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ALL-TIME GIANTS: THE LARGEST ANIMALS AND  
THEIR PROBLEMS

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**ABSTRACT.** The largest known swimming, walking and flying animals are all vertebrates. They include the blue whale (up to 190 tonnes), the largest sauropod dinosaurs (probably about 80 tonnes) and two flying animals estimated to have had masses of at least 75 kg, the pterosaur *Quetzalcoatlus* and the bird *Argentavis*. Even larger sizes might be physically possible, but may not have been attained because problems associated with size may make excessively large animals competitively inferior. These problems are discussed with frequent reference to basic consequences of geometric similarity (areas are proportional to the squares of lengths and volumes to the cubes) and to the empirical rule that metabolic rates of similar animals tend to be proportional to (body mass)<sup>0.75</sup>. Excessively large animals would be liable to overheat, both in water and on land. Larger animals tend to have fewer individuals in each species, suggesting the possibility that the largest whales and dinosaurs approach the limits of size above which numbers would be unlikely to be large enough for long term viability. Even the largest dinosaurs seem to have been well able to support their weight on land. Flying animal size may have been limited more by the problem of taking off than by the power requirement for flight. The largest swimming animals are filter feeders and the largest land animals were herbivores, so neither are at the top of a long food chain.

THIS paper reviews the largest animals known to have lived, at any time in the Earth's history. I will consider the problems associated with their size, and ask why they did not evolve to be even larger. Aquatic, terrestrial and flying animals will be considered separately. Invertebrates cannot match the size of the largest vertebrates, so I will be concerned almost exclusively with vertebrates. Colonial animals such as corals are excluded from consideration.

PRINCIPLES OF ALLOMETRY

It may be helpful to start by noting some of the consequences of size differences, starting with a geometrical point. Bodies of identical shape, but different sizes (that is, geometrically similar bodies) have surface areas proportional to the squares of their lengths and volumes proportional to the cubes of their lengths: for example, a cube with sides twice as long as another has faces of four (= 2<sup>2</sup>) times the area and has eight (= 2<sup>3</sup>) times the volume. If the bodies are made of the same material, they have masses proportional to their volumes. Thus for different-sized animals of the same shape we expect to find

mass proportional to (length)<sup>3</sup>

from which follows

length proportional to (mass)<sup>0.33</sup>

and since area is proportional to length squared

area proportional to (mass)<sup>0.67</sup>

Plainly, even closely related animals of different sizes are not precisely the same shape. Lions have relatively smaller brains and eyes than domestic cats (Davis 1962) but, in many other respects, groups of animals are remarkably close to geometric similarity. For example, the lengths of whales ranging from 30 kg dolphins to 100 tonne blue whales are proportional to (body mass)<sup>0.34</sup> (Economos 1983). The lengths of the limb bones of mammals ranging from shrews to elephants are proportional to (body mass)<sup>0.35</sup> (Alexander *et al.* 1979). However, in some cases we find marked deviations from geometric similarity. If Bovidae (antelopes, etc.) are considered separately from other mammals, their limb bone lengths are proportional to (mass)<sup>0.26</sup> (Alexander *et al.* 1979). The wing spans of birds other than hummingbirds tend to be proportional to (mass)<sup>0.39</sup> and those of hummingbirds to (mass)<sup>0.53</sup> (Rayner 1988).

Further to those geometrical points, we need to note that the pace of life is generally slower for larger animals. These generally make repetitive movements at lower frequencies than small animals: for example, sparrows in flight make about 20 wing beat cycles per second and swans about three cycles per second (see Rayner 1988). There is a tendency, in groups of related animals, for frequencies to be about proportional to (body mass)<sup>-0.25</sup>. For example, wing beat frequencies of birds (excluding hummingbirds) are proportional to (mass)<sup>-0.27</sup> (Rayner 1988) and heart frequencies of mammals to (mass)<sup>-0.25</sup> (Stahl 1967). However, not all frequencies scale so steeply. The stride frequencies of mammals using corresponding gaits are about proportional to (shoulder height)<sup>-0.5</sup> and so to (mass)<sup>-0.17</sup> (Pennycuik 1975).

Another aspect of the slower pace of life for larger animals is that metabolic rates do not increase in proportion to body mass. The metabolic rate of a 2000 kg elephant is not 10000 times that of a 0.2 kg rat, but only about 1000 times. More generally, metabolic rates of similar animals of different sizes are found to be about proportional to (body mass)<sup>0.75</sup>. This applies not only to resting rates (Calder 1984), but also approximately to field metabolic rates and maximum aerobic rates, both of which are proportional, for mammals, to (mass)<sup>0.81</sup> (Weibel and Taylor 1981; Nagy 1987). There are marked differences between groups, notably between ectotherms and endotherms; even with its body at a mammal-like temperature of 37 °C, a typical lizard uses oxygen only about one-quarter as fast as a mammal of equal mass (see Alexander 1981, fig. 11-4). However, within each group the 0.75 power law holds well.

Most of the attempts that have been made to explain this law apply only to a limited range of organisms. However, a recent very general theory (West *et al.* 1997) derives the law by considering the energy cost of distributing resources through a branching network of tubes (for example a blood system) in organisms of different sizes.

The 0.75 power law of metabolic rate is related to the -0.25 law of frequencies. Consider two muscles that exert equal stresses while shortening by equal fractions of their lengths. The forces they exert are proportional to their cross sectional areas, and the distances they shorten are proportional to their lengths, so the amounts of work they do (force multiplied by distance) are proportional to their volumes, and so to their masses. If these muscles make up equal fractions of body mass and contract with frequencies proportional to (body mass)<sup>-0.25</sup>, their power outputs are proportional to (mass)<sup>0.75</sup>.

There is another general rule (in this case, a very imprecise one) that is useful. Large species tend to have fewer members than small ones so that in most cases, for instance, the world population of a species of elephant will be fewer in number than the world population of a species of mouse. There is a general tendency for the population density of a species to be proportional to (body mass)<sup>-0.75</sup> (Cotgreave 1993). This has been interpreted as implying an energetic equivalence rule: if species of different sizes have numbers proportional to (mass)<sup>-0.75</sup> and metabolic rates proportional to (mass)<sup>0.75</sup>, total rate of food intake will be the same for species of all sizes. However, several points should be noted. First, there is a great deal of scatter about the regression line: in many cases, a common species is 1000 times as numerous as a rare one of similar size. Second, some studies of particular groups have found exponents markedly different from -0.75. And finally, carnivore species tend to have many fewer members than herbivore species of similar size (Peters and Raelson 1984).

