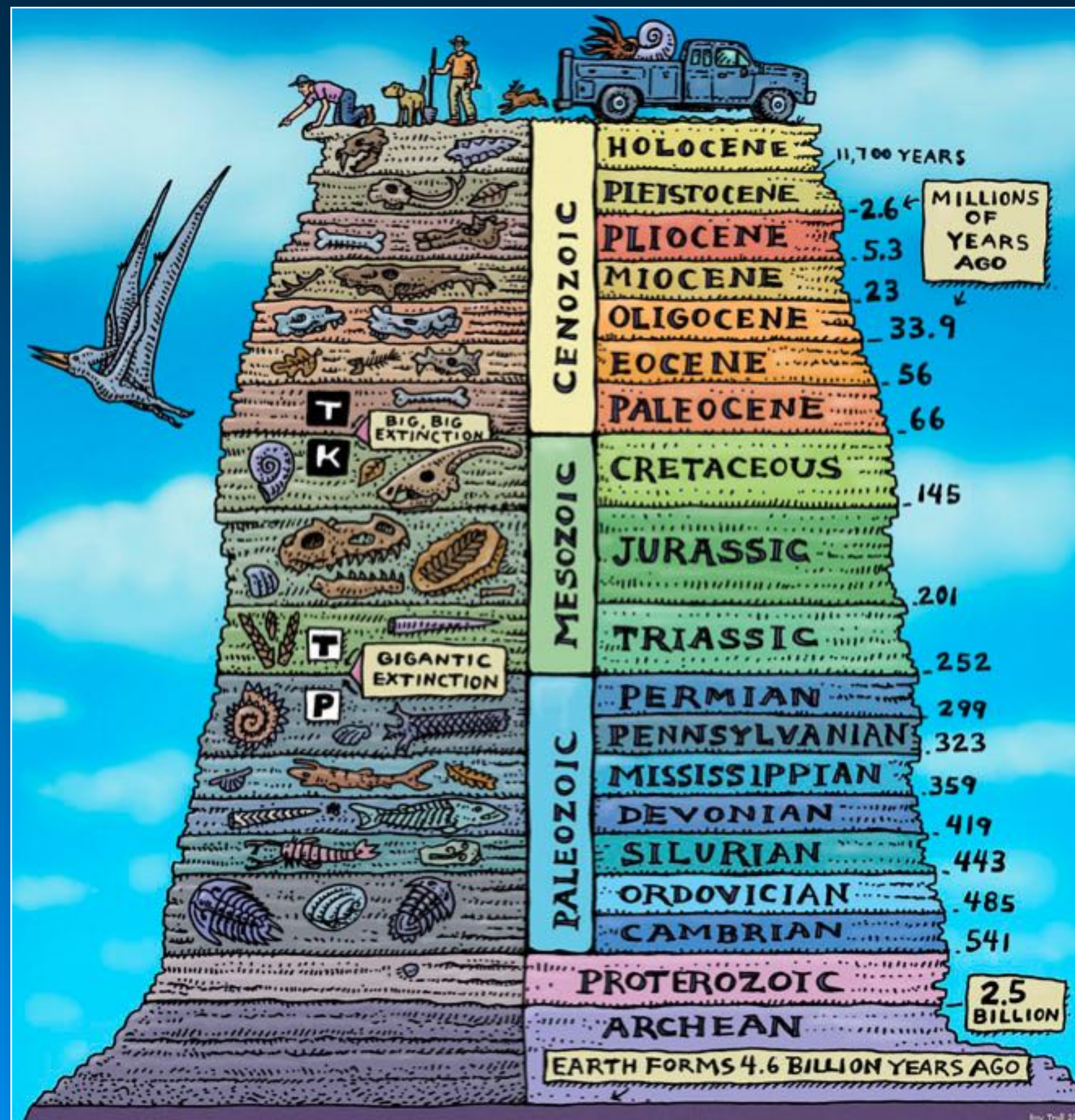


# Principles of Paleobiology

## The Nature of the Fossil Record





# The Nature of the Fossil Record

# What is a fossil?





# The Nature of the Fossil Record

## What is a fossil?

The preserved remains, impression or trace of any once-living thing from any past time in earth history.



Vertebrate



Invertebrate



Plant



Microfossil



Trace



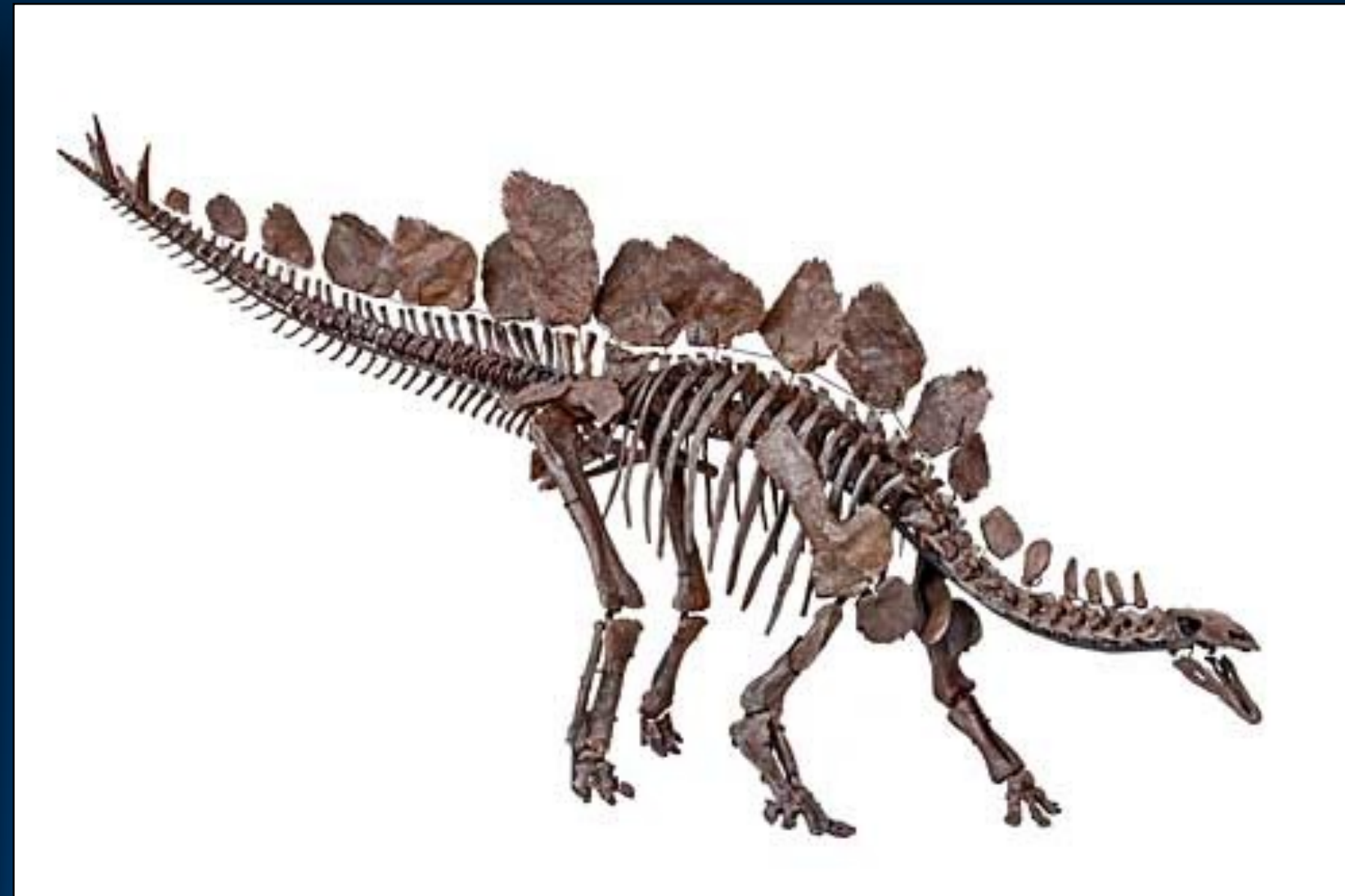
# The Nature of the Fossil Record

## Body Fossils

Fossil whose original materials have been replaced by minerals, either alternative forms of the original mineral or minerals precipitated from groundwater.



Ammonite



Dinosaur



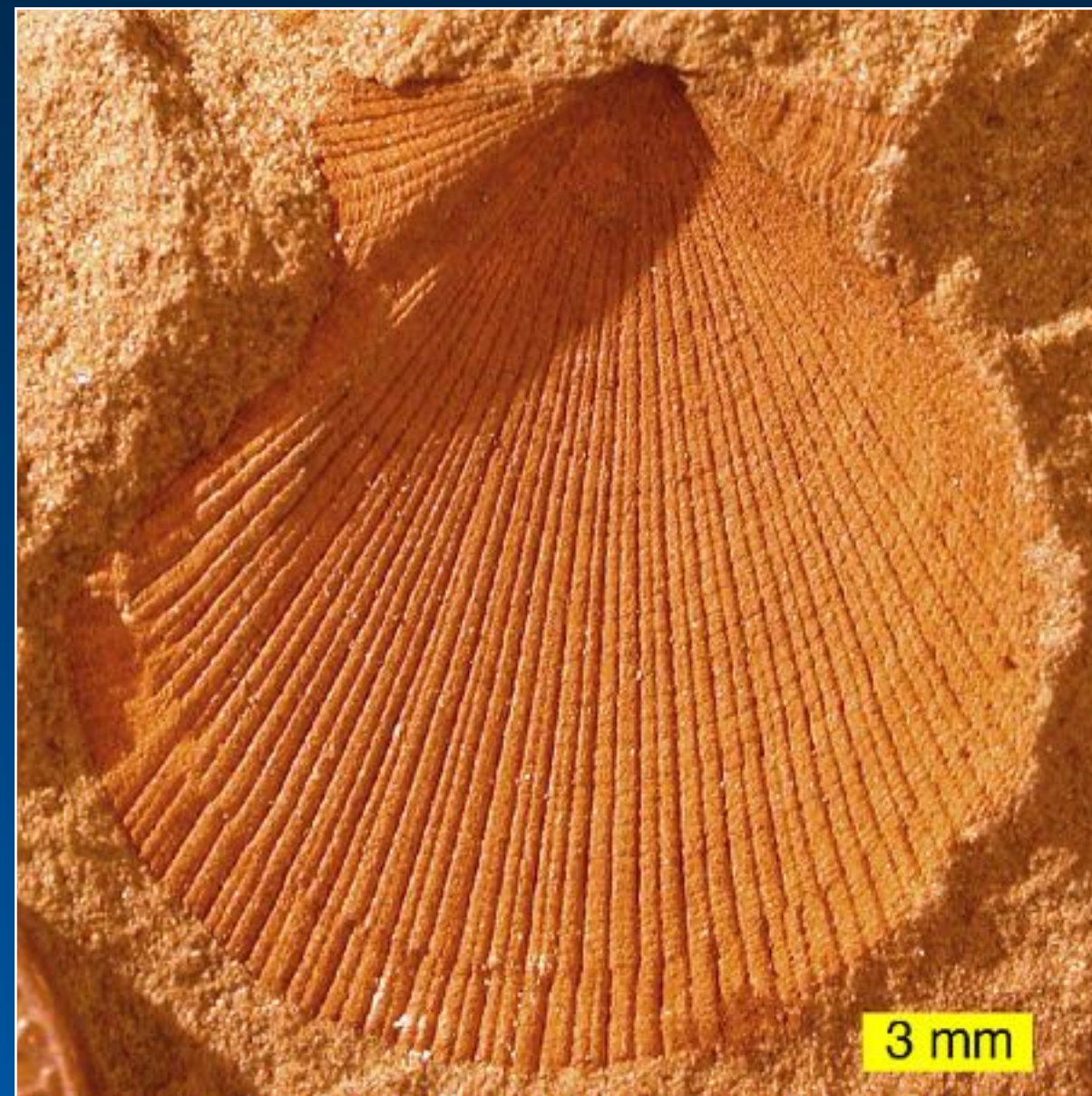
Trilobite



# The Nature of the Fossil Record

## Castes & Moulds

Fossils whose original materials dissolved completely leaving a fossil-shaped void in the surrounding sediment (mould) that may become filled with sediment or mineral crystals subsequently (cast).



Mould



Cast



Mould



# The Nature of the Fossil Record

---

## Trace Fossils

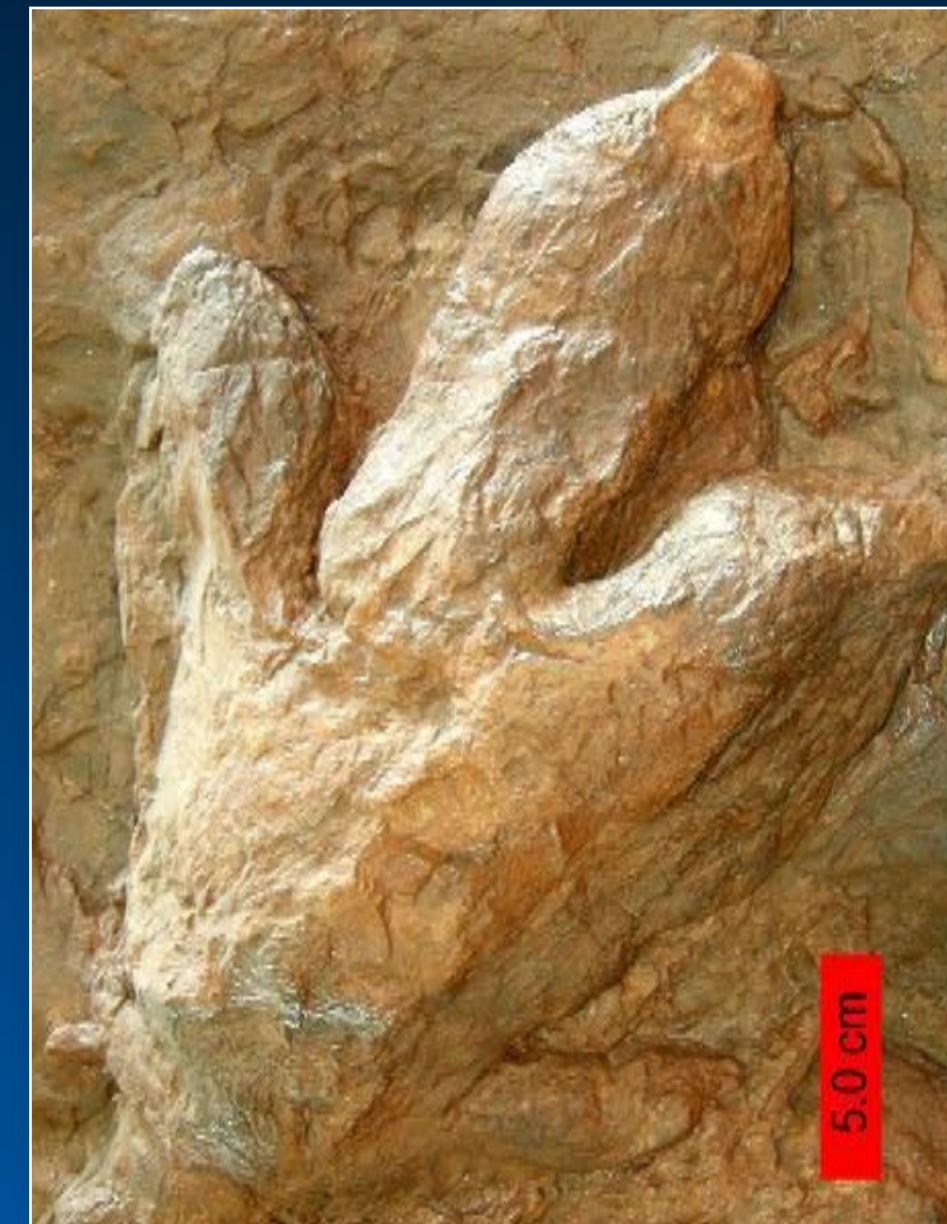
Naturally preserved impressions and/or excavations in inorganic materials made as a result of biological activity.



Borings



Burrows



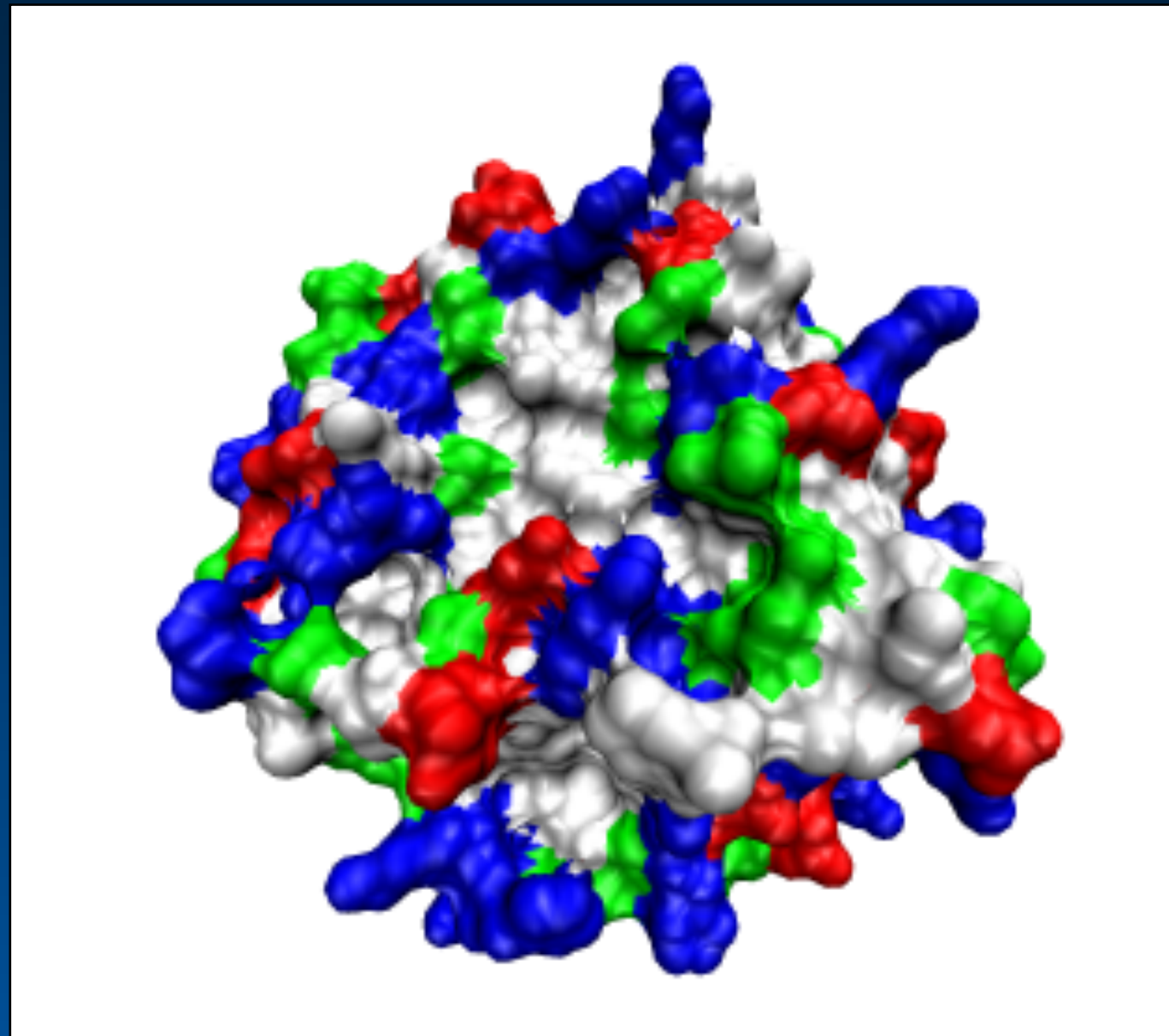
Track



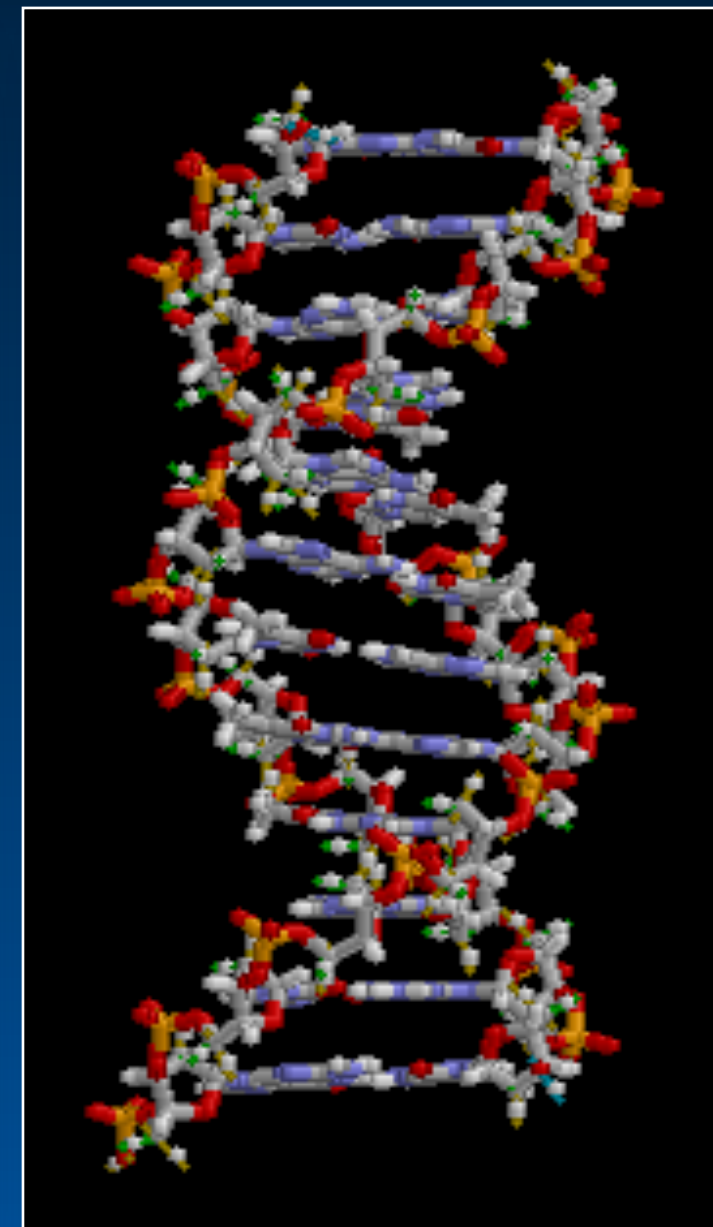
# The Nature of the Fossil Record

## Fossil Molecules

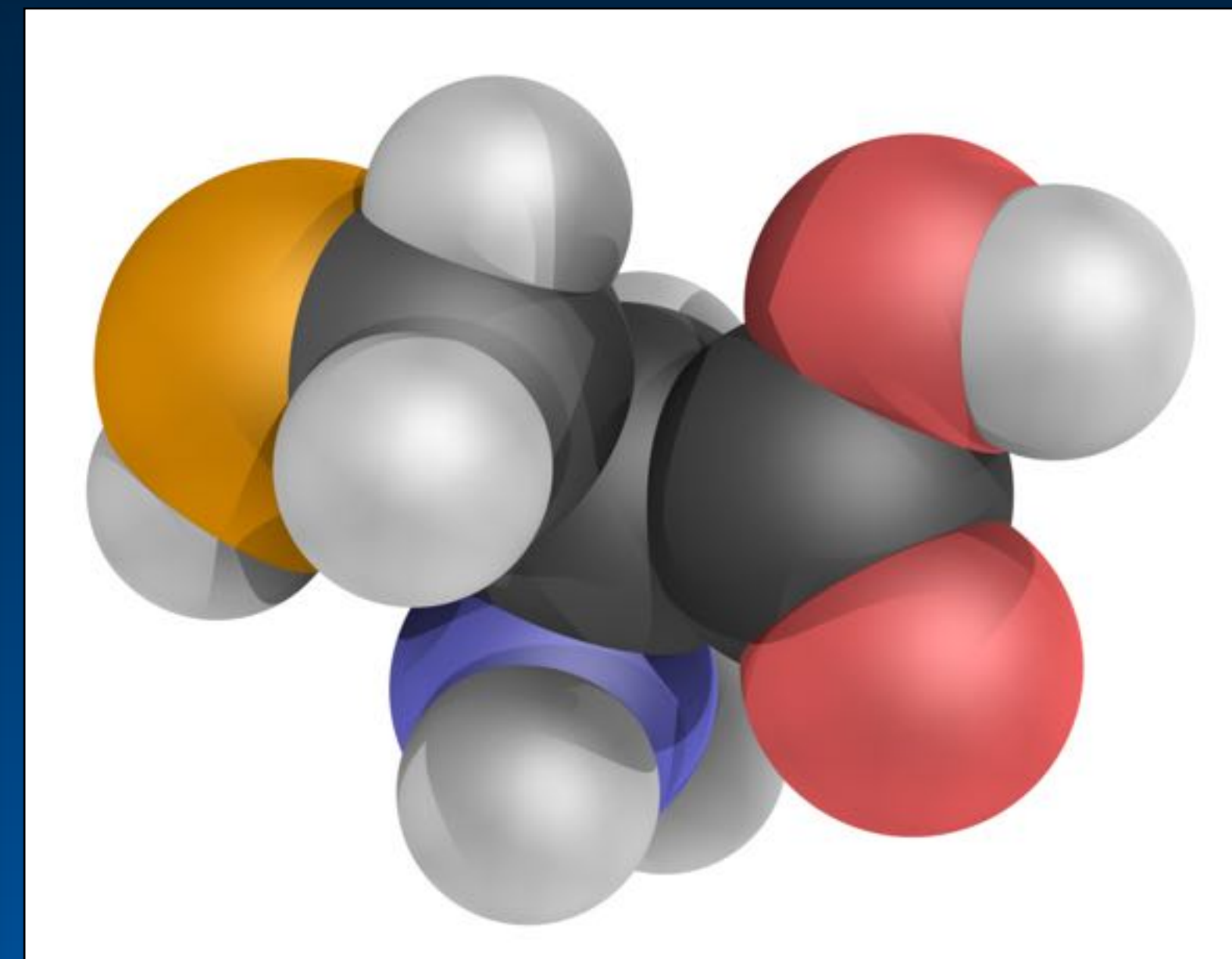
The remains of the molecular constituents of organisms preserved in the sediment record in whole, partial, or altered states.



Protein



DNA



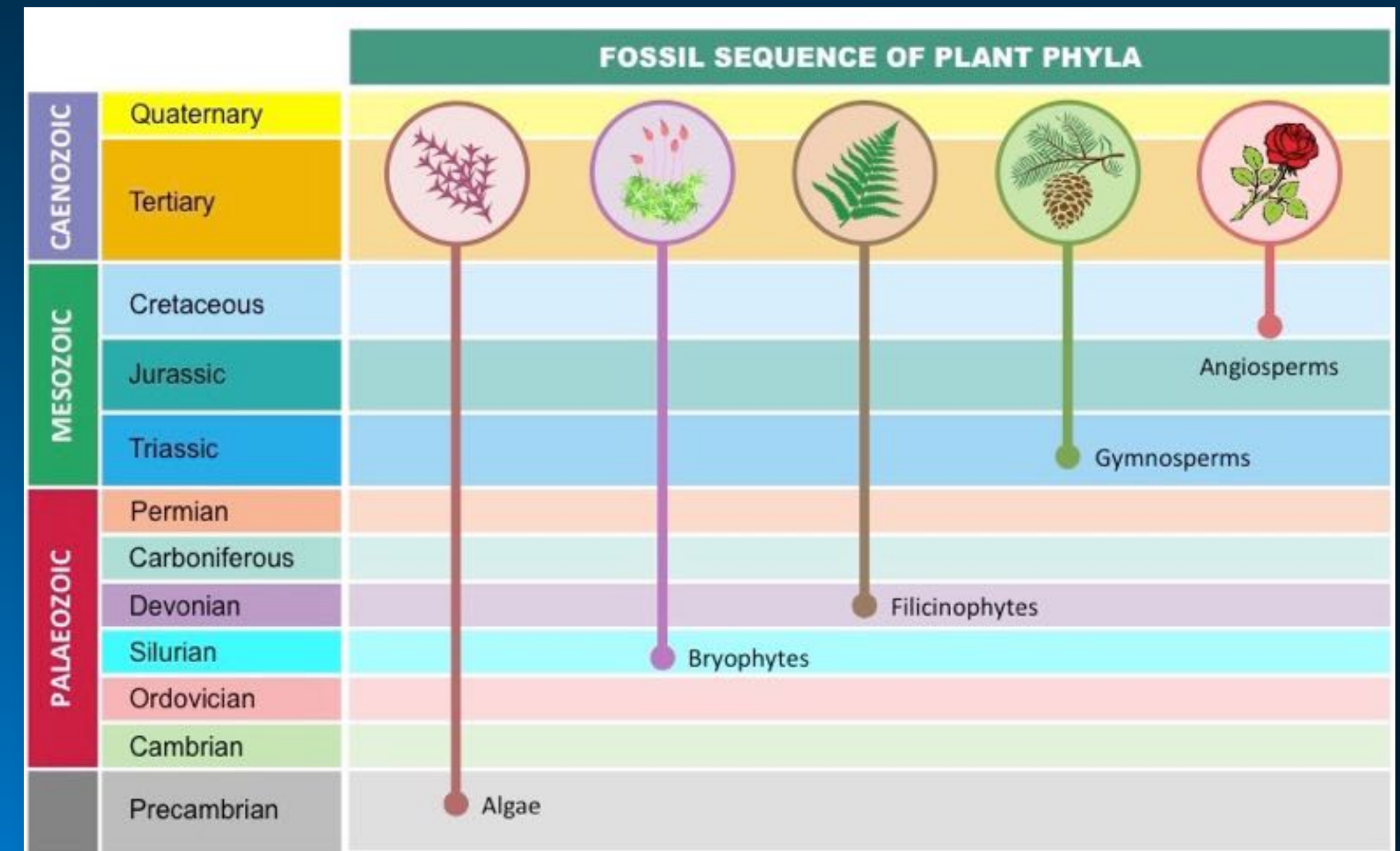
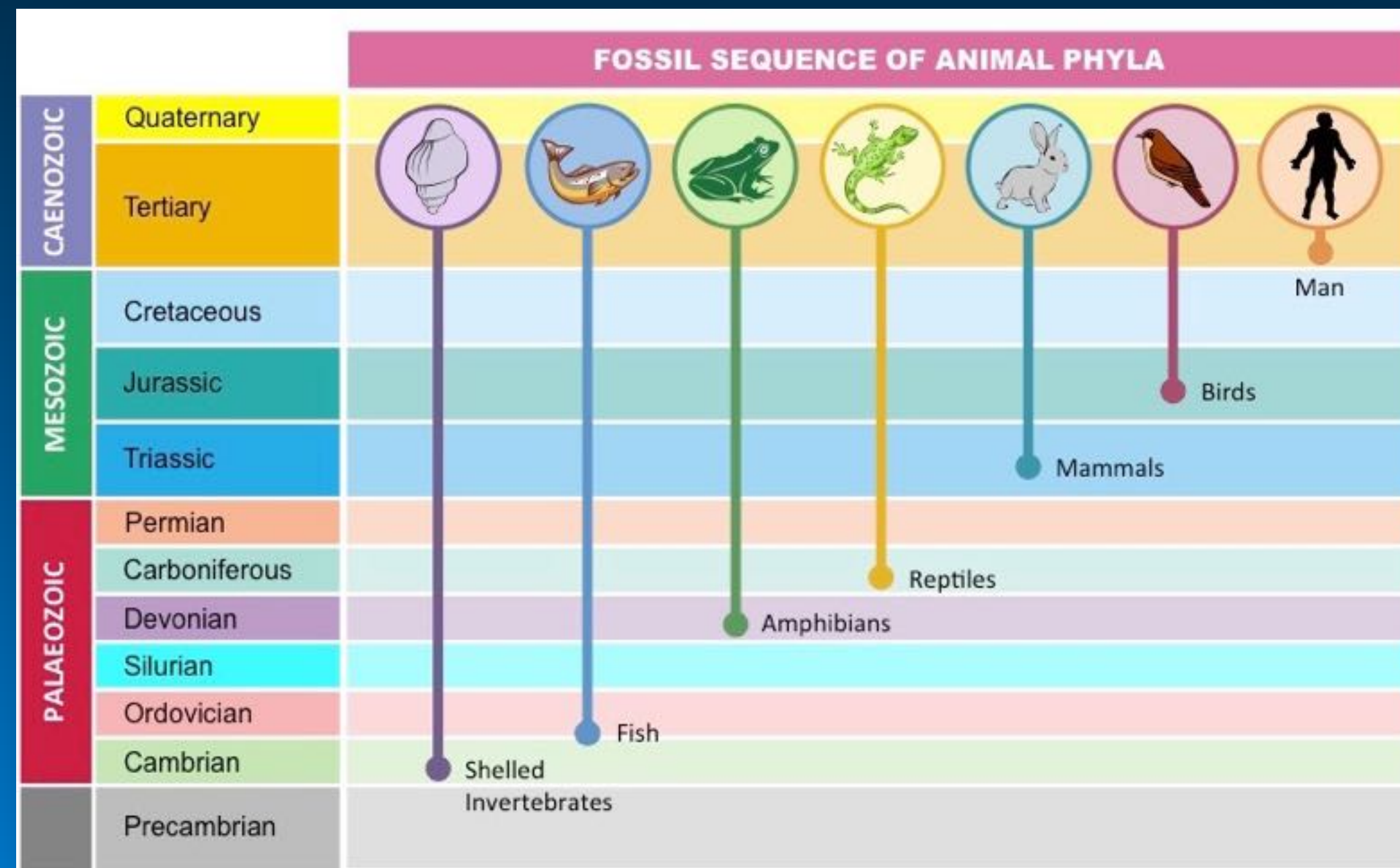
Amino Acid



# The Nature of the Fossil Record

## What is the fossil record?

The totality of fossils of all types, both discovered and undiscovered.

