Growth Evolution in Dinosaurs

- causes and consequences -

Marcus Clauss

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Vetsuisse Faculty, University of Zurich, Switzerland

Bruxelles 18.10.2019

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Research Unit 533 Sauropod Biology
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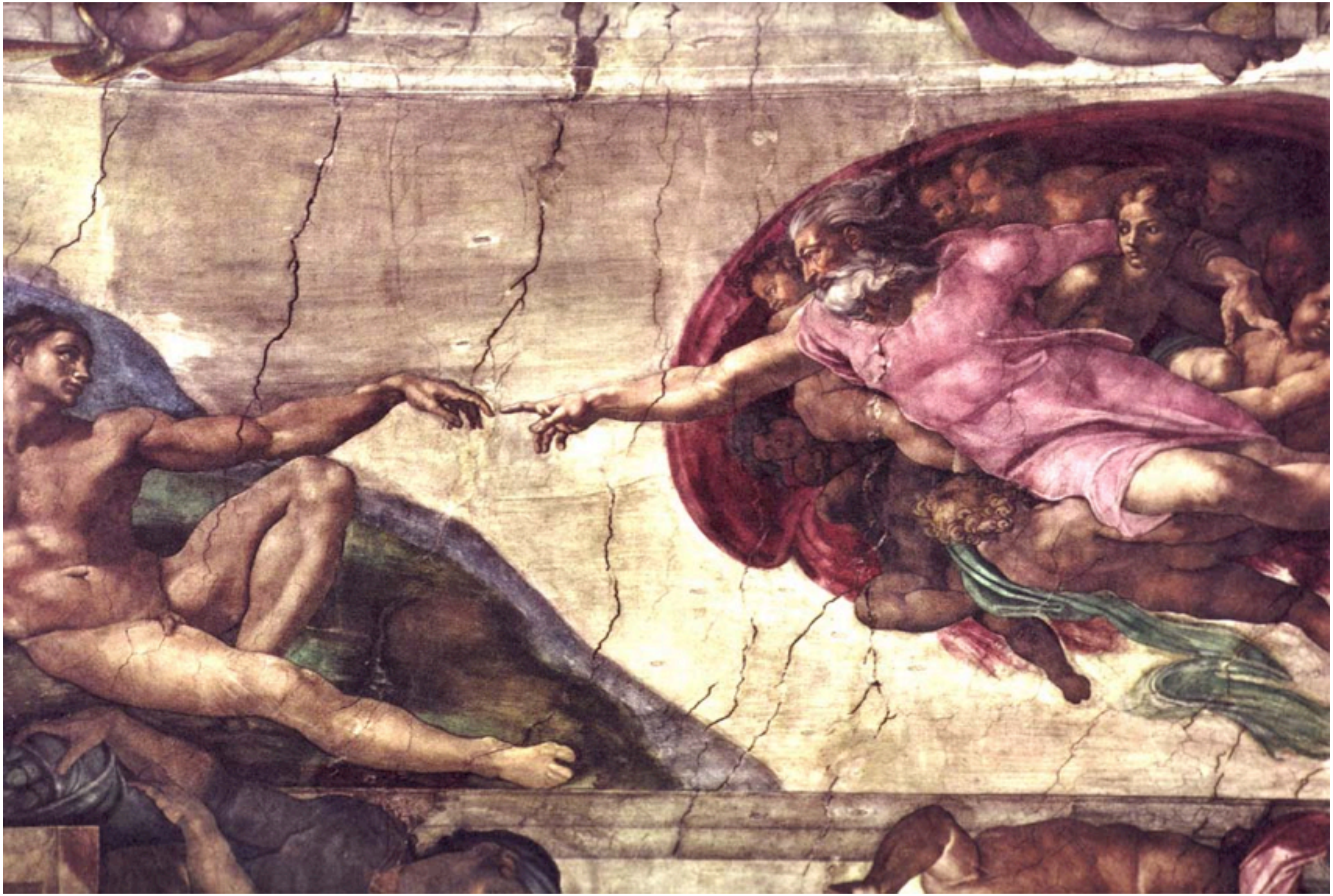
better late than never
SAUROPOD NUTRITION SQUAD

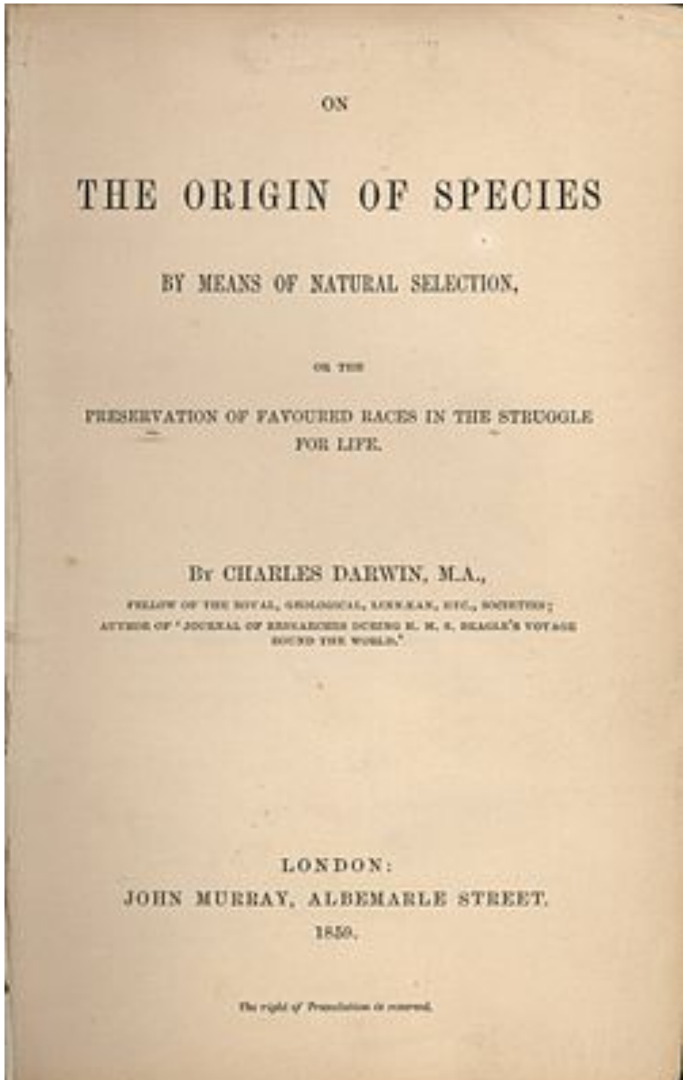
What is your story ?

Storytellers: competing for scope

The greatest story ever told



The greatest story ever told



ON

THE ORIGIN OF SPECIES

BY MEANS OF NATURAL SELECTION,

OR THE

PRESERVATION OF FAVOURED RACES IN THE STRUGGLE FOR LIFE.

BY CHARLES DARWIN, M.A.,

FELLOW OF THE ROYAL, GEOLOGICAL, LINNÆAN, ETC., SOCIETIES;
AUTHOR OF 'JOURNAL OF RESEARCHES DURING H. M. S. BEAGLE'S VOYAGE ROUND THE WORLD.'

LONDON:
JOHN MURRAY, ALBEMARLE STREET.
1859.

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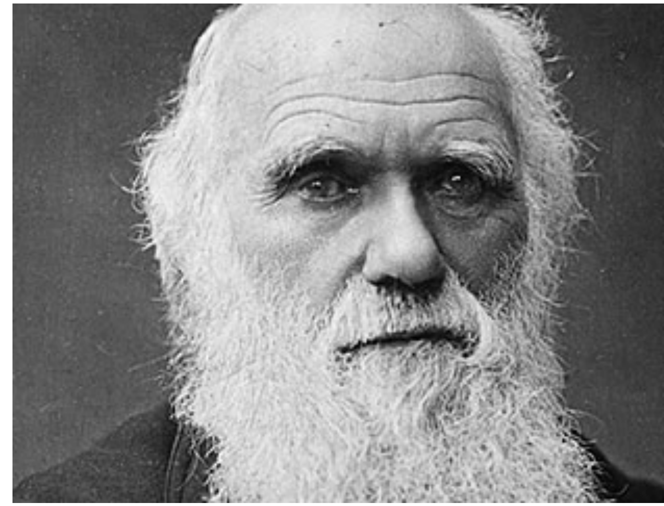
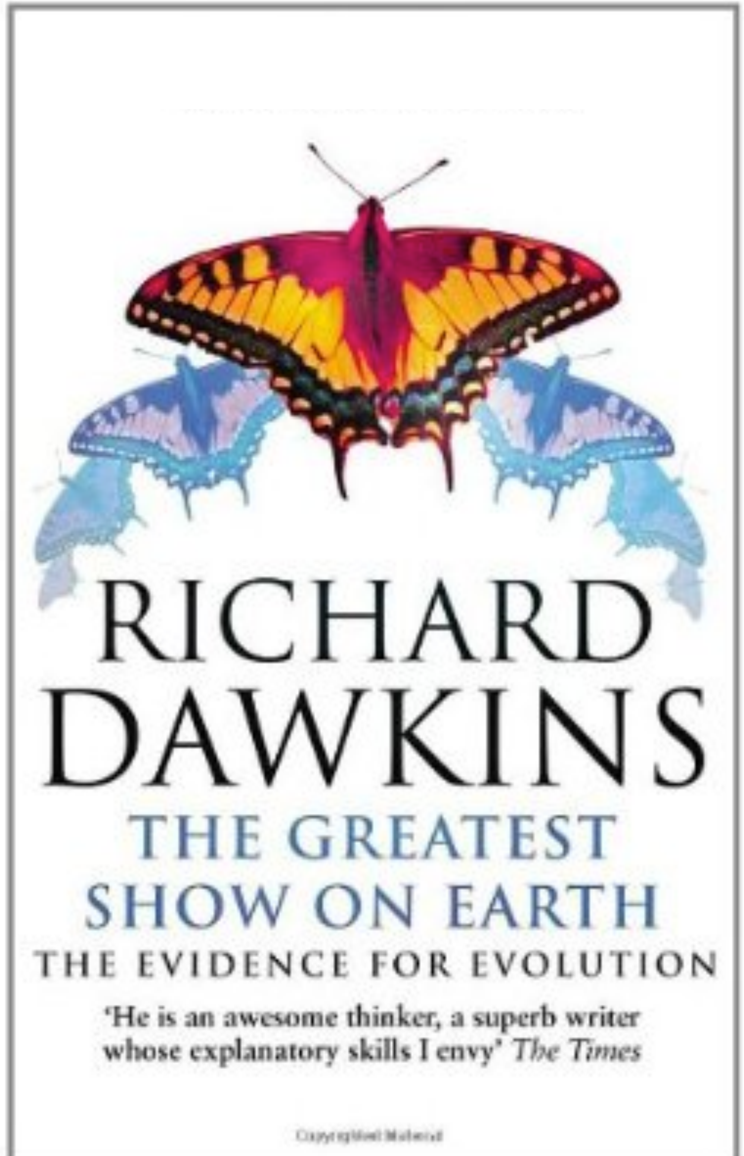
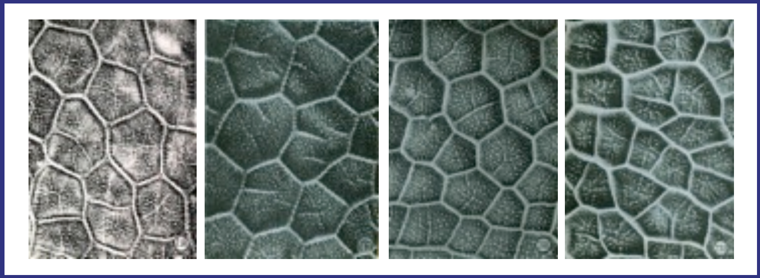


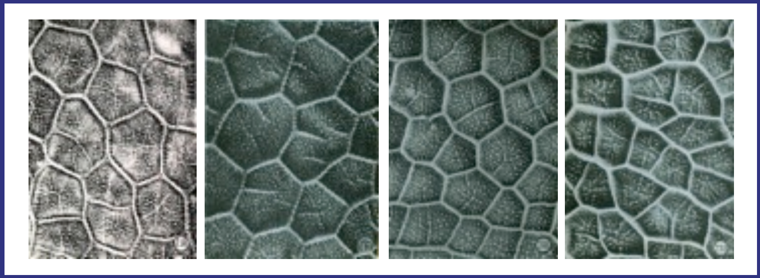
The greatest story ever told





from Hofmann (1969 & 1973)

Why does the depth of the reticular honeycomb pattern vary among different ruminant species?



from Hofmann (1969 & 1973)

from Hofmann (1969 & 1973)

How did dinosaurs become so large?

Why did dinosaurs become so large?

Why did dinosaurs die out?

PALEONTOLOGY

Sauropod Gigantism

How did sauropod dinosaurs reach body sizes that remain unsurpassed in land-living animals?

P. Martin Sander[1] and Marcus Clauss[2]

Sauropod dinosaurs were the largest animals ever to inhabit the land (see the figure). At estimated maximum body masses of 50 to 80 metric tons, they surpassed the largest terrestrial mammals and nonsauropod dinosaurs by an order of magnitude. With body lengths of more than 40 m and heights of more than 17 m, their linear dimensions also remain unique in the animal kingdom. From their beginnings in the Late Triassic (about 210 million years ago), sauropods diversified into about 120 known genera. They dominated ecosystems for more than 100 million years from the Middle Jurassic to the end of the Cretaceous, setting a record that mammalian herbivores will only match if they can double their current geological survival time. Thus, sauropods were not only gigantic but also, in evolutionary terms, very successful. Recent advances bring us closer to understanding the enigma of their gigantism (*1*–*3*).

Extrinsic causes have repeatedly been advanced to explain the success of sauropod dinosaurs and the gigantism seen in the dinosaur era. However, physical and chemical conditions in the Mesozoic (250 to 65 million years ago) were probably less favorable for plant and animal life than they are today; for example, atmospheric O_2 concentrations were much lower (*4*). The variation of other factors (such as land mass size, ambient temperature, and atmospheric CO_2 concentrations) through time is not tracked by variations in sauropod body size (*2*, *5*). Thus, the clue to sauropod gigantism must lie in their unusual biology (see the figure).

Sauropods had an elephantine body supported by four columnar legs and ending in a long tail. From the body arose a long neck bearing a small skull. Sauropods exhibit diverse oral, dental, and neck designs, indicating dietary niche differentiation; this variety makes reliance on any particular food source (*6*) as the reason for gigantism unlikely. However, one evolutionarily primitive character truly sets sauropods apart: In contrast to mammals and advanced bird-hipped dinosaurs (duck-billed and horned dinosaurs), they did not masticate their food; nor did they grind it in a gastric mill, as did some other herbivorous dinosaurs (*7*). Because gut capacity increases with body mass (*8*), the enormous gut capacity of sauropods would have guaranteed the long digestion times (*6*) necessary for degrading unchewed plant parts, even at a relatively high food intake.

The lack of a masticatory apparatus allowed sauropod heads to remain small and was one prerequisite for their long neck to

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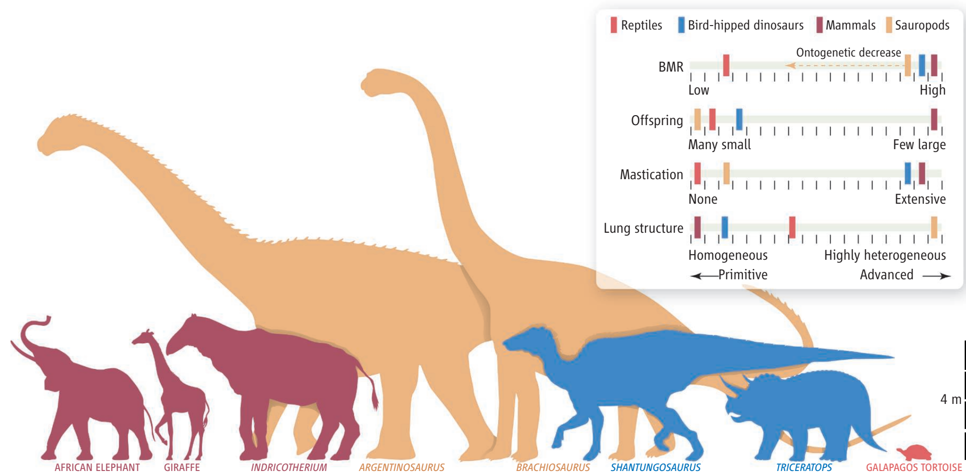

Toward understanding sauropod dinosaur gigantism. The sauropod dinosaurs *Brachiosaurus* and *Argentinosaurus* were much larger than the largest bird-hipped dinosaurs *Shantungosaurus* and *Triceratops*, the fossil rhinoceros *Indricotherium* (the largest known land mammal), the African elephant, the giraffe, and the Galapagos tortoise (the largest living herbivorous reptile). (**Inset**) The main biological properties that control the upper limits of body size in terrestrial herbivores—sauropod dinosaurs, bird-hipped dinosaurs, mammals, and ectothermic herbivorous reptiles—are visualized as sliders, with the evolutionarily primitive state to the left and the advanced state to the right. The slider position for each herbivore group (color-coded to match the images) indicates the specific combination of primitive and advanced states that led to the maximal body size of this group. The unique gigantism of sauropod dinosaurs was made possible by a high basal metabolic rate (BMR, advanced), many small offspring (primitive), no mastication (primitive), and a highly heterogeneous lung (advanced). We hypothesize that ontogenetic flexibility of BMR was also important.

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Biology of the sauropod dinosaurs: the evolution of gigantism

P. Martin Sander[1], Andreas Christian[2], Marcus Clauss[3], Regina Fechner[4], Carole T. Gee[1], Eva-Maria Griebeler[5], Hanns-Christian Gunga[6], Jürgen Hummel[7], Heinrich Mallison[8], Steven F. Perry[9], Holger Preuschoft[10], Oliver W. M. Rauhut[4], Kristian Remes[1,4], Thomas Tütken[11], Oliver Wings[8] and Ulrich Witzel[12]

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ABSTRACT

The herbivorous sauropod dinosaurs of the Jurassic and Cretaceous periods were the largest terrestrial animals ever, surpassing the largest herbivorous mammals by an order of magnitude in body mass. Several evolutionary lineages among Sauropoda produced giants with body masses in excess of 50 metric tonnes by conservative estimates. With body mass increase driven by the selective advantages of large body size, animal lineages will increase in body size until they reach the limit determined by the interplay of bauplan, biology, and resource availability. There is no evidence, however, that resource availability and global physicochemical parameters were different enough in the Mesozoic to have led to sauropod gigantism.

We review the biology of sauropod dinosaurs in detail and posit that sauropod gigantism was made possible by a specific combination of plesiomorphic characters (phylogenetic heritage) and evolutionary innovations at different levels which triggered a remarkable evolutionary cascade. Of these key innovations, the most important probably was the very long neck, the most conspicuous feature of the sauropod bauplan. Compared to other herbivores, the long neck allowed more efficient food uptake than in other large herbivores by covering a much larger feeding envelope and making food accessible that was out of the reach of other herbivores. Sauropods thus must have been able to take up more energy from their environment than other herbivores.

The long neck, in turn, could only evolve because of the small head and the extensive pneumatization of the sauropod axial skeleton, lightening the neck. The small head was possible because food was ingested without mastication. Both mastication and a gastric mill would have limited food uptake rate. Scaling relationships between gastrointestinal tract size and basal metabolic rate (BMR) suggest that sauropods compensated for the lack of particle reduction with long retention times, even at high uptake rates.

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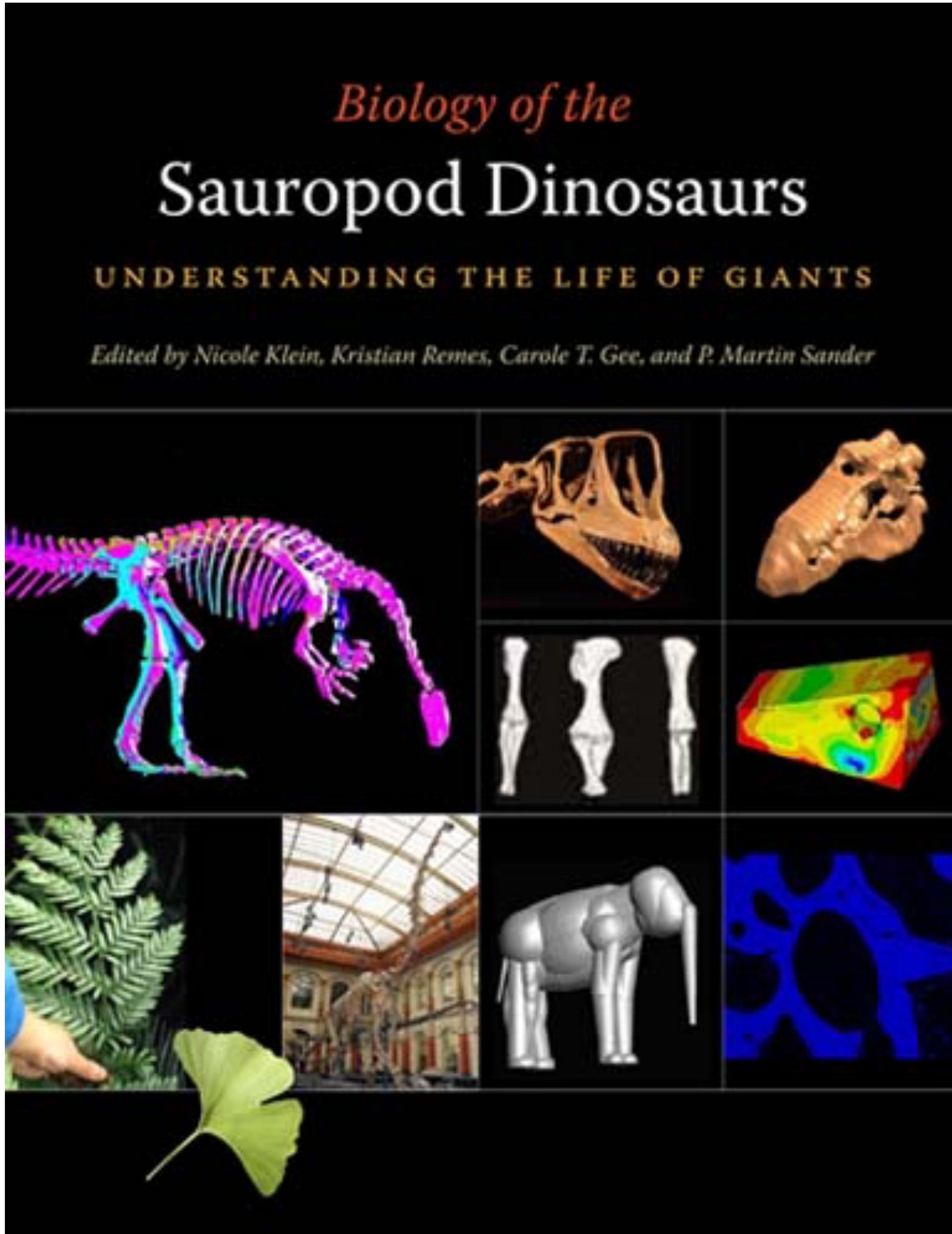
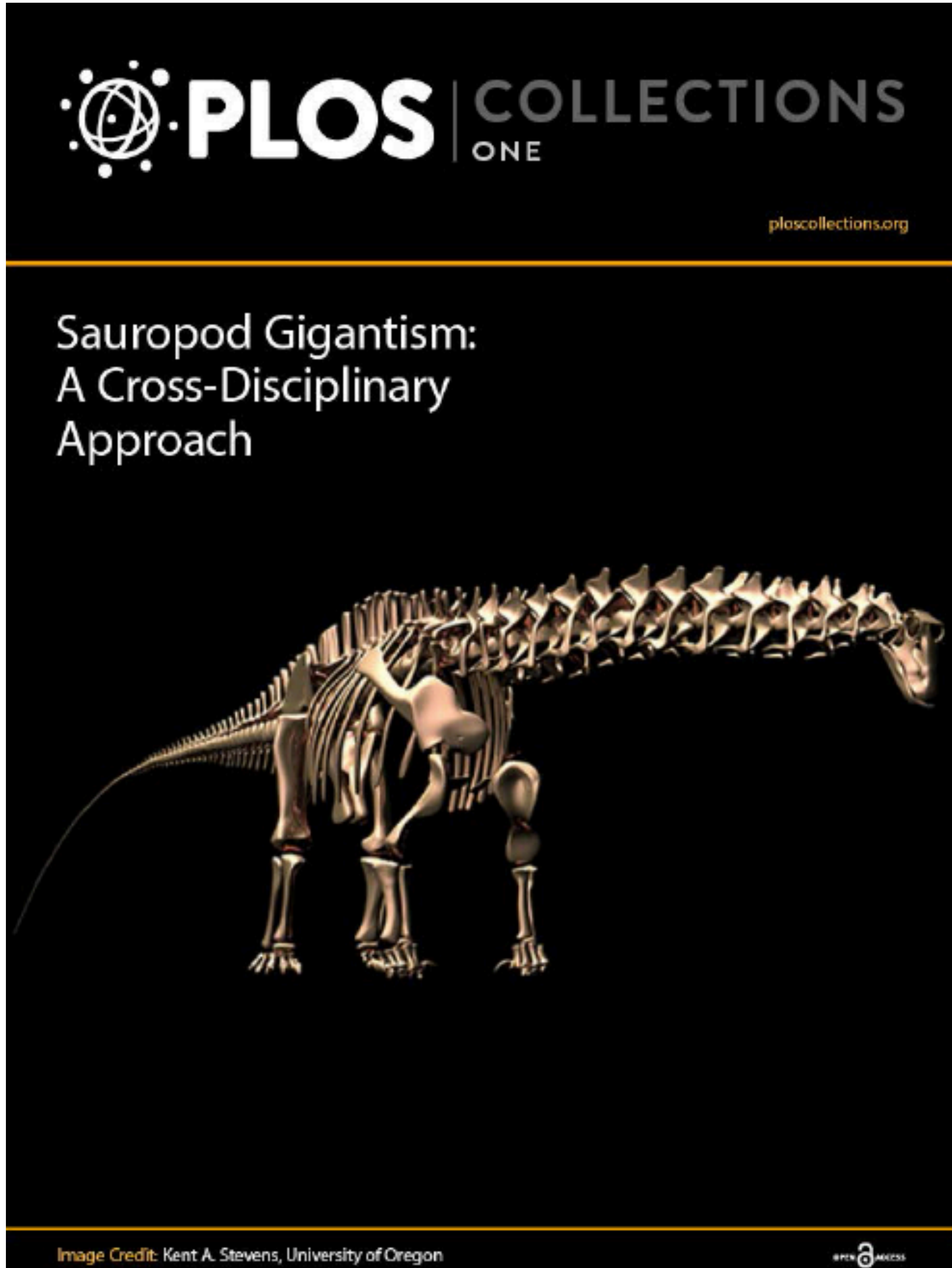

Biology of the
Sauropod Dinosaurs
UNDERSTANDING THE LIFE OF GIANTS
Edited by Nicole Klein, Kristian Remes, Carole T. Gee, and P. Martin Sander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Sauropod Gigantism:
A Cross-Disciplinary
Approach
Image Credit: Kent A. Stevens, University of Oregon

biology letters
Evolutionary biology

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Ontogenetic niche shifts in dinosaurs influenced size, diversity and extinction in terrestrial vertebrates

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Given the physiological limits to egg size, large-bodied non-avian dinosaurs experienced some of the most extreme shifts in size during post-natal ontogeny found in terrestrial vertebrate systems. In contrast, mammals—the other dominant vertebrate group since the Mesozoic—have less complex ontogenies. Here, we develop a model that quantifies the impact of size-specific interspecies competition on abundances of differently sized dinosaurs and mammals, taking into account the extended niche breadth realized during ontogeny among large oviparous species. Our model predicts low diversity at intermediate size classes (between approx. 1 and 1000 kg), consistent with observed diversity distributions of dinosaurs, and of Mesozoic land vertebrates in general. It also provides a mechanism—based on an understanding of different ecological and evolutionary constraints across vertebrate groups—that explains how mammals and birds, but not dinosaurs, were able to persist beyond the Cretaceous–Tertiary (K–T) boundary, and how post-K–T mammals were able to diversify into larger size categories.

Keywords: allometry; body mass; Mesozoic vertebrates; size-specific competition

1. INTRODUCTION

Dinosaurs and mammals have successively dominated terrestrial life for more than 200 Myr. Yet, they differ in the most fundamental biological trait—reproduction, with dinosaurs being oviparous, and mammals viviparous. A peculiar constraint on oviparous taxa is that offspring (total clutch sizes) are very small relative to adults (compared with similar-sized viviparous taxa) [1,2]. This occurs because of upper limits to eggshell thickness (the shell must be sufficiently thin to allow gaseous exchange) [3,4]. Not surprisingly, scaling exponents from adult–neonate mass allometries are lower among extant herpetofauna and birds (approx. 0.4–0.7) than mammals (approx. 0.8–1) (reviewed in [5]). Among extinct dinosaurs, the adult-to-neonate mass ratio estimated for a approximately 4 tonne titanosaur was 2500 : 1, over two orders of magnitude greater than that of the Asian elephant, *Elephas maximus* [1].

Thus, dinosaurs have more complex ontogenetic life histories than similar-sized mammals, implying more extensive ecological niche shifts through their development [6]. Previously, it was hypothesized that the ability of dinosaurs to disperse into a wider variety of niches, coupled with higher reproductive rates [7], meant their populations were more resilient to environmental perturbations, which played a large part in their dominance of terrestrial life for *ca* 180 Myr [2].

However, wider intraspecific niche breadths imply more interspecific niche overlaps, hence greater potential for competition [6]. This competition should be especially pronounced in assemblages comprising very large taxa, whose offspring are considerably smaller than the adults. Here, we develop a simple, deterministic model to explore the influence of size-specific competition on populations of differently sized dinosaurs and mammals, and its implications for body size distributions of the dominant terrestrial vertebrate groups of the Mesozoic and Cenozoic.

2. MATERIAL AND METHODS

Our simulated dinosaur assemblage comprises species from 27 size categories (populations), from $\log_2 M = -9$ to 17 (approx. 2 g to 131 tonnes). Our mammal assemblage comprises 24 categories (up to $\log_2 M = 14$, approx. 16 tonnes). These ranges represent the smallest and largest estimated body masses of extinct dinosaurs and mammals, respectively [8,9]. Each population was structured according to size classes of $\log_2 M$ increments from neonate to adult, where $M_{neonate}$ was estimated from M_{adult} using allometric equations (scaling exponents are 0.6 for dinosaurs, and 0.9 for mammals; see above). Taking into account inter- and intraspecific allometric effects on size-specific mortality, reproductive output [5] and abundance [10] (see electronic supplementary material, part A), our model estimates changes in population abundances owing to competition-induced mortalities among similarly sized individuals. Competition is strictly interspecific, in that abundances of each mass class are reduced by the frequency occurrence of that class among other populations in the assemblage, weighted by the Lotka–Volterra competition coefficient α. Values for α are non-empirical, simply reflecting the number of individuals of a mass class assumed to die owing to competition from one other individual of that class. We defined unique α values for interactions among dinosaurs (α_{DD}) or mammals (α_{MM}), and among each other (α_{DM} and α_{MD}). Finally, we explore implications of a mass extinction event, such as that occurred at the Cretaceous–Tertiary (K–T) boundary, which primarily affected large-bodied land animals [11,12]. To mimic the K–T, we set initial conditions to exclude all individuals larger than an arbitrary mass threshold of 25 kg.

