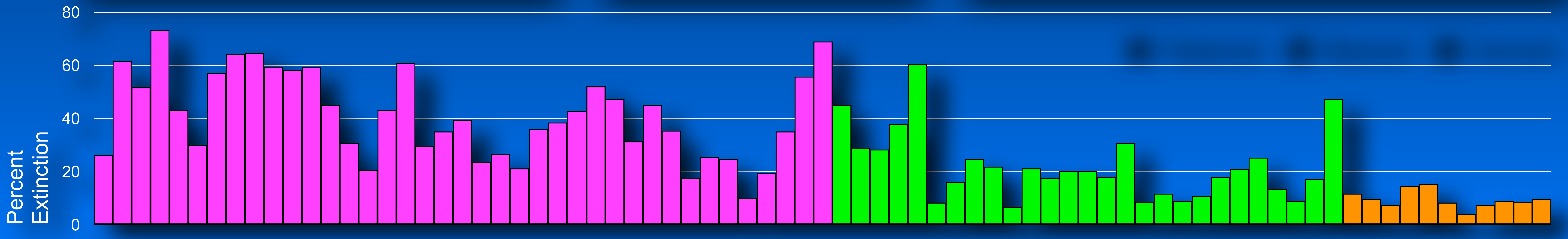
NJU Course

Principles of Paleobiology

Patterns & Modes of Extinction



What is Extinction?

Entry of the Animals into Noah’s Ark (1613)
Jan Brueghel the Elder

Patterns & Modes of Extinction

Types of Extinction

- Extinct species - a taxon, all of whose members have died without leaving any progeny.
- Extripated species - a taxon that has ceased to exist in a geographic area while still existing elsewhere.
- Ghost species - a taxon declared extinct, but which has been sighted by non-professional observers at a later date.
- Lazarus species - a taxon declared to have become extinct, but which has been (re)discovered by qualified observers at a later date.
- Zombie species* - a fossil that has been eroded and then redeposited in younger sediments.
- Elvis species - a taxon that has been rediscovered after being presumed extinct, but has been discovered not to belong to the extinct taxon subsequently.

Triceratops horridus

* Also, an extant taxon whose individuals have lost the ability to reproduce.

Types of Extinction

Mammuthus primigenius
(Woolly Mammoth)

Camelinae
(Camels)

Thylacinus cinocephalus
(Tasmanian Tiger)

Jurassic ammonite collected
from Cretaceous sediments

Coelacanth
(Lobe-Finned Fish)

Lobothyris subgregaria
(formerly *Rhaetina gregaria*)

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Types of Extinction

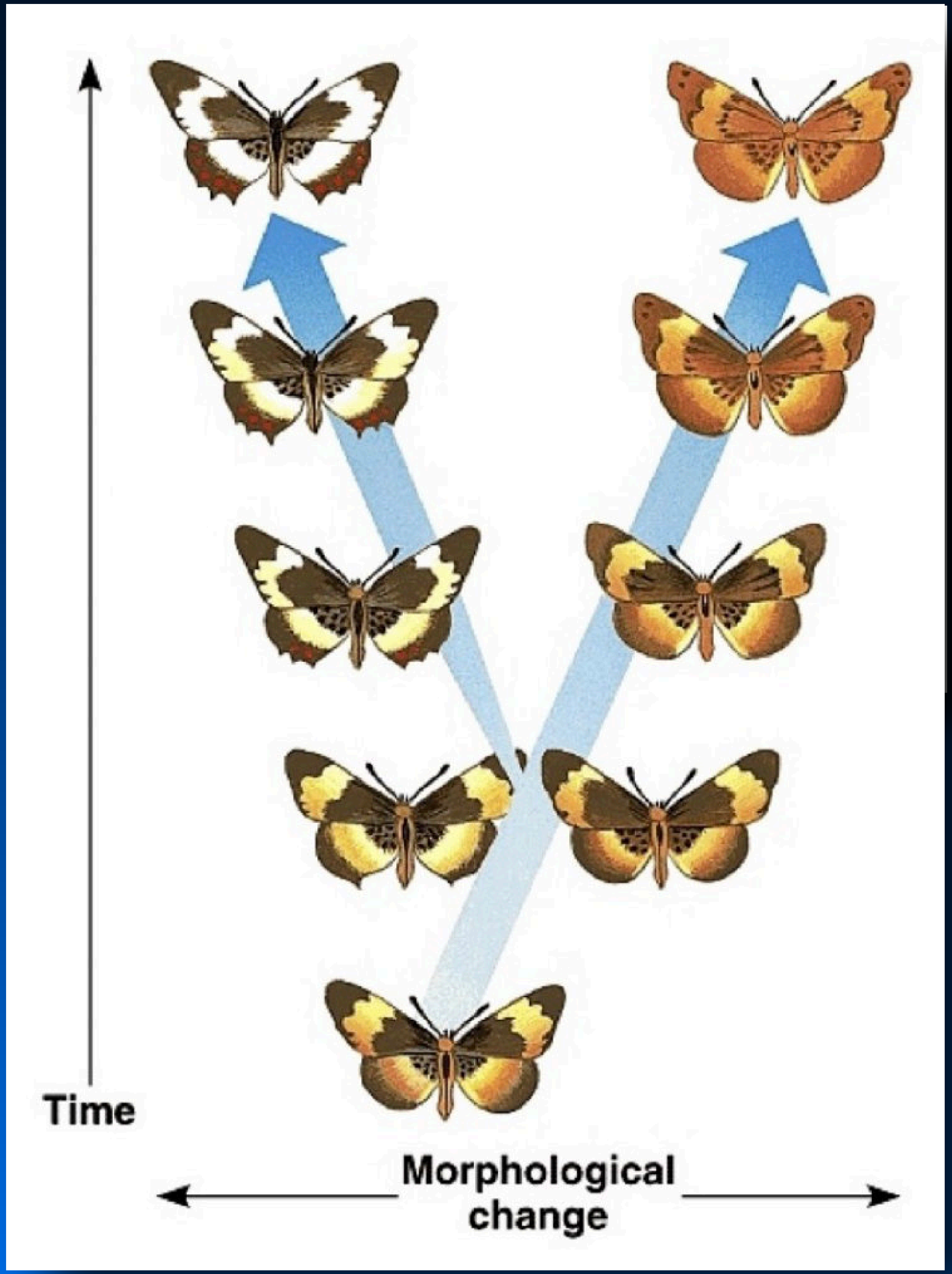
Pseudoextinction - a taxonomic artifact resulting from the practice of giving a new name to members of an evolving taxon when morphological divergence from the ancestral form reaches a point where, in the taxonomist's opinion, advantage is gained through designation under a new name.

Possible Advantages

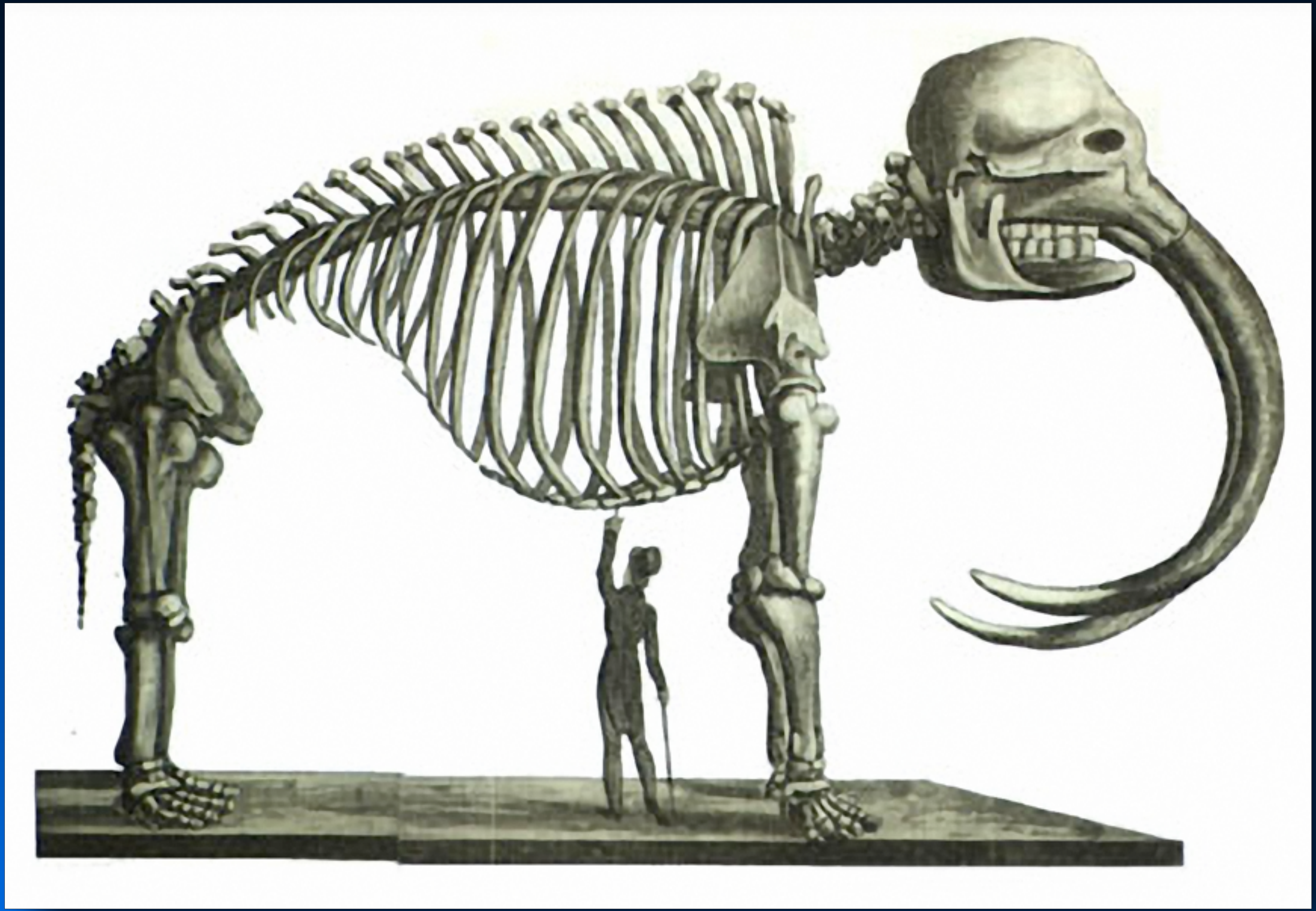
- Biostratigraphic utility - under the new name(s) a fossil taxon can be used in the definitions of progressively younger biozones.
- Assumption that reproductive isolation is gained through morphological change.

Paleobiological Disadvantages

- This practice inflates the number of apparent originations and extinctions artificially and so constitutes an important source of bias in these data.



History of Extinction Studies



American incognitum
(1799)

History of Extinction Studies

The "First" Extinction

Raphus cucullatus
(Dodo)

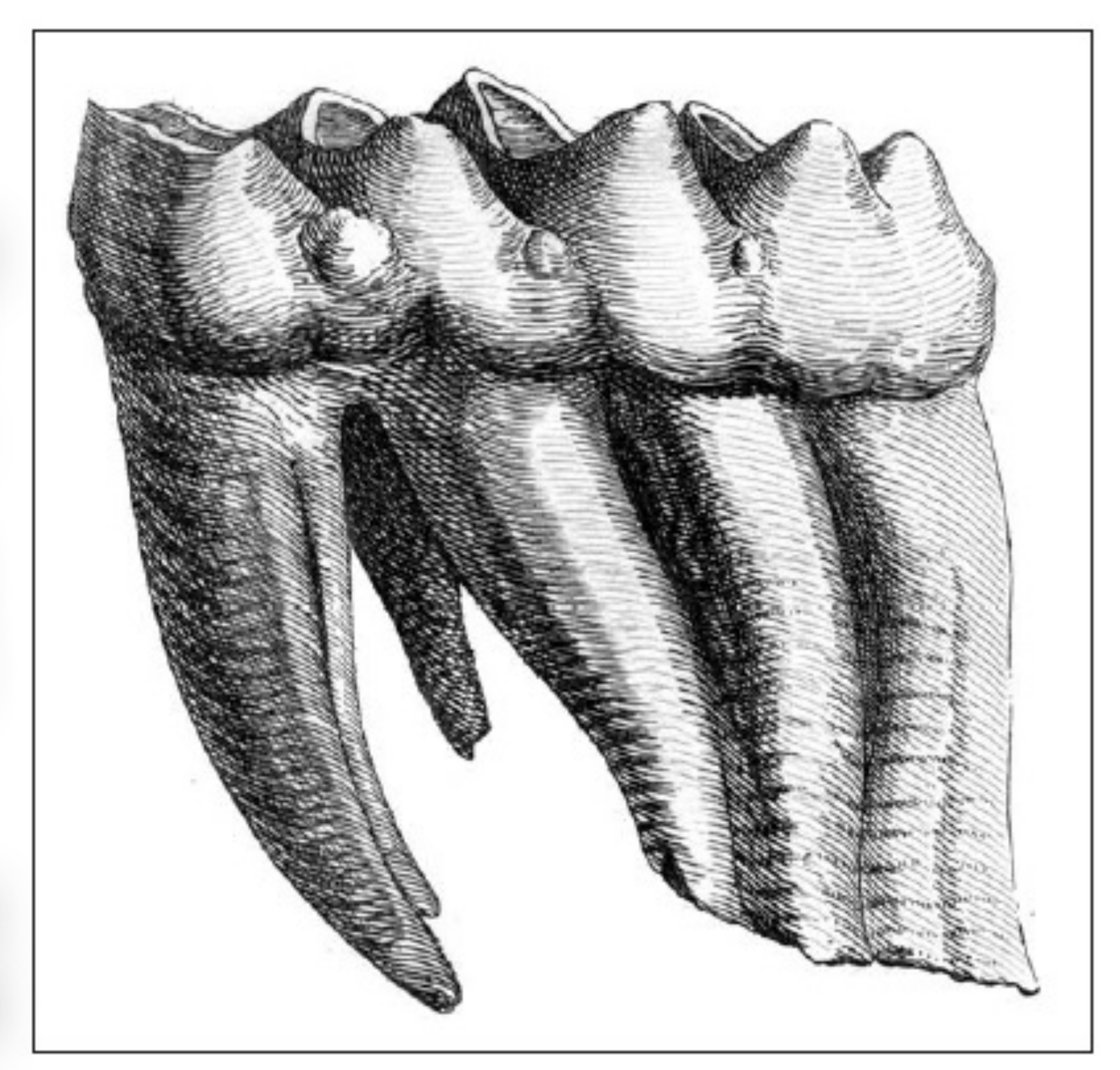
A large, flightless pigeon endemic to the island of Mauritius first reported by Dutch sailors in 1598. Following their discovery Dodo's were exploited as an easily obtained food resource by passing sailors. Mass killings of dodos were reported in ships logs, but subsequent investigation of Dodo remains indicates this was not a significant factor in their extinction. More importantly the Dodo's habitat was changed by animals (incl. dogs, pigs, cats, rats and a predatory macaque) which disrupted Dodo nesting sites, eggs and food resources.

The increasing rarity of Dodos was first noted in print in the 1660s and its complete extinction is estimated to have occurred between 1664 and 1674. However, the Dodo was not acknowledged to have been driven extinct until 1833. Whatever, the specific cause(s) of its extinction, they are unquestionably linked to human activities. As a result, the Dodo has been regarded as an icon for extinction since 1833.

History of Extinction Studies

The American Incognitum

Drawing of a molar recovered in 1739 by French soldiers from the "Big Bone Lick" locality in Kentucky. This molar, along with other bones was sent to the Cabinet du Roi (Royal Museum) in Paris in 1762 where Louis Jean-Marie Daubenton identified the long bones as belonging to a large elephant and the teeth as belonging to a hippopotamus.



History of Extinction Studies

The American Incognitum

Georges-Louis Leclerc, Comte de Buffon (1707–1788)

Georges-Louis Leclerc (Comte de Buffon) was the Director of the Cabinet du Roi in 1739 and became prominent in biological circles for his development of a “degeneration” theory of racial origins.

This held that non-Caucasian races were derived from Caucasian ancestors but had “degenerated” as a result of environmental factors and poor diets, which he held to be reversible.

Buffon extended this theory to biology in 1749 by arguing that, because of their smaller, weaker and generally inferior character, New World quadrupeds were degenerate forms of European ancestors.

History of Extinction Studies

The American Incognitum

William Hunter
(1718–1783)

The British physician and anatomist William Hunter suggested in 1799 that the large bones and teeth recovered from Big Bone Lick might belong to an extinct elephant species. Hunter, who was also an avid collector of natural history objects, books and coins, founded the Hunterian Museum in London.

History of Extinction Studies

The American Incognitum

Georges Cuvier
(1769 - 1832)

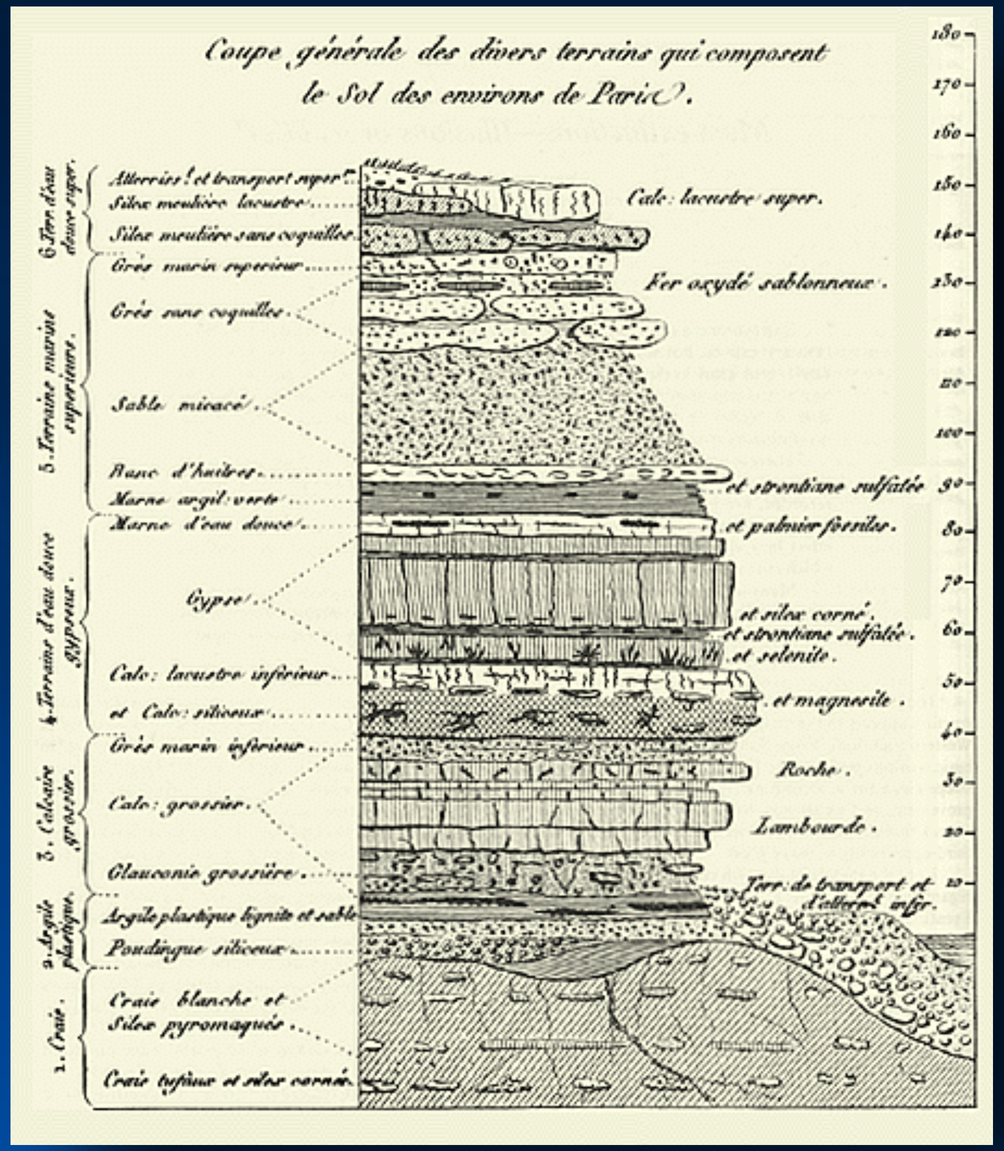
Georges Cuvier finally solved the mystery of the American Incognitum in 1806 by using the principles of comparative anatomy to demonstrate that the “animal de l’Ohio” differed from modern elephants and from the (European) Siberian mammoth. Cuvier erected a new genus for the American Icongnitum, referring to is as a “Mastodon” because of the pronounced conical cusps of its molar teeth. Finally, Cuvier reasoned that, since this animal was too large to have been overlooked by previous expeditions to different parts of the world it was, most likely, an extinct species — the first extinct species to be widely recognized as such by the scientific community.