Subsequent sections of this paper apply the principles expounded in this one, in discussions of the consequences of large size for aquatic, terrestrial and flying animals. Crocodiles divide their time between land and water; they will be treated here as aquatic.

### SWIMMING ANIMALS

(Text-fig. 1)

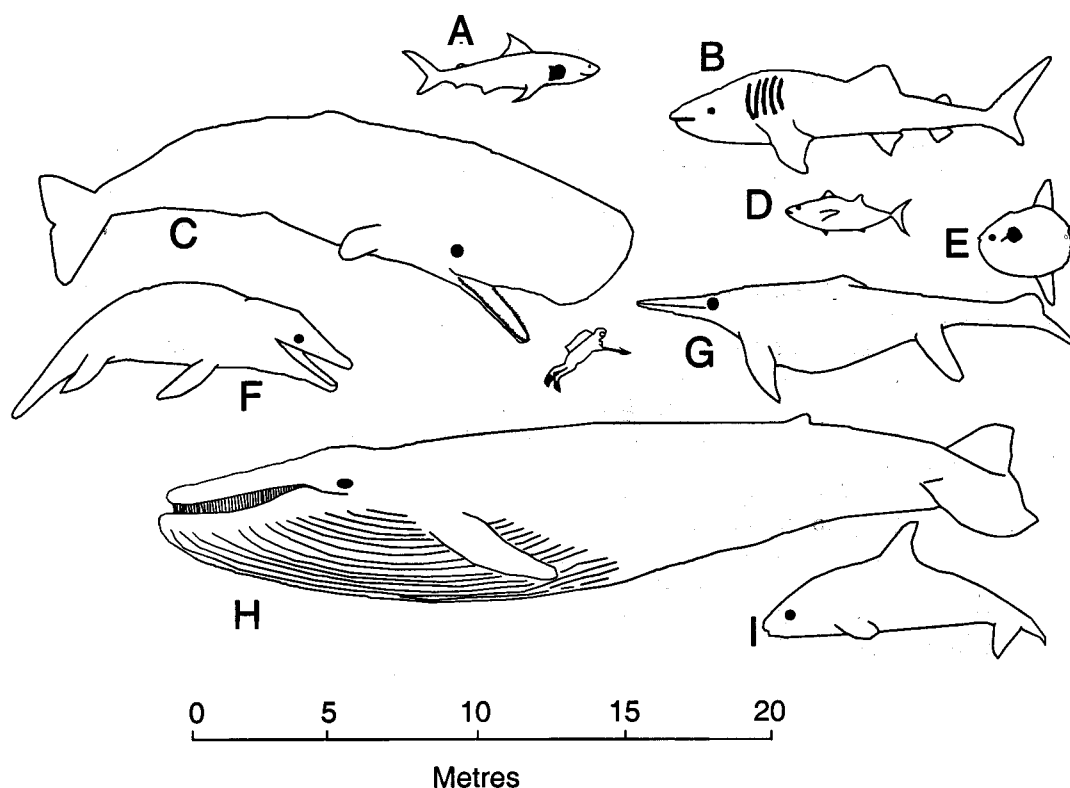
First, I shall consider aquatic animals. Before discussing the consequences for them of large size, I shall review some of the largest of them. The blue whale (*Balaenoptera musculus*) is not only the heaviest modern animal, but also the heaviest known to have lived at any time. Adult females, which grow larger than males, reach lengths of 30 m and masses (determined by weighing the carcass in pieces) of over 120 tonnes (Lockyer 1976). The heaviest recorded weighed 190 tonnes. There are eight other species of baleen whales, with adult masses ranging from 7 tonnes (the minke whale, *B. acutorostrata*) upwards. All of them are filter feeders, using the fringes of their baleen to strain small crustaceans or fishes from the plankton. Antarctic krill (Euphausioida, about 50 mm long) are particularly important for the blue whale, but other species, with differently spaced bristles on their baleen, take mainly copepods or fishes (Nowak 1991).

There is a marked tendency for very large swimming animals to be filter feeders. The largest modern fishes are the whale shark, *Rhincodon typus*, which grows up to 13 m long with an estimated mass of at least 15 tonnes; and the basking shark, *Cetorhinus maximus*, which reaches 11 m and 8 tonnes (Matthews 1995). The basking shark feeds largely on copepods and crab larvae (Matthews and Parker 1950). The whale shark also feeds on zooplankton, but I know of no more precise description of its diet. Both these large sharks obtain their tiny prey by filtering. The largest known teleost fish, the Jurassic *Leedsichthys* (Martill 1988), was another filter feeder. It is known only from fragments, but these include the tail fin whose span of 2.7 m suggests a body length of 13 m.

Some other very large aquatic animals are predators on larger prey, mainly fishes and squid. By far the largest is the sperm whale, *Physeter catodon*, which attains 19 m and over 50 tonnes (Lockyer 1976). It feeds mainly on ammoniacal squid from substantial depths, prey whose bloated form suggests that they may not swim fast (Denton 1974). The killer whale (*Orcinus orca*; males reach 10 m and 9 tonnes) eats seals as well as fishes and squid (Nowak 1991). Male elephant seals, *Mirounga leonina*, have masses up to 3.7 tonnes and again feed mainly on fishes and squid (Nowak 1991). The great white shark, *Carcharodon carcharias*, preys on seals and dolphins as well as fishes (Wheeler 1975). The largest recorded modern specimen was 6.4 m long with a mass of 3.2 tonnes, but there are fossil *Carcharodon* teeth whose size indicates a body length of 13 m (Randall 1973). The largest known aquatic reptiles include the Cretaceous pliosaur *Kronosaurus* (12 m long; Romer 1959); the Triassic ichthyosaur *Shonisaurus* (14 m; Kosch 1990); and the Cretaceous crocodylian *Deinosuchus* (15 m; Steel 1989). All of these were apparently predators, but we have no direct evidence of their diets.