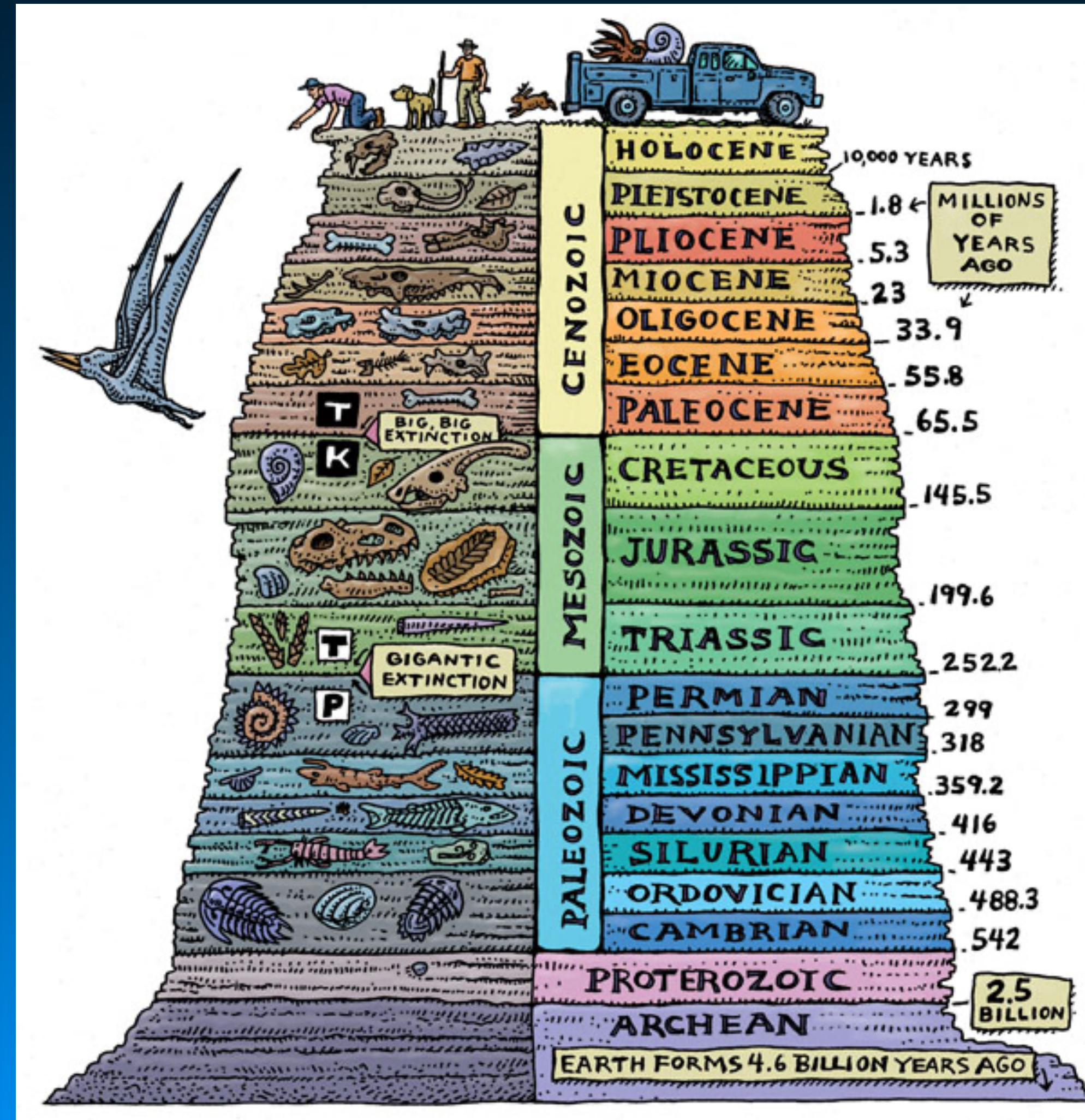


There are two primary principles used to organize the fossil record: stratigraphic (time) order and taxonomic ("evolutionary") order.



# The Nature of the Fossil Record

## Stratigraphy





# The Nature of the Fossil Record

## Stratigraphy - Steno's "Laws"



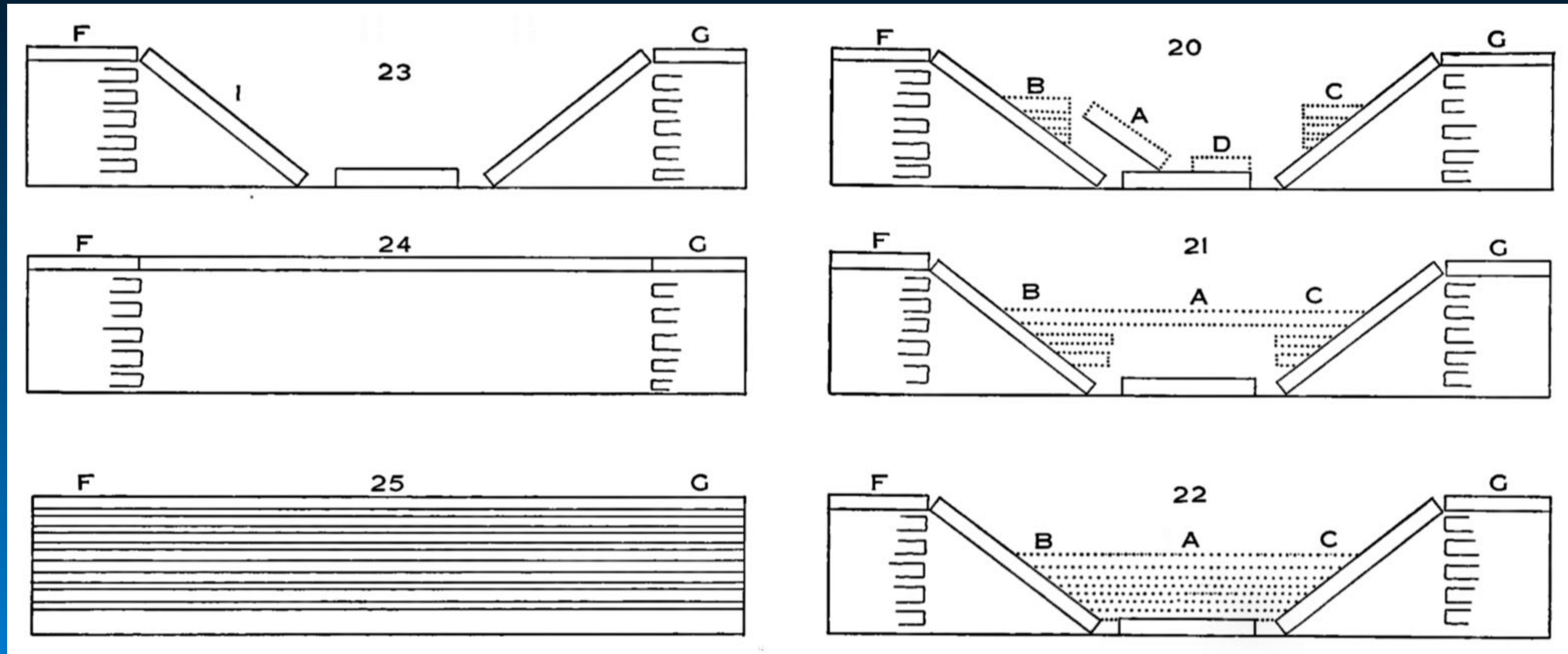
Nicholas Steno  
(1638 - 1686)

- **Original Horizontality** - unconsolidated sediments deposited on a solid base must have formed horizontal layers originally.
- **Original Continuity** - unconsolidated sediments deposited on a solid base would have formed continuous sheets or bands of material.
- **Superposition** - since each layer of unconsolidated sediment deposited on a solid base must have formed after the basal layer has been deposited, overlying layers of sediment are younger than underlying layers.



# The Nature of the Fossil Record

## Stratigraphy



Steno's stratigraphic analysis of the natural history of Tuscany.



# The Nature of the Fossil Record

## Stratigraphy



James Hutton  
(1726 - 1797)



**Cross-cutting relations** - Synonymous in concept with super-position, Hutton used this principle to show that rock bodies such as granite were formed by crystallization from an originally molten state (plutonism) rather than by precipitation from seawater (neptunism).

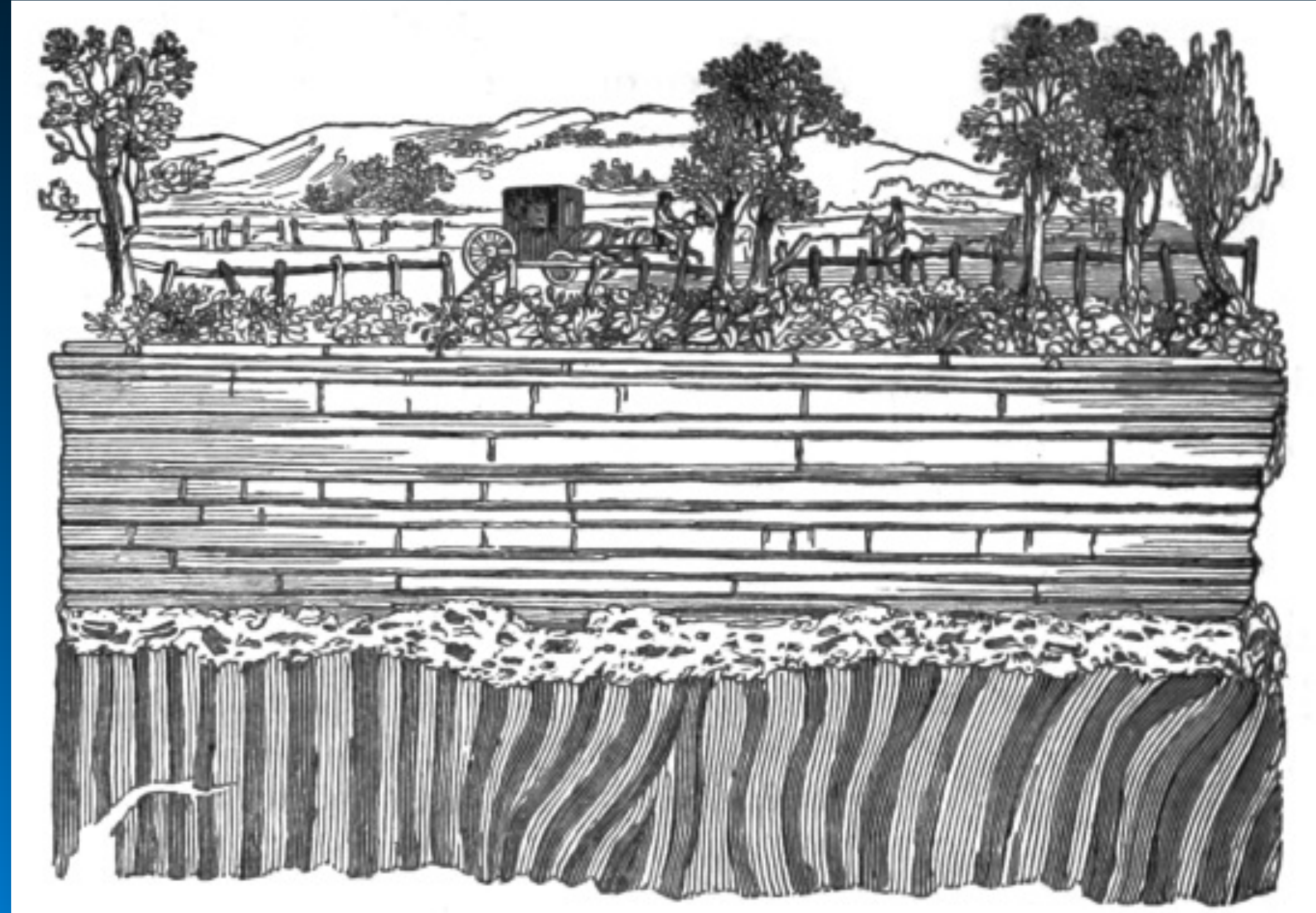


# The Nature of the Fossil Record

## Theories of the Earth



James Hutton  
(1726 - 1797)

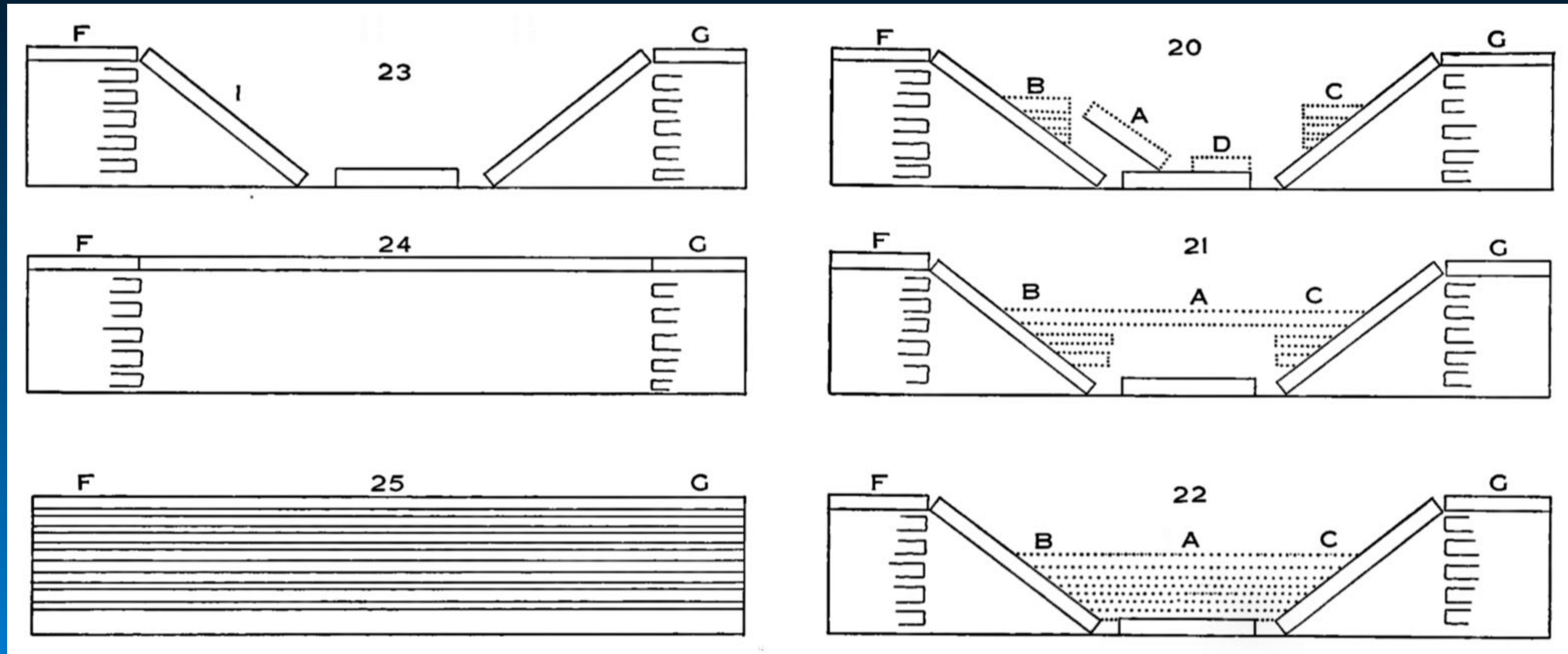


**Uniformitarianism** - The commonly observed physical earth processes of sediment deposition, uplift, deformation, and erosion were self-renewing, and proceeded in a cyclic manner with “no vestige of a beginning, no prospect of an end”.



# The Nature of the Fossil Record

## Stratigraphy



Steno's stratigraphic analysis of the natural history of Tuscany.

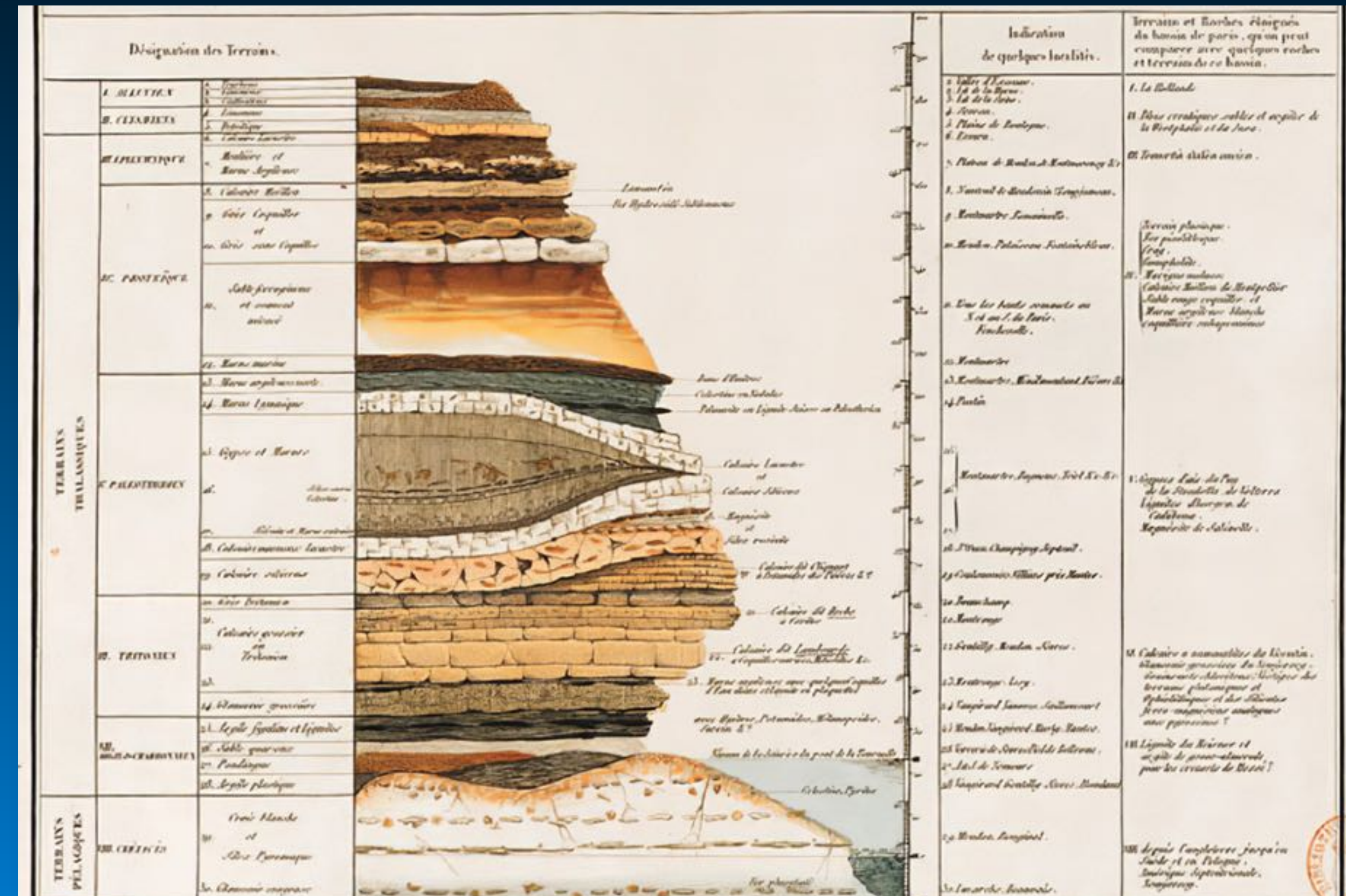


# The Nature of the Fossil Record

## Theories of the Earth



Georges Cuvier  
(1769 - 1832)



**Catastrophism** - Changes to landscapes on Earth over geological history resulted chiefly from sudden, violent and unusual events caused ultimately by cooling and thermal contraction of the Earth's core.

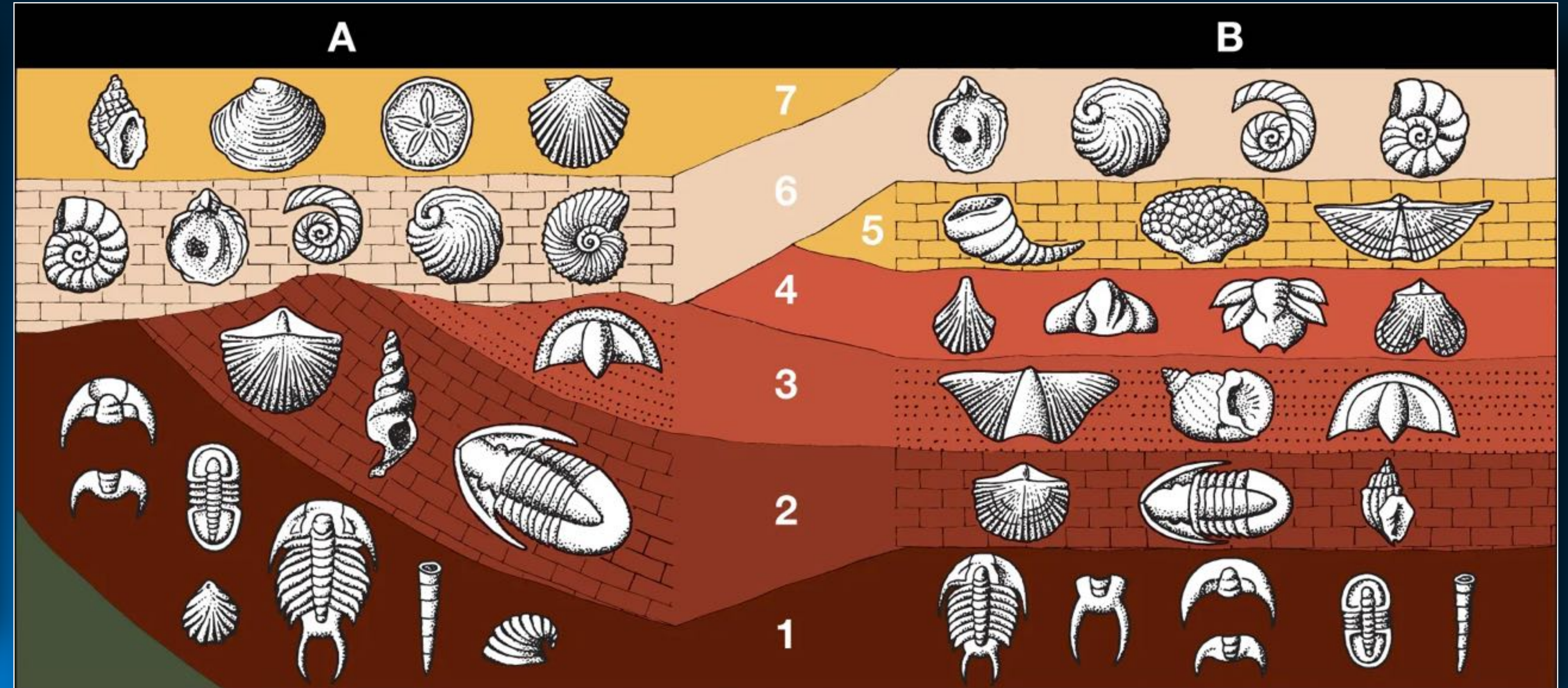


# The Nature of the Fossil Record

## Stratigraphy



William Smith  
(1769 - 1839)



**Principle of Faunal Succession** - Bodies of fossiliferous strata can be characterized and arranged in their correct superposition sequence on the basis of their unique fossil content, irrespective of the sequence of lithologies.



# The Nature of the Fossil Record

## Stratigraphy



Charles Lyell  
(1797 - 1875)

### Types of Uniformitarianism

- **Uniformity of Law** - the laws that govern natural processes are unchanging.
- **Uniformity of Process** - the processes of the natural world that operated in the Earth's distant past are the same as can be seen operating today (actualism).
- **Uniformity of Rate** - The rates at which geological processes operated in the Earth's distant past are the same as can be seen operating today (gradualism).
- **Uniformity of State** - Throughout earth history there has been no net progress in any inexorable direction (non-progressionism).

Note how far from these precepts of of Lyell's uniformitarianism depart from Hutton's uniformitarianism of endless cycles.

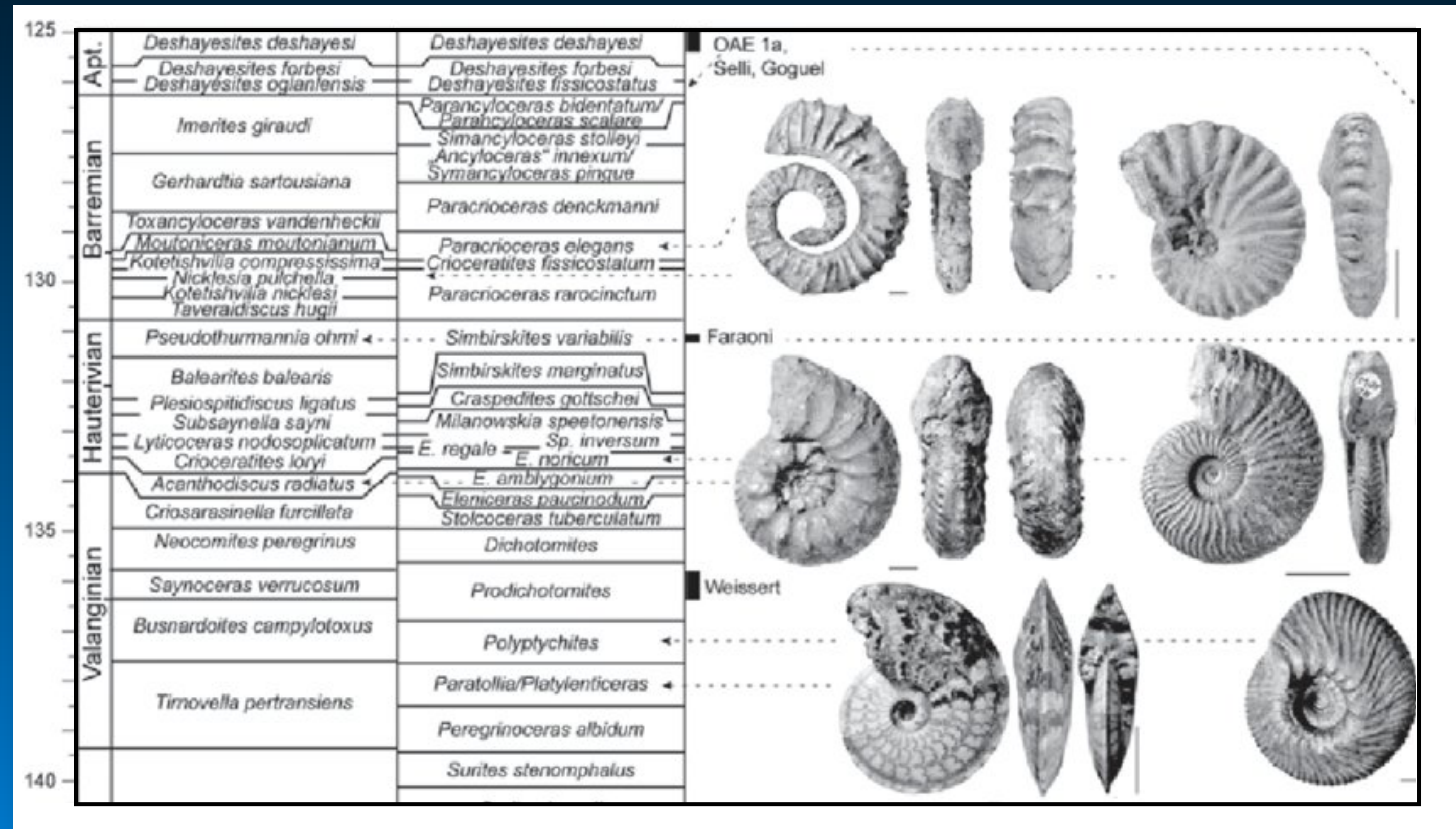


# The Nature of the Fossil Record

## Stratigraphy



Albert Oppel  
(1831 - 1865)



**Biozone** - following on from the work of Alcide d'Orbigny, Oppel used assemblages of ammonite fossils to define sequences of zones that subdivided d'Orbigny's stages into finer time intervals, using a single taxon as the nominal index.