History of Extinction Studies

Cuvier & Catastrophism

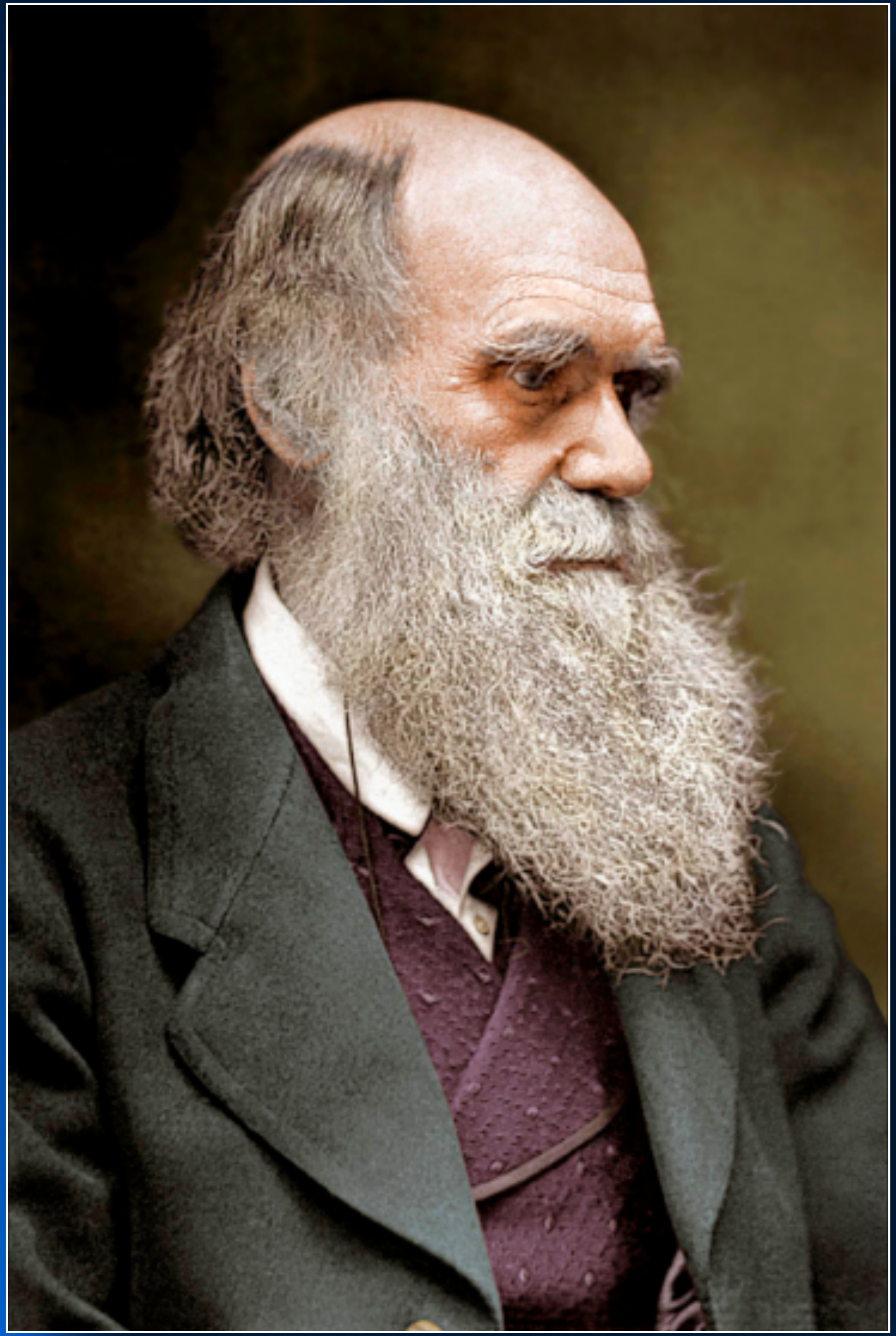
Georges Cuvier
(1769 - 1832)

Based on his fossil studies Cuvier proposed that most fossils were the remains of extinct species. The rapid changes he saw in the fossil fauns preserved in the Paris Basin led him to become a prominent supporter of the theory of catastrophism, which held that the Earth periodically went through short intervals of extreme environmental change in which most or all of the animals and plants that existed at the time became extinct. This theory had the advantage of being consistent with many of the facts that had been established by geologists of the time and to religious doctrine.



History of Extinction Studies

Darwin & Gradualism



Charles Darwin
(1808 - 1882)

In the midst of this ferment about extinct species, Charles Darwin wrote and published in book On the Origin of Species (1959). Darwin was skeptical of Cuvier's claims regarding catastrophic extinctions, preferring to invoke the incompleteness of the fossil record and the long span of geological time to argue that both speciation and extinction occur very slowly. Darwin regarded natural selection as the process by which progressive evolution takes place and extinction as its (inevitable) outcome.

"... the complete extinction of the species of a group is generally a slower process than their production" (p. 218).

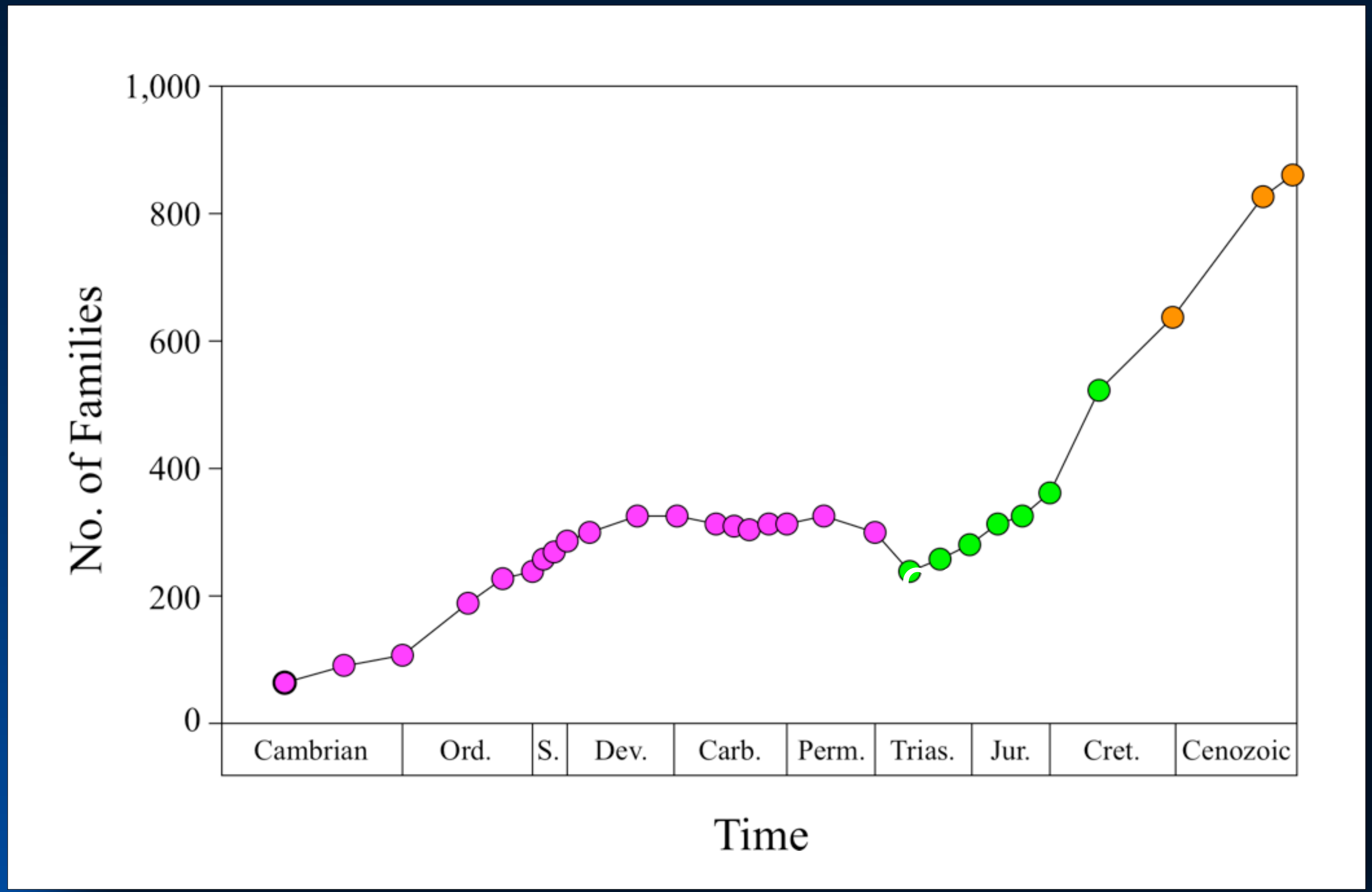
"With respect to the apparently sudden extermination of whole families or orders [such as those of the trilobites and ammonites] we must remember ... the probable wide intervals of time between ... consecutive formations and in these intervals there may have been much slower extermination." (pp. 321-322).

From *On the Origin of Species* (1859)

History of Extinction Studies

Rehabilitation of Extinction

Otto Schindewolf
(1896 - 1971)



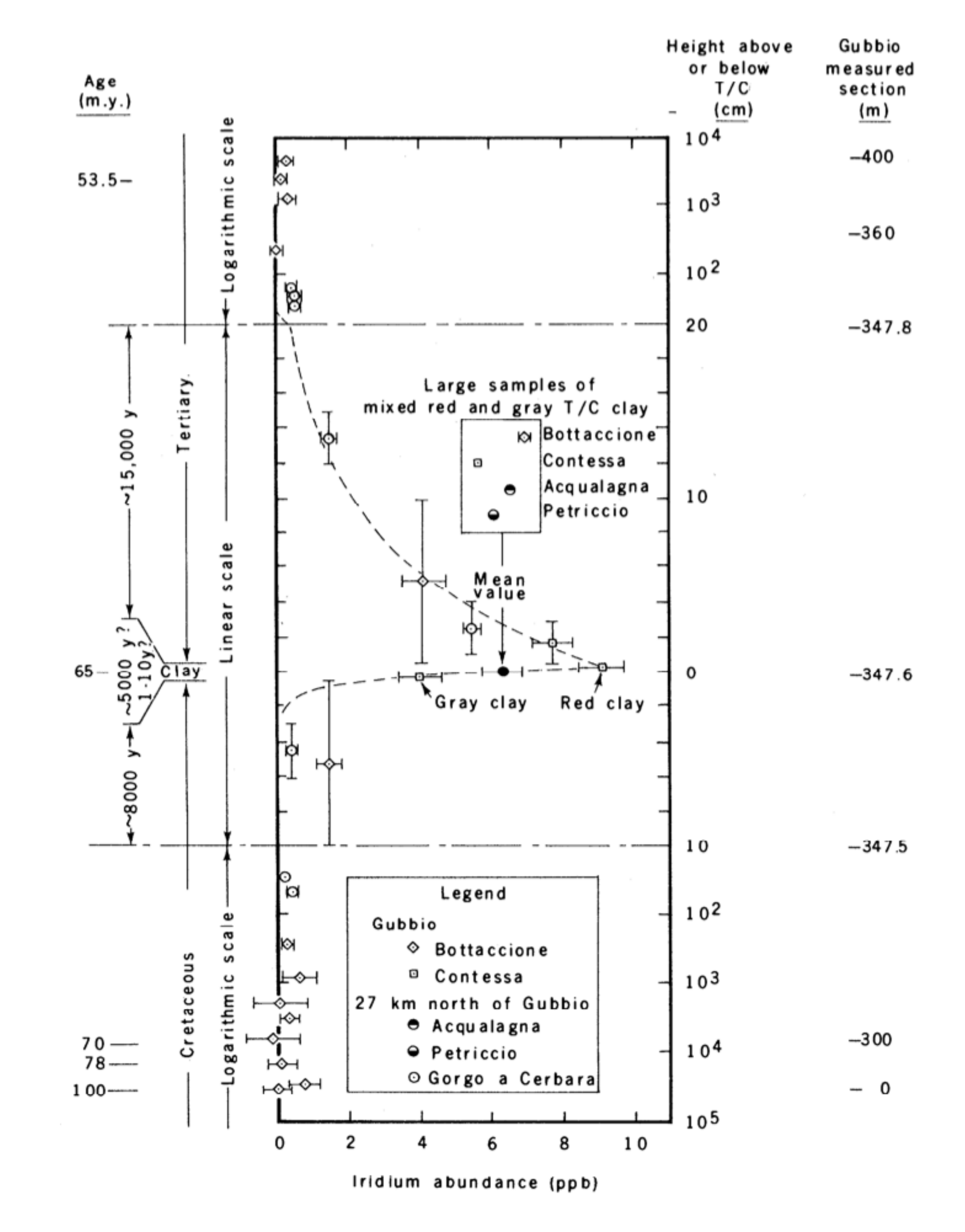
Norman Newell
(1919 - 2004)

"At or near the close of the Permian period nearly half of the known families of animals throughout the world disappeared. The German paleontologist Otto Schindewolf noted that 24 orders and superfamilies also dropped out at this point. At no other time in history, save possibly the close of the Cambrian, has the animal world been so decimated. Recovery to something like the normal variety was not achieved until late in the Triassic period, 15 or 20 million years later.".

Newell (1963, p. 79)

History of Extinction Studies

The Extraterrestrial Connection



Alvarez, L. W., Alvarez, W., Asaro, F., & Michel, H. (1980). Extraterrestrial cause for the Cretaceous-Tertiary extinction. Science, 208(4448), 1095–1108.

History of Extinction Studies

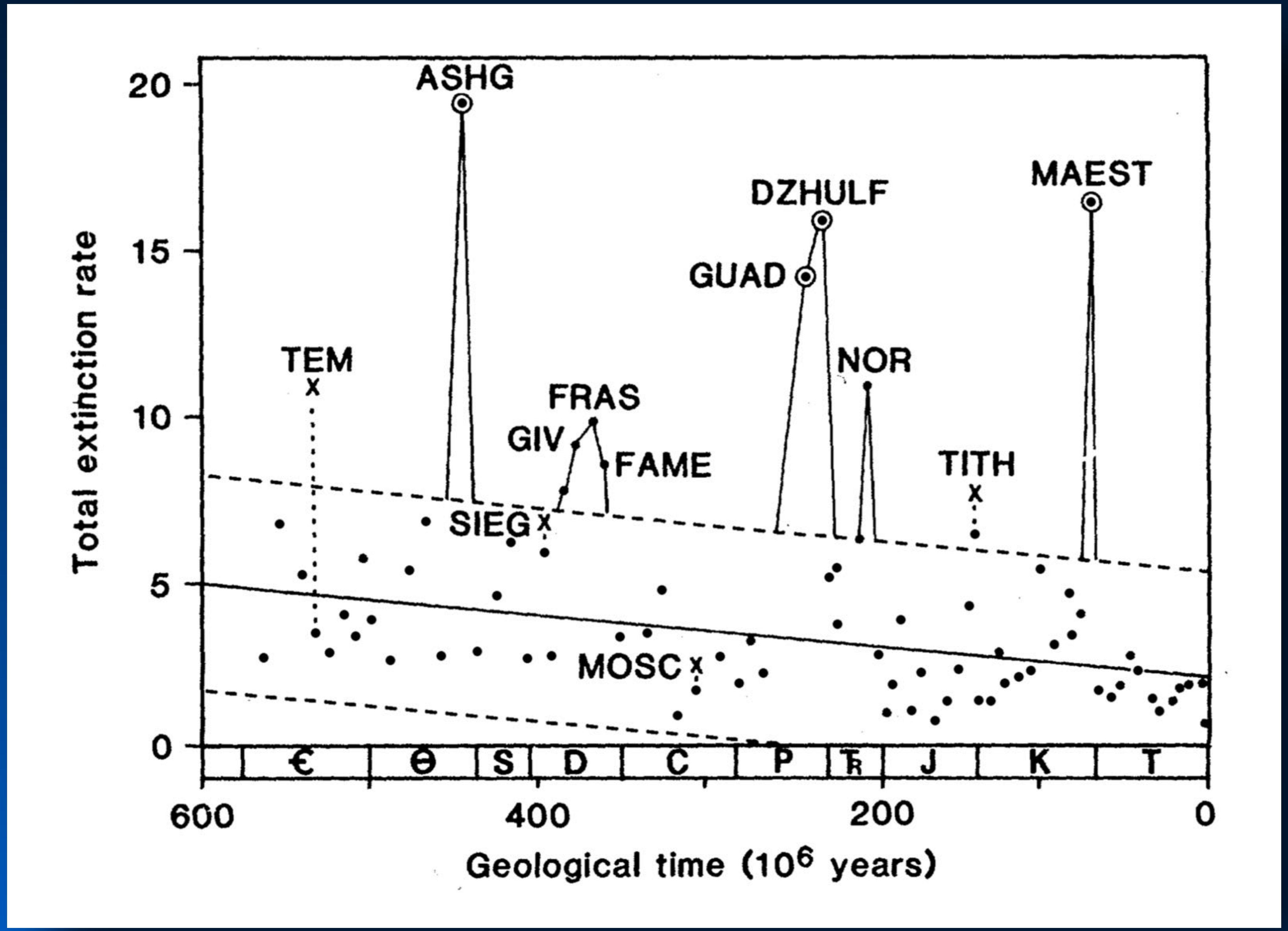
The Extraterrestrial Connection

190 Identified Structures (= confirmed & suspect craters)

Earth Impact Database: http://www.passc.net/EarthImpactDatabase/New%20website_05-2018/Index.html

