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Patterns In Palaeontology: Trends of body-size evolution in the fossil record - a growing field

by [Mark Bell](#)*¹

Introduction:

The body size of an animal is often considered the most important part of its biology. Large body size brings many advantages, which can include better ability to capture prey, success in evading predators, intelligence, longevity and reproductive success; it also makes a greater range of resources available. A larger animal has a lower surface area to volume ratio than a smaller animal, which results in less heat loss to the surroundings, allowing it to remain warmer for longer in a cold environment. However, one major disadvantage is that larger organisms are, in general, more specialized, and can require more food for example. This can put species at higher risk of extinction caused by rapid environmental change.

Since the work of nineteenth-century palaeontologists such as Edward Drinker Cope and Othniel Marsh, the occurrence of both giant and dwarf species has been of interest to palaeontologists (for more information on Cope and Marsh see this [Palaeontology \[online\]](#) article). Studies of body-size patterns in the fossil record range from examinations of the entire history of life to more focused research into individual groups of vertebrates, invertebrates, [microfossils](#) or plants.

One of the reasons for the large number of studies in this area is that body size of an individual is readily preserved in the fossil record and so can be easily compared between individuals or species. Fossils of vertebrate animals are rarely preserved complete, and we are often restricted to isolated teeth or bones, but even these skeletal parts are strong predictors for either the length or mass of an individual, allowing the creatures to be used in macroevolutionary analyses (studies of evolutionary trends across a large number of species).

Giants in the fossil record:

The largest animal to have ever lived is the blue whale (*Balaenoptera musculus*), which can measure up to 27 metres long. However, the fossil record is replete with instances of gigantism throughout the [Phanaerozoic eon](#) — a period of time that covers the past 542 million years, since the first animals with hard parts began to appear in the fossil record. Figure 1 shows examples of the largest species known in all major animal clades (groups of a species and all its descendants), including extant and extinct species. During the