3. RESULTS

The ecological relevance of relatively small offspring in dinosaurs is most pronounced among larger mass classes. Around the mass range where increases in dinosaur M_{adult} no longer result in major increases in $M_{neonate}$, simulated populations include substantially more ontogenetic niche steps, and interspecific size (niche) overlaps, compared with similarly sized mammals (see electronic supplementary material, figure S2). The impact on model outcomes is clear: while species abundances decrease steadily with increases in M_{adult} (figure 1*a*), size-specific competition (positive α_{DD}) reduces population abundances of intermediate-sized

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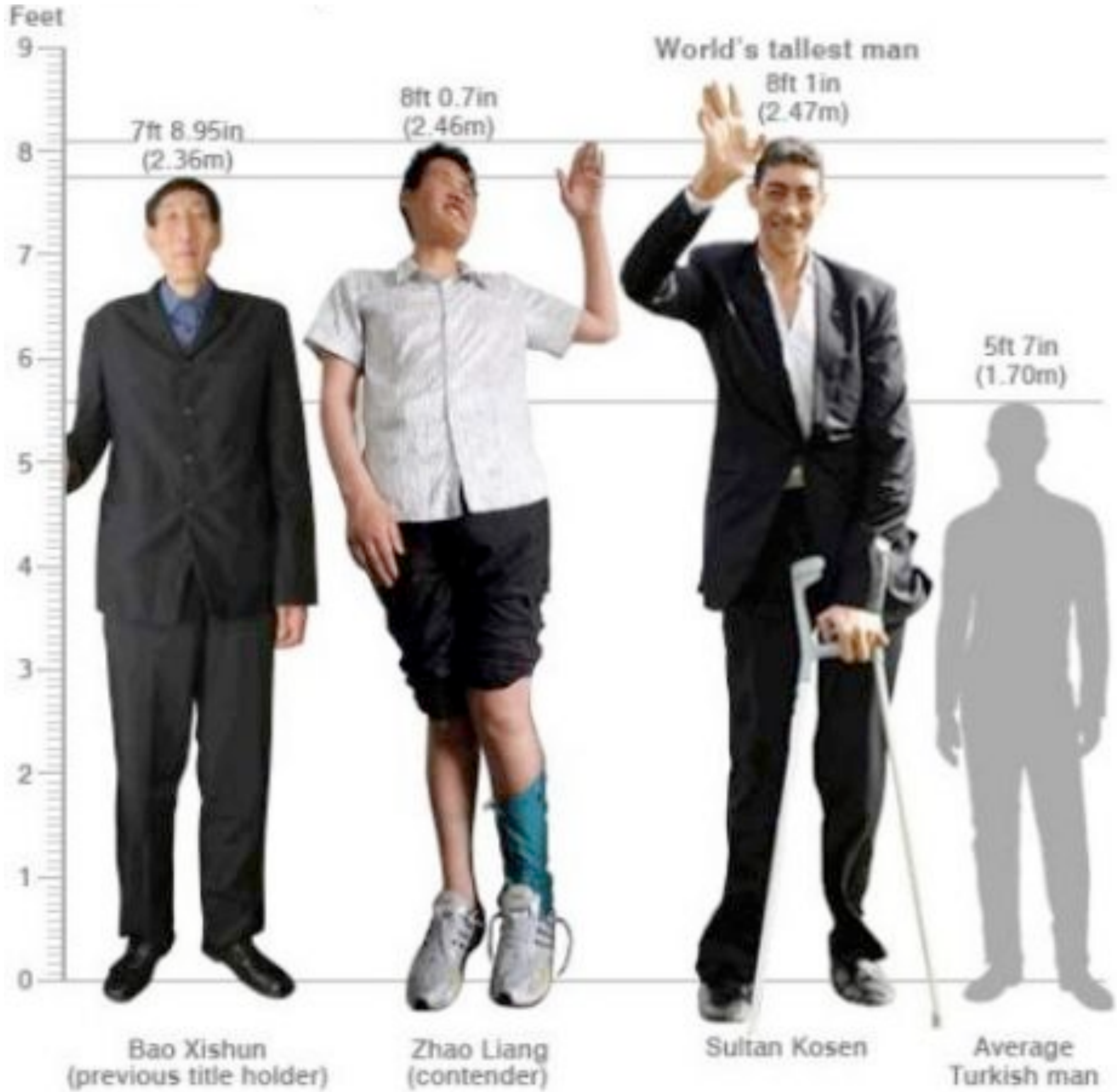
Gigantism


Feet
9
8
7
6
5
4
3
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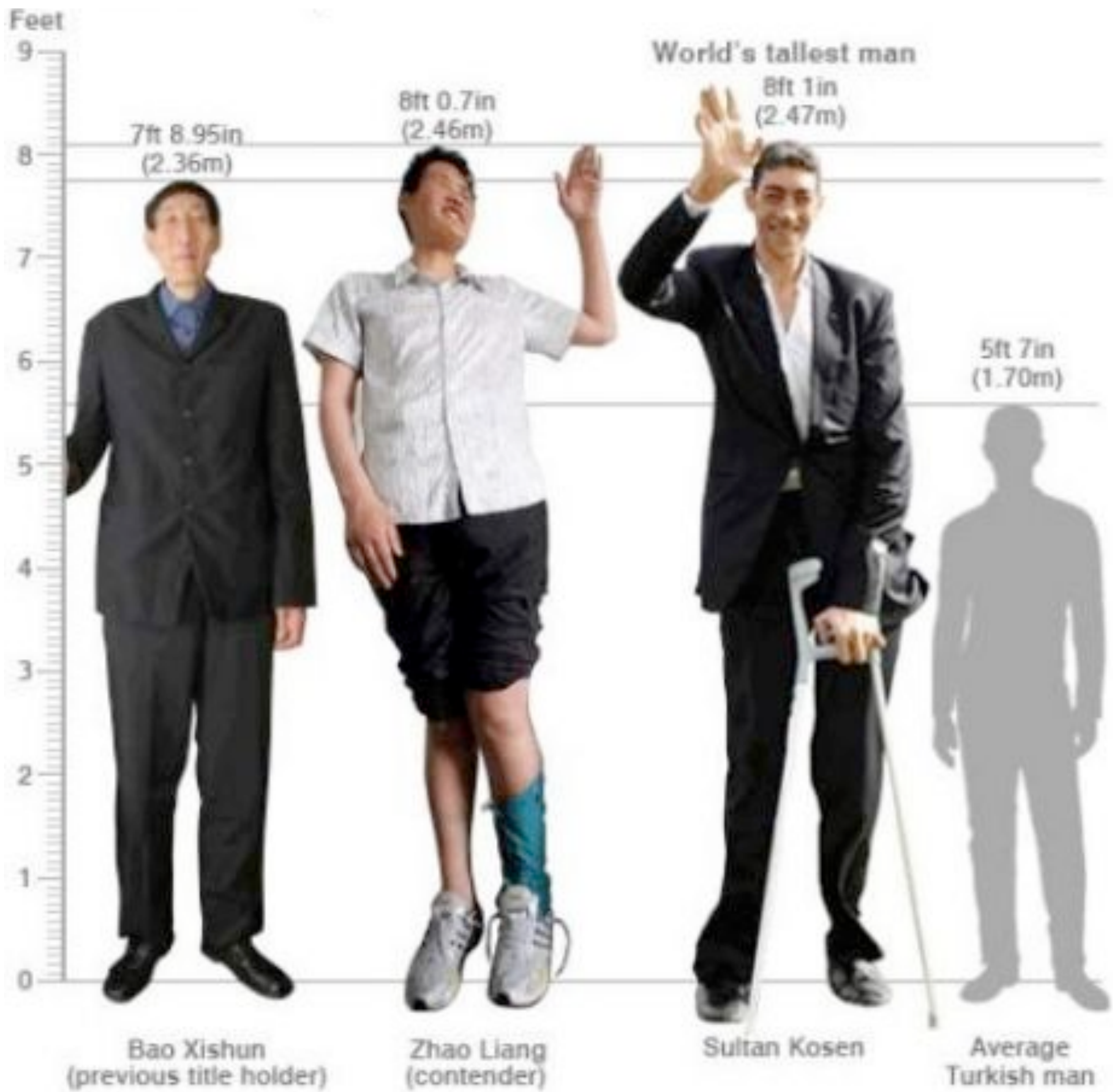
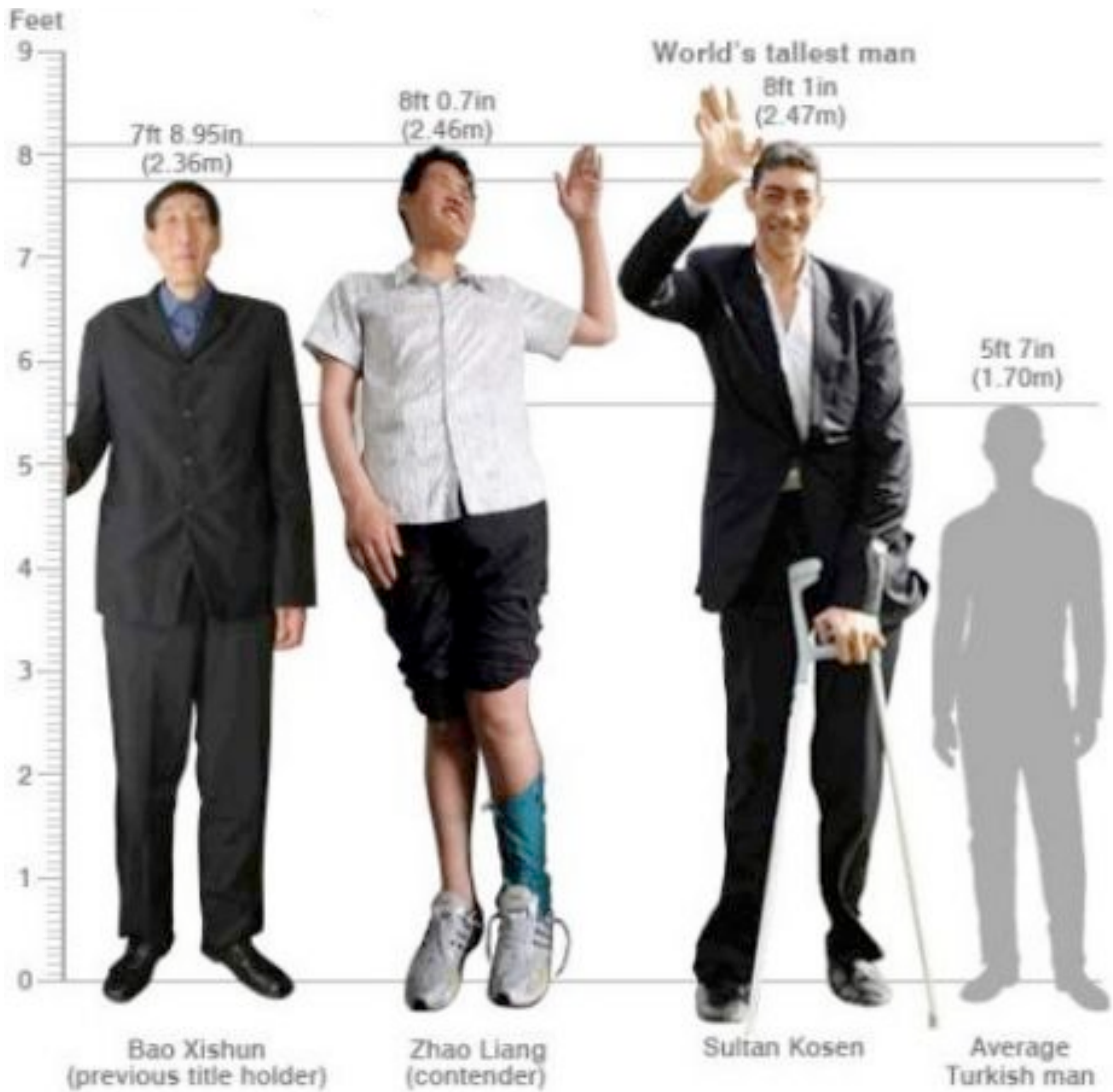
World's tallest man
7ft 8.95in
(2.36m)
8ft 0.7in
(2.46m)
8ft 1in
(2.47m)
5ft 7in
(1.70m)
Bao Xishun
(previous title holder)
Zhao Liang
(contender)
Sultan Kosen
Average
Turkish man

Gigantism



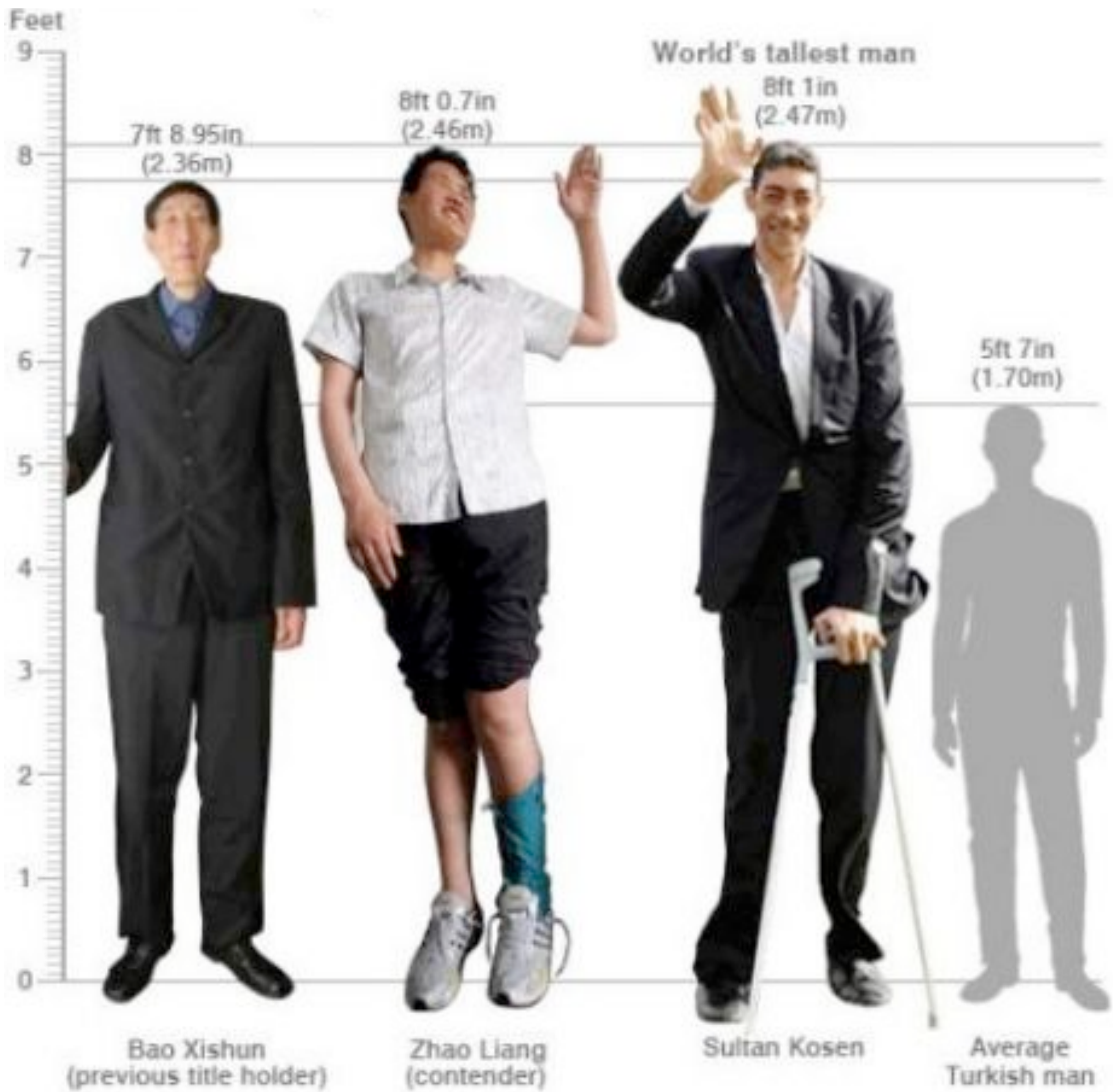
- etiopathology (endocrinology)

Gigantism



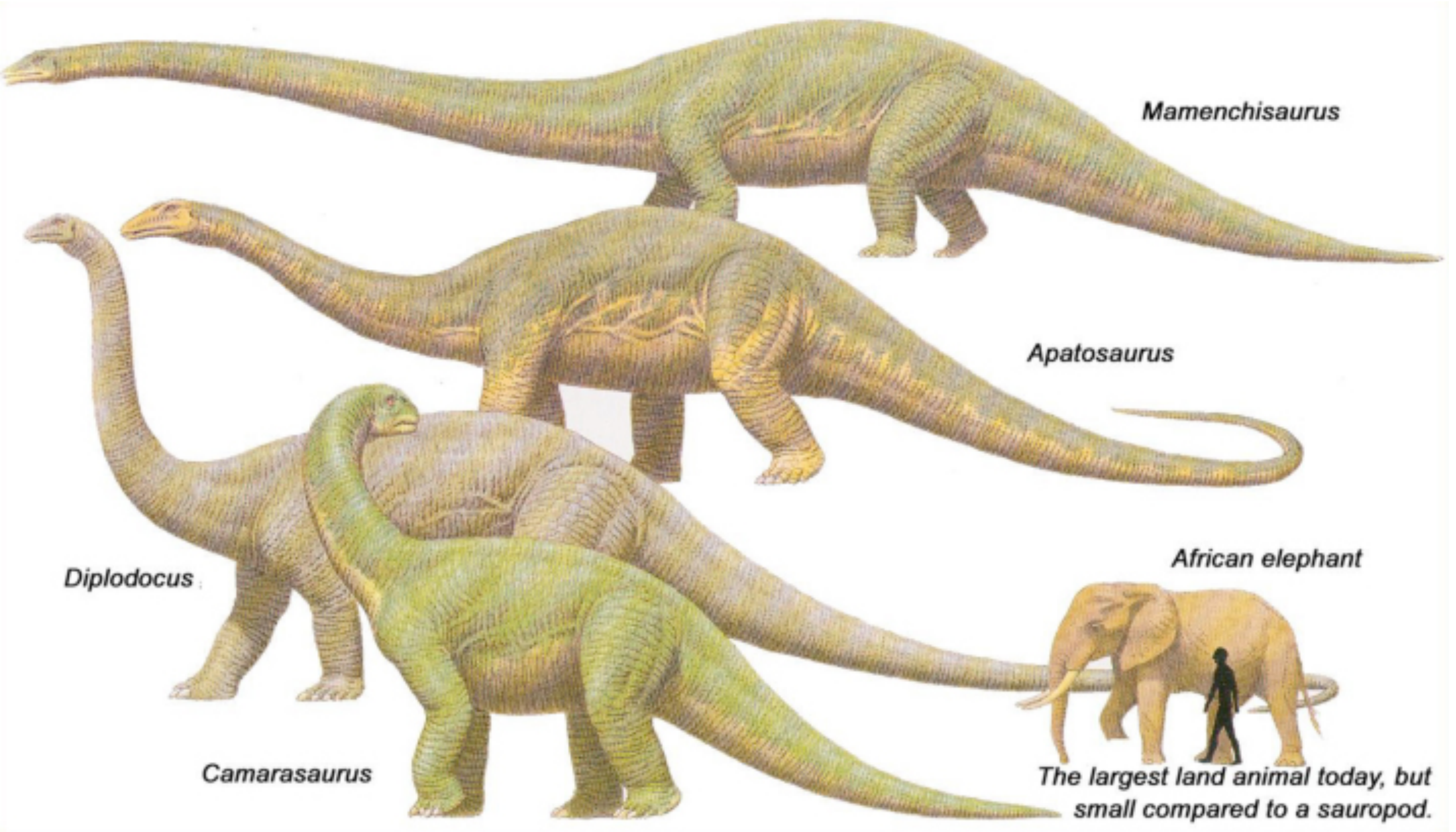
- etiopathology (endocrinology)
- physiological consequences

Gigantism



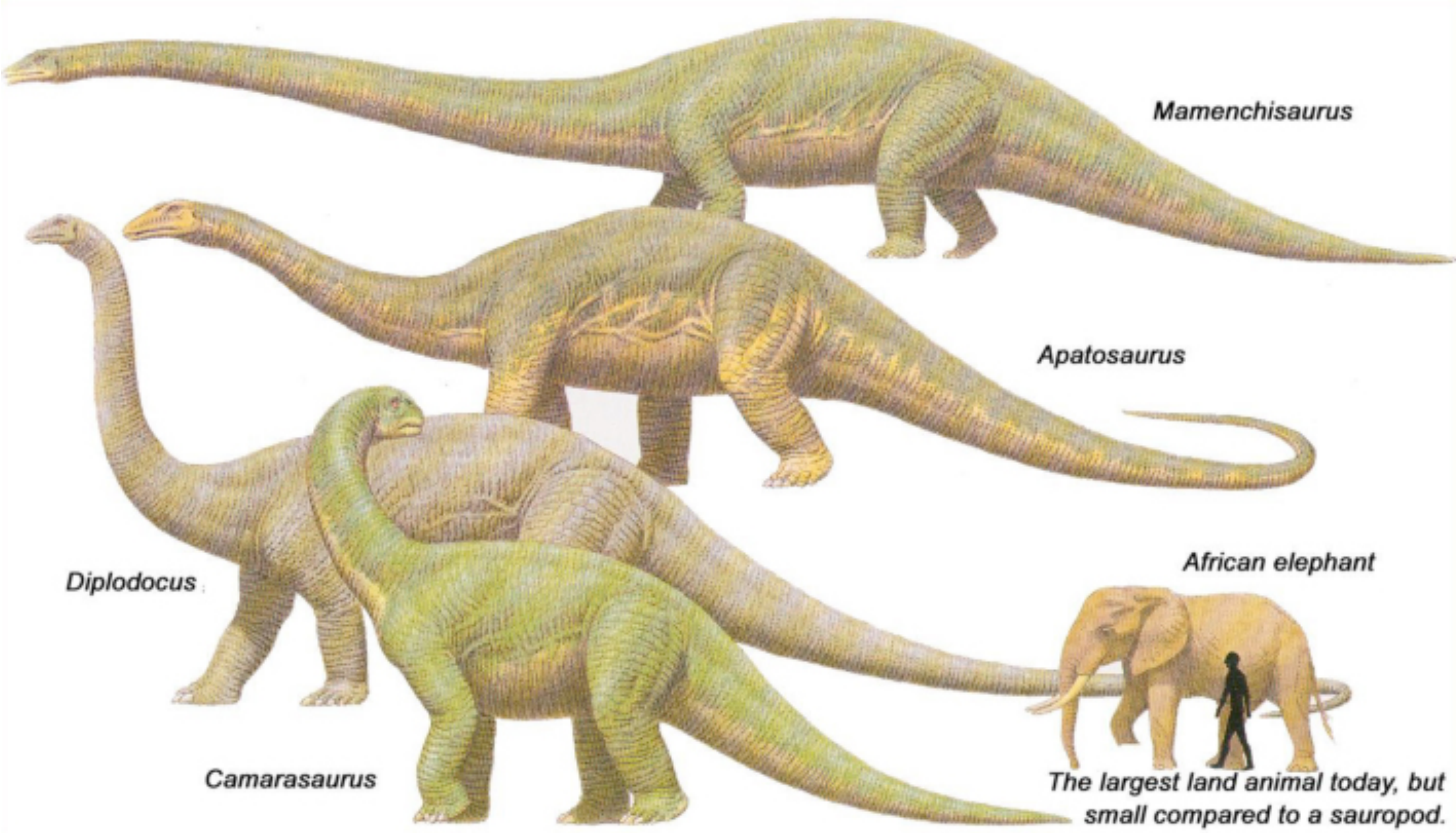
- etiopathology (endocrinology)
- physiological consequences
- social consequences

Gigantism


Mamenchisaurus
Apatosaurus
Diplodocus
Camarasaurus
African elephant
The largest land animal today, but
small compared to a sauropod.