# The Nature of the Fossil Record

## Stratigraphy



Albert Oppel  
(1831 - 1865)

### Characteristics of “Index Fossils”

- **Ease of identification** - for maximum reproducibility.
- **Narrow stratigraphic range** - for maximum stratigraphic resolution.
- **Wide geographic distribution** - for maximum practical correlation utility.
- **Facies independence** - for maximum independence and minimum bias.



Whereas Oppel never referred to his assemblage-occurrence intervals as “zones”, and used the term “index” only to refer to the assembled name-holders taxon, his concepts have come down to us as biozones, defined by index taxa.



# The Nature of the Fossil Record

## Stratigraphy



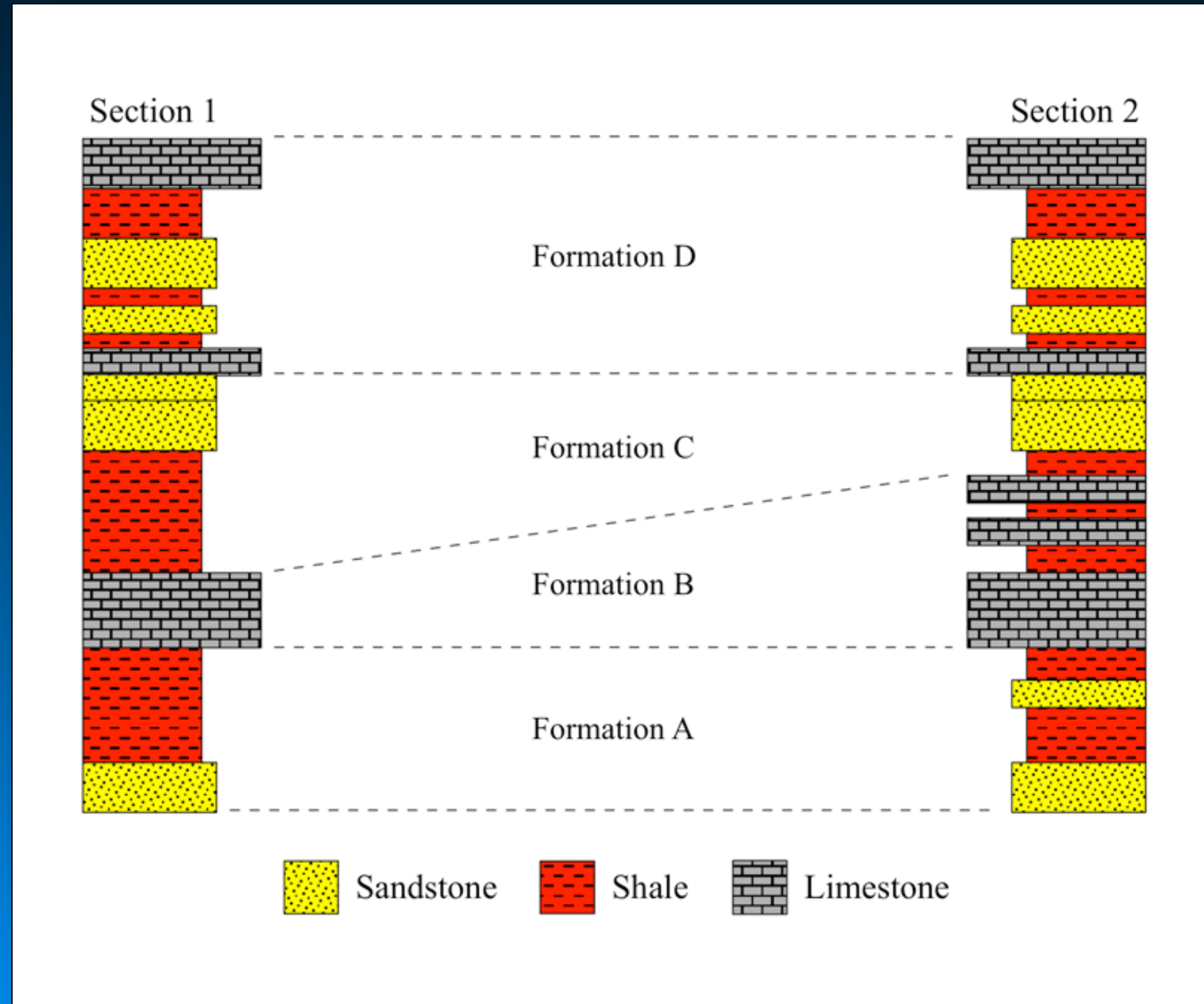
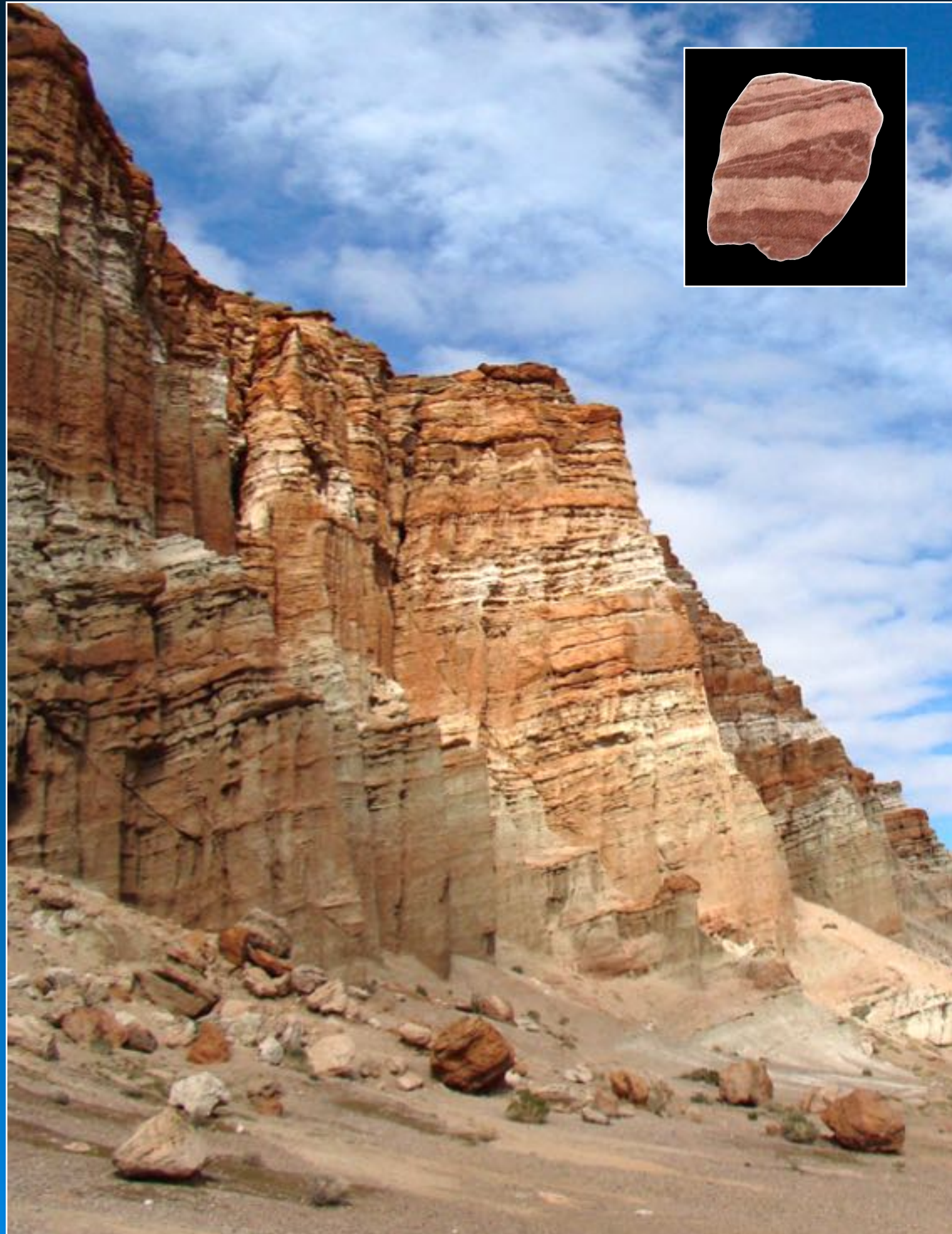
The branch of geology involved with the study of rock layers.

- Lithostratigraphy - focus on lithologic constituents.
- Biostratigraphy - focus on fossil constituents.
- Magnetostratigraphy - focus on paleomagnetic constituents.
- Chemostratigraphy - focus on chemical (elemental, molecular, isotopic) constituents.
- Chronostratigraphy - focus on relative time sequences.
- Geochronology - focus on numerical dating.



# The Nature of the Fossil Record

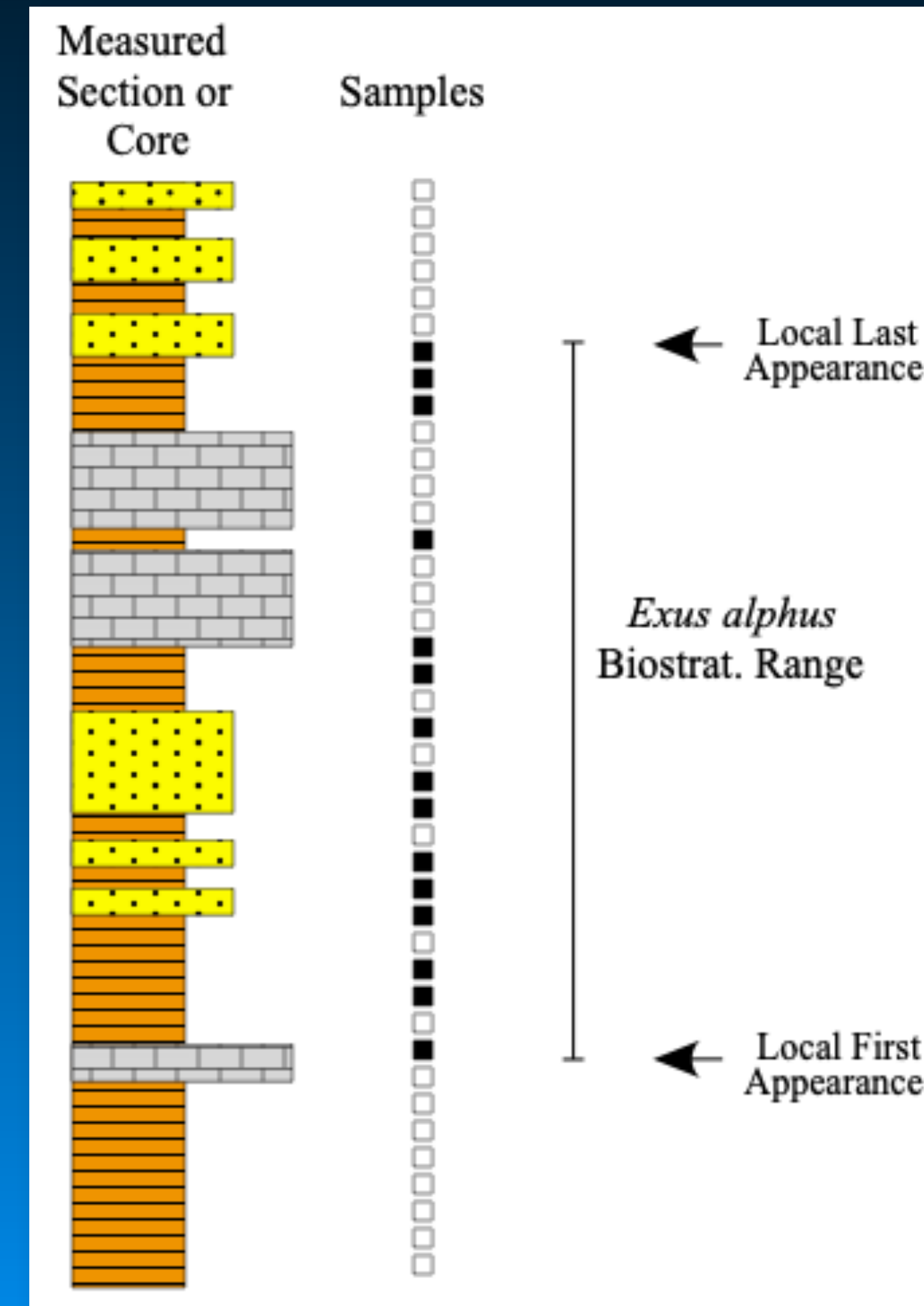
# Lithostratigraphy





# The Nature of the Fossil Record

## Biostratigraphy



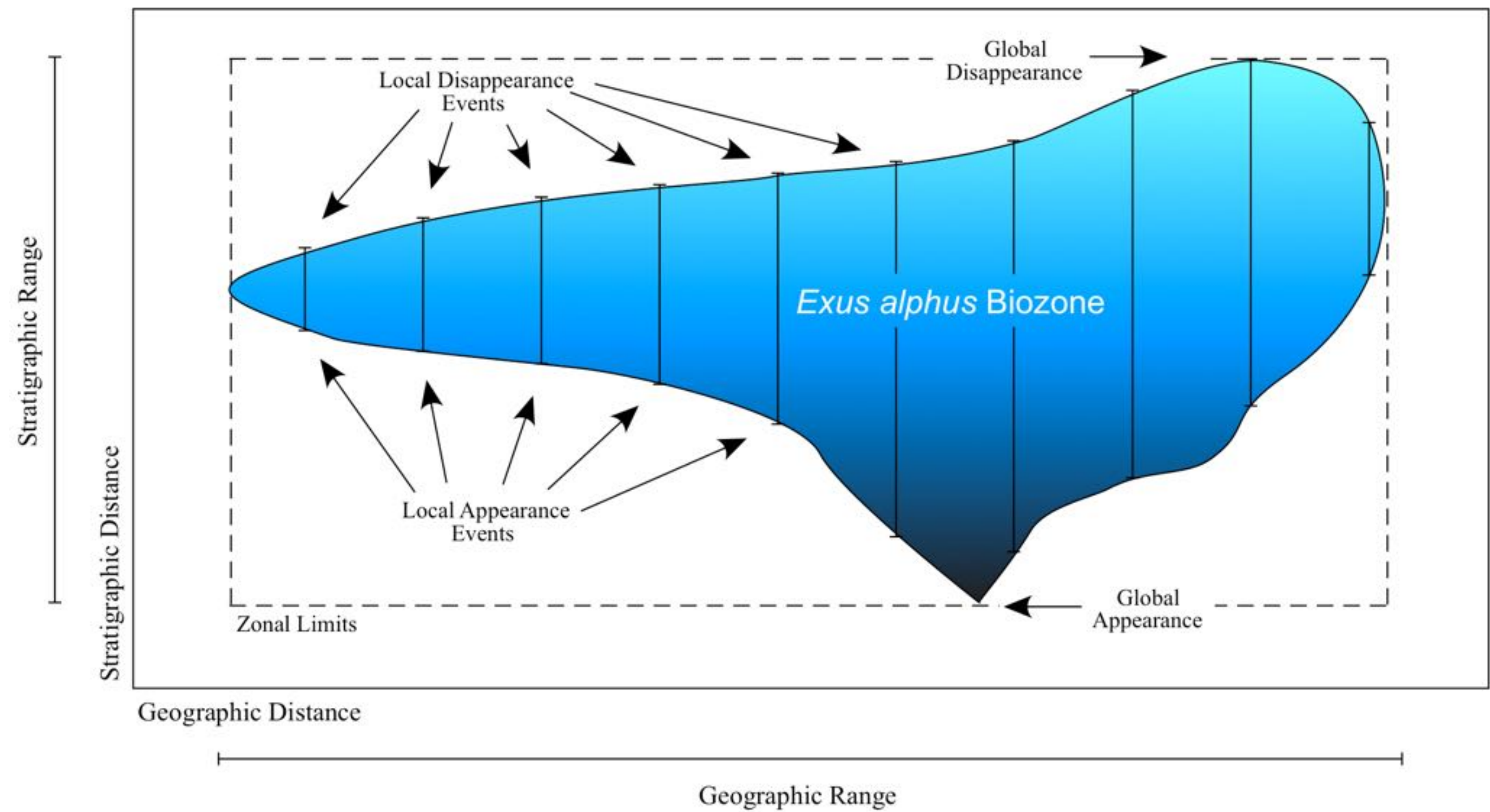


# The Nature of the Fossil Record

## Biostratigraphy



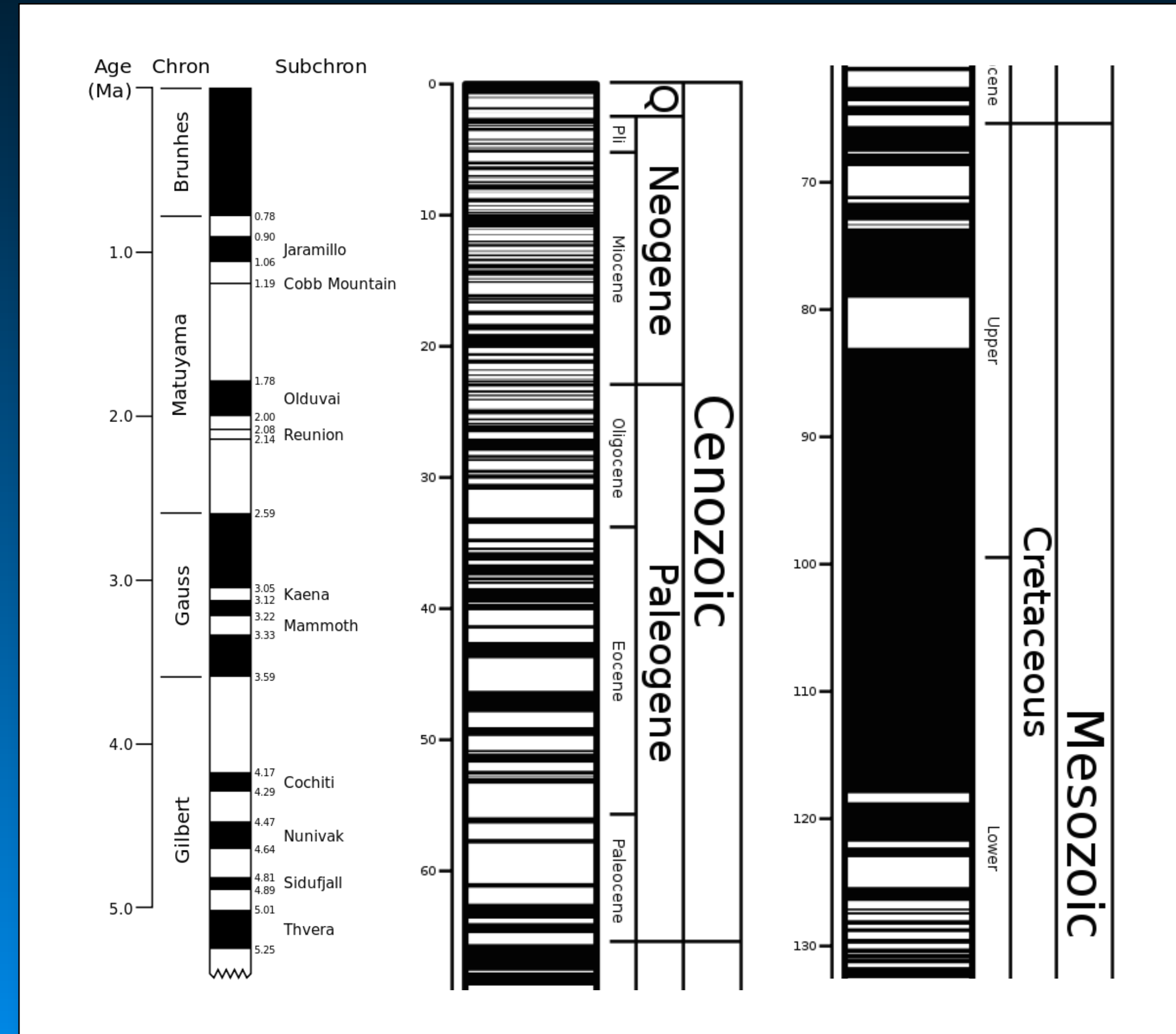
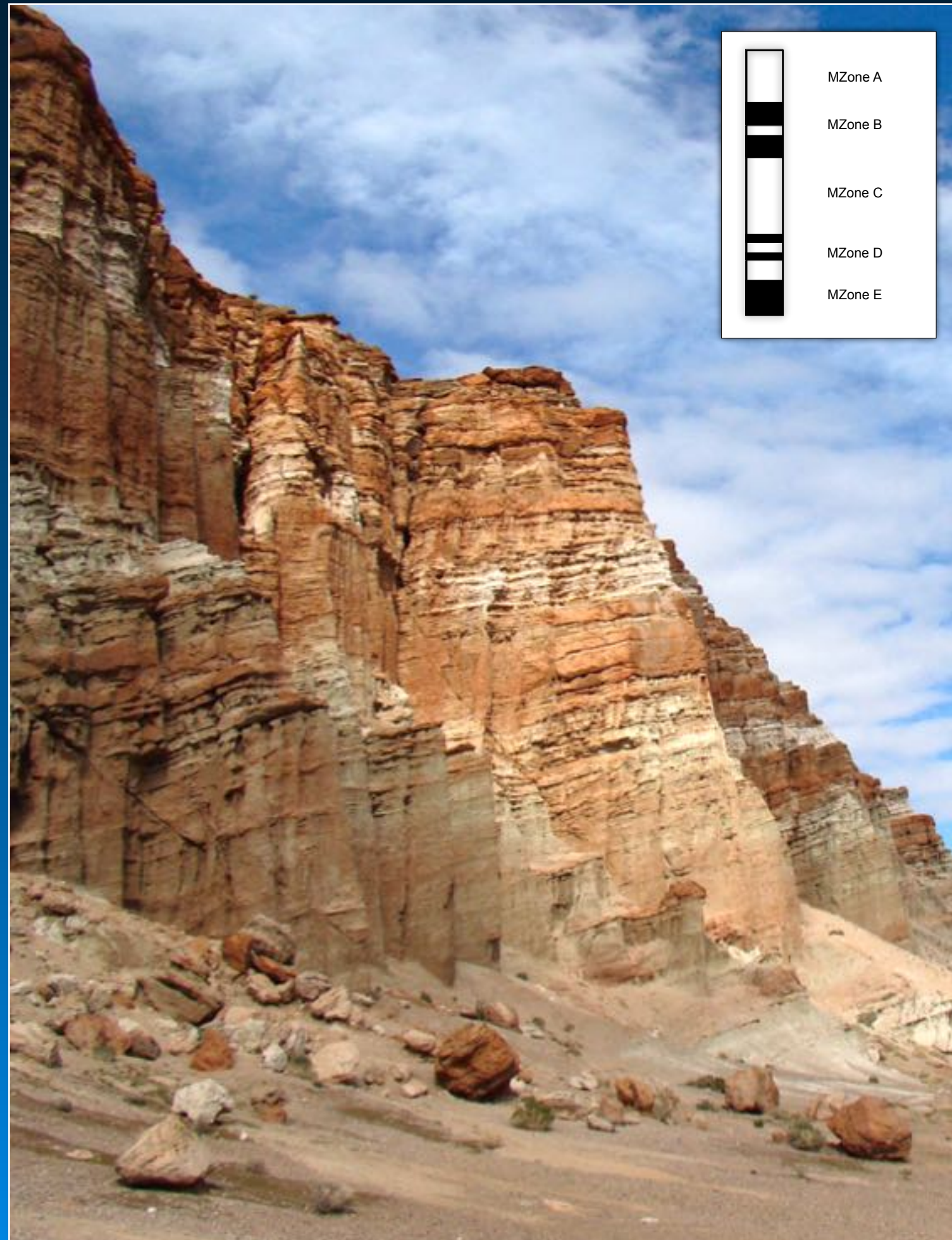
### Taxon Range Zone





