variety	Any	Sum	$s = \sum_{j=1}^{m} (max(x_j) - min(x_j))$	Sum of ranges across all variables

From Wills (1994)

Morphological Disparity

Measuring Disparity

A Plethora of Disparity Indices

Measure	Data	Index Type	Equation	Description
Morph. Range	Phenetic	Distance	$\bar{d}_{group} = \frac{\sum_{j=1}^{group} \sum_{i=1}^{n_{group}} \sum_{k=1}^{m} \sqrt[2]{(x_{ik} - x_{group_{jk}})^2}}{n}$	Mean Euclidean distance from group centroid
Morph. Range	Phenetic	Distance	$\bar{\bar{d}}_{group} = \frac{\sum_{i=1}^{n} \sum_{k=1}^{m} \sqrt[2]{(x_{ik} - \bar{\bar{x}}_{group_k})^2}}{n}$	Mean Euclidean distance from grand centroid
Morph. Range	Phenetic	Distance	$\bar{d}_{anc} = \frac{\sum_{i=1}^{n} \sum_{k=1}^{m} \sqrt[2]{(x_{ik} - x_{anc_k})^2}}{n}$	Mean Euclidean distance from hypothetical ancestral morphology
Morph. Range	Phenetic	Distance	$\bar{d} = \frac{\sum_{i=1}^{n} \sum_{j=1}^{n} \sum_{k=1}^{m} \sqrt[2]{(x_{ik} - x_{jk})^2}}{n^2}$	Mean Euclidean distance between all taxa
Morph. Range	Phenetic	Distance	$d_1 = \frac{\sum_{i=1}^{n} \sum_{j=1}^{n} \sum_{k=1}^{m} \lvert x_{ik} - x_{jk} \rvert}{n^2}$	Mean Manhatten distance between all taxa

From Wills (1994)

Morphological Disparity

Measuring Disparity

A Plethora of Disparity Indices

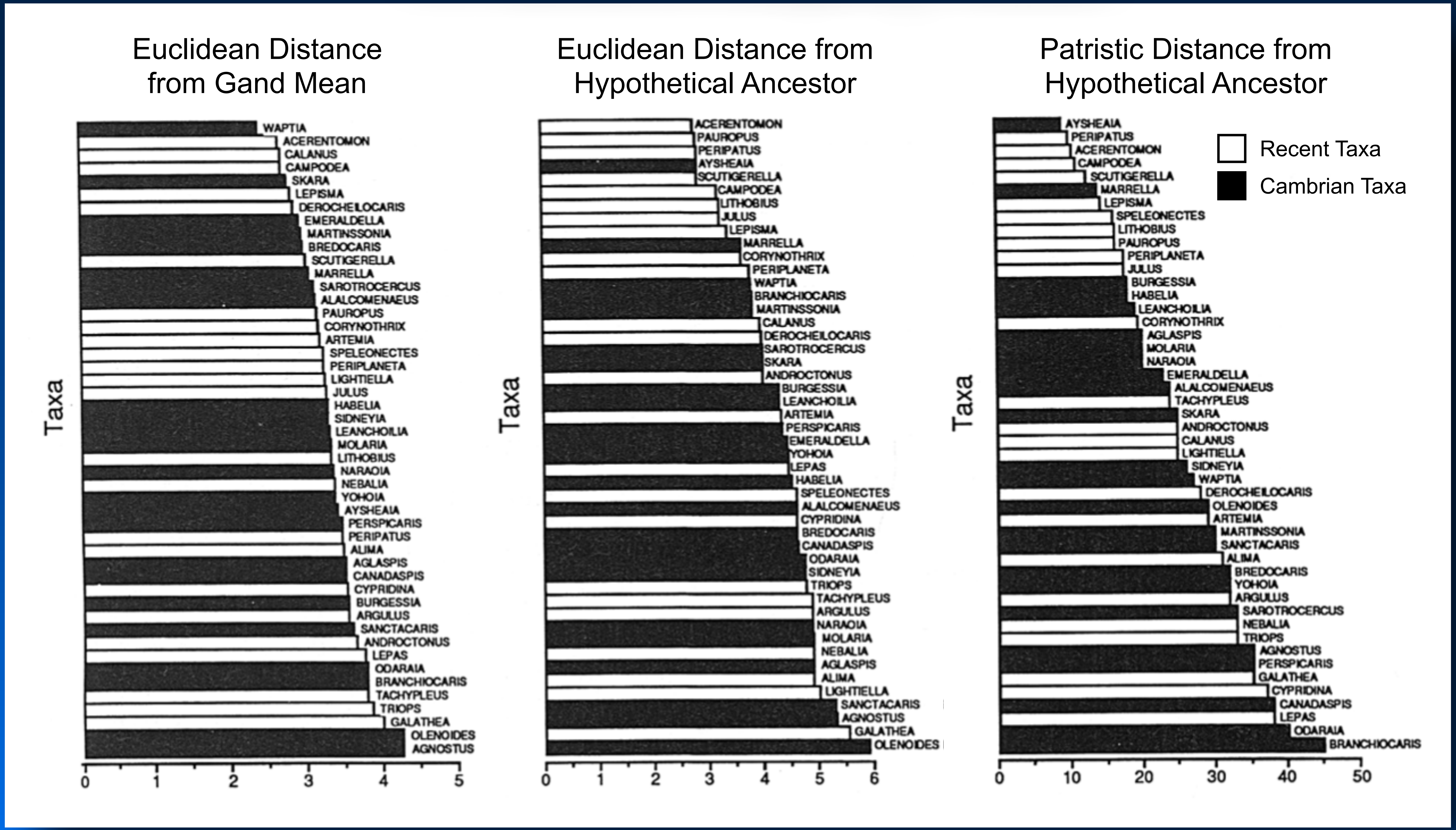
Measure	Data	Index Type	Equation	Description
Morph. Range	Cladistic	Distance	$\bar{d}_{patristic-anc} = \frac{\sum_{i=1}^{n} branchlength(taxon_i <=> ancestor)}{n_{branchlengths}}$	Mean patristic distance from hypothetical ancestor
Morph. Range	Cladistic	Distance	$\bar{d}_{patristic} = \frac{\sum_{i=1}^{n} \sum_{j=1}^{n} branchlength(taxon_i <=> taxon_j)}{n^2}$	Mean patristic distance between all taxa

From Wills (1994)

Morphological Disparity

Measuring Disparity

A Plethora of Disparity Indices



Euclidean Distance from Gand Mean

Euclidean Distance from Hypothetical Ancestor

Patristic Distance from Hypothetical Ancestor

From Wills (1994)

Morphological Disparity

Measuring Disparity

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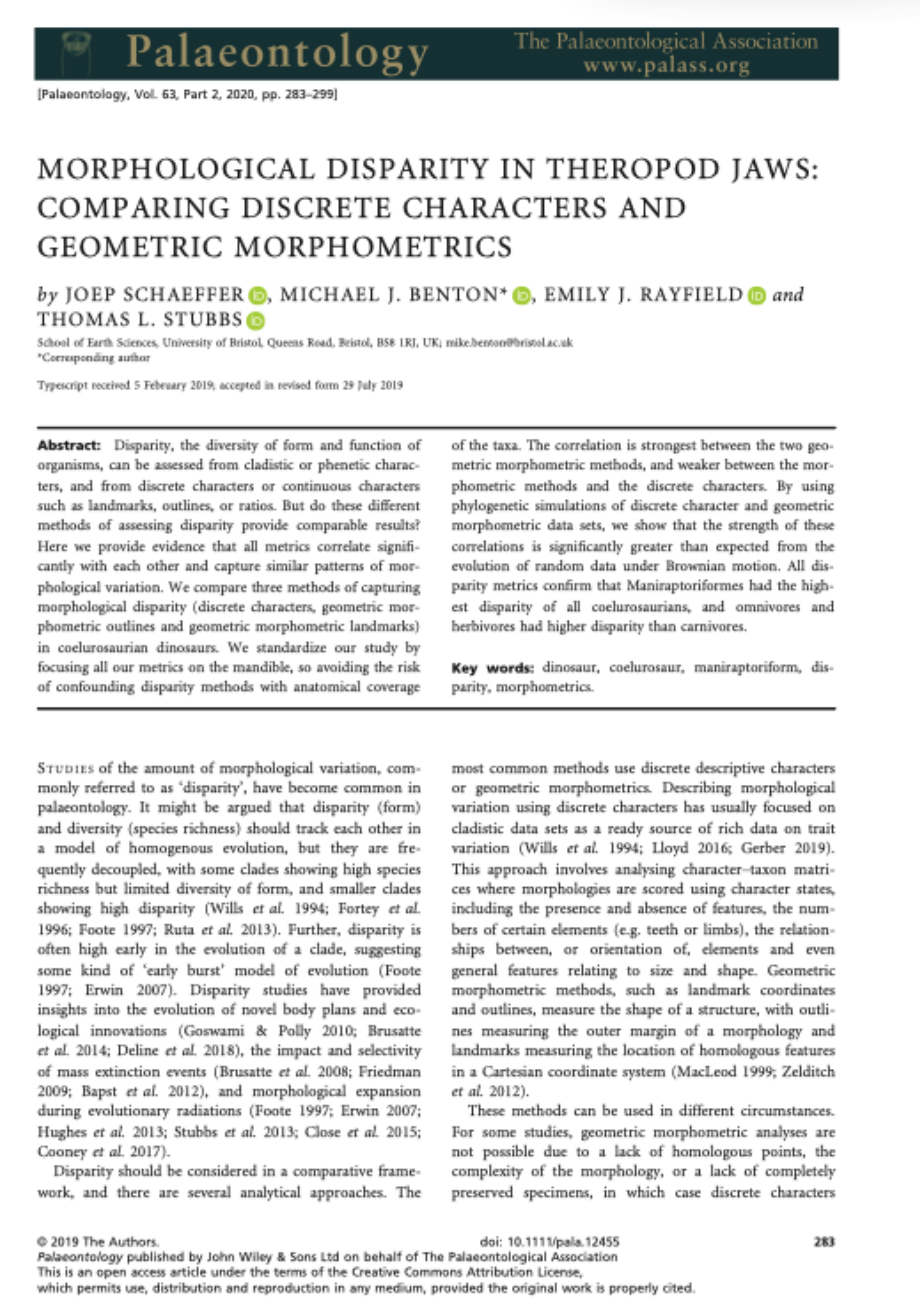
- ☑ … measure density, range, clumping, and a host of other properties that determine differential filling of this totality.
- ☑ …. be able to assess the variation in this differential filling through time.