History of Extinction Studies

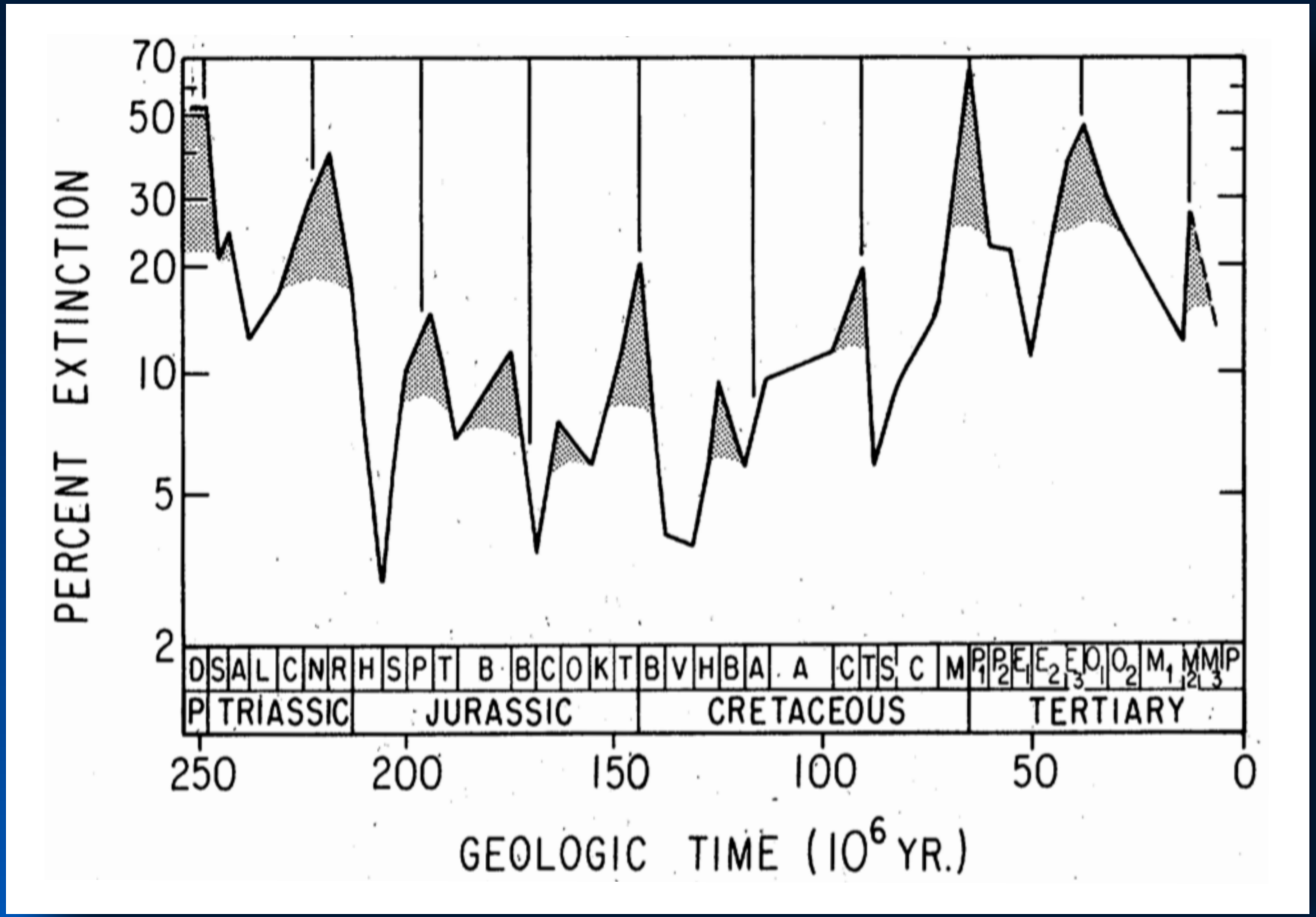
Big Five "Mass Extinction" Events



Raup, D. M., and J. Sepkoski, John J. 1982: Mass extinctions in the marine fossil record. Science 215:1501–1503.

History of Extinction Studies

Big Five “Mass Extinction” Events



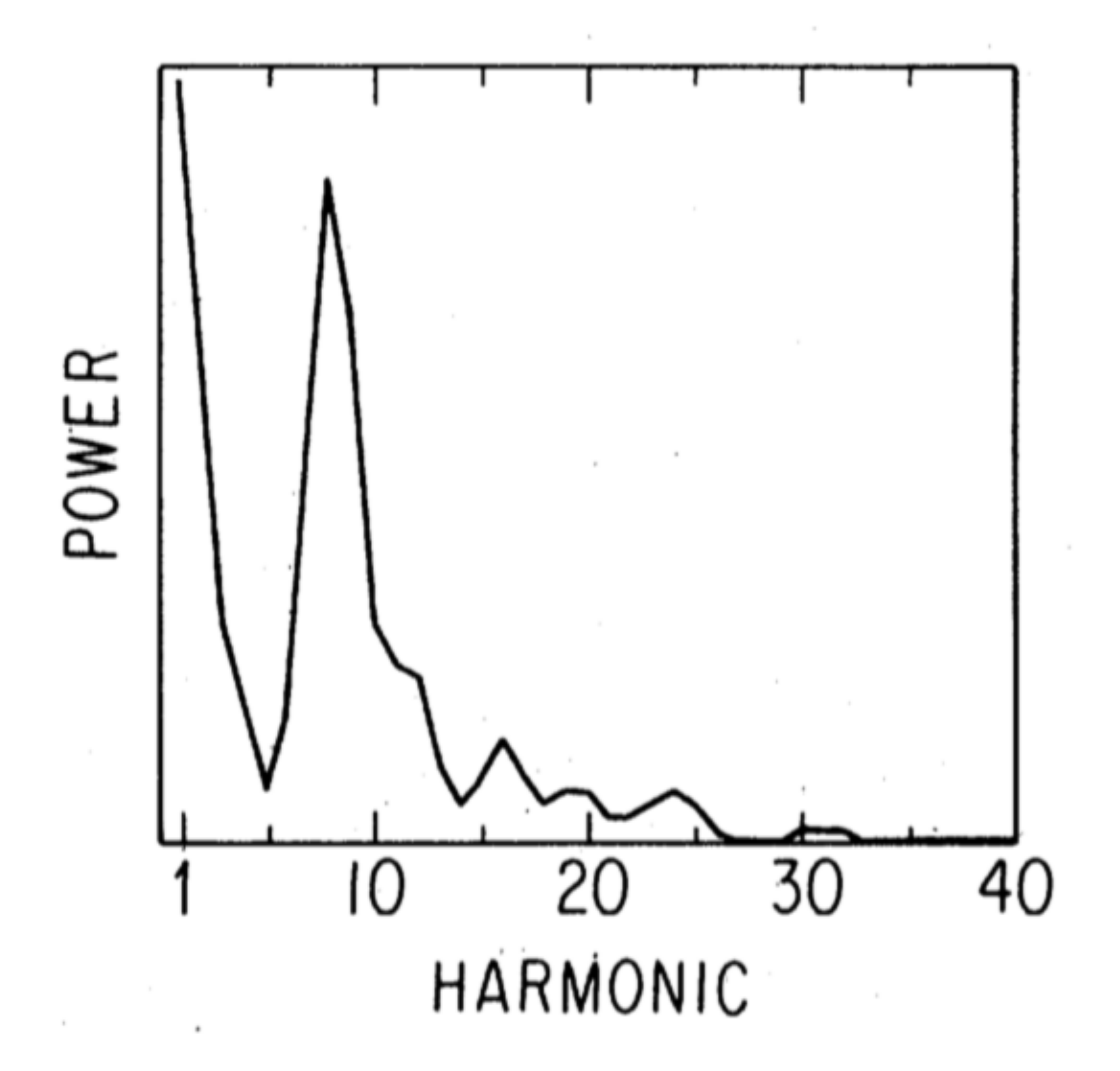
Raup, D. M., and J. Sepkoski, John J. 1984: Periodicity of extinctions in the geologic past. Proceedings of the National Academy of Sciences of the United States of America 81:801–805.

History of Extinction Studies

Extinction Periodicity

Pros

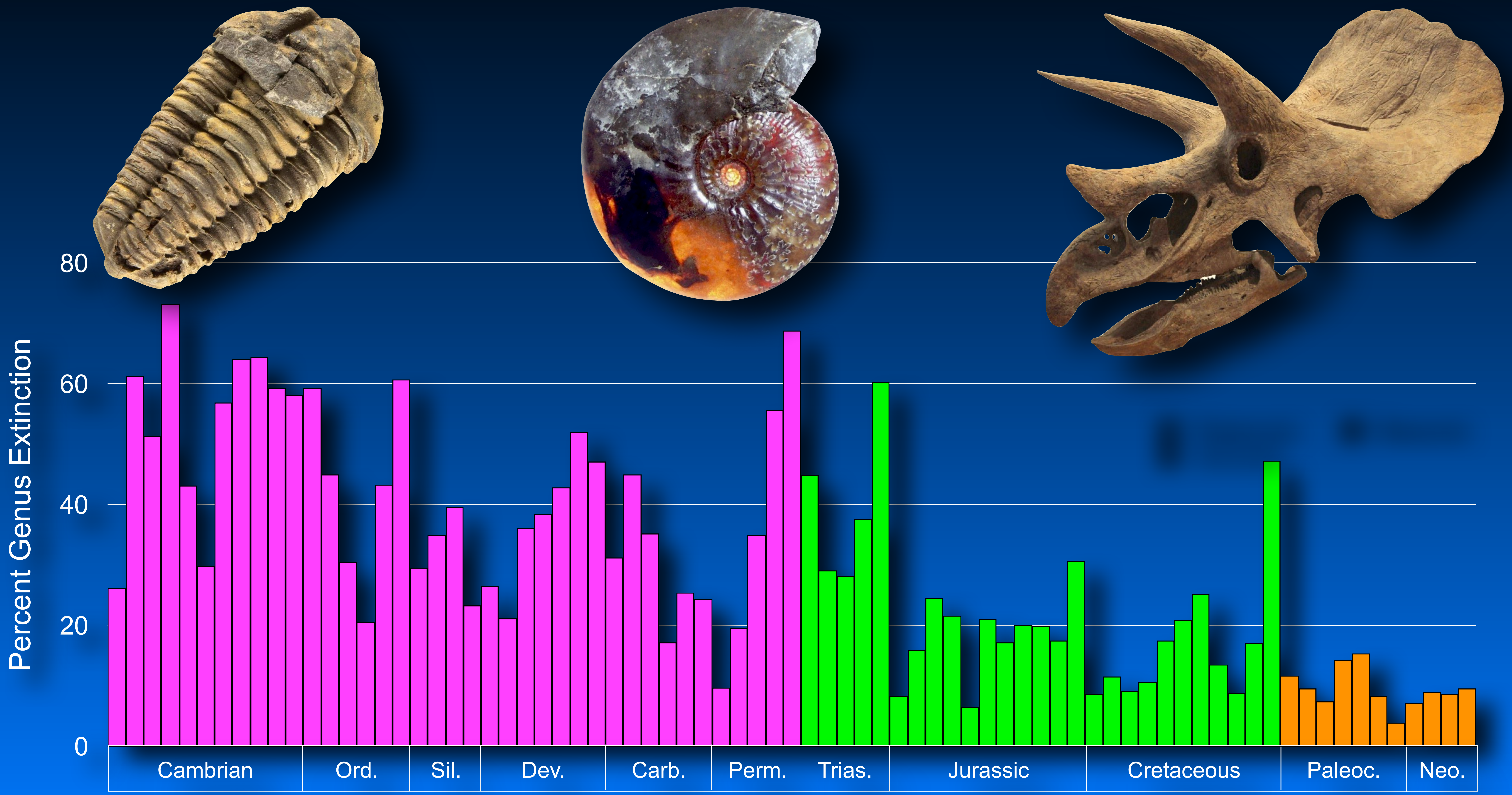
- Periodic patterns at around the 26 m.y. to 30 m.y. level have been found repeatedly in a number of different extinction-related datasets.
- This periodic interval suggests an extraterrestrial forcing mechanism which agrees with some data from well-studied extinction events (e.g. K-Pg).



Cons

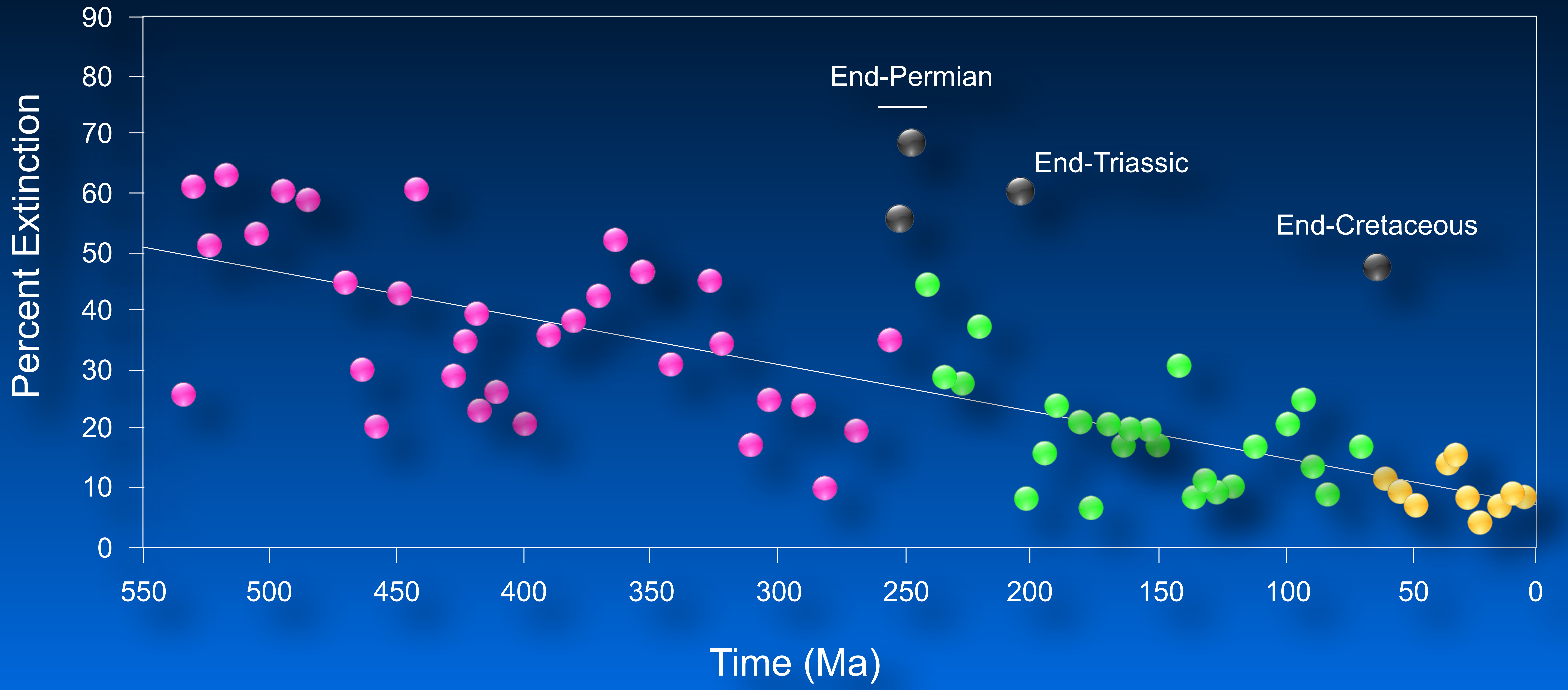
- Strict conformance to the periodic model has not been found by any analysis.
- No periodic signal has been found in the record of impact crater ages.
- Statistical significance of the periodic signal has been questioned by expert statisticians.
- Extra-terrestrial forcing is not the only mechanism implied by the finding of periodicity. A quasi-periodic signal may be induced as a result of the time lag necessary for biodiversity to reach the point where a major extinction event can be identified.

The Extinction Record



The Extinction Record

Phanerozoic Extinction-Intensity Gradient

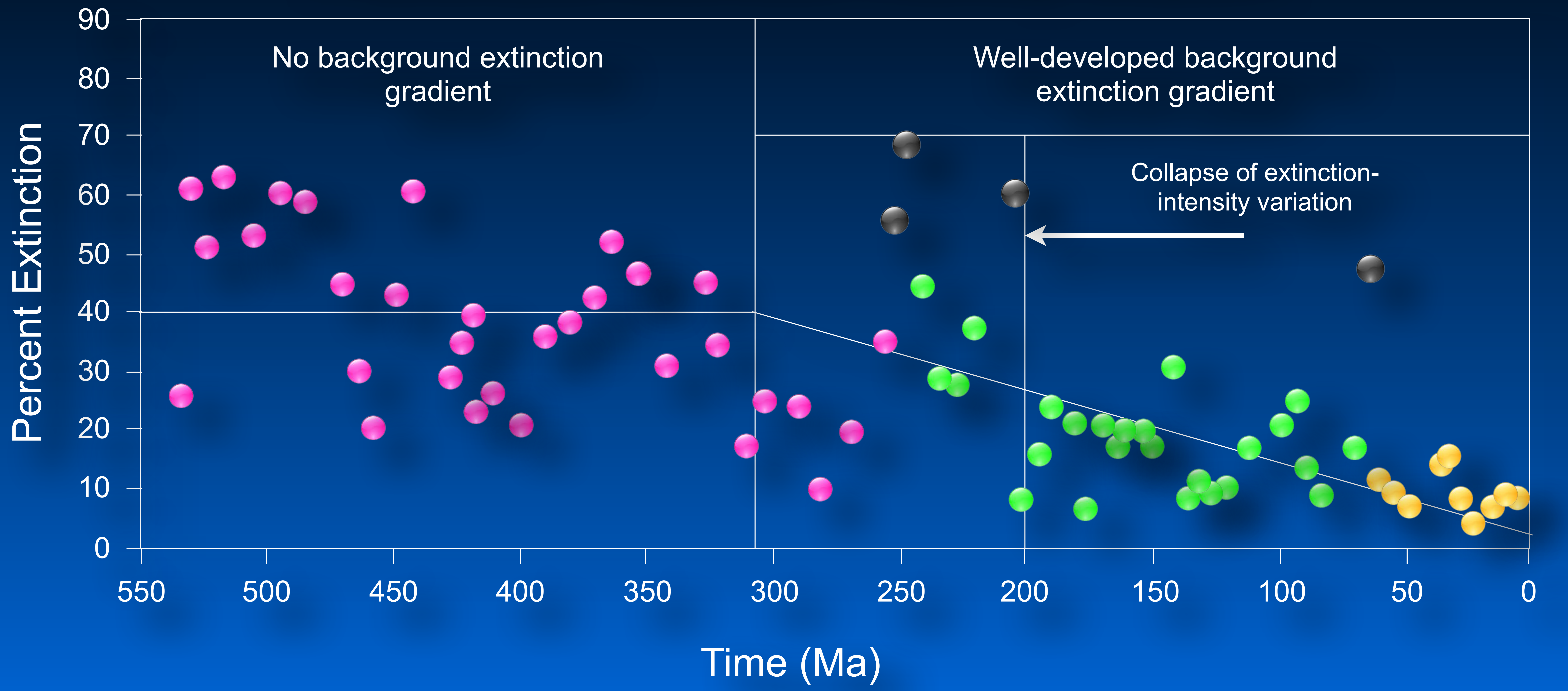


A number of explanations have been offered to account for this intriguing pattern.