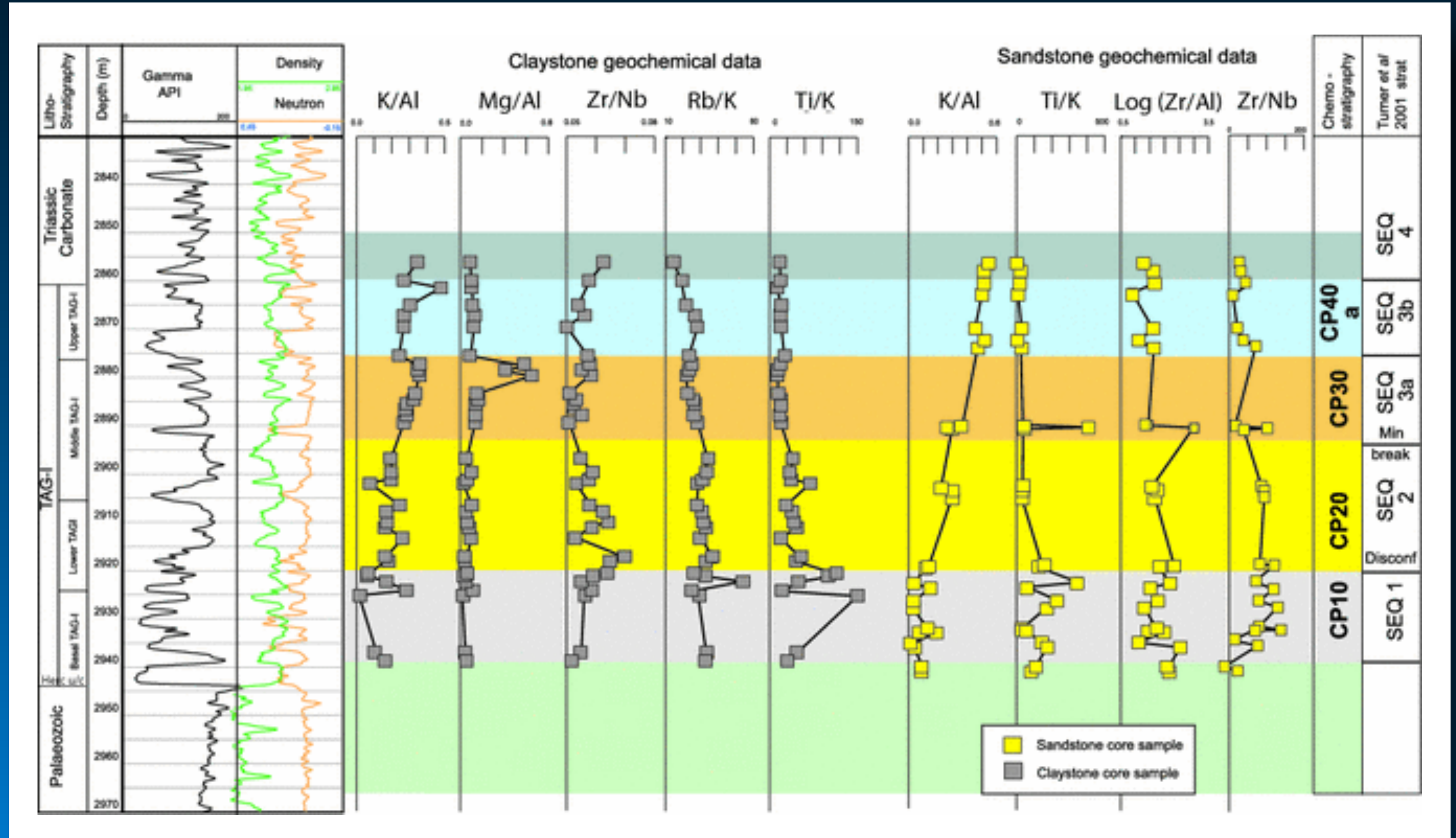
# The Nature of the Fossil Record

## Magnetostratigraphy





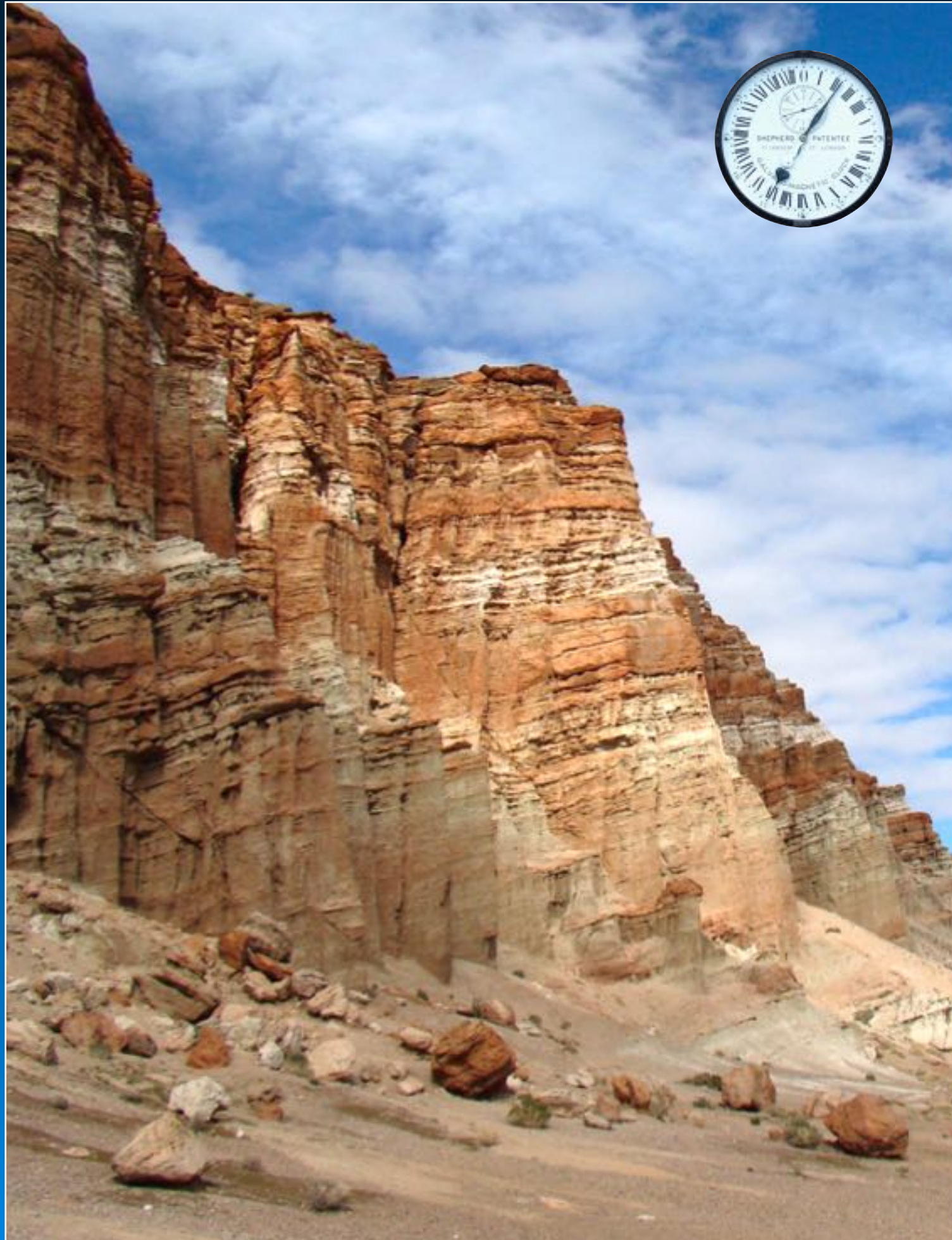
# Chemostratigraphy





# The Nature of the Fossil Record

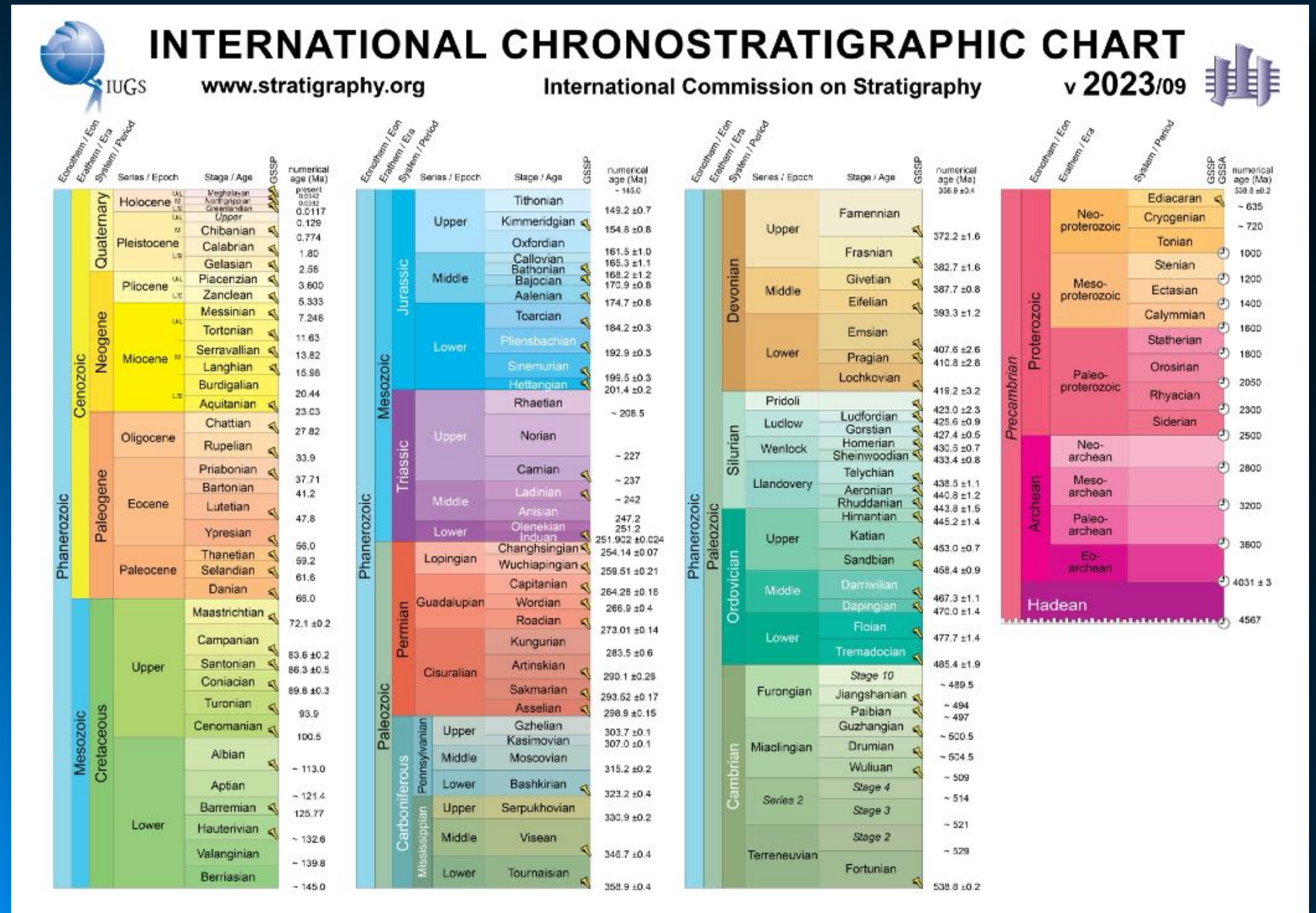
## Chronostratigraphy





# The Nature of the Fossil Record

## Chronostratigraphy





# The Nature of the Fossil Record

Everyone agrees the stratigraphic record is incomplete. But how incomplete is it?

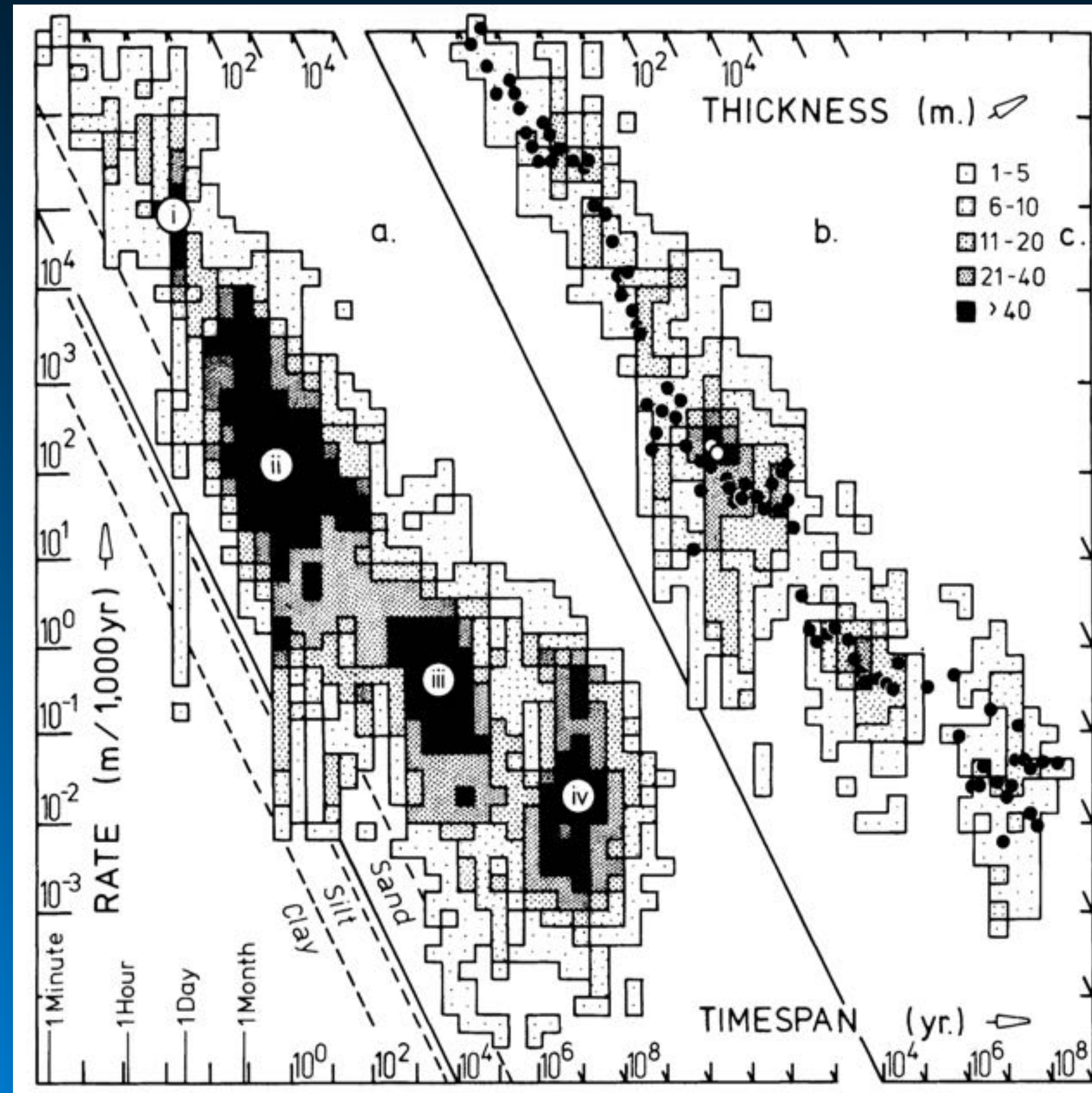


Popular metaphor likening the stratigraphic (and fossil) record to the pages of a book or newspaper.

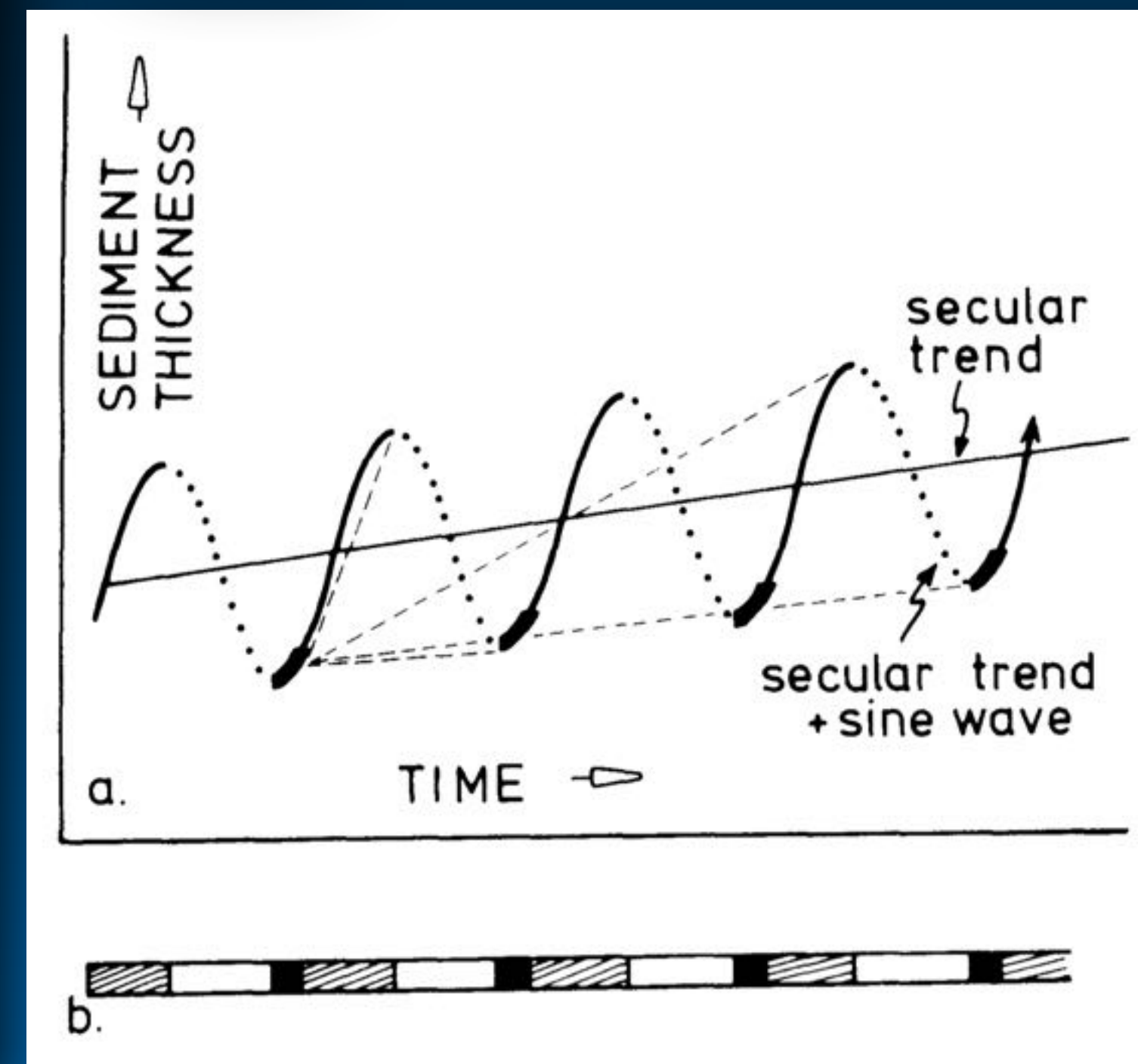


# The Nature of the Fossil Record

## Completeness of the Sedimentological Record



Based on 25,000 rock-accumulation records



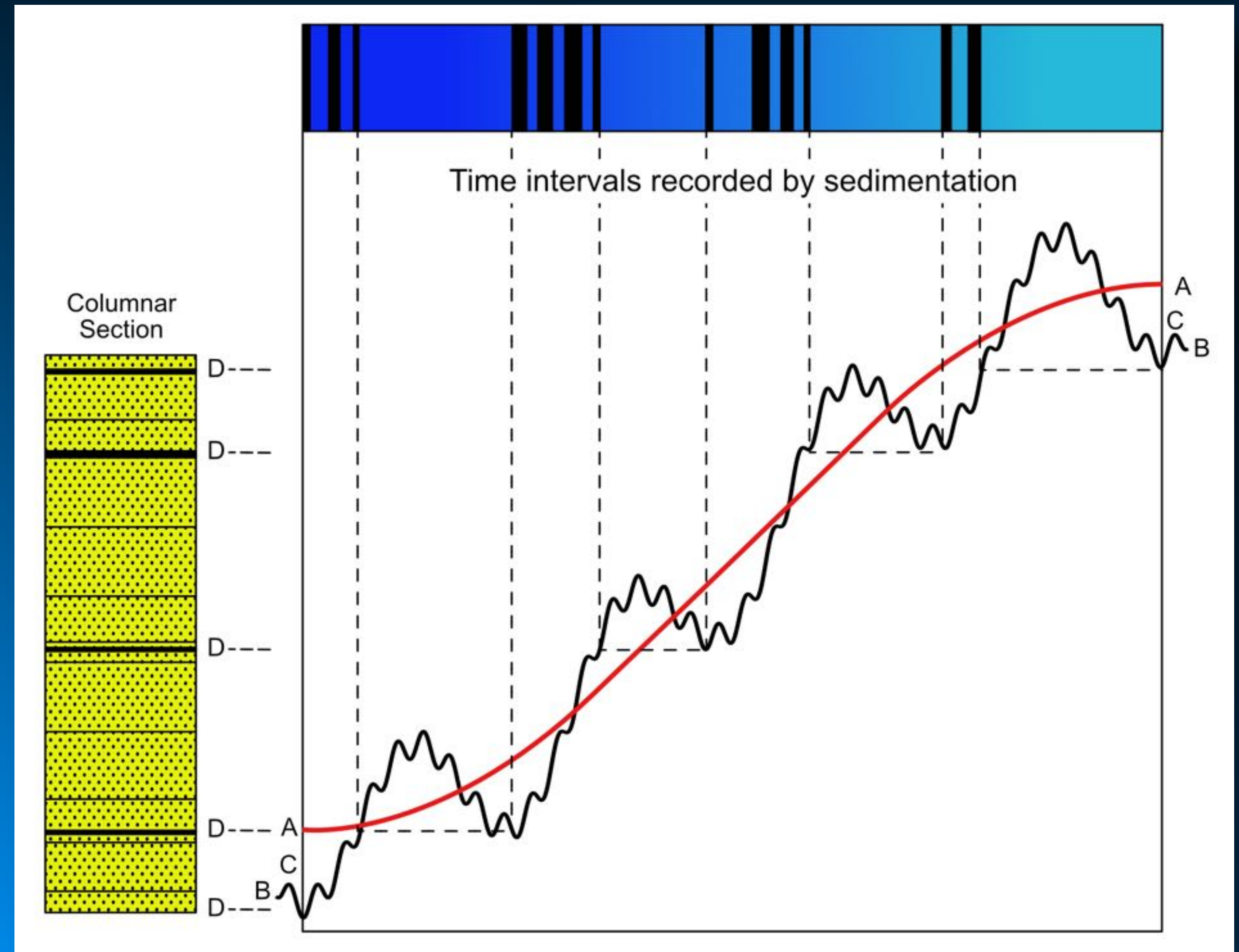
Owing to the nature of sedimentary processes only a small proportion of time is preserved by net sediment accumulation. This means all sedimentary series are riven by gaps in time.



# The Nature of the Fossil Record



## Completeness of the Sedimentological Record





# The Nature of the Fossil Record

## Questions for Paleobiologists



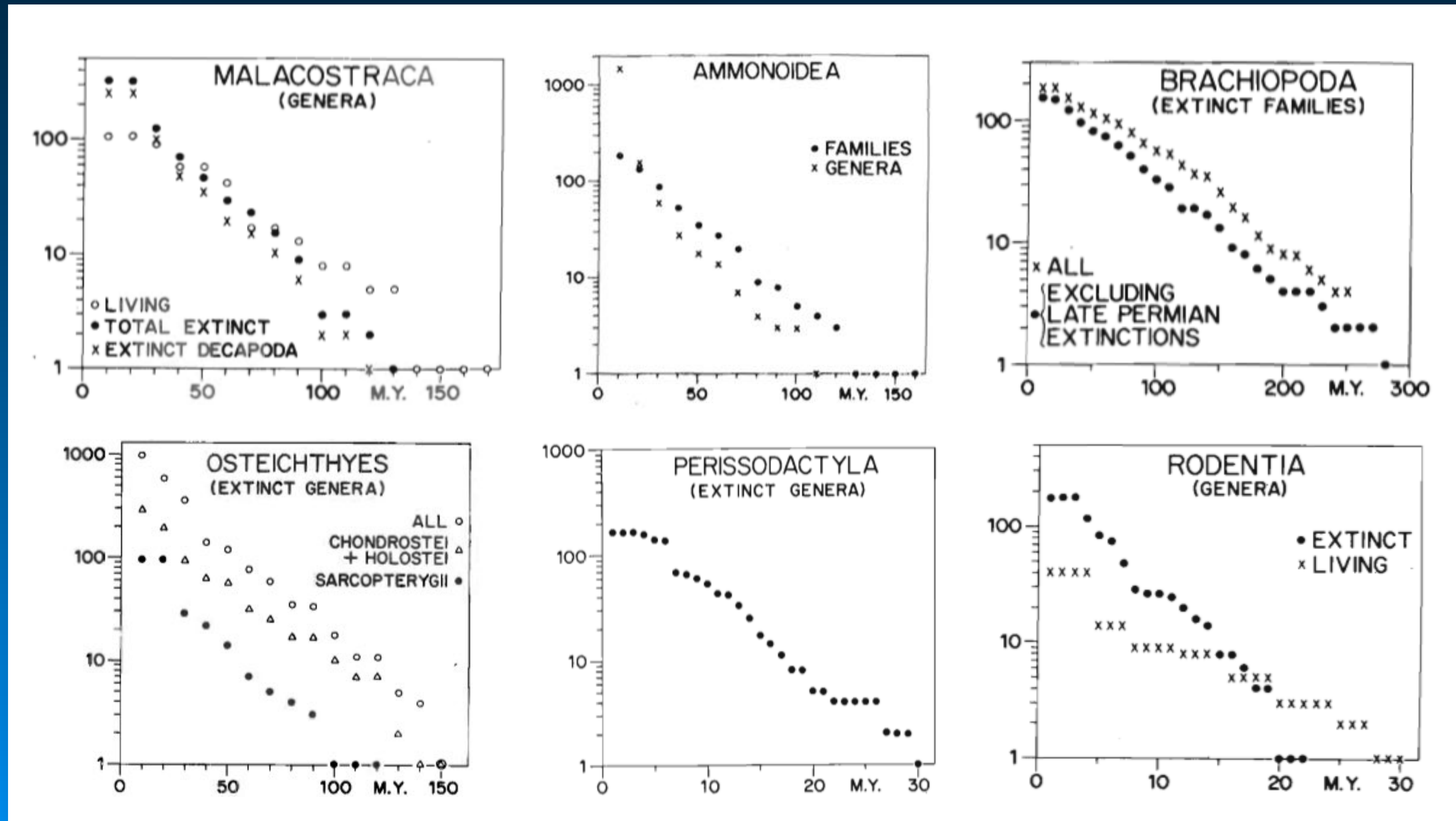
- What proportion of life is represented in the fossil record?
- How much rock of different ages is accessible for sampling?
- How do different organismal groups differ in the preservation potential?
- Are different ancient environments equally represented in the stratigraphic record?



# The Nature of the Fossil Record

What Proportion of Life is Present in the Fossil Record?

What is the average duration of a species?





# The Nature of the Fossil Record

What Proportion of Life is Present in the Fossil Record?

What is the average duration of a species?

Taxon	Avg. Duration (myr.)
Cenozoic Mammals	1 - 2
All Mammals	1
Cenozoic Bivalves	10
Marine Invertebrates	5 - 10
All Invertebrates	11
Avg. Species Duration	c. 5.0

$$8.7 \times 10^6 \text{ modern species} \times \frac{541 \times 10^6 \text{ myr}}{5.0 \times 10^6 \text{ myr}} = 941.34 \times 10^6 \text{ species}$$



# The Nature of the Fossil Record

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What Proportion of Life is Present in the Fossil Record?

What is the average duration of a species?

Est. Global Phanerozoic Species Richness:  $941.34 \times 10^6$

Est. No. of Described Fossil Species: 250,000

Est. Percent Represented in Fossil Record: 0.000265

Est. Percent Absent from Fossil Record: 99.999735



# The Nature of the Fossil Record

What Proportion of Life is Present in the Fossil Record?

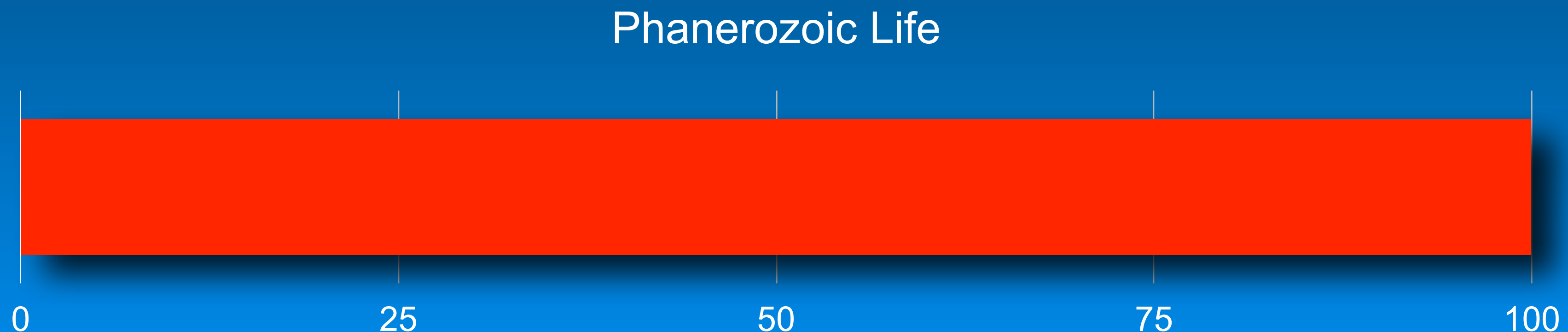
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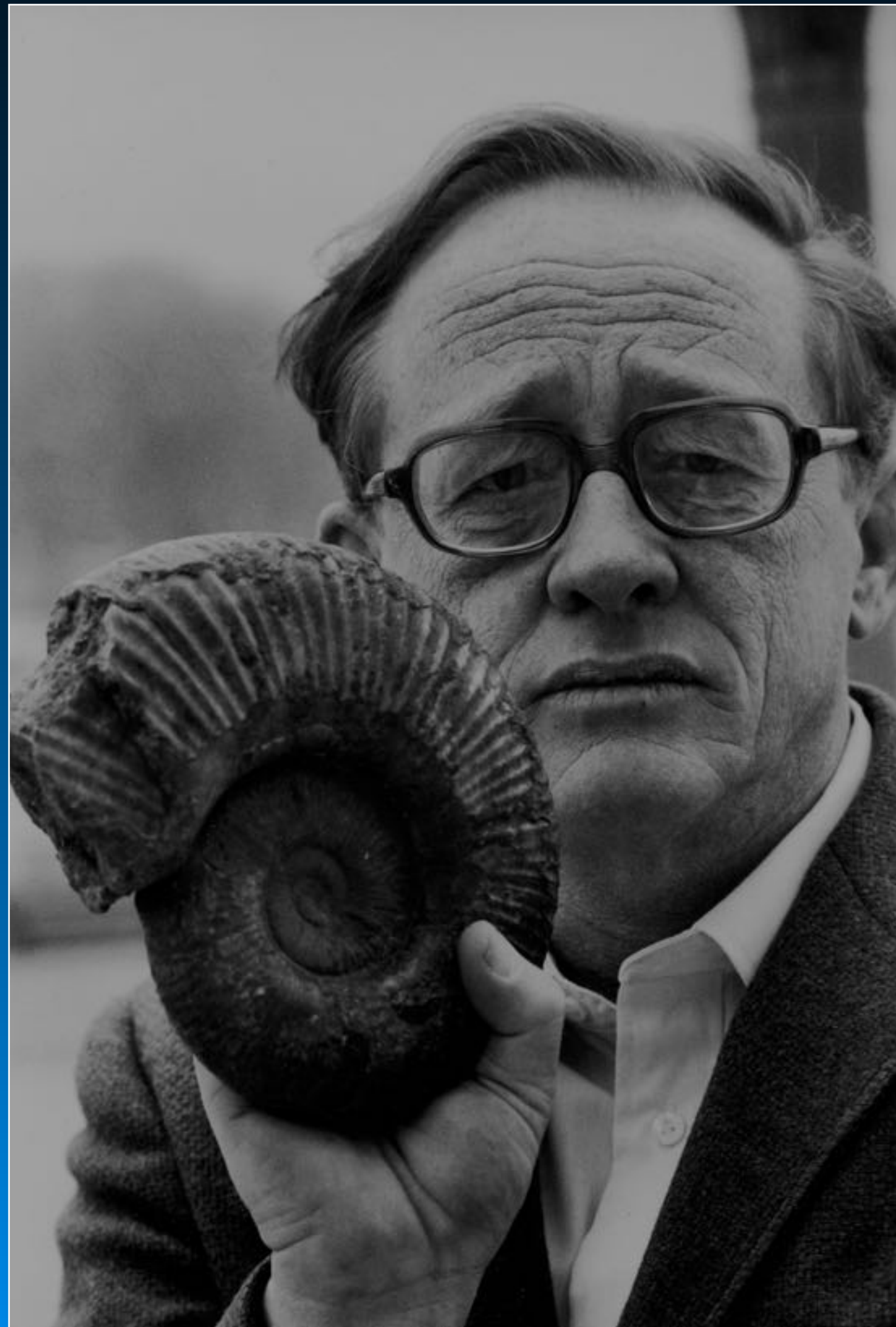
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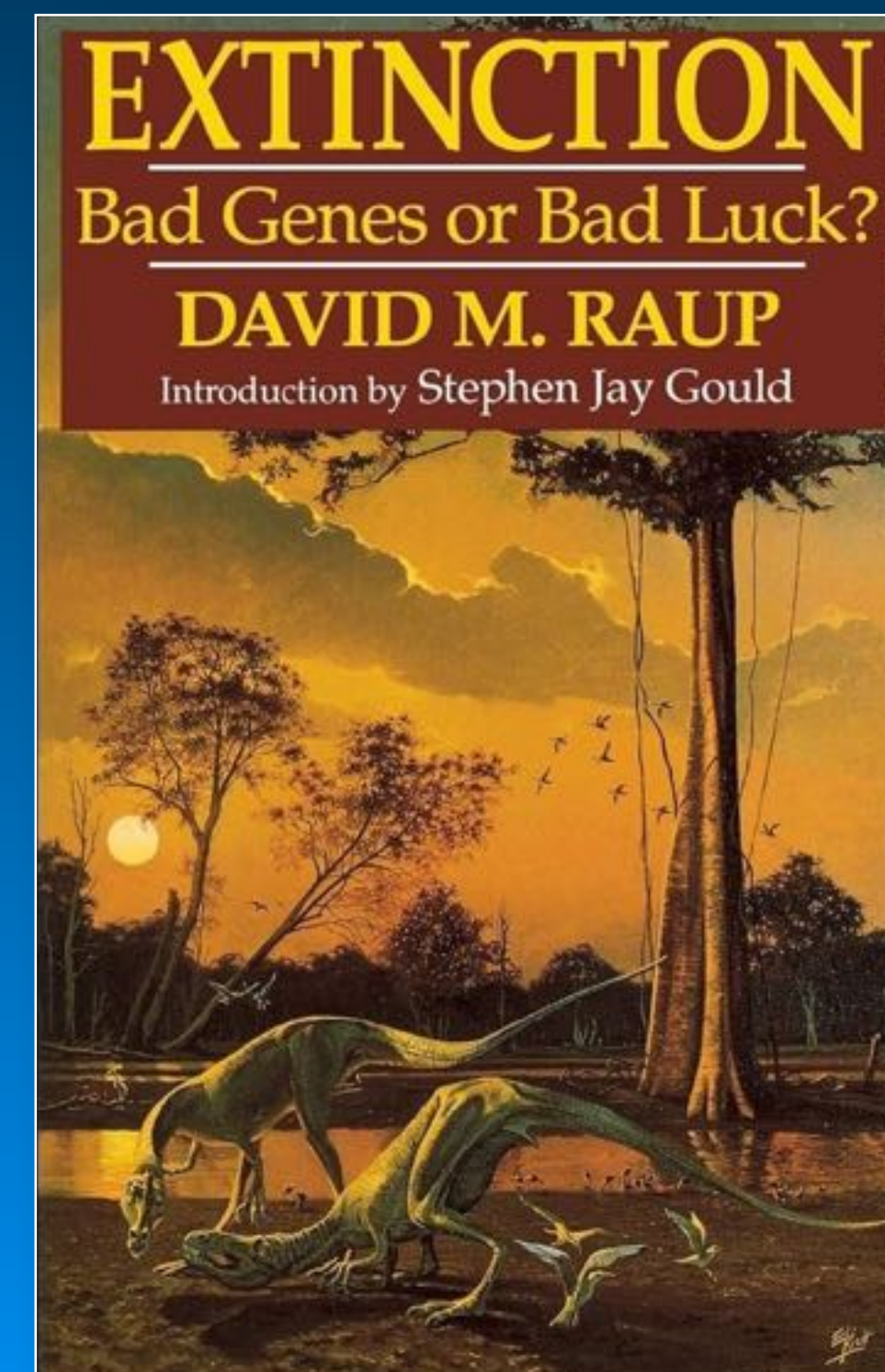


# The Nature of the Fossil Record



“To a first approximation,  
all life on Earth is  
extinct.”