The best of the lot (so far). However, scaling of the phylogenetic characters is problematic as is the inclusion of taxa with radically different body plans. In addition, use of overall variances of taxa scattered across a morphospace assumes all intermediate conditions are realizable. Of course, there’s also the issue of how correct the pattern of phylogenetic relations might be.

Morphological Disparity

Measuring Disparity



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MORPHOLOGICAL DISPARITY IN THEROPOD JAWS: COMPARING DISCRETE CHARACTERS AND GEOMETRIC MORPHOMETRICS

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Abstract: Disparity, the diversity of form and function of organisms, can be assessed from cladistic or phenetic characters, and from discrete characters or continuous characters such as landmarks, outlines, or ratios. But do these different methods of assessing disparity provide comparable results? Here we provide evidence that all metrics correlate significantly with each other and capture similar patterns of morphological variation. We compare three methods of capturing morphological disparity (discrete characters, geometric morphometric outlines and geometric morphometric landmarks) in coelurosaurian dinosaurs. We standardize our study by focusing all our metrics on the mandible, so avoiding the risk of confounding disparity methods with anatomical coverage of the taxa. The correlation is strongest between the two geometric morphometric methods, and weaker between the morphometric methods and the discrete characters. By using phylogenetic simulations of discrete character and geometric morphometric data sets, we show that the strength of these correlations is significantly greater than expected from the evolution of random data under Brownian motion. All disparity metrics confirm that Maniraptoriformes had the highest disparity of all coelurosaurians, and omnivores and herbivores had higher disparity than carnivores.

Key words: dinosaur, coelurosaur, maniraptoriform, disparity, morphometrics.

STUDIES of the amount of morphological variation, commonly referred to as 'disparity', have become common in palaeontology. It might be argued that disparity (form) and diversity (species richness) should track each other in a model of homogenous evolution, but they are frequently decoupled, with some clades showing high species richness but limited diversity of form, and smaller clades showing high disparity (Wills *et al.* 1994; Fortey *et al.* 1996; Foote 1997; Ruta *et al.* 2013). Further, disparity is often high early in the evolution of a clade, suggesting some kind of 'early burst' model of evolution (Foote 1997; Erwin 2007). Disparity studies have provided insights into the evolution of novel body plans and ecological innovations (Goswami & Polly 2010; Brusatte *et al.* 2014; Deline *et al.* 2018), the impact and selectivity of mass extinction events (Brusatte *et al.* 2008; Friedman 2009; Bapst *et al.* 2012), and morphological expansion during evolutionary radiations (Foote 1997; Erwin 2007; Hughes *et al.* 2013; Stubbs *et al.* 2013; Close *et al.* 2015; Cooney *et al.* 2017).

Disparity should be considered in a comparative framework, and there are several analytical approaches. The most common methods use discrete descriptive characters or geometric morphometrics. Describing morphological variation using discrete characters has usually focused on cladistic data sets as a ready source of rich data on trait variation (Wills *et al.* 1994; Lloyd 2016; Gerber 2019). This approach involves analysing character–taxon matrices where morphologies are scored using character states, including the presence and absence of features, the numbers of certain elements (e.g. teeth or limbs), the relationships between, or orientation of, elements and even general features relating to size and shape. Geometric morphometric methods, such as landmark coordinates and outlines, measure the shape of a structure, with outlines measuring the outer margin of a morphology and landmarks measuring the location of homologous features in a Cartesian coordinate system (MacLeod 1999; Zelditch *et al.* 2012).

These methods can be used in different circumstances. For some studies, geometric morphometric analyses are not possible due to a lack of homologous points, the complexity of the morphology, or a lack of completely preserved specimens, in which case discrete characters

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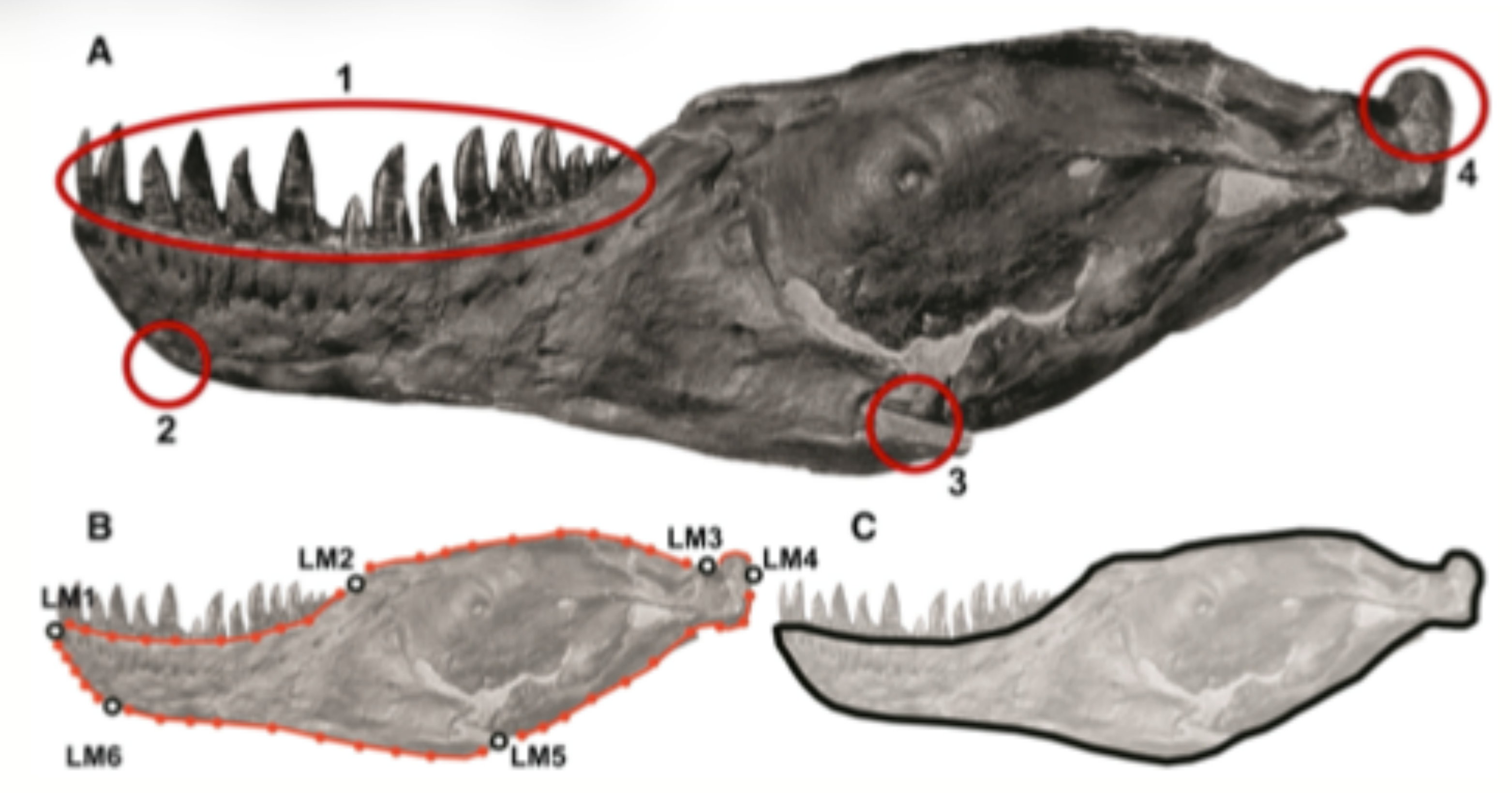