Data from Sepkoski (1998)

Ancient Background Extinctions

Phanerozoic Extinction-Intensity Gradient

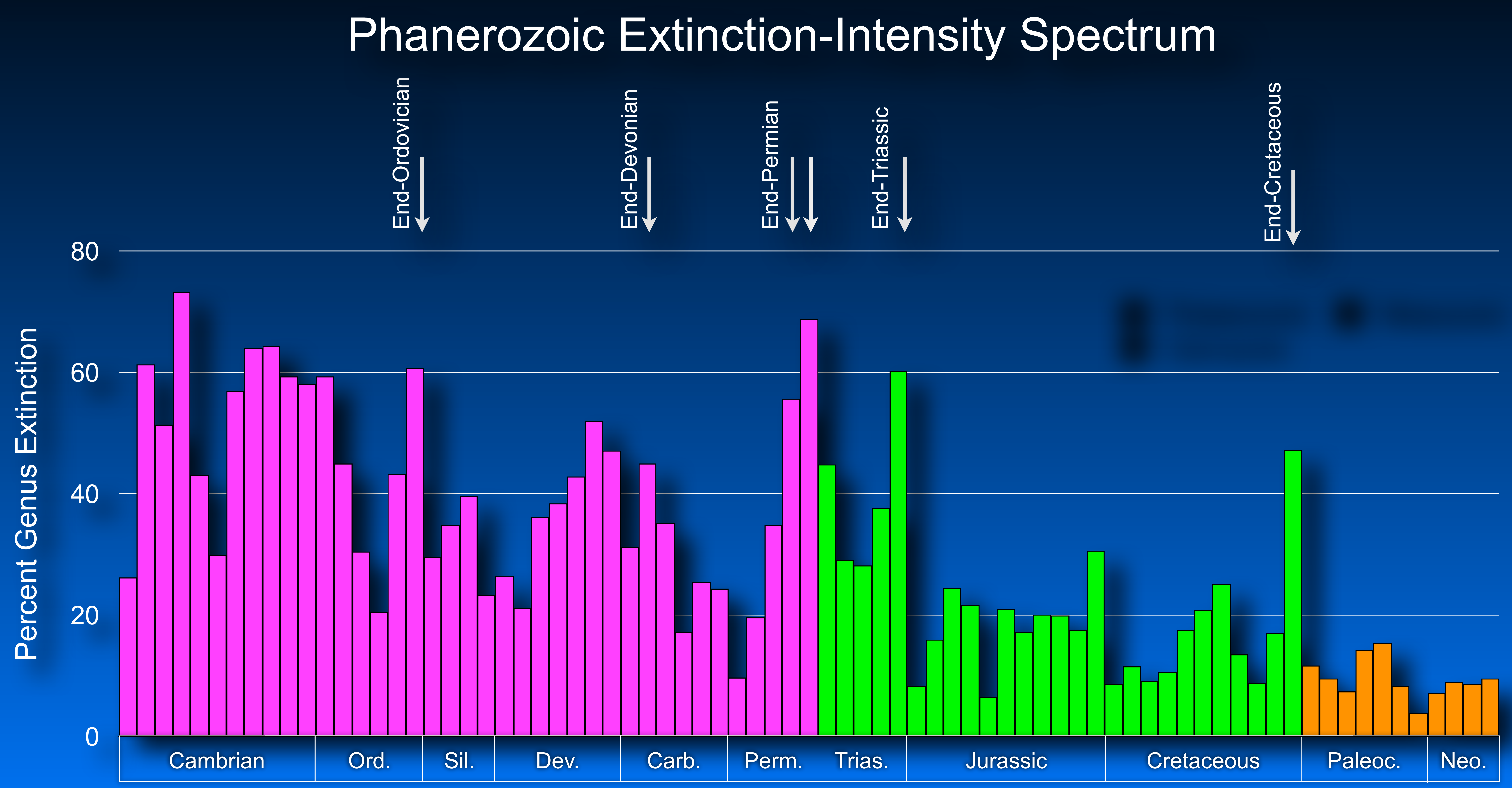


First forests and thick soils

Appearance of modern marine phytoplankton groups

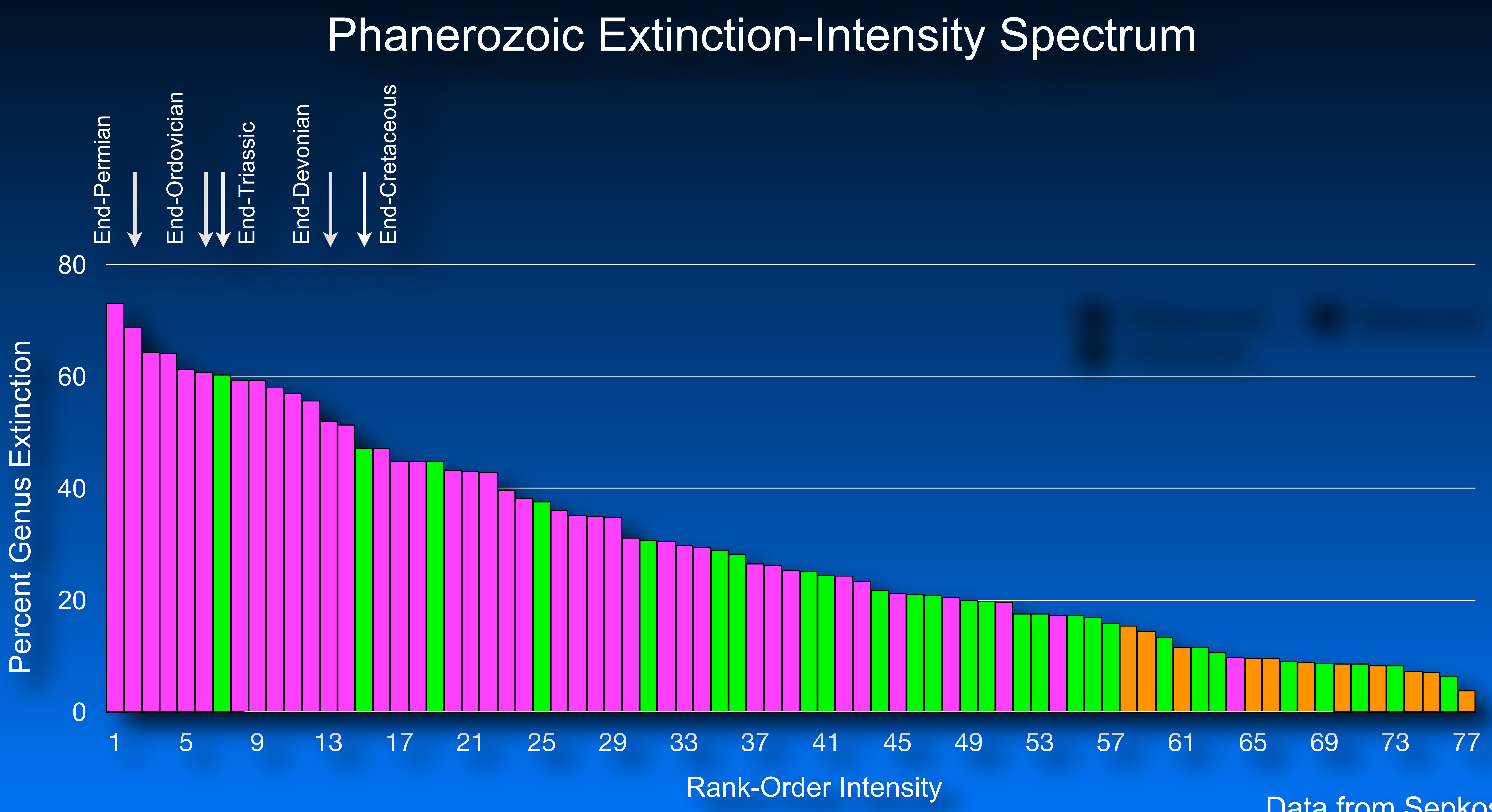
Data from Sepkoski (1998); interpretation from MacLeod (2004)

The Extinction Record



Data from Sepkoski (1998)

The Extinction Record



Data from Sepkoski (1998)

The Extinction Record

Phanerozoic “Mass Extinction”Intensity

Stage	Age (Myr)	Families (%)	Genera (%)	Species (%)
End-Ordovician	439	26 ± 1.9	60 ± 4.4	
End-Devonian	367	22 ± 1.7	52 ± 3.3	
End-Permian	245	51 ± 2.3	69 ± 3.8	
End-Triassic	208	22 ± 2.2	60 ± 4.4	
End-Cretaceous	66	16 ± 1.5	47 ± 4.1	

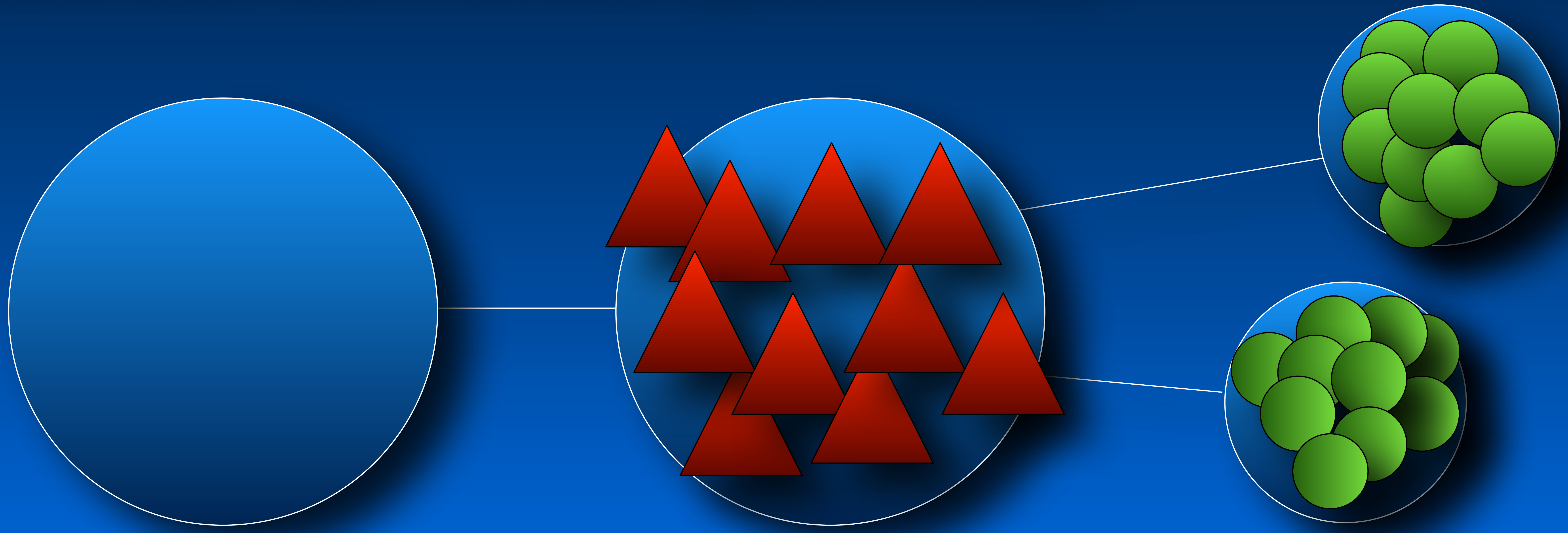
Higher taxonomic groups are one thing. But in order to provide a realistic ecological context within which to understand “mass extinction” events it is necessary to estimate species-level extinction intensities.

Data from Jablonski (1995)

The Extinction Record

Field-of-Bullets Model

A simulation based on the concept of constant extinction susceptibility that takes a sample of families, genera and species and asks the question "on average how many species extinctions does it take to eliminate a genus or a family?"



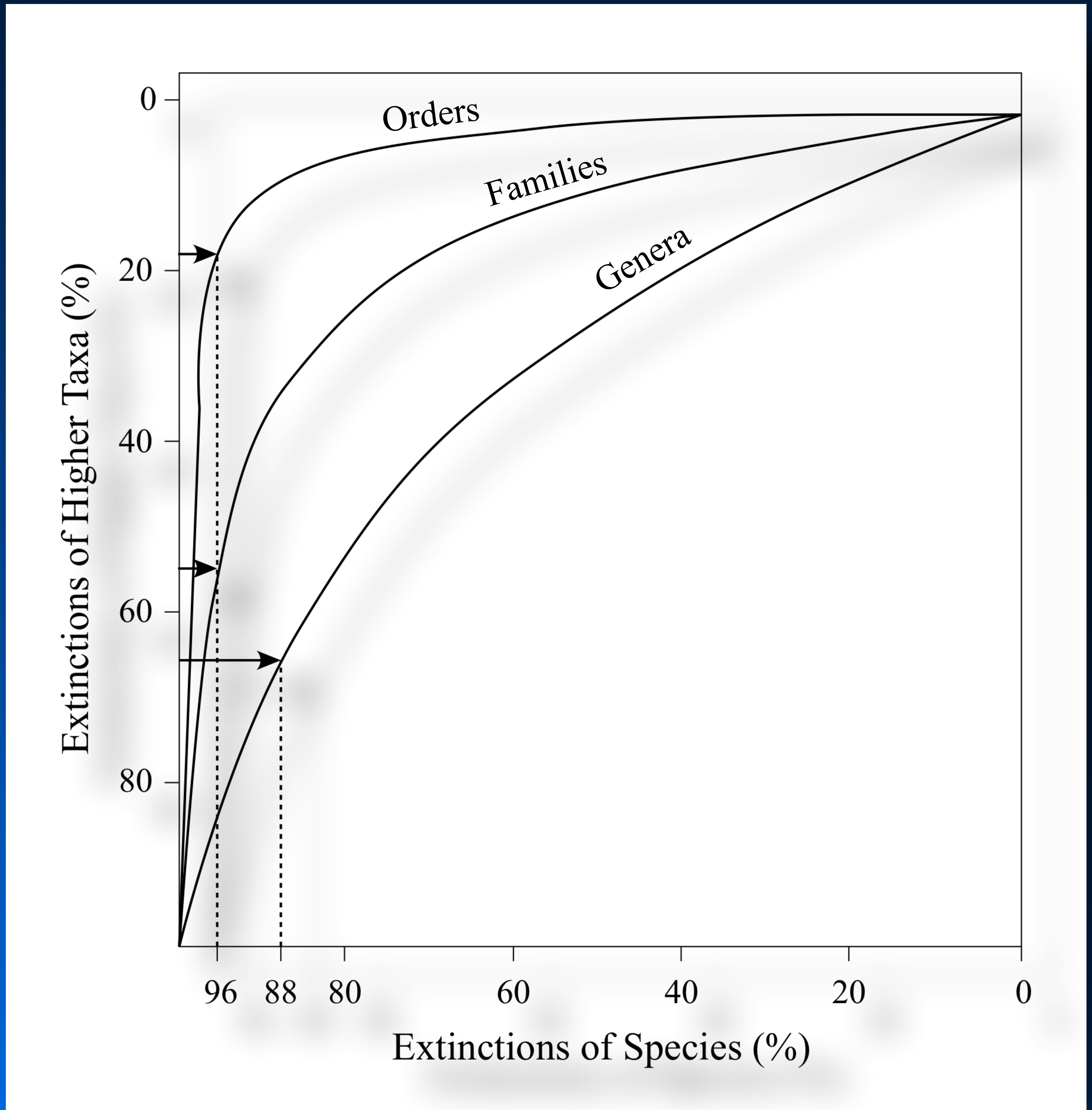
10 Families

10 Genera/Family

10 Species/Genus

The Extinction Record

Taxonomic Rarefaction



These curves summarize a series of simulation experiments in which random elimination of species (= equal probability of extinction) was used to estimate how many species extinctions would be necessary into to remove larger taxonomic groups. These curves look reasonable insofar as their inflection points grow more pronounced and migrate to the left as taxonomic generality increases. But they do assume a taxonomic structure that's far from reality.

The Extinction Record

Phanerozoic “Mass Extinction”Intensity

Stage	Age (Myr)	Families (%)	Genera (%)	Species (%)
End-Ordovician	439	26 ± 1.9	60 ± 4.4	85 ± 3.0
End-Devonian	367	22 ± 1.7	52 ± 3.3	83 ± 4.0
End-Permian	245	51 ± 2.3	69 ± 3.8	95 ± 2.0
End-Triassic	208	22 ± 2.2	60 ± 4.4	80 ± 4.0
End-Cretaceous	66	16 ± 1.5	47 ± 4.1	76 ± 5.0

Despite the various assumptions and caveats that pertain to such estimates, these magnitudes appear astonishingly large.

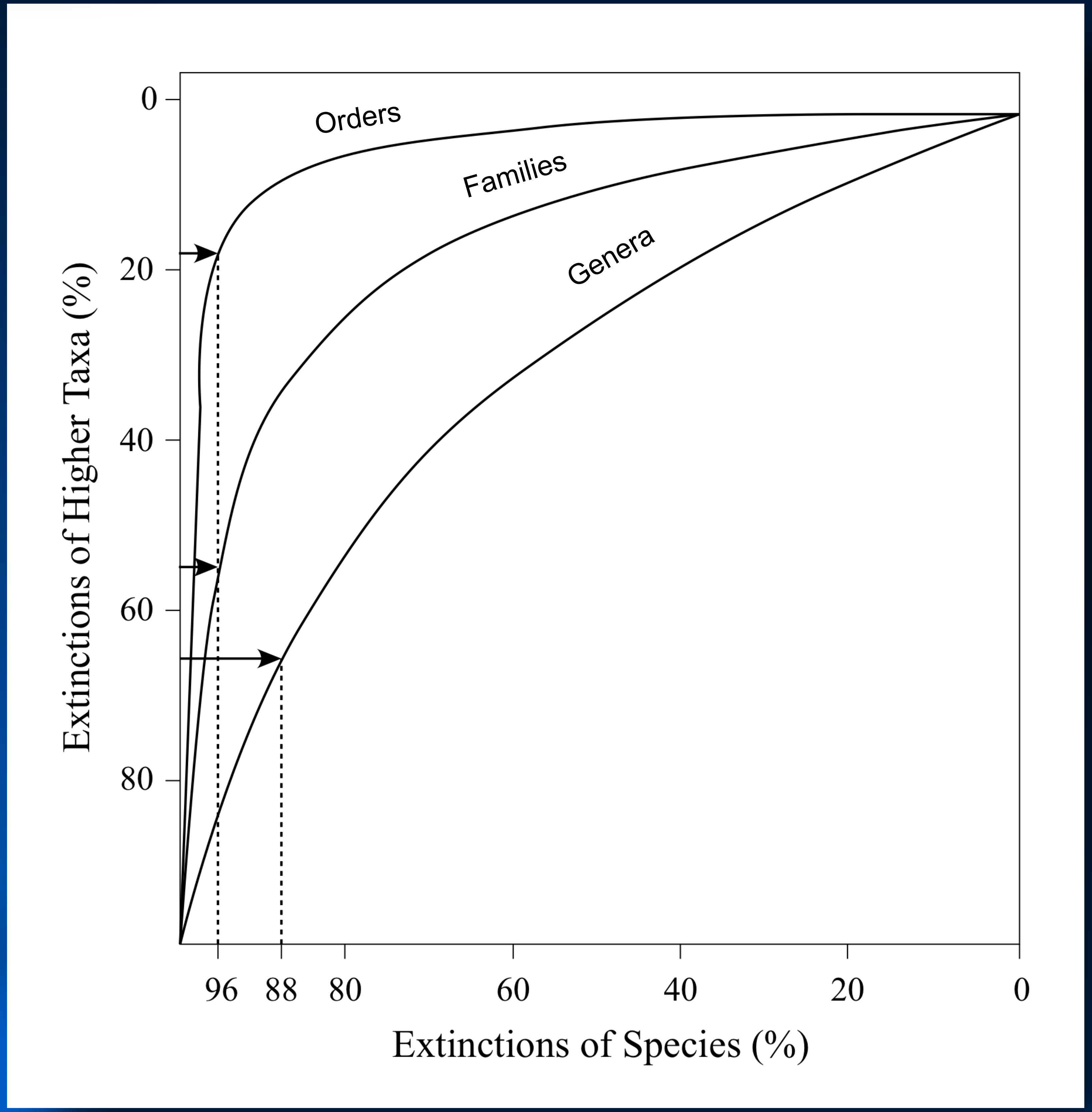
Data from Jablonski (1995)

The Extinction Record

Taxonomic Rarefaction

Pros

- Constitute a means to estimate statistically expected percent species extinction based on data at any taxonomic level.
- Results susceptible to empirical verification.
- Can be used to estimate mechanism-specific ‘kill curves’.