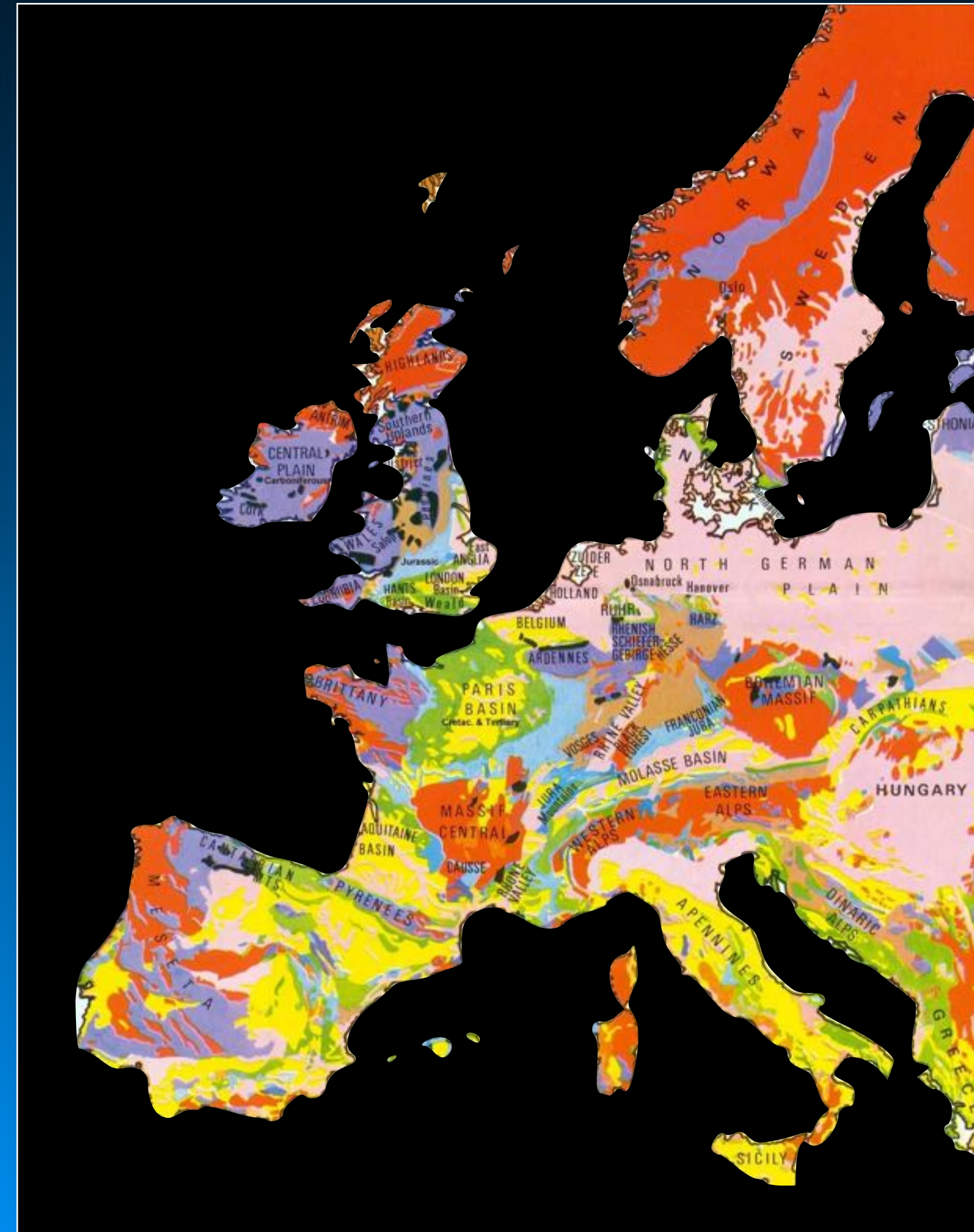
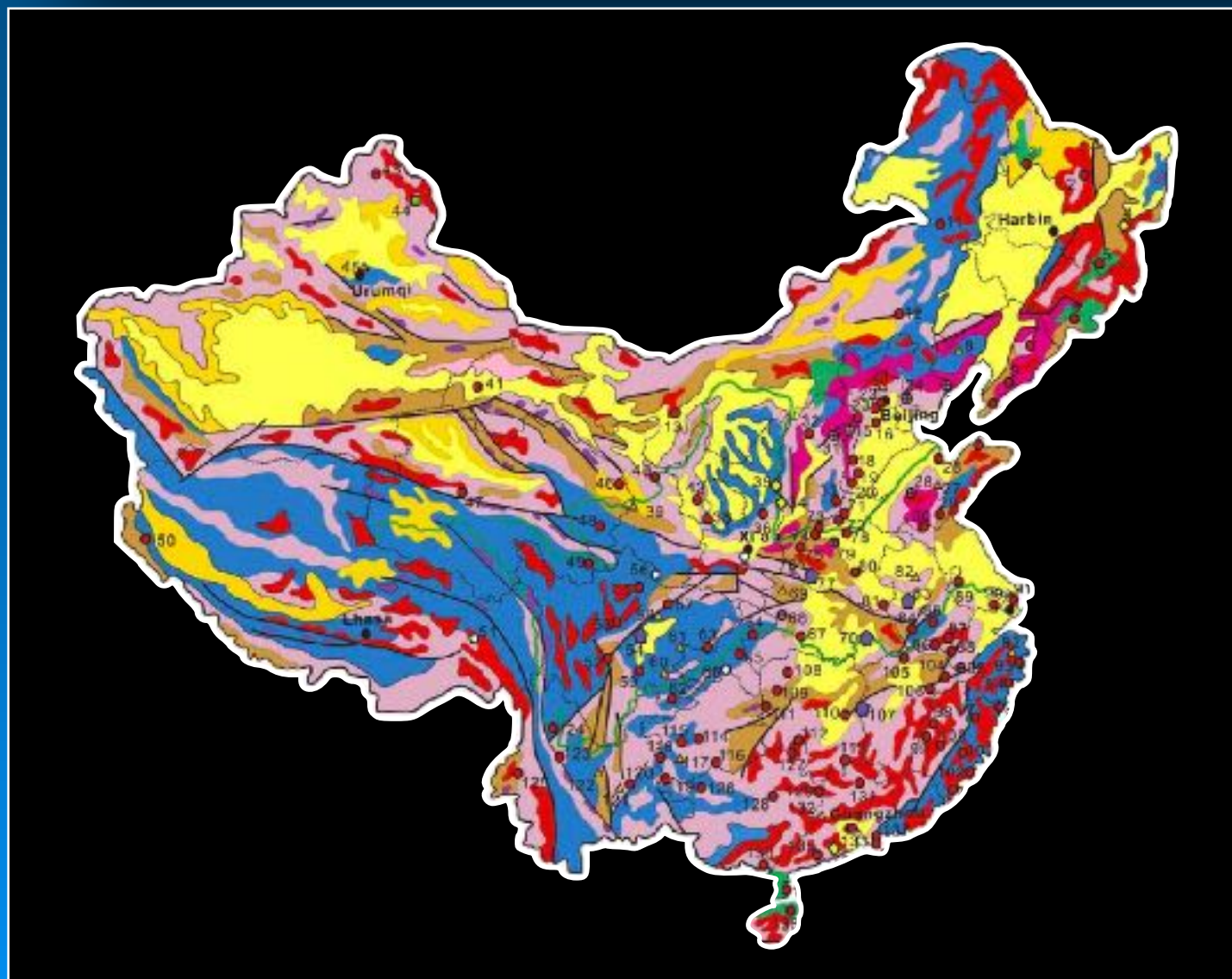
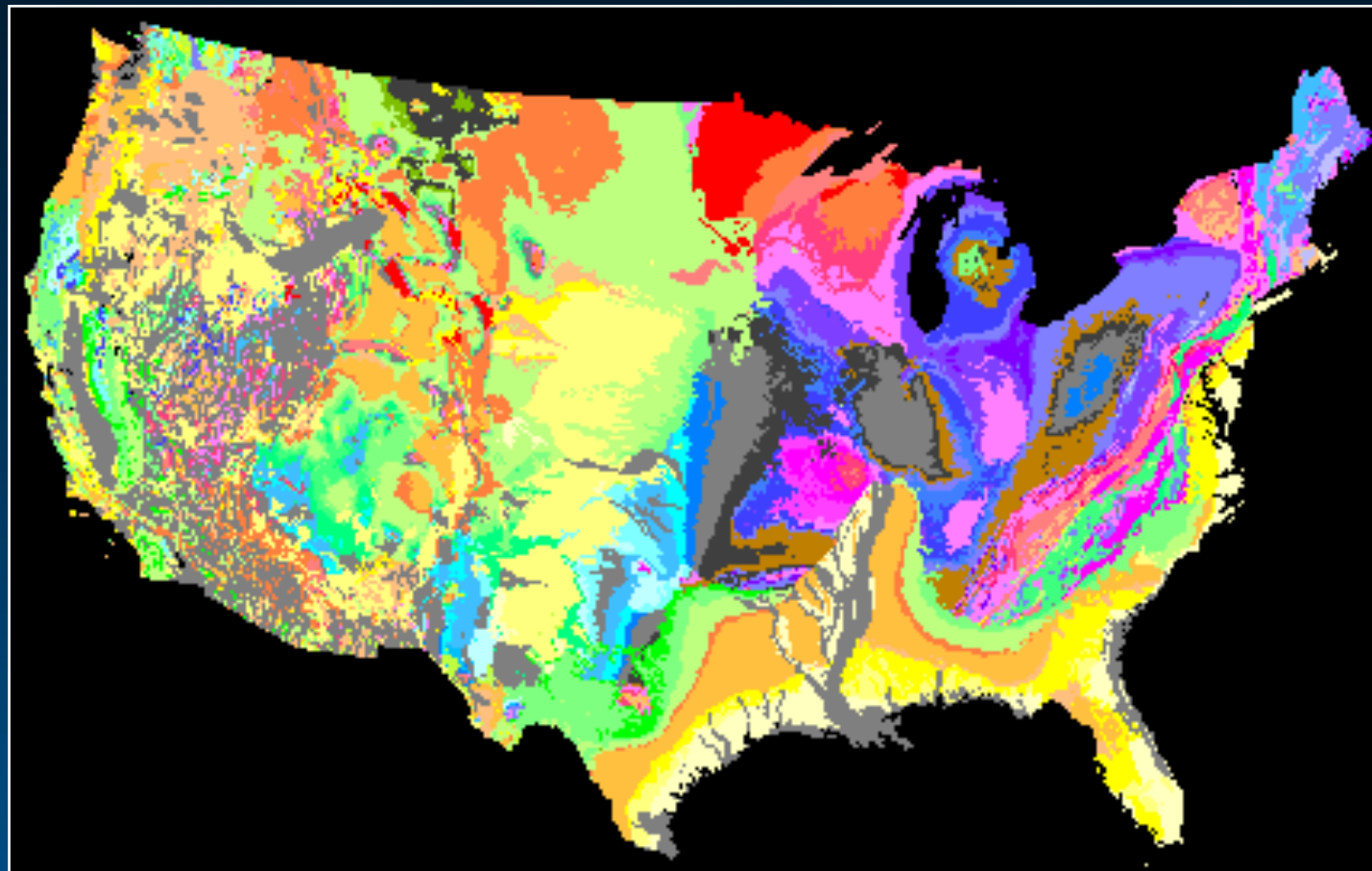
Raup (1991)





# The Nature of the Fossil Record

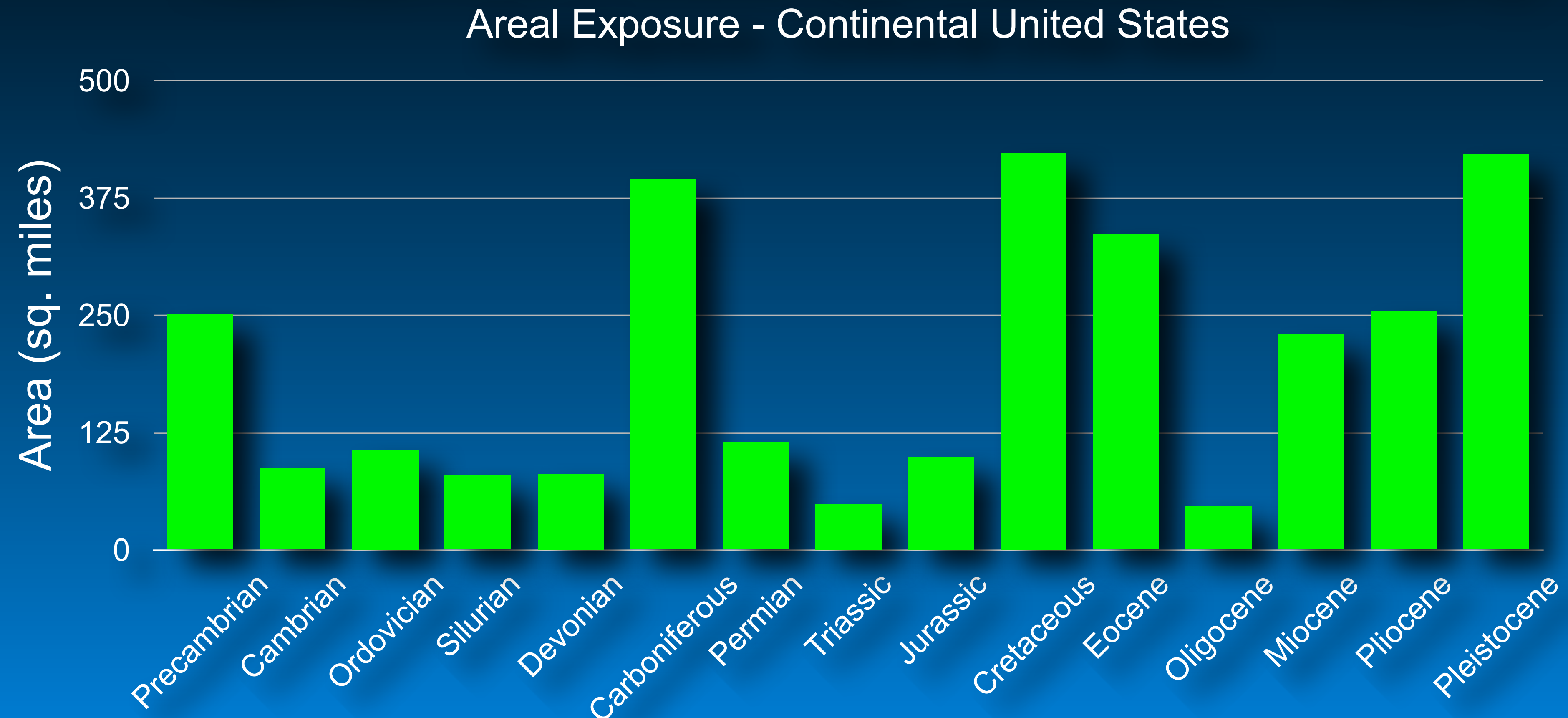
How much rock of different ages is accessible for sampling?





# The Nature of the Fossil Record

How much rock of different ages is accessible for sampling?

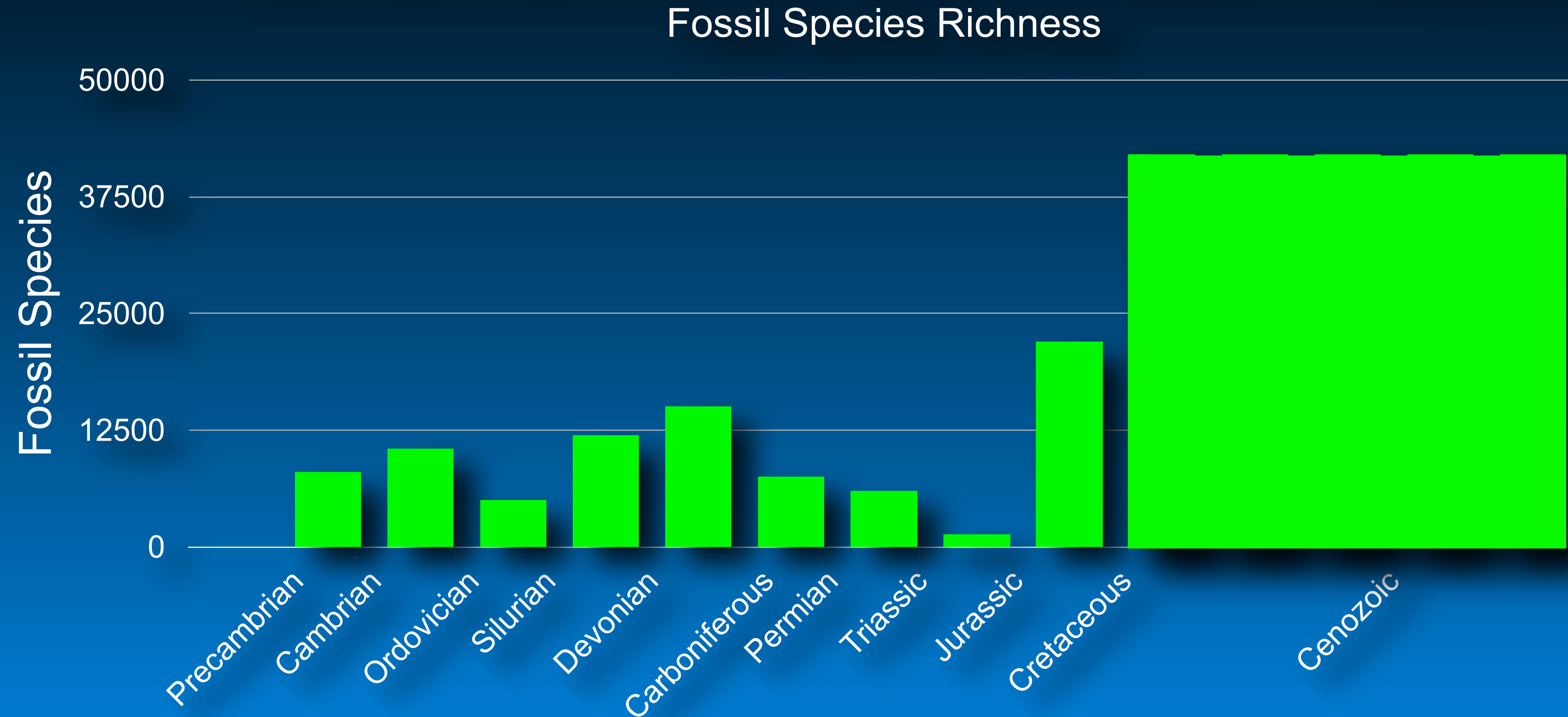


There are several patterns present in these data: (i.) duration of stratigraphic stages, (ii.) outcrop area, (iii.) enhanced recovery from Cenozoic sediments.



# The Nature of the Fossil Record

How much rock of different ages is accessible for sampling?



There are several patterns present in these data: (i.) duration of stratigraphic stages, (ii.) outcrop area, (iii.) enhanced recovery from Cenozoic sediments.

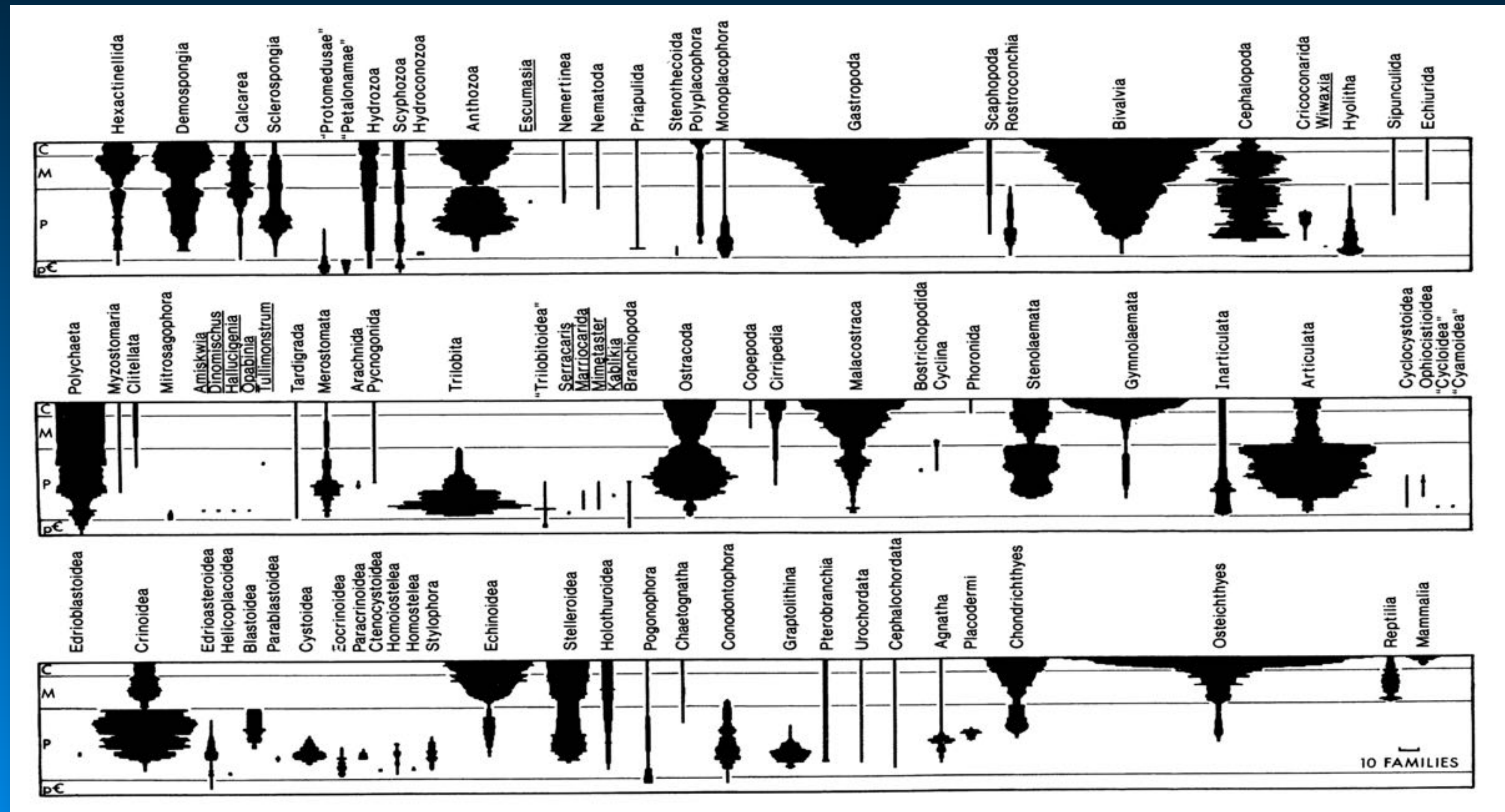






# The Nature of the Fossil Record

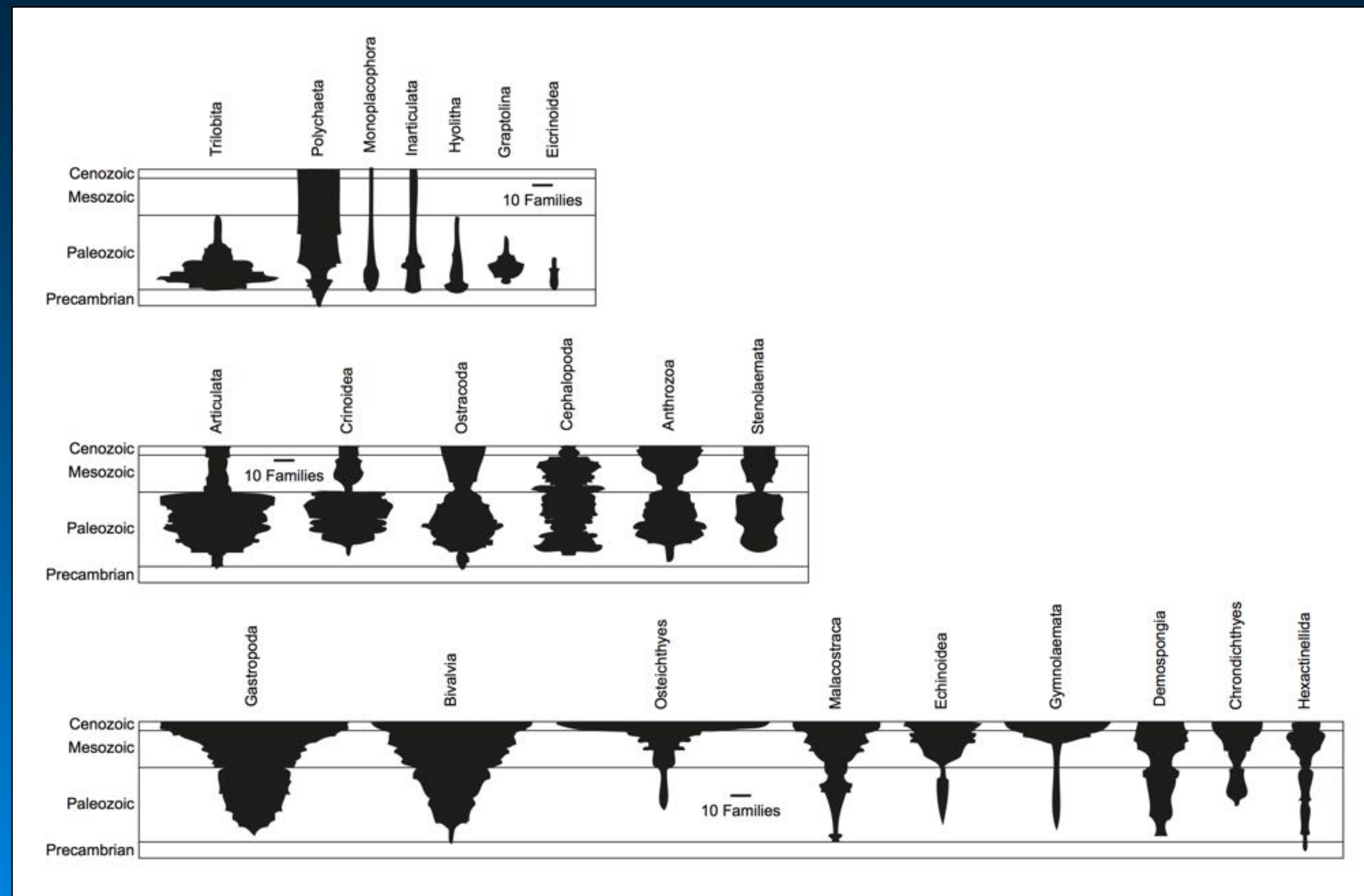
Richness (or “diversity”) charts reflect the evolutionary & ecological histories of major groups ...





# The Nature of the Fossil Record

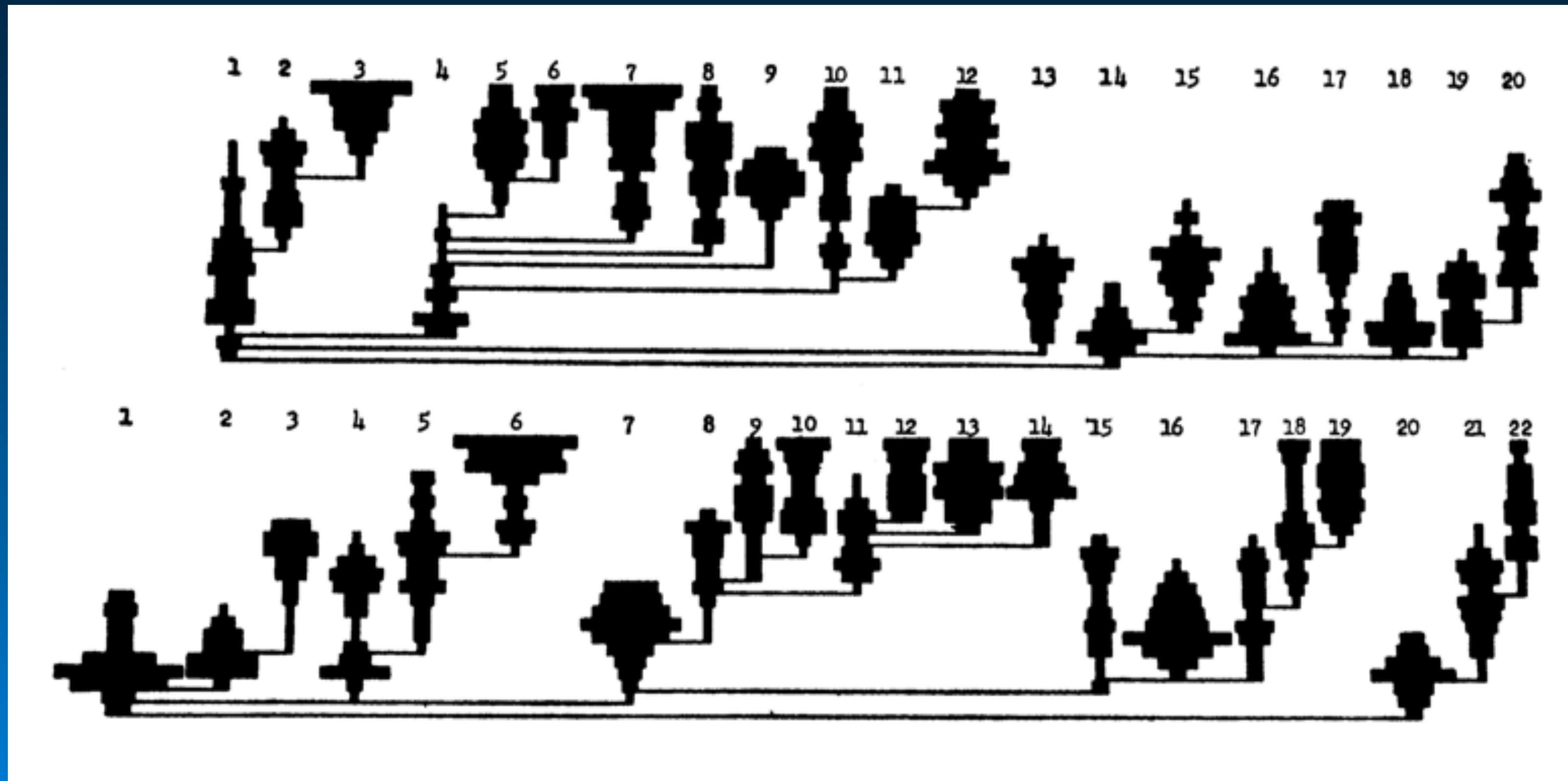
... and there is a strong tendency among paleontologists to construct stories about such data.





