

## 2.10 Evolution of Large Size

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### Introduction

Many plants and animals of the past and present are very large compared to the human scale. In particular, vertebrates, gymnosperms, and angiosperms achieved giant dimensions on occasion, and apparently several times independently in each group (Table 1; Fig. 1). The focus here, however, will be on truly large organisms on the human scale. The key macroevolutionary questions to be asked are:

- 1 Why do certain groups achieve giant size while others do not? Is it simply chance, or are there historical and mechanical reasons?
- 2 Why do some groups never produce giants?
- 3 Does evolution always go from small to large, or can it reverse?
- 4 How long does it take for large size to evolve in a lineage?
- 5 Are large organisms better adapted than small ones?

### Giants and mechanical constraints

The bony internal skeleton of vertebrates is ideally suited to supporting great weights in terrestrial giants. The acquisition of a fully upright posture in both dinosaurs and mammals, where the limb bones are tucked immediately beneath the body, permitted giants to evolve.

The major constraints on large size in a terrestrial vertebrate are limits to the strength of bones and to the power of muscles. As animals become larger, the bones and muscles in the legs come under increasing strain, and there have to be modifications in their shape and design. Hokkanen (1986) made simple biomechanical calculations of bone and muscle strengths in order to determine the size of the largest feasible terrestrial tetrapod.

Each leg bone must be strong enough to support one-quarter of the total body weight, or more if the weight is concentrated at the back, as is often the case, and there has to be a fairly large safety factor in order to allow the animal to walk or run. The strength of a bone is proportional to its cross-sectional area (a two-dimensional measure), while

body weight is proportional to volume (a three-dimensional measure). Thus, bone cross-sectional area has to increase relatively faster than body weight, which is why elephants and dinosaurs have legs like tree trunks (Fig. 2). Under high stress, leg bones can buckle, or they can break without bending much. The strength of muscles also limits the size of an animal. A large animal has to be able to pull itself up from a lying position, and the heavier the animal is the more massive its muscles must be. So, muscle dimensions and muscle strength also limit the maximum size of a land animal.

Locomotion is yet another limiting factor. A hypothetical animal weighing 140 tonnes could stand safely enough, but if it walked its legs would break. This is because, in walking, the force of the weight of the animal is expressed at an angle through the leg bones. Even if a giant animal could stand safely with its legs positioned vertically beneath it, it might not be able to walk because the breaking force of the bone is relatively greater. Hokkanen (1986) concluded that the heaviest possible animal able to walk on four legs would have weighed no more than 100 tonnes.

The largest dinosaurs have estimated weights in the range of 80–140 tonnes, but the larger forms are poorly known. The 78 tonne weight of *Brachiosaurus* is the greatest generally accepted weight known for a terrestrial animal. The strength of bone and muscle, as described above, would have limited *Brachiosaurus* to a sedate walking pace of about 1 m/s with strides of only 2.5 m or so (quite short for an animal with 3 m legs) (Alexander 1985).

In land plants, the continuously growing supporting tissues (lignin-lined xylem cells) within a tree trunk allow vast heights and weights to be achieved. The maximum height is probably limited in part by the ability of a plant to raise sap. Water has to be 'pumped' from the ground and raised up the trunk, against the force of gravity, by means of osmosis (the sap has a higher salt content than the ground water), and the hydrostatic effect of transpiration (water loss through leaves exposed to the air).

There are also mechanical constraints imposed by

**Table 1** A selection of large organisms, giving some key dimensions. Fossil forms are preceded by †, and the weights quoted for these are estimates (a question mark implies that estimates are very uncertain because complete skeletons are unknown).