Gigantism

- evolutionary opportunity



Ecological niches

Ecological niches

Elephant

Tenrek

Hedgehog

Ecological niches

Elephant

Tenrek

Hedgehog

Ecological niches

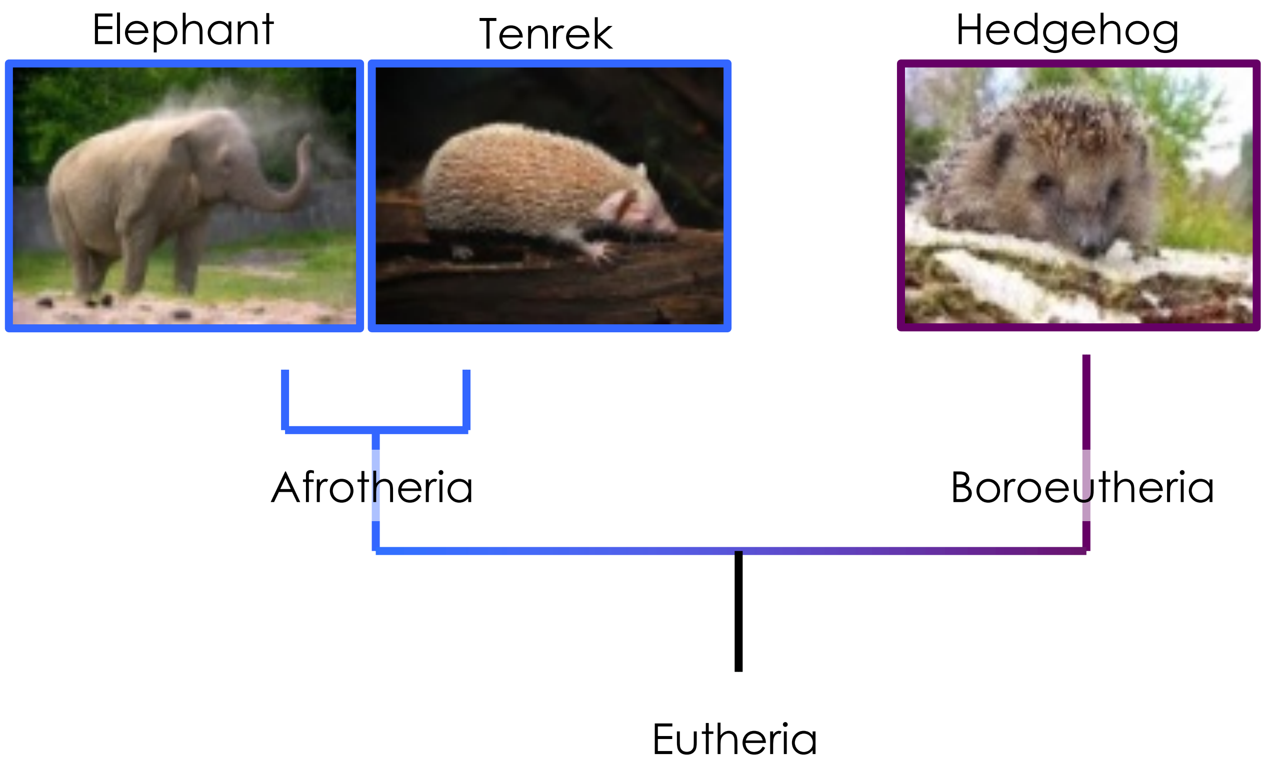
Elephant

Tenrek

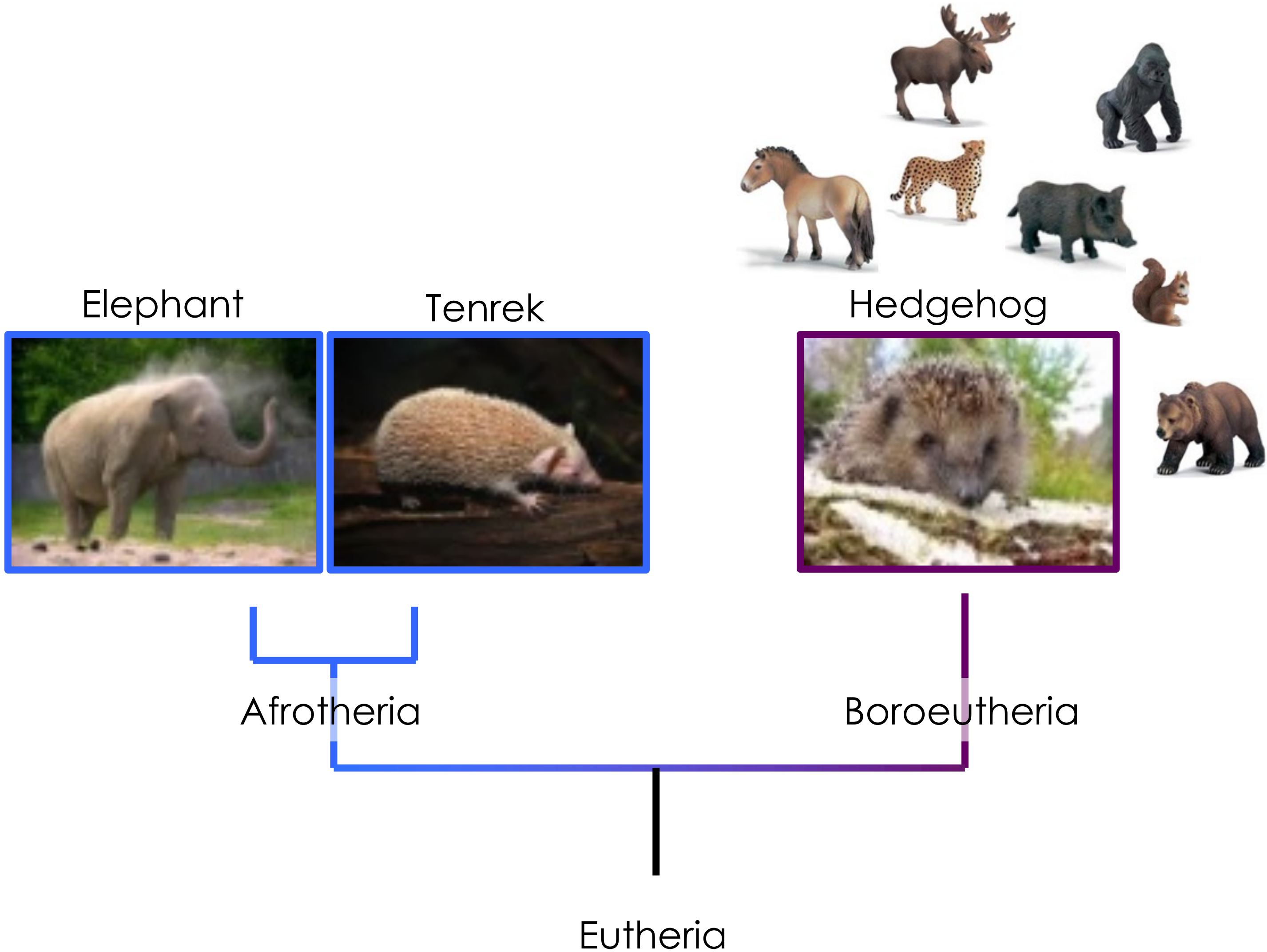
Hedgehog

Eutheria

Ecological niches



Ecological niches



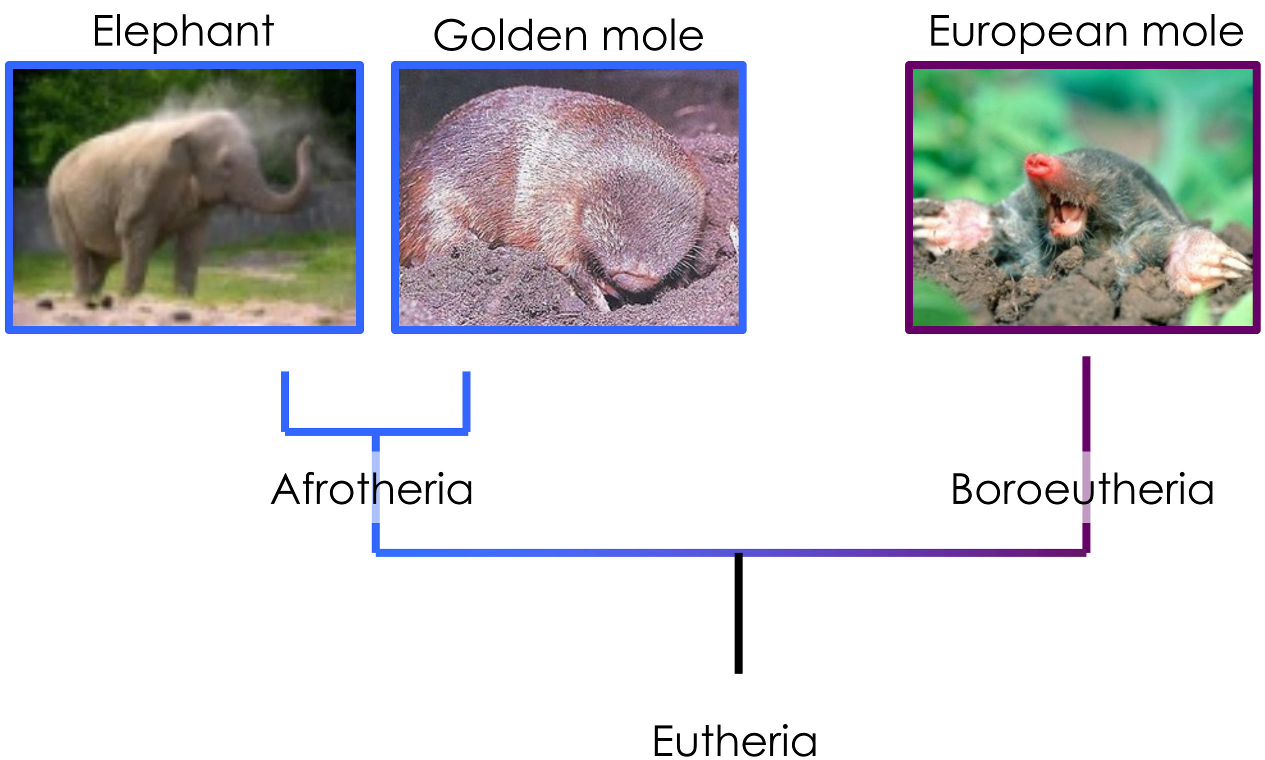
Ecological niches

Elephant

Golden mole

European mole

Ecological niches



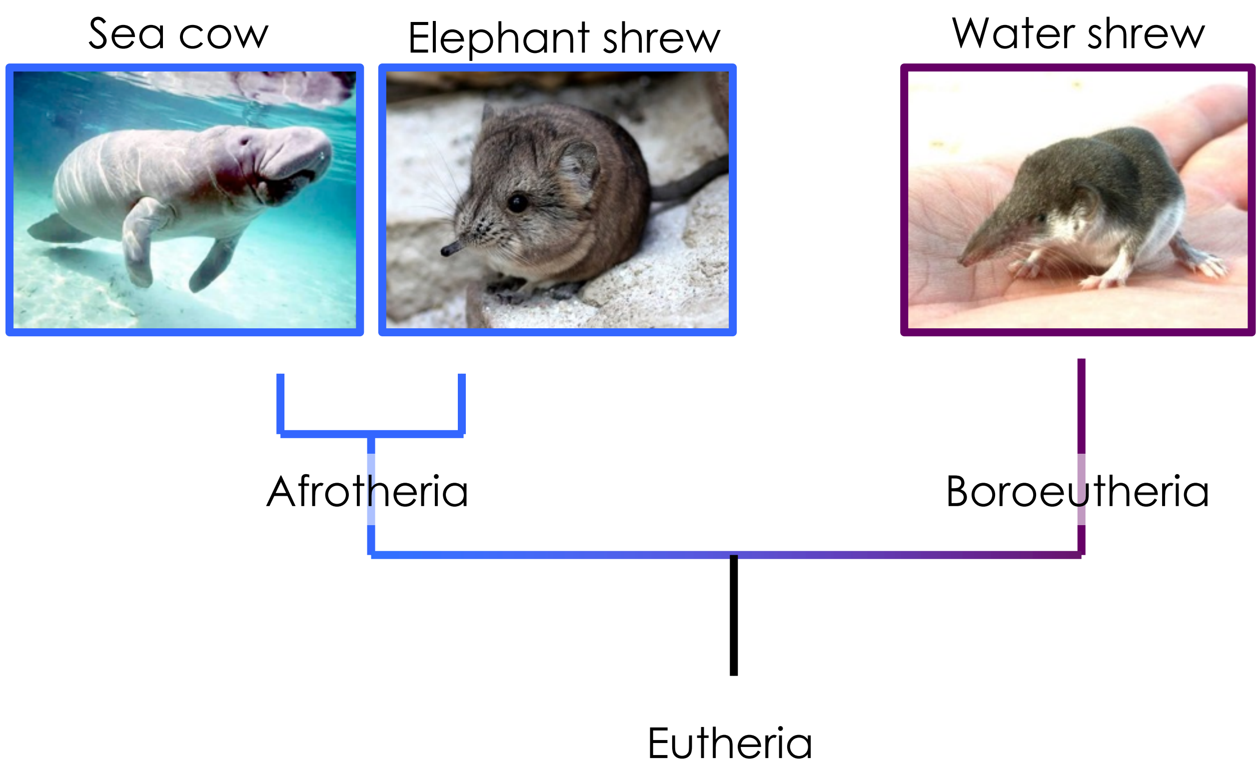
Ecological niches

Sea cow

Elephant shrew

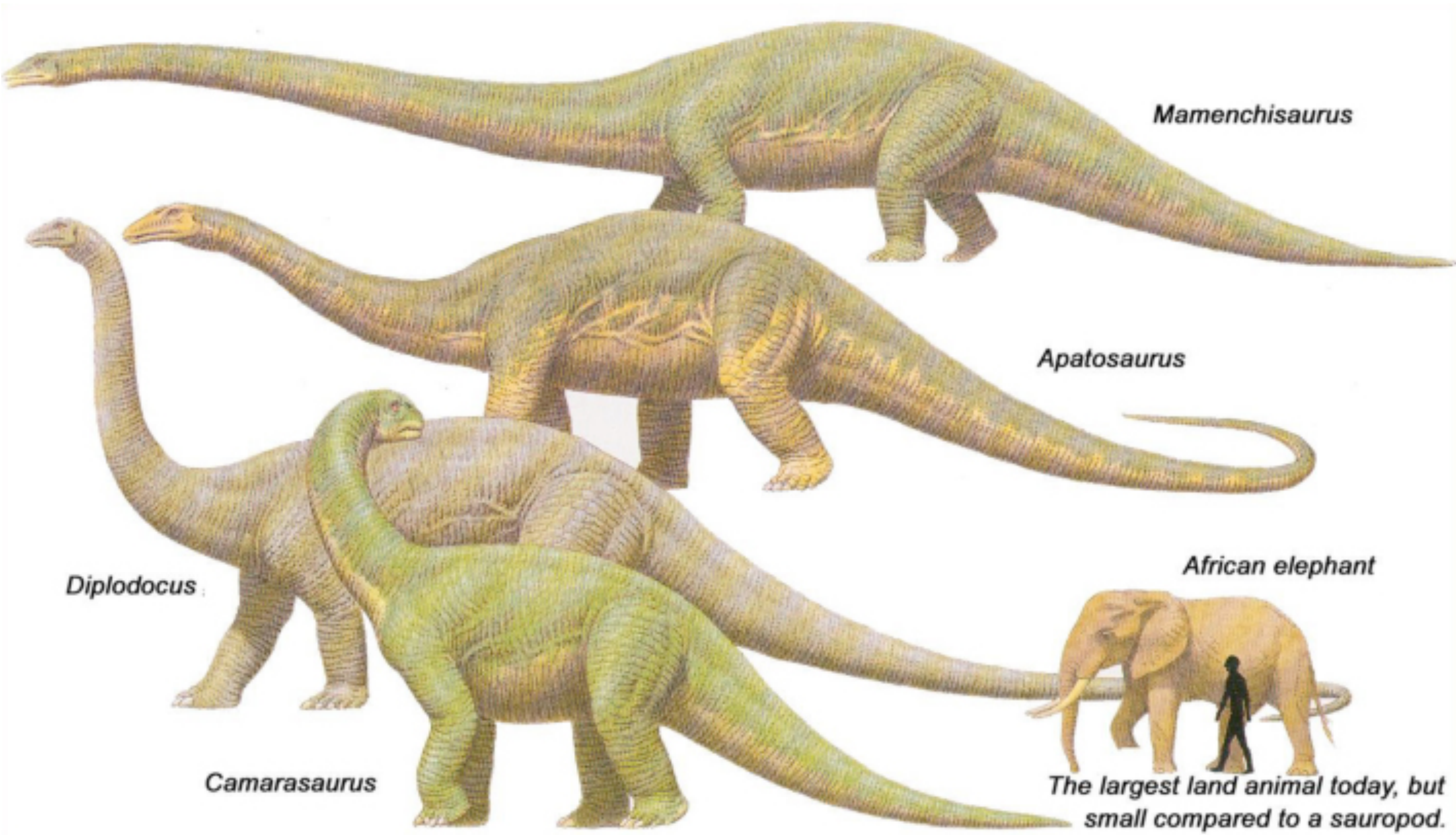
Water shrew

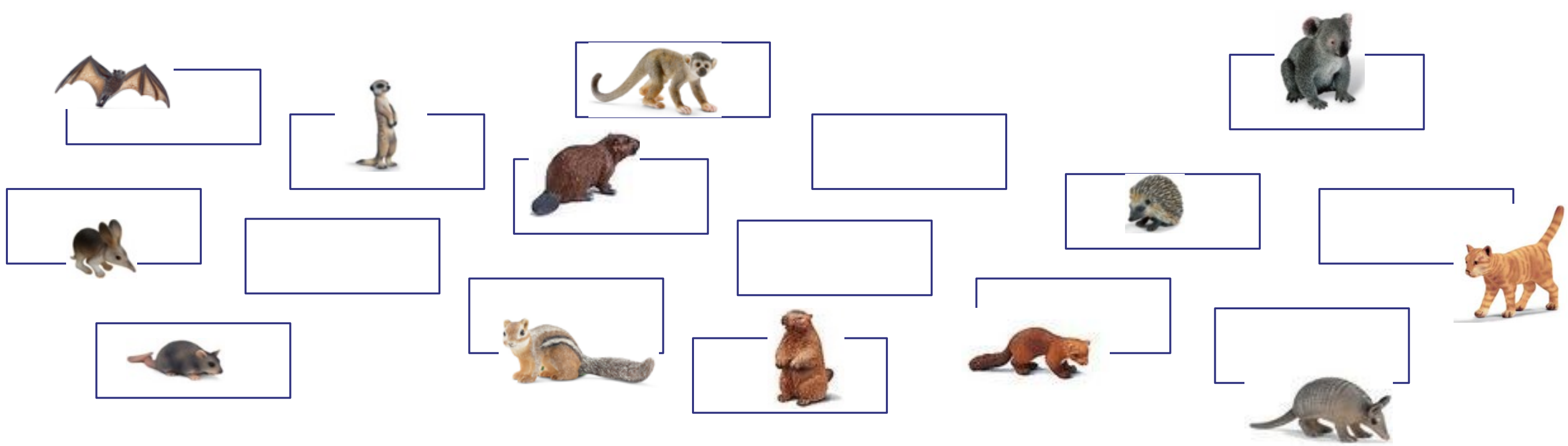
Ecological niches



Gigantism

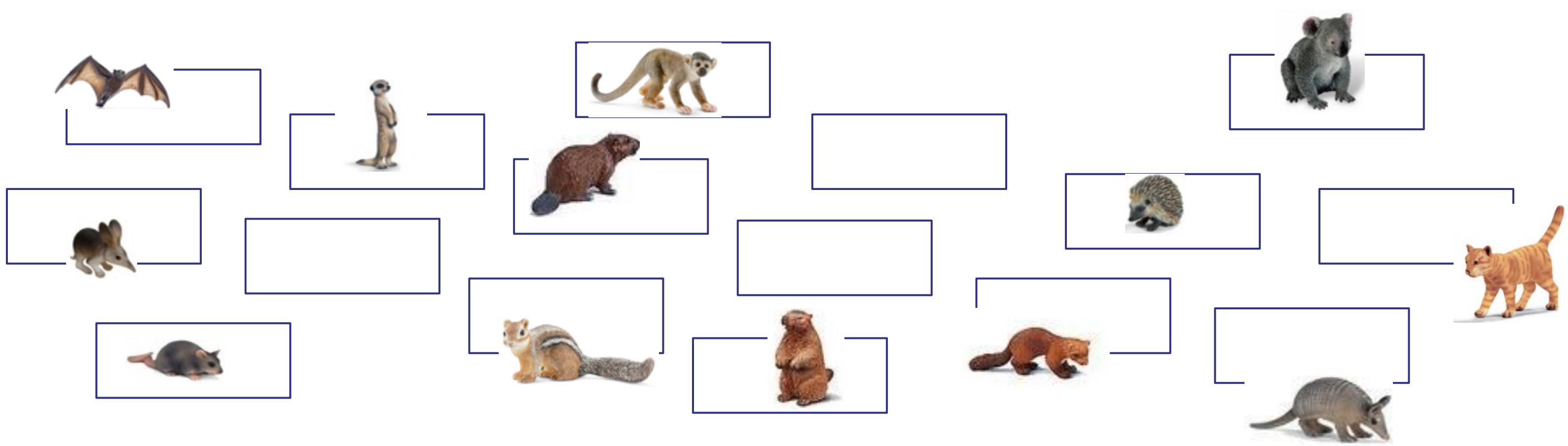
- evolutionary opportunity



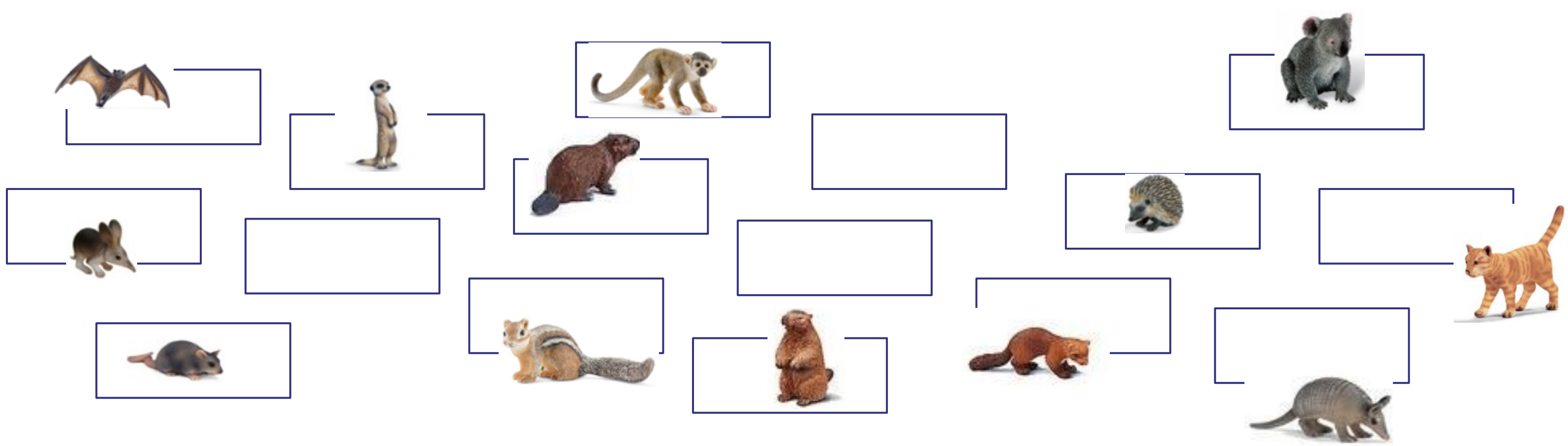


There are many niches for small things.

There are a few niches for large things



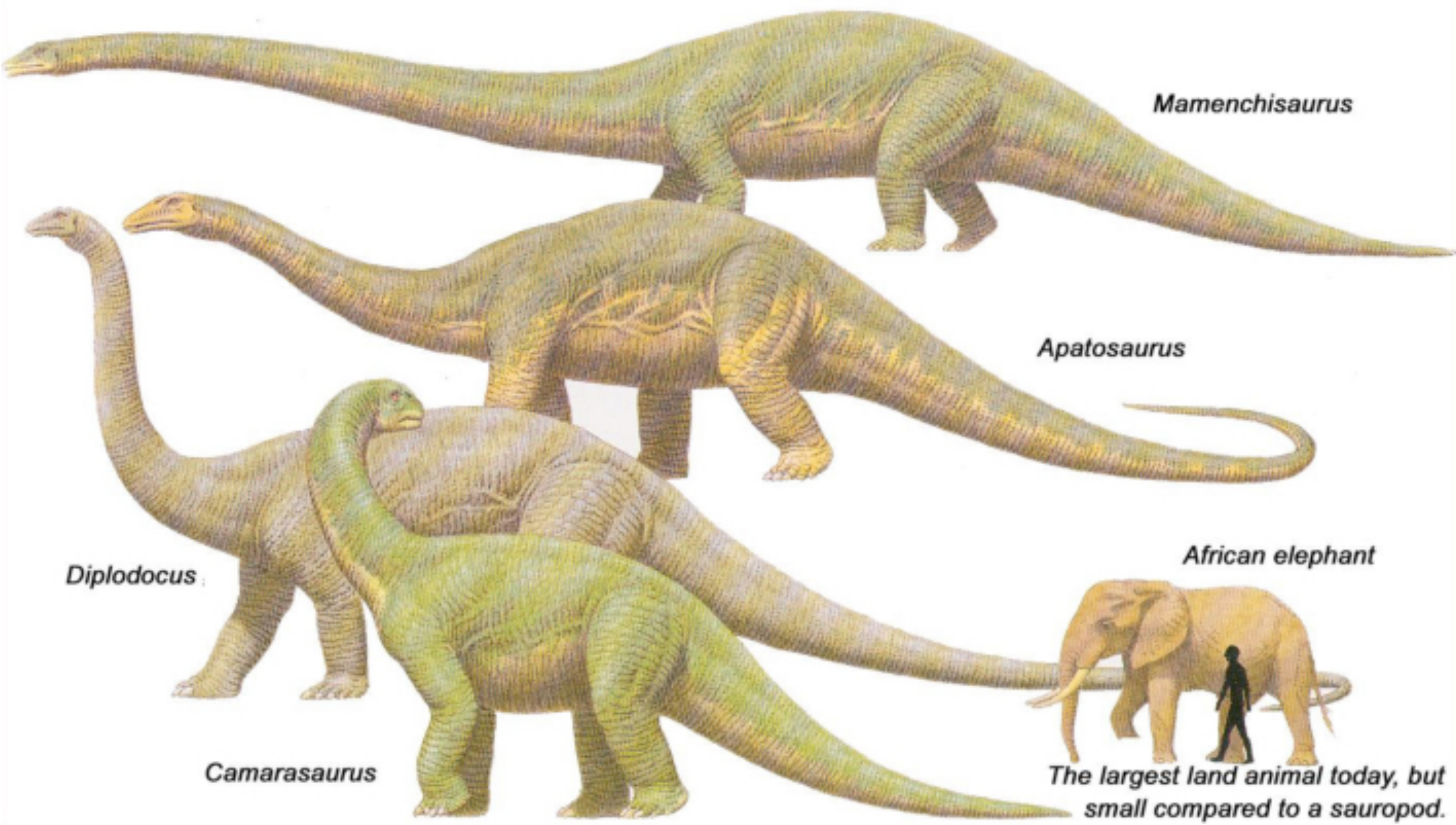
There are many niches for small things.

There are many niches for small things.

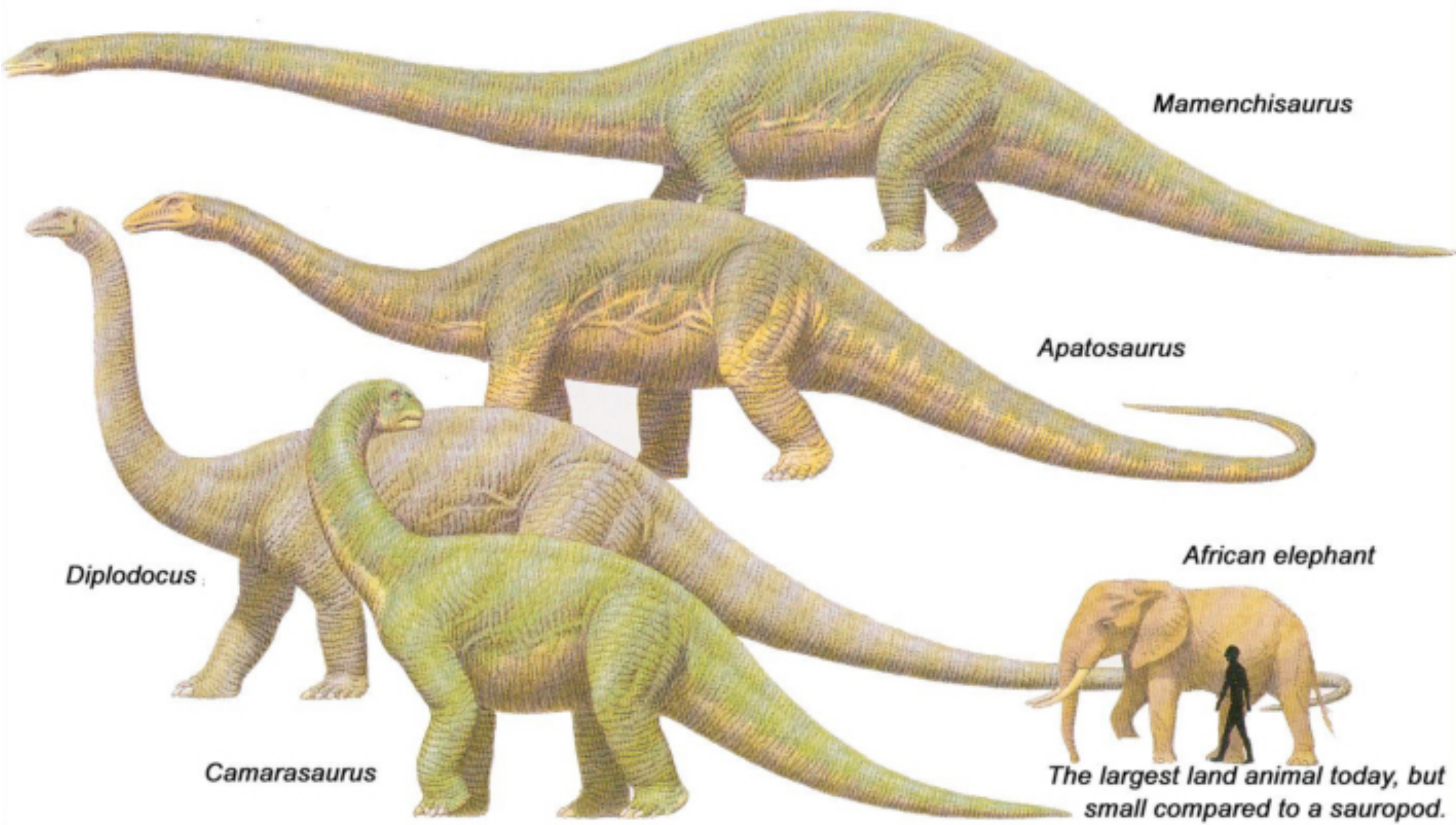
Gigantism

- evolutionary opportunity



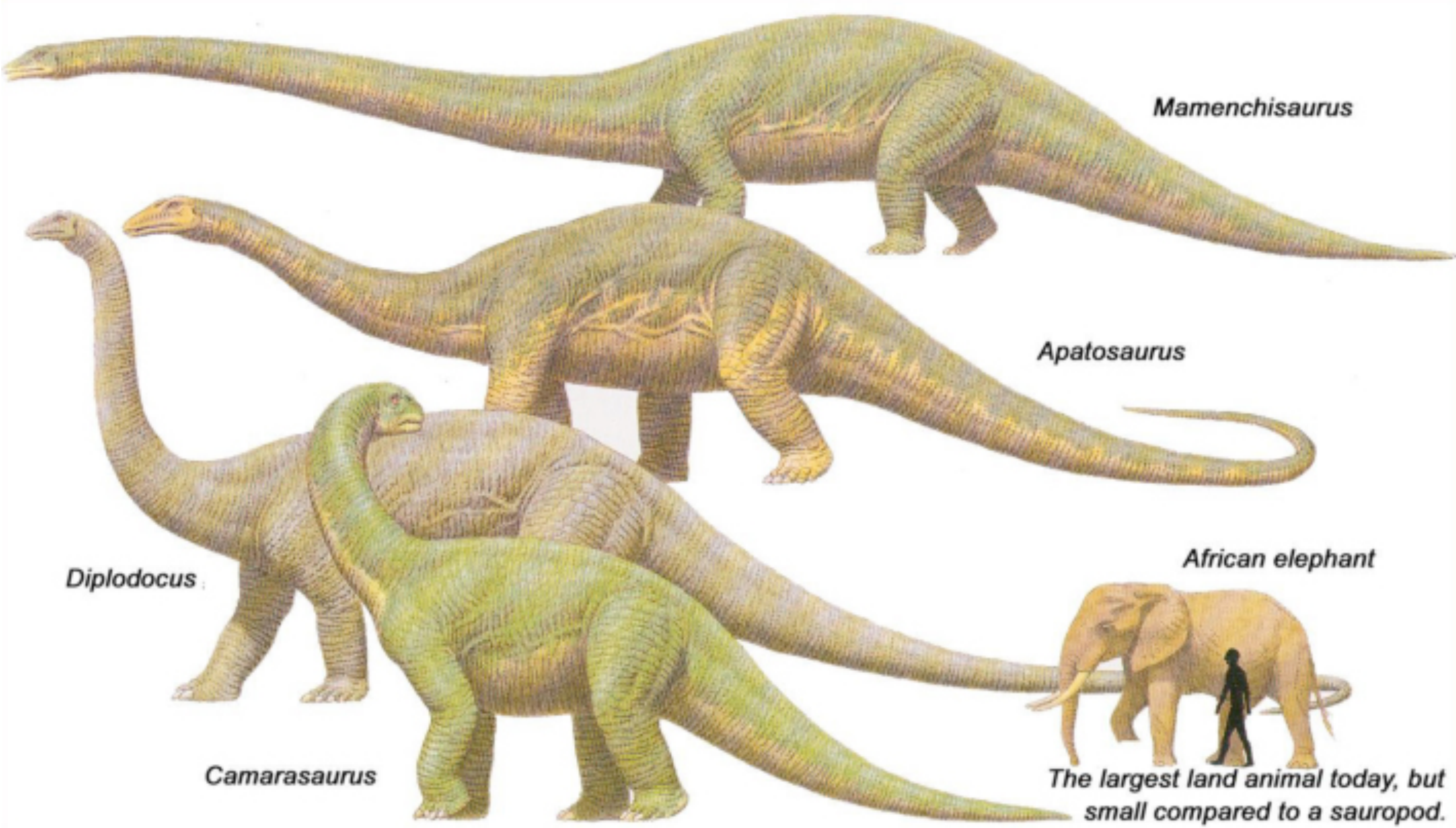
Gigantism

• evolutionary opportunity • physiological prerequisites and consequences



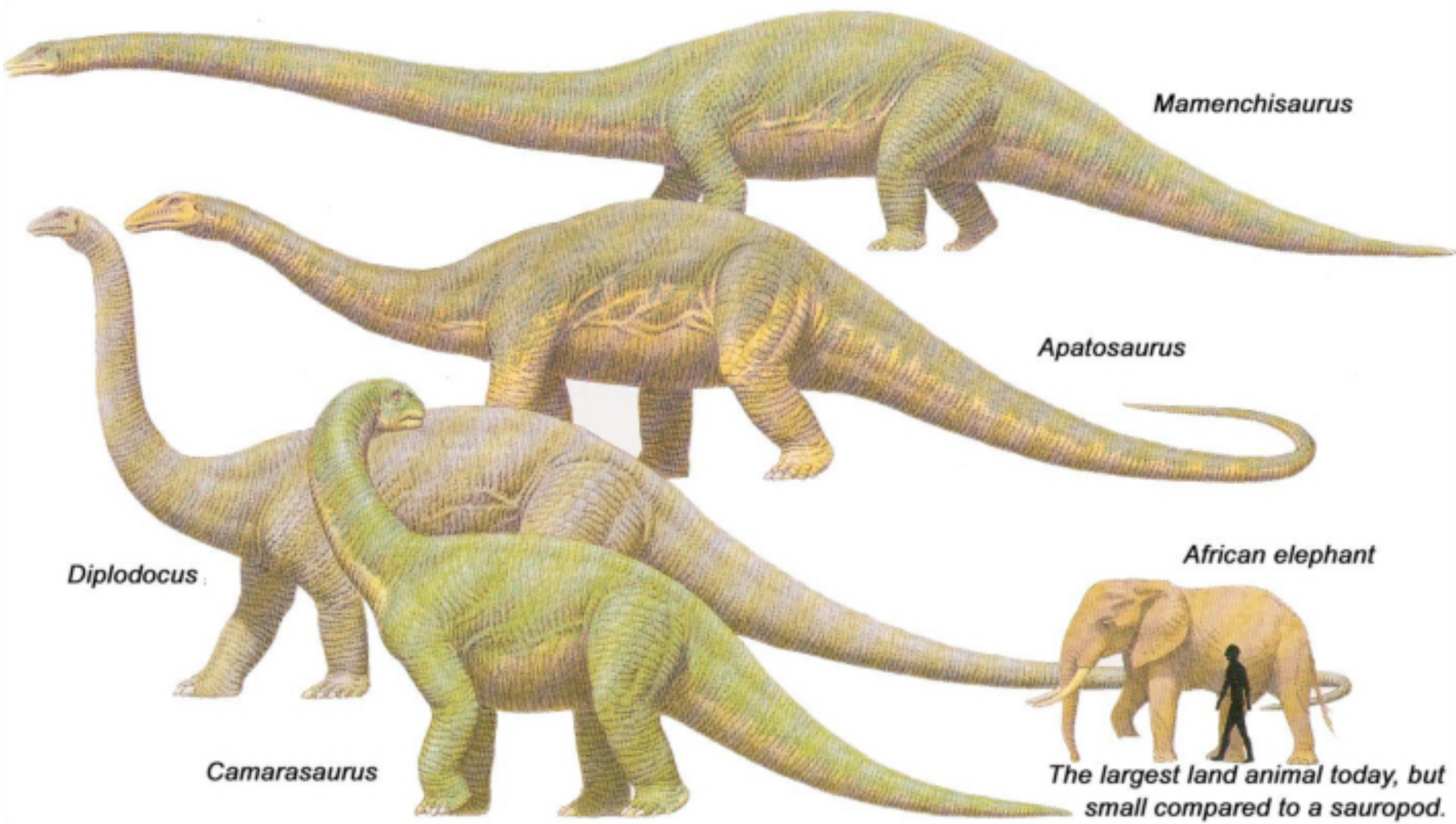
Gigantism

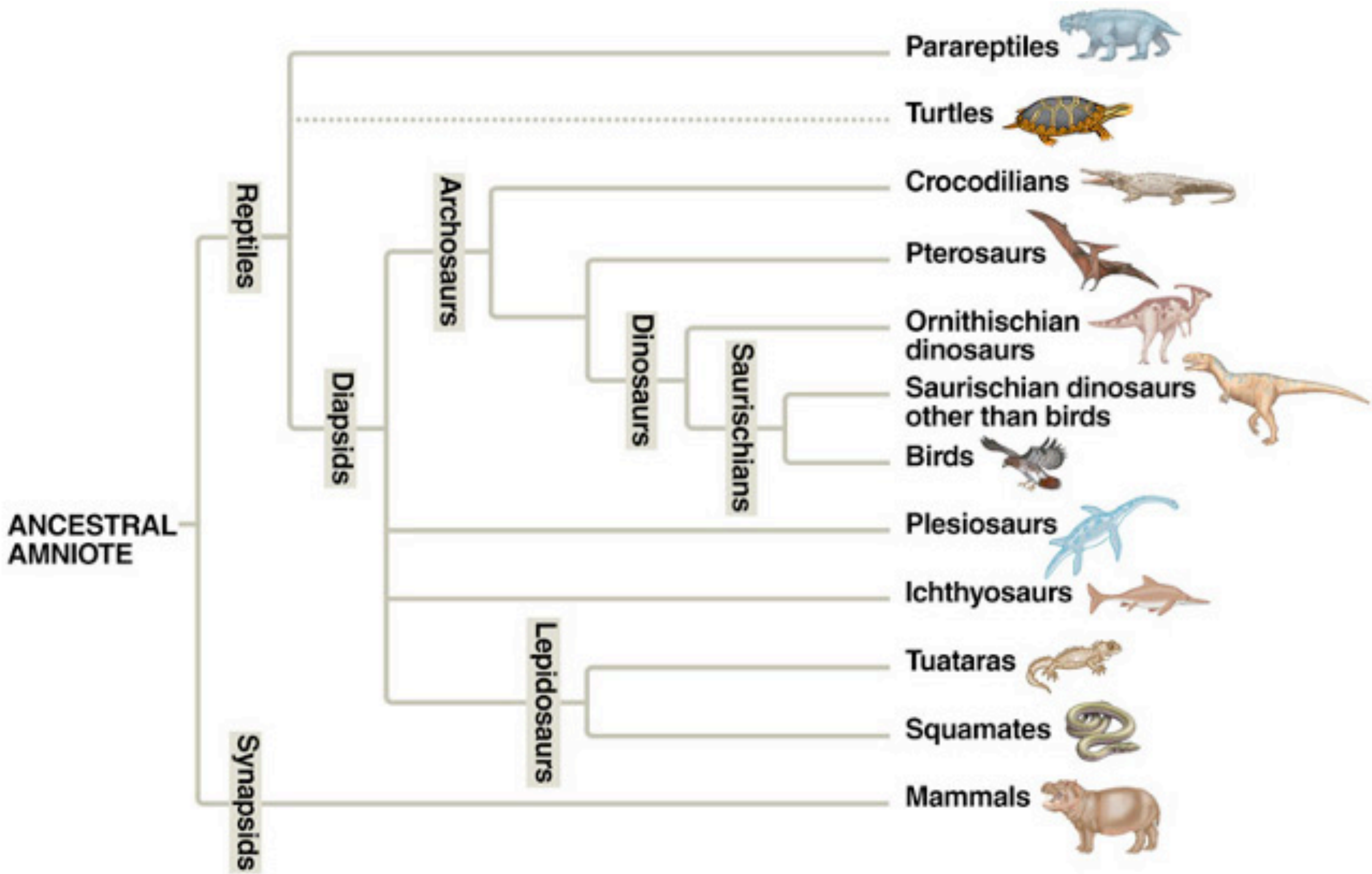
- evolutionary opportunity
- ecological consequences
- physiological prerequisites and consequences

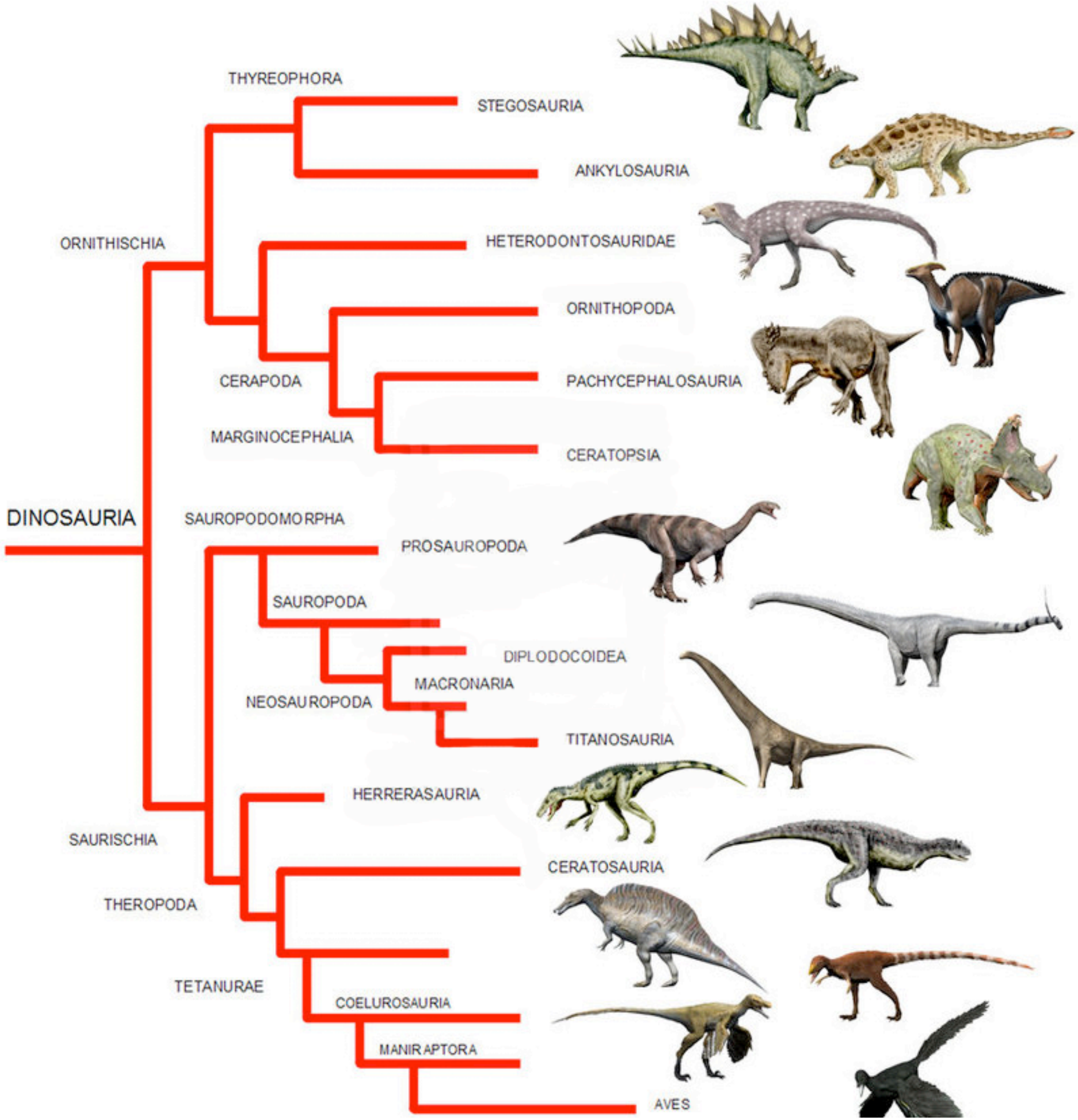


Gigantism

- evolutionary opportunity
- ecological consequences
- physiological prerequisites and consequences
- extinction



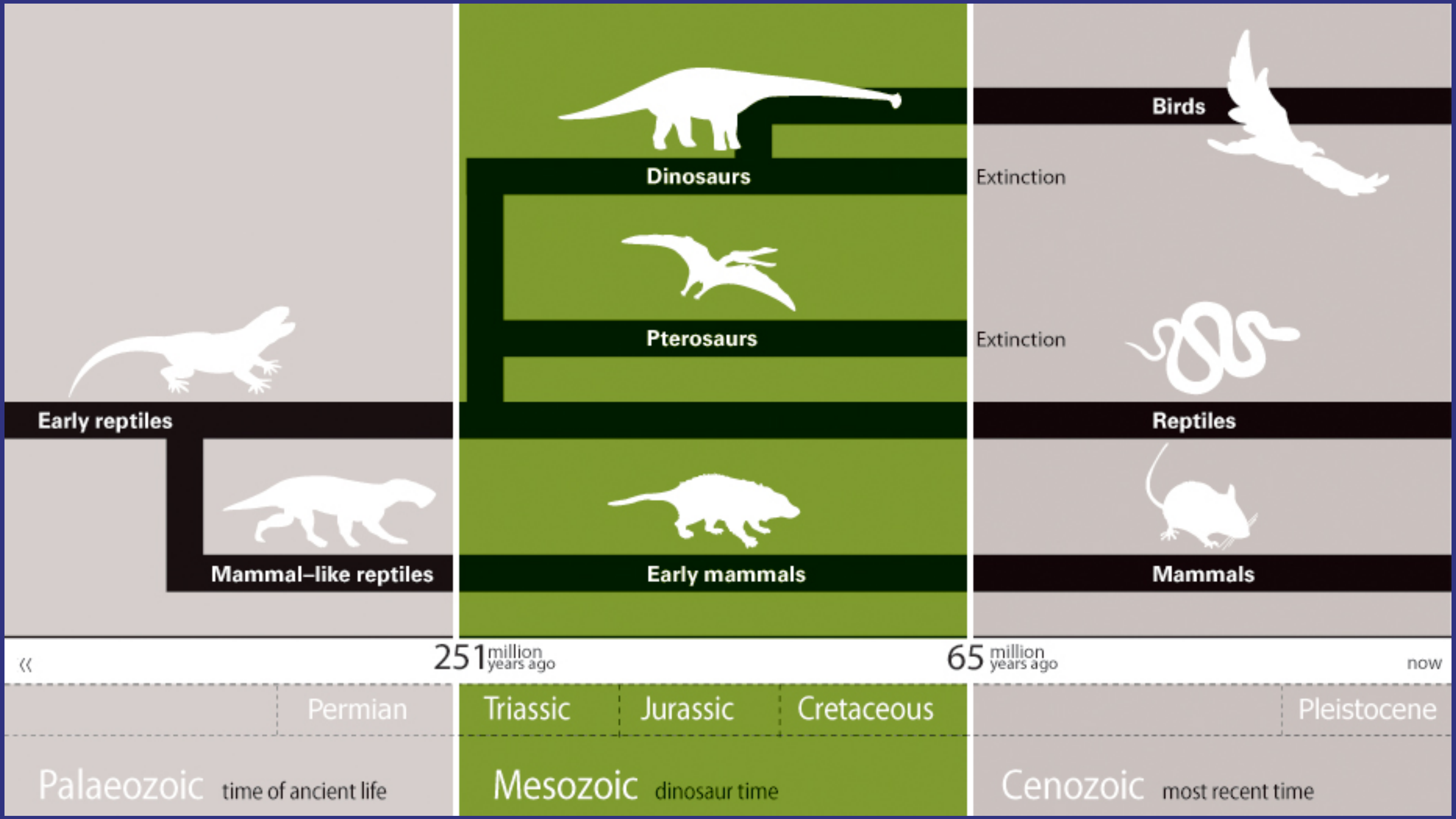

ANCESTRAL AMNIOTE
Reptiles
Diapsids
Archosaurs
Dinosaurs
Saurischians
Lepidosaurs
Synapsids
Parareptiles
Turtles
Crocodilians
Pterosaurs
Ornithischian dinosaurs
Saurischian dinosaurs other than birds
Birds
Plesiosaurs
Ichthyosaurs
Tuataras
Squamates
Mammals


THYREOPHORA
STEGOSAURIA
ANKYLOSAURIA
ORNITHISCHIA
HETERODONTOSAURIDAE
ORNITHOPODA
CERAPODA
PACHYCEPHALOSAURIA
MARGINOCEPHALIA
CERATOPSIA
DINOSAURIA
SAUROPODOMORPHA
PROSAUROPODA
SAUROPODA
DIPLODOCOIDEA
MACRONARIA
NEOSAUROPODA
TITANOSAURIA
HERRERASAURIA
SAURISCHIA
CERATOSAURIA
THEROPODA
TETANURAE
COELUROSAURIA
MANIRAPTORA
AVES

Dinosaurs did not die out !