# The Nature of the Fossil Record

But in the absence of some appropriate standard of comparison it is very difficult to avoid confirmation bias.



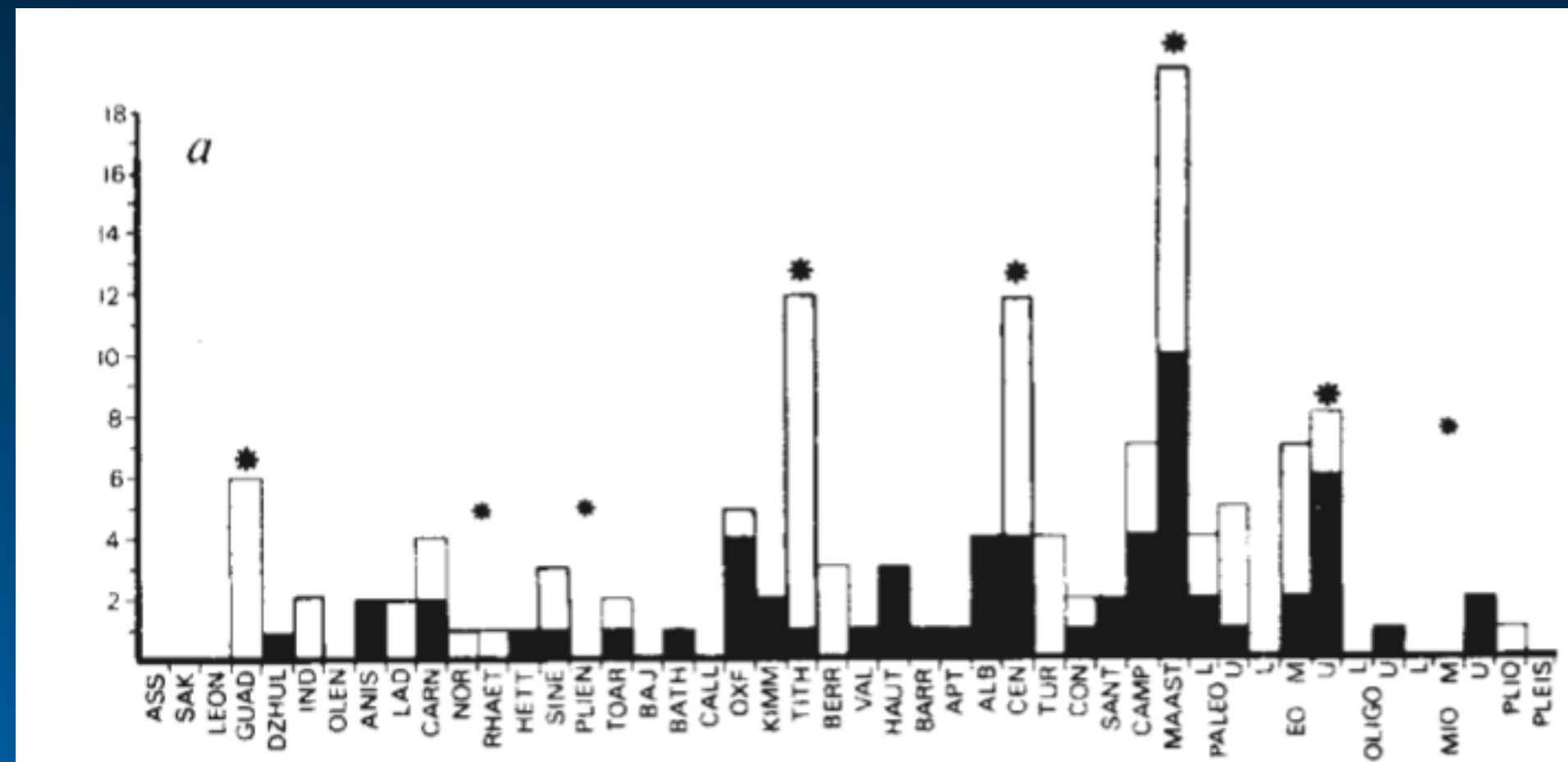
Simulated Random Taxon-Richness Histories



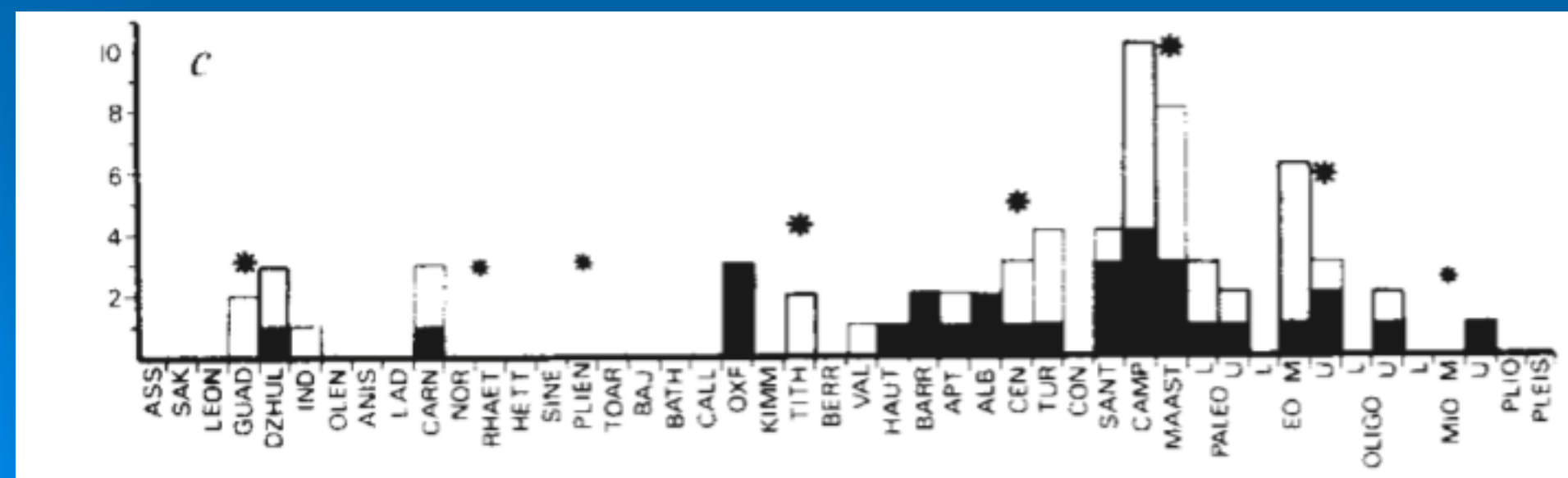
# The Nature of the Fossil Record

## Can we trust the taxonomy in databases?

### The Curious Case of Mass Extinction Periodicity



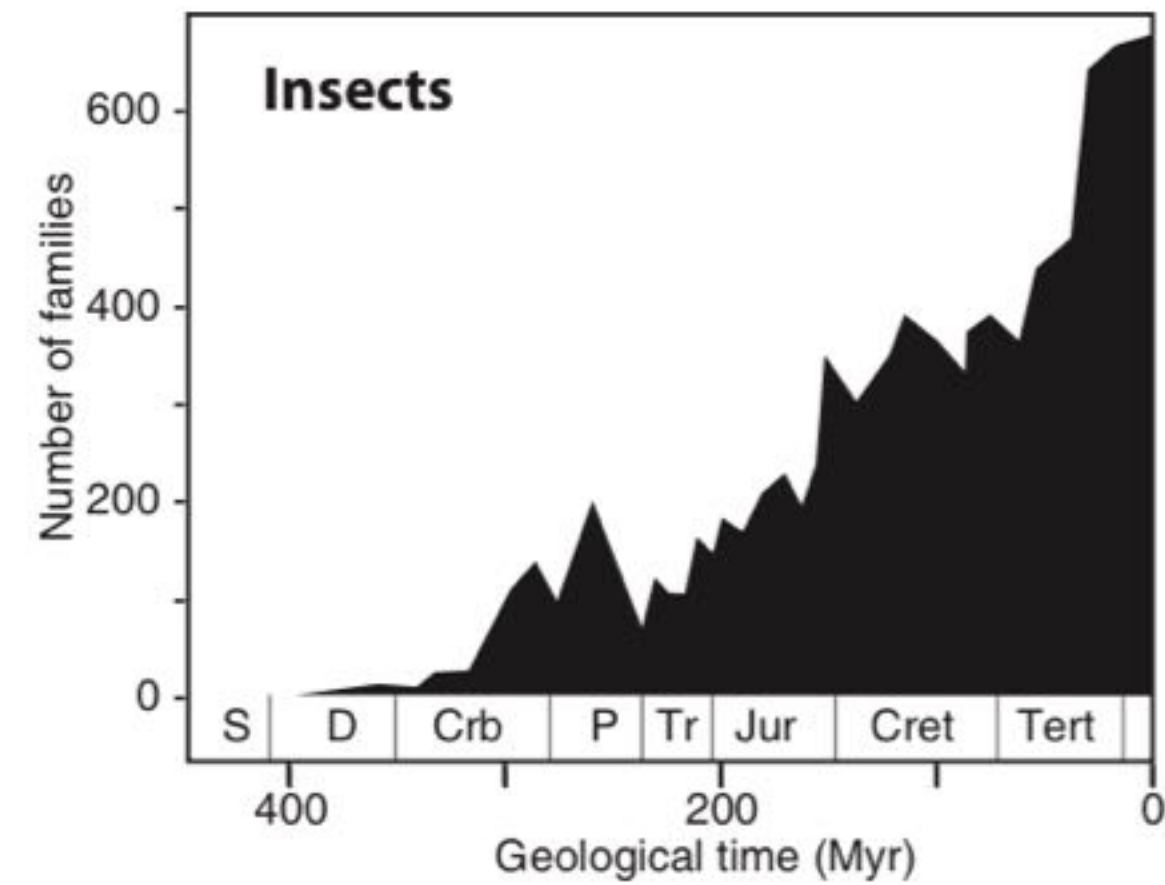
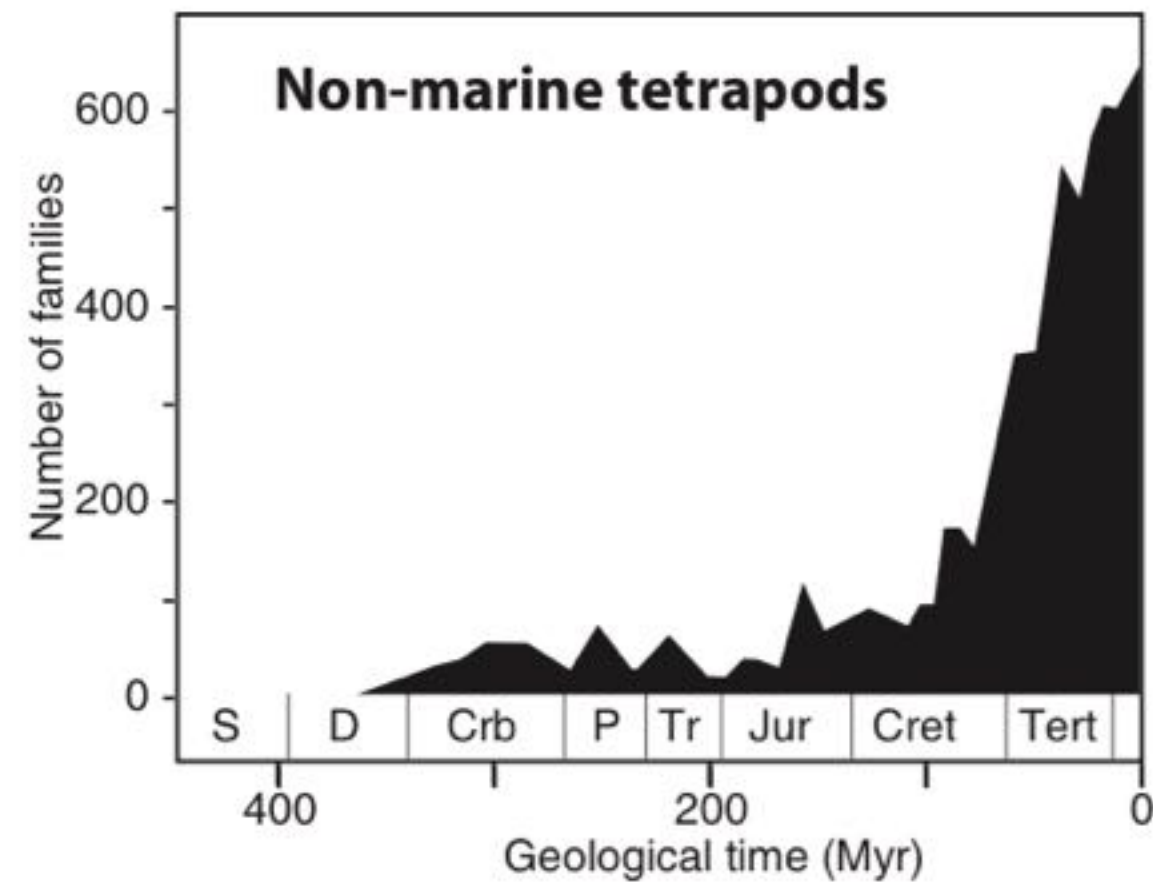
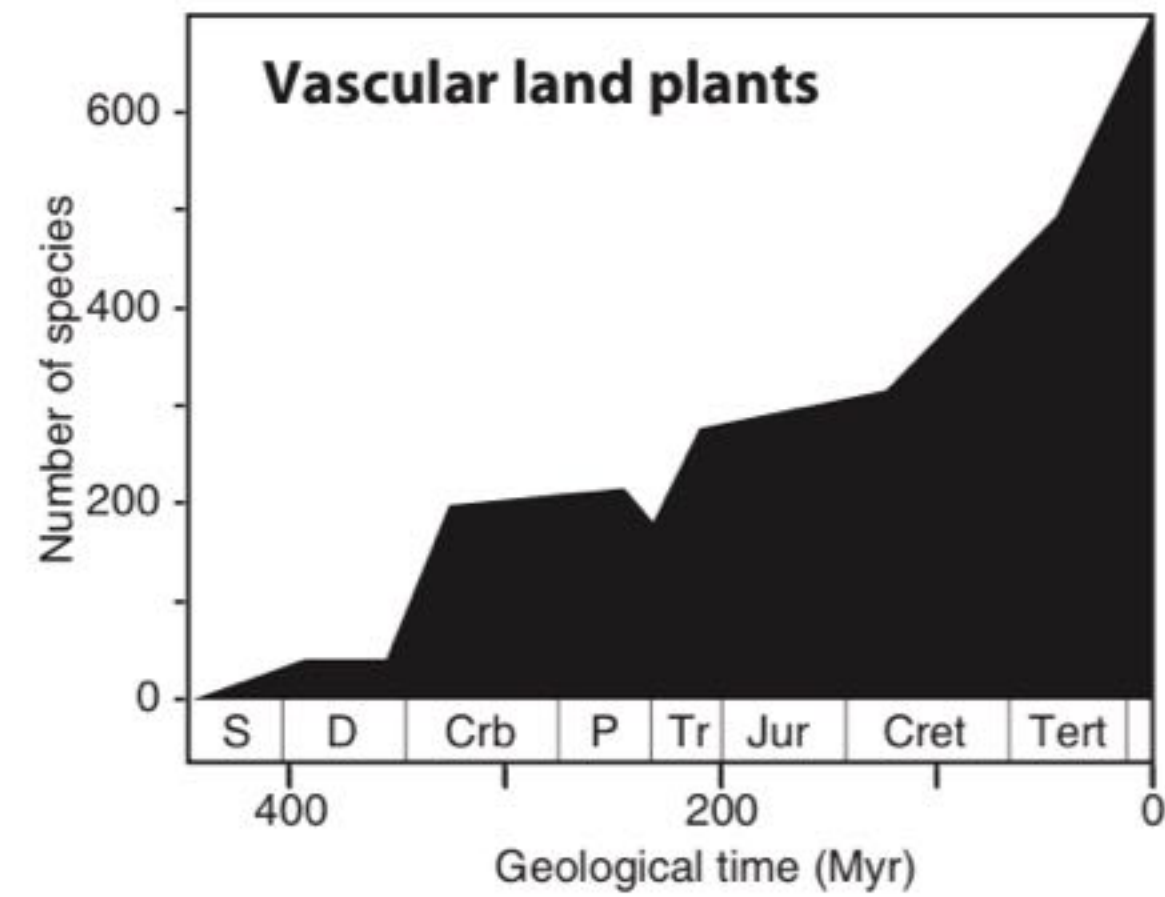
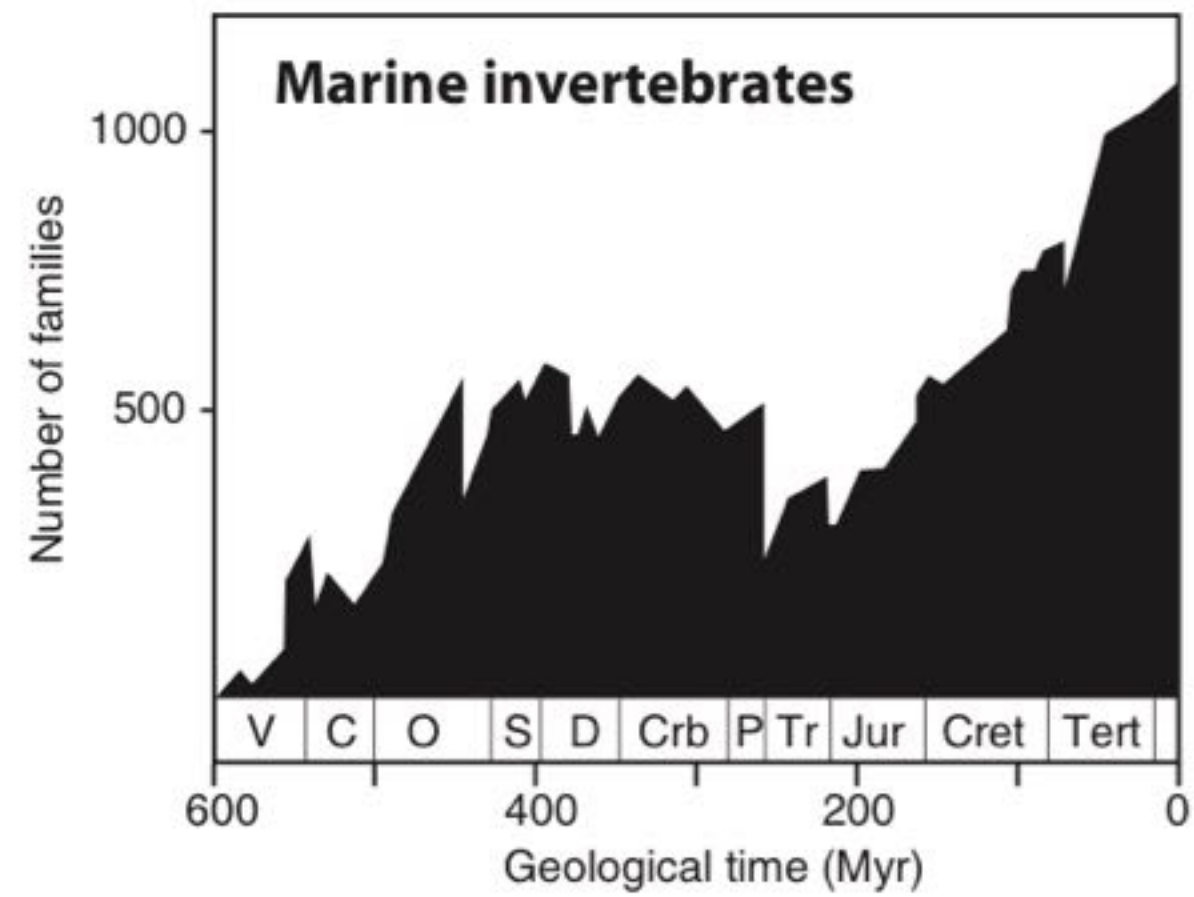
Phanerozoic family-level extinction counts for fish (white) and echinoderms (black) compiled by Sepkoski (1982).



Valid Phanerozoic family-level extinction counts for fish (white) and echinoderms (black) as revised by Patterson and Smith (1987).



# The Nature of the Fossil Record





# The Nature of the Fossil Record

## Summary

Fossil Taxa	
Group	Preservation Probability*
Brachiopoda	0.90
Cephalopoda	0.80 - 0.90
Trilobita	0.70 - 0.90
Bryozoa	0.70 - 0.75
Graptolina	0.65 - 0.90
Echinoidea	0.55 - 0.65
Ostracoda	0.50
Gastropoda	0.40 - 0.55
Porifera	0.40 - 0.45
Bivalvia	0.45 - 0.50
Cnidaria	0.40 - 0.50
Crinoidea	0.40
Asterozoa	0.25
Malacostraca	0.20 - 0.35
Elasmobrancha	0.10 - 0.15
Bony Fish	0.15 - 0.30
Polychaeta	0.05

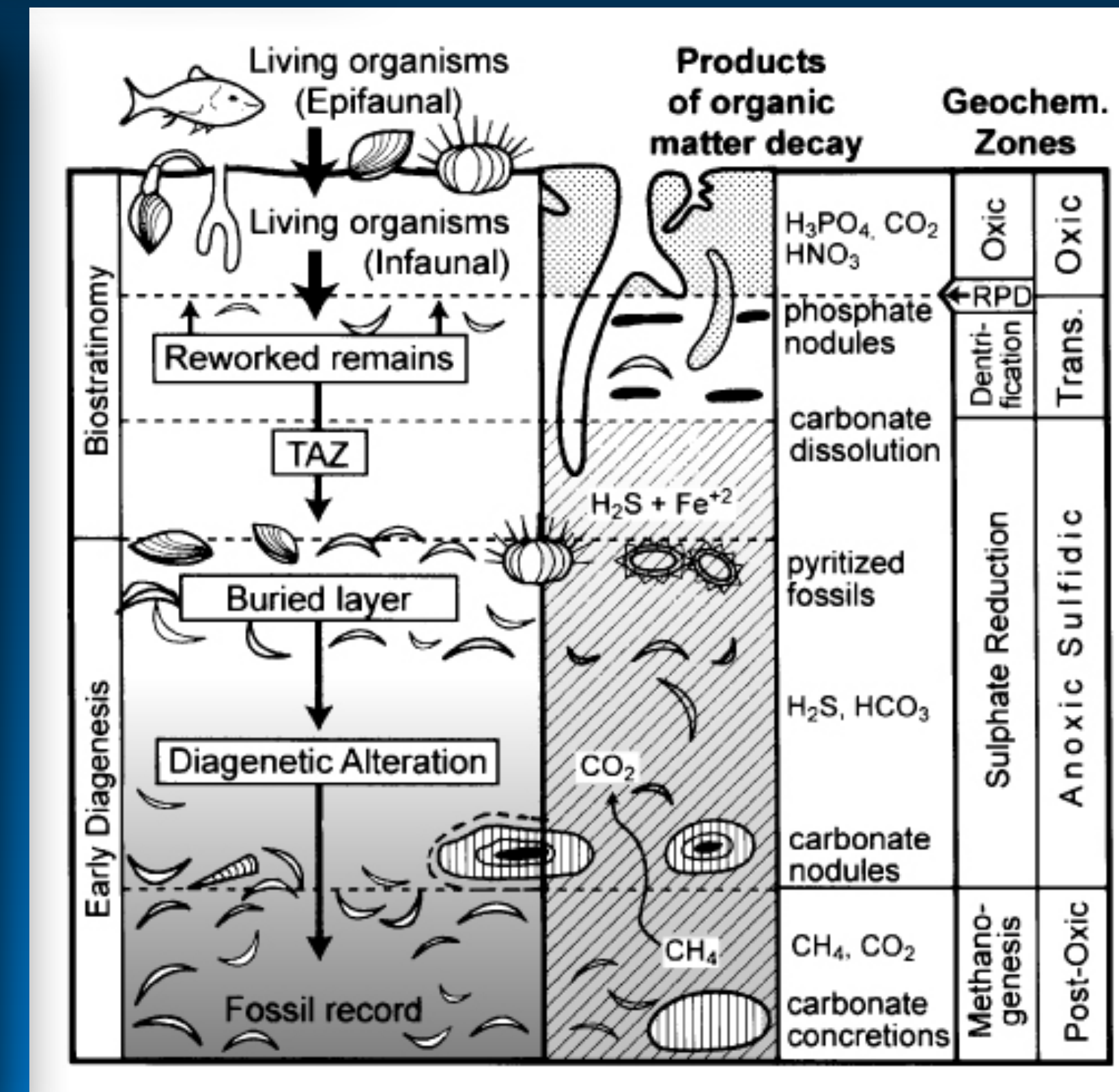
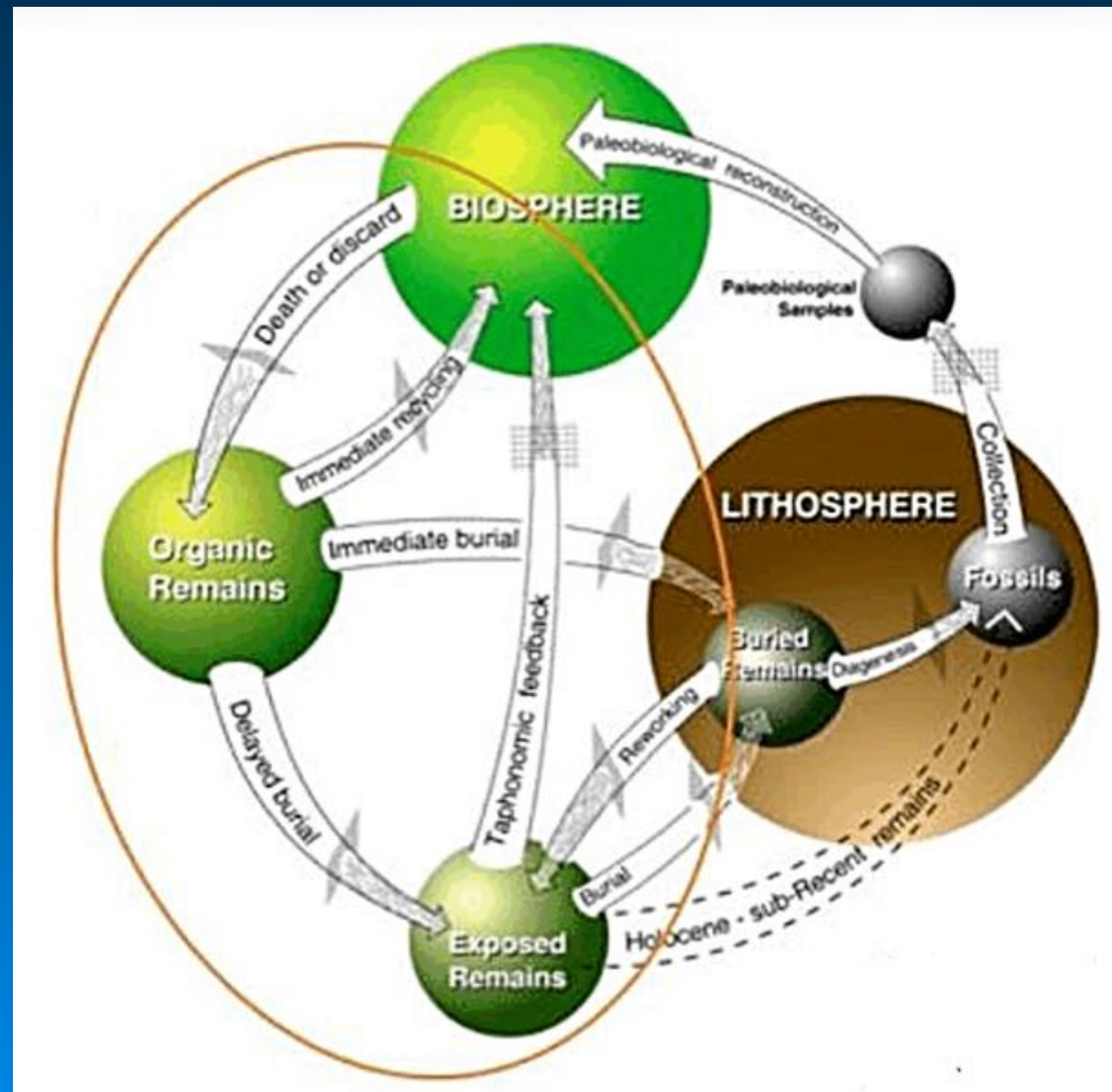
Recent Taxa w/ Fossil Record (%)		
Group	Family	Genus
Brachiopoda	100	77
Bivalvia	95	76
Elasmobranchs	95	-
Echinoidea	89	41
Ostracoda	82	42
Bryozoa	74	-
Bony Fish	62	-
Gastropoda	59	-
Asterozoa	57	5
Crinoidea	50	-
Porifera	48	-
Polychaetes	35	-
Cnidaria	32	-
Cephalopoda	20	-
Malacostraca	19	-
Arthropoda	2	-



# The Nature of the Fossil Record

## Taphonomy

The study of how organic remains pass from the biosphere to the lithosphere, including all processes affecting remains from the time of death (or the discard of shed parts) through decomposition, burial, and preservation as mineralized fossils or other stable biomaterials.





# The Nature of the Fossil Record

Different organismal groups differ in the materials their bodies are composed of and so have different preservation potentials.