Organism	Max. length (m)	Max. height (m)	Max. weight (t)
<i>Plants</i>			
<i>Algae</i>			
<i>Macrocystis</i> , Pacific giant kelp	60	—	—
<i>Gymnospermophyta</i>			
<i>Sequoiadendron</i> , Giant sequoia	—	84–112	c. 2500
<i>Pseudotsuga</i> , Douglas fir	—	126.5	—
<i>Angiospermae</i>			
<i>Eucalyptus</i> , Mountain ash	—	114.3	—
<i>Animals: Vertebrata</i>			
<i>Class Placodermi</i>			
<i>Dunkleosteus</i>	9	—	—
<i>Class Chondrichthyes</i>			
<i>Cetorhinus</i> , Basking shark	10.5	—	—
† <i>Carcharodon</i>	13	—	—
<i>Rhincodon</i> , Whale shark	12.6	—	15
<i>Class Reptilia</i>			
<i>Suborder Squamata</i>			
<i>Eunectes</i> , Anaconda snake	8.4	—	0.23
<i>Python</i>	10	—	—
† <i>Kronosaurus</i> , Pliosaur	15.2	—	—
<i>Suborder Crocodylia</i>			
† <i>Deinosuchus</i>	16	—	—
<i>Suborder Pterosauria</i>			
† <i>Quetzalcoatlus</i>	wing span 11–12	—	0.09
<i>Suborder Dinosauria</i>			
† <i>Brachiosaurus</i>	23–27	12	40–78
† <i>Diplodocus</i>	27	—	18.5
† <i>Antarctosaurus</i>	30	—	80
† ‘ <i>Supersaurus</i> ’	?24–30	?15	?75–100
† ‘ <i>Ultrasaurus</i> ’	?30–35	?16–17	?100–140
† ‘ <i>Seismosaurus</i> ’	?30–36	—	80+
<i>Class Mammalia</i>			
<i>Order Perissodactyla</i>			
† <i>Indricotherium</i> (= <i>Baluchitherium</i> )	11.3	c. 6	20
<i>Order Artiodactyla</i>			
<i>Giraffa</i> , Giraffe	—	5–6	—
<i>Order Proboscidea</i>			
<i>Loxodonta</i> , African elephant	7–10	3–4.4	2–10
<i>Elephas</i> , Indian elephant	6	3	4
<i>Order Cetacea</i>			
<i>Balaenoptera</i> , Blue whale	33.5	—	190
<i>Physeter</i> , Sperm whale	20.7	—	—
† <i>Basilosaurus</i>	21.3	—	—

the vast weight of a tall tree and the possible strength of its trunk. The weight acts vertically down the trunk, but winds can cause tremendous stresses as the crown of a tree is pushed from side to side. Experiments show that winds with speeds of 60–65

km/h exert a lateral force on the tree equal to its weight (Fraser 1962). The girth of the tree then increases in proportion to the weight (i.e. relatively more rapidly than the height increases). At 100 m tall, a tree may be as much as 30 m in circumference