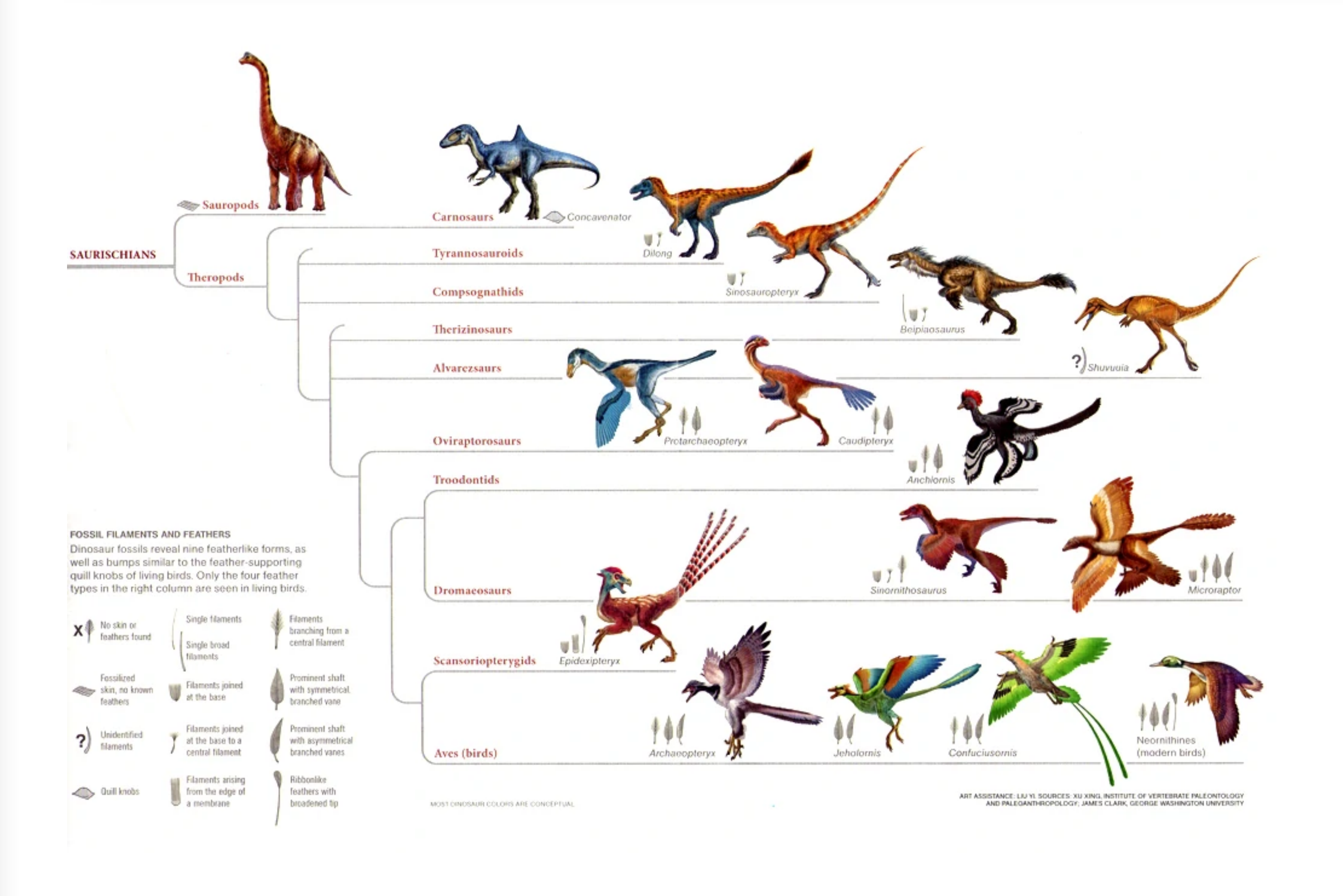

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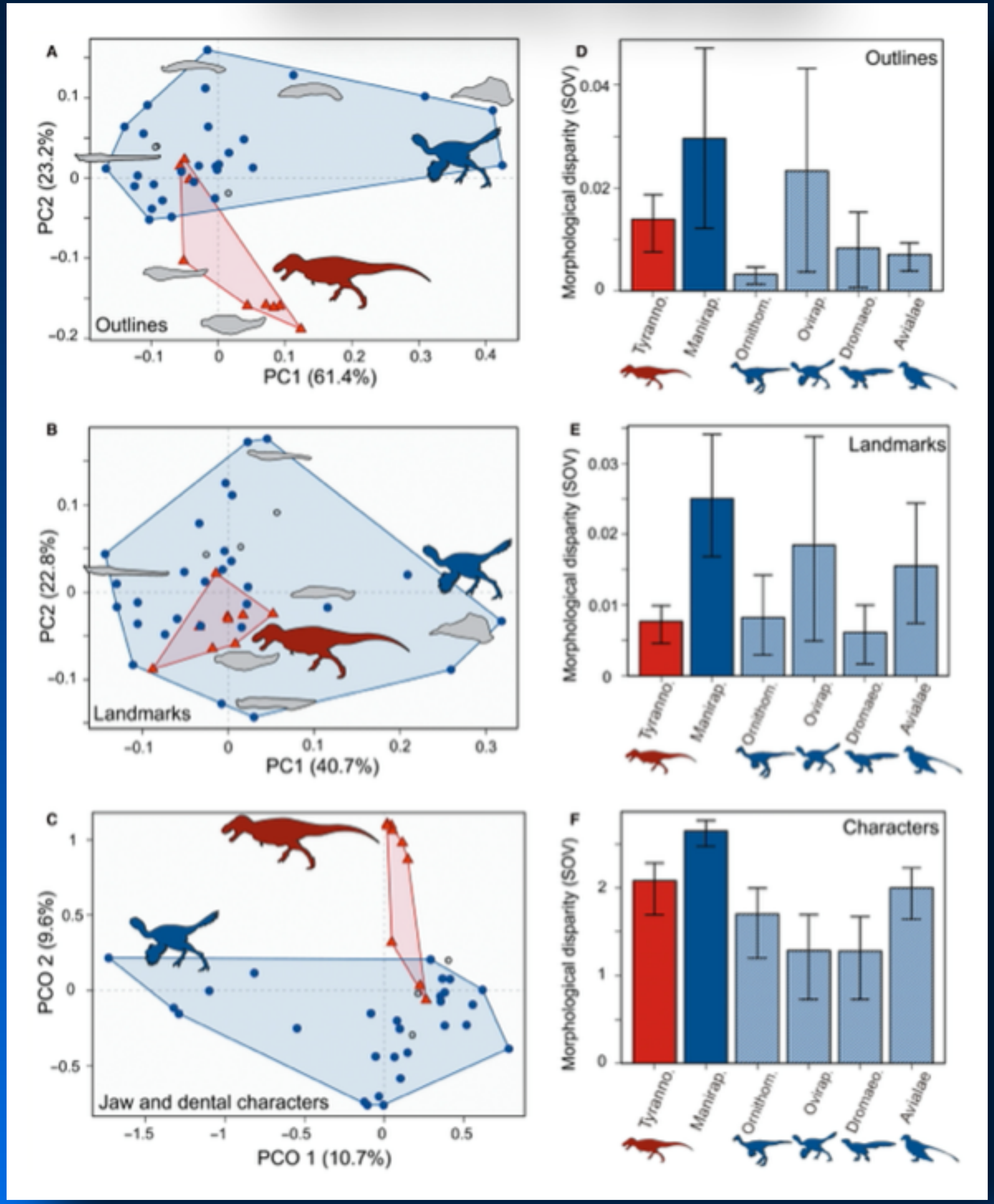
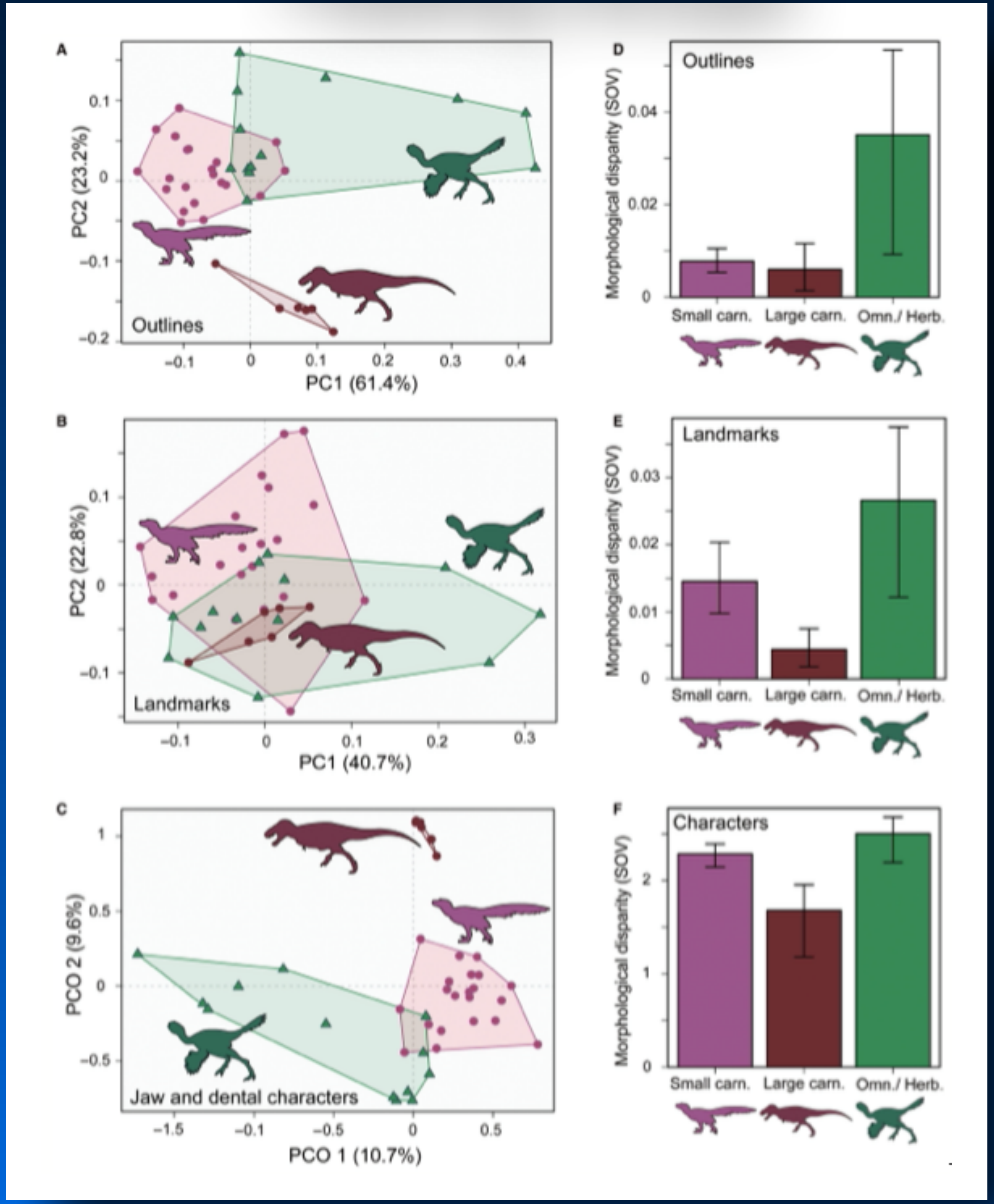
Taxonomy Groups



Feeding Groups



Diagrams from Schaeffer et al. (2020)

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Measuring Disparity

To accomplish this task Gould noted, “We need to …

- ☑ … define a full range of the abstract (and richly multivariate) space into which all organisms may fit (the morphospace).
- ☑ … be able to characterize individual organisms and plot them within this encompassing space.
- ☑ … measure density, range, clumping, and a host of other properties that determine differential filling of this totality.
- ☑ …. be able to assess the variation in this differential filling through time.

It’s notable (to me) that the same mistakes are being committed now (in 2020) as in 1991. A dinosaur mandible is not the same thing as a dinosaur and, whatever the disparity of mandible morphology might be, it does not constitute an adequate proxy for the rest of the body. Moreover, the manner in which disparity is estimated fails to take the degree to which the entire space is filled (or not) into consideration.