Dinosaurs were an evolutionary failure?

Dinosaurs were no evolutionary failure!



Dinosaurs ...

Dinosaurs ...

- ... stimulate our phantasy

 Dinosaurs ... 

- ... stimulate our phantasy
- ... challenge our understanding of quantities

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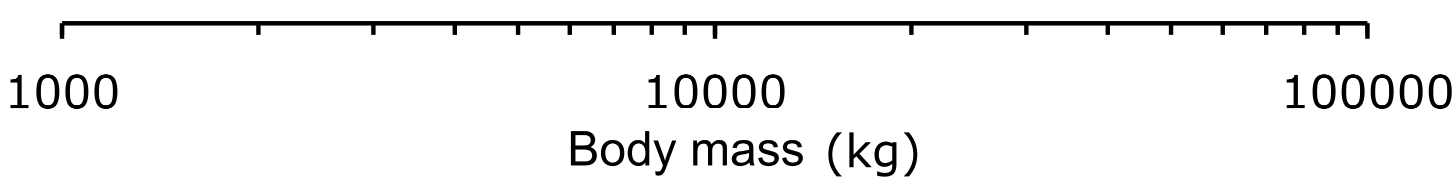
- ... stimulate our phantasy
- ... challenge our understanding of quantities

What is "gigantic"?

Sizing up dinosaurs



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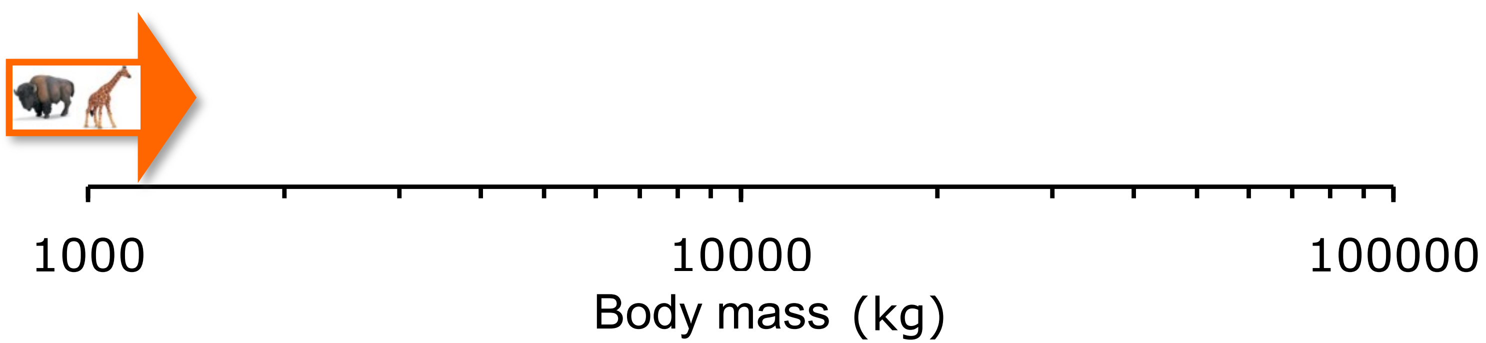

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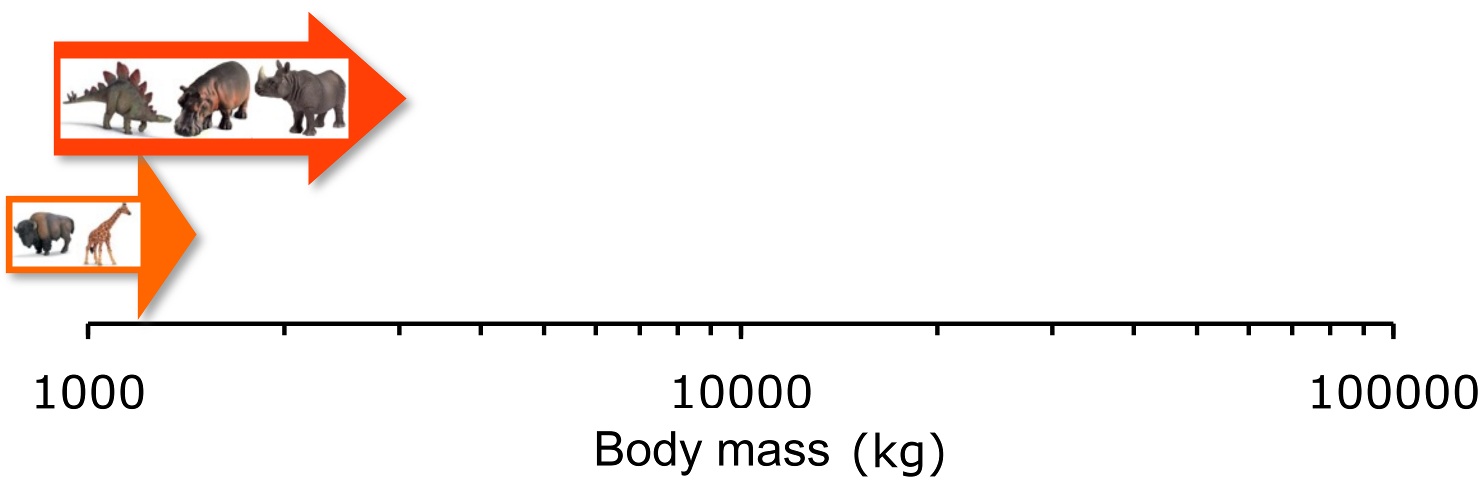

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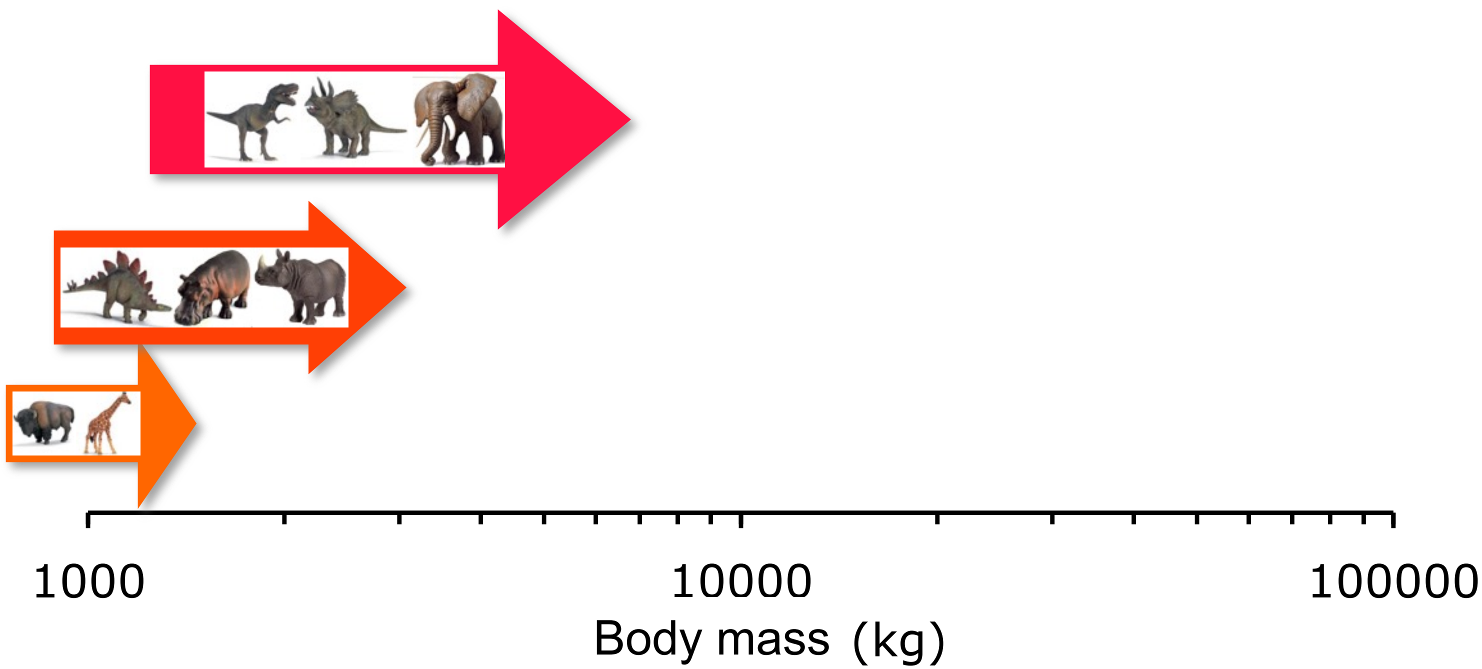

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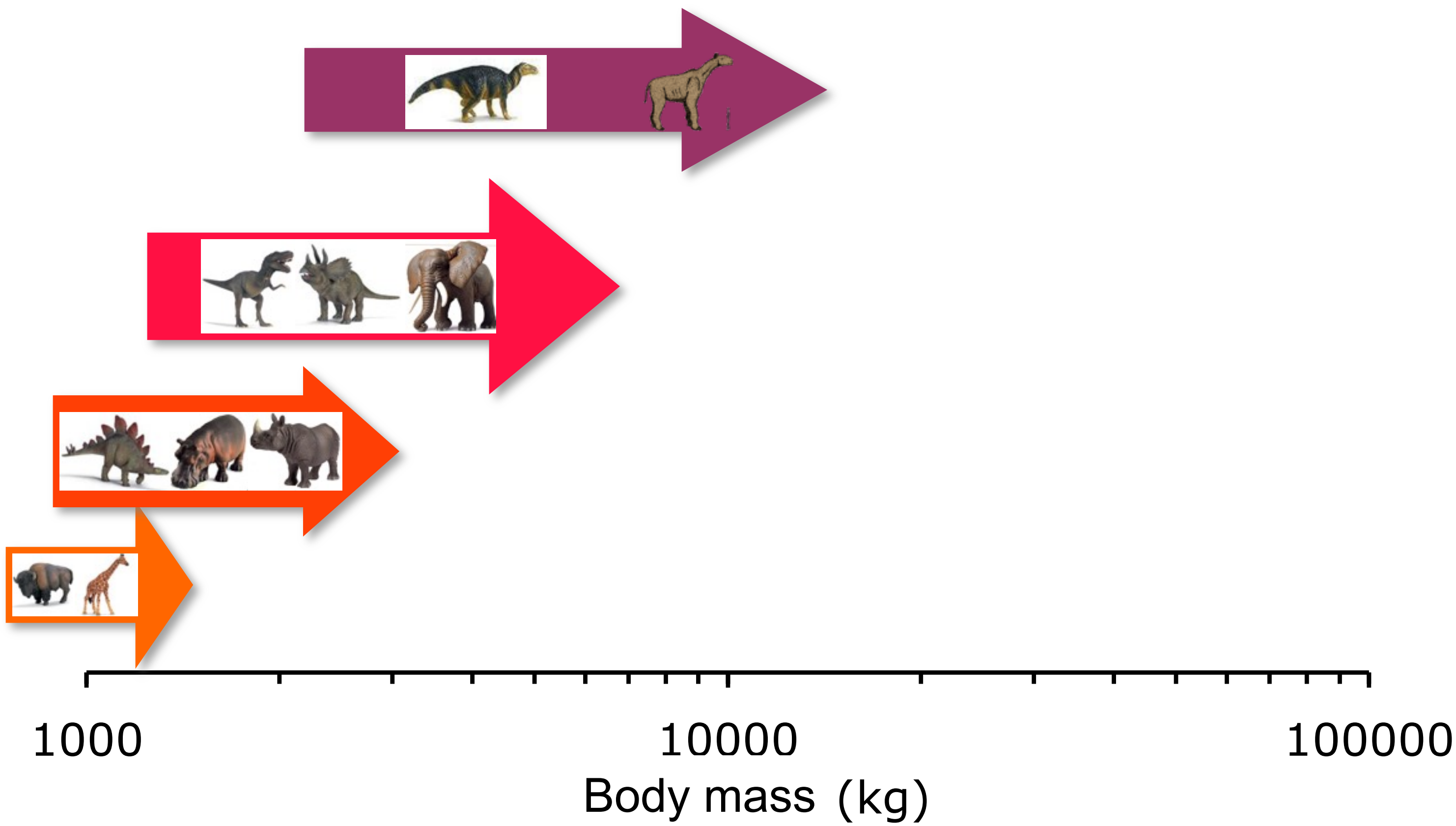
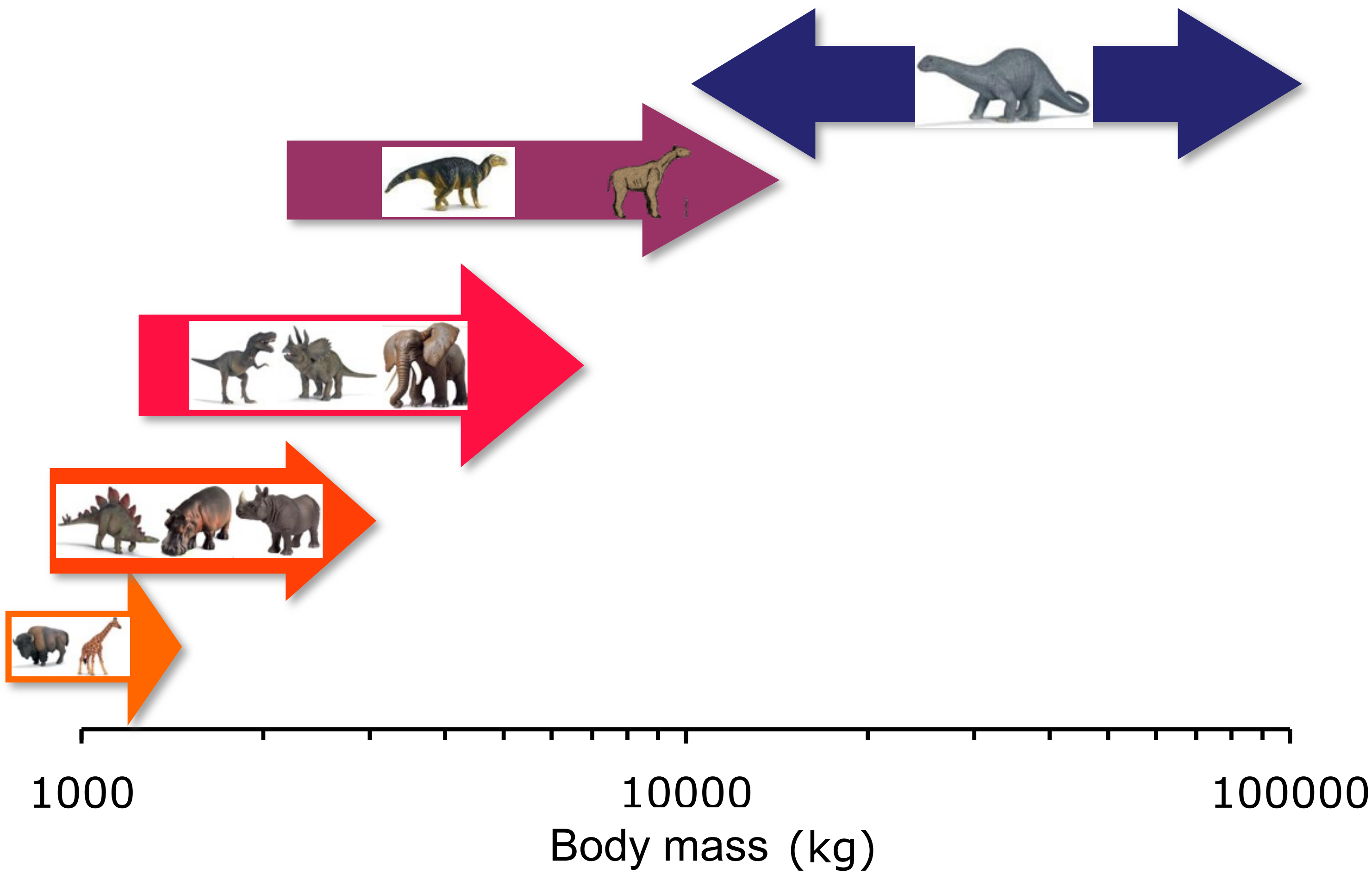


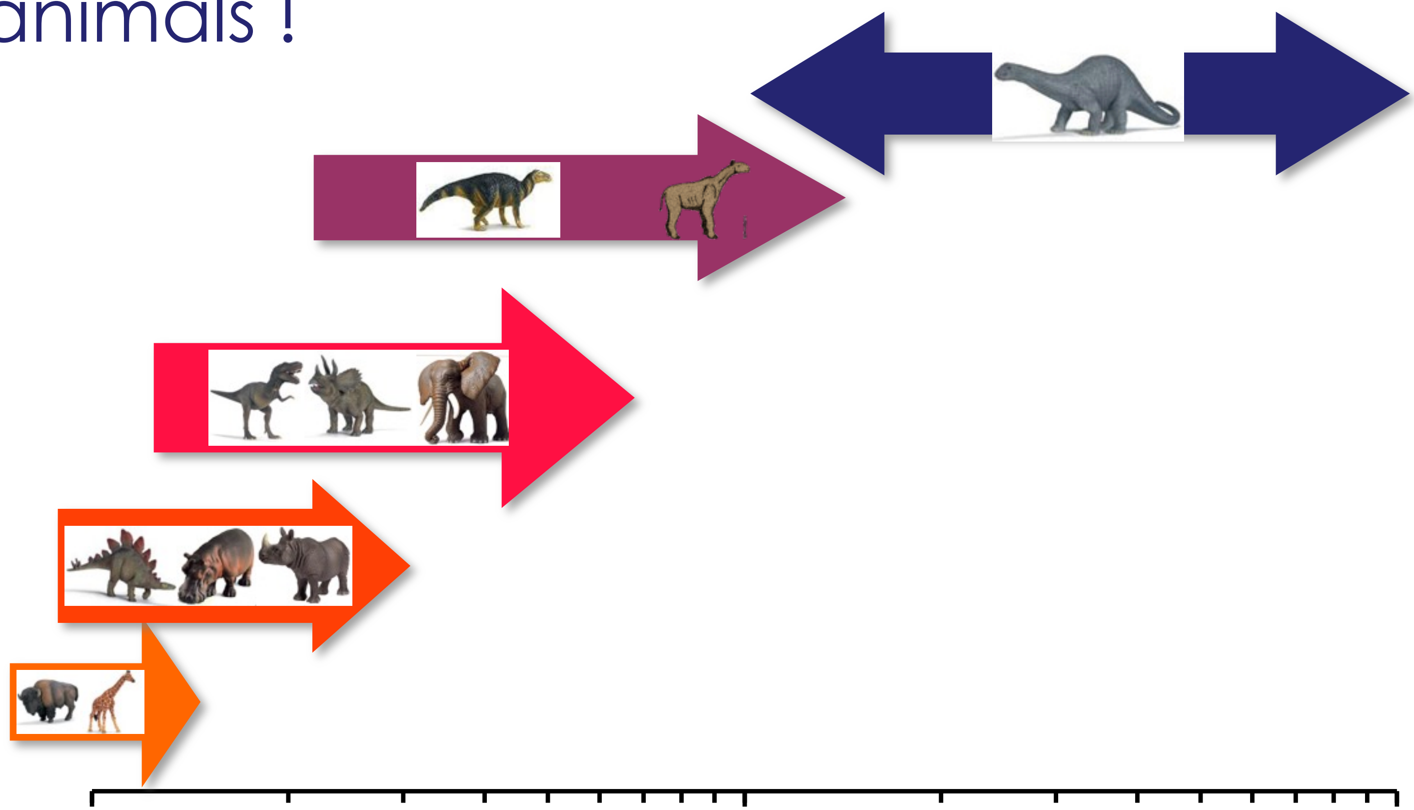

(C) NHK

Sizing up dinosaurs

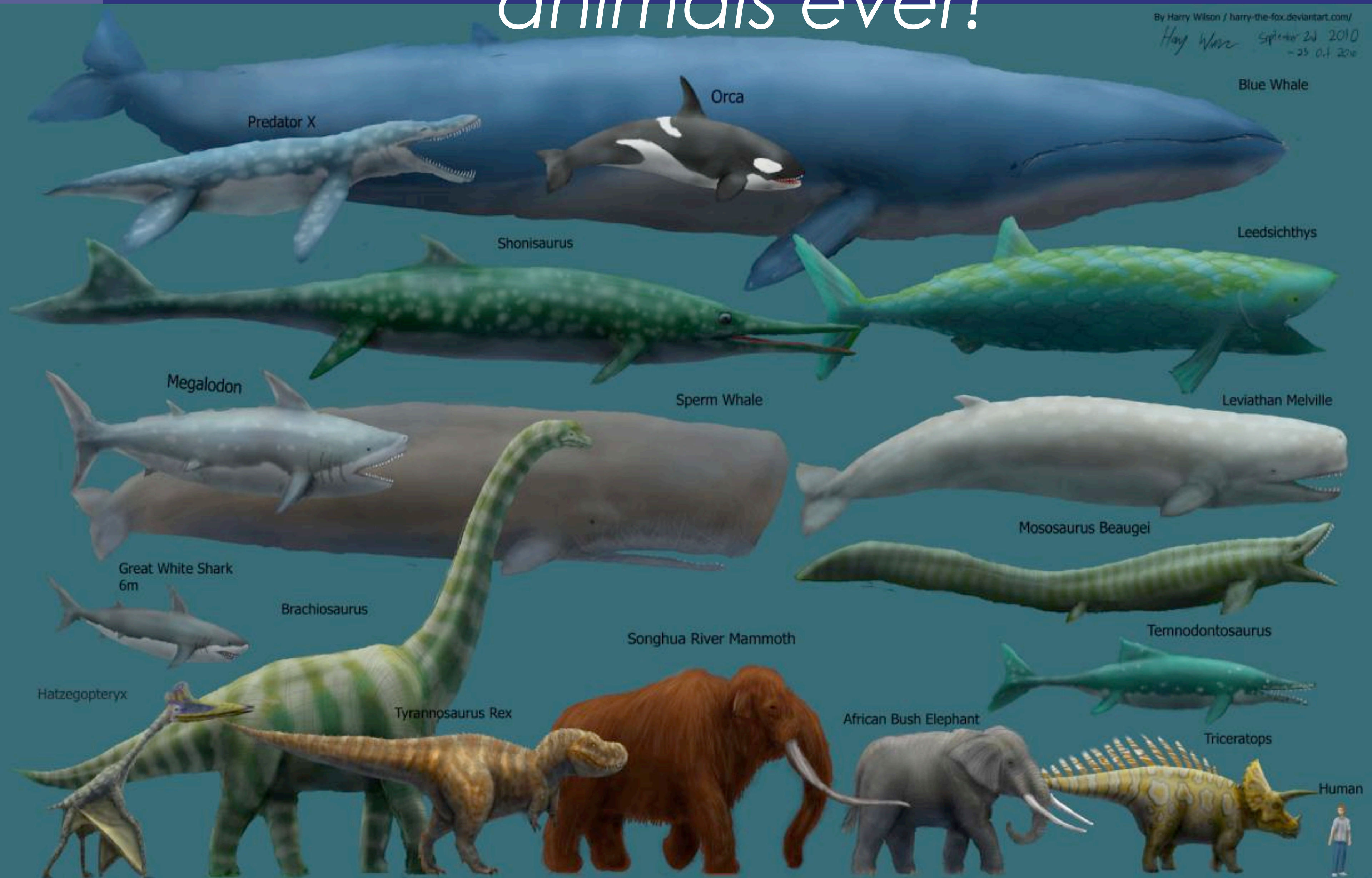


Sizing up dinosaurs

- Sauropods were the biggest of all terrestrial animals !



Dinosaurs were not the biggest animals ever!



Gigantism - Prerequisites

To become gigantic …

To become gigantic ...

- ... the niche must be empty

To become gigantic ...

- ... the niche must be empty
- ... you need resources

Gigantism and land mass

Dinosaurs, dragons, and dwarfs: The evolution of maximal body size

Gary P. Burness*†, Jared Diamond*‡, and Timothy Flannery§

*Department of Physiology, University of California School of Medicine, Los Angeles, CA 90095-1751; and §South Australian Museum, North Terrace, Adelaide 5000, SA, Australia

Contributed by Jared Diamond, October 15, 2001

Among local faunas, the maximum body size and taxonomic affiliation of the top terrestrial vertebrate vary greatly. Does this variation reflect how food requirements differ between trophic levels (herbivores vs. carnivores) and with taxonomic affiliation (mammals and birds vs. reptiles)? We gathered data on the body size and food requirements of the top terrestrial herbivores and carnivores, over the past 65,000 years, from oceanic islands and continents. The body mass of the top species was found to increase with increasing land area, with a slope similar to that of the relation between body mass and home range area, suggesting that maximum body size is determined by the number of home ranges that can fit into a given land area. For a given land area, the body size of the top species decreased in the sequence: ectothermic herbivore > endothermic herbivore > ectothermic carnivore > endothermic carnivore. When we converted body mass to food requirements, the food consumption of a top herbivore was about 8 times that of a top carnivore, in accord with the factor expected from the trophic pyramid. Although top ectotherms were heavier than top endotherms at a given trophic level, lower metabolic rates per gram of body mass in ectotherms resulted in endotherms and ectotherms having the same food consumption. These patterns explain the size of the largest-ever extinct mammal, but the size of the largest dinosaurs exceeds that predicted from land areas and remains unexplained.

The size and taxonomic affiliation of the largest locally present species ("top species") of terrestrial vertebrate vary greatly among faunas, raising many unsolved questions. Why are the top species on continents bigger than those on even the largest islands, bigger in turn than those on small islands? Why are the top mammals marsupials on Australia but placentals on the other continents? Why is the world's largest extant lizard (the Komodo dragon) native to a modest-sized Indonesian island, of all unlikely places? Why is the top herbivore larger than the top carnivore at most sites? Why were the largest dinosaurs bigger than any modern terrestrial species?

A useful starting point is the observation of Marquet and Taper (1), based on three data sets (Great Basin mountaintops, Sea of Cortez islands, and the continents), that the size of a landmass's top mammal increases with the landmass's area. To explain this pattern, they noted that populations numbering less than some minimum number of individuals are at high risk of extinction, but larger individuals require more food and hence larger home ranges, thus only large landmasses can support at least the necessary minimum number of individuals of larger-bodied species. If this reasoning were correct, one might expect body size of the top species also to depend on other correlates of food requirements and population densities, such as trophic level and metabolic rate. Hence we assembled a data set consisting of the top terrestrial herbivores and carnivores on 25 oceanic islands and the 5 continents to test 3 quantitative predictions.

1. Within a trophic level, body mass of the top species will increase with land area, with a slope predictable from the slope of the relation between body mass and home range area.
2. For a given land area, the top herbivore will be larger than the top carnivore by a factor predictable from the greater amounts of food available to herbivores than to carnivores.
3. Within a trophic level and for a given area of landmass, top species that are ectotherms will be larger than ones that are endotherms, by a factor predictable from ectotherms' lower food requirements.

On reflection, one can think of other factors likely to perturb these predictions, such as environmental productivity, over-water dispersal, evolutionary times required for body size changes, and changing landmass area with geological time. Indeed, our database does suggest effects of these other factors. We propose our three predictions not because we expect them always to be correct, but because we expect them to describe broad patterns that must be understood in order to be able to detect and interpret deviations from those patterns.

Data

For continents and oceanic islands with a good fossil record for the last 65,000 years, Table 1 lists the identity and mean adult body mass of the top herbivore and top carnivore, most of them known only as Late Pleistocene or Holocene fossils. We chose a cutoff of 65,000 years ago because that is the approximate time of emergence of behaviorally modern humans (2), who may have been responsible for the subsequent extinctions of most of these top species.

We used mean adult mass of each species rather than mass of the largest known individual. In studies providing only a range of masses, we averaged the range. To generate a species mean, we averaged male and female body masses. When calculating the mean mass of extant reptiles, we included only mass estimates for individuals of breeding age and/or size. When no body mass values were available (e.g., for many extinct species), we estimated body mass from linear dimensions through comparisons with related extant species of known body mass, using regression equations (refs. 3 and 4; P. Christiansen, personal communication), or else assuming body mass to increase as the cube of linear dimensions.

In some cases, a top species occurred on multiple islands within an archipelago but was unlikely to disperse often among islands, hence each island must have had a nearly self-sustaining population. We report such a species only once, using the area of the largest island on which it was the top herbivore or carnivore. Because some avian carnivores (e.g., sea eagles *Haliaeetus* sp.) readily cross water gaps, we excluded them if they occurred on islands less than an arbitrarily defined 50 km from a larger landmass.

We included terrestrial and freshwater crocodiles known or suspected to prey on terrestrial vertebrates. We excluded salt-

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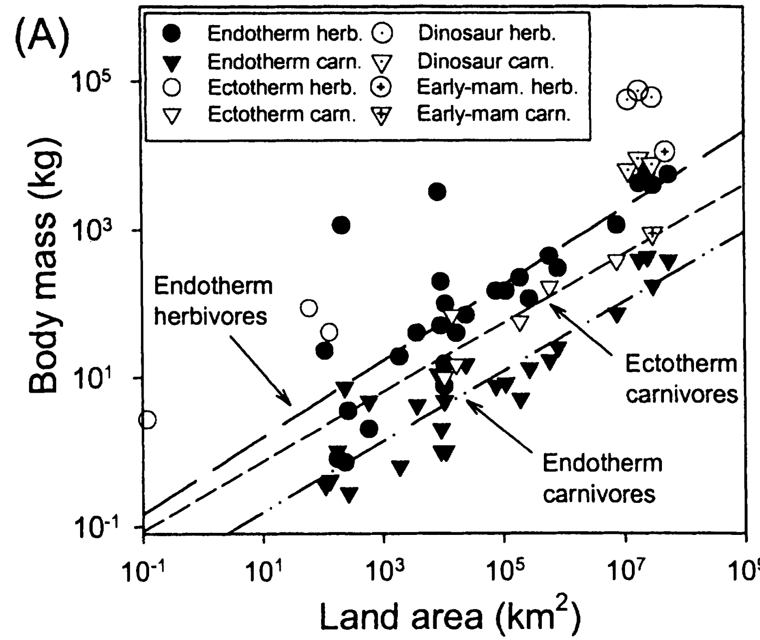
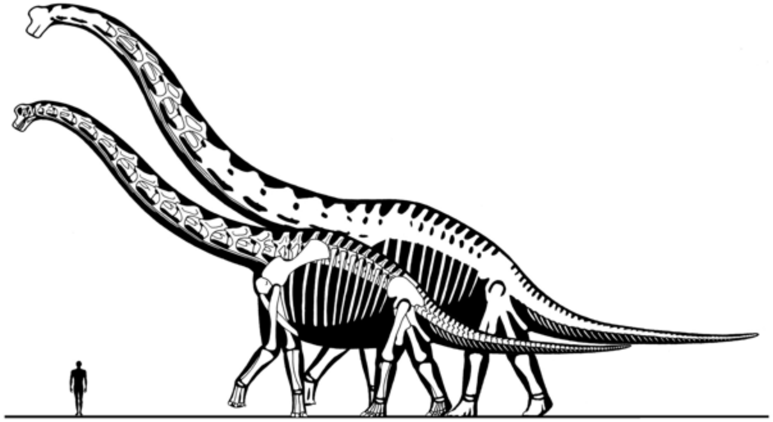


Gigantism and land mass



Gigantism and land mass

Vol 441|8 June 2006|doi:10.1038/nature04633 nature

LETTERS

Bone histology indicates insular dwarfism in a new Late Jurassic sauropod dinosaur

P. Martin Sander[1], Octávio Mateus[2], Thomas Laven[3] & Nils Knötschke[3]

Sauropod dinosaurs were the largest animals ever to inhabit the land, with truly gigantic forms in at least three lineages[1–3]. Small species with an adult body mass less than five tonnes are very rare[4,5], and small sauropod bones generally represent juveniles. Here we describe a new diminutive species of basal macronarian sauropod, *Europasaurus holgeri* gen. et sp. nov., and on the basis of bone histology we show it to have been a dwarf species. The fossils, including excellent skull material, come from Kimmeridgian marine beds of northern Germany[6,7], and record more than 11 individuals of sauropods 1.7 to 6.2 m in total body length. Morphological overlap between partial skeletons and isolated bones links all material to the same new taxon. Cortical histology of femora and tibiae indicates that size differences within the specimens are due to different ontogenetic stages, from juveniles to fully grown individuals. The little dinosaurs must have lived on one of the large islands around the Lower Saxony basin[8]. Comparison with the long-bone histology of large-bodied sauropods suggests that the island dwarf species evolved through a decrease in growth rate from its larger ancestor.