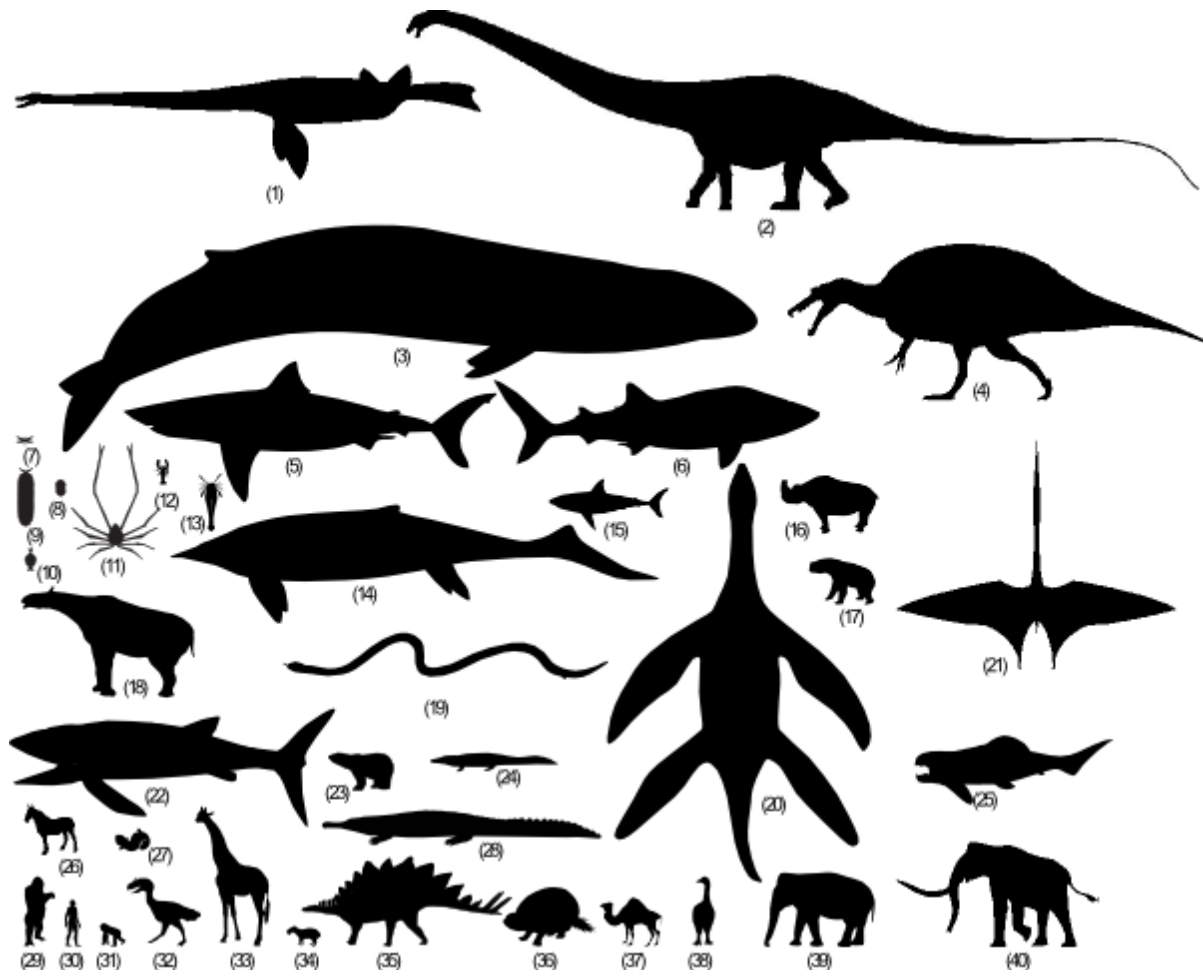


FIGURE 1 — A SELECTION OF SOME OF THE LARGEST SPECIES IN THE RECENT AND FOSSIL RECORD: (1) *MAUISAURUS HAASTI*, PLESIOSAUR [20 m]; (2) *SUPERSAURUS* [34 m]; (3) *BALAEOPTERA MUSCULUS*, BLUE WHALE [30 m]; (4) *SPINOSAURUS AEGYPTIACUS* [18 m]; (5) *CARCHAROCLES MEGALODON* [16 m]; (6) *RHINCODON TYPUS*, WHALE SHARK [14 m]; (7) *MEGANEURA* (75-CM WINGSPAN); (8) *ISOTELUS REX*, TRILOBITE (0.7 m); (9) *ARTHROPLEURA* (2.5 m); (10) *ANOMALOCARIS* (1 m); (11) *MACROCHEIRA KAEMPFERI*, JAPANESE SPIDER CRAB (3.8-M ARM SPAN); (12) *HOMARUS AMERICANUS*, AMERICAN LOBSTER (1.1 m); (13) *JAEKELOPTERUS RHENANIAE*, EURYPTERID [3.5 m]; (14) *SHASTASAURUS SIKANNIENSIS*, ICHTHYOSAUR [21 m]; (15) *CARCHARODON CARCHARIAS*, GREAT WHITE SHARK [5.2 m]; (16) *EMBLOTHERIUM* [2.5 m TALL]; (17) *DIPROTODON OPTATUM* [2 m TALL]; (18) *PARACERATHERIUM* [4.8 m TALL]; (19) *TITANOBOA CERREJONENSIS* [13 m]; (20) *PLIOSAURUS MACROMERUS* [18 m]; (21) *QUETZALCOATLUS NORTHROPI* [12-M WINGSPAN]; (22) *LEEDSICHTHYS PROBLEMATICUS* [14 m]; (23) *URSUS MARITIMUS*, POLAR BEAR [1.6 m HIGH]; (24) *CROCODYLUS POROSUS*, SALTWATER CROCODILE [5.5 m]; (25) *DUNKLEOSTEUS TERRELLI* [30 m]; (26) *EQUUS FERUS* [2.2 m TALL]; (27) *ANDRIAS DAVIDIANUS*, CHINESE GIANT SALAMANDER [1.8 m]; (28) *SARCOSUCHUS IMPERATOR* [12 m]; (29) *GIGANTOPITHECUS GARSTINI* [3 m]; (30) *HOMO SAPIENS* [1.8 m]; (31) *GORILLA GORILLA* [1 m TALL]; (32) *BRONTORNIS BURMEISTERI* [3 m]; (33) *GIRAFFE CAMELOPARDALIS* [6 m TALL]; (34) *HYDROCHOREUS HYDROCHAERIS*, CAPYBARA [0.9 m TALL]; (35) *STEGOSAURUS ARMATUS* [9 m]; (36) *GLYPTODON* [4 m]; (37) *CAMEL DROMEDARIS* [2.1 m TALL]; (38) *DROMORNIS STIRTONI*, ELEPHANT BIRD [3 m TALL]; (39) *LOXODONTA AFRICANA*, AFRICAN BUSH ELEPHANT [3.2 m TALL]; (40) *MAMMATHUS TROGONOTHERII* [4.5 m TALL]. SOURCE: (1–6, 12–40) SILHOUETTES FROM PHYLOPIC.ORG; (7–9, 11) RUDKIN ET AL. (2003); (10) TRILOBITES.INFO..