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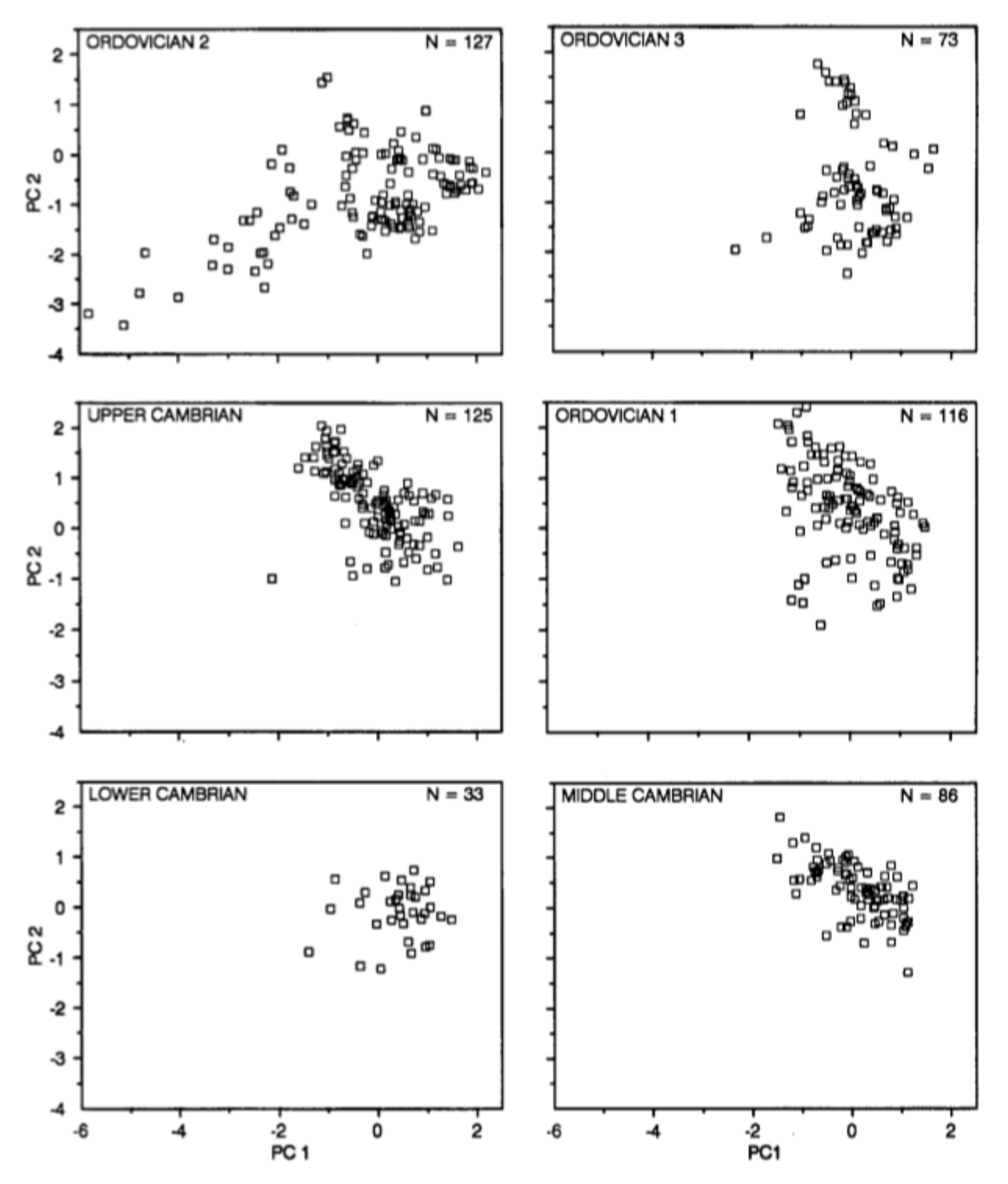
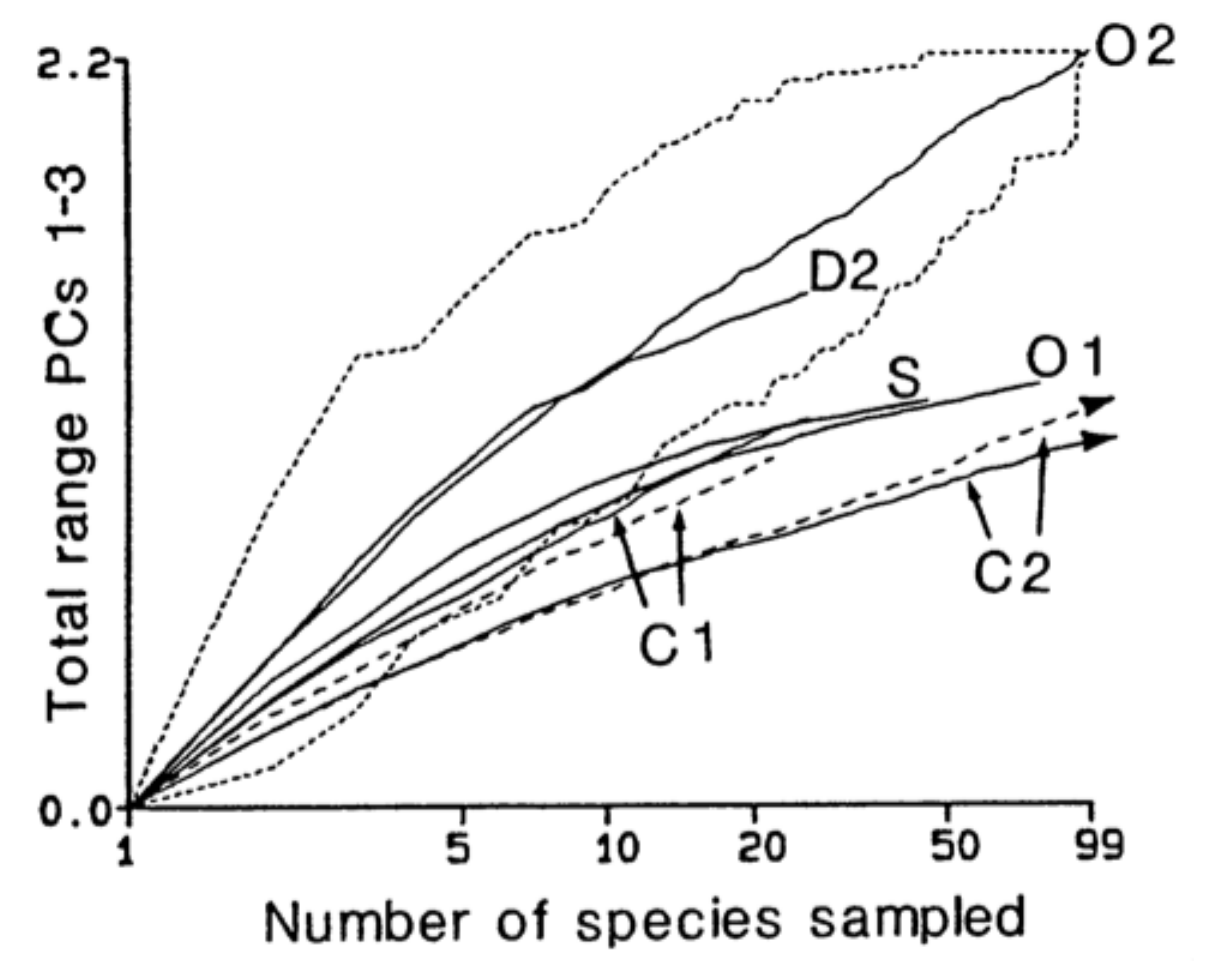
Obviously, the estimate of morphological disparity are, to some extent, dependent on the number of taxa recovered from the stratigraphic interval in question. Fortunately, some of the same methods use to correct taxic richness estimates for sample size variation can be repurposed to correct disparity data.





Diagrams from Foote (1991; left) and Foote (1992; right)

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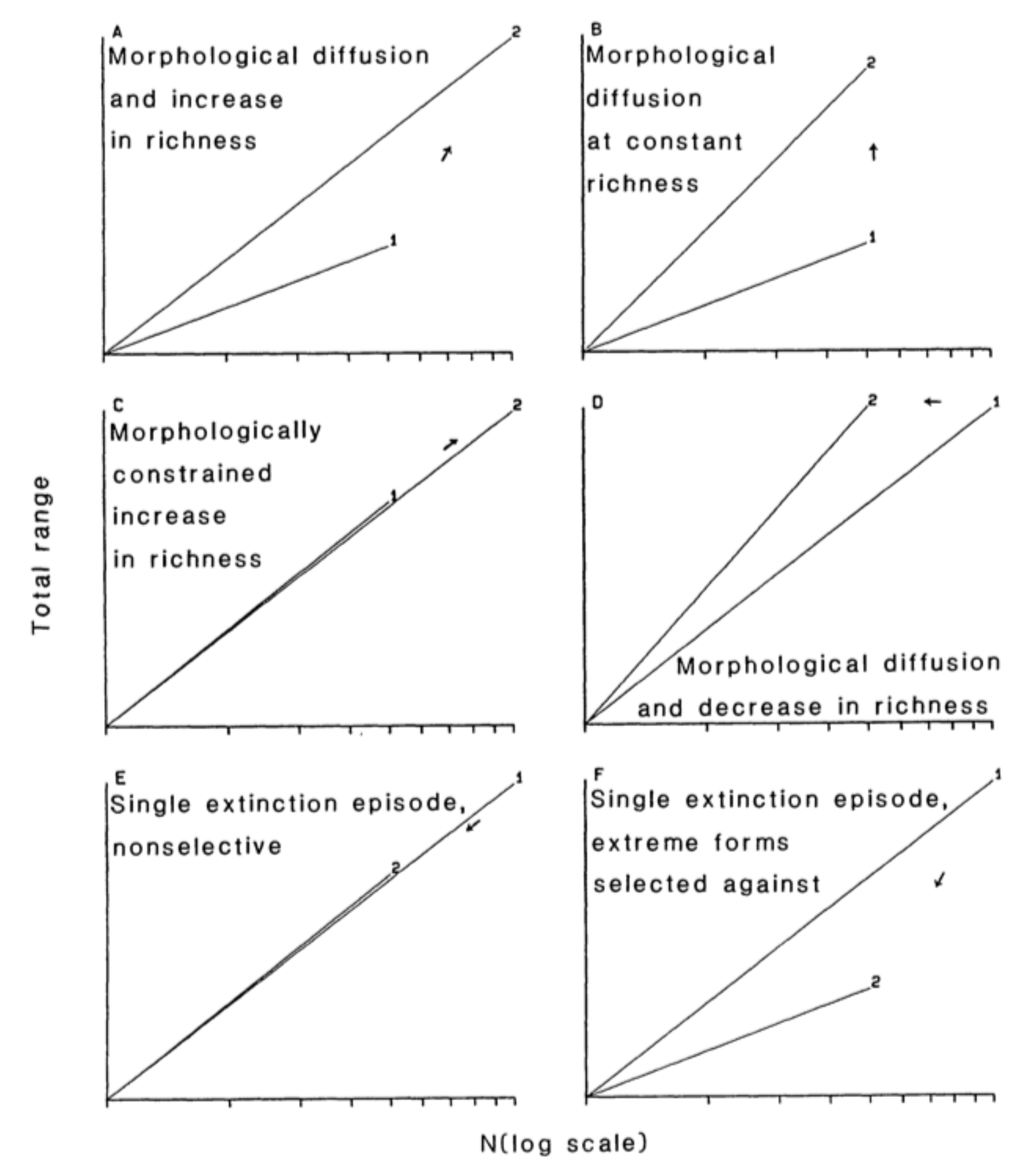
Rarefaction Curves



- Morphological diffusion with constant richness (A) cannot be distinguished from diffusion with true richness increase but decreased sample size (B).
- Morphologically constrained richness increase (C) cannot be distinguished from simple increase in sample size.
- If extinction is morphologically non-selective and takes place over multiple events disparity is maintained or increases despite richness decrease (D).
- Since nonselective extinction events yield a pattern identical to simple richness decrease (E).
- Single extinction events selecting against morphologically extreme forms yield lower richness and lower disparity.