Sauropoda Marsh, 1878
Neosauropoda Bonaparte, 1986
Macronaria Wilson and Sereno, 1998
Europasaurus holgeri gen. et sp. nov.

Etymology. The generic name means 'reptile from Europe', after Europe and the Greek *sauros* for lizard; *holgeri* after Holger Lüdtke, who discovered the first bones.
Holotype. DFMMh/FV 291: disarticulated left premaxilla; right maxilla; right quadratojugal; occipital region; left laterosphenoid–orbitosphenoid complex; right surangular; right angular; left dentary; teeth; cervical and sacral vertebrae; and cervical and dorsal ribs of one individual (see Fig. 1 and Supplementary Information). DFMMh/FV: Dinosaurier-Freilichtmuseum Münchehagen/Verein zur Förderung der Niedersächsischen Paläontologie (e.V.), Germany.
Referred material. Cranial and postcranial elements of at least ten individuals, preserved as isolated bones to partially articulated skeletons, including young juveniles (estimated body length 1.7 m) to adults (body length 6.2 m).
Horizon and locality. Late Jurassic, middle Kimmeridgian marine carbonate rock, bed 93 of section at Langenberg quarry[7], Lower Saxony basin, Oker near Goslar, Niedersachsen, northern Germany (see Supplementary Information).
Diagnosis. *Europasaurus holgeri* gen. et sp. nov. shows the following unambiguous autapomorphies (see also Supplementary Information): nasal process of premaxillary projecting anterodorsally; medial notch on posterior dorsal margin of cervical vertebral centra; scapular acromion with a prominent posterior projection; and transverse width of astragalus twice its dorsoventral height and anteroposterior length. *Europasaurus* differs from *Camarasaurus* in the wing-shaped posterior process of the postorbital being slightly longer and wider than the anterior process, whereas it is much shorter in *Camarasaurus*. *Europasaurus* also differs from *Camarasaurus* in its short nasal–frontal contact; rectangular parietal in posterior view; and undivided presacral neural spines. *Europasaurus* differs from *Brachiosaurus* in the shorter muzzle, quadratojugal contacting squamosal; participation of jugal in ventral margin of skull; short nasal–frontal contact; and humerus flat anteromedially with proximal and distal epiphyses not aligned. *Europasaurus* differs from *Lusotitan atalaiensis*[25] in the shape of the ilium and the astragalus, and from the potentially valid '*Cetiosaurus*' *humerocristatus*[4] in its shorter and less prominent deltopectoral crest. *Europasaurus* differs from almost all known neosauropods in its diminutive adult body size.

Phylogenetic analysis (see Supplementary Information) indicates that *Europasaurus holgeri* gen. et sp. nov. is a macronarian that is more derived than *Camarasaurus*, and is the sistergroup of Brachiosauridae and all (more-derived) Titanosauromorpha. It also indicates that the diminutive body size of *Europasaurus* is derived.

Six individuals that represent the full body-length range known for *Europasaurus* were sampled histologically from one or two long bones each. The bones selected were femora and tibiae, and the bone tissues examined were those of the cortex (see Supplementary Information). The bone cortex of the smallest individual (body length 1.75 m; DFMMh/FV 009) is primary bone of the fibrolamellar complex with a reticular vascular network that grades into a laminar network (Fig. 2a). The bone matrix consists of fibrous tissue with plump osteocyte lacunae. Only a thin veneer of lamellar bone lines the vascular canals (incipient primary osteons). There are no growth marks in the cortical bone. The inner cortex lacks any indication of secondary remodelling, except for large erosional cavities. These features indicate a rapidly growing juvenile[9–11].

The next-largest individual (body length 2 m; DFMMh/FV 291.9) differs from the previous one in that the fibrolamellar bone is of the laminar type, the vascular network being organized into a predominantly circumferential pattern. The vascular canals have a lining of lamellar bone, forming primary osteons. In the next-largest individual (body length 3.5 m; DFMMh/FV 001), the primary osteons in the fibrolamellar complex are mature with a narrow central vascular canal. Notably, there are two cyclical growth marks (annuli) in the fibrolamellar bone of the outer cortex.

A slightly larger individual (body length 3.7 m; DFMMh/FV 495) was sampled from its tibia and femur. Both bones have the same histology of laminar fibrolamellar bone interrupted by growth marks (Fig. 2b), the spacing of which diminishes towards the outer bone surface, indicating a decrease in growth rate. However, the vascular canals in the outermost cortex are large and open to the bone surface, indicating active growth at the time of death. The next-largest individual (body length 4.6 m; DFMMh/FV 153) has the same primary bone histology as the previous ones, preserving five growth

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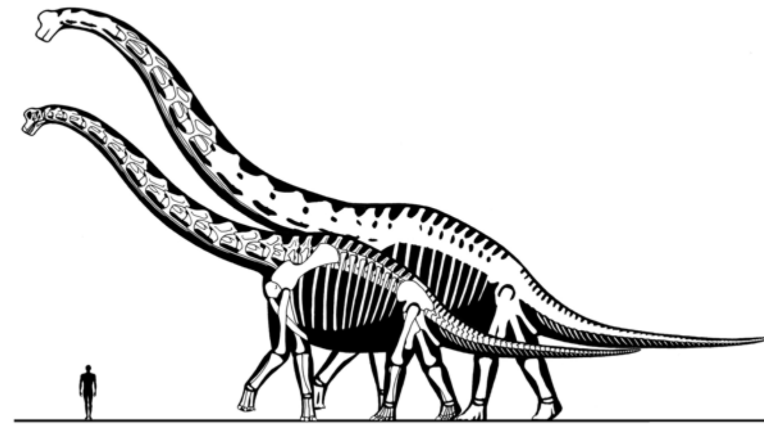

Gigantism and land mass

Vol 441|8 June 2006|doi:10.1038/nature04633 nature

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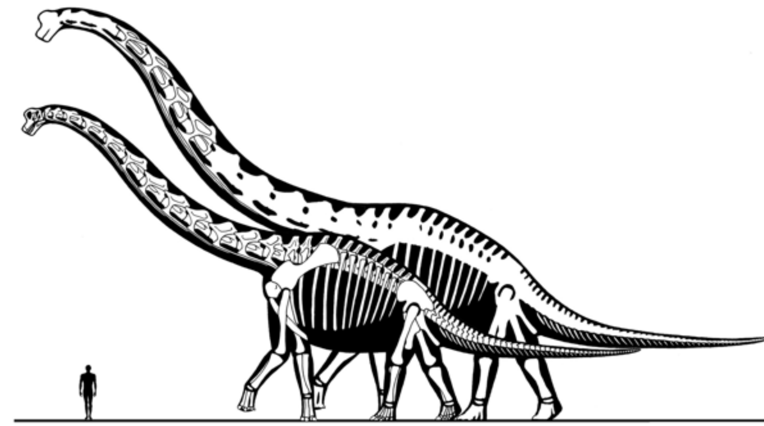
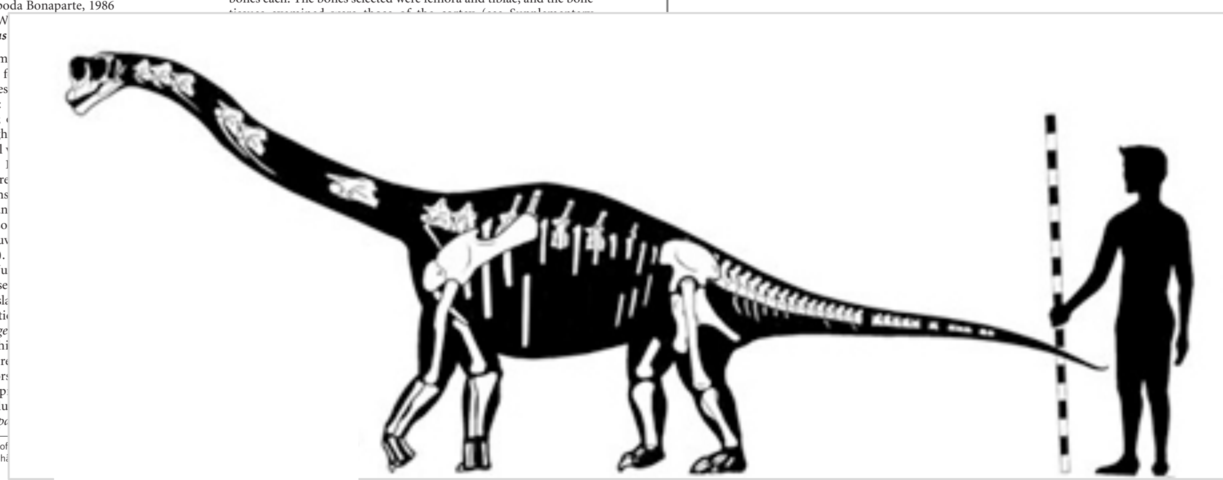
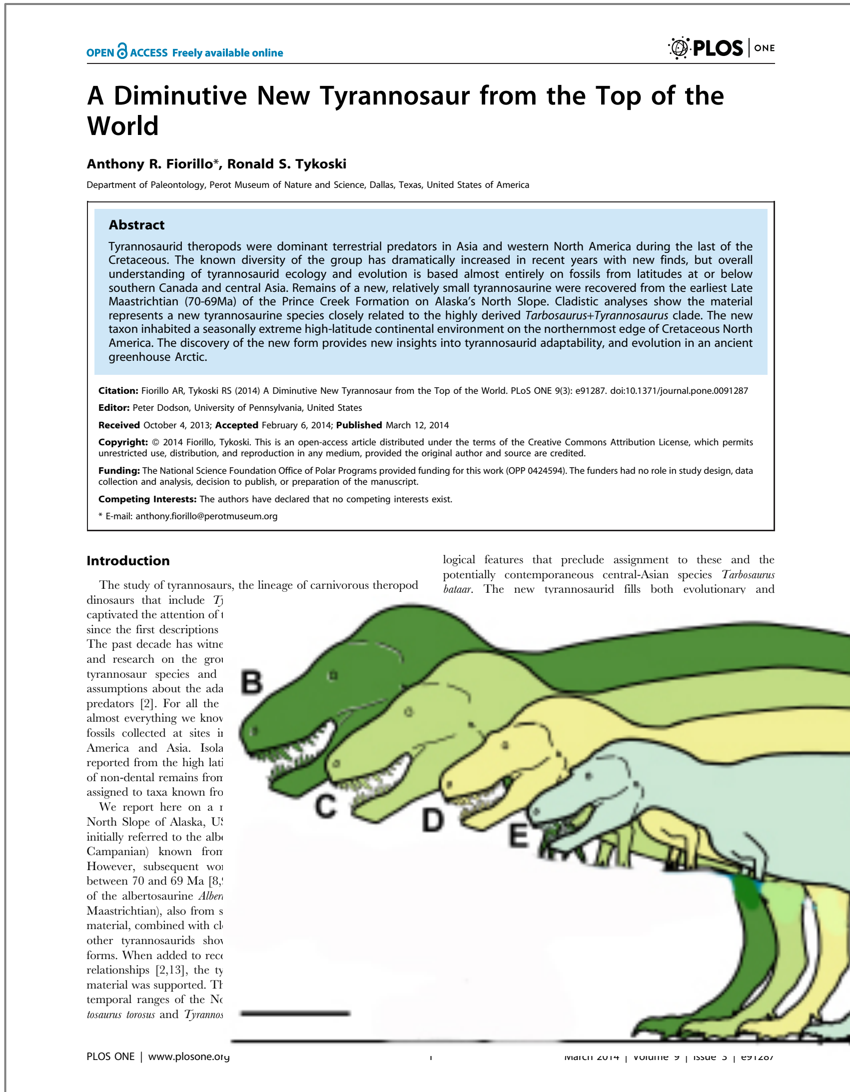




Gigantism and land mass



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A Diminutive New Tyrannosaur from the Top of the World

Anthony R. Fiorillo*, **Ronald S. Tykoski**

Department of Paleontology, Perot Museum of Nature and Science, Dallas, Texas, United States of America

Abstract

Tyrannosaurid theropods were dominant terrestrial predators in Asia and western North America during the last of the Cretaceous. The known diversity of the group has dramatically increased in recent years with new finds, but overall understanding of tyrannosaurid ecology and evolution is based almost entirely on fossils from latitudes at or below southern Canada and central Asia. Remains of a new, relatively small tyrannosaurine were recovered from the earliest Late Maastrichtian (70-69Ma) of the Prince Creek Formation on Alaska's North Slope. Cladistic analyses show the material represents a new tyrannosaurine species closely related to the highly derived *Tarbosaurus*+*Tyrannosaurus* clade. The new taxon inhabited a seasonally extreme high-latitude continental environment on the northernmost edge of Cretaceous North America. The discovery of the new form provides new insights into tyrannosaurid adaptability, and evolution in an ancient greenhouse Arctic.

Citation: Fiorillo AR, Tykoski RS (2014) A Diminutive New Tyrannosaur from the Top of the World. PLoS ONE 9(3): e91287. doi:10.1371/journal.pone.0091287

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Competing Interests: The authors have declared that no competing interests exist.

* E-mail: anthony.fiorillo@perotmuseum.org

Introduction

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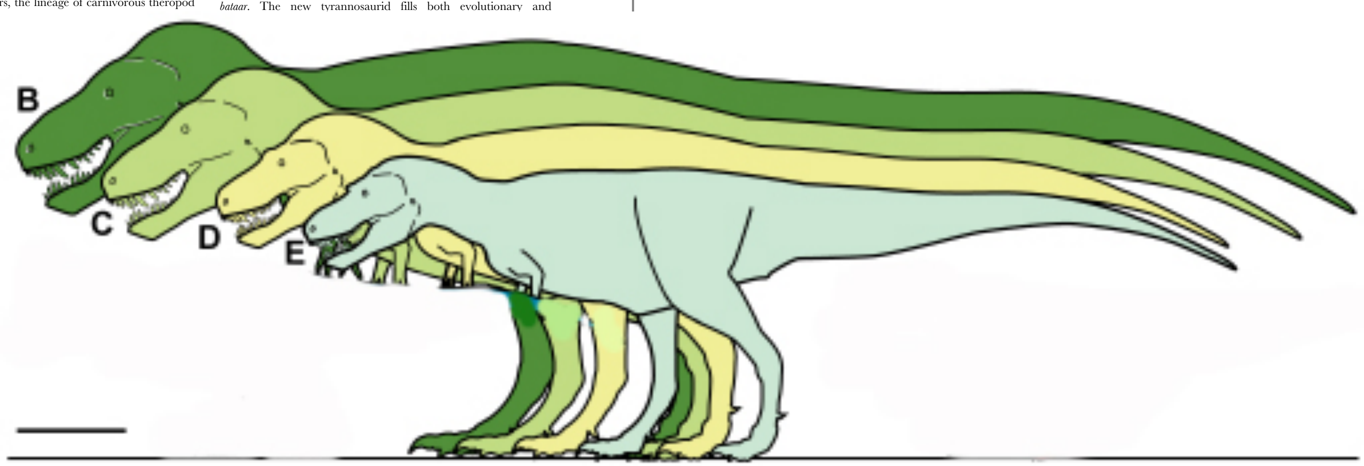
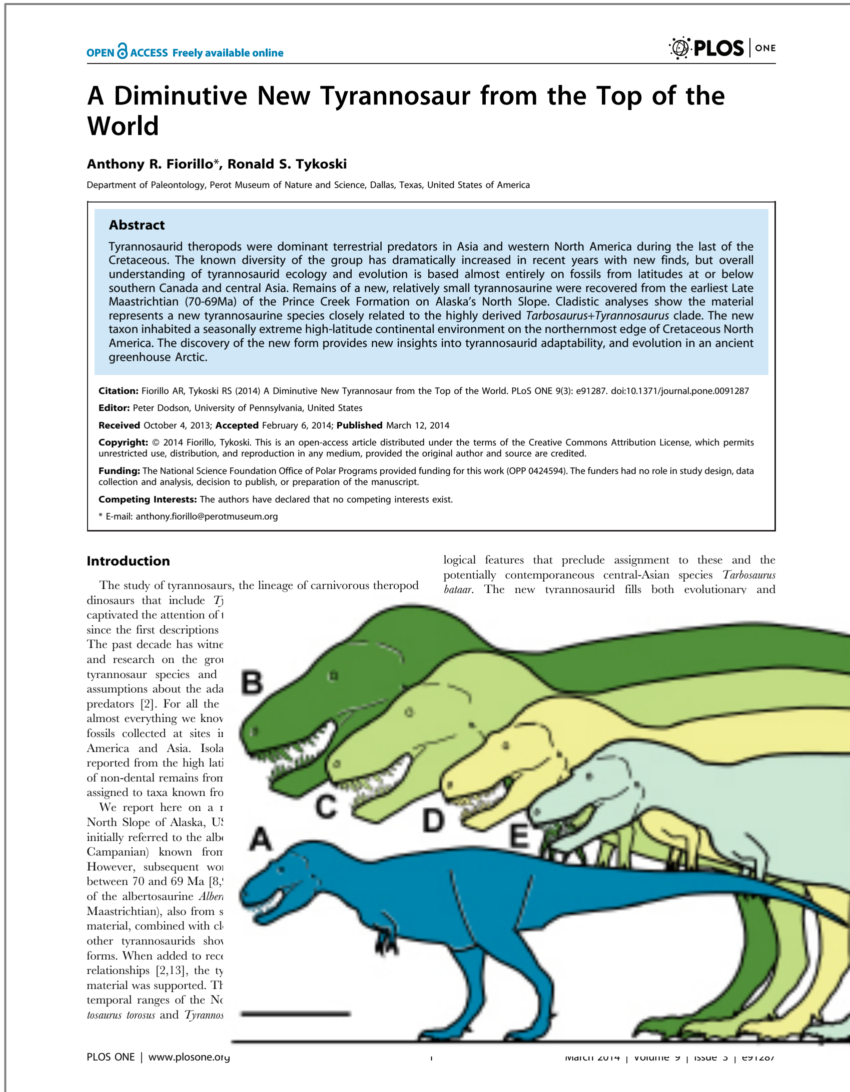


Gigantism and land mass



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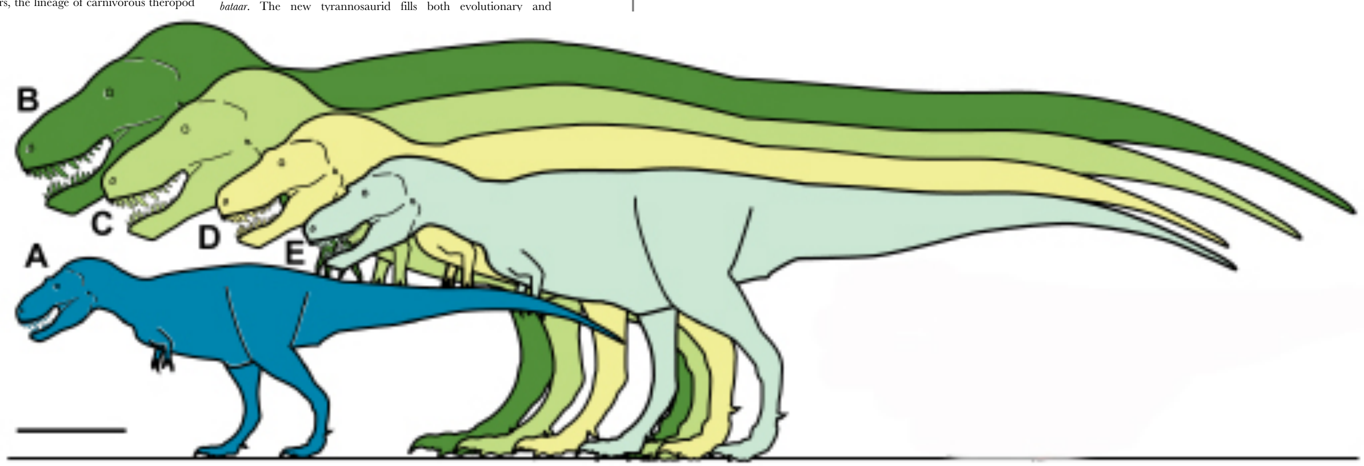
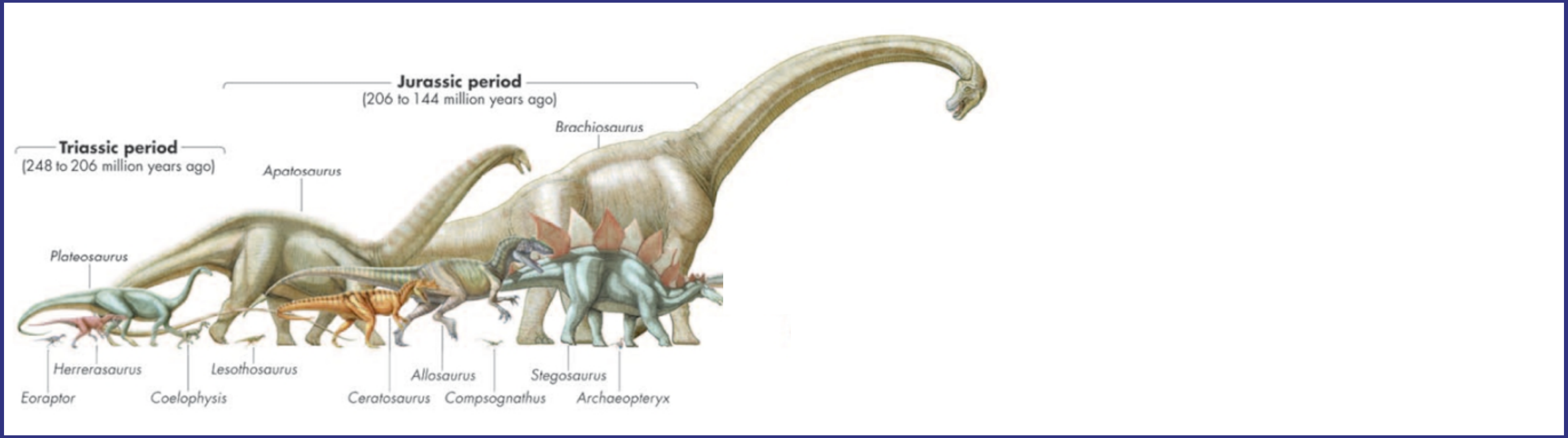


Tectonic changes



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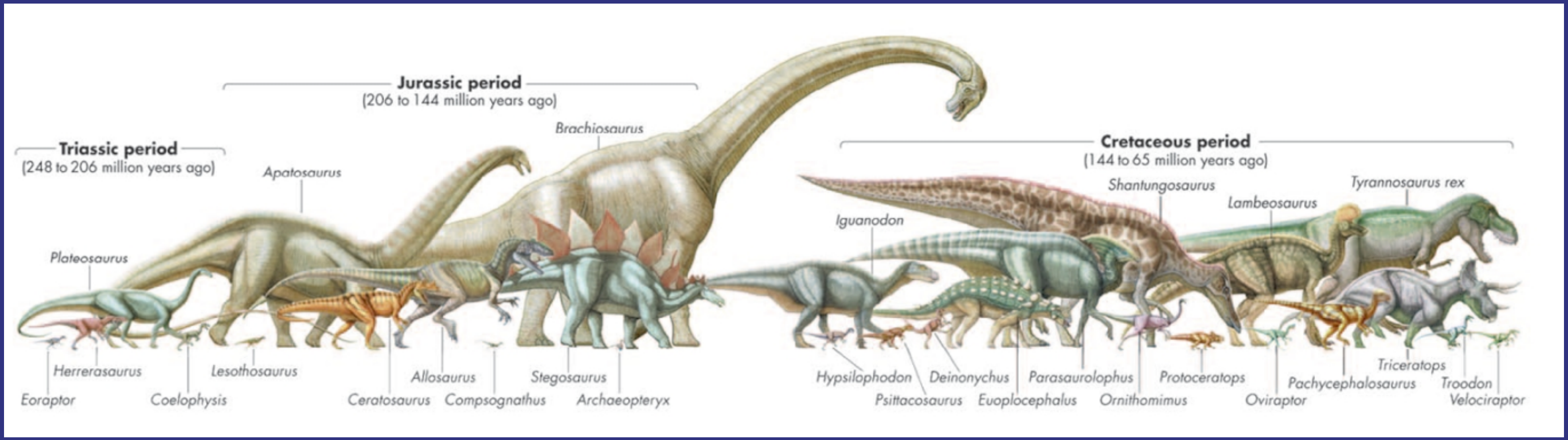


To become gigantic ...

- ... the niche must be empty
- ... you need resources

To become gigantic ...

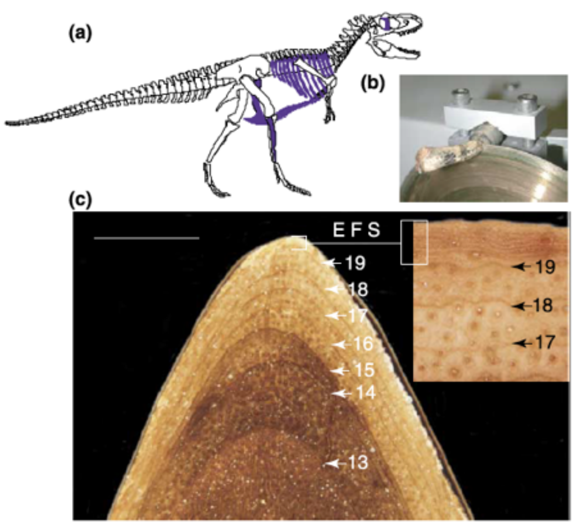
- ... the niche must be empty
- ... you need resources
- ... you have to grow (fast)

Fast growth

Gigantism and comparative life-history parameters of tyrannosaurid dinosaurs

Gregory M. Erickson[1,2], Peter J. Makovicky[3], Philip J. Currie[4], Mark A. Norell[2], Scott A. Yerby[5] & Christopher A. Brochu[6]

NATURE | VOL 430 | 12 AUGUST 2004



Fast growth

Gigantism and comparative life-history parameters of tyrannosaurid dinosaurs

Gregory M. Erickson[1,2], Peter J. Makovicky[3], Philip J. Currie[4], Mark A. Norell[2], Scott A. Yerby[5] & Christopher A. Brochu[6]

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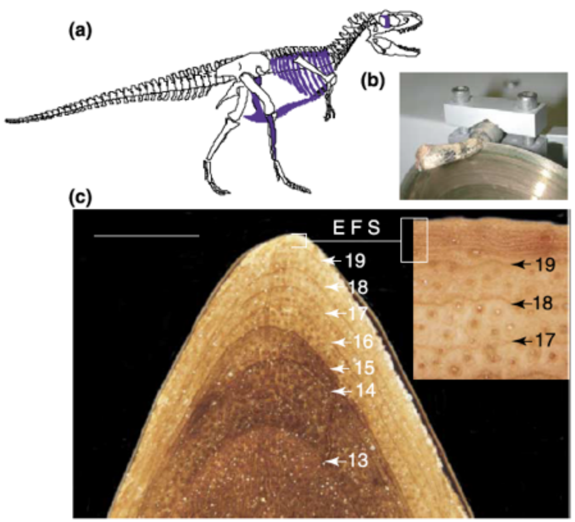

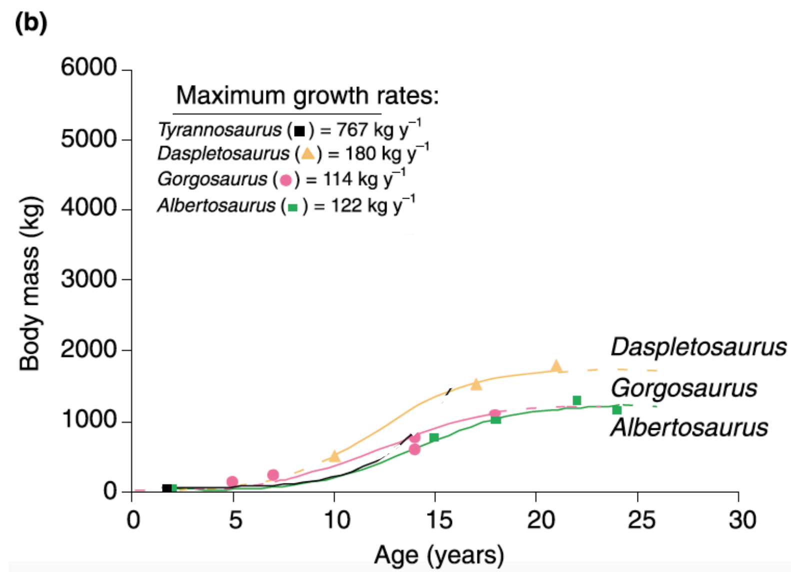

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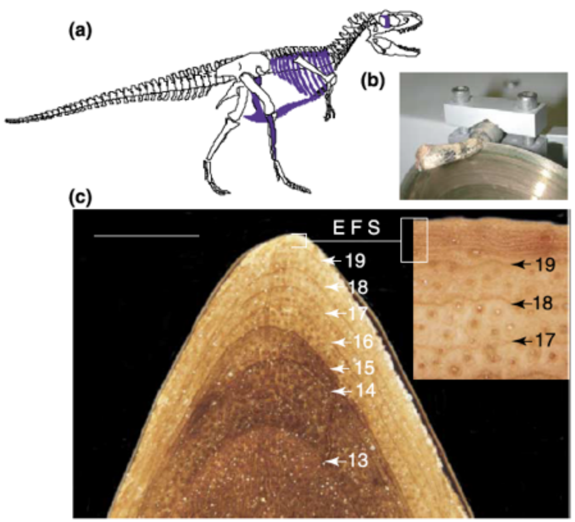
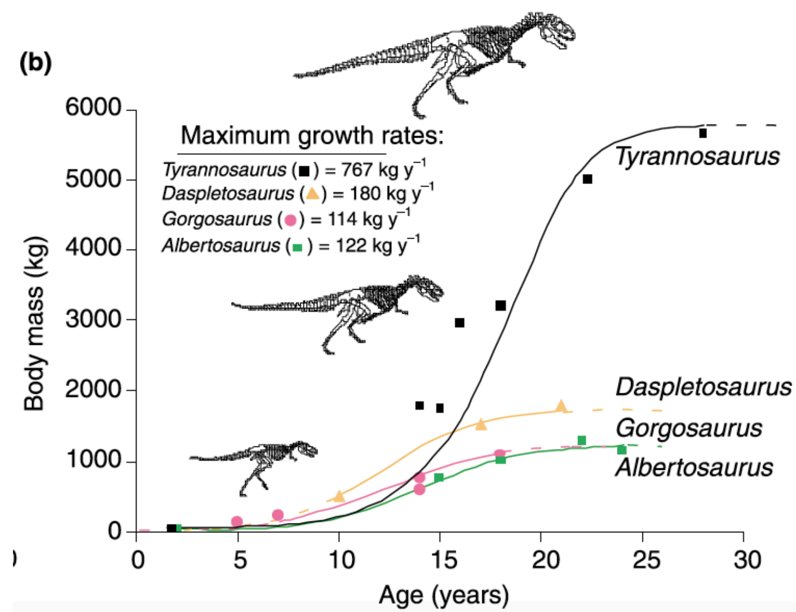




Fast growth

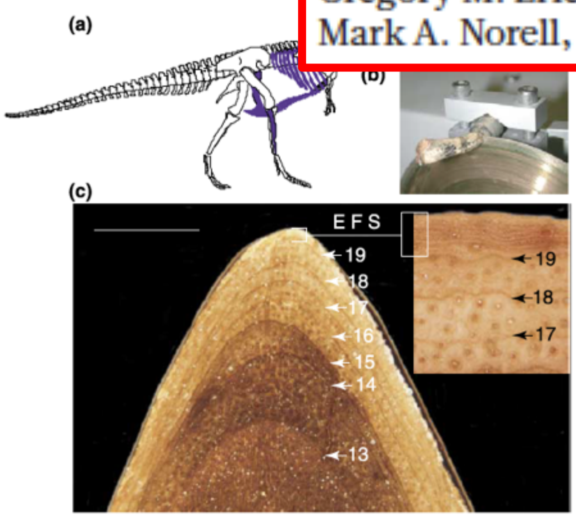
Gigantism and comparative life-history parameters of tyrannos

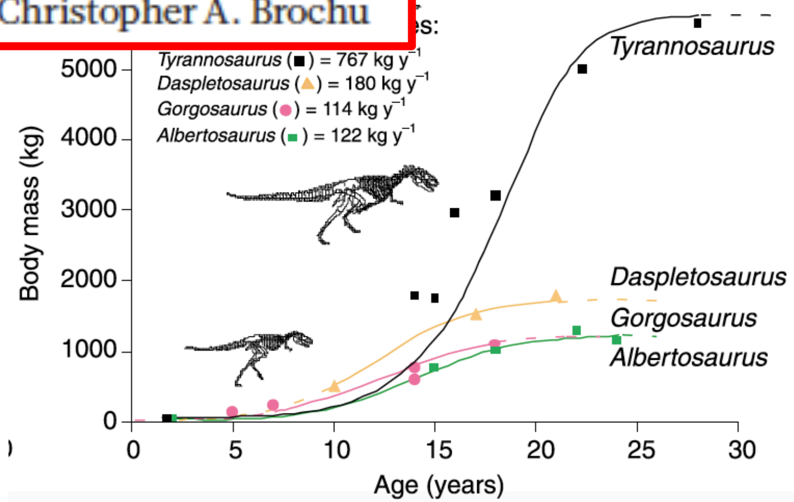
Gregory M. Erick
Mark A. Norell[2],

NATURE | VOL 430 | 12

Corrigendum: Gigantism and comparative life-history parameters of tyrannosaurid dinosaurs

Gregory M. Erickson, Peter J. Makovicky, Philip J. Currie, Mark A. Norell, Scott A. Yerby & Christopher A. Brochu



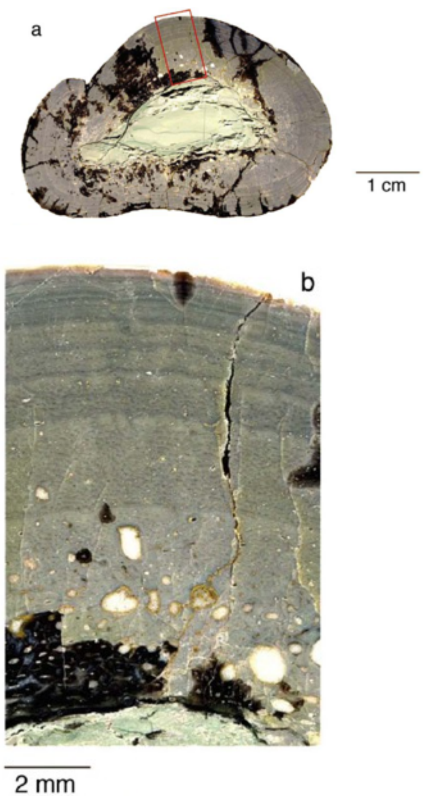


Fast growth

Adaptive radiation in sauropod dinosaurs: bone histology indicates rapid evolution of giant body size through acceleration