Cons

- Dependent on accuracy (and reality) of taxonomic data.
- Results dependent of appropriateness of the model used to simulate the range of actual taxonomic groups (e.g., no. of monospecific genera & families).
- Assumption that all species are equally susceptible to extinction is generally regarded as unrealistic.

The Extinction Record

Phanerozoic “Mass Extinction”Intensity

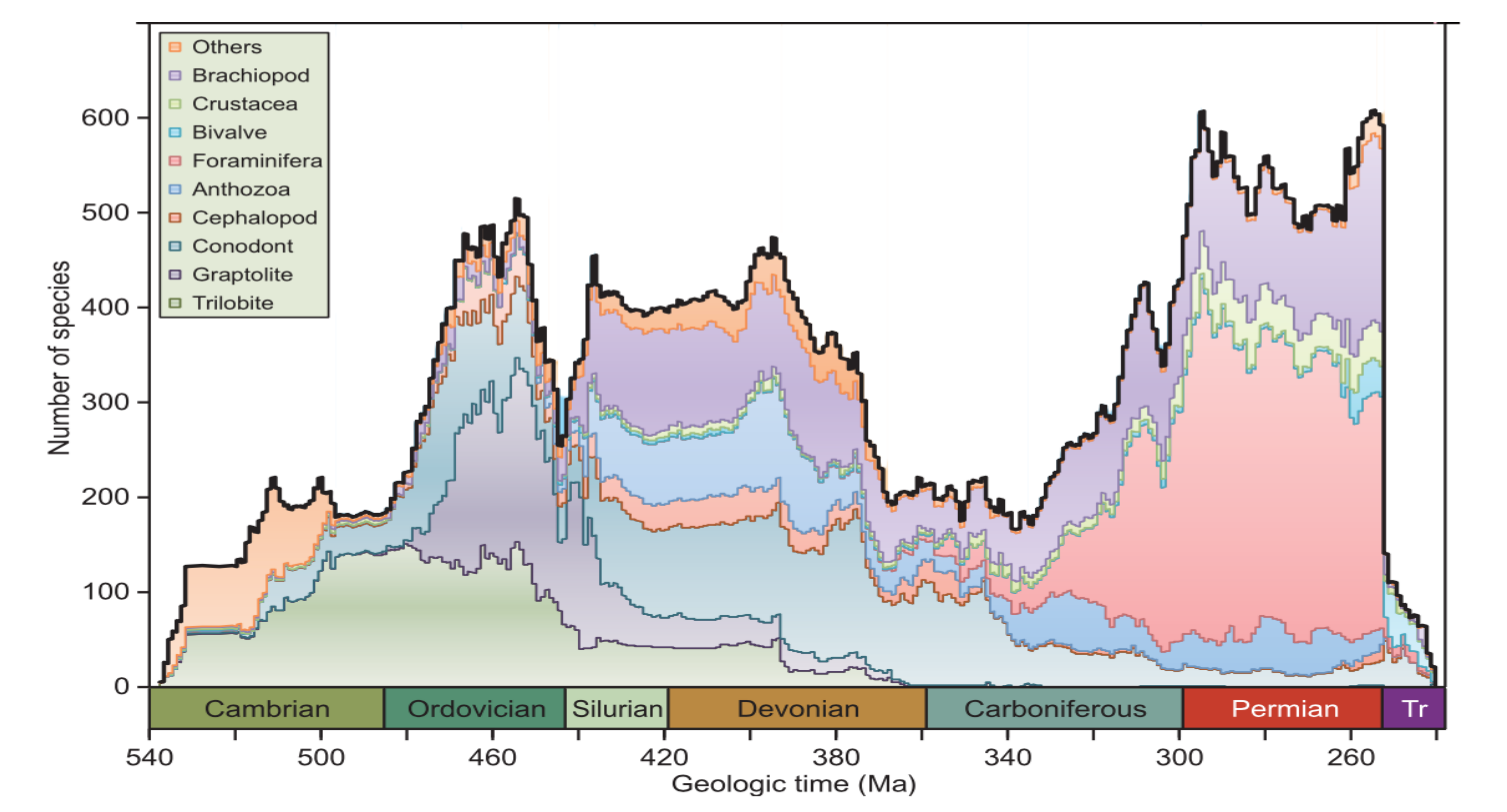
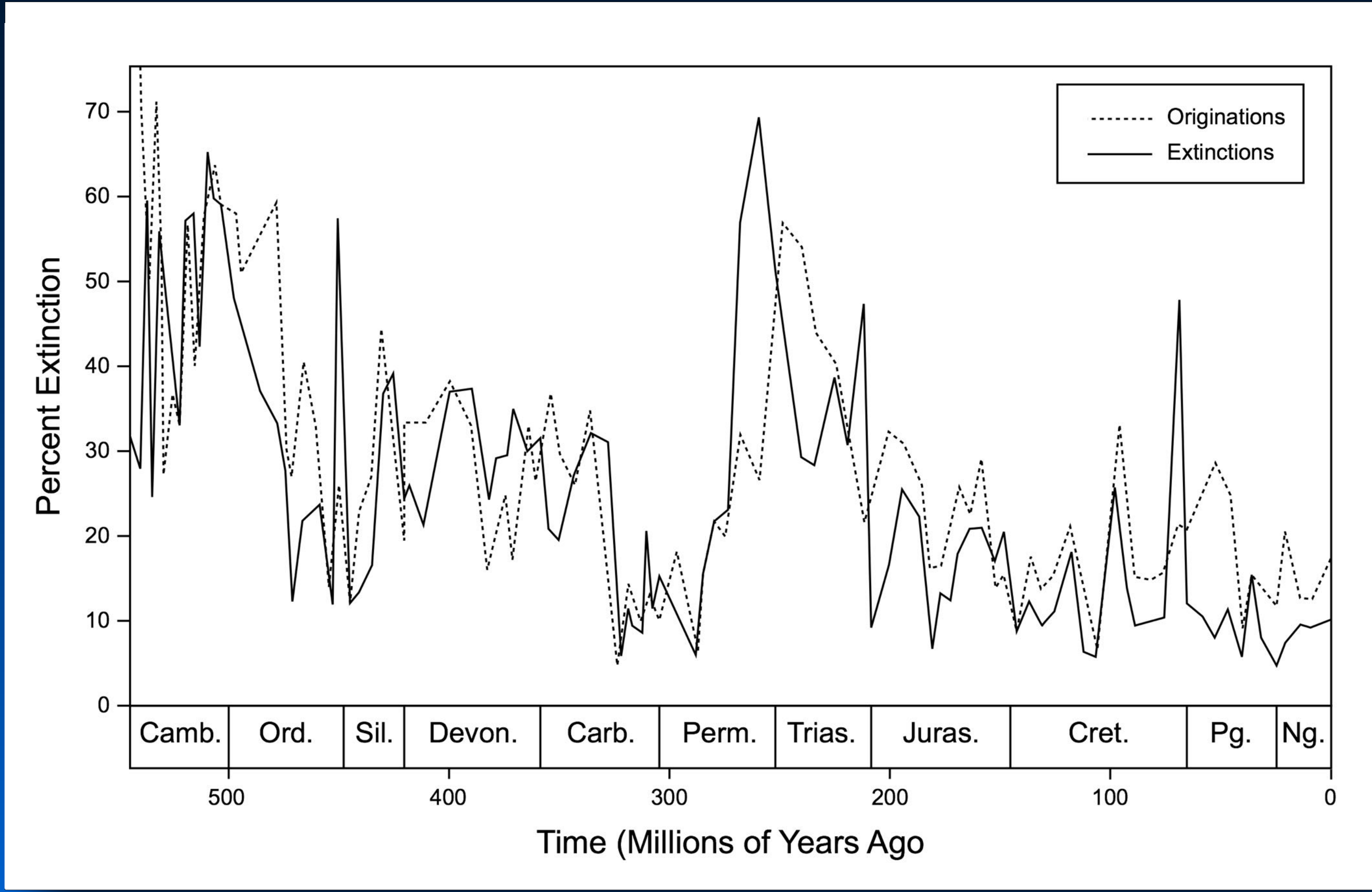


Chart from Fan et al. (2020)

The Extinction Record

Dynamic Interplay Between Extinctions and Originations



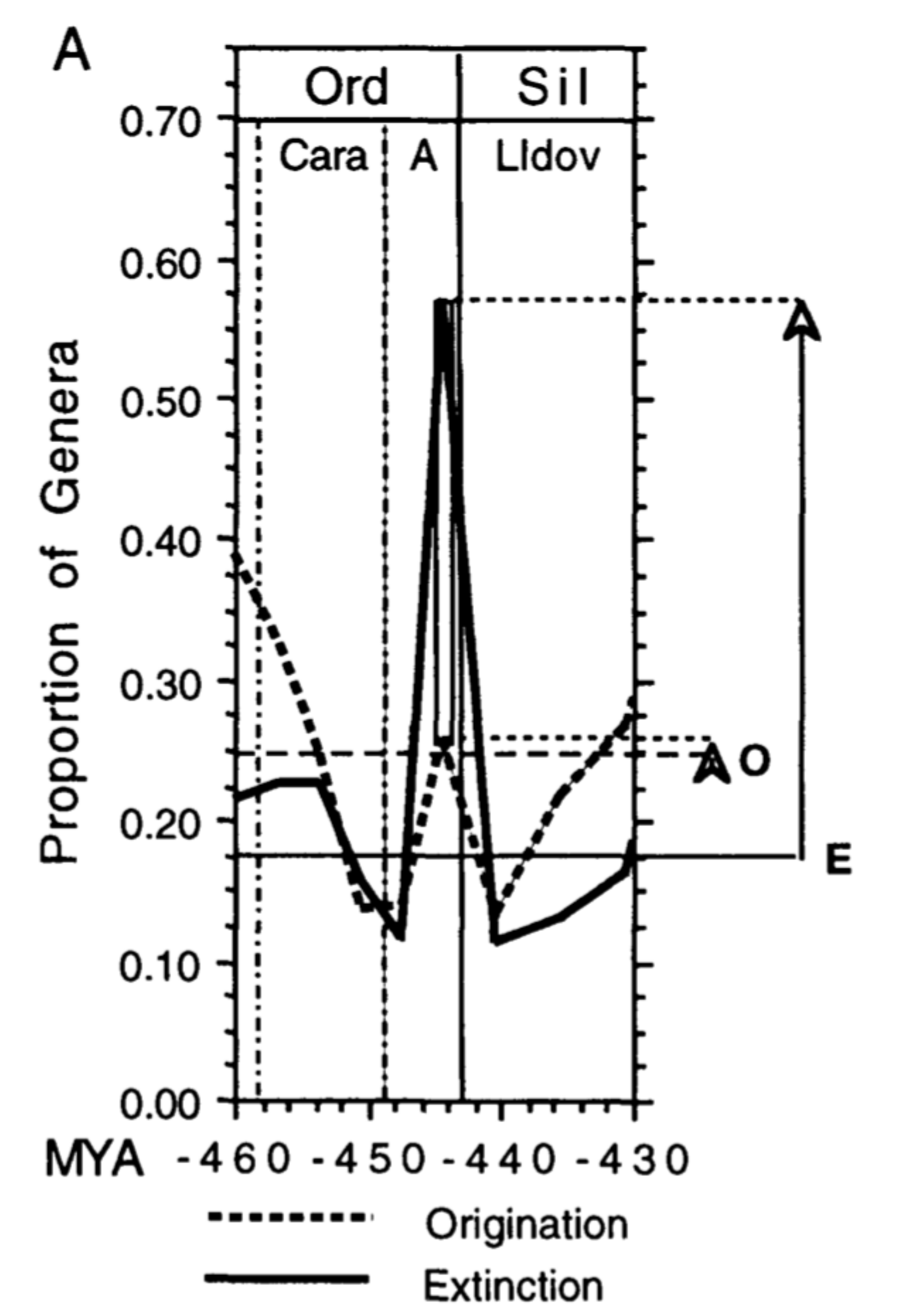
Extinction metrics are sensitive to the proportion of extinctions *and* the proportion of originations that occur in given time intervals.

From Bambach et al. (2004)