In comparison with these giants, the largest predatory teleosts are unimpressive. Current angling records are 0.71 tonnes for black marlin (*Makaira indica*) and 0.68 tonnes for bluefin tuna (*Thunnus thynnus*; Matthews 1995). Both feed mainly on schooling fish (Wheeler 1975). The ocean sunfish *Mola* grows larger, apparently to more than one tonne, but eats smaller prey such as jellyfishes and young fish (Wheeler 1975). Giant squid (*Architeuthis harveyi*) have immensely long tentacles, but the mantle is seldom more than 3 m long, and large specimens probably have masses of around 1 tonne (Clarke 1966).

We may ask why very large swimmers tend to be filter feeders. Consider first the rate (volume per unit time) at which water must be filtered. For animals taking the same food, this must be proportional to metabolic rate, and so to (body mass)<sup>0.75</sup>. Blue whales and other rorquals take mouthfuls of water, which are then squeezed out through the baleen to filter out the food. If mouth volume is proportional to body mass and mouth-filling frequency (like other physiological frequencies, see above) to (mass)<sup>-0.25</sup>, the rate of filtration will be proportional to (mass)<sup>0.75</sup>, as



TEXT-FIG. 1. Some of the largest known swimming animals, drawn to a uniform scale. The names of extinct animals are asterisked. A, *Carcharodon*; B, *Rhinocodon*; C, *Physeter*; D, *Thunnus*; E, *Mola*; F, *Kronosaurus*\*; G, *Shonisaurus*\*; H, *Balaenoptera*; and I, *Orcinus*.

required. Large size will present no problem. Right whales (*Balaena*) and filter-feeding sharks swim with their mouths open, straining out food with their baleen or gill rakers. Their rates of filtration will be mouth area multiplied by swimming speed. Geometric similarity would make mouth area proportional to  $(\text{mass})^{0.67}$  so larger animals would have to swim a little faster to make filtration rates proportional to  $(\text{mass})^{0.75}$  as required.

Considerations of energy cost suggest problems for very large filter feeders. Animals taking the same prey can be expected to have filters of equal mesh size, even if their bodies are very different in size. To obtain volumetric flow rates proportional to  $(\text{mass})^{0.75}$  through filters whose areas are proportional to  $(\text{mass})^{0.67}$ , linear flow rates and so pressure drops must be proportional to  $(\text{mass})^{0.08}$ . The power required for filtration is the volumetric flow rate multiplied by the pressure drop, and so will be proportional to  $(\text{mass})^{0.75} \times (\text{mass})^{0.08} = (\text{mass})^{0.83}$ . Thus larger filter feeders may have to use a larger proportion of their food intake to drive the filtration process than smaller filter feeders. However, this conclusion could be avoided if fractal design made filter area increase with slight positive allometry (see Pennycuik 1992 on fractals). Also, at least some of the baleen whales appear to have fore stomachs which function as fermentation chambers, like the rumen of cattle (Herwig *et al.* 1984). If the chitin of crustacean exoskeletons is fermented, this may improve food utilization and so reduce the volume of water that must be filtered, alleviating the problem of energy cost for these very large filter feeders. In any case, the arguments in this paragraph fail to explain why the largest aquatic animals are filter feeders.

Now consider predation on prey which are too large to be filtered and must be pursued

individually. Slow prey may be able to escape from larger predators if they are better at swerving; the critical property is lateral acceleration (Howland 1974). The forces available for swerving can be expected to be proportional to muscle cross sectional area and so to  $(\text{mass})^{0.67}$ , and the accelerations they will provide will be proportional to  $(\text{mass})^{-0.33}$ . Thus predators can be expected to have trouble catching smaller prey. If the discrepancy of size between predators and prey is greater for larger predators, these may have most difficulty in catching prey. It may be significant that sperm whales feed largely on (probably) sluggish ammoniacal squid and killer whales hunt in groups, improving their chances of catching prey by making it harder for prey to escape by swerving (Howland 1974).

These arguments seem inconclusive; they fail to make it clear why so many of the largest swimmers are filter feeders. Another possible reason relates to the problem of maintaining a population of viable size, of very large animals. Filter feeders, taking food from relatively low in the food chain, have a more abundant energy supply than predators taking prey from higher in the food chain. If size were limited by the problem of obtaining enough energy to support a viable population, we would expect filter feeders to evolve to larger sizes than predators on large prey. Similarly, among terrestrial mammals herbivores have evolved to larger sizes than carnivores, and herbivore species have higher population densities than carnivore species of similar size. Similar reasoning might lead us to expect that because endotherms such as whales need more energy than ectotherms of similar size such as sharks, the largest animals should be ectotherms, which they are not. Similarly, terrestrial mammals need more energy than similar-sized (ectothermic) reptiles; thus we might expect reptiles to be more abundant than mammals of equal size, but they are not (Peters, 1983). These discrepancies show that we should be cautious in formulating arguments of this kind.

It seems unlikely that the blue whale has reached the maximum size consistent with a viable population. Prior to human exploitation, it is estimated that the world population comprised 200 000 individuals (Nowak 1991). A recent estimate that the minke whale population of the north-east Atlantic is now about 120 000 has raised confidence in the viability of this species to such an extent that it has been suggested that some hunting could be permitted (Motluk 1996). In their guidelines for assessing threats of extinction, Mace and Lande (1991) associated their lowest level of threat ('vulnerable') with a population size of only 10 000 or less. However, they were concerned with extinction in periods of the order of centuries, whereas our concern is with viability over periods of millions of years. If smaller populations were viable, larger animals would be possible.