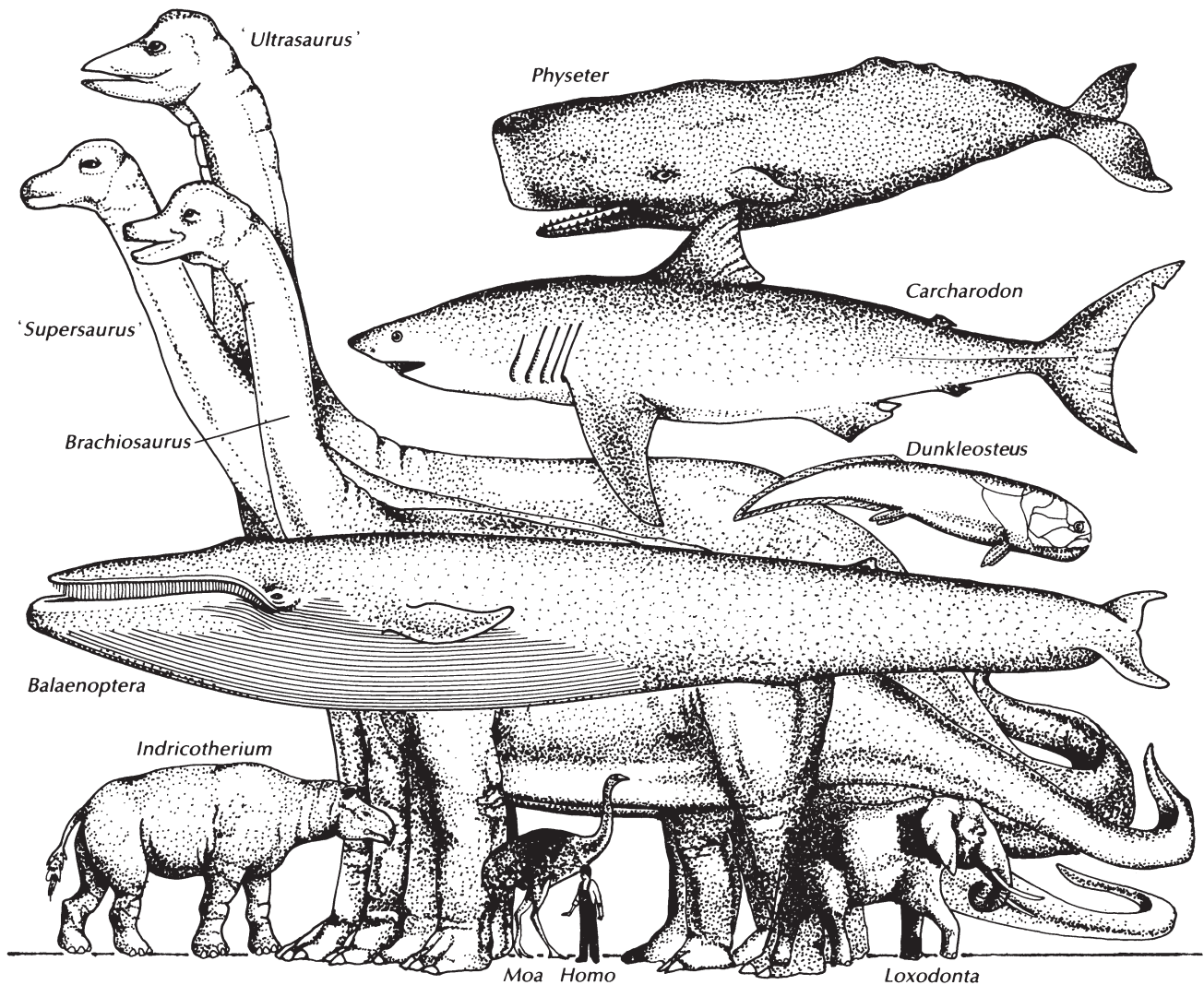


Fig. 1 A selection of large animals drawn to scale. Measurements are given in Table 1. (Drawing by Elizabeth Mulqueeny.)

(Table 1), and at much greater heights, the circumference would tend to approach the height.

### Why so few giants?

Most other groups of organisms appear to be restricted from achieving large size by mechanical and physiological constraints. For example, arthropods have an external skeleton which has to be moulted frequently as the animal grows. After each moult, the animal is soft-bodied for a while, and hence vulnerable. The shed skeleton also represents a loss of body materials that have to be replaced. To achieve giant size, an arthropod would suffer the cost of moulting dozens of times. A more important constraint on large size is probably the respiratory system of tubes in the exoskeleton that allow air to

diffuse throughout the body passively. At moderate to large size, this technique would not allow all body tissues to receive an adequate supply of oxygen.

There are similar constraints on large size in most other invertebrates — e.g. the respiratory system of annelids and nematodes (simple diffusion into the body); the filter-feeding habits of brachiopods, most molluscs, coelenterates, bryozoans, graptolites, and some echinoderms; and mechanical constraints of the exoskeleton of brachiopods, most molluscs, and most echinoderms. It is assumed that filter-feeding by means of exposed cilia cannot sustain a large organism. The shells of brachiopods and molluscs can reach large sizes (e.g. the giant clam, *Tridacna*, 1 m across), but as body size increases, shell thickness has to increase in proportion to body weight to