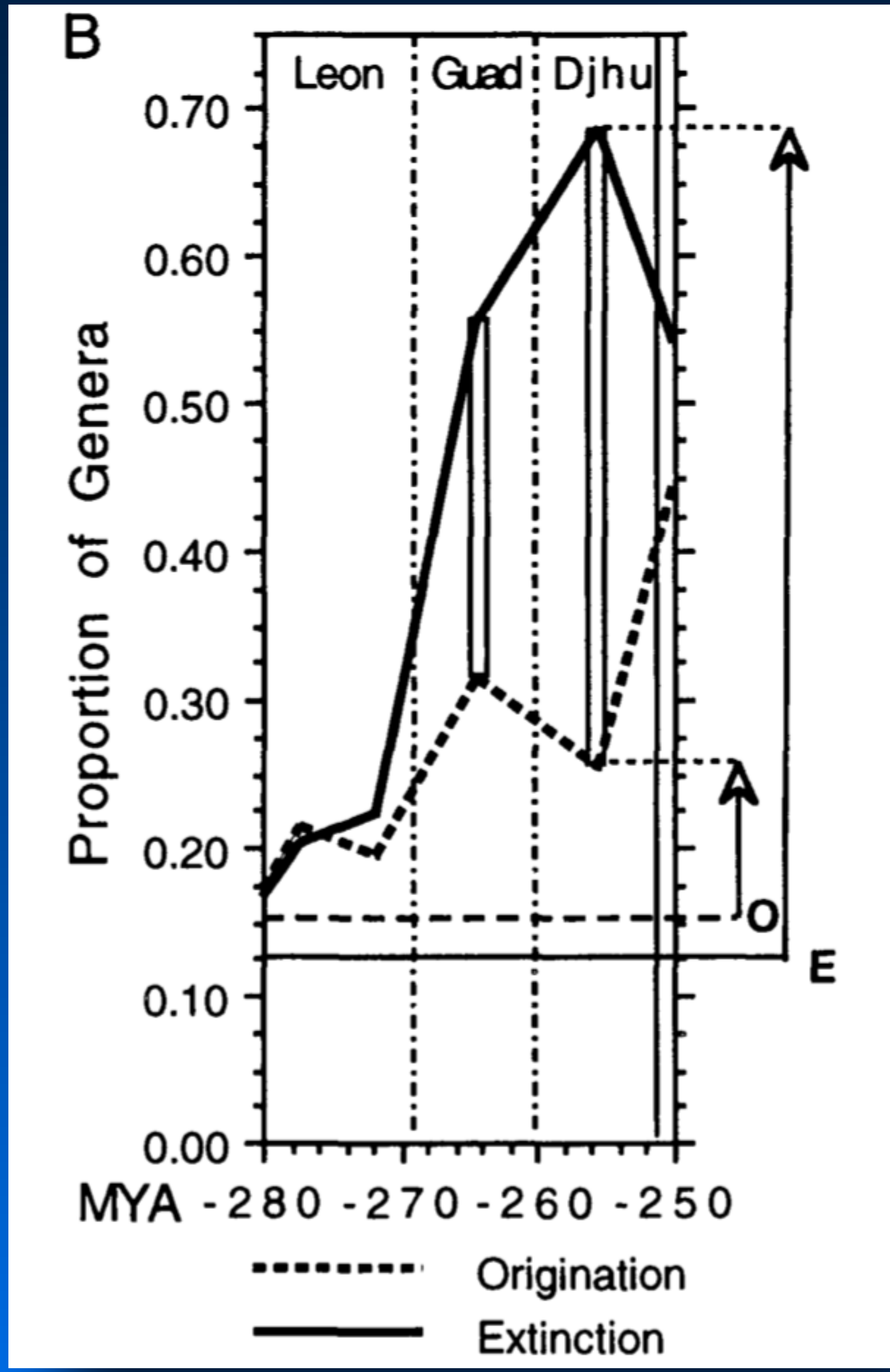
The Extinction Record

Dynamic Interplay Between Extinctions and Originations

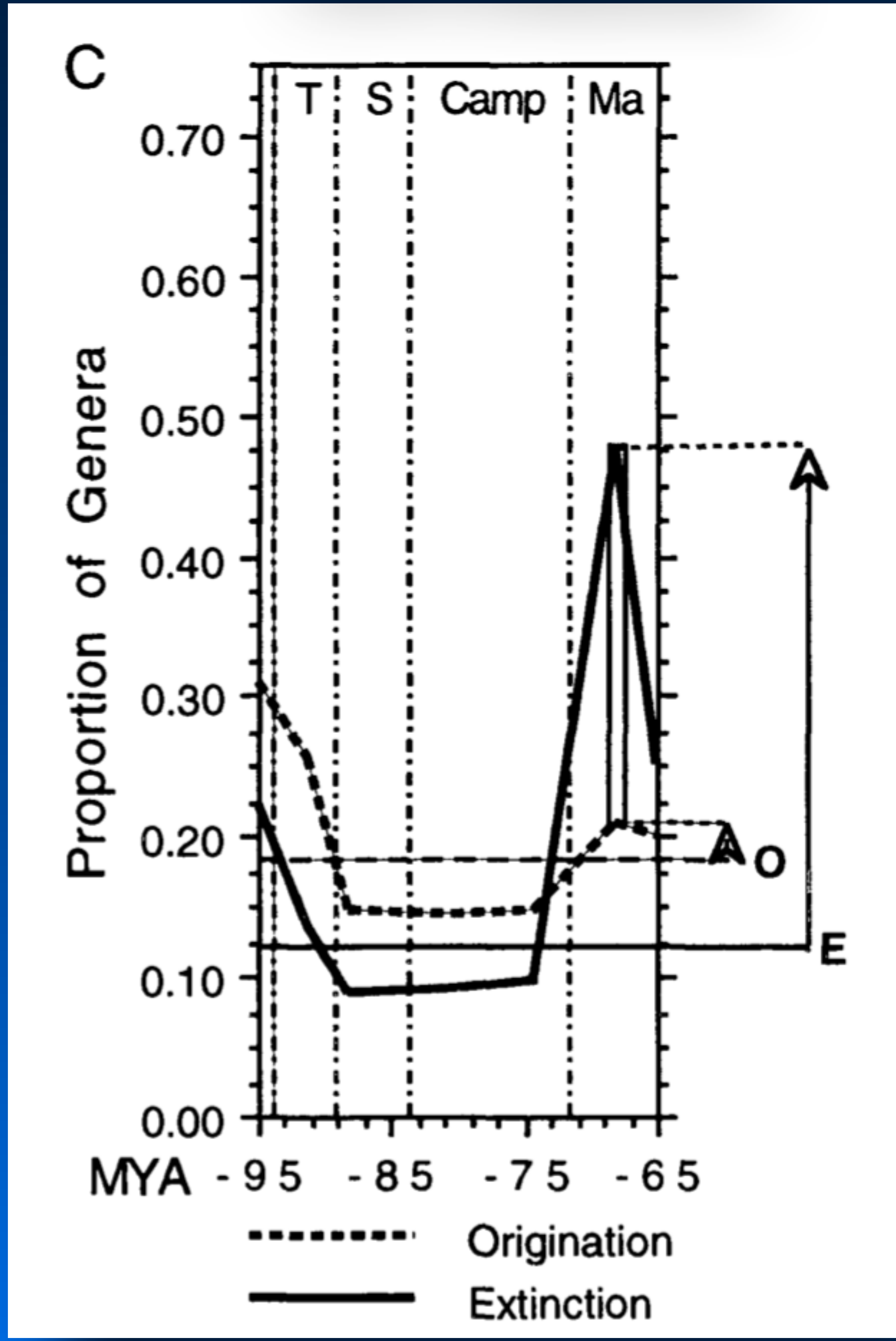
End-Ordovician



End-Permian



End-Cretaceous

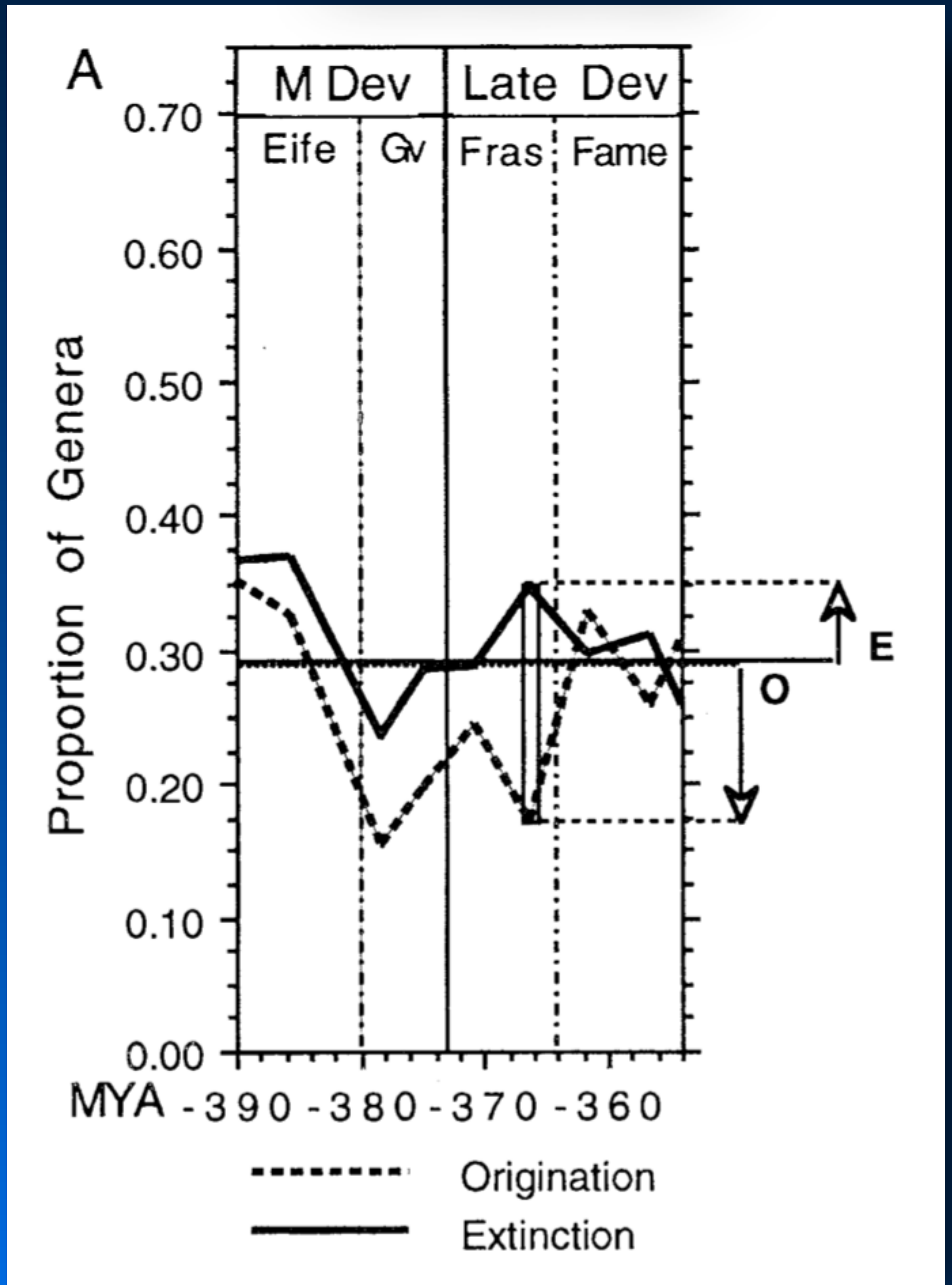


From Bambach et al. (2004)

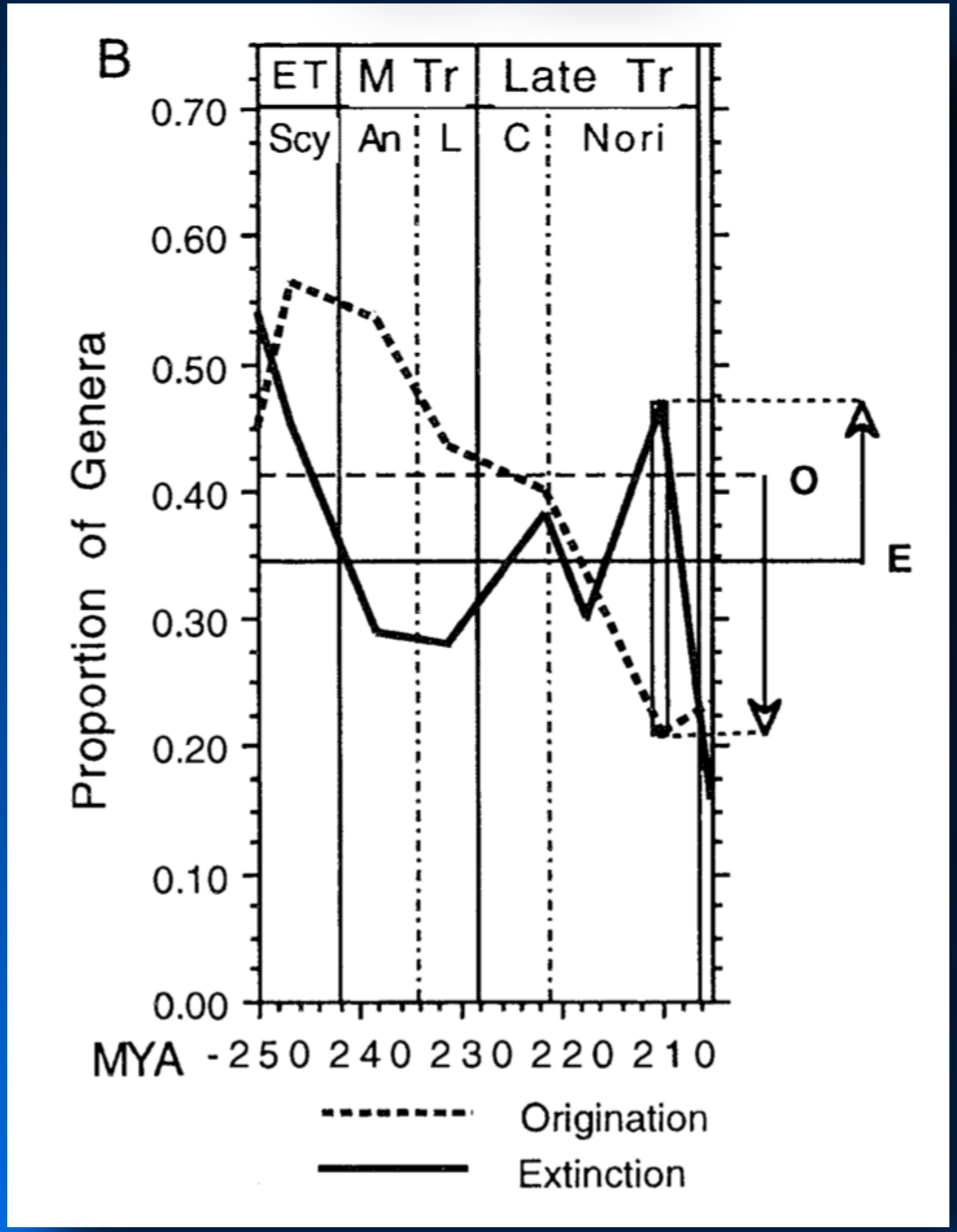
The Extinction Record

Dynamic Interplay Between Extinctions and Originations

End-Devonian



End-Triassic



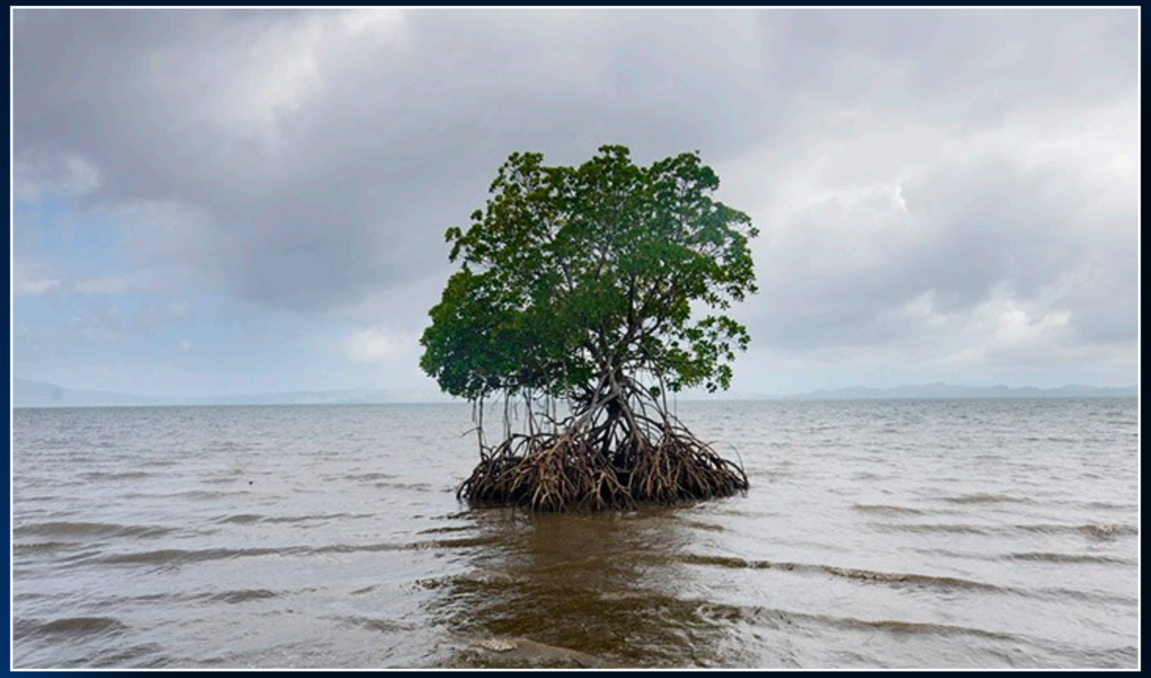
From Bambach et al. (2004)

The Extinction Record

Dynamic Interplay Between Extinctions and Originations

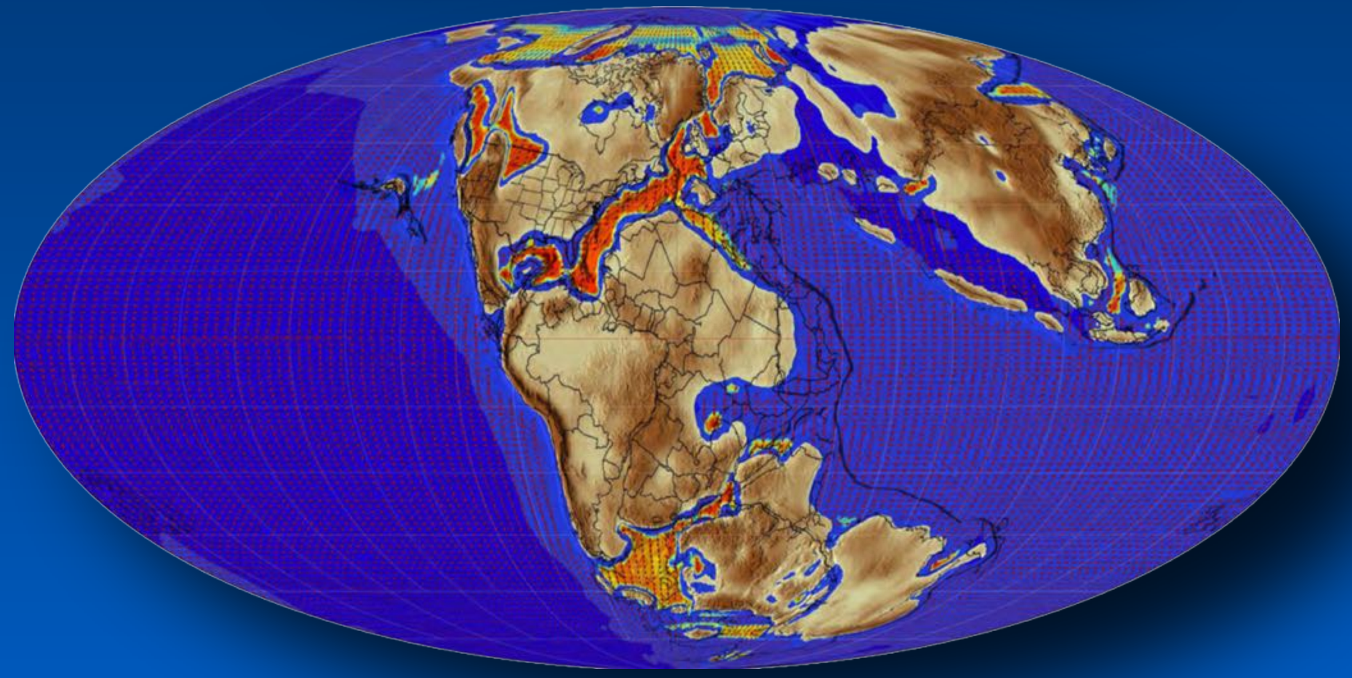
- The dynamic between origination and extinction plays an important role in determining the magnitude of each of the major extinction events.
- Three of the ‘Big Five’ geological extinction events are associated with excess extinctions: end-Ordovician, end-Permian, end-Cretaceous.
- Two of the ‘Big Five’ geological extinction events are associated with significant downturns in origination: end-Devonian, end-Triassic.
- To understand extinction we must understand the processes that suppress origination as well as those that cause extinctions.