P. Martin Sander[a,*], Nicole Klein[a], Eric Buffetaut[b], Gilles Cuny[c,d], Varavudh Suteethorn[e], Jean Le Loeuff[f]

Organisms, Diversity & Evolution 4 (2004) 165–173



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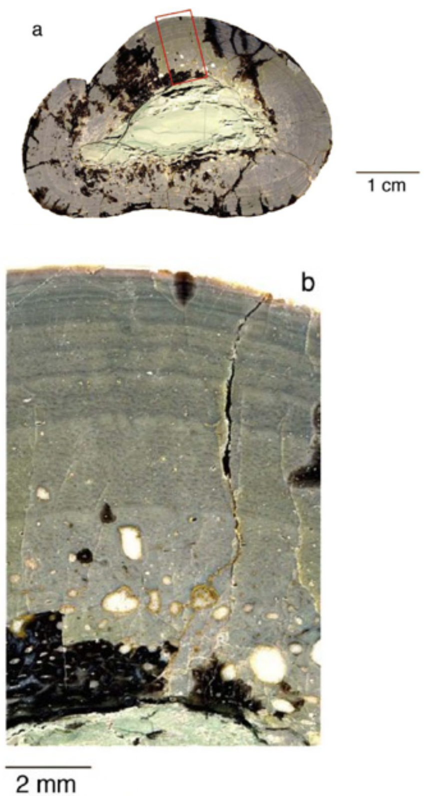

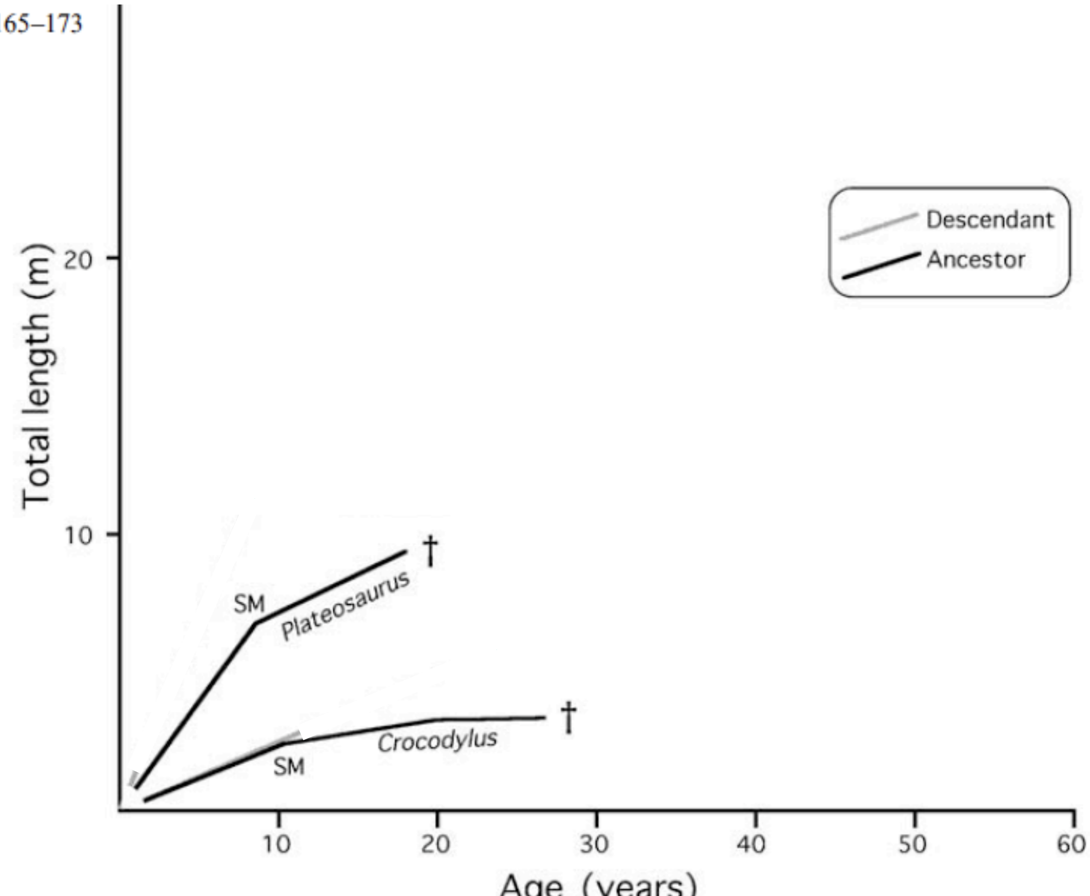

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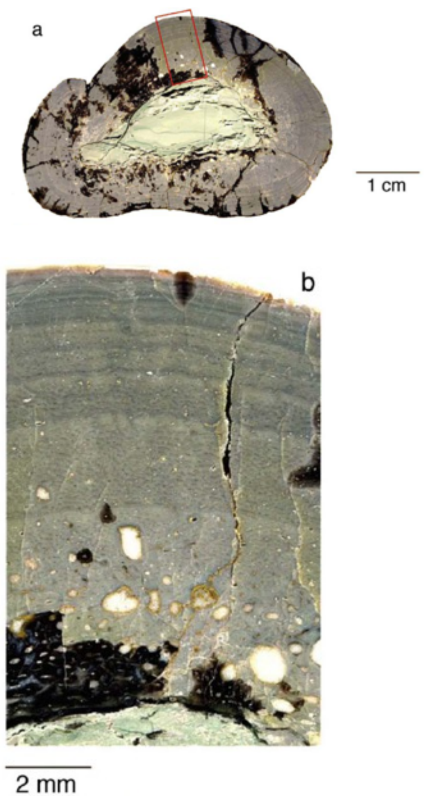

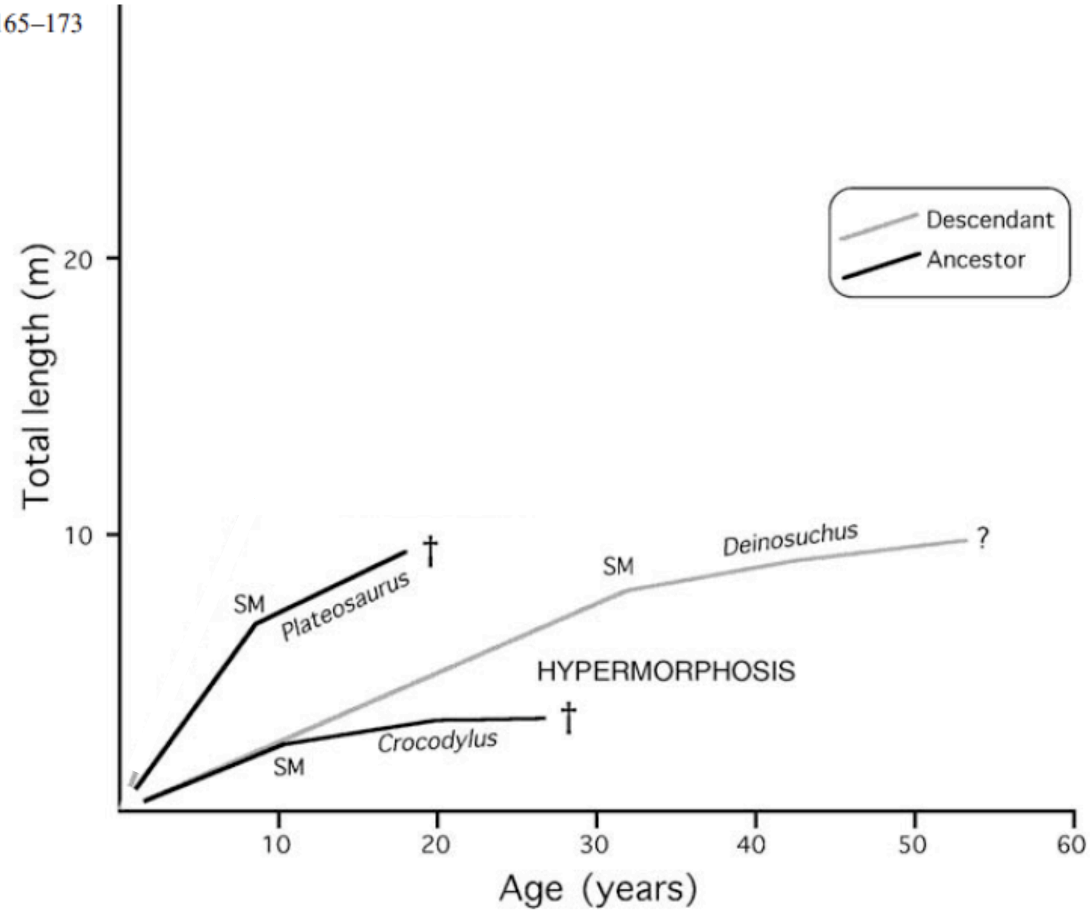

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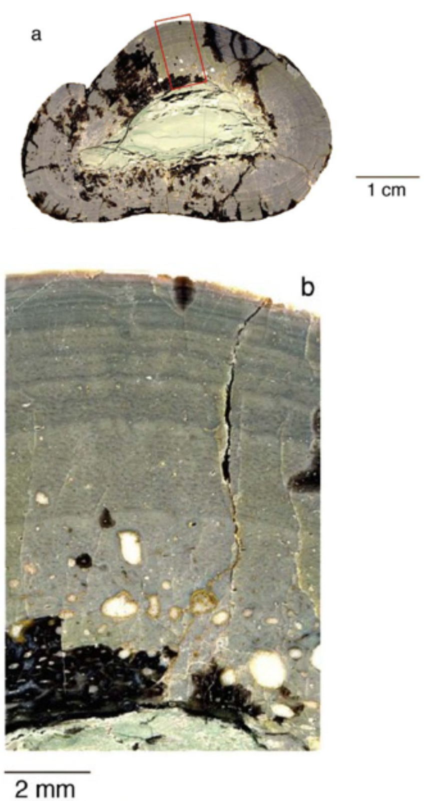

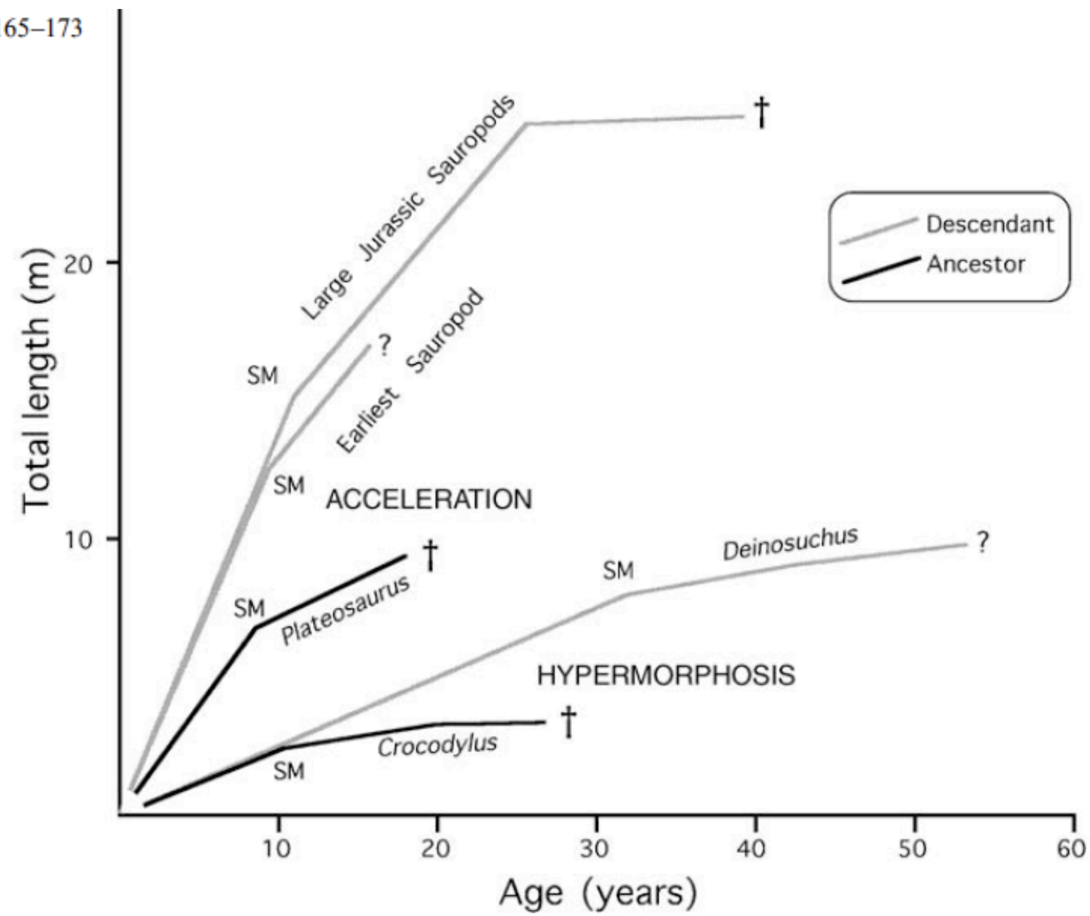

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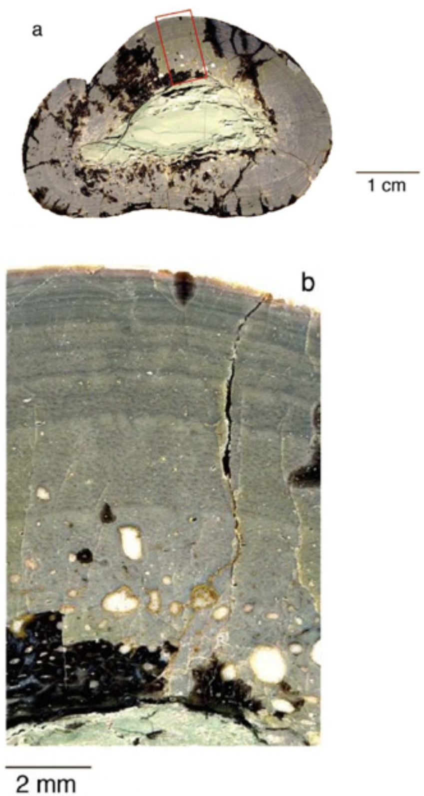
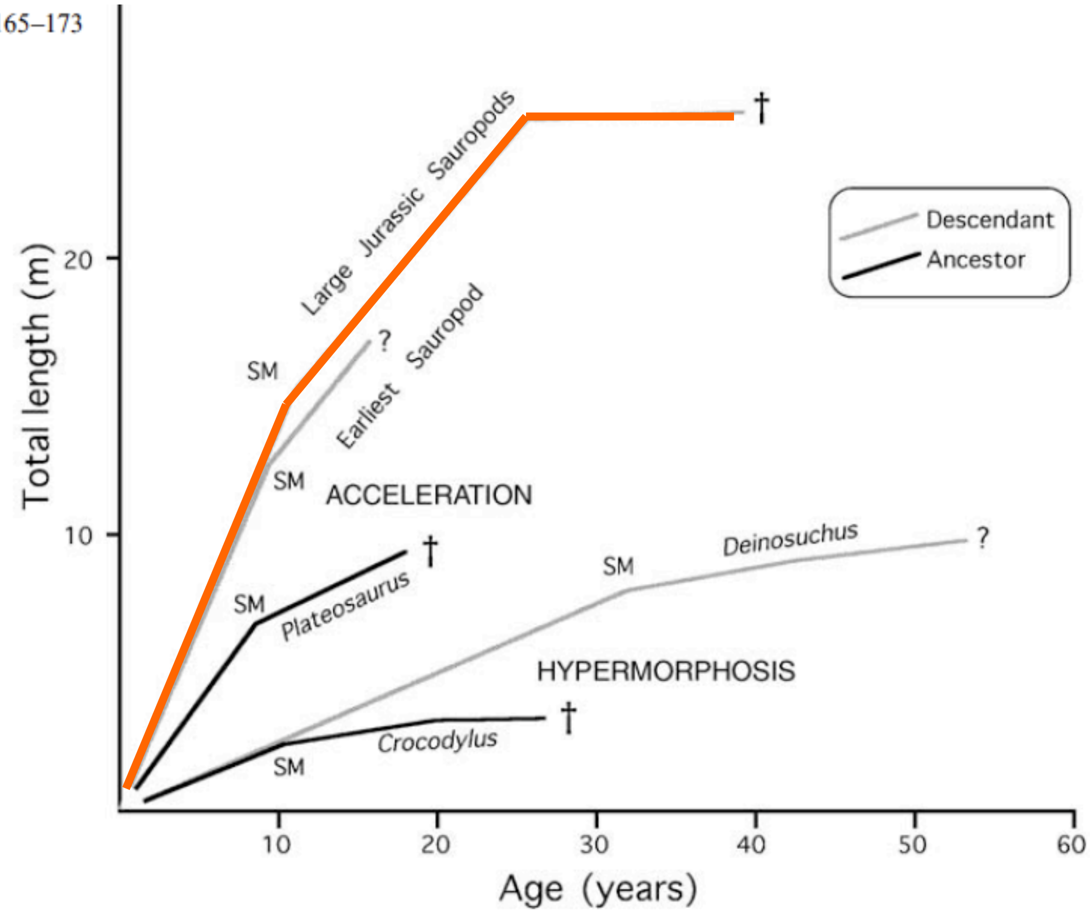
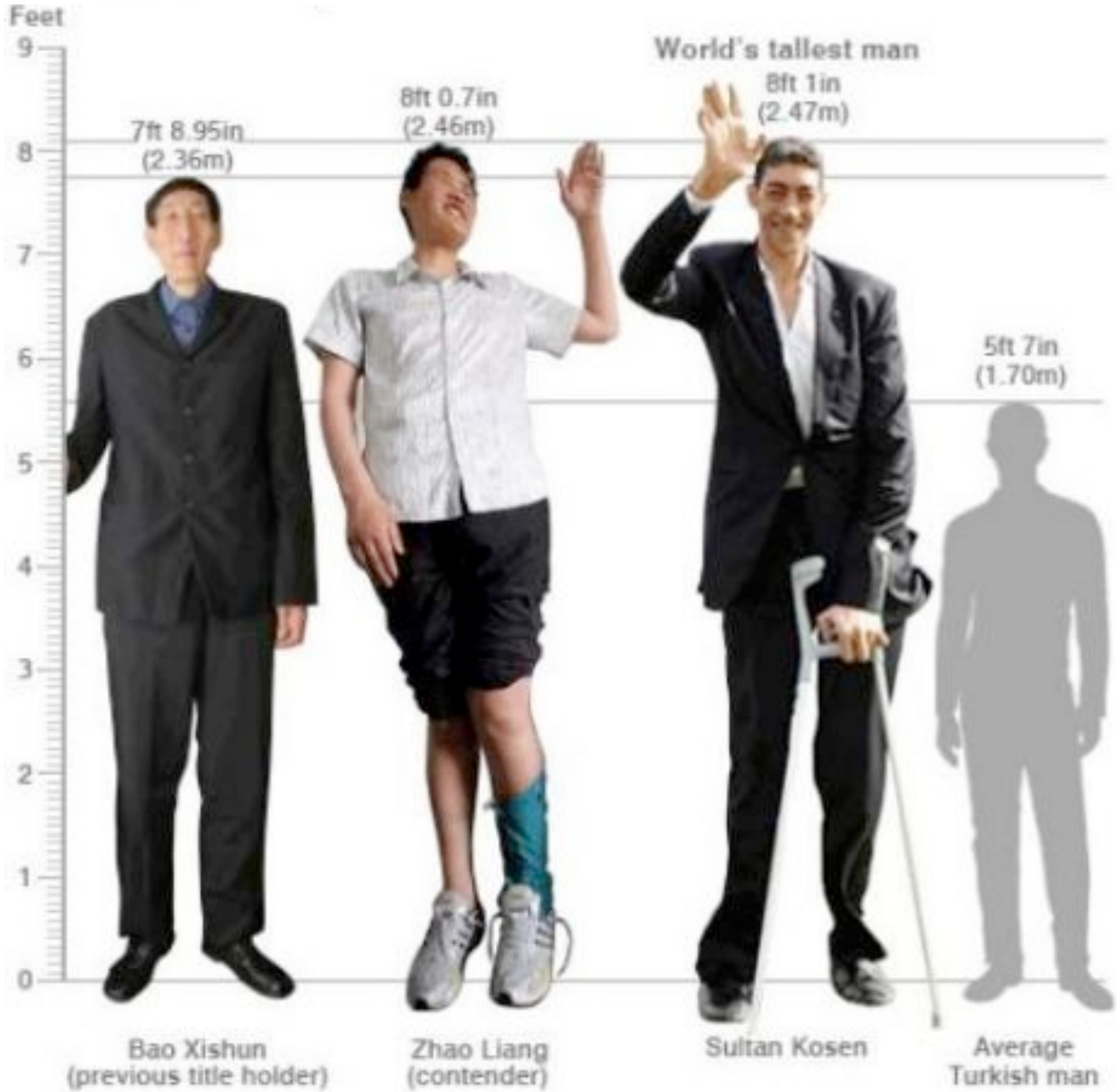




Growth speed

Growth speed



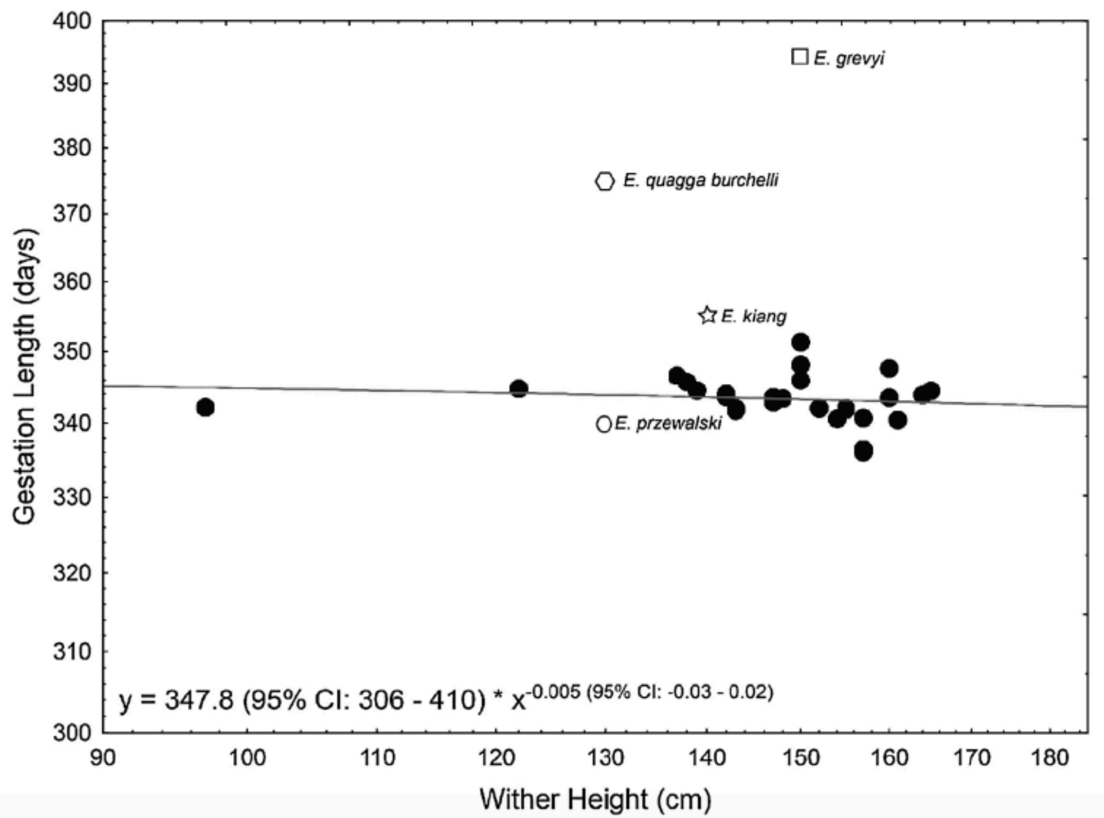
Within species (with determinate growht), large individuals do not grow longer but faster!

Growth speed

Gestation length variation in domesticated horses and its relation to breed and body size diversity

Laura Heck[a,*], Marcus Clauss[b], Marcelo R. Sánchez-Villagra[a]

Mammalian Biology 84 (2017) 44–51



Within species (with determinate growht), large breeds do not grow longer but faster!

Growth speed

Days of gestation period (to apparently similar level of precociality)

Cattle:
Horse:
Dromedary:
Okapi:

Growth speed

Days of gestation period (to apparently similar level of precociality)

Cattle: app. 280 days

Horse:

Dromedary:

Okapi:

Growth speed

Days of gestation period (to apparently similar level of precociality)

Cattle:	app. 280 days
Horse:	app. 340 days
Dromedary:	
Okapi:	

Growth speed

Days of gestation period (to apparently similar level of precociality)

Cattle:	app. 280 days
Horse:	app. 340 days
Dromedary:	app. 390 days
Okapi:	

Growth speed

Days of gestation period (to apparently similar level of precociality)

Cattle:	app. 280 days
Horse:	app. 340 days
Dromedary:	app. 390 days
Okapi:	app. 440 days

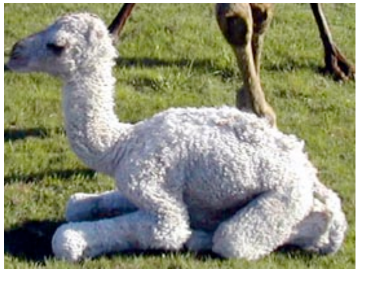
Growth speed

Days of gestation period (to apparently similar level of precociality)

Cattle:	app. 280 days
Horse:	app. 340 days
Dromedary:	app. 390 days
Okapi:	app. 440 days

Nobody knows why.






Growth speed

Days of gestation period (to apparently similar level of precociality)

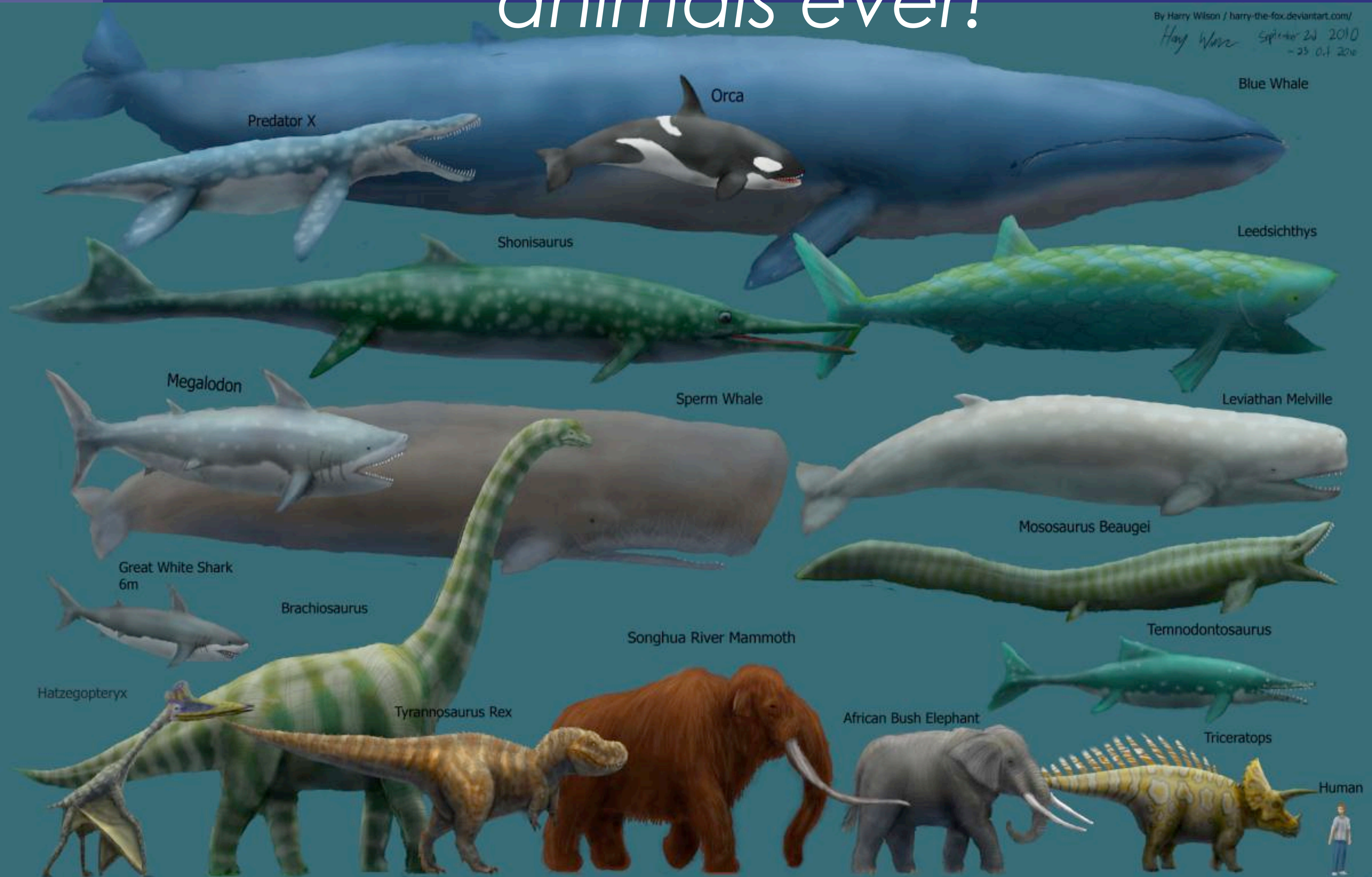
Cattle:	app. 280 days
Horse:	app. 340 days
Dromedary:	app. 390 days
Okapi:	app. 440 days

Nobody knows why.

But it is evident that there are large differences between species in intra-uterine growth speed.




Dinosaurs were not the biggest animals ever!

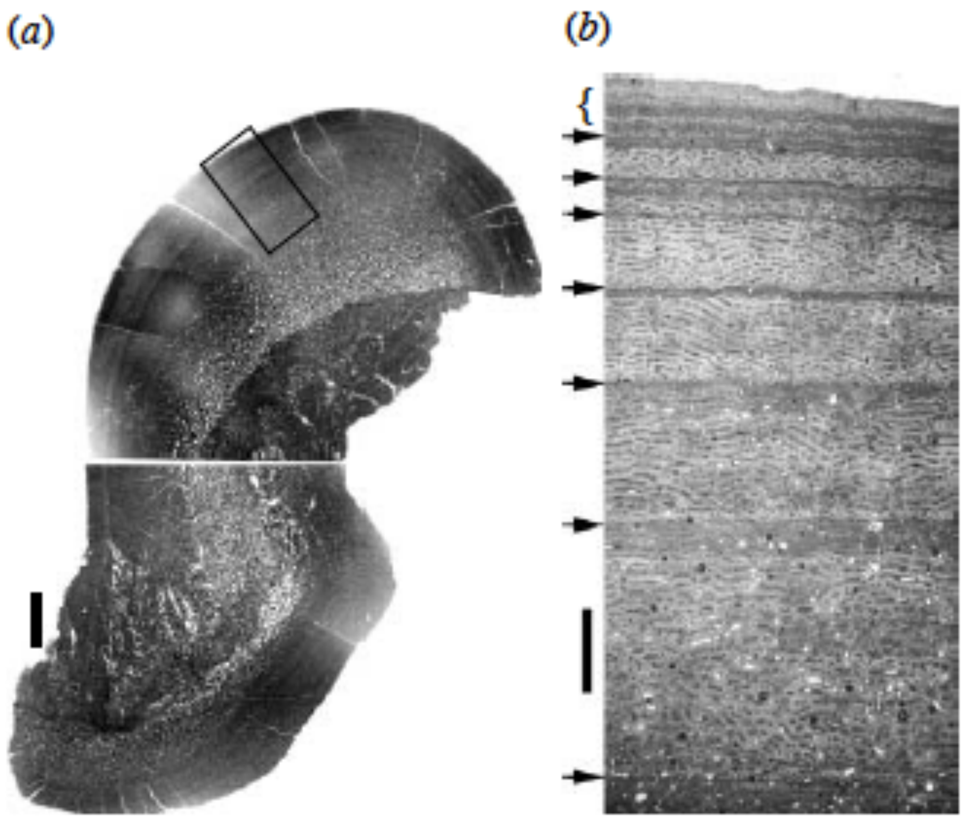


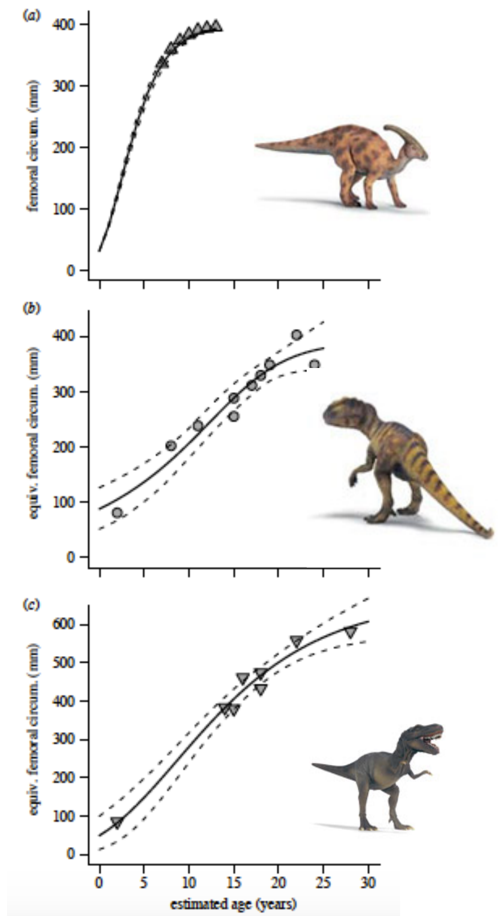
Fast growth

Relative growth rates of predator and prey dinosaurs reflect effects of predation

Lisa Noelle Cooper[1,2], Andrew H. Lee[3,*], Mark L. Taper[4] and John R. Horner[5]

Proc. R. Soc. B (2008) 275, 2609–2615





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Revisiting the Estimation of Dinosaur Growth Rates

Nathan P. Myhrvold*

Intellectual Ventures, Bellevue, Washington, United States of America

Abstract

Previous growth-rate studies covering 14 dinosaur taxa, as represented by 31 data sets, are critically examined and reanalyzed by using improved statistical techniques. The examination reveals that some previously reported results cannot be replicated by using the methods originally reported; results from new methods are in many cases different, in both the quantitative rates and the qualitative nature of the growth, from results in the prior literature. Asymptotic growth curves, which have been hypothesized to be ubiquitous, are shown to provide best fits for only four of the 14 taxa. Possible reasons for non-asymptotic growth patterns are discussed; they include systematic errors in the age-estimation process and, more likely, a bias toward younger ages among the specimens analyzed. Analysis of the data sets finds that only three taxa include specimens that could be considered skeletally mature (*i.e.*, having attained 90% of maximum body size predicted by asymptotic curve fits), and eleven taxa are quite immature, with the largest specimen having attained less than 62% of predicted asymptotic size. The three taxa that include skeletally mature specimens are included in the four taxa that are best fit by asymptotic curves. The totality of results presented here suggests that previous estimates of both maximum dinosaur growth rates and maximum dinosaur sizes have little statistical support. Suggestions for future research are presented.