Diagram from Foote (1992)

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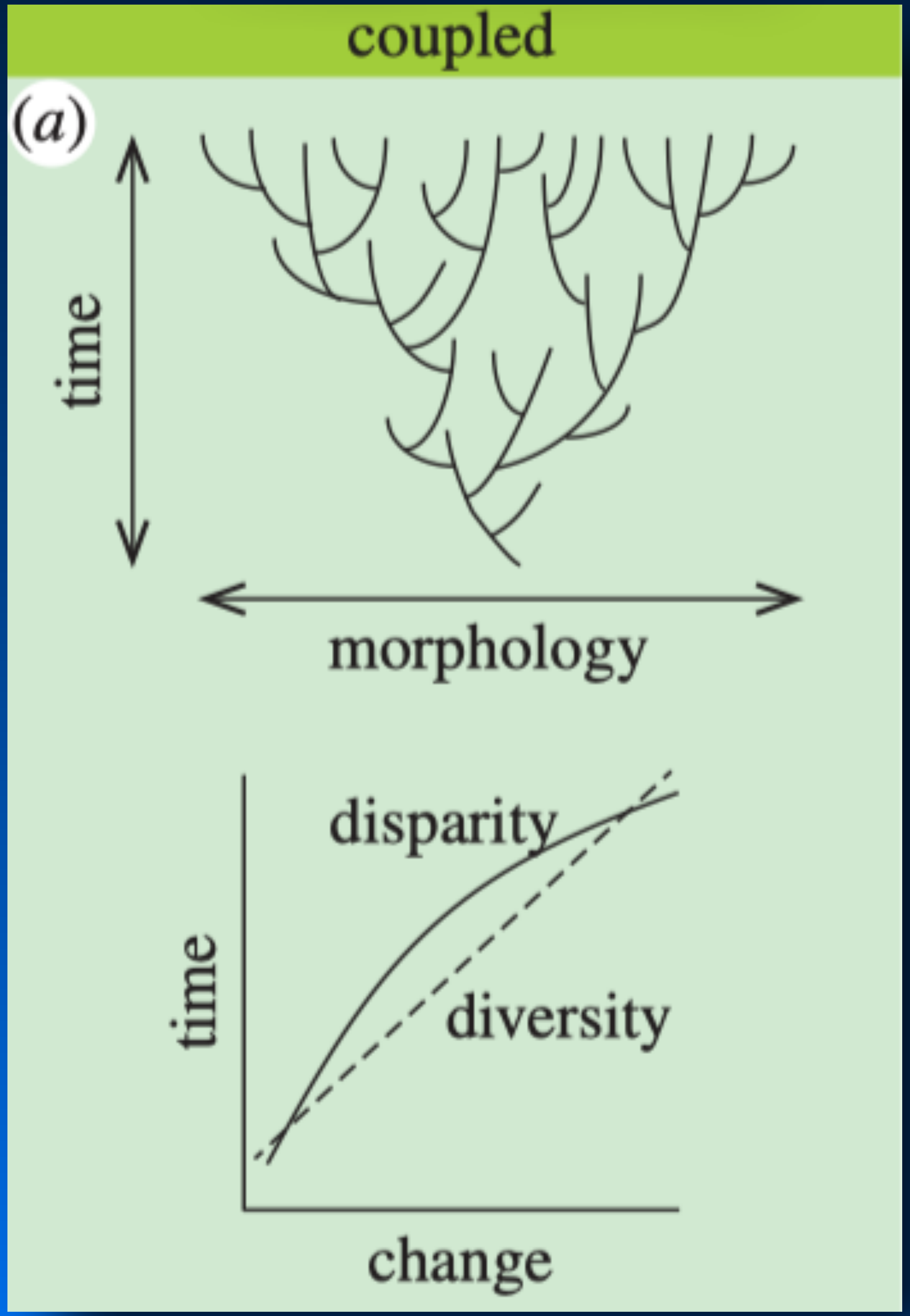
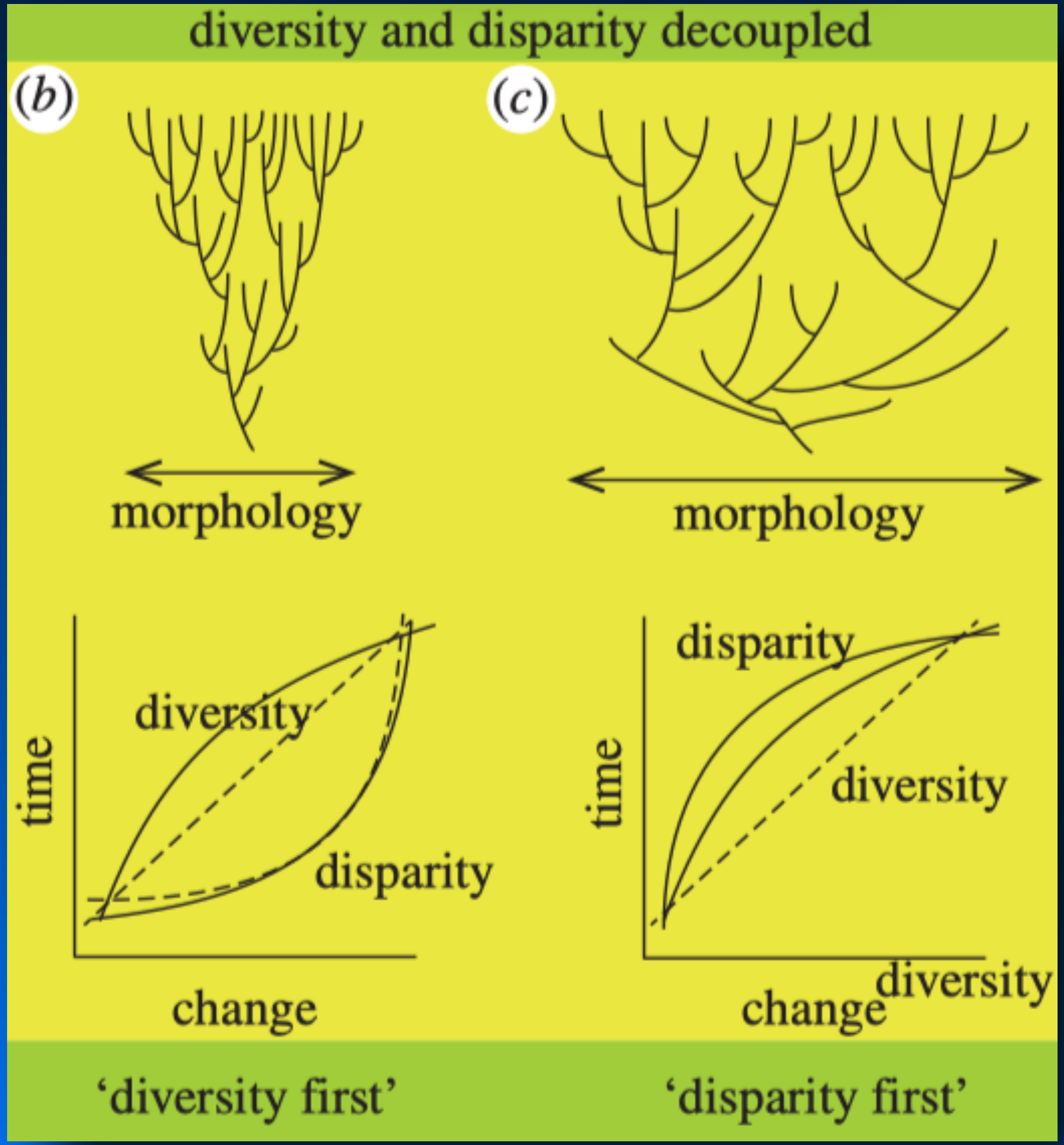
Richness versus Disparity

Coupled Geometry



Decoupled Geometries



Diagrams from Benton et al. (2015)

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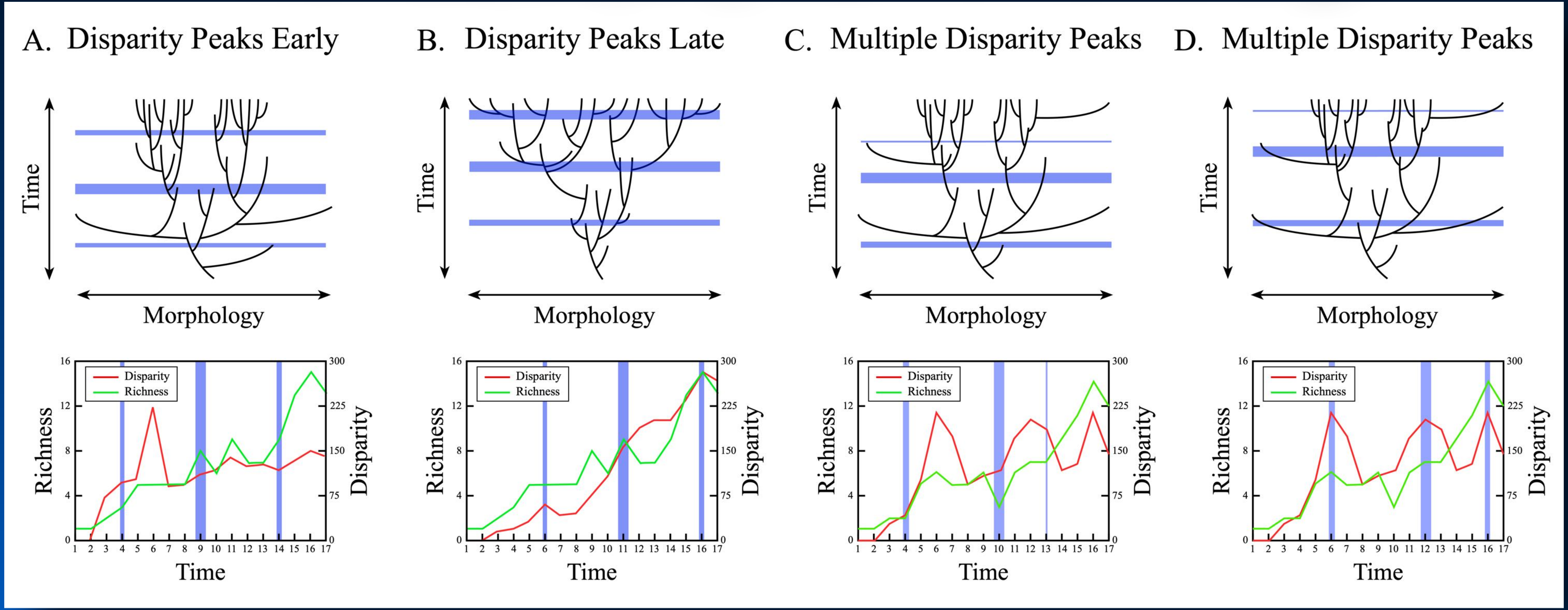
Richness, Disparity & Environment Change



If we combine assessments of taxic richness and morphological disparity with the timing of environmental events it is possible to develop association tests that can identify the causes of taxic richness increases/decreases and morphological disparity increases/decreases.