Ancient Extinctions: Causes

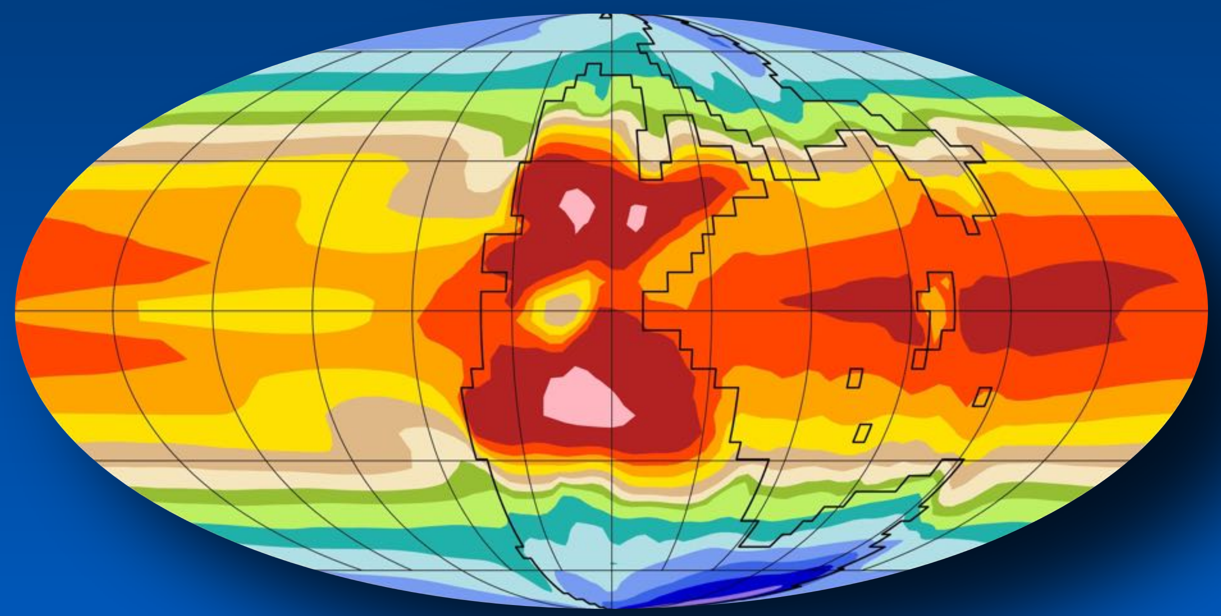


Sea-Level Change

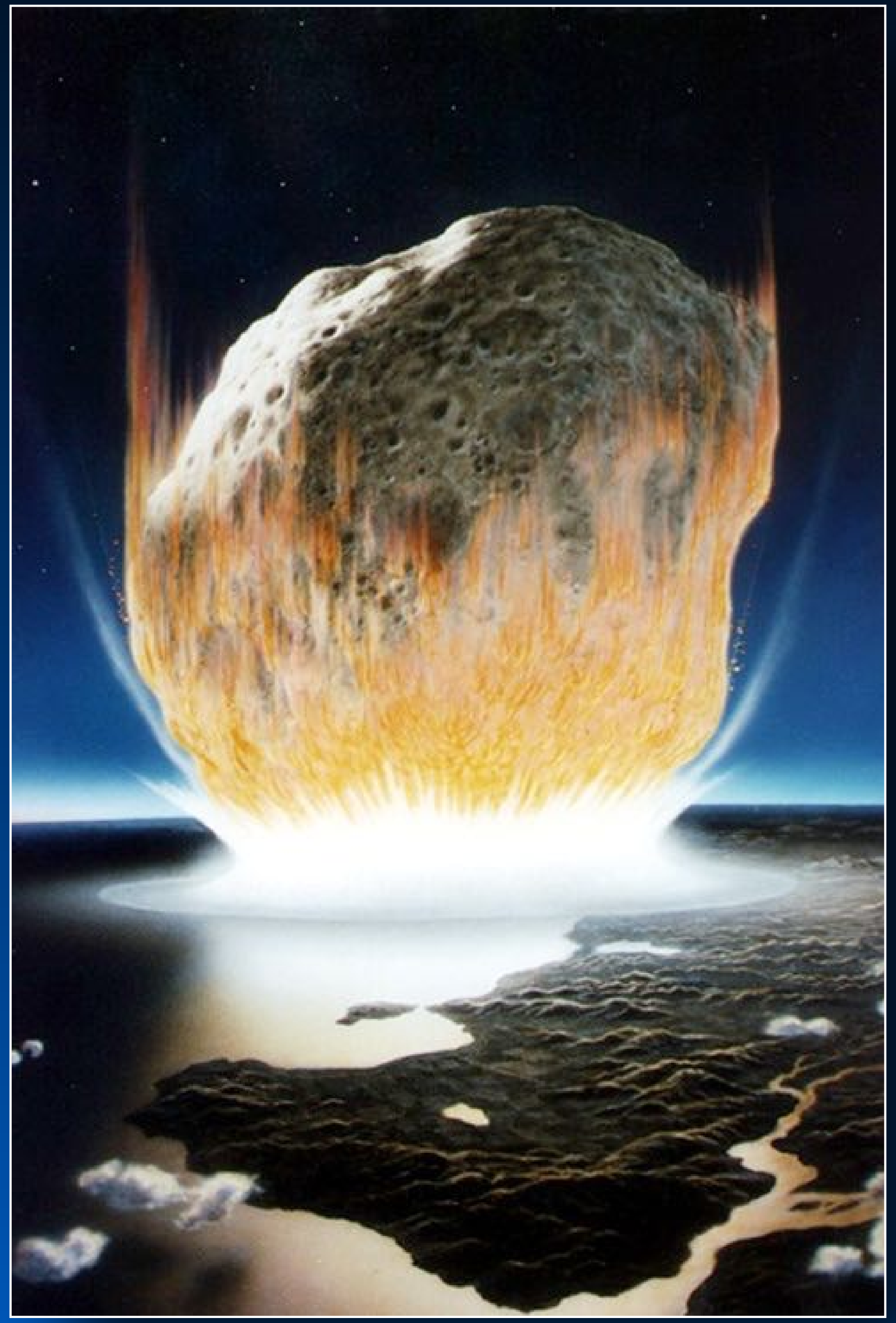
Volcanism



Marine Anoxia



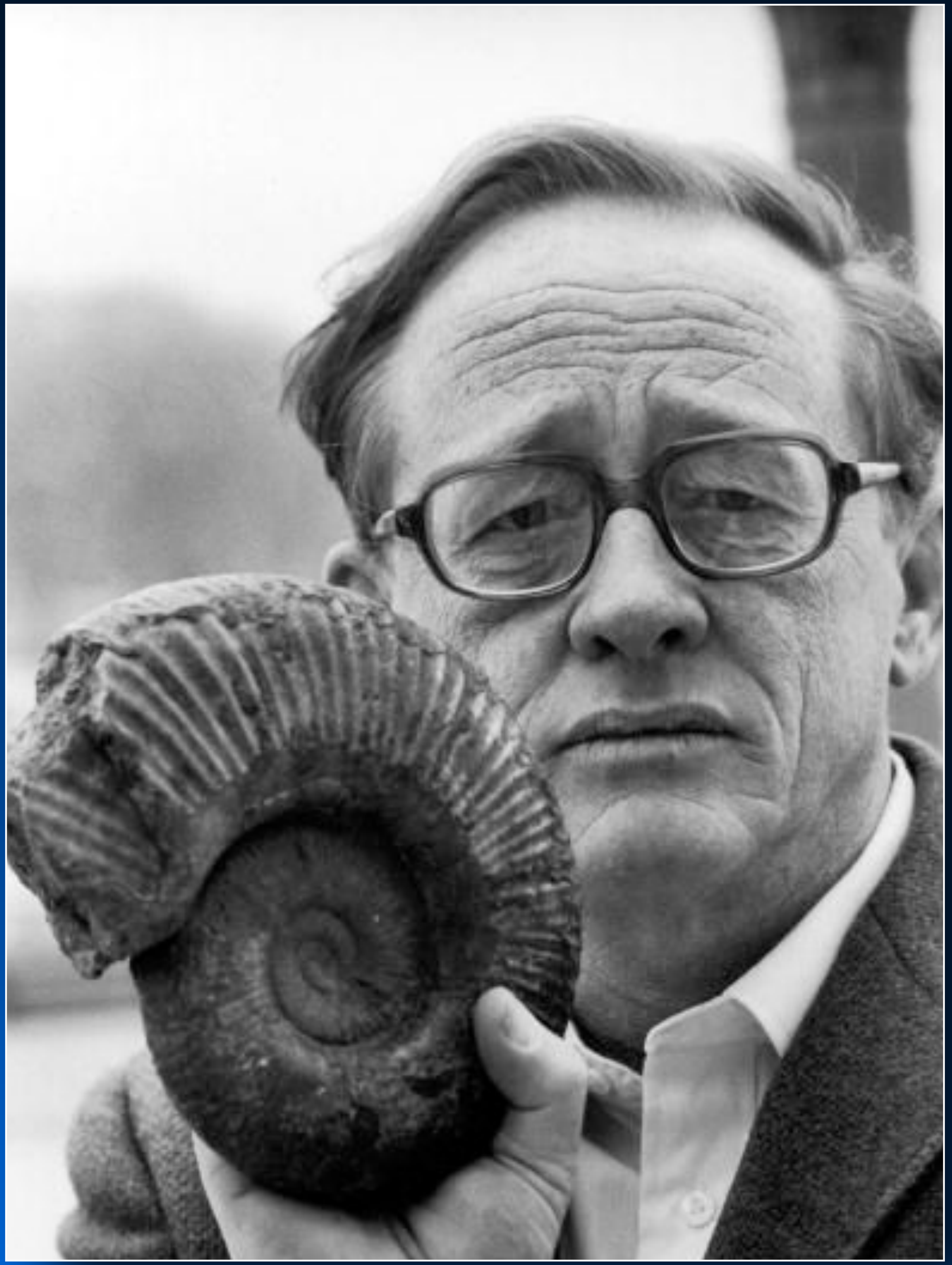
Climate Change



Bolide Impact

The list of causal mechanisms that have been put forward in the scientific literature ranges into the 100s. However, these are the most popular mechanisms currently and the ones that have received the most extensive testing.

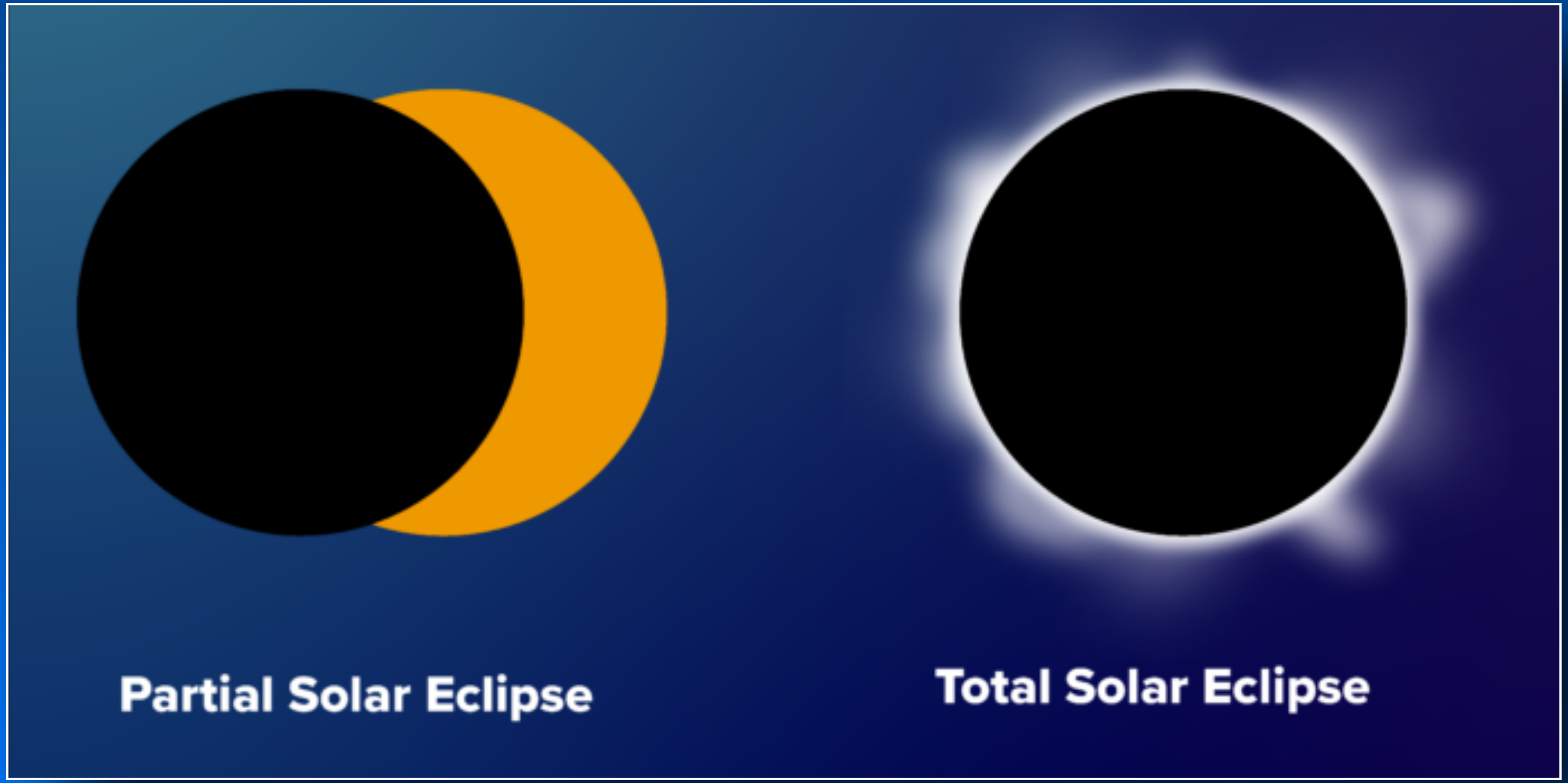
Testing Hypotheses with Historical Data



David Raup
(1933 – 2015)

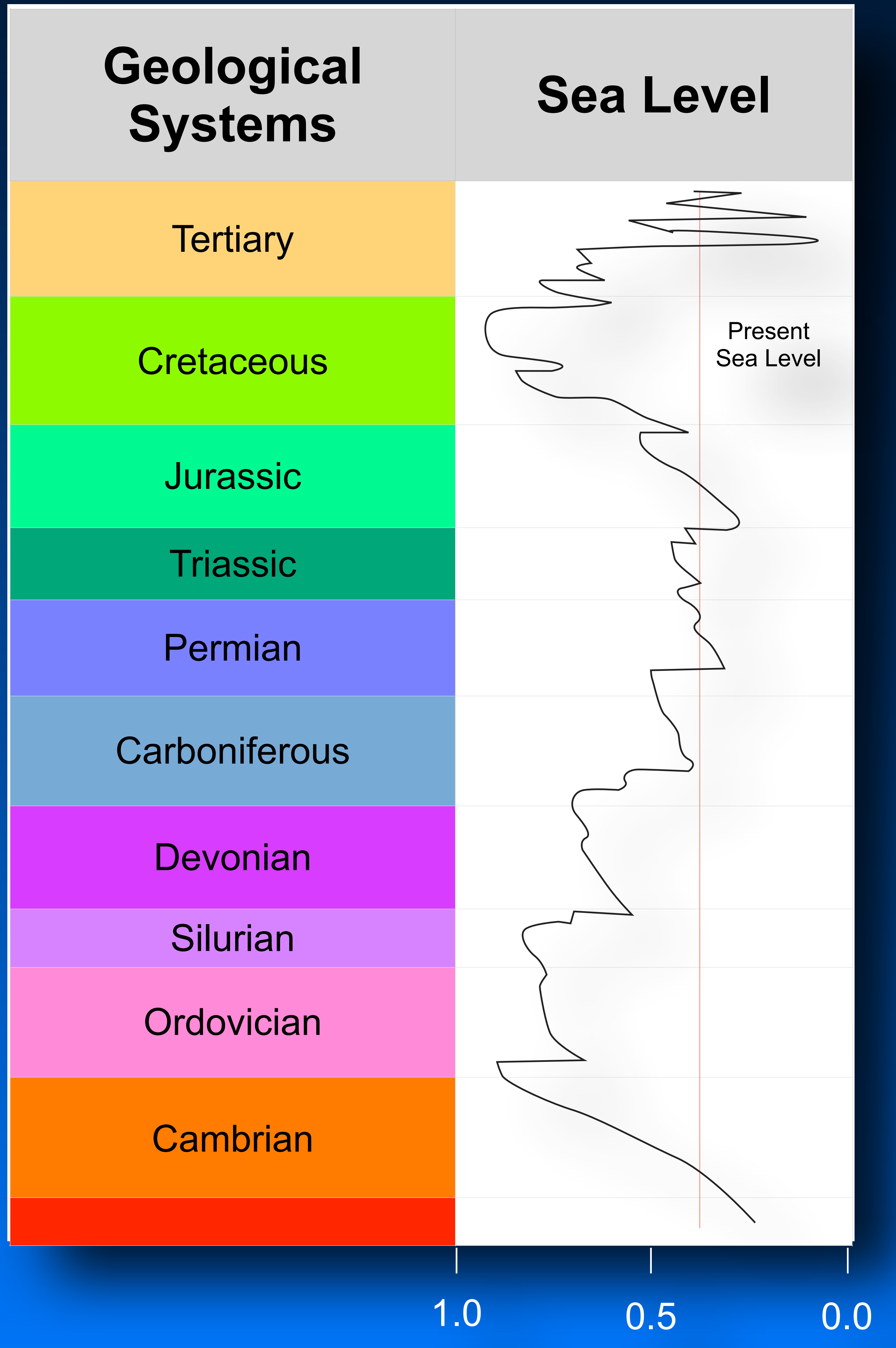
"There is no way of assessing cause and effect [in historical data] except to look for patterns of coincidence — and this requires multiple examinations of each cause-and-effect pair. If all extinction events are different the deciphering of any one of them will be next to impossible.”

David Raup
Bad Genes or Bad Luck, p. 151



Extinction Mechanisms

Sea-Level Change

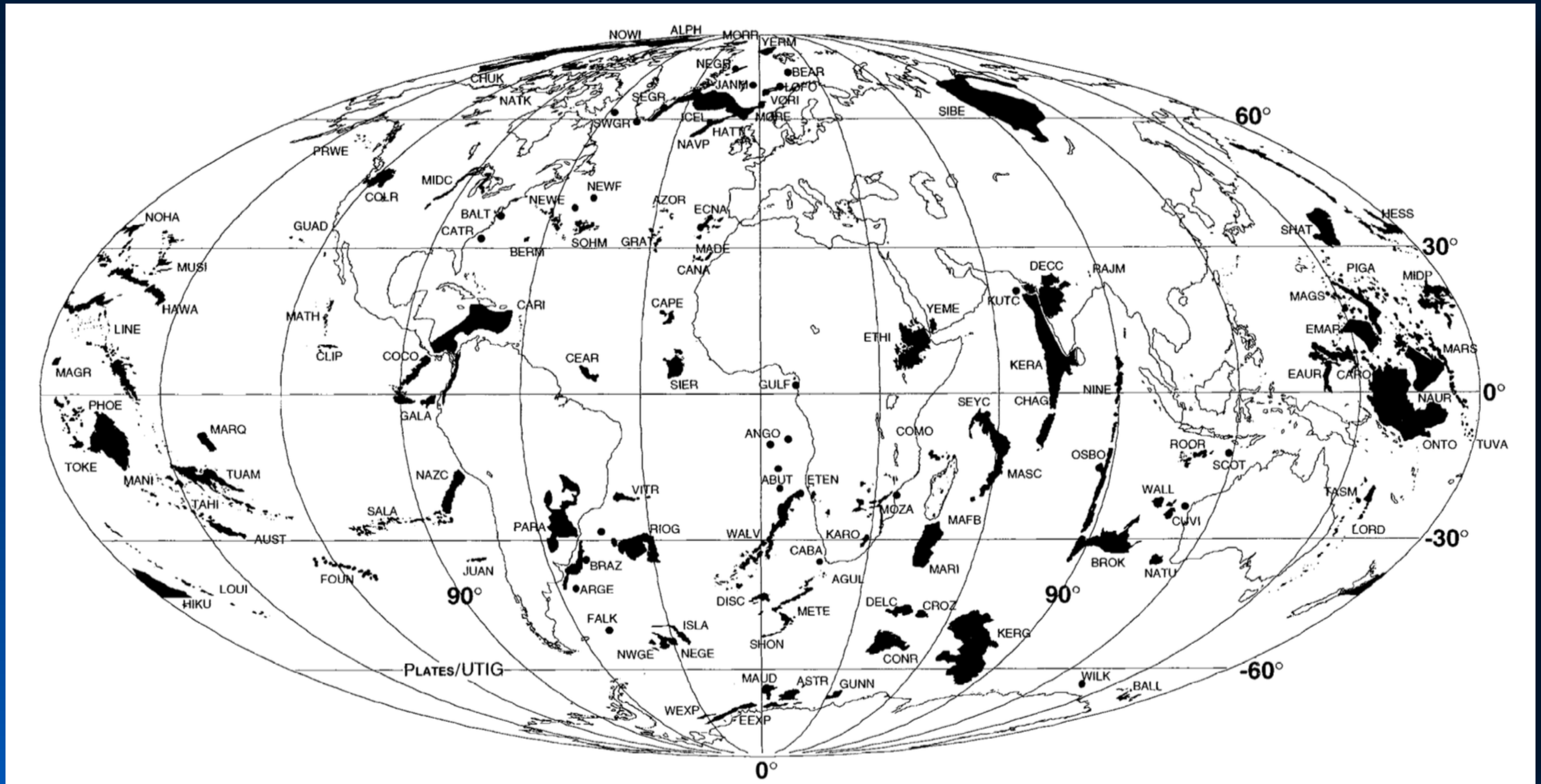


- Reduced shelf area (habitat destruction, ecological crowding)
- Increased continentality (climate change)
- Increased albedo (cooling)
- Greenhouse gases emissions (warming)

Changes in the level of the oceans have happened repeatedly throughout Earth history and have long been regarded as potential causes of major extinction events. Fluctuations of 100s of meters are not uncommon. Minor changes in sea level (0.1 - 5.0 m) can take place rapidly (1000s of years), but major eustatic events (c. 100 – 200 m) take place over quite long intervals of geological time (e.g., 10s x 10^6 years).

Extinction Mechanisms

Volcanism: Large Igneous Provinces (LIPs)



- Local devastation (physical damage)
- Increased albedo (cooling)
- Increased greenhouse gases (warming)
- Acid rain (habitat damage)
- Quasi-continuous disruption of global cycles

Large Igneous Province volcanism has happened repeatedly throughout Earth history and has led to the emplacement of (literally) millions of cubic miles of lava and other volcanic deposits on the earth's surface. Time scales for such eruptions stretch to as much as several million years.

Diagram from Coffin & Eldholm (1994)

Extinction Mechanisms

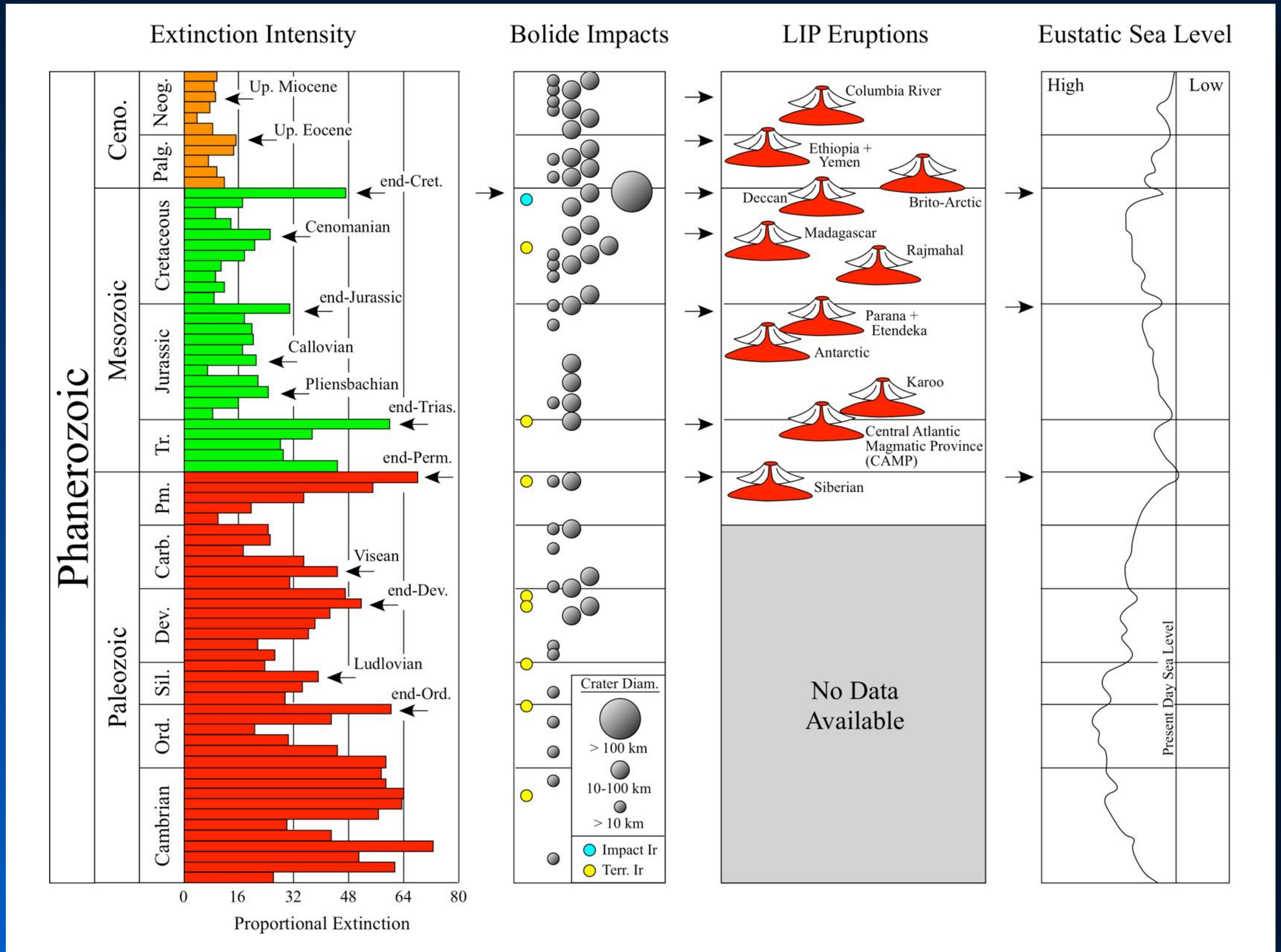
Bolide Impact

- Thermal flash (wildfires)
- Shock wave (physical damage)
- Global darkness (cooling)
- Increased albedo (cooling)
- Increased greenhouse gases (warming)
- Acid rain (habitat damage)

Because this mechanism represents a short, sharp, shock to the biosphere, timing considerations and recurrence patterns are paramount. Direct global effects of a large bolide impact are estimated not to last more than 100 years.