Palaeozoic era (542 million to 251 million years ago), several arthropod groups reached what may be their upper size limit. One of the earliest examples of gigantism occurred in a period of rapid diversification of life called the Cambrian explosion, at the beginning of the Phanerozoic. During this time, there arose a group of arthropods known as anomalocaridids, which had no mineralized parts, and survived until the Devonian period (416 million to 359 million years ago). Of these, *Anomalocaris*

(Fig. 1(10)) is considered to have been a predator, and is thought to have grown up to 2 metres long. In the marine realm, the early Devonian eurypterid *Jaekelopterus rhenaniae* (Fig. 1(13)) is estimated to have grown to more than 3 metres long. The largest-ever terrestrial arthropod, the millipede-like myriapod *Arthropleura* (Fig. 1(9)), existed in the Carboniferous period (359 million to 299 million years ago), reached more than 2 metres in length and would have fed on plant detritus on the floor of a rainforest.

During the early Palaeozoic, invertebrates would have been the largest animals and the apex predators. However, their dominance was quickly superseded with the rise of fish in the Devonian. At this time came armoured fish called placoderms, such as *Dunkleosteus* (Fig. 1(25)), which reached upwards of 10 metres and have been suggested as the cause of the decline of the eurypterids. The peak of terrestrial body size for vertebrates came with the rise of herbivorous sauropod dinosaurs in the late Triassic period (251 million to 200 million years ago), which regularly reached lengths estimated in excess of 30 metres. After the non-avian dinosaurs became extinct, mammals began to diversify and rapidly increased in body size.

Dwarfs and dwarfing in the fossil record:

Gigantism is common in the fossil record, but the reverse pattern of dwarfism has also been extensively documented. Vertebrate groups often conform to an ecological principle called the Island rule, or insular dwarfing, in which larger animals will decrease in size when available resources are reduced, such as when the species are isolated on an island. Examples of this effect in the Quaternary period (2.6 million years ago to the present) include pygmy mammoths, elephants, hippos and even hominins (such as the 'hobbit' *Homo floresiensis*, Fig. 2). During the late Jurassic period (200 million to 146 million years ago), the dwarf sauropod *Europasaurus* (6–7 metres in length) is thought to have lived on islands in the Lower Saxony Basin of Germany that would not have had enough resources to sustain large sauropods.



FIGURE 2 — A SELECTION OF DWARFS IN THE RECENT AND FOSSIL RECORD. LEFT: THE BORNEO PYGMY ELEPHANT (*ELEPHAS MAXIMUS BORNEENSIS*, [SOURCE](#)). MIDDLE: A BABY PYGMY HIPPOPOTAMUS STANDS WITH ITS PARENT (*CHOEROPSIS LIBERIENSIS*). RIGHT: THE FOSSIL HOMININ *HOMO FLORESIENSIS*, SCALE BAR 1 CM. [SOURCE](#).

The miniaturization of species has also been noted in the aftermath of extinction. Named after the island in Jonathan Swift's 1726 book *Gulliver's Travels*, the 'Lilliput effect' describes faunas with lots of animals, but few different species, all of generally small size (Fig. 3). Originally noted in foraminifera around the time of the extinction of the dinosaurs, it has since been shown to occur

mainly in invertebrate groups (including graptolites, corals, gastropods and echinoids) across almost all the major mass-extinction events.