Citation: Myhrvold NP (2013) Revisiting the Estimation of Dinosaur Growth Rates. PLoS ONE 8(12): e81917. doi:10.1371/journal.pone.0081917

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Introduction

Knowledge of the life histories of extinct species has increased enormously in recent decades, advanced by bone histology [1–16] and the measurement of ontogenetic growth rates for many species [17–19]. Histological estimation of age depends primarily on analysis of features known as lines of arrested growth (LAGs) [20], which are seen in thin sections of fossilized bone [6]. Strong evidence from extant amphibians, reptiles, birds and mammals suggests that, in many dinosaur taxa, LAGs were deposited annually while the animal was alive. Even in bones in which LAGs are not visible, "polish lines" sometimes appear, and Sander has argued [21] that these also represent markers for annual growth. Although the inference that each LAG represents one year of growth is still a subject of debate [22] and the number and distribution of LAGs varies in some specimens from one bone to another or is obscured by inter-element remodeling [10,11,13–15,21–23], the analysis presented here adopts the common assumption in paleobiology that LAGs and polish lines are indeed annual markers.

Many of the other assumptions on which studies of dinosaur growth have routinely depended are more questionable, however, as are some of the statistical methodologies used. Insufficient attention has been given to problematic issues in estimating the ages and masses that dinosaurs achieved during their lives, in fitting growth curves to the data sets available, and in interpreting the results of curve fits.

Two distinct analytical approaches, the whole-bone method and the longitudinal method, have been used to gather age/size data sets, from which biological growth parameters can be calculated. Each approach involves similar steps – age estimation, mass estimation and growth curve fitting – but they differ in their details between approaches, and between studies. Both approaches require careful handling of the uncertainties involved in the estimation of ages and masses, and of the assumptions and statistical methods used to fit growth curves to observed and derived data.

Whole-bone Method

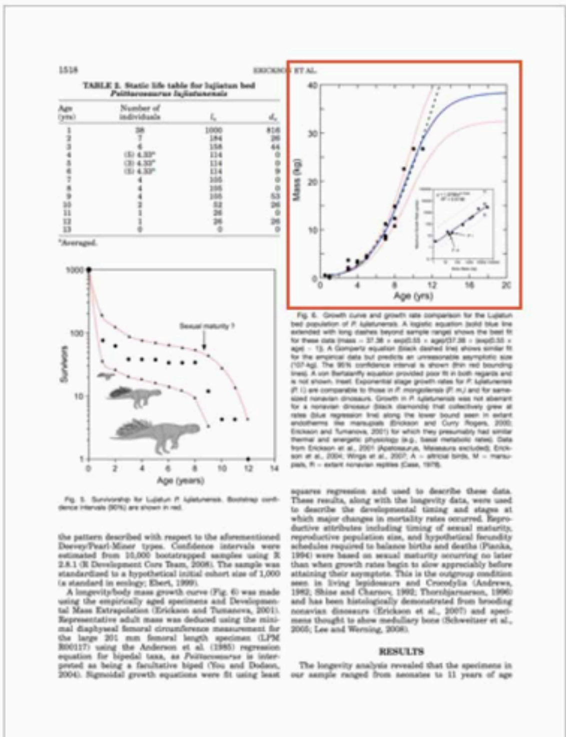
Chinsamy-Turan [6] appears to have been the first to use the "whole-bone" method to fit growth curves for dinosaurs by using the linear dimension of a whole bone as the size metric and a count of LAGs in a bone to estimate age at time of death. Erickson and Tumanova [24] extended the method to estimate the mass of an animal from the length of a long bone, and the approach was extended further in later studies [16–18,24–29]. The method has been applied to 11 dinosaur taxa by Erickson and coworkers and to three additional taxa by Bybee *et al.*, Lehman, and Lee and Werning (Table 1). Werning [30] and Lee and Werning [31] applied a variation of the whole-bone method to the ornithopod *Tenontosaurus* (without the developmental mass extrapolation (DME) step, discussed below), although bone dimensions have not been published. Bybee *et al.* [32] presented data that can be used for the method.

Although details of the whole-bone method vary slightly in the literature, it generally includes two or more of the following steps:

(1) **Estimate ages.** LAGs are counted by microscopic examination of thin sections of bone, typically cut from the femur but sometimes from other bones. Age at the time of death is then estimated by adjusting or supplementing the raw LAG count:

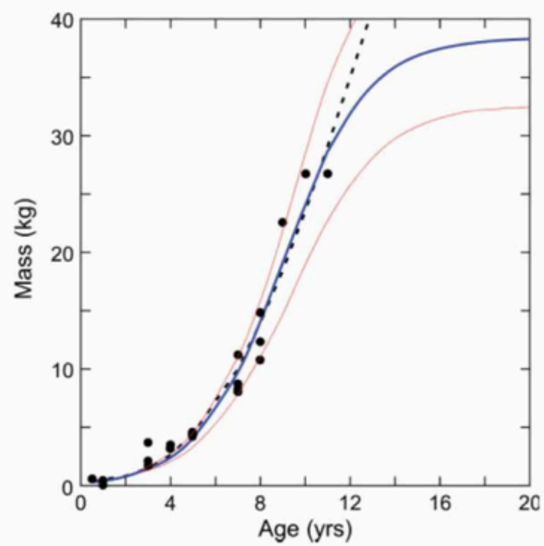
Dinosaurs and Statistics

A new paper by Nathan P. Myhrvold, the former chief technology officer of Microsoft, highlights possible statistical problems in a series of papers on dinosaur growth rates. Two examples are shown below. Related Article »



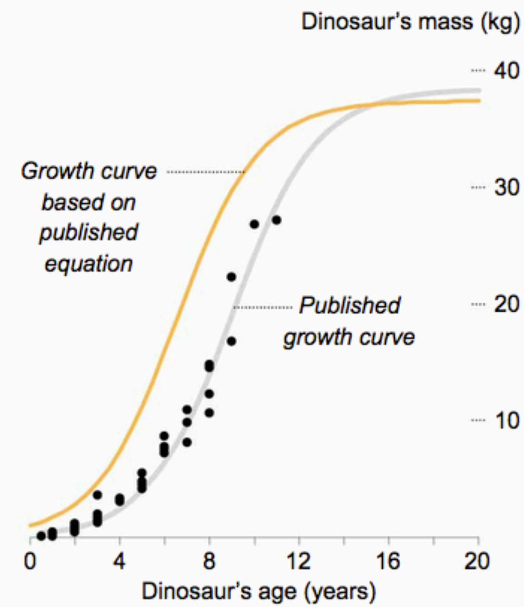
AN EXAMPLE FROM 2009

One questioned paper, published in the Anatomical Record, includes a chart showing the growth rate (—) of Psittacosaurus lujiatunensis, a beaked dinosaur. The data points are shown below in black.



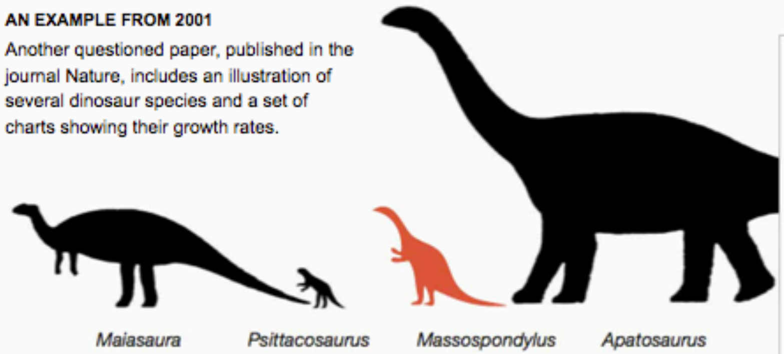
RECREATING THE CHART

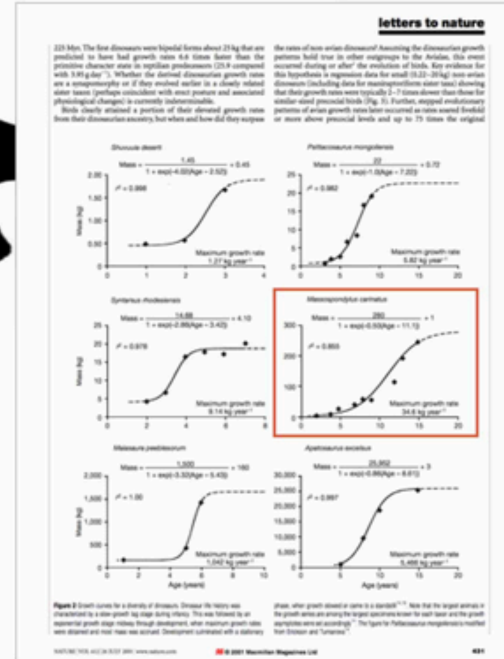
But when Dr. Myhrvold tried to recreate the curve using the equation given in the paper, the resulting growth curve (—) was very different.



AN EXAMPLE FROM 2001

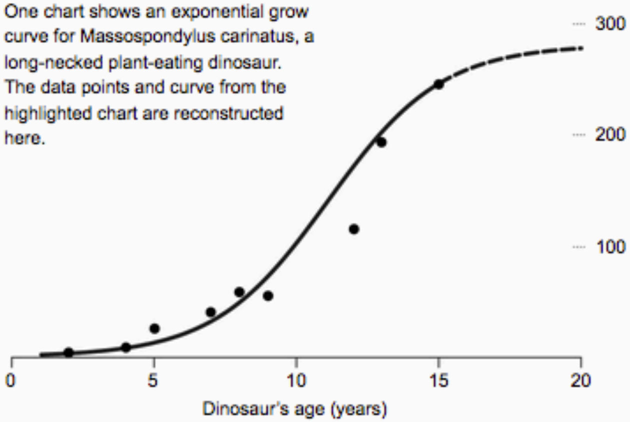
Another questioned paper, published in the journal Nature, includes an illustration of several dinosaur species and a set of charts showing their growth rates.





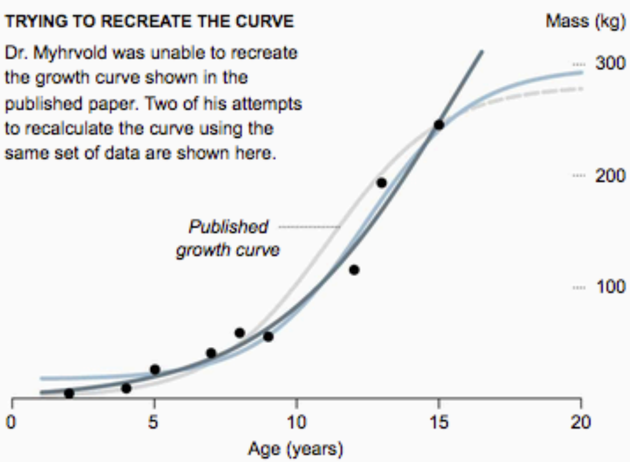
PUBLISHED GROWTH CURVE

One chart shows an exponential grow curve for Massospondylus carinatus, a long-necked plant-eating dinosaur. The data points and curve from the highlighted chart are reconstructed here.



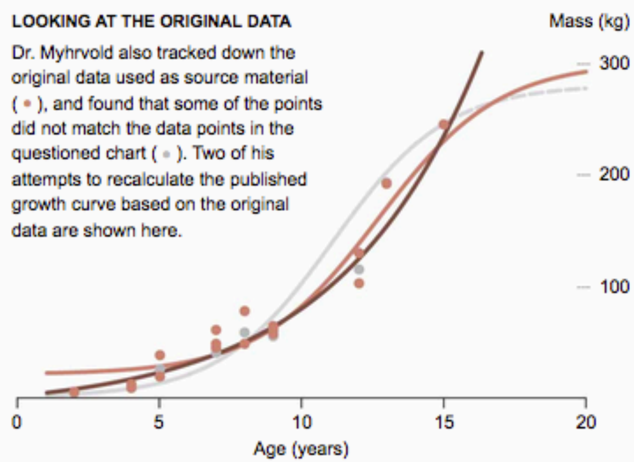
TRYING TO RECREATE THE CURVE

Dr. Myhrvold was unable to recreate the growth curve shown in the published paper. Two of his attempts to recalculate the curve using the same set of data are shown here.



LOOKING AT THE ORIGINAL DATA

Dr. Myhrvold also tracked down the original data used as source material (•), and found that some of the points did not match the data points in the questioned chart (•). Two of his attempts to recalculate the published growth curve based on the original data are shown here.



About two and half years ago, Dr. Myhrvold came across a 2009 paper by Dr. Erickson as he was trying to answer the question, “Why were dinosaurs big?” He said data in two of the graphs, one plotting the length of the thigh bone versus age, the other mass versus age, conflicted with each other. “I instantly knew that this couldn’t be correct,” Dr. Myhrvold said.

Dr. Myhrvold said he contacted Dr. Erickson, asking for the original data. While Dr. Erickson answered some questions, he said the data was on a computer he had gotten rid of and later that he did not have time to answer more questions, Dr. Myhrvold said.

Dr. Myhrvold was able to obtain some of the data from other researchers and thought he could do a better statistical analysis. Last year, he submitted a paper with his calculations — a fairly esoteric scientific disagreement about how best to extract reasonable generalizations from a limited number of fossils.

Dr. Erickson was one of the reviewers and argued strongly against publication. While praising Dr. Myhrvold’s accomplishments and saying the calculations appeared to be numerically correct, Dr. Erickson said the paper would not advance scientific understanding.

“In fact it will hurt our field by producing inherently flawed growth curves, misrepresenting the work of others, and stands to drive a wedge between labs that are currently cordial with one another,” he wrote.

CORRIGENDUM

doi:10.1038/nature16488

Corrigendum: Dinosaurian growth patterns and rapid avian growth rates

Gregory M. Erickson, Kristina Curry Rogers & Scott A. Yerby

Nature **412**, 429–433 (2001); doi:10.1038/35086558

Questions have been raised about the methods used in the construction of dinosaurian growth curves in this Letter[1]. These were caused by ambiguity with regard to how curve-fitting functions were utilized, and insufficient explanation for how maximum growth rates were calculated. Taken together, these omissions gave the impression that we were able to fit very specific curves even in cases where data were seemingly too scarce to justify them. We apologise for the confusion. However, the main conclusions of the paper were not affected. A detailed rationale is available in the Supplementary Methods and Supplementary Discussion of this Corrigendum and the source data are provided as Supplementary Data. We thank N. Myhrvold for bringing these issues to our attention.

In our reanalysis we found the following translational mistakes, which do not appear to have contributed to Myhrvold's concerns; however, we take this opportunity to rectify them. The growth rates for *Psittacosaurus mongoliensis* were incorrectly reported as $5.82\,\mathrm{kg\,yr^{-1}}$ versus $5.28\,\mathrm{kg\,yr^{-1}}$ in Fig. 2 and $12.5\,\mathrm{g\,d^{-1}}$ in the legend to Fig. 3. Fortunately, the correct value of $14.1\,\mathrm{g\,d^{-1}}$ was used in the comparative regression calculations. Finally, the mass estimate used for one of the *Apatosaurus* specimens was incorrectly transcribed. This modestly affected the growth curve parameters in Fig. 2. Details can be found in the Supplementary Methods and Discussion to this Corrigendum along with the corrected Fig. 2. The change causes a negligible shift in the overall dinosaur regression line slope (see the Supplementary Data to this Corrigendum) and does not compromise our conclusion that dinosaurs grew like endotherms.

Supplementary Information is available in the online version of the Corrigendum.

1. Myhrvold, N. P. Revisiting the estimation of dinosaur growth rates. *PLoS ONE* **8**, http://dx.doi.org/10.1371/journal.pone.0081917 (2013).

CORRIGENDUM

doi:10.1038/nature16487

Corrigendum: Gigantism and comparative life-history parameters of tyrannosaurid dinosaurs

Gregory M. Erickson, Peter J. Makovicky, Philip J. Currie, Mark A. Norell, Scott A. Yerby & Christopher A. Brochu

Nature **430**, 772–775 (2004); doi:10.1038/nature02699

Questions have been raised about the methods used and conclusions reached in this Letter[1]. In revisiting the work, we realized that we did not provide sufficient methodological details regarding the many steps that went into our growth curve analysis, although the main conclusions of the paper were not affected. We regret any misunderstanding that might have resulted. A detailed rationale is available in the Supplementary Methods and Discussion of this Corrigendum and the source data are provided as Supplementary Data. We thank N. Myhrvold for bringing these issues to our attention.

In our reanalysis we found a minor translational mistake affecting the reported growth for *Tyrannosaurus*, which does not appear to have contributed to Myhrvold's concerns (details can be found in the Supplementary Methods and Discussion to this Corrigendum.) The correct equation is $\mathrm{Mass} = (5{,}649/[1 + e^{-0.55(\mathrm{Age}-16.2)}]) + 5$. This produces a maximal growth rate of $758\,\mathrm{kg\,yr^{-1}}$ using points closely bounding the inflection point and $774\,\mathrm{kg\,yr^{-1}}$ using the instantaneous equation. The reported value was $767\,\mathrm{kg\,yr^{-1}}$. This slight discrepancy (see the corrected Fig. 2 in the Supplementary Methods and Discussion to this Corrigendum) does not compromise our conclusion that *Tyrannosaurus* primarily achieved gigantism through evolutionary acceleration.

Supplementary Information is available in the online version of the Corrigendum.

1. Myhrvold, N. P. Revisiting the estimation of dinosaur growth rates. *PLoS ONE* **8**, http://dx.doi.org/10.1371/journal.pone.0081917 (2013).

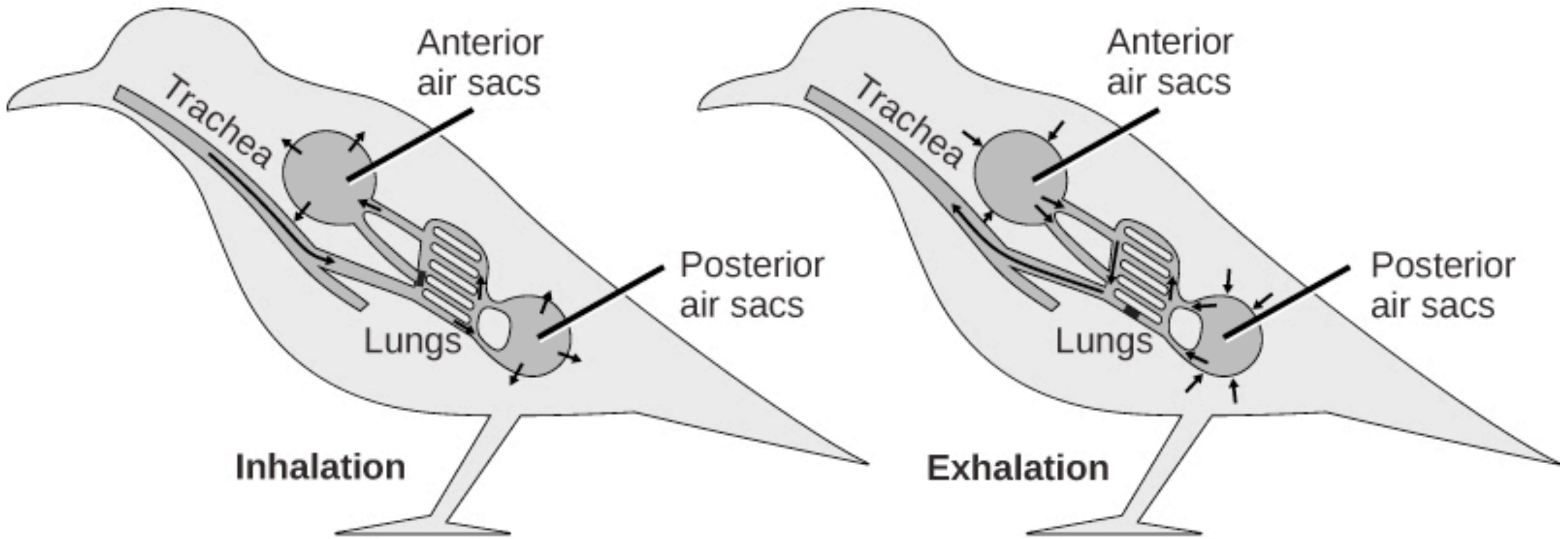
To become gigantic ...

- ... the niche must be empty
- ... you need resources
- ... you have to grow (fast)

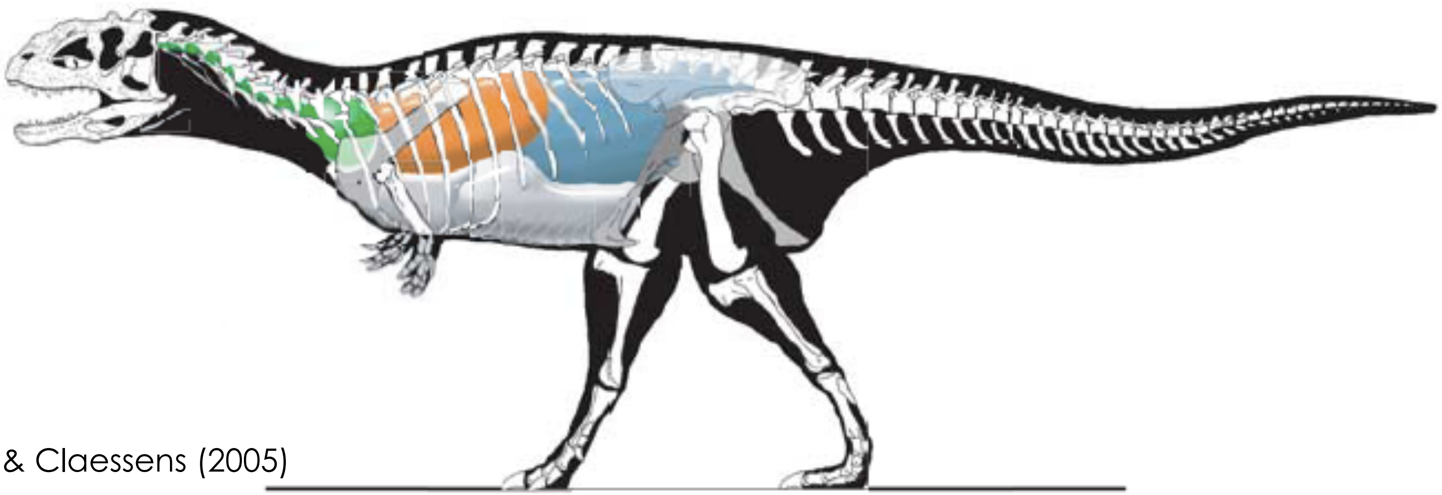
To become gigantic ...

- ... the niche must be empty
- ... you need resources
- ... you have to grow (fast)
- ... you should have a lightweight construction

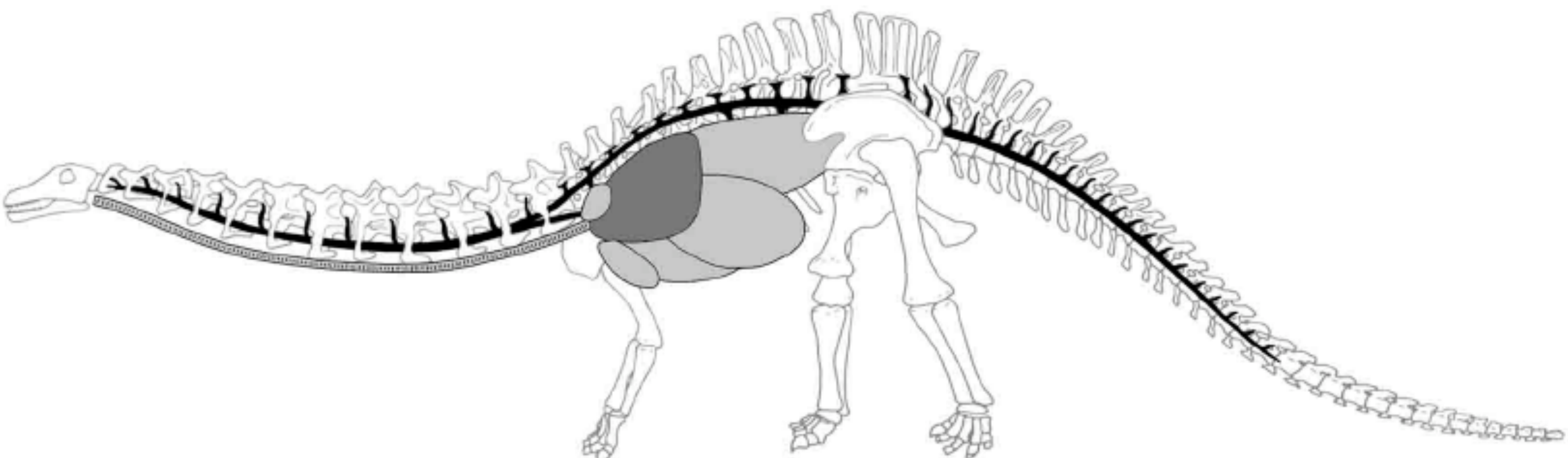
Respiration system



Respiration system

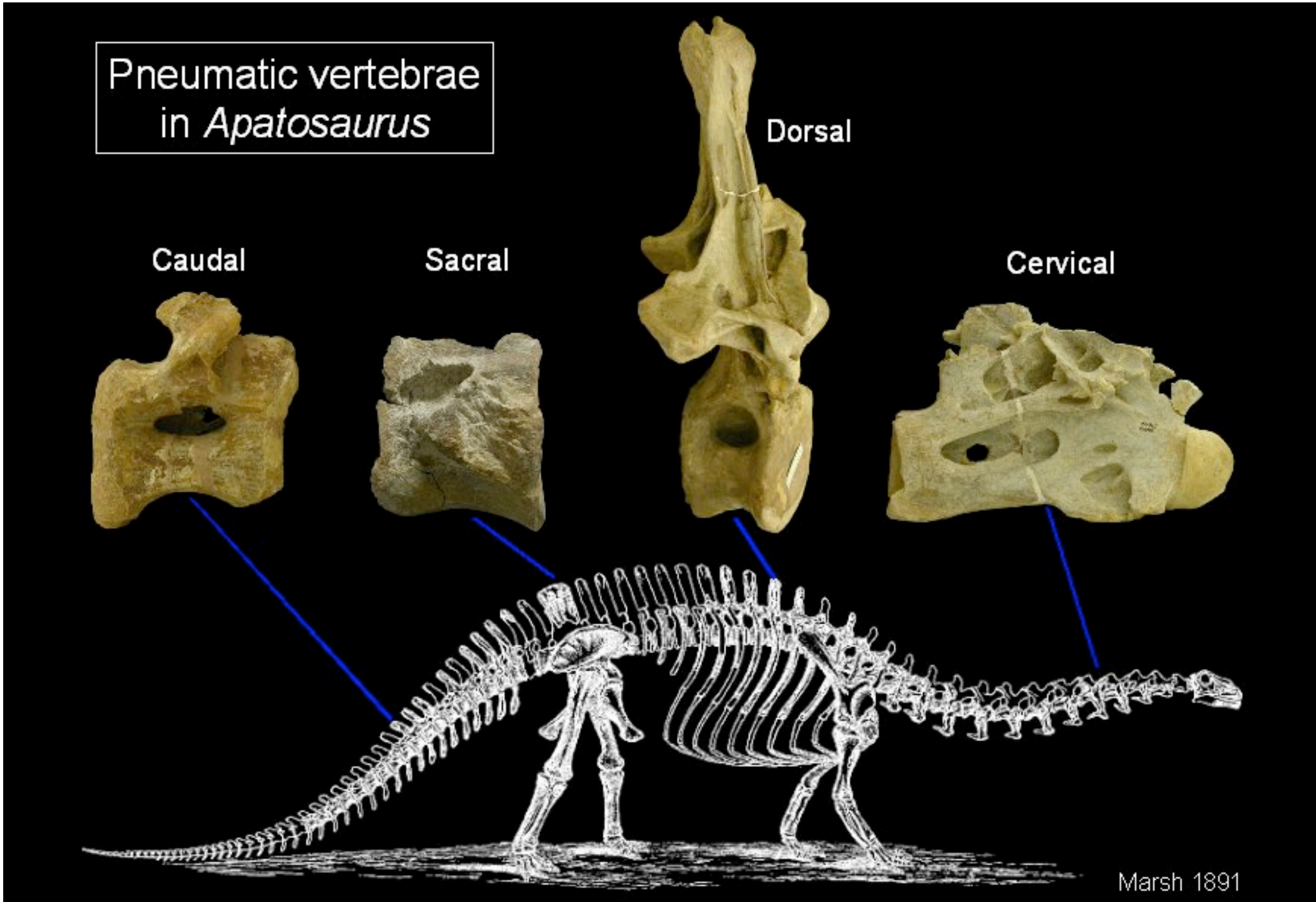


O'Connor & Claessens (2005)



Wedel (2005)

Respiration system



To become gigantic ...

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To become gigantic ...

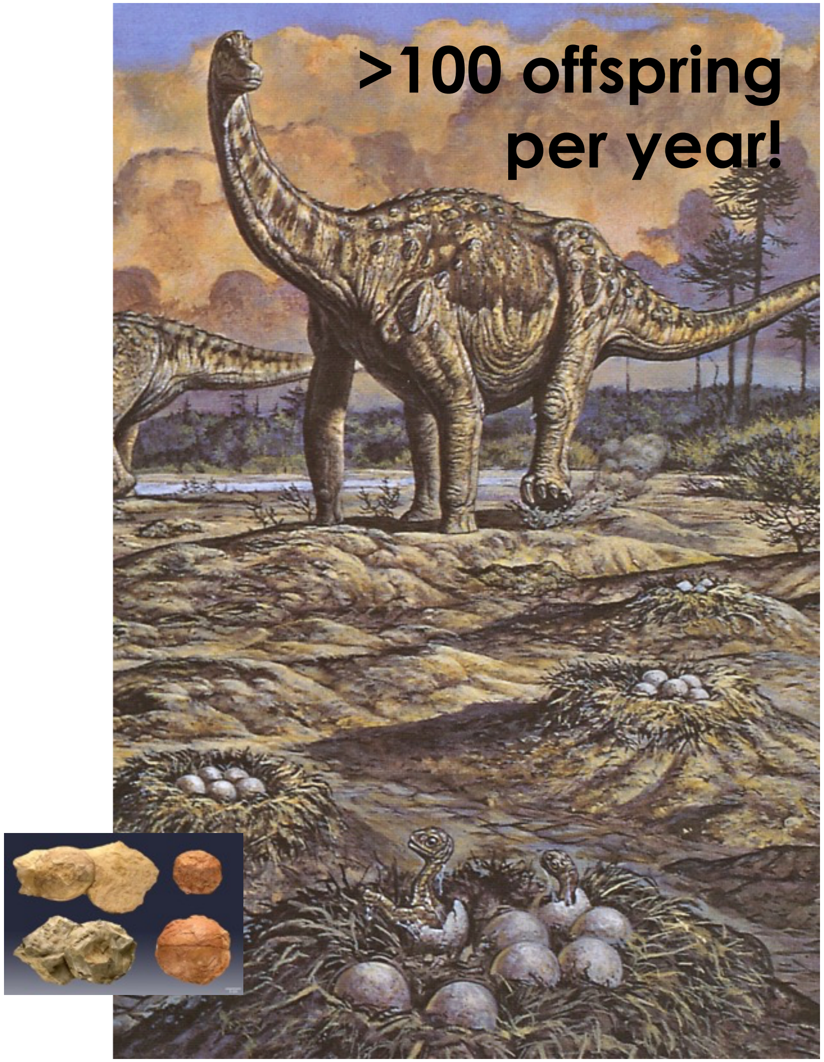
- ... the niche must be empty
- ... you need resources
- ... you have to grow (fast)
- ... you should have a lightweight construction
- ... you should have no intrinsic limitation

To become gigantic ...

- ... the niche must be empty
- ... you need resources
- ... you have to grow (fast)
- ... you should have a lightweight construction
- ... you should have no intrinsic limitation
  - reproduction
  - mastication (chewing)

Re-Generation

Re-Generation



from Curry Rogers and Wilson (2005)

Re-Generation

OPEN ACCESS Freely available online

PLoS one

Reproductive Biology and Its Impact on Body Size: Comparative Analysis of Mammalian, Avian and Dinosaurian Reproduction

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Abstract

Janis and Carrano (1992) suggested that large dinosaurs might have faced a lower risk of extinction under ecological changes than similar-sized mammals because large dinosaurs had a higher potential reproductive output than similar-sized mammals (JC hypothesis). First, we tested the assumption underlying the JC hypothesis. We therefore analysed the potential reproductive output (reflected in clutch/litter size and annual offspring number) of extant terrestrial mammals and birds (as "dinosaur analogs") and of extinct dinosaurs. With the exception of rodents, the differences in the reproductive output of similar-sized birds and mammals proposed by Janis and Carrano (1992) existed even at the level of single orders. Fossil dinosaur clutches were larger than litters of similar-sized mammals, and dinosaur clutch sizes were comparable to those of similar-sized birds. Because the extinction risk of extant species often correlates with a low reproductive output, the latter difference suggests a lower risk of population extinction in dinosaurs than in mammals. Second, we present a very simple, mathematical model that demonstrates the advantage of a high reproductive output underlying the JC hypothesis. It predicts that a species with a high reproductive output that usually faces very high juvenile mortalities will benefit more strongly in terms of population size from reduced juvenile mortalities (e.g., resulting from a stochastic reduction in population size) than a species with a low reproductive output that usually comprises low juvenile mortalities. Based on our results, we suggest that reproductive strategy could have contributed to the evolution of the exceptional gigantism seen in dinosaurs that does not exist in extant terrestrial mammals. Large dinosaurs, e.g., the sauropods, may have easily sustained populations of very large-bodied species over evolutionary time.