Diagram from MacLeod (2021)

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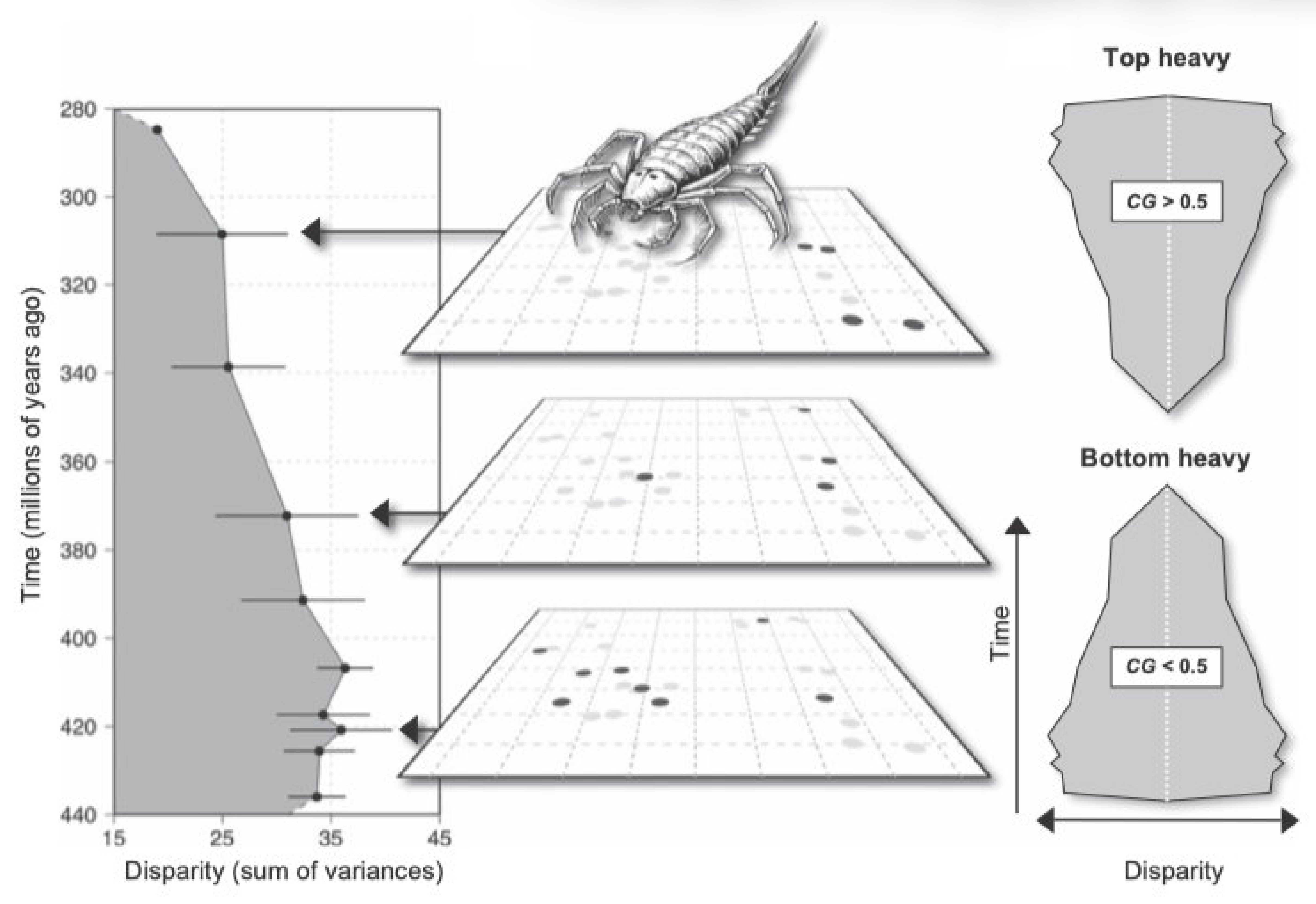
Trends in Disparity Data



In order to test Gould’s original (1991) assertion — based on the Burgess Shale data — that taxic richness and taxic disparity are decoupled with disparity peaking early in a clade’s history Hughes et al. (2013) examined results from 98 Phanerozoic clades.

Diagrams from Hughes et al. (2013)

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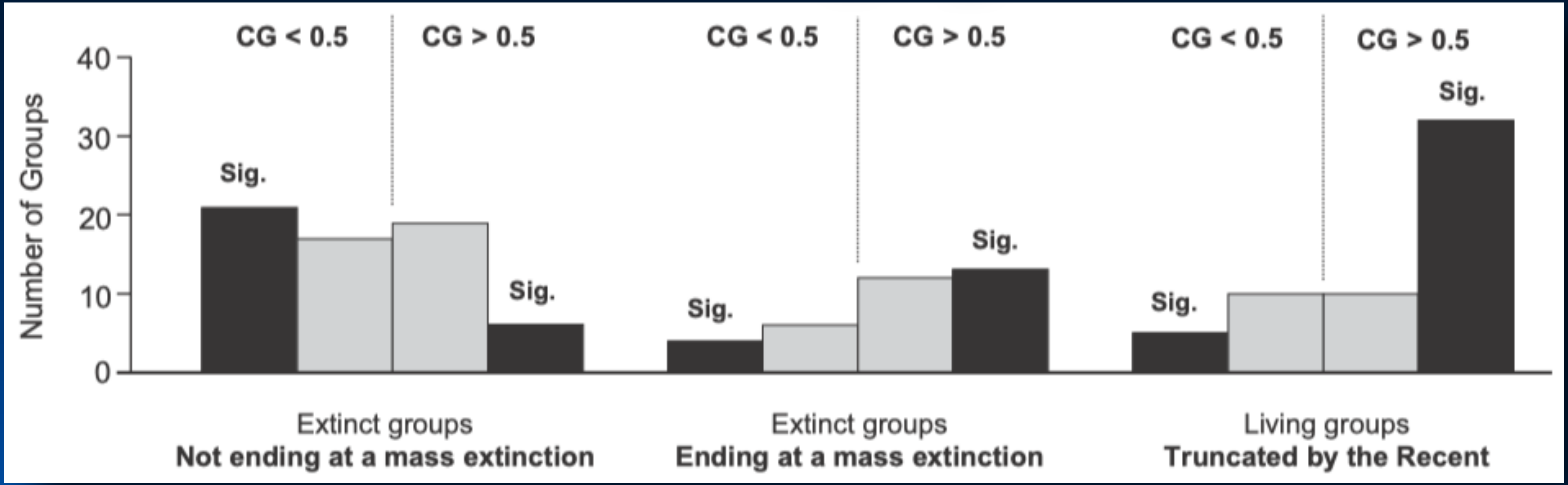
Trends in Disparity Data



Results suggested that Gould's (1991) assertion was correct for clades whose termination did not coincide with one of the five generally accepted mass extinctions or whose taxic richness values were not biased by the "pull of the Recent".

Nevertheless, these results indicate that the majority of clades considered in this analysis did not conform to Gould's bottom-heavy disparity model.

Diagrams from Hughes et al. (2013)

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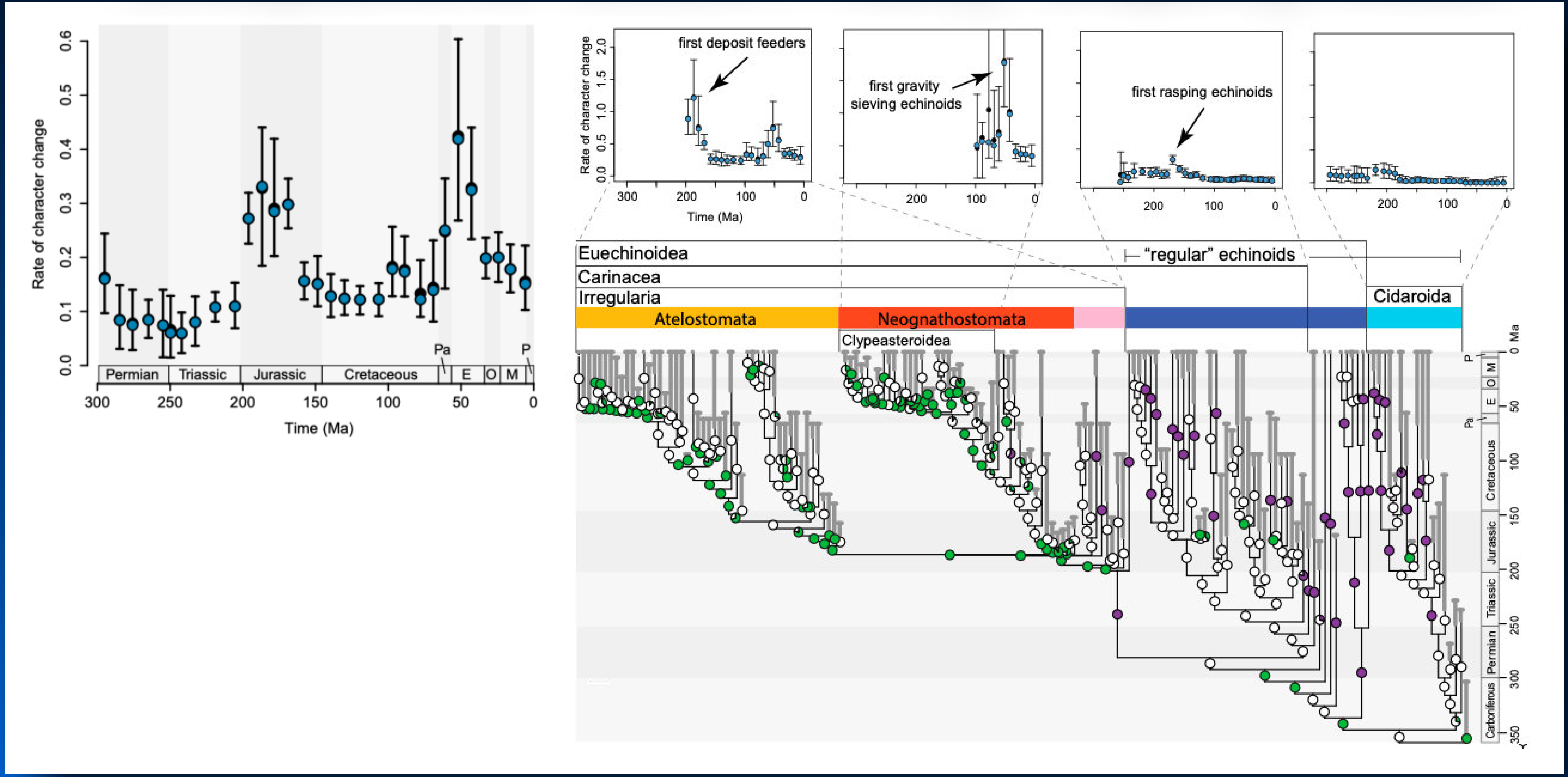
Exceptions to “Bottom-Heavy” Disparity Model



However, Hopkins & Smith (2015) have shown recently that echinoids exhibited bursts of rapid morphological diversification across their phylogenetic history. These coincided with adaptive feeding innovations.