Another potential problem for very large animals is that excessively large ones would overheat. An animal may be thought of as a core, in which heat is liberated by metabolism and in which blood circulation maintains uniform temperature; enclosed by an insulating layer of skin with (in some cases) blubber, fur or feathers. The physics of heat conduction tells us that the temperature difference across the insulating layer is proportional to the metabolic rate divided by the thermal conductance of the insulation. Metabolic rate can be expected to be proportional to  $(\text{body mass})^{0.75}$ , as previously noted. Conductance should be proportional to surface area divided by insulation thickness, and so to  $(\text{mass})^{0.67}/(\text{mass})^{0.33} = (\text{mass})^{0.33}$ . Then the temperature difference across the insulating layer will be proportional to  $(\text{mass})^{0.75}/(\text{mass})^{0.33} = (\text{mass})^{0.42}$ , and excessively large animals would overheat. Ryg *et al.*'s (1993) calculations indicate that when a blue whale makes full use of the heat-insulating potential of its blubber, its basal metabolism is enough to heat it 40 K (centigrade degrees) above ambient, maintaining a typical mammalian body temperature of 38 °C in sea water at its freezing point of -2 °C. Field metabolic rates of large mammals are typically twice basal rates (Nagy 1987), so the whale's problem is not to keep warm, but to avoid overheating. It does this by sending blood to the dermis, bypassing the blubber. Hokkanen (1990) calculated that with maximal blood flow to the dermis, a blue whale metabolizing at 1.5 times the estimated basal rate could just avoid overheating in water at 29 °C. Tropical surface water temperatures are about 27 °C. These data suggest that the largest whales may be near the maximum size set by the overheating problem.

Even if this is the case, the largest fishes and aquatic reptiles are in no danger of overheating. They are much smaller than the blue whale, and their metabolic rates are presumably far below

those of similar-sized mammals. Tunnies and other 'warm blooded' fishes owe their elevated body temperatures more to vascular heat exchangers than to their size (Carey 1982). Leatherback turtles (*Dermochelys coriacea*) have metabolic rates intermediate between predictions for reptiles and mammals of their mass, enabling a 400 kg specimen to keep its body 18 K warmer than the water (Paladino *et al.* 1990).

### TERRESTRIAL ANIMALS

(Text-fig. 2)

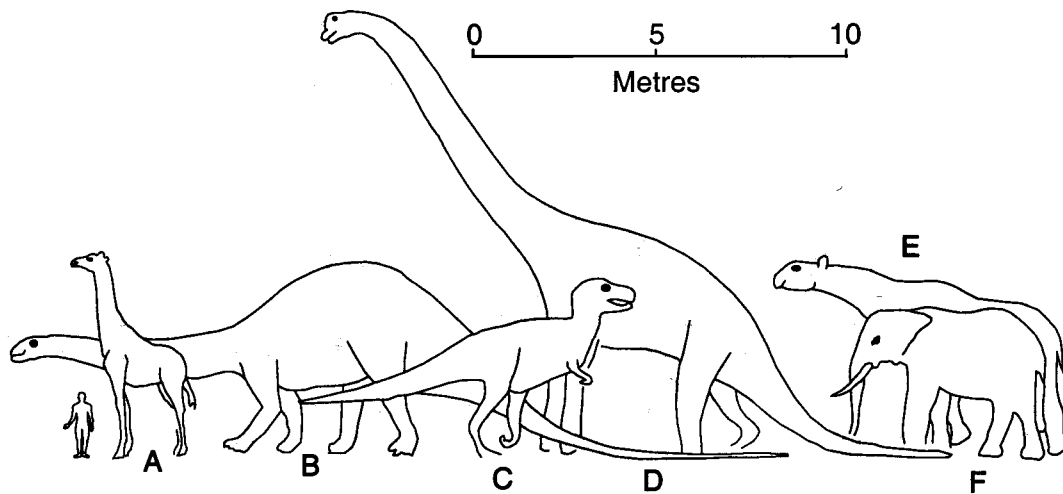
Now I will review and discuss the largest terrestrial animals. Among these, the largest known are sauropod dinosaurs, all of them extinct. The linear dimensions of sauropods are known from skeletons but their masses can only be estimated. This has been attempted in two ways. First, scale models have been made of the animals as they are believed to have appeared in life and their volumes have been determined, preferably by a method that depends on Archimedes' Principle. Then the volume of the living animal has been estimated by scaling up from the model, and the animal's mass calculated by assuming a density in the range observed for related modern animals (see Alexander 1985). Alternatively, the circumferences of fossil leg bones have been used to estimate body mass, by extrapolating from empirical relationships established for modern mammals (Anderson *et al.* 1985). A relationship based on mammals seems appropriate because we know from fossil footprints that dinosaurs did not adopt the sprawling stance of modern reptiles, but walked more like mammals (Thulborn 1990; Lockley 1991).

The largest dinosaur known from a reasonably complete (albeit composite) skeleton is *Brachiosaurus brancai*. It is about 25 m long, measured along the vertebral column (Paul 1988). Its mass has been estimated by both methods, yielding values ranging from 32 to 87 tonnes (Alexander 1989). Paul (1988) and Alexander (1989) both give values of 45–50 tonnes, and these are probably the best estimates. The Chicago skeleton of *B. altithorax* is a little smaller (Paul 1988). Other large sauropods known by more-or-less complete skeletons are *Apatosaurus louisae* (about 35 tonnes according to Alexander 1989, although Paul, who prefers very 'skinny' reconstructions, gives it only half that mass), and *Diplodocus carnegiei* (estimates range from 6 to 19 tonnes).

A few bones are known of sauropods that may have been heavier than *Brachiosaurus*. The bones described as '*Ultrasaurus*' seem to be from large specimens of *B. altithorax* of about 50 tonnes (Paul 1988). '*Supersaurus*' may be a *Diplodocus* species (Paul 1988). Its scapulocoracoid is 2.7 m long, compared with 1.542 m for *Diplodocus carnegiei*. Hence if *D. carnegiei* had a mass of 15 tonnes (within the range of estimates given above) the mass of *Supersaurus* may have been  $15 \times (2700/1542)^3 = 80$  tonnes. The huge femur of *Antarctosaurus* is 2.31 m long, compared with 1.785 m for *Apatosaurus louisae*. If the latter had a body mass of 35 tonnes, geometric scaling suggests a mass for *Antarctosaurus* of  $35 \times (2310/1785)^3 = 75$  tonnes. However, the circumference of the femur is only 0.8 m, suggesting a more slender build and a lower mass (Paul 1988). It has been claimed that *Seismosaurus* may have had a mass of 100 tonnes (Gillette 1994), but the sparse remains (including no limb bones) seem inadequate to support the claim. These data suggest that the heaviest dinosaurs may have been between 50 and 80 tonnes. This is immensely heavier than the largest modern land animal, the African elephant (*Loxodonta africana*: large males are around 5.5 tonnes; Laws 1966). Adult male masses for other very large land mammals include 2.2 tonnes for white rhinoceros (*Ceratotherium simum*), 1.5 tonnes for hippopotamus (*Hippopotamus amphibius*) and 1.2 tonnes for giraffe (*Giraffa camelopardalis*; Owen-Smith 1988).