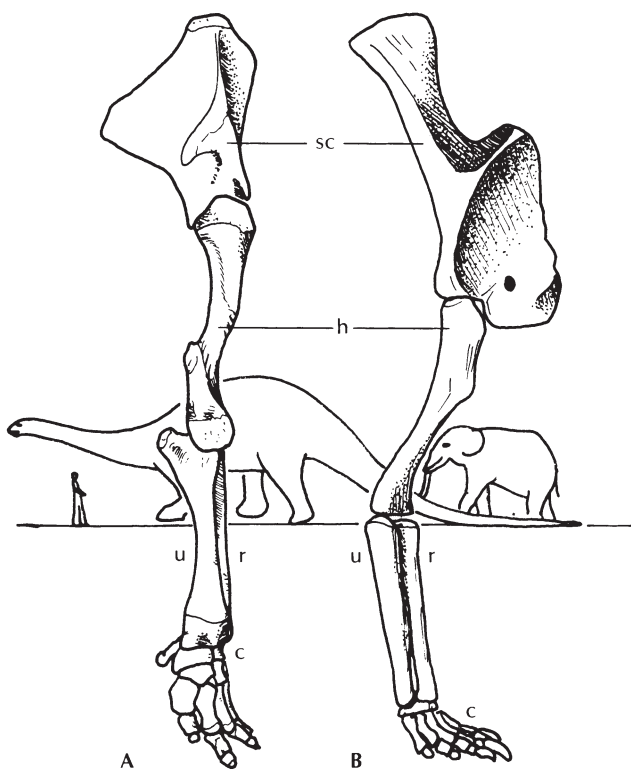


Fig. 2 The pillar-like skeleton of the forelimb of A, *Elephas*, the Indian elephant and B, *Diplodocus*, a sauropod dinosaur, showing convergent graviportal (weight-bearing) adaptations: columnar arrangement of shoulder girdle (sc=scapula) and limb bones, relatively long humerus (h), large separate radius (r) and ulna (u), block-like carpal bones (c), and relatively short finger bones spreading out over a cushioning pad.

maintain the strength of the shell. The potential weight of the shell, and the amount of particulate calcium carbonate to be extracted from the seawater, tend to prevent huge size. The same is probably true for echinoids.

### Cope's Rule

In 1887, E.D. Cope presented a new principle of evolution, that organisms always tend towards large size. He could find no examples in which a lineage or clade of plants or animals evolved towards smaller size. Although Cope never explicitly defined this as a 'law' of evolution, it has since come to be known as Cope's Rule.

In considering Cope's Rule, many authors have focused on particular advantages of evolving large size (see below). However, Stanley (1973) argued that Cope's Rule had general application, not because of any particular advantages of large size, but since groups tend to arise at small body size relative

to their ecological optimum. Amongst mammals, for example, the original members of most clades in the Cretaceous and Palaeocene were small carnivores or insectivores. On the other hand, large forms are unlikely ancestors for major new lineages since they tend to be specialized to particular habitats, often by virtue of the physiological demands imposed by large size. Stanley (1973) surveyed a range of animal taxa, and found that the ancestors of a clade were generally smaller, on average, than a random sample of their descendants. Histograms of body size tended to be concentrated initially at small sizes and to be rather symmetrical. Through time, the histograms developed longer and longer tails to the right as larger body sizes arose (Fig. 3).

Size decrease also does take place in many lineages, but it is rare. For example, modern horsetails and clubmosses are midgets in comparison with their Carboniferous tree-like ancestors. Certain vertebrate groups have also shown reductions in size since the Pleistocene, but some of the former giants (e.g. mammoth, aurochs, giant kangaroo and wombat, giant ground sloth, glyptodon, moa) may have suffered because of human influence (see also Section 2.13.8).

### Evolution of large size

The evidence of the fossil record is that giant size can evolve very quickly in certain groups. For example, the first (small) dinosaurs of the late Triassic date from the Carnian. By mid-Norian times, 5–10 million years later, prosauropods such as *Plateosaurus* had reached body lengths of 5 m. The sauropodomorph line then achieved a length of 12 m with *Melanorosaurus* in the Early Jurassic, and sizes continued to increase rather slowly until the Late Jurassic when the largest known dinosaurs occurred (Table 1). This last phase of size increase towards giantism — a leap from body lengths of about 12 m and weights of 10 tonnes to maxima of 30 m and 80 tonnes or more, occurred between the Bathonian and the Kimmeridgian, a time of about 20 million years.