Diagrams from Hopkins & Smith et al. (2015)

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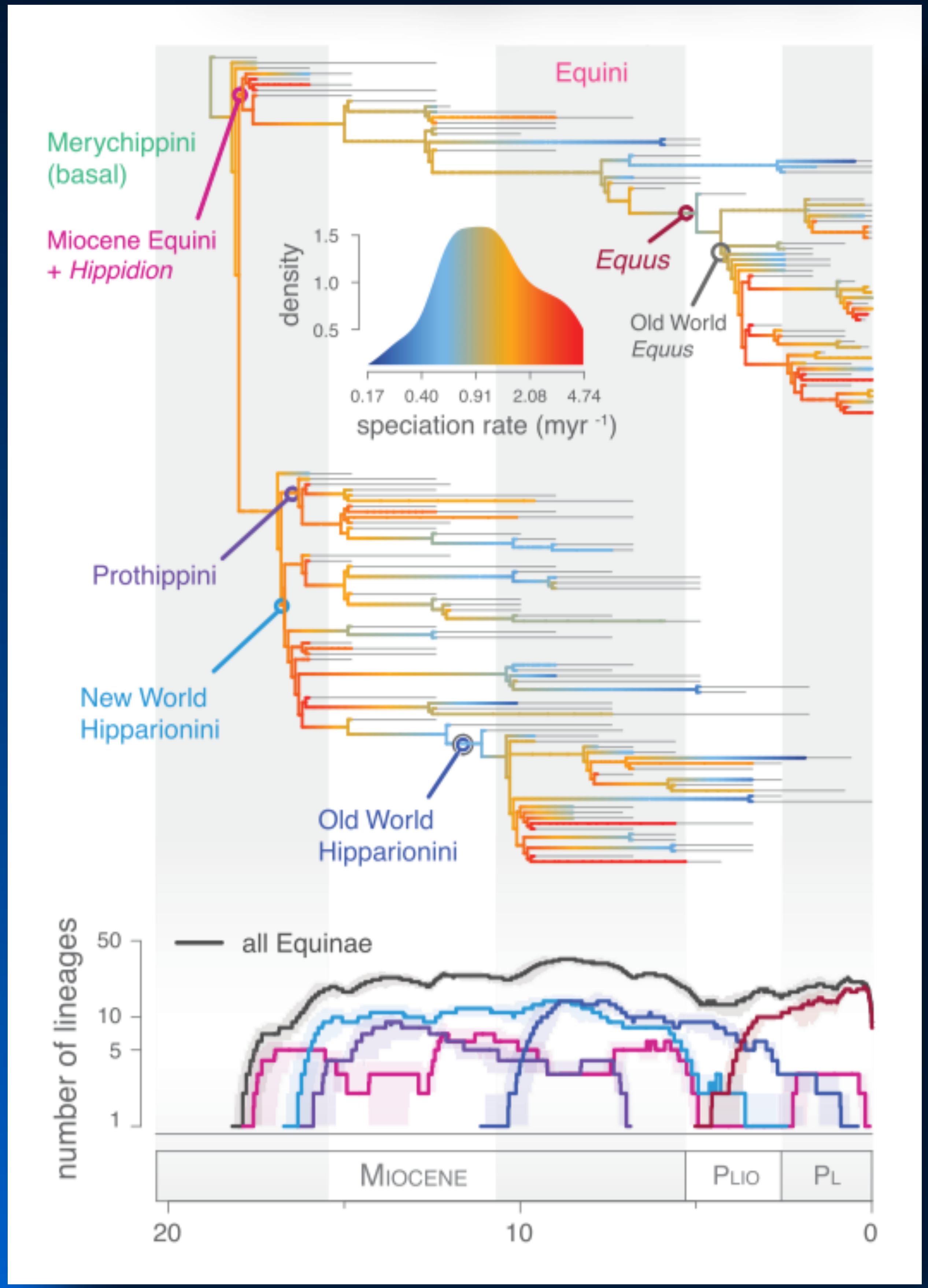
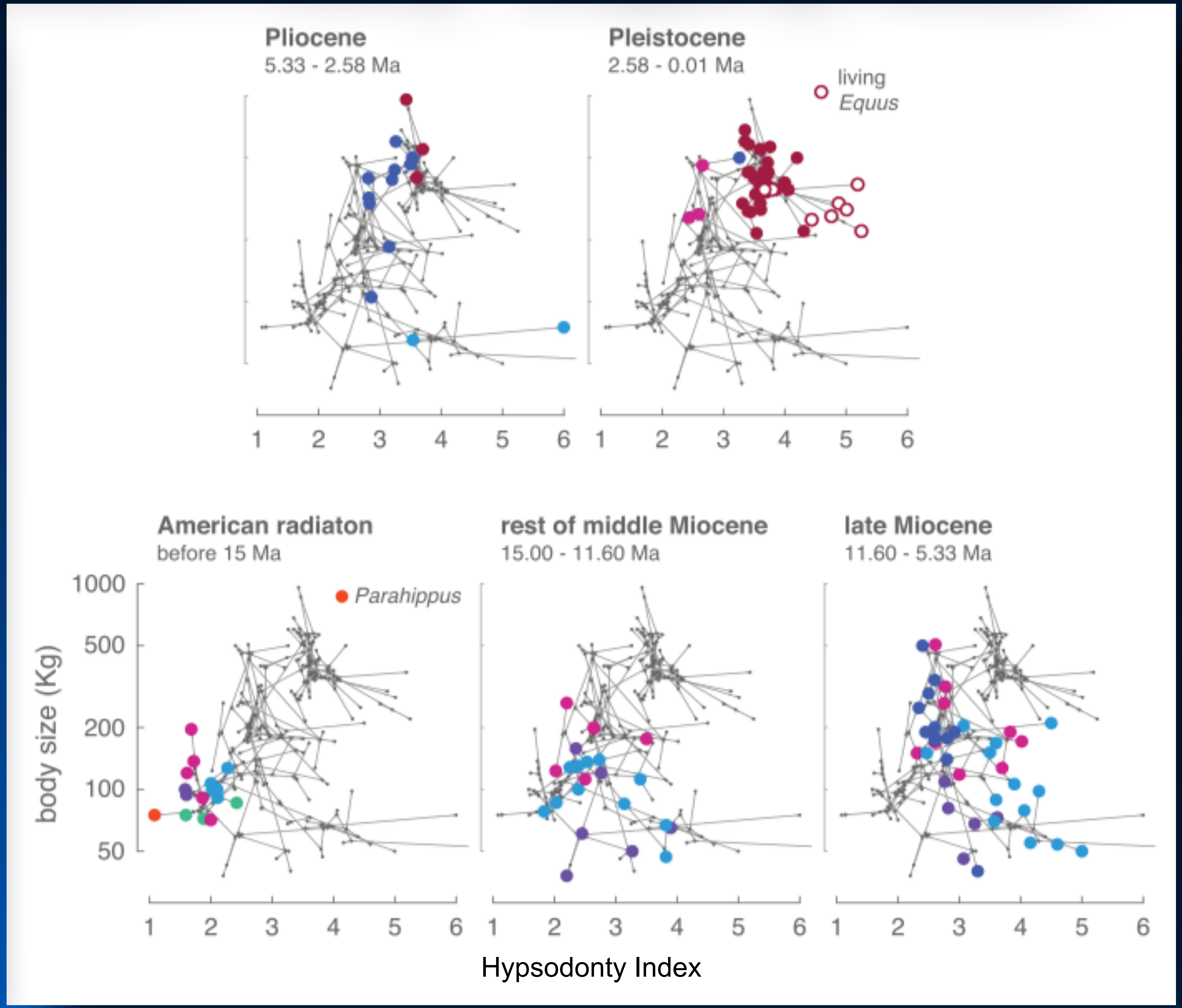
Exceptions to “Bottom-Heavy” Disparity Model





Much the same can be said of Neogene-Quaternary horse lineages according to Cantalapiedra et al. (2017). Here diversity dynamics appear to have been controlled by ecological limits.

Diagrams from Cantalapiedra et al. (2017)