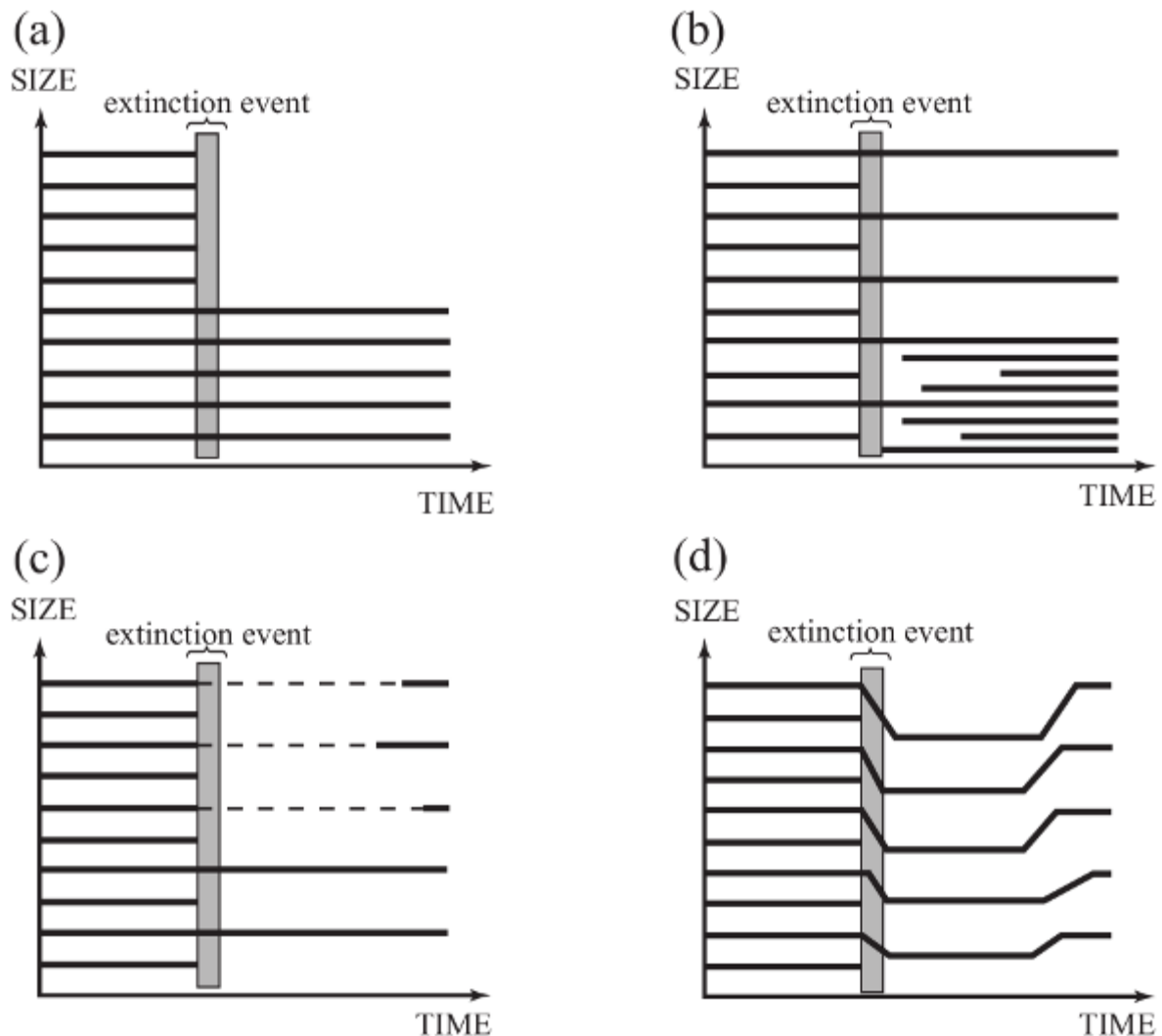


FIGURE 3 — POTENTIAL MECHANISMS FOR THE LILLIPUT EFFECT. (A) LOSS OF LARGER FORMS; (B) SPECIATION OF SMALL FORMS AFTER THE EXTINCTION; (C) TEMPORARY DISAPPEARANCE OF SPECIES FROM THE FOSSIL RECORD AFTER THE EXTINCTION; (D) REDUCTION IN SIZE OF GROUPS THAT SURVIVE. SOURCE: TWITCHETT (2007).

As with other potential controls on body-size evolution that affect multiple species at once, the mechanisms behind the Lilliput effect are still poorly understood. UK palaeontologist Richard Twitchett has discussed several mechanisms by which it could occur: the extinction of larger, more specialized taxa; the splitting apart of one species into new, smaller species immediately after the extinction; the temporary disappearance of some larger species from the fossil record, without going extinct; actual reduction in size of species; or a combination of these four processes.

Environmental controls and Bergmann's rule:

Of the suggested controllers of body-size evolution, fluctuations in environmental conditions are

undoubtedly important. For example, increases in atmospheric oxygen content throughout the Phanerozoic eon have been linked to several evolutionary innovations, including the first multicellular animals, the first flying insects, the radiation of Quaternary mammal groups and especially increased body size of several animal groups. Increased size in the Carboniferous is often associated with increased partial pressure of oxygen at this time; its effects are seen in arthropod groups such as the dragonfly-like insect *Meganeura* (Fig. 1(7)), which had a wingspan of around 65 centimetres.