Extinction Mechanisms

Multiple Causes



- Thermal flash (wildfires)
- Shock wave (physical damage)
- Global darkness (cooling)
- Increased albedo (cooling)
- Increased greenhouse gases (warming)
- Acid rain (habitat damage)
- Quasi-continuous disruption of global cycles
- Reduced shelf area (habitat destruction)
- Increased continentality (climate change)

Since it's unquestionable that impacts, eruptions, sea-level changes and anoxia events were taking places various times in earth history, all may have played a role in driving the extinctions recorded there.

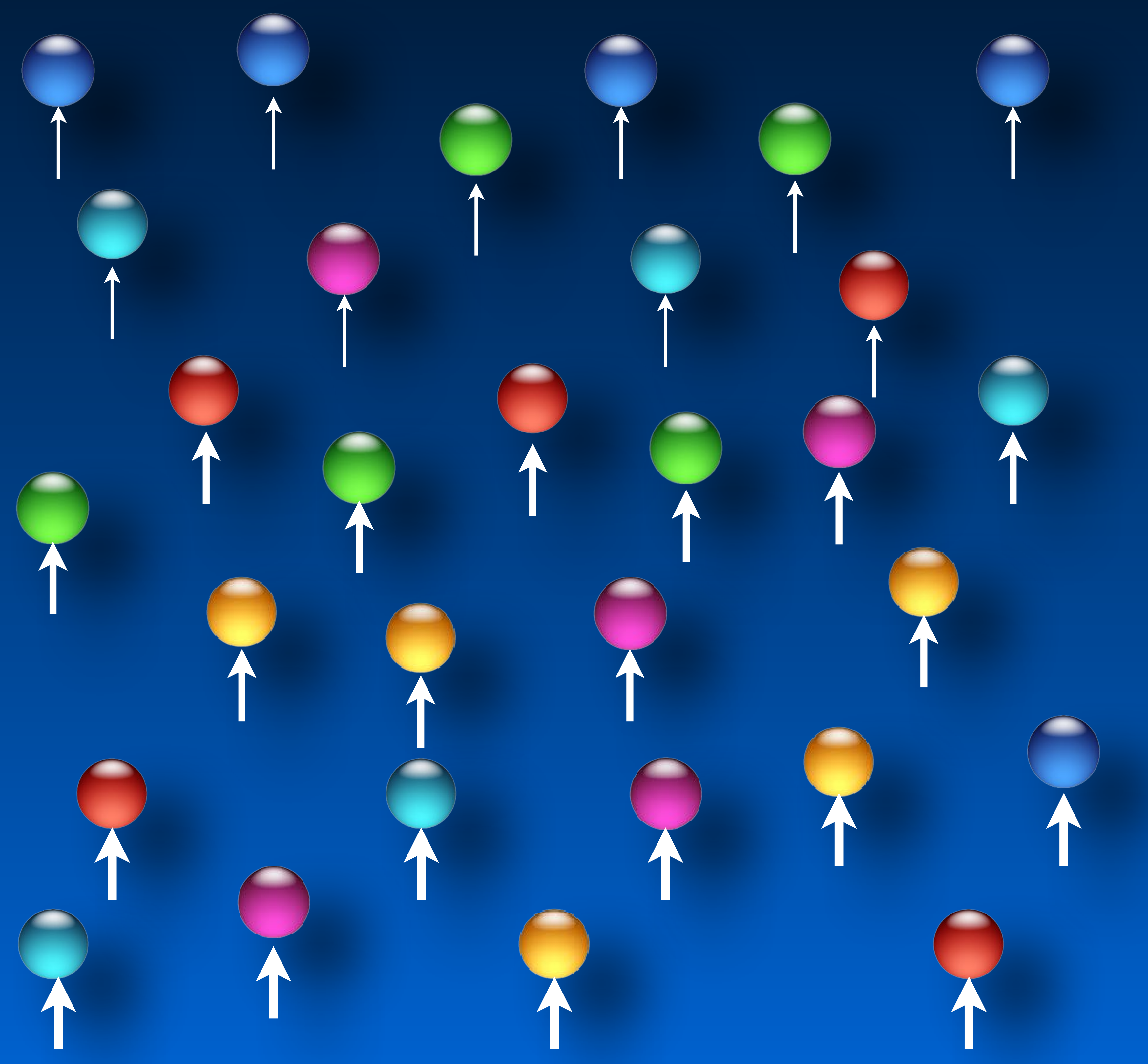
Ancient Extinctions: Effects

Alteration of Selective Regimes

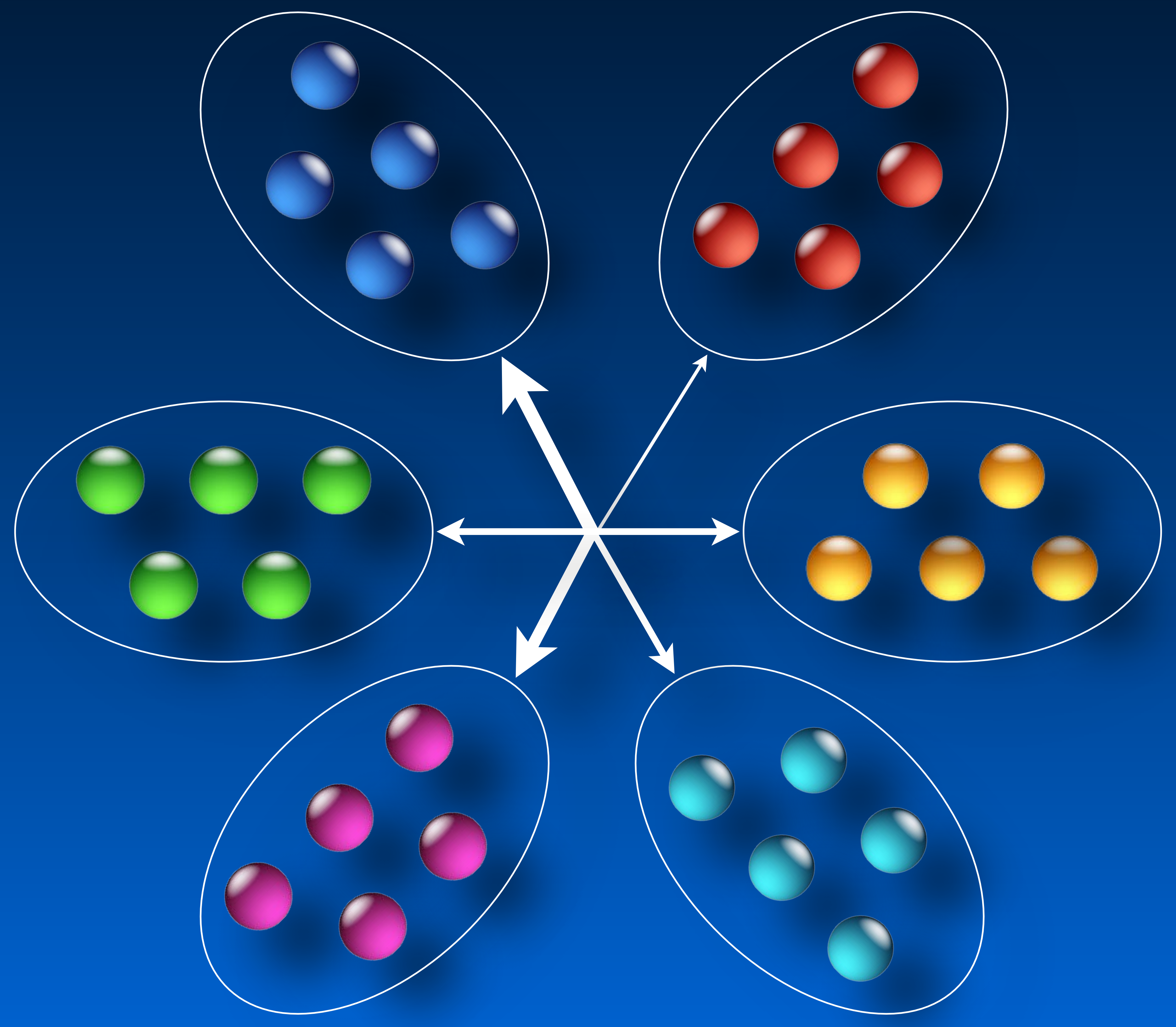
- Large extinction events that happen suddenly can alter the character of natural selection profoundly from selective regimes extant during normal times (e.g., emphasize survival of physical changes in the environment as opposed to competitive interactions between species).
- Pervious species-specific adaptive advantages may not confer the same survivorship potential during the former, as opposed to the latter, intervals.
- The role of chance in determining patterns of survivorship increases (e.g., bad genes or bad luck).

Ancient Extinctions: Effects

Alteration of Selective Regimes



Selection for Individual



Selection for Group

Ancient Extinctions: Effects

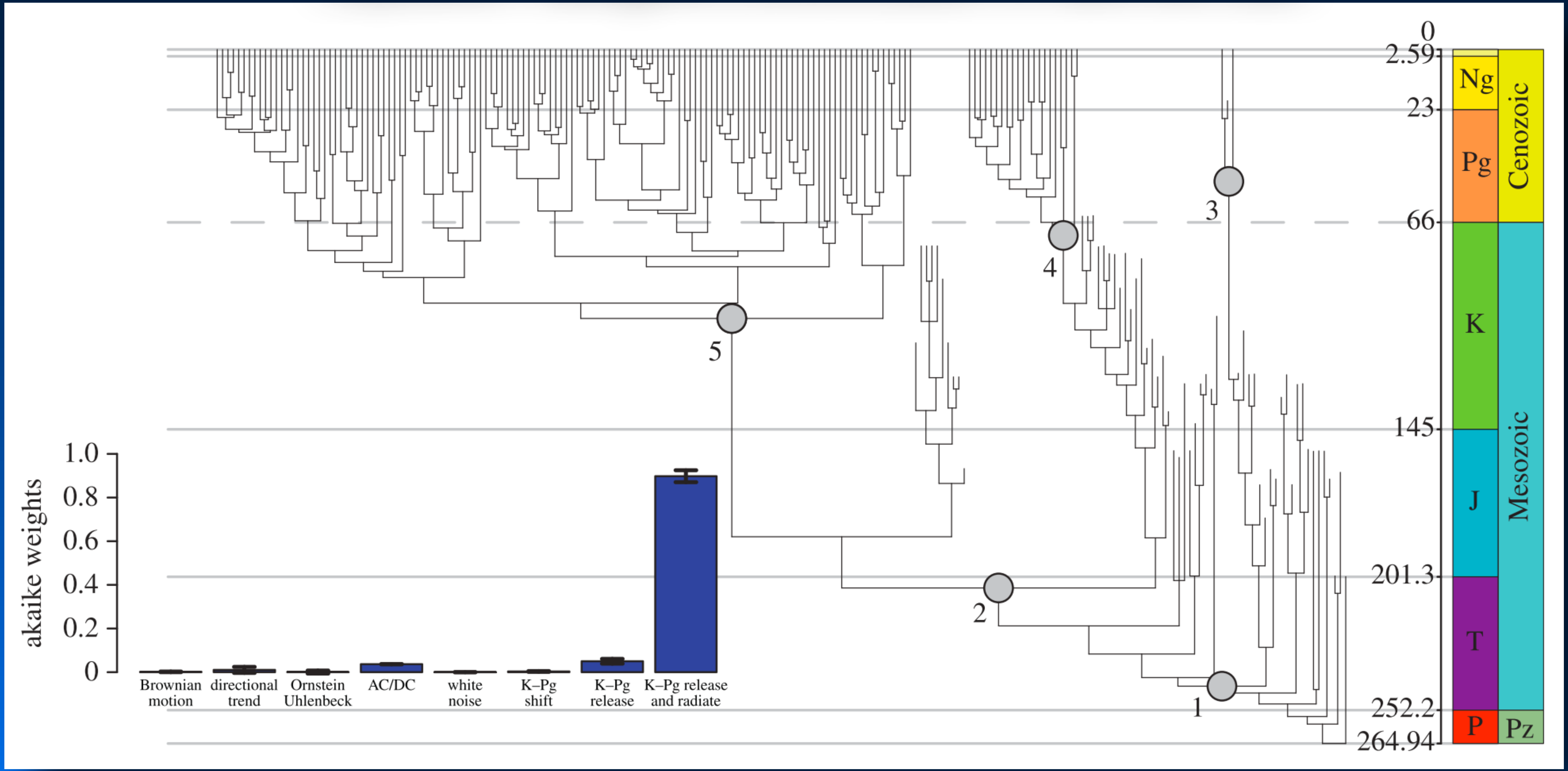
Reduction of Incumbency Advantage

- Clades the diversify early can block the diversification of equally well-adapted clades (e.g., dinosaurs vs mammals).
- Large & sudden extinction events can act to release this blockage by changing the character of selection and increasing the likelihood of both fair competition and opportunistic survivorship.
- There are a number of examples in the history of life in which this mechanism appears to have operated and resulted in dramatic changes to both faunas and floras over rapid time scales.

Ancient Extinctions: Effects

Reduction of Incumbency Advantage

Explosive Paleogene Diversification of Mammal Size



Slater (2013)

Ancient Extinctions: Effects

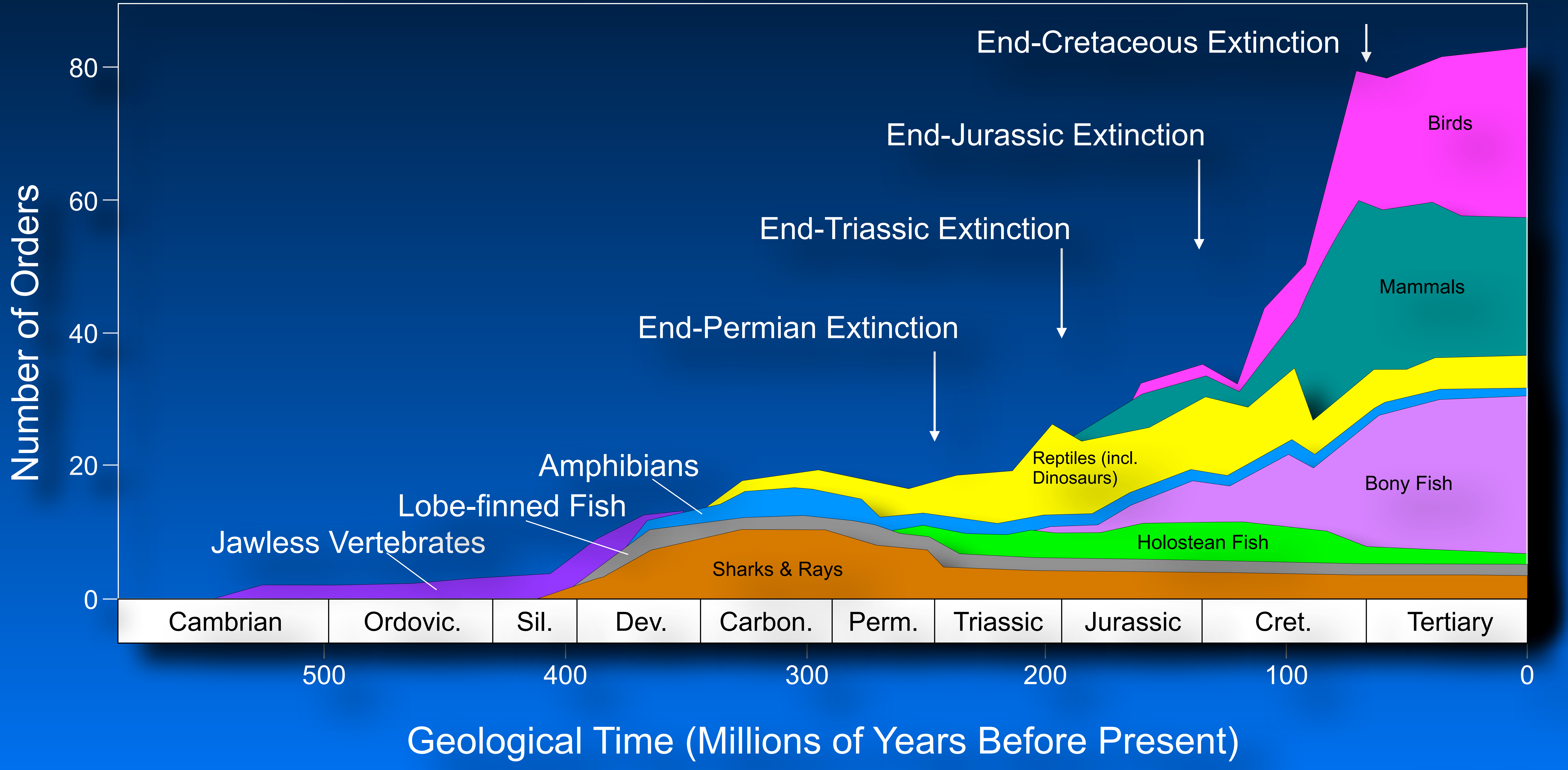
Biodiversity Enhancement Through Evolutionary-Ecological Stacking

- While large numbers of extinctions take place during large extinction events, it is rare that all members of previously diverse groups are eliminated (e.g., the end-Permian extinction eliminated trilobites, but not arthropods).
- This persistence leads to and evolutionary stacking of clades over time as extinction provides opportunities for new evolutionary innovation without dispensing completely with older designs.

Ancient Extinctions: Effects

Biodiversity Enhancement Through Evolutionary-Ecological Stacking

Accumulation of Vertebrate Biodiversity



Data from Romer (1966)

NJU Course

Principles of Paleobiology

Patterns & Modes of Extinction