Although the large dinosaurs were sauropods, several other groups had members that were at least as heavy as any modern terrestrial animals. Mass estimates for herbivores include 5 tonnes for *Iguanodon* and 6 tonnes or more for *Triceratops* (Alexander 1989).

The only terrestrial animals known to have approached the size of the large sauropods are a few gigantic mammals. The largest of these was probably *Indricotherium*, a hornless Oligocene rhinocerotoid which Economos (1981) estimated to have had a mass of 20 tonnes. Others, including myself (Alexander 1989) have suspected it of being even heavier, up to 34 tonnes. However, it now appears that the early restoration on which these mass estimates were based is misleading. A careful



TEXT-FIG. 2. Some of the largest known terrestrial animals, drawn to scale. In the case of extinct animals (asterisked), only those known from reasonably complete skeletons are included. A, *Giraffa*; B, *Apatosaurus*\*; C, *Tyrannosaurus*\*; D, *Brachiosaurus*\*; E, *Indricotherium*\*; and F, *Loxodonta*.

analysis by Fortelius and Kappelman (1993) led to the conclusion that the bones that have been found come from specimens with an average mass of only 11 tonnes and that the largest specimens were probably little more than 15 tonnes. Two species of the related genus *Paraceratherium* were only a little smaller, and Fortelius and Kappelman argued that the largest complete mammoth (*Mammuthus*) skeleton may be from a 14 tonne animal. Other large extinct herbivores include pareiasaurs, dinocephalians and dicynodonts, but these were no larger than the largest modern mammals.

The largest known terrestrial carnivores are much smaller than the sauropods. The best known is *Tyrannosaurus rex*, which was about 12 m long with a mass of about 7 tonnes (Alexander 1989; Farlow *et al.* 1995). Two other theropods, *Giganotosaurus* (Coria and Salgado 1995) and *Carcharodontosaurus* (Sereni *et al.* 1996), may have been a little heavier.

The largest raiisuchids (early archosaurs) attained lengths of 6 m (Benton 1997). Apart from these, and the theropods, there seem to have been no terrestrial carnivores of more than 1 tonne, at any time. The largest modern examples are polar bears (*Ursus maritimus*; adult males are about 500 kg) and Siberian tigers (*Panthera tigris altaica*, about 250 kg; Nowak 1991). The crocodylians have been discussed already, as aquatic carnivores.

The question has often been asked, whether the largest dinosaurs could have supported their weight on land? The alternative would have been for them to have waded in water deep enough to have supported much of their weight by buoyancy. The question arises because for geometrically similar animals made of the same materials, weight increases as the cube of length, but bone and muscle cross sectional areas (and so strength) only in proportion to the square. Therefore, larger animals are expected to be less able to support their own weight.

Evidence that the large sauropods could support their weight on land comes from several sources. First, morphological comparisons with terrestrial mammals such as rhinoceroses and elephants, and with the semiaquatic hippopotamus, favour terrestrial habits (Bakker 1971). Second, many sauropod footprints are more sharply defined than seems consistent with their having been formed under water (Thulborn 1990). Third, the dimensions of leg bones of large sauropods such as *Apatosaurus* indicate that they were amply strong enough to support the animals' estimated weight. Alexander (1985) pointed out that bending moments due to components of force at right angles to

the long axes of bones are more likely to set up dangerous stresses than are axial forces. With that in mind, I defined a 'strength indicator' which expressed the strength in bending of a leg bone (estimated from its dimensions) in relation to the load that the weight of the body would impose on it. If the bones of an extinct animal have strength indicators equal to those of homologous bones of a similarly proportioned modern one, they were strong enough to allow the extinct animal to move in dynamically similar fashion to the modern one. The legs of *Apatosaurus* are quite similar in the relative lengths of the bones to those of the African elephant *Loxodonta*, and homologous leg bones of the two species have very similar strength indicators. This implies that *Apatosaurus* had leg bones strong enough for it to have moved as athletically as elephants, which easily support their weight on land and indeed can run moderately fast, although they cannot jump. Hokkanen (1986) discussed how large a dinosaur could be, and concluded that even a sauropod of well over 100 tonnes could have legs strong enough to support itself on land. Thus sauropod size seems not to have been limited by problems of support.

Another possibility we should consider is that dinosaur size was limited by the danger of overheating. Suppose first, as Bakker (1986) does, that the dinosaurs were endotherms with metabolic rates as estimated by extrapolation for mammals of their mass. We know that whales larger than any known dinosaur survive without overheating, even in the tropics where surface water temperatures may be as high as 27 °C. The effective temperatures of terrestrial habitats (averaged over day and night since we are considering very large animals which will heat and cool slowly) are probably seldom higher than this at the present day. In the Mesozoic, temperatures that we think of as tropical extended to higher latitudes than now, and equatorial temperatures seem to have been a few degrees higher (Hallam 1985).

It seems necessary to explain what I mean by the effective temperature of a habitat. Different parts of the environment (air, ground, vegetation, sky) will be at different temperatures, and heat balance may also be affected by solar radiation. The 'equivalent blackbody temperature' (Campbell 1977) is the temperature at which a body that was not producing heat or evaporating water would reach equilibrium in the environment. By the effective environmental temperature I mean the equivalent blackbody temperature averaged over 24 h. The observation that whales can live in tropical seas suggests that the largest dinosaurs could have avoided overheating at similar effective environmental temperatures on land, even if their metabolic rates were as high as would be predicted for mammals of the same mass. In this argument I have not referred to the difference in heat loss rates in air and in water because, although small animals lose heat much faster in water, the difference is trivial for animals of more than 100 kg (Bell 1980).

In another approach to the problem of overheating, Alexander (1989) considered the heat balance of a brachiosaur with mammal-like metabolism, estimating its rate of loss of heat by extrapolation from Bell's (1980) data on cooling rates for smaller reptiles. I estimated that, unless it dissipated excess heat by evaporation of water, an endothermic brachiosaur would be at least 60 K warmer than its environment, which would be lethal except in extreme cold. Comparison with whales (as in the previous paragraph) suggests that this temperature difference has been overestimated, but even so we must doubt the viability of a brachiosaur with mammal-like metabolism, especially in warm Mesozoic climates, where the quantities of water that would have to evaporate to prevent overheating would be enormous. A more sophisticated analysis by Hokkanen (1989) led to a similar conclusion, that a *Brachiosaurus* with mammal-like metabolism would probably not be viable in a hot climate.