Another environmental factor that can affect body size is changes in temperature. In 1847, German biologist Carl Bergmann noted that if two closely related species differ only in size, then the smaller species requires a warmer climate. This pattern is termed Bergmann's rule. It has been examined most extensively for warm-blooded vertebrates, but several studies have shown support for a similar trend in invertebrates such as amphipod crustaceans: these have been shown to have larger body sizes in colder waters, where more oxygen is available.

One of the major discussion points about Bergmann's rule, as with all ecological and evolutionary rules, is how it should be defined and when it should be applied. Originally Bergmann discussed it with respect to patterns within a species (intraspecific). Some studies have shown Bergmann's rule to apply across species (interspecific), but there is little to indicate whether such patterns are caused by the same mechanisms. Another issue is what causes Bergmann's rule. A common explanation in warm-blooded animals is heat conservation: the larger an animal is, the lower its surface area to volume ratio and therefore the less heat it loses to the environment. Other mechanisms have also been suggested, including that species of larger mass generally spread out to a wider geographic area than smaller species, or that larger species are less likely to starve in resource-scarce environments such as polar regions.

Cope's rule:

One of the most well-known and frequently studied macroevolutionary concepts is known as Cope's rule. In general, it describes an increase in body size over time. The theory is commonly attributed to the works of Edward Drinker Cope in the late nineteenth century, although Cope never actually stated the rule; the term was coined by German evolutionary biologist Bernhard Rensch in 1948.

Regardless of who discovered the trend of increasing body sizes, there is discussion over how it should be defined and which clades show examples of it. In 1973, US palaeontologist Steven Stanley provided one of the first attempts to define Cope's rule, making a distinction between what he termed active and passive trends. With an active trend, the population as a whole grows bigger over time and smaller individuals disappear; this is sometimes called Cope's rule *sensu stricto*. In a passive system, the mean size increases through a process whereby the maximum size grows but the minimum size either remains constant or decreases, so the total range of possible sizes gets wider over time. This is termed Cope's rule *sensu lato*, meaning 'in the broadest sense'. The reverse of both these patterns can also occur (Fig. 4).