Group	Inorganic				Organic				
	CaCO <sub>3</sub>	PO <sub>4</sub>	SiO <sub>2</sub>	FeO	Chitin	Cellulose	Lignin	Collagen	Keratin
Prokaryotes	●	○		○		○			
Algae	●		○		○	●			
Plants	○		○	○		●	●		
Unicellular Eukaryotes	●		●	●	○				
Fungi	○	○		○	●	●			
Porifera	●		●	○				●	
Cnidaria	●				●			○	
Bryozoa	●	●			●			○	
Brachiopoda	●	○	○	○	○			○	
Mollusca	●	●		○	○			●	
Annelida	●	●	○	○	●			○	
Arthropoda	○	○	○					●	
Echinodermata		●						●	●
Chordata	●								

● Major Constituent

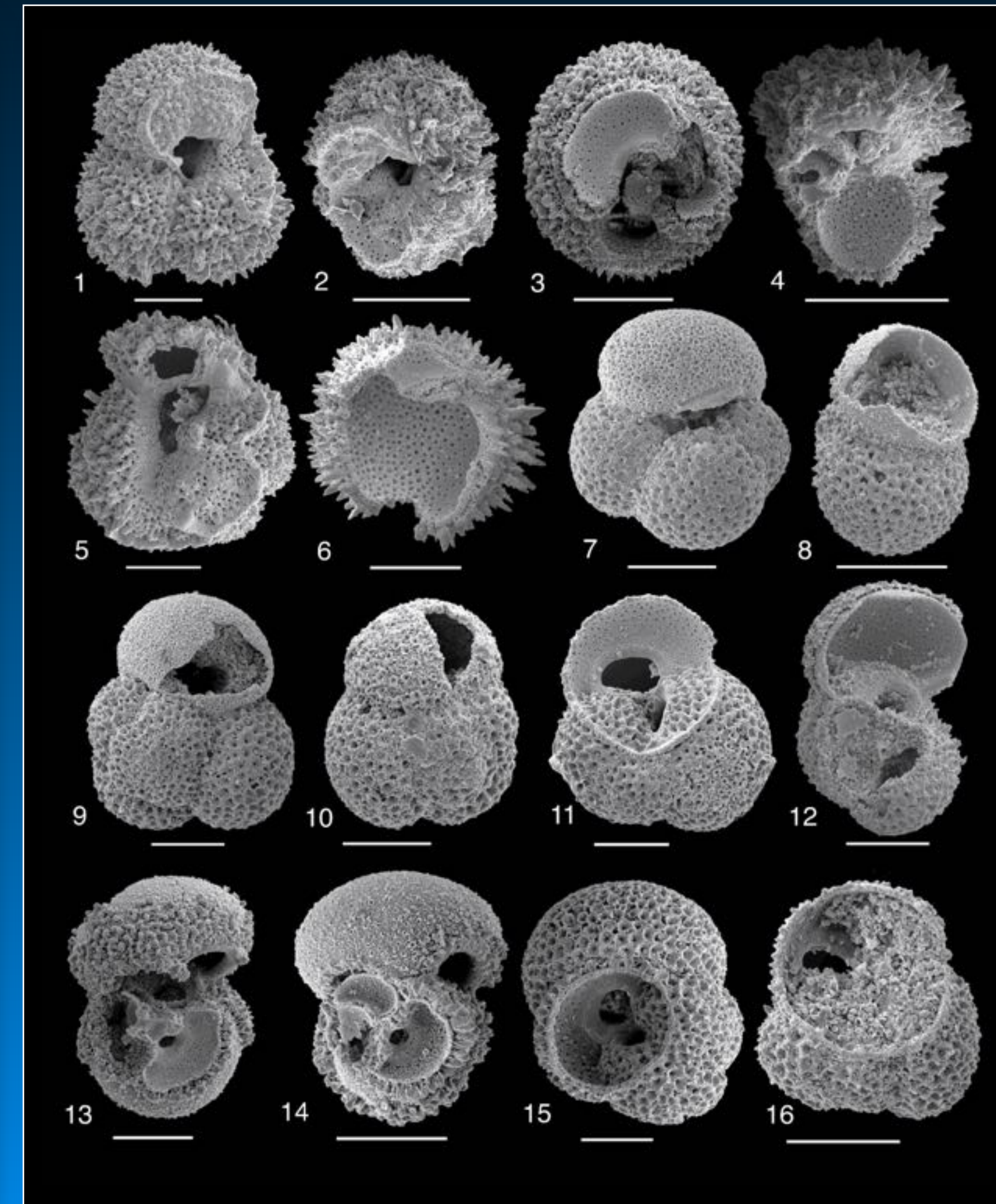
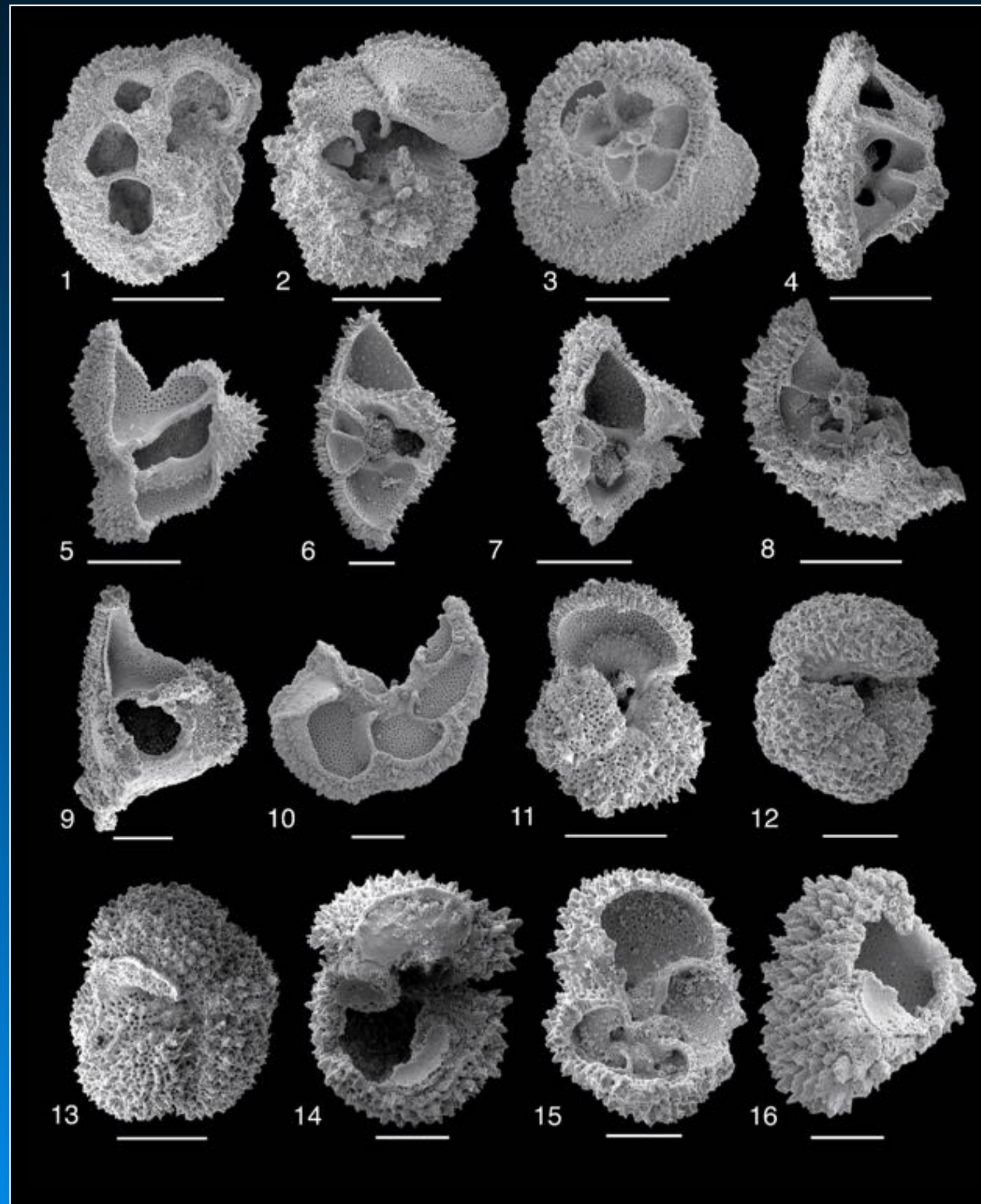
○ Minor Constituent

Towe (1987)



# The Nature of the Fossil Record

## Observational Taphonomy

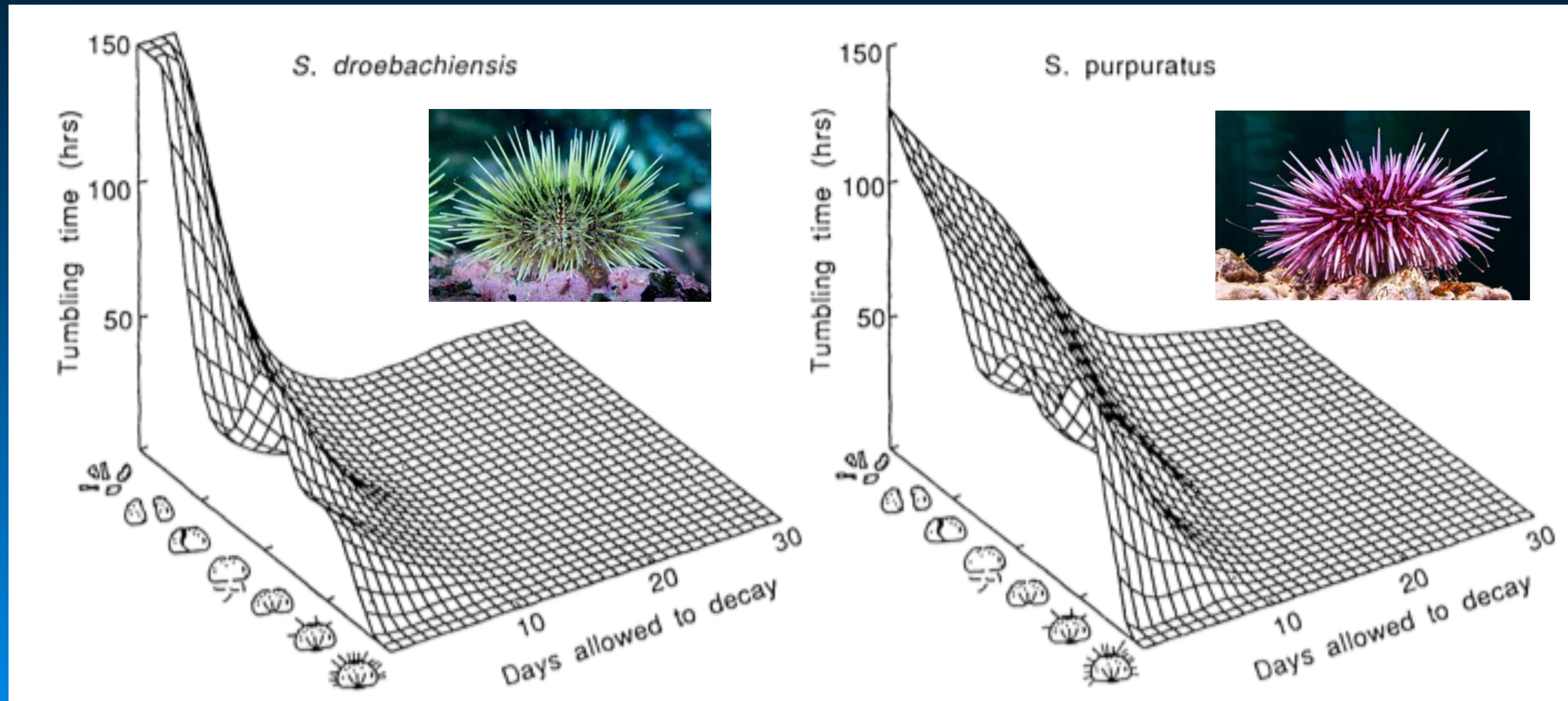




# The Nature of the Fossil Record

## Experimental Taphonomy

This experiment measured susceptibility to fragmentation as a function of the prior decay level.

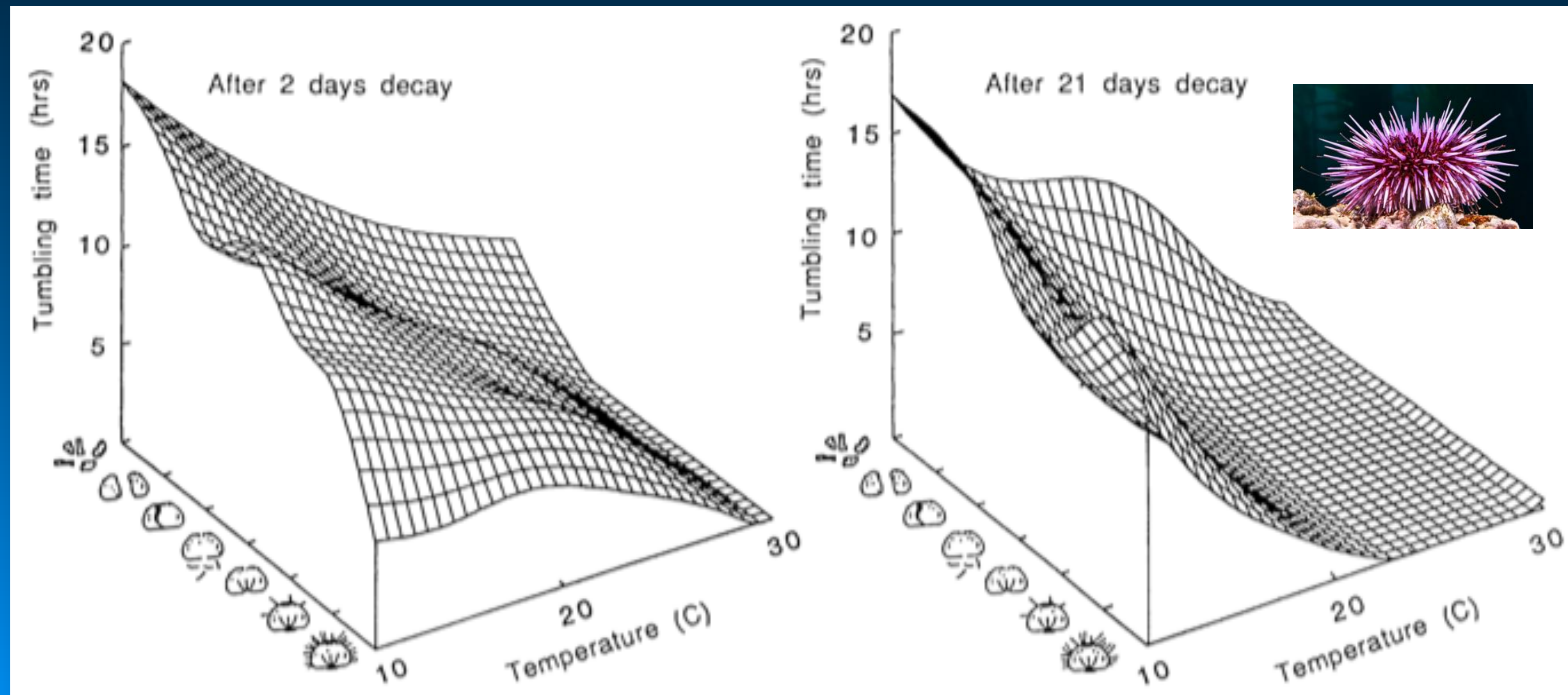




# The Nature of the Fossil Record

## Experimental Taphonomy

This experiment measured susceptibility to fragmentation as a function of both the prior decay level and temperature.

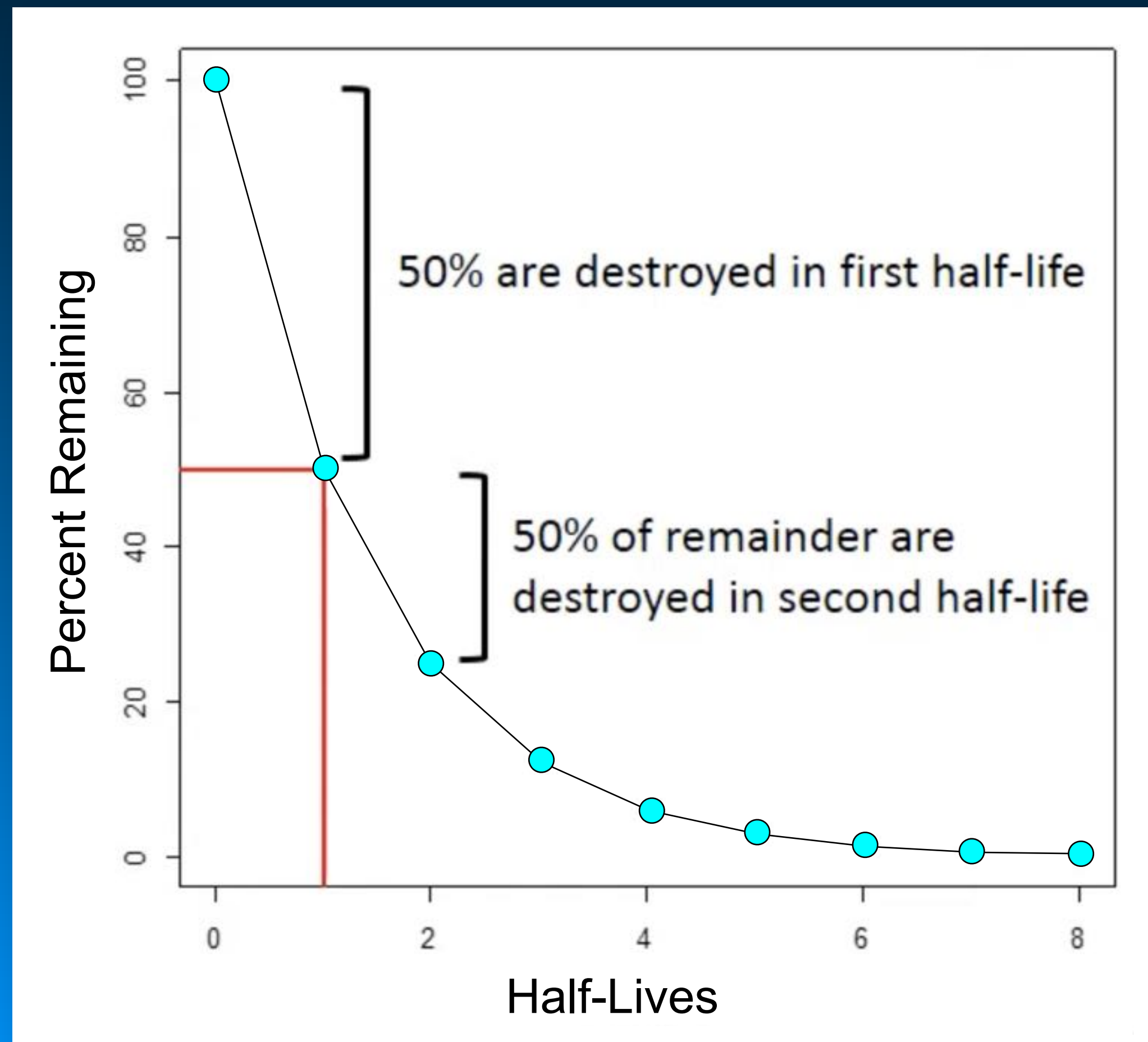




# The Nature of the Fossil Record

## Analytic Taphonomy

### Taphonomic Half-Life



### Factors Effecting Taphonomic Half-Life

- Proportion of shell/skeletal material
- Mineralogy
- Body size
- Environment

Short Half-Life = Lower preservation potential.

Long Half-life - Higher preservation potential.

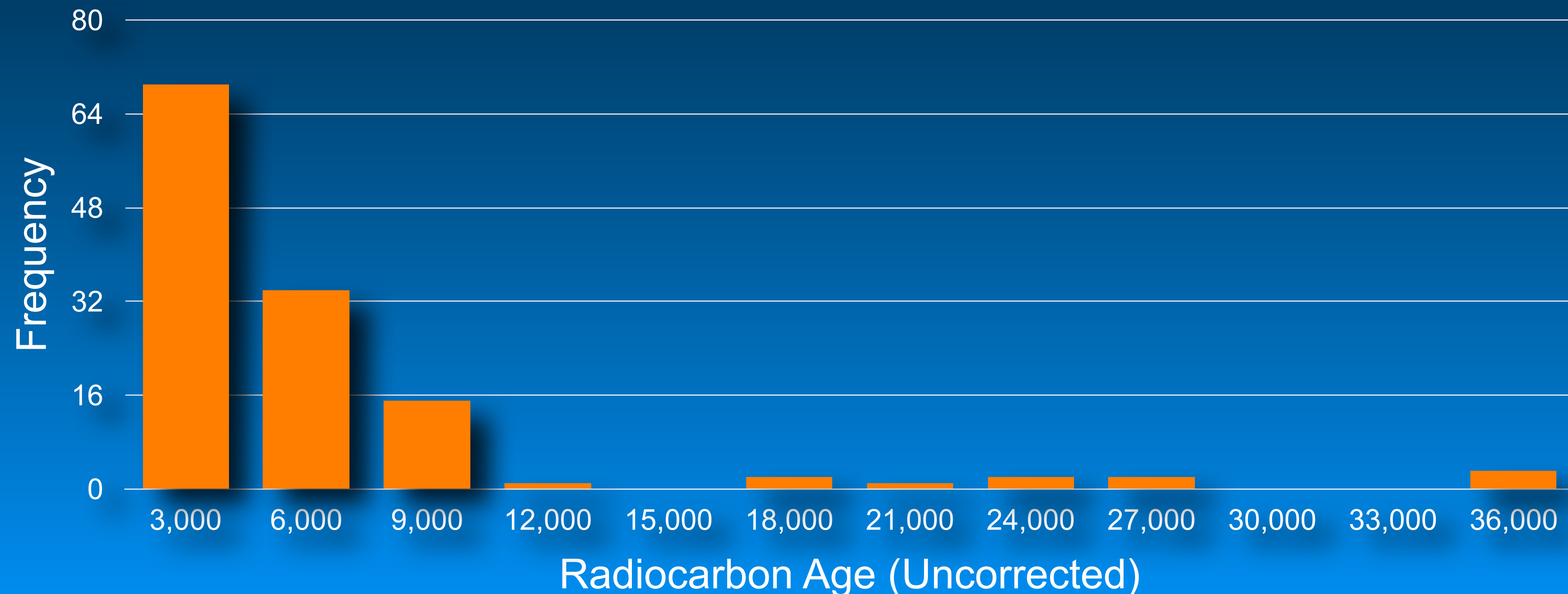


# The Nature of the Fossil Record

## Analytic Taphonomy

### Shell-Age Paradox

When the ages of subfossil shells are measured very old shells almost always comprise a significant proportion of the assemblage.

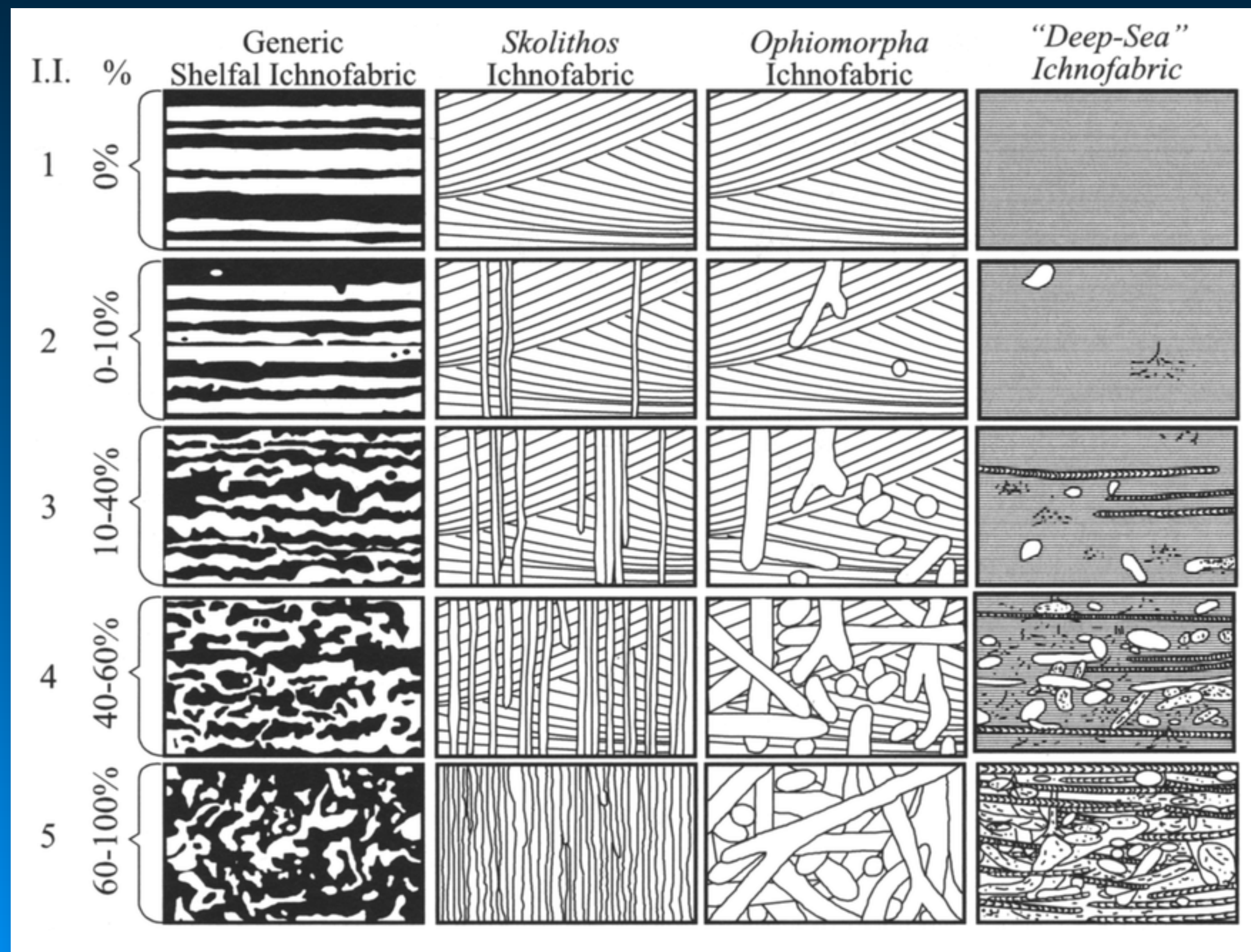




# The Nature of the Fossil Record

## Analytic Taphonomy

### Shell-Age Paradox





# The Nature of the Fossil Record

## Analytic Taphonomy

### Time Averaging

The average amount of time a shell/skeleton remains in the time averaged zone (TAZ). “Event beds” (or Lagerstätten) are fortuitous situations where organisms spend only days in the TAZ.

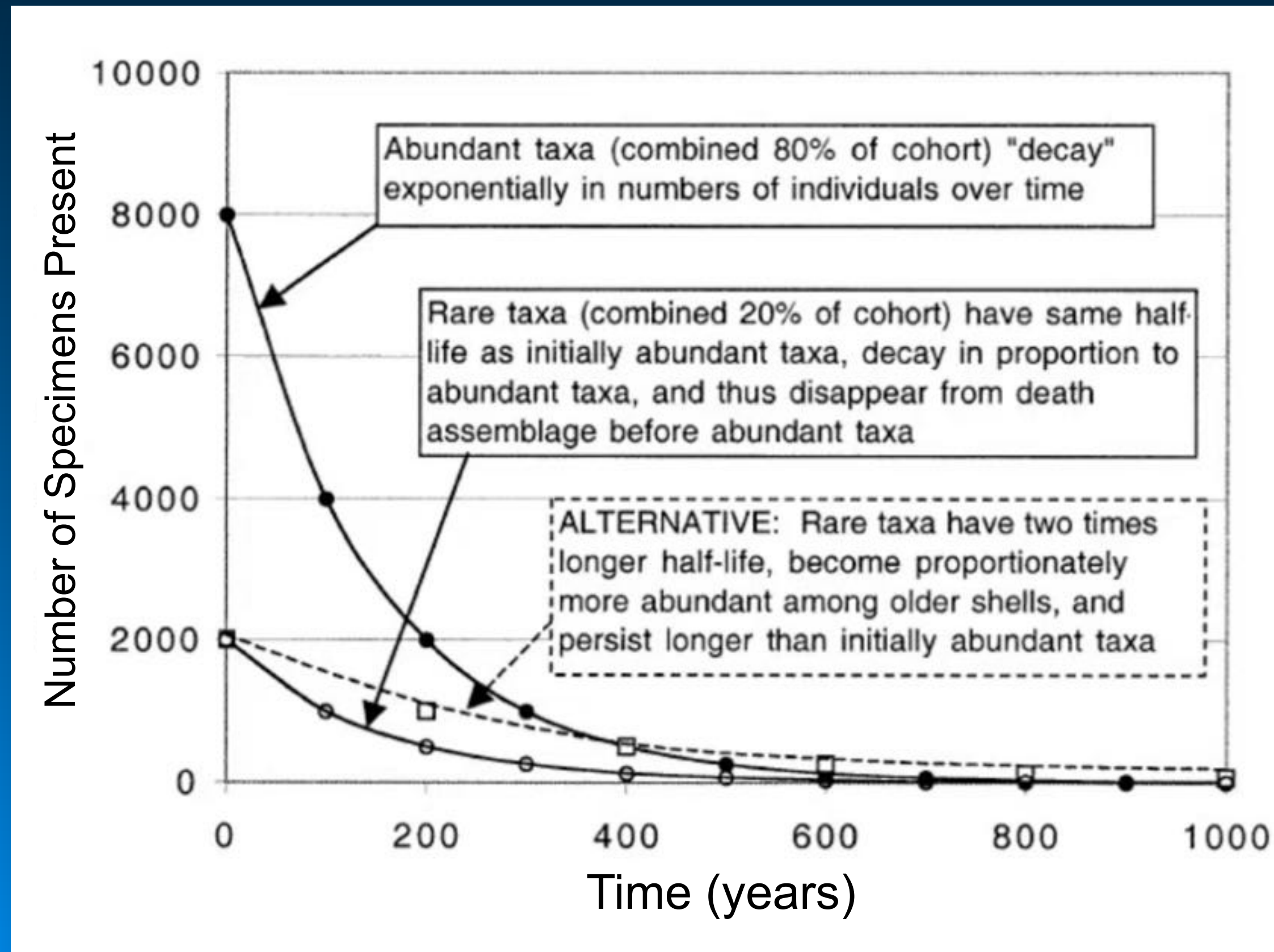




# The Nature of the Fossil Record

## Analytic Taphonomy

### Effect of Time-Averaging: Excess Taxic Richness



Severity of this effect is controlled, counterintuitively, by the taphonomic half-life of rare taxa. The longer their half-life the greater the apparent (but not real) taxic richness.