Alexander (1989) also estimated body temperatures for ectothermic brachiosaurs, with metabolic rates as predicted for modern reptiles of equal mass. Unfortunately, my table 7.1 contained arithmetic inconsistency which has been pointed out to me by Dr Brian Bodenbender, to whom I am grateful. Also, my argument was simplistic: it should have taken account of the dependence of a reptile's resting metabolic rate on body temperature. A corrected form of the argument follows.

An animal with body temperature  $T_{\text{body}}$  in an environment at temperature  $T_{\text{env}}$  loses heat at a rate  $(T_{\text{body}} - T_{\text{env}}) C / \tau$ , where  $C$  is the heat capacity of the body and  $\tau$  is the thermal time constant (the quantity given by Bell 1980, for many reptiles). This formula is explained by Alexander (1989). At



equilibrium this heat loss is balanced by metabolic heat production at a rate  $R(m, T_{\text{body}})$ , that is at a rate that depends both on body mass and on body temperature.

$$(T_{\text{body}} - T_{\text{env}}) C/\tau = R(m, T_{\text{body}}),$$

Bennett and Dawson (1976) gave equations relating metabolic rate to body mass, for several groups of reptiles at several temperatures. I will use their equations for lizards, which cover the widest temperature range. These give metabolic rates for a 50 tonne brachiosaur of 770 W at a body temperature of 20 °C, 3270 W at 30 °C and 4840 W at 37 °C. These enable us to estimate the metabolic rate of a brachiosaur with reptile-like metabolism at any likely body temperature.

The specific heat capacity of animal tissue is about 3500 J kg<sup>-1</sup> K<sup>-1</sup>, so a 50 tonne brachiosaur would have a heat capacity  $C$  of 175 MJ K<sup>-1</sup>. We will assume a thermal time constant of  $6 \times 10^5$  s (8 days). This is the shorter of the two estimates given by Alexander (1989; the other was 20 days), and is also shorter than an estimate of 12 days obtained by extrapolation from Loveridge's (1984) data for crocodiles. The shortest estimate has been chosen as the least likely to predict overheating. Thus  $C/\tau$  will be taken to be 300 W/K and a temperature difference ( $T_{\text{body}} - T_{\text{env}}$ ) of 10 K would be needed for equilibrium with a metabolic rate of 3000 W, the rate predicted for a body temperature of 29 °C. This tells us that with no evaporative cooling, a brachiosaur with a body temperature of 29 °C could be at equilibrium in an environment at 19 °C. Similarly, a brachiosaur with a body temperature of 38 °C could be at equilibrium in an environment at 23 °C. It seems unlikely that a brachiosaur with reptile-like metabolism could avoid overheating in hotter climates except by evaporative cooling.

The latent heat of vaporization of water at 30–40 °C is 2.4 MJ kg<sup>-1</sup>, so the whole of the 4840 W produced by a brachiosaur at 37 °C could be dissipated by evaporation of 2 g of water per second, or 170 kg per day. This rate of loss seems entirely feasible; for example, a 3.7 tonne elephant lost 20 kg water per day by evaporation (Benedict 1936). Thus a brachiosaur with reptile-like metabolism could avoid overheating even in the hottest climates, provided it had an adequate water supply.

Thus the size of large dinosaurs may have been limited by the danger of overheating if they had a mammal-like metabolism but not if they had a reptile-like metabolism. Dinosaur metabolic rates have been controversial since Bakker (1972) put the case for endothermy, but most of the points made have been inconclusive. Bakker's most persuasive argument was that endothermic predators need bigger prey populations than ectothermic ones would do, to support their higher metabolic rates. He claimed to show that the ratio of predator to prey biomasses for dinosaur populations indicated endothermy, but Farlow (1976) showed that the evidence was equivocal. Weaver (1983) argued that *Brachiosaurus* could not have had mammal-like metabolism because, with a head of about the same size as that of a one tonne giraffe, it could not have eaten fast enough. If their metabolic rates are proportional to (body mass)<sup>0.75</sup> (see above) a 50 tonne endothermic brachiosaur would need to eat  $50^{0.75} = 19$  times as much food as a 1 tonne giraffe with a similar-sized head. Barrick and Showers (1994) used the ratio of oxygen isotopes in *Tyrannosaurus* bone to argue that this dinosaur had a constant, uniform body temperature, like mammals (but see criticisms in Morell 1994 and Millard 1995). By contrast, Ruben *et al.* (1996) used computed axial tomography to show that the dinosaurs *Nanotyrannus*, *Dromaeosaurus* and *Hypacrosaurus* had no nasal turbinates. These structures are present in both birds and mammals, and serve as heat exchangers, cooling air as it is breathed out and condensing out much of its water vapour. Ruben *et al.* (1996) argued that, without nasal turbinates, endotherms with mammal-like metabolic rates would lose so much heat and water in their breath that endothermy was unlikely; dinosaurs were probably reptile-like in their metabolism.

Whether the dinosaurs had mammal-like or reptile-like metabolic rates, *Indricotherium* was presumably mammal-like. For it, overheating may have been a serious problem.

Another possibility is that dinosaur size was limited by the problem of maintaining a viable population (see Farlow 1993). Terrestrial habitats are more diverse and fragmented than the oceans, so world populations of terrestrial animals cannot be expected to comprise as many individuals as

populations of ocean-living animals of equal body mass. Africa was supporting a population of 1.3 million elephants in 1979 (Nowak 1991). Population densities tend to be proportional to (body mass)<sup>-0.75</sup> (Damuth 1981), with no clear difference between vertebrate ectotherms and endotherms (Peters 1983), so a continent capable of supporting 1.3 million 3 tonne elephants should be adequate to support 150 000 50 tonne brachiosaurs, which would probably be enough for long-term (millions of years) viability.

We have seen that the largest terrestrial carnivores were a great deal smaller than the largest herbivores. Similarly, modern carnivorous mammal species have lower population densities than similar-sized herbivores (Peters and Raelson 1984) and the largest carnivores are much smaller than the largest herbivores.