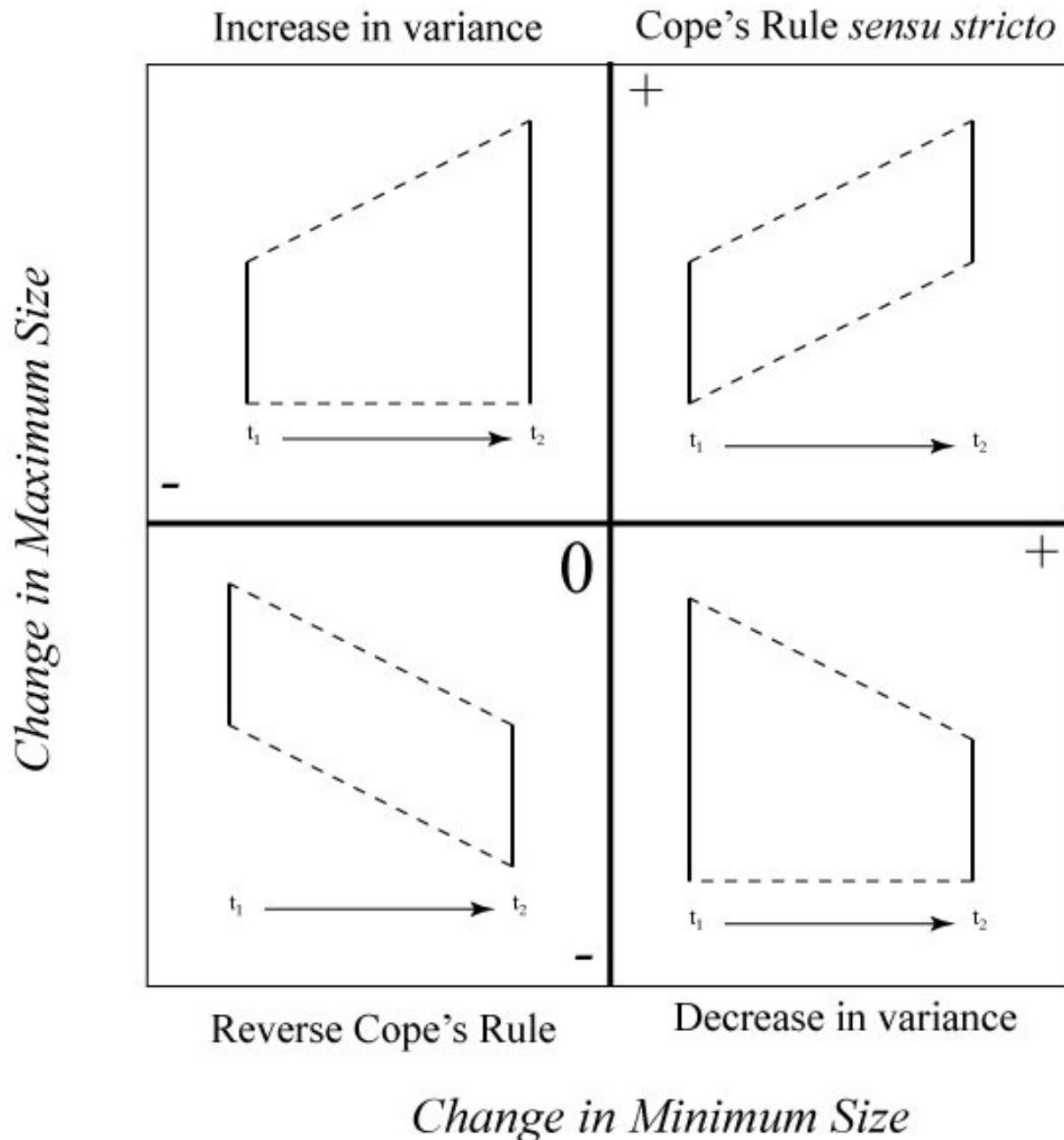


FIGURE 4 — ACTIVE VERSUS PASSIVE TRENDS IN BODY-SIZE EVOLUTION. (TOP LEFT) INCREASE IN VARIANCE; (TOP RIGHT) COPE'S RULE *SENSU STRICTO*; (BOTTOM LEFT) REVERSE COPE'S RULE; (BOTTOM RIGHT) DECREASE IN VARIANCE. SOURCE: JABLONSKI (1997).

More recently, patterns of body-size evolution have been investigated using several evolutionary models, through a method called maximum likelihood. There are three commonly used models: Brownian motion (or a random walk), a directional model and stasis (Fig. 5). Under Brownian motion, increase and decrease in body size are equally likely. With a directional model, either increases or decreases are preferred over time. Finally, in stasis there is no net change over time. Simulations of evolution are run using each model; in the maximum-likelihood method, the model that produces a pattern that best fits the pattern seen in the fossils is considered the most likely explanation. Using this method, it has been shown that directional evolution (that is, Cope's rule *sensu stricto*) is not as

common as either Brownian motion or stasis across a wide range of groups.

Summary:

The body size of an animal is the product of the interaction between many and varied environmental and ecological factors. Databases featuring measurements of a wide range of fossils, and methods such as computer simulations allow us to achieve a much greater understanding of these factors.

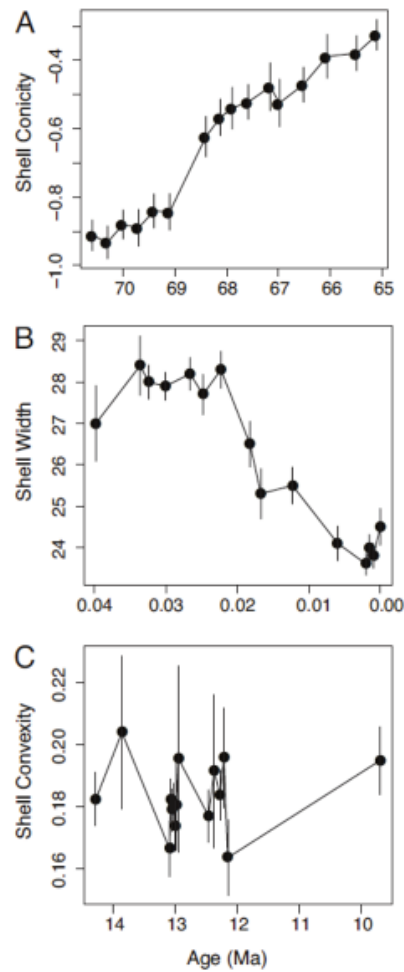


FIGURE 5 — MODELS OF PHENOTYPIC EVOLUTION. (A) DIRECTIONAL MODEL OR GENERALIZED RANDOM WALK; (B) BROWNIAN MOTION OR UNBIASED RANDOM WALK; (C) STASIS. SOURCE: HUNT (2007).

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