Mammals achieved large size just as rapidly, if not more so. From a maximum of cat size just before the end of the Cretaceous, rhinoceros-sized uinatheres and astrapotheres are known 10 million years later in the Late Palaeocene and Early Eocene. The largest land mammal of all time, the rhinoceros *Indricotherium*, was in existence by the Early Oligocene, 30 million years after the radiation began. Whales achieved large size even more



teristics that are subject to species selection (since these are not organism-level features). They could also potentially be interpreted as examples of the 'effect hypothesis' (Vrba 1983; see also Section 2.6). This hypothesis suggests that species-level characteristics, such as species duration or broad ecological adaptation, may be incidental effects of individual characters, such as dietary or habitat preferences. Natural selection, acting on organisms, might select for large body size, which in turn might produce higher extinction rates within a lineage. These higher rates could be interpreted as an incidental *effect* of natural selection, rather than as a result of species-level selection. These ideas are still highly controversial.

## References

Alexander, R.McN. 1985. Mechanics of posture and gait of

- some large dinosaurs. *Zoological Journal of the Linnean Society* **83**, 1–25.
- Bakker, R.T. 1977. Tetrapod mass extinctions — a model of the regulation of speciation rates and immigration by cycles of topographic diversity. In: A. Hallam (ed.) *Patterns of evolution as illustrated by the fossil record*, pp. 439–468. Elsevier, Amsterdam.
- Fraser, A.I. 1962. Wind tunnel studies of the forces acting on the crowns of small trees. *Reports on Forest Research* **1962**, 178–183.
- Hokkanen, J.E.I. 1986. The size of the largest land animal. *Journal of Theoretical Biology* **118**, 491–499.
- Stanley, S. M. 1973. An explanation for Cope's Rule. *Evolution* **27**, 1–26.
- Stanley, S.M. 1979. *Macroevolution: pattern and process*. W.H. Freeman, San Francisco.
- Vrba, E.S. 1983. Macroevolutionary trends: new perspectives on the roles of adaptation and incidental effect. *Science* **221**, 387–389.

## 2.11 Rates of Evolution — Living Fossils

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### Introduction

The study of rates of evolution encompasses a wide variety of approaches to characterization of the amount of evolutionary change within particular groups of organisms, over specified time intervals. The high level of interest that palaeontologists and evolutionary biologists have shown in this subject is not surprising, since rates are a common focus in the analysis of any process. The importance of rates, however, is often only marginally attributable to intrinsic interest in 'how rapidly' or 'how slowly' a process operates. Rather, information on rates tends to be used as a means of investigating the underlying dynamics of the process in question, or sometimes as input for analysing the dynamics of a related process. Much of the work on rates of evolution has thus been directed toward a better understanding of the dynamics of evolutionary change. Studies have been designed with the intent of comparing rates of evolution in a variety of ways — within and between particular taxonomic groups, ecological settings, and lineage geometries (e.g.,

ancestor–descendant sequences that include lineage splitting versus ones that do not). While interesting generalizations are emerging, a greater appreciation is also being gained of the difficulties of quantifying rates of evolution.

'Living fossils' is a term frequently used to denote extant representatives of groups of organisms that have survived with relatively little change over a long span of geological time. Such groups are implicitly recognized as having displayed unusually low rates of evolution. In both professional and popular literature, living fossils collectively appear to have attracted more attention than have groups displaying unusually high rates of evolution. This may be partly because, in keeping with the inherent paradox of the term 'living fossil', evolutionary history is expected to involve conspicuous change, and it is surprising when it does not. In addition, evolutionary rate statements are commonly (though not exclusively) framed in terms of putative ancestor–descendant pairs, and it is easier to recognize these when the total amount of change has been small than when it has been large. Instances of