#### FLYING ANIMALS

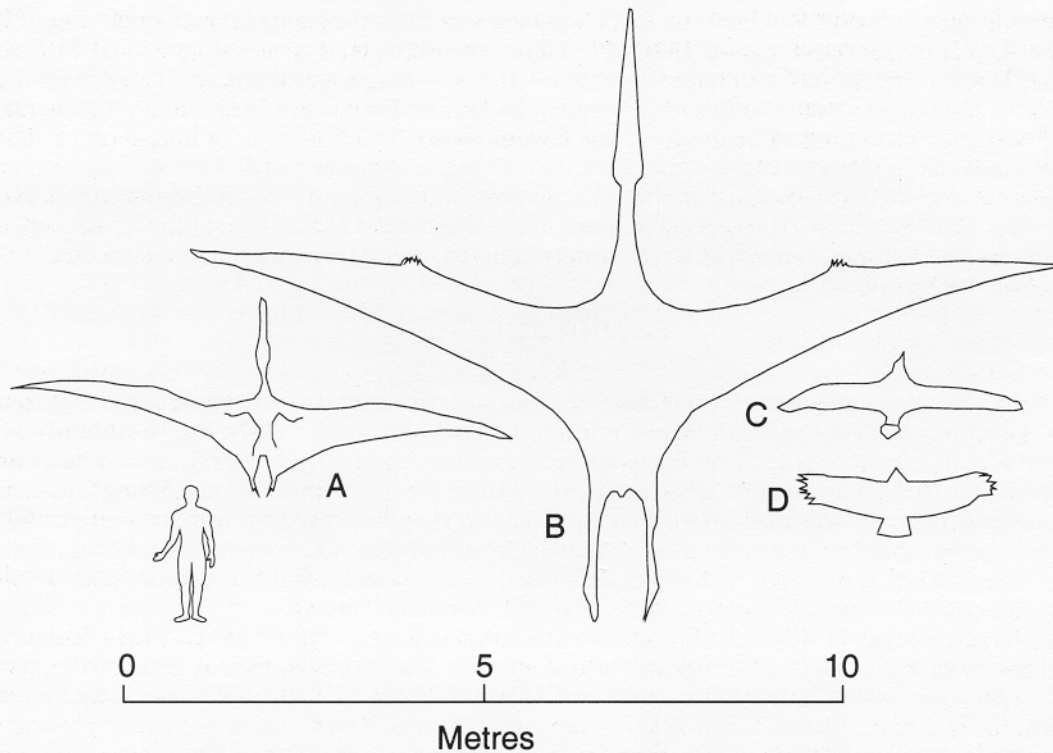
(Text-fig. 3)

Finally, I will review and discuss the largest flying animals. The Kori bustard (*Ardeotis kori*) seems to be the largest modern one, with masses of up to 16 kg (Maloiy *et al.* 1979). It takes off only with difficulty, and often runs instead of flying when approached. The largest albatrosses, vultures and swans all have masses around 10 kg and are much stronger fliers. The wandering albatross, *Diomedea exulans*, spends much of its time airborne, slope soaring over waves (Bevan *et al.* 1995). Vultures spend most of the day airborne, soaring either in thermals (*Gyps* species in Africa; Pennycuik 1972) or over the windward slopes of mountains (*Condor*; Pennycuik and Scholey 1984). By contrast, swans travel by flapping flight rather than soaring.

The largest extinct birds, like the largest modern ones, were plainly flightless; their wings are rudimentary or even absent. The elephant bird *Aepyornis* stood 3 m tall, with an estimated mass of 450 kg (Amadon 1947). The largest known birds with well developed wing skeletons are the vulture-like teratorns (Campbell and Tonni 1983). The largest of these, *Argentavis*, is unfortunately known from only a few bones. Its mass has been estimated from the circumference of the tibiotarsus as 80 kg, five times the mass of the Kori bustard. This estimate is very imprecise, with 95 per cent confidence limits of 37 and 166 kg, but even the lower limit is far heavier than any modern flying bird. If the wing span was in the same proportion to humerus length as in condors, it was about 6 m, far greater than the 2.7 m span of the condor or the largest of all modern spans, the 3.4 m of the wandering albatross.

All known pterosaurs had well developed wing skeletons and could presumably fly. Among them *Pteranodon ingens* is the largest known by a reasonably complete skeleton. Its wing span was 7 m, but it was remarkably lightly built, with an estimated mass of only 15 kg (Brower 1983). This mass was obtained by calculating the volume of the body and multiplying by 900 kg m<sup>-3</sup>, approximately the density of a plucked bird. A larger species, *P. sternbergi*, is estimated to have had a span of 9 m, a typical span for an ultralight aircraft (Frey and Martill 1996). *Quetzalcoatlus northropi* was even larger (Lawson 1975; Langston 1981). Only an incomplete wing skeleton has been found, but there is better material of smaller *Quetzalcoatlus*, either young specimens or a smaller species. The wing span of the large individual must have been about 12 m. If it were geometrically similar to *Pteranodon* (span 7 m) it would have been (12/7)<sup>3</sup> times as heavy, about 75 kg. In fact, the wing skeleton was far from being geometrically similar to that of *Pteranodon* (the phalanges made up a smaller fraction of the span), so this estimate cannot be relied upon. Paul (1991) has estimated the mass of *Quetzalcoatlus northropi* as 250 kg. *Arambourgiania* (known only from a very few bones) may have had a slightly larger span than *Quetzalcoatlus* (Frey and Martill 1996).

Now I will consider whether large animals can be expected to be able to generate the power needed for flight. A simple argument predicts that for geometrically similar aircraft, the power required for flight will be proportional to (mass)<sup>1.17</sup> (see Rayner 1988), but the following argument predicts a lower exponent. Well-designed gliders of all sizes, from small gliders to large passenger-carrying craft, lose height at 0.5–1.0 m s<sup>-1</sup> when gliding at optimum speed (Tucker and Parrott 1970). Thus they lose potential energy at rates proportional to their masses. This is the energy that keeps them airborne, so this observation suggests that the power required for flight is proportional



TEXT-FIG. 3. Some of the largest known flying animals, drawn to a uniform scale. Names of extinct animals are asterisked. A, *Pteranodon ingens*\*; B, *Quetzalcoatlus northropi*\*; C, *Diomedea*; and D, *Condor*.

to  $(\text{mass})^{1.0}$ . Whether power requirements increase in proportion to  $(\text{mass})^{1.17}$  or to  $(\text{mass})^{1.0}$ , they increase faster than available metabolic power, which is expected to increase only in proportion to  $(\text{mass})^{0.75}$ . Thus large flying animals will have less power in reserve, and there must be an upper limit to the mass of flying animals.