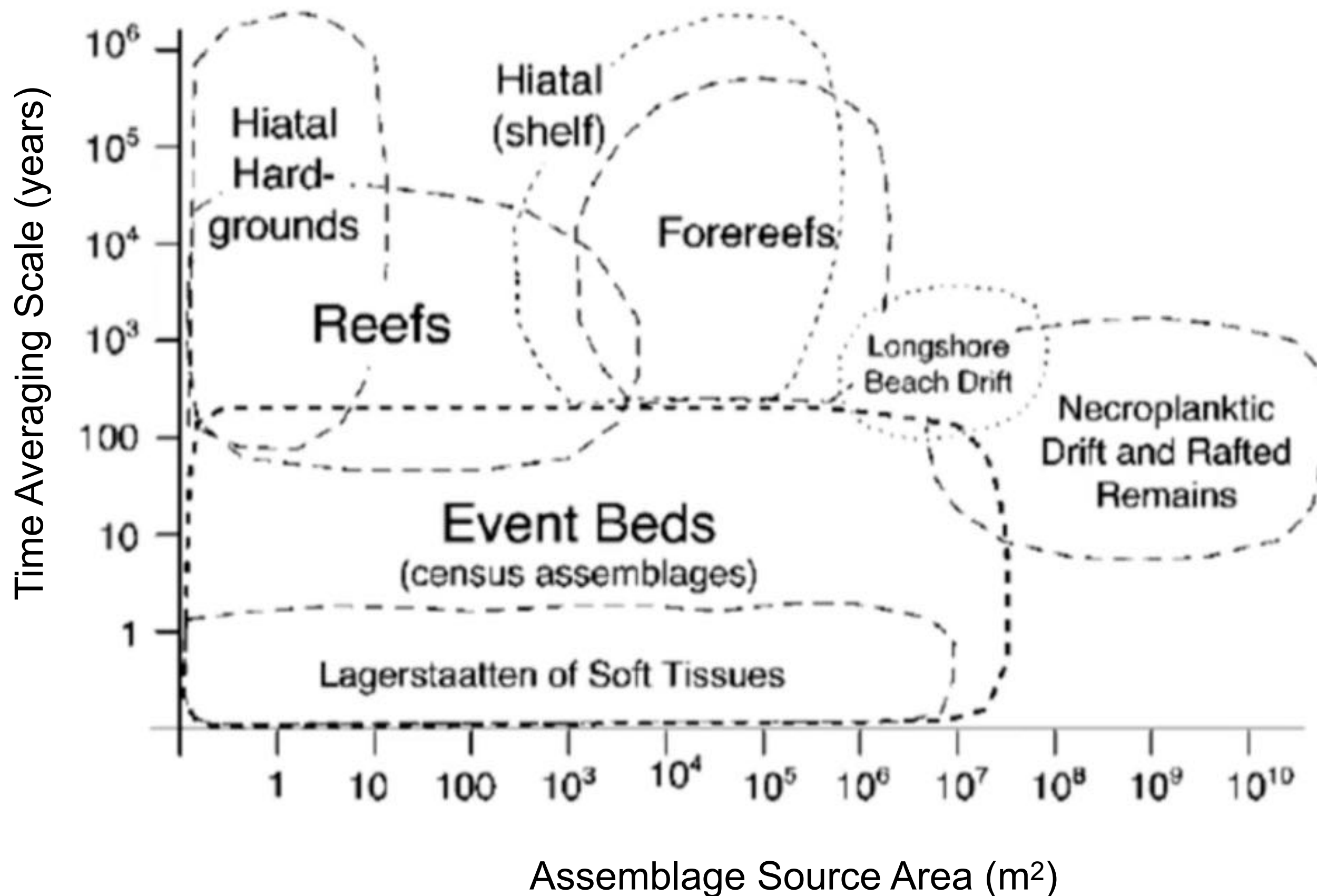
Abundant taxa are also often smaller and thinner-shelled which creates a further bias.



# The Nature of the Fossil Record

## Analytic Taphonomy

### Spatial Averaging



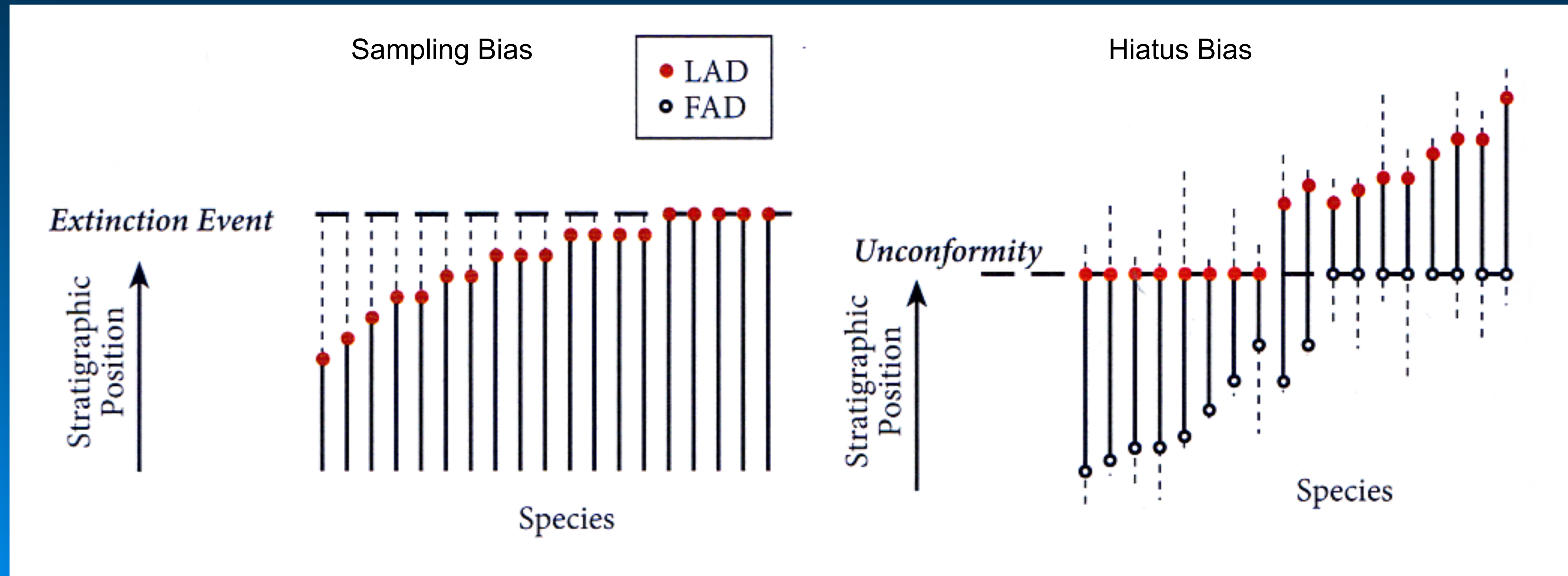
This source of averaging occurs as well, but present data suggest it to be an insignificant source of bias due to cross-environment “leakage”.



# The Nature of the Fossil Record

## Bias in Apparent Stratigraphic Ranges

Stratigraphic ranges cannot be accepted uncritically as true representations of a taxon's distribution in time because each stratigraphic section/core is effected by various complications and inconsistencies that disrupt the simple-minded assumption that position in a spatial sequence = position in time.

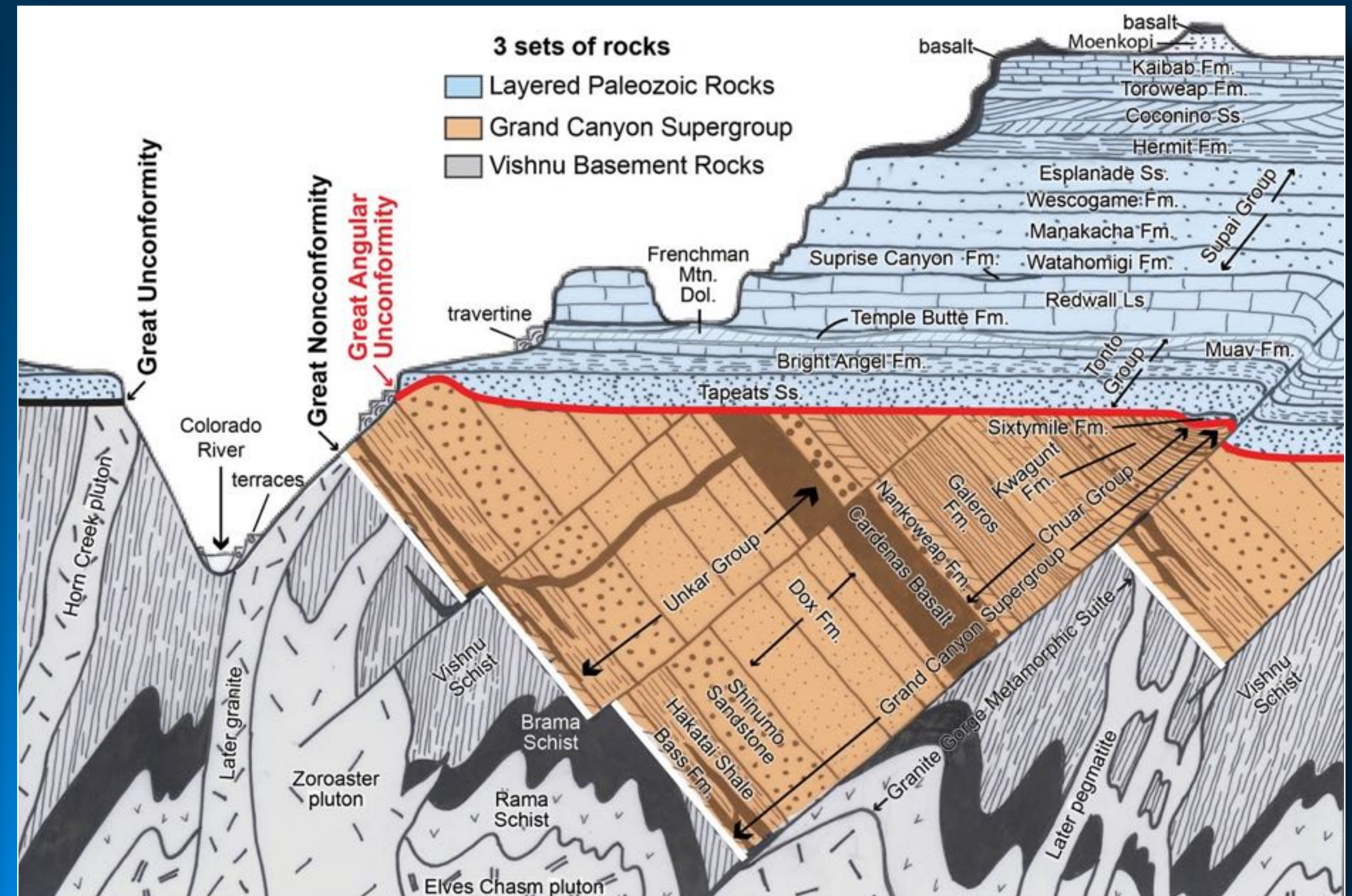




# The Nature of the Fossil Record

## Stratigraphy

Can we trust the data we observe in stratigraphic sequences?

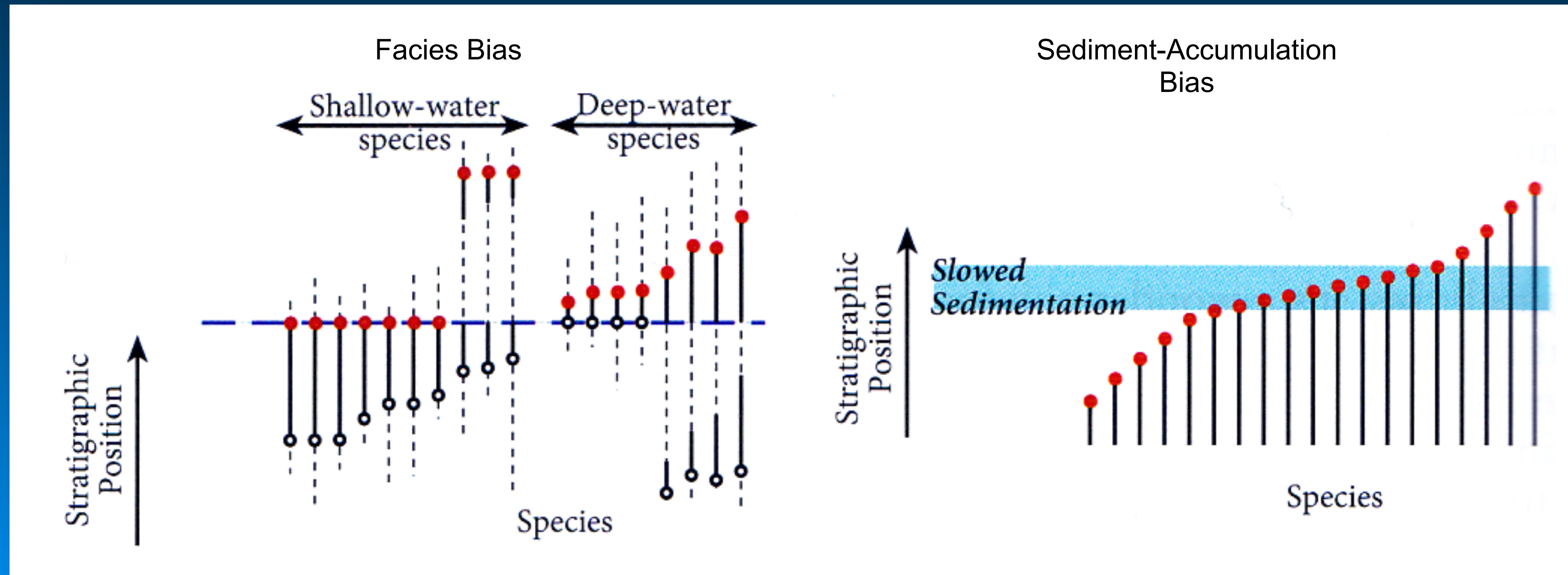




# The Nature of the Fossil Record

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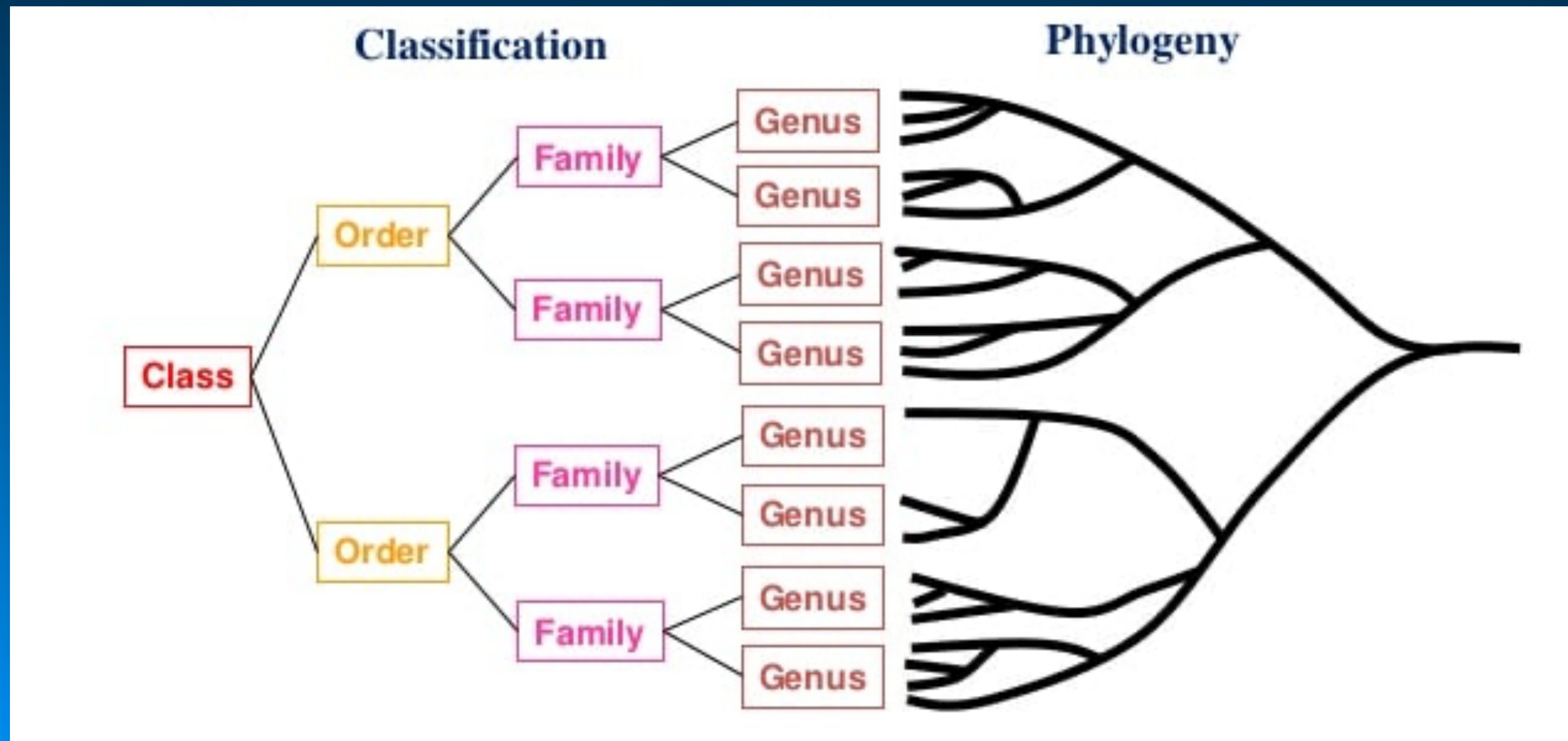




# The Nature of the Fossil Record

## Phylogenetic Validation of Taxon Ranges

A fundamental problem is that, until recently, there has been no alternative to the fossil record for estimating the ages of taxa. However, an alternative source of age data now exists for some well-studied modern groups in the form of well-supported and chronologically calibrated phylogenies.

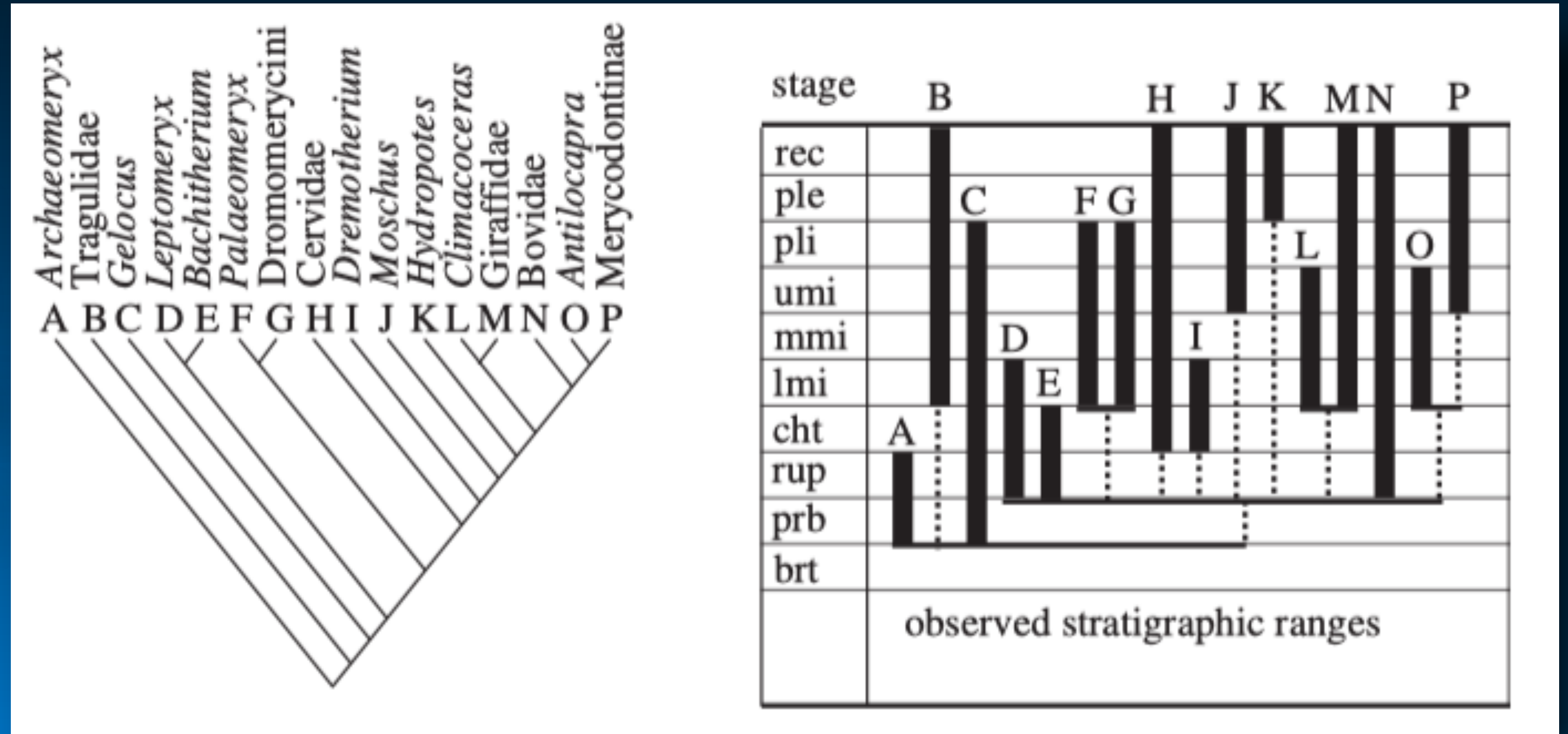




# The Nature of the Fossil Record

## Phylogenetic Validation of Taxon Ranges

- Stratigraphic Completeness Index (SCI) - ratio of stratigraphically consistent to stratigraphically inconsistent nodes (Huelsenbeck, 1994).
- Relative Completeness Index (RCI) - ratio between ghost ranges and observed ranges (Benton and Storrs, 1994).
- Gap Excess Ratio (GER) - Congruence between the phylogeny and the fossil record taking account of uncertainty in ghost range estimates (Wills, 1999).

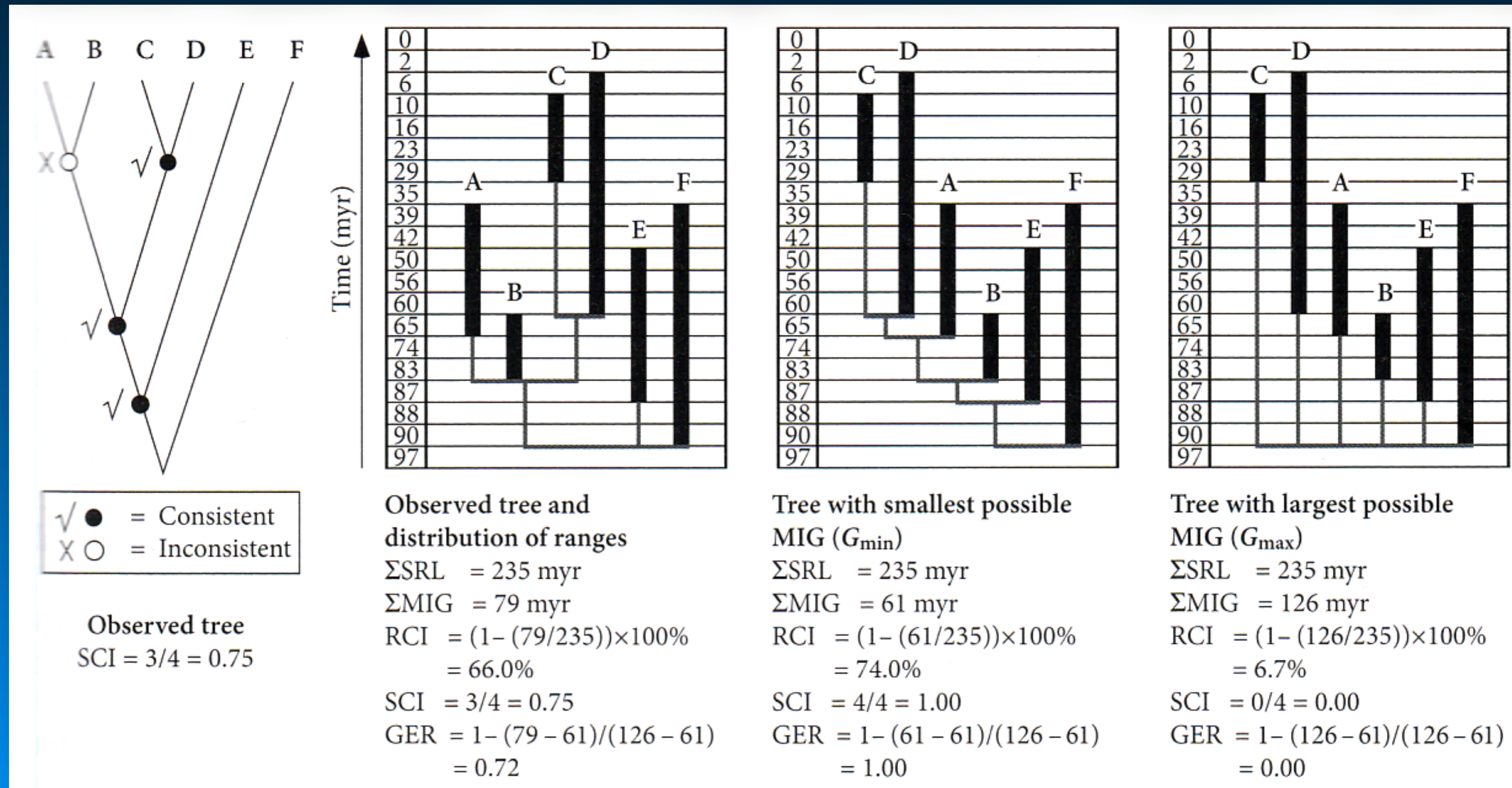




# The Nature of the Fossil Record

## Phylogenetic Validation of Taxon Ranges

MIG = Minimum Implied Gap (or Ghost Range Duration); SRL = Standard or total range length





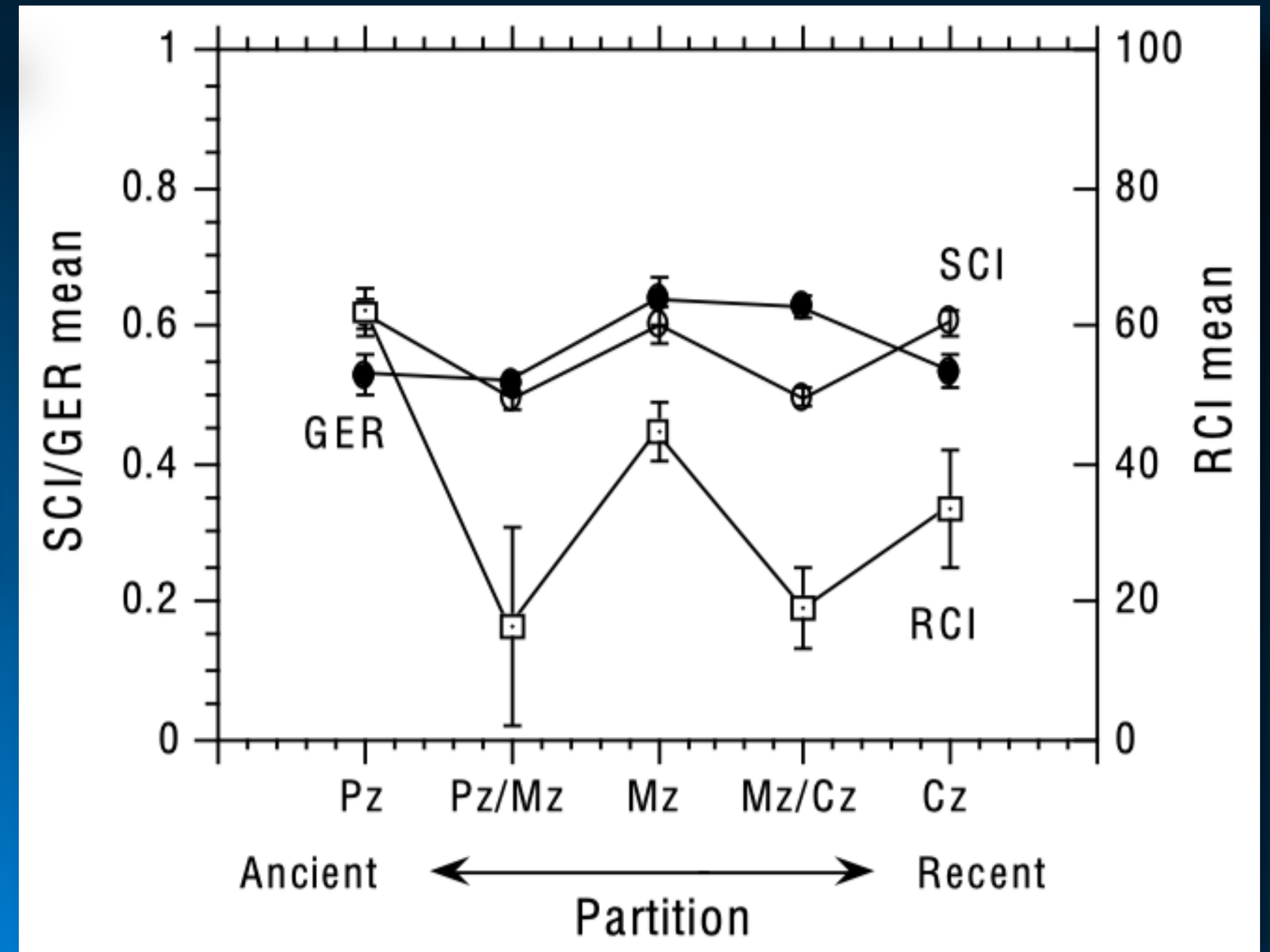
# The Nature of the Fossil Record

## Phylogenetic Validation of Taxon Ranges

Comparisons between the observed fossil records and estimated phylogenies for 1,000 cladograms (morphological and molecular) covering five Phanerozoic intervals.

This study demonstrates fairly good agreement between stratigraphic and morphologic-evolutionary data sources. The low RCI values can be accounted for by the fact that this index takes total geologic time into consideration.

Thus, inferences from stratigraphic data seem more-or-less reliable for rank-order considerations, but not for precise chronostratigraphic purposes.





# Principles of Paleobiology

## The Nature of the Fossil Record