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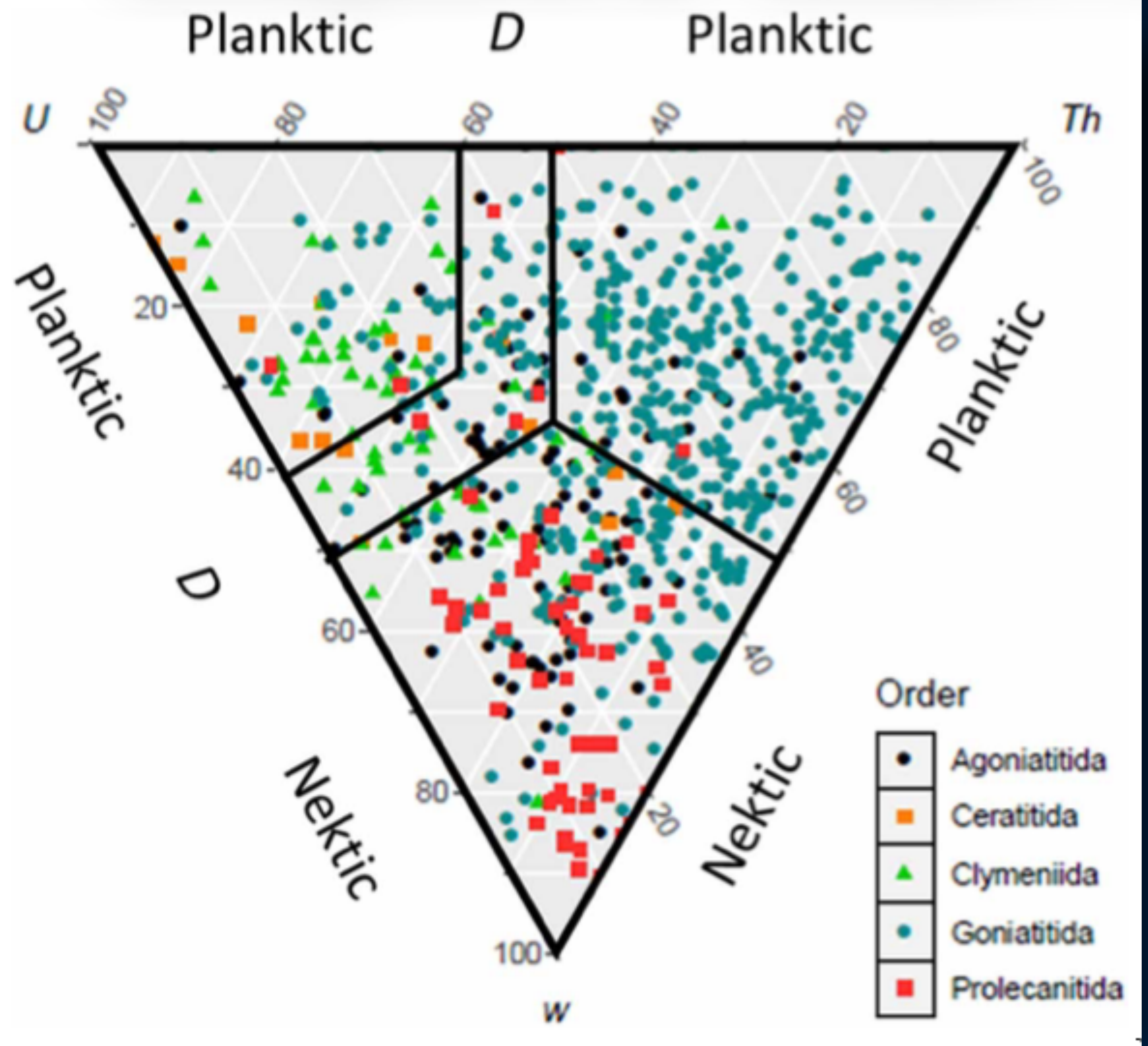
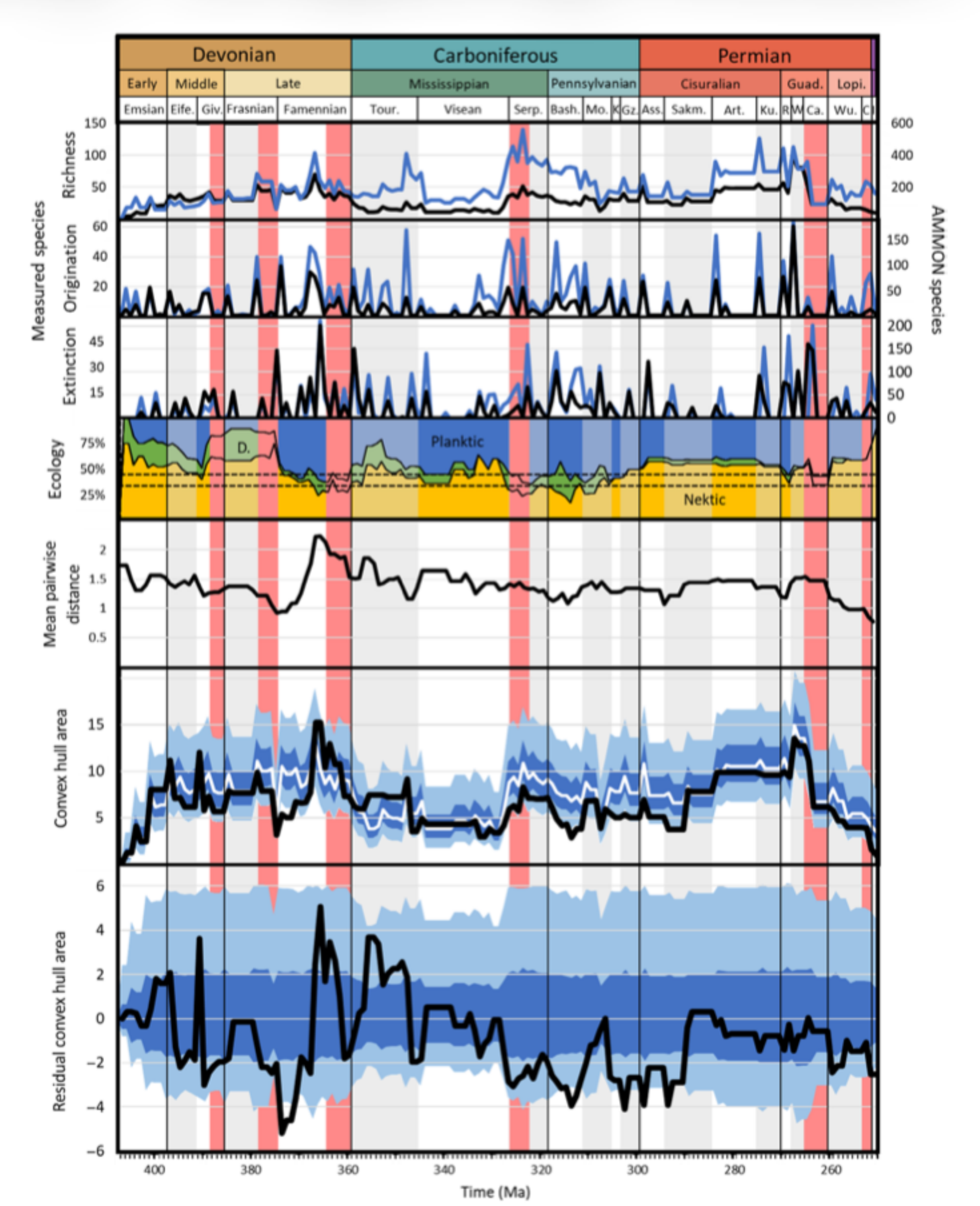
Exceptions to “Bottom-Heavy” Disparity Model





Similarly, Whalen et al. (2020) saw no early busts of eco-morphological disparity in their (very generalized) Paleozoic ammonoid data. This study agrees with the findings of studies on extant clades and rules out the idea that bottom-heavy patterns can only be developed over long timespans.

Diagrams from Whalen et al. (2020)

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The Current Consensus

In the most comprehensive analysis published to date (1,767 characters, 212 extant taxa, 34 phyla) it is clear that, while some clades do exhibit a bottom-heavy distparity structure, many (arthopods, annelids echinoderms, moluscs, chordates) do not.

Interestingly, many of the clades exhibiting the highest "late-stage" disparities did so as the body plans of descendant species were modified to allow invasion of terrestrial environments.

Increased propensity for late-stage disparity Increase was also associated with clades characterized by large genome sizes and diverse microRNA structure.

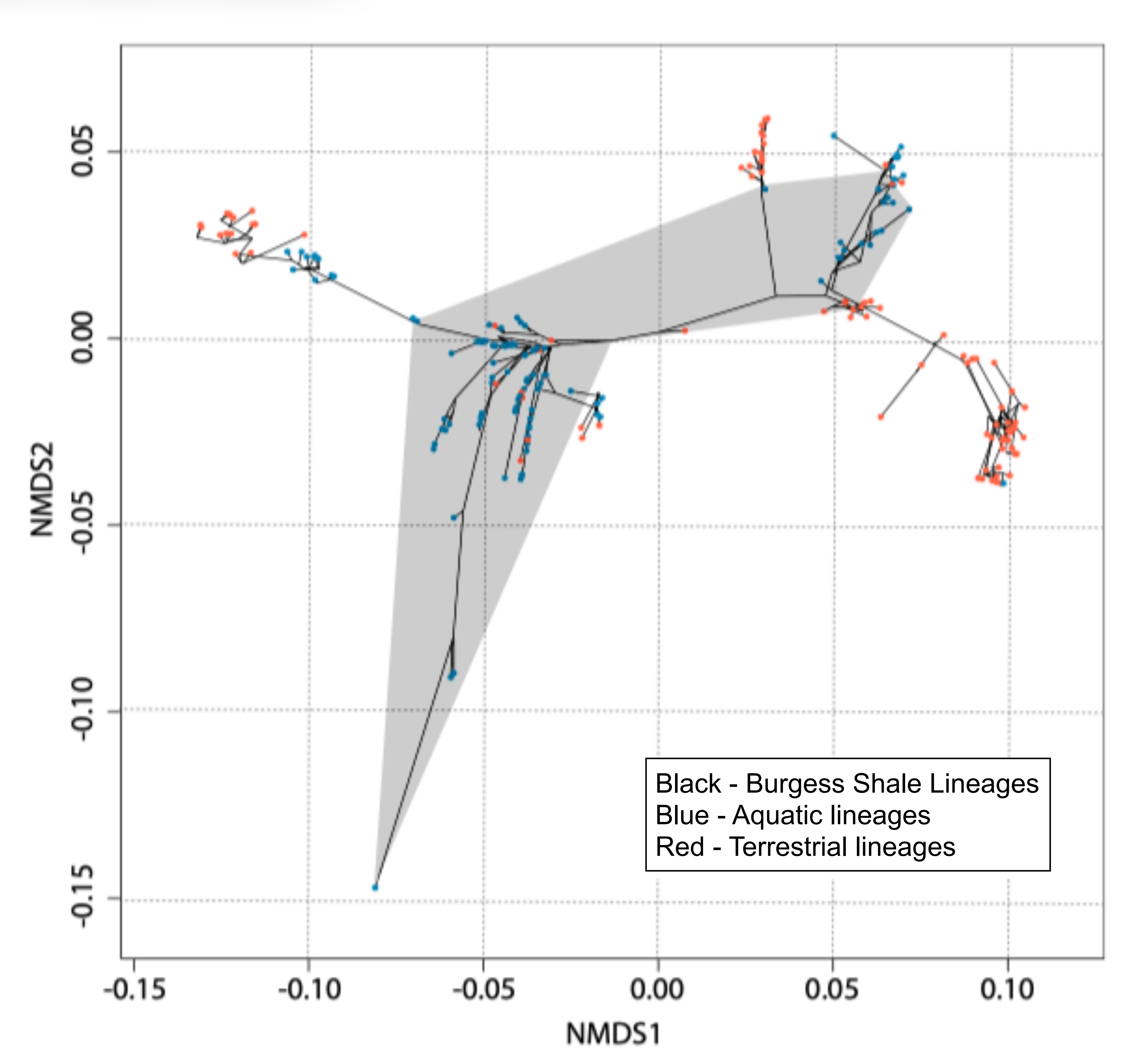

Diagram from Deline et al. (2018)

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