A glider sinking at  $0.5 \text{ m s}^{-1}$  is losing potential energy at a rate of  $5 \text{ W kg}^{-1}$  of body mass. To do work at this rate, muscles operating at the expected efficiency of about 25 per cent. (Åstrand and Rodahl 1986) would have to use metabolic energy at a rate of  $20 \text{ W kg}^{-1}$  body mass. The maximum metabolic rates (calculated from oxygen consumption) of human endurance athletes are also about  $20 \text{ W kg}^{-1}$  (Åstrand and Rodahl 1986), suggesting that a man-sized bird such as *Argentavis* might be just able to fly. Confirmation of this seems to be provided by the *Gossamer Albatross*, an ultra-light propeller-driven aircraft powered by a pedalling athlete which flew successfully across the English Channel in 1979 (MacCready 1995). Some animals are much better endurance athletes than humans; maximum metabolic rates of  $40 \text{ W kg}^{-1}$  have been recorded for 500 kg horses, and a remarkable  $100 \text{ W kg}^{-1}$  for the pronghorn antelope (*Antilocapra americana*; mass about 32 kg; Lindstedt *et al.* 1991). Thus animals even larger than *Argentavis* and *Quetzalcoatlus* might well be able to produce enough power for flight.

A flying bird (or pterosaur) probably needs some capacity for powered flight, but most very large birds (albatrosses, vultures, etc.) spend most of their airborne time soaring. The success of man-made gliders serves as evidence that craft much larger than *Argentavis* and *Quetzalcoatlus* can soar successfully, both in thermals and on the windward sides of slopes.

There remains the question of whether such large animals could take off. Small birds can take off simply by jumping from the ground, hovering to keep themselves airborne, and then building up

speed. Simple helicopter theory tells us that the power needed for hovering is much greater than for forward flight and (for geometrically similar craft) increases in proportion to (mass)<sup>1.17</sup> (Alexander 1982). Therefore, large birds cannot hover, even to take off. They may take off by diving from a high perch, but to take off from level ground they often have to run like taxiing aircraft, as bustards and vultures do. Similarly, swans run over the surface of water to take off.

The speed that a taxiing aircraft must reach, to take off, is the least speed at which the wings can provide enough lift to support it. It should correspond to the minimum gliding speed, which is between 5 and 10 m s<sup>-1</sup> for various birds and a bat (Alexander 1982). Thus, animals that rely on running to take off may have to run moderately fast. The minimum speed is proportional to the square root of wing loading (that is, of body weight divided by wing area; Alexander 1982). It will generally be larger for larger animals because wing area is proportional only to (mass)<sup>0.67</sup>, in geometrically similar animals.

*Pteranodon* is the largest flying animal for which wing loading, and so take-off speed, can be estimated with any confidence. Even in this case there is considerable uncertainty; the mass estimate may be inaccurate, and there has been controversy about the area of the wings. Estimates for a *Pteranodon* of 7 m span range from 2.1 to 4.6 m<sup>2</sup> (Hazlehurst and Rayner 1992). Alexander (1994) argued on the basis of Unwin and Bakhurina's (1994) interpretation of the shape of pterosaur wings that an intermediate value, perhaps 3.4 m<sup>2</sup>, was likely. If we accept this together with Brower's (1983) mass of 15 kg, and assume a maximum lift coefficient of 1.5, Brower's equation 2 gives a minimum speed of only 7 m s<sup>-1</sup>. It seems unlikely that *Pteranodon* could run as fast as this (it is about the speed of a men's 1500 m race), but if the wind were blowing at 7 m s<sup>-1</sup> or faster (a moderate breeze) it could take off simply by facing into the wind and spreading its wings. This depends on its wings being remarkably large for its weight; its estimated wing loading of 43 N m<sup>-2</sup> is much lower than those of the largest albatrosses and vultures (about 170 and 100 N m<sup>-2</sup>, respectively; Brower 1983).

*Quetzalcoatlus* is estimated to have had 1.7 times the span of *Pteranodon*, so if it had the same aspect ratio its wing area was 1.7<sup>2</sup> times that of *Pteranodon*, and can be estimated as 10 m<sup>2</sup>. A 75 kg *Quetzalcoatlus* with this wing area would have had a wing loading of 74 N m<sup>-2</sup>, still a little lower than those of the largest vultures. That does not necessarily mean that it could have taken off as easily as a vulture; its enormous wings must have been difficult to manage, while it was still on the ground. If, however, it had the 250 kg mass estimated by Paul (1991), its wing loading would have been 245 N m<sup>-2</sup>, considerably higher than for albatrosses. Its minimum speed would then have been about 16 m s<sup>-1</sup>, in the speed range of galloping racehorses. *Argentavis* is estimated to have had double the span, four times the wing area and eight times the mass of a large vulture. This would give it twice the wing loading of a vulture and 2<sup>0.5</sup> = 1.4 times the take-off speed. The problem of taking off may well have set the upper limit to the size of flying animals.

## CONCLUSIONS

It is tempting to look for limits to the range of animal sizes and then to ask whether animals have ever reached them, and if not why not. That approach seems misguided for two reasons. First, all postulated limits depend on assumptions based on extant animals which may be false for extinct ones. For example, the metabolic rate of an unknown or extinct large animal may not be as predicted by allometric equations based on modern animals. Second, the evolution of larger animals will not necessarily occur whenever larger animals are possible; it will occur only when larger animals are favoured by natural selection. Very large animals may fail to evolve because their movements would be cumbersome, or because their activity would be constrained by the precautions they would have to take to avoid overheating, or for some other reason, even if they would be capable of life in the absence of competition. This paper does not show that larger animals than have evolved would be physically impossible, but it does suggest reasons why they might have been at a disadvantage.

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