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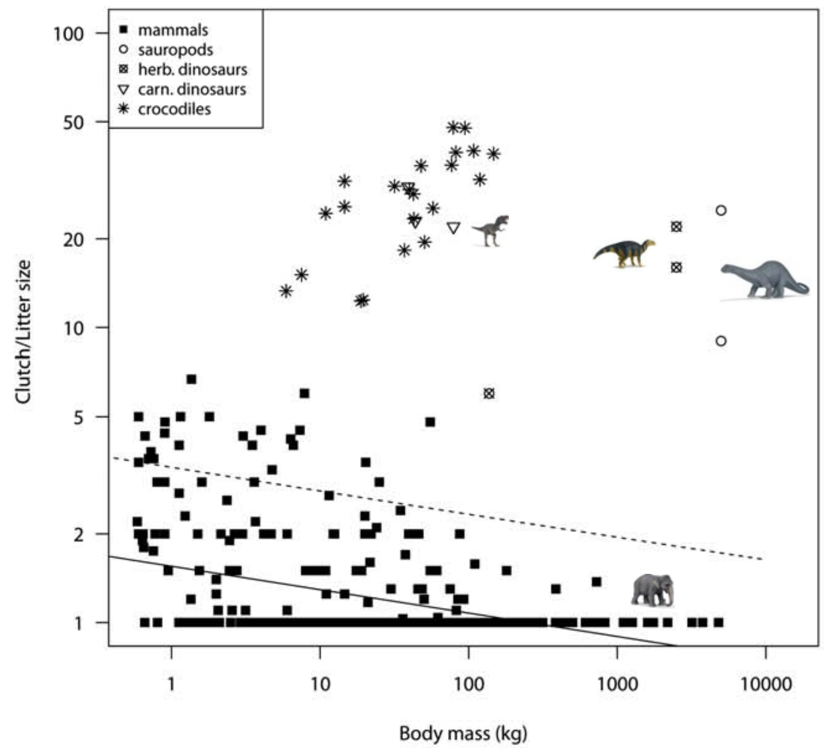
Introduction

Body size is one of the most fundamental attributes of any organism [1,2]. While body size maxima for some organisms can be directly studied in living species, the largest terrestrial animals that have ever existed on earth, the sauropod dinosaurs, must be studied from the fossil record. Sander and Clauss [3] have argued that the gigantism of these animals must result from their unusual biology. Their thesis is supported by the observation that body size influences nearly every aspect of the biology of currently existing organisms and that many life history variables correlate with body size [4–6]. Variables such as mortality, age at sexual maturity, size or number of offspring are important for understanding life history strategies and population extinction risk, because such factors are directly related to the fitness of an organism [7–10]. These variables reflect several important trade-offs, e.g., investment of energy in somatic versus gonadic growth, in continuous or intermittent breeding, and in the investment in either many small or a few large offspring [11].

Kurtén [12] already pointed out that body size limits of a taxon reflect not only mechanical or physiological constrains, but also the scaling of its reproductive parameters [4,11,13–15]. Following the idea by Kurtén [12], Janis and Carrano (abbreviated hereafter as JC [16]) stated that terrestrial non-passerine birds, taken as a model for dinosaurs, differ from terrestrial mammals in terms of their reproductive biology. They found that, for terrestrial mammals, body mass was negatively correlated with litter size (number of offspring per litter; clutch size = number of offspring per clutch), breeding frequency (number of clutches/litters per year) and annual offspring number (total number of offspring per year = clutch/litter size × number of broods per year), whereas such relationships were absent in non-passerine birds.

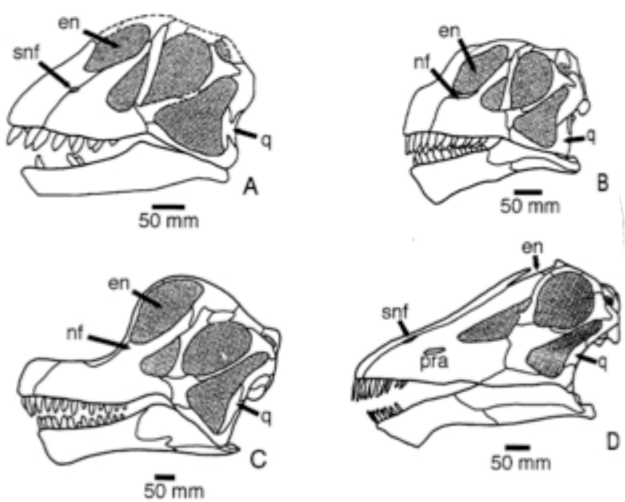
Using terrestrial non-passerine birds as "dinosaur analogs", JC put forward the hypothesis (henceforth called the JC hypothesis) that different reproductive strategies in dinosaurs and mammals (ovipary in birds and dinosaurs versus vivipary plus lactation in mammals) resulted in a different ability of dinosaurs and mammals to evolve and sustain large-bodied species over evolutionary time. JC suggested that, given their higher potential reproductive output (reflected in clutch size or number of offspring per year) compared to similar-sized mammals, large dinosaurs may have faced a lower risk of population extinction under ecological changes than mammals.

A higher potential reproductive output is advantageous when the size of a population is reduced, e.g., by a catastrophic event.



No chewing in sauropods

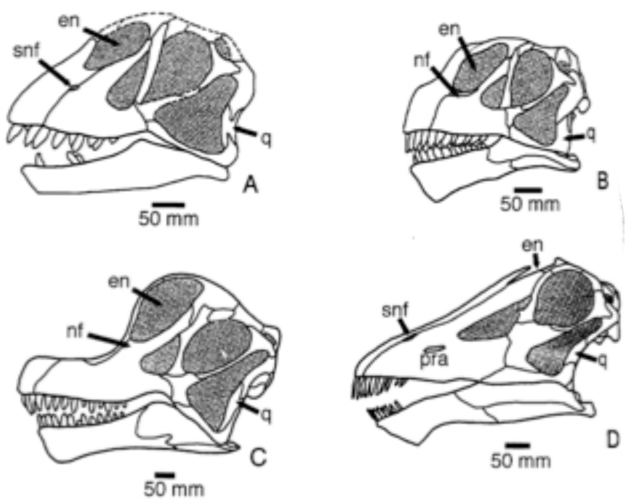
Absence of mastication apparatus (no grinding teeth, no cheeks)

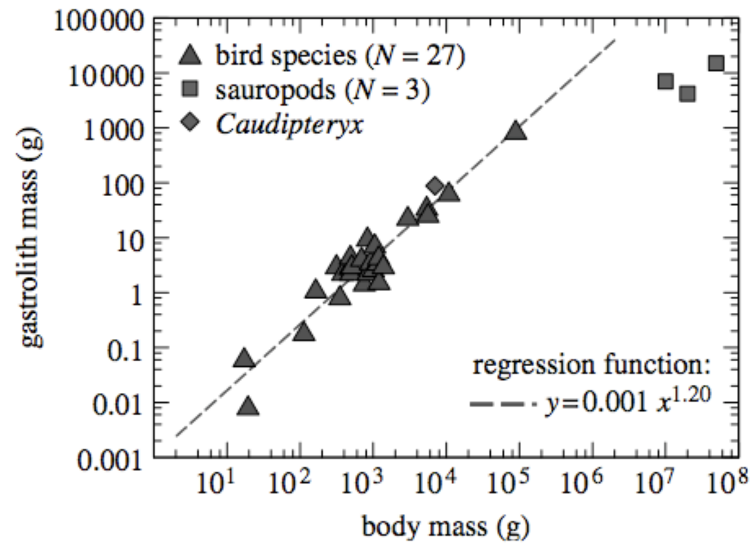


from Calvo (1994)

No chewing in sauropods

Absence of mastication apparatus (no grinding teeth, no cheeks) and absence of gastric mill



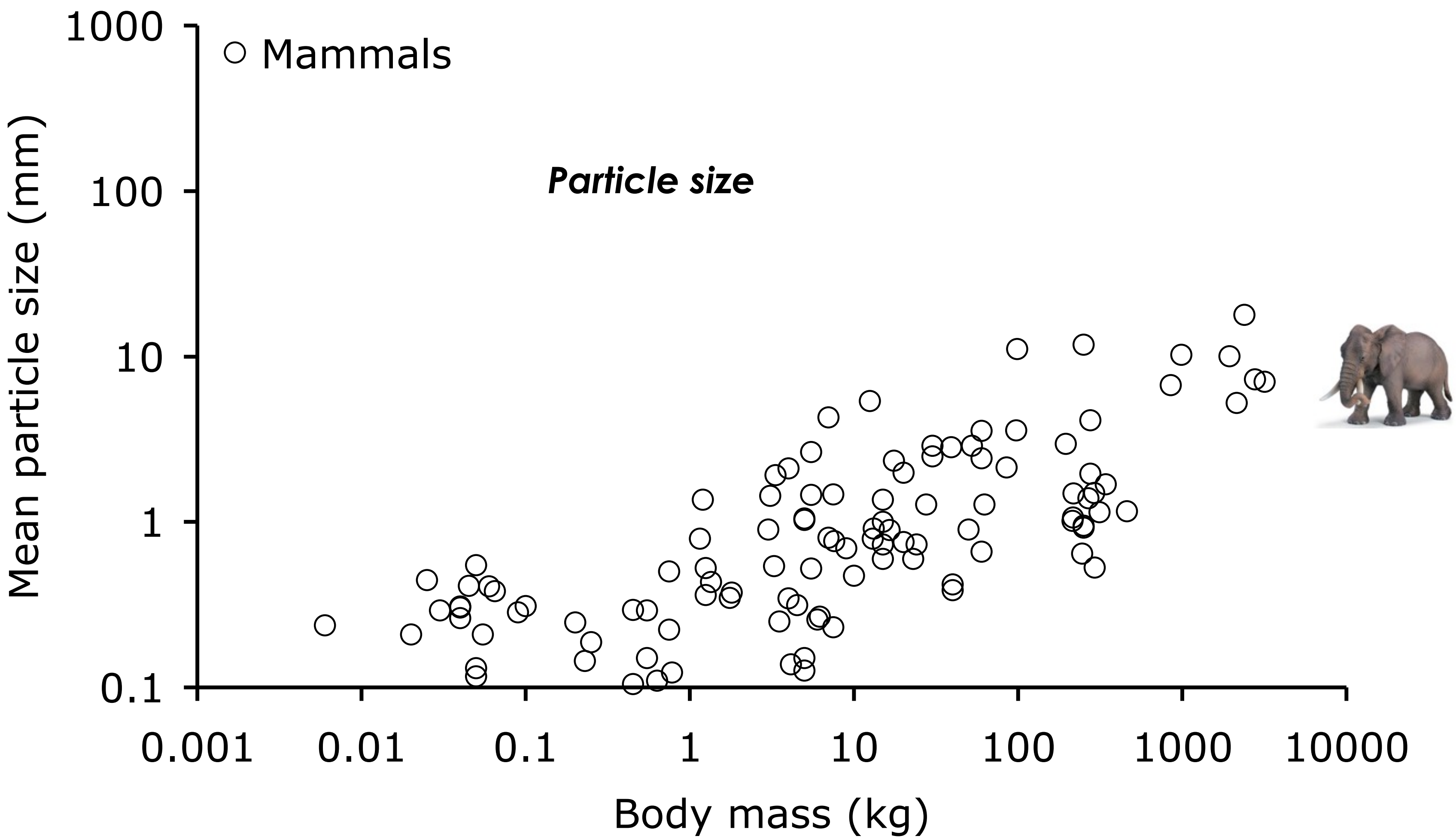


sauropods are special - they did not chew their food

from Calvo (1994)

from Wings & Sander (2007)

Extrapolating to sauropods



(Fritz et al. 2009, 2010, 2011)

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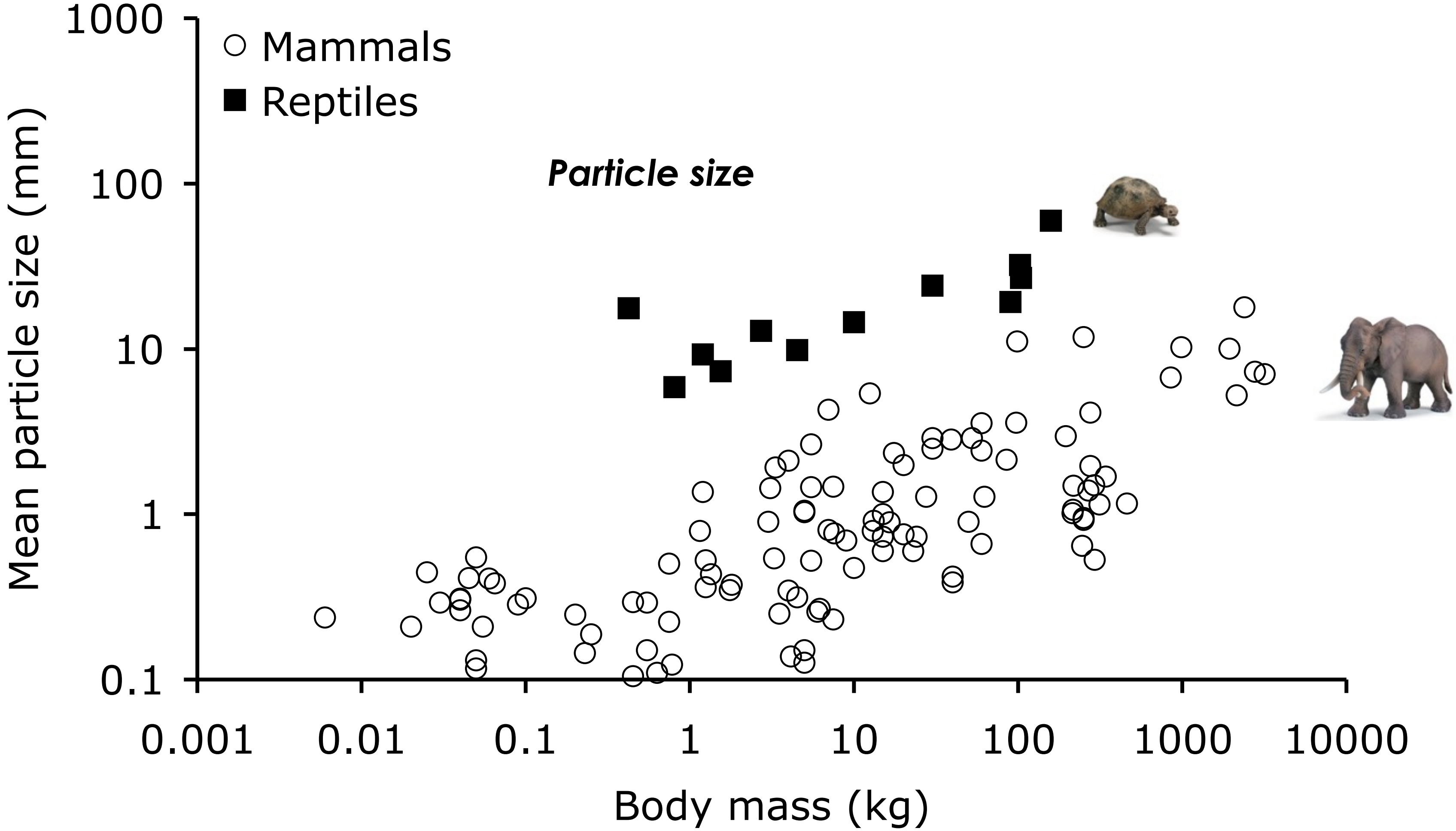

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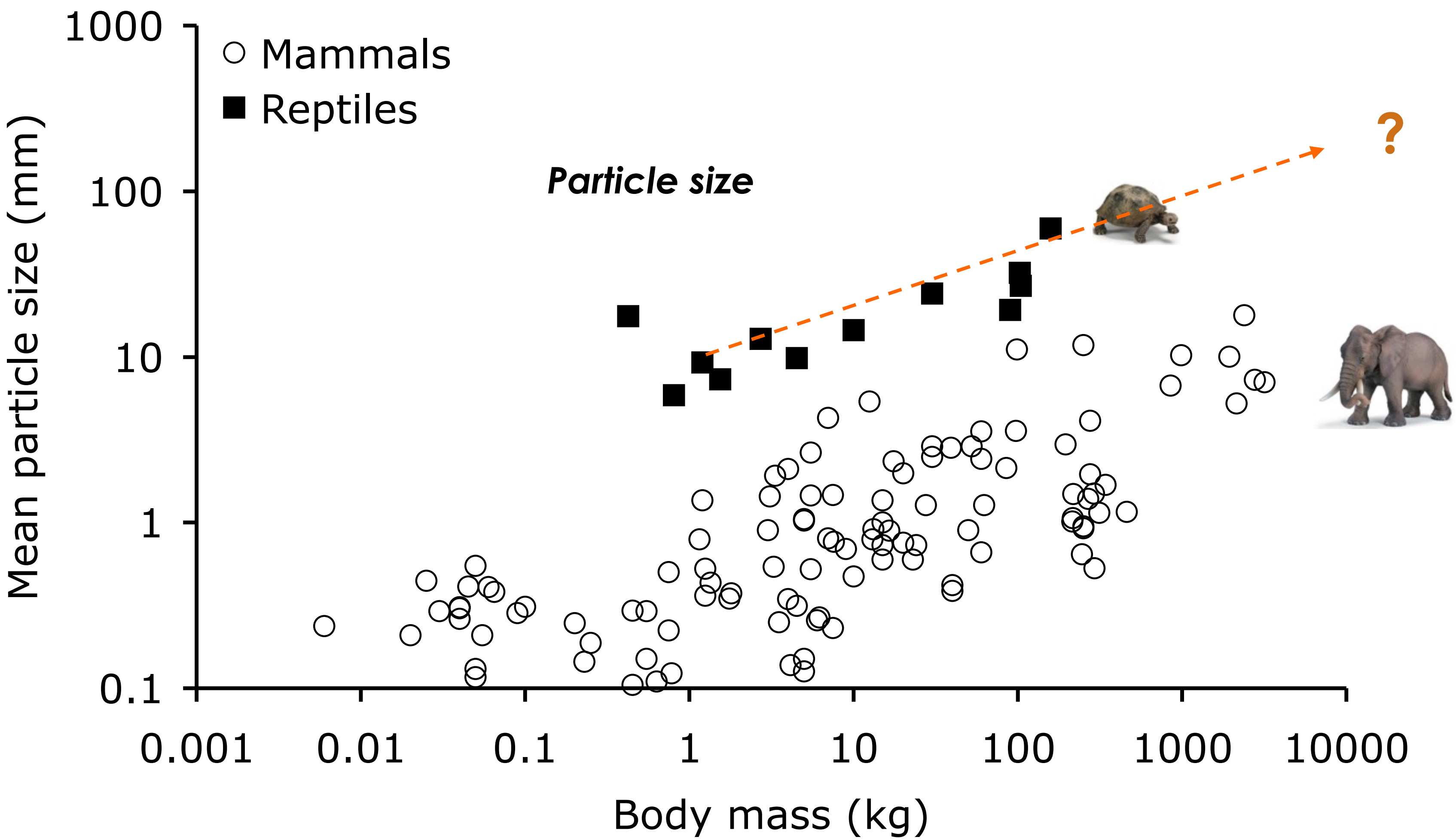
Extrapolating to sauropods



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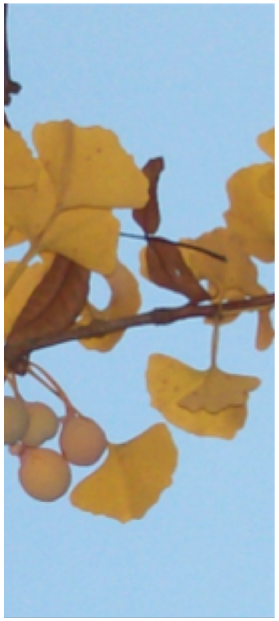
General allometric considerations

At a certain body mass, digesta particle size will only depend on plant morphology



General allometric considerations

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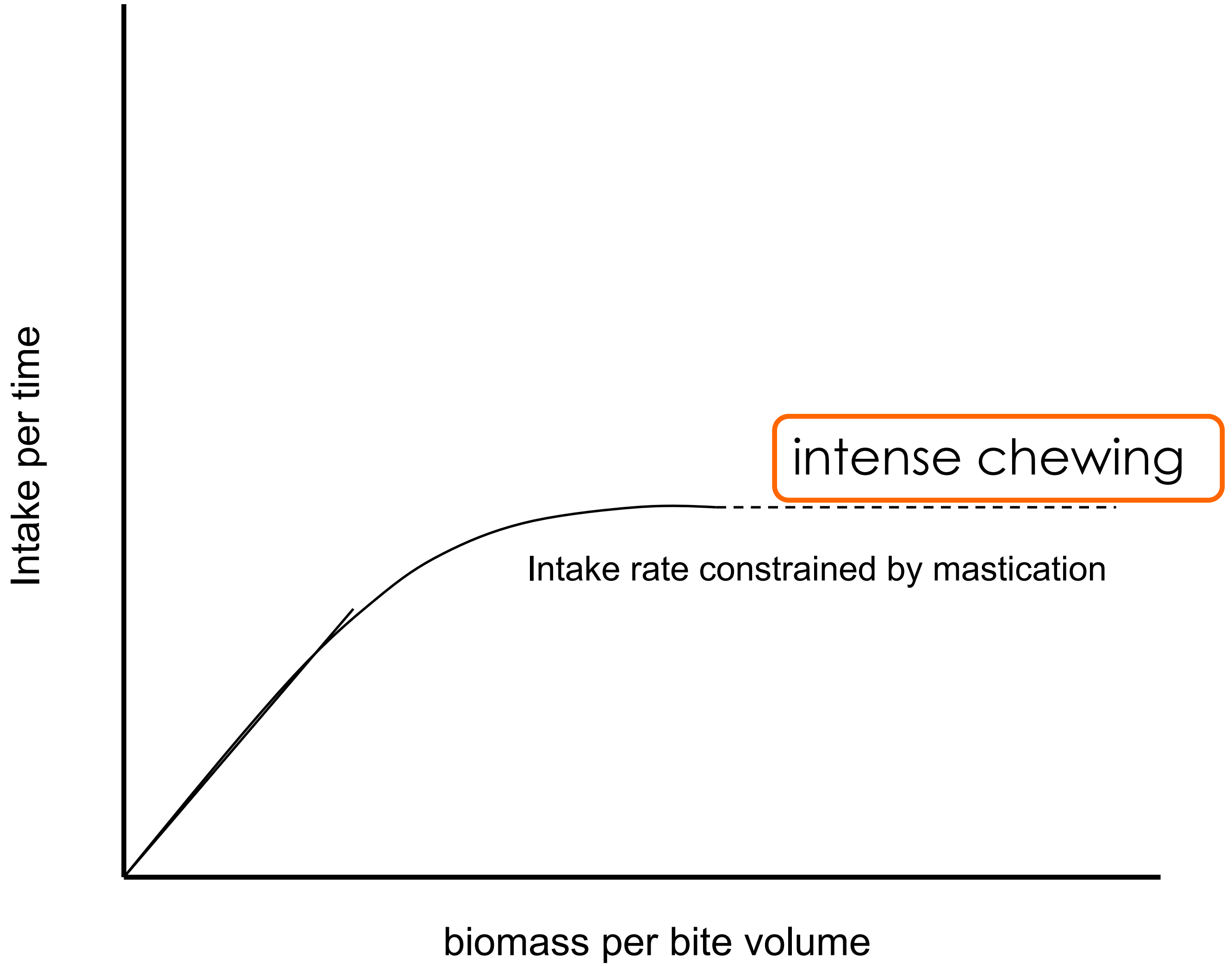
At a certain body mass, digesta particle size will only depend on plant morphology

Feeding time and body size



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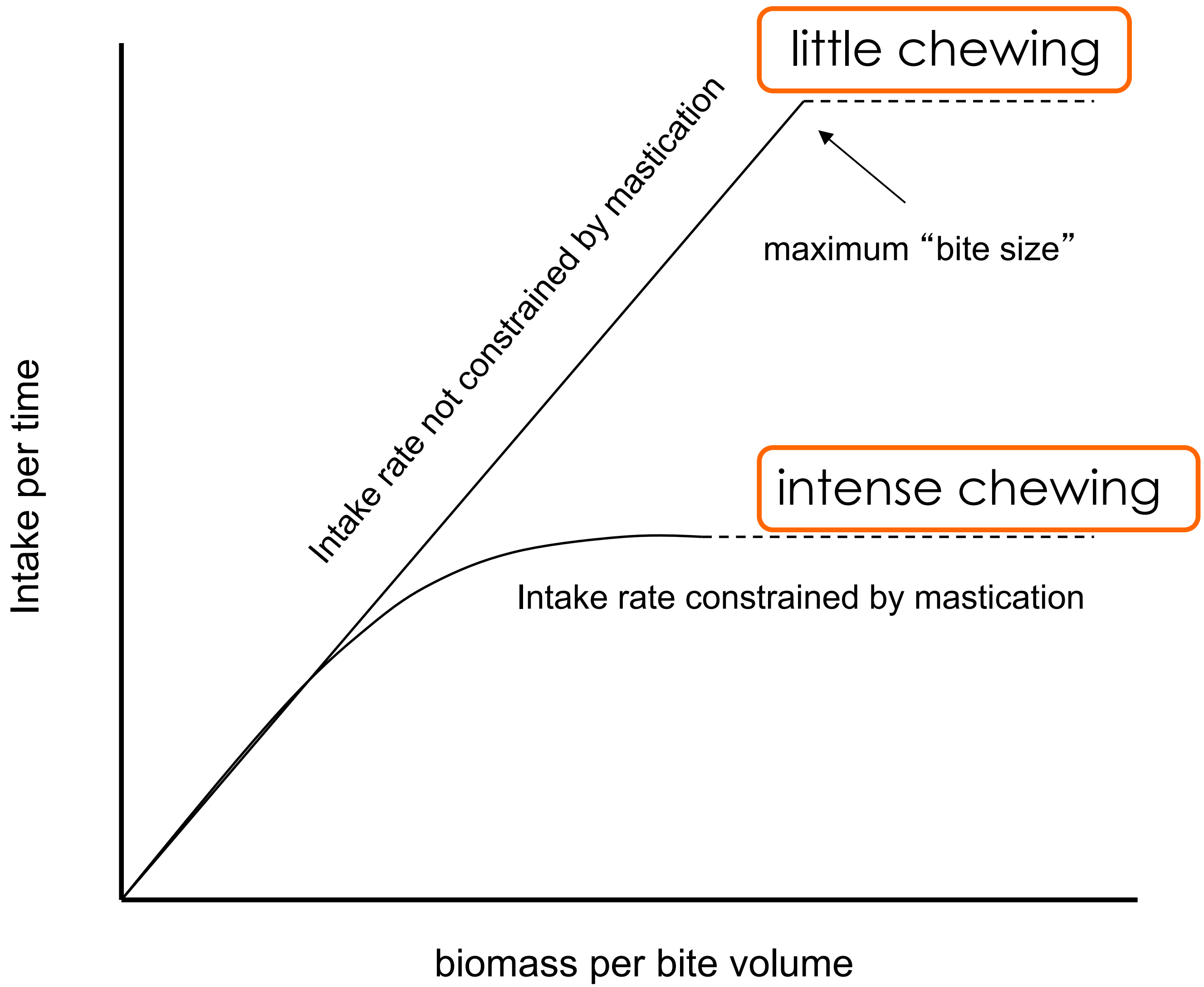

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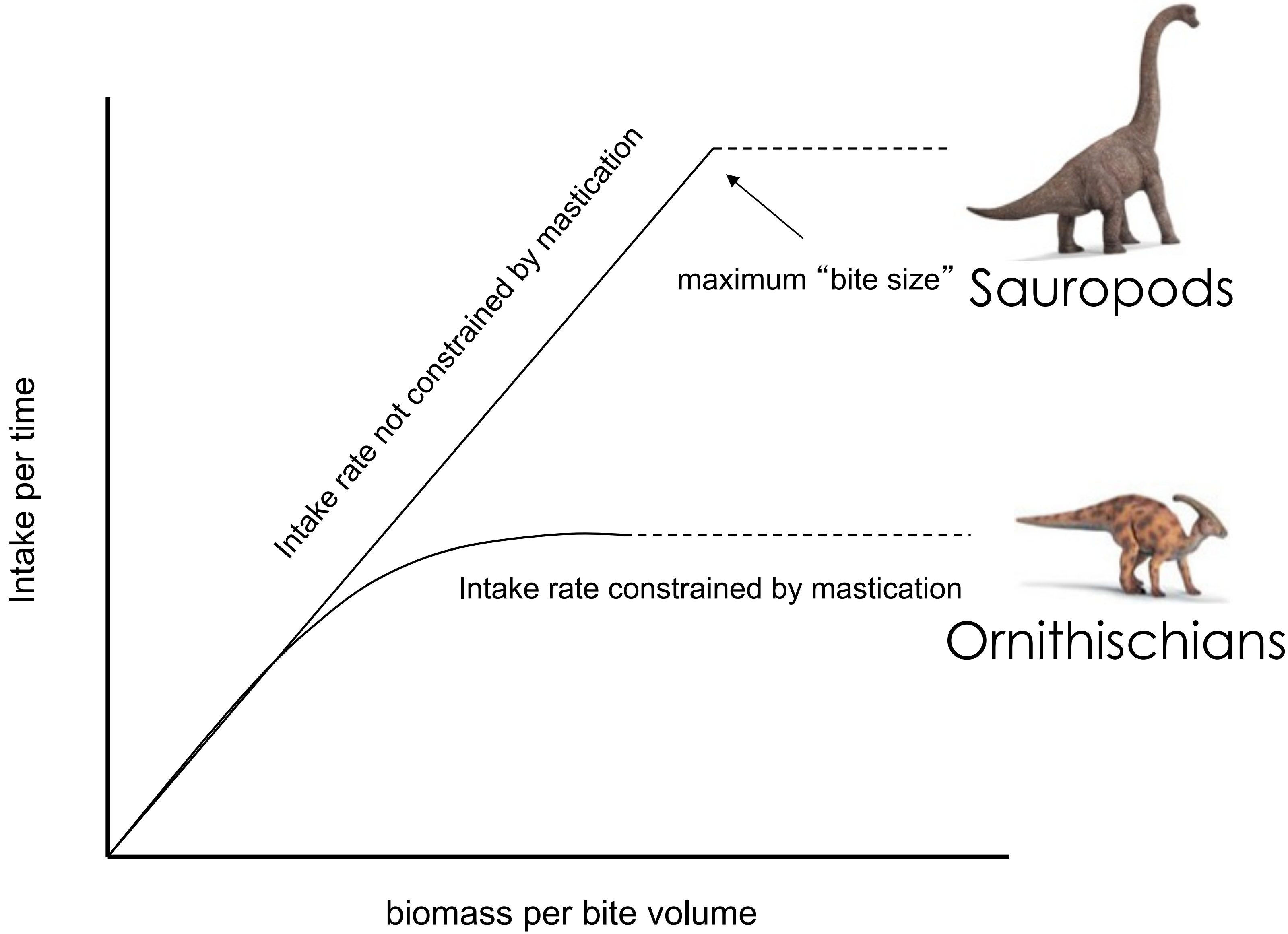
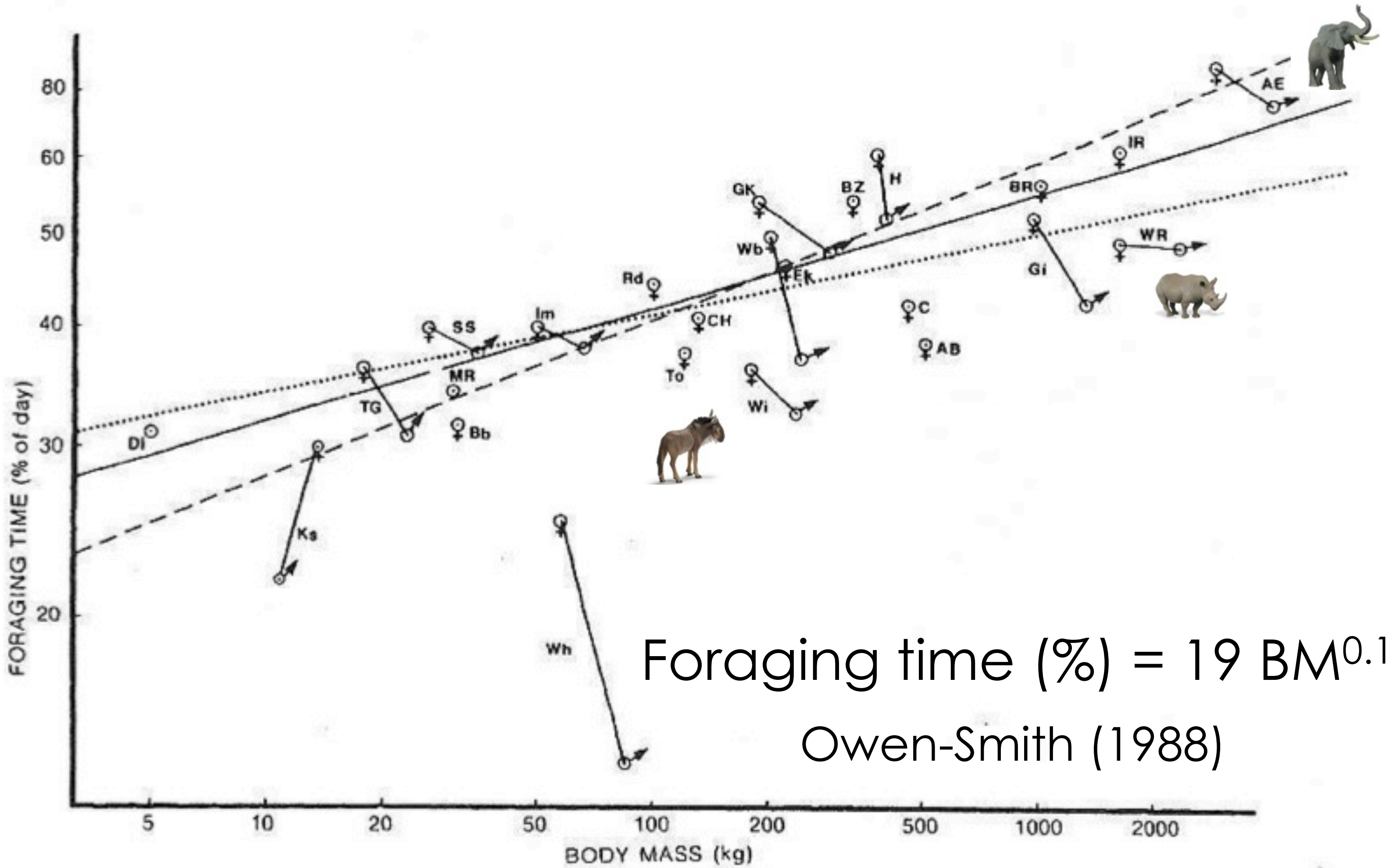


Foraging time and body size



Foraging time (%) = 19 $BM^{0.17}$

Owen-Smith (1988)

Foraging: Sum of searching, cropping ***and chewing***

Chewing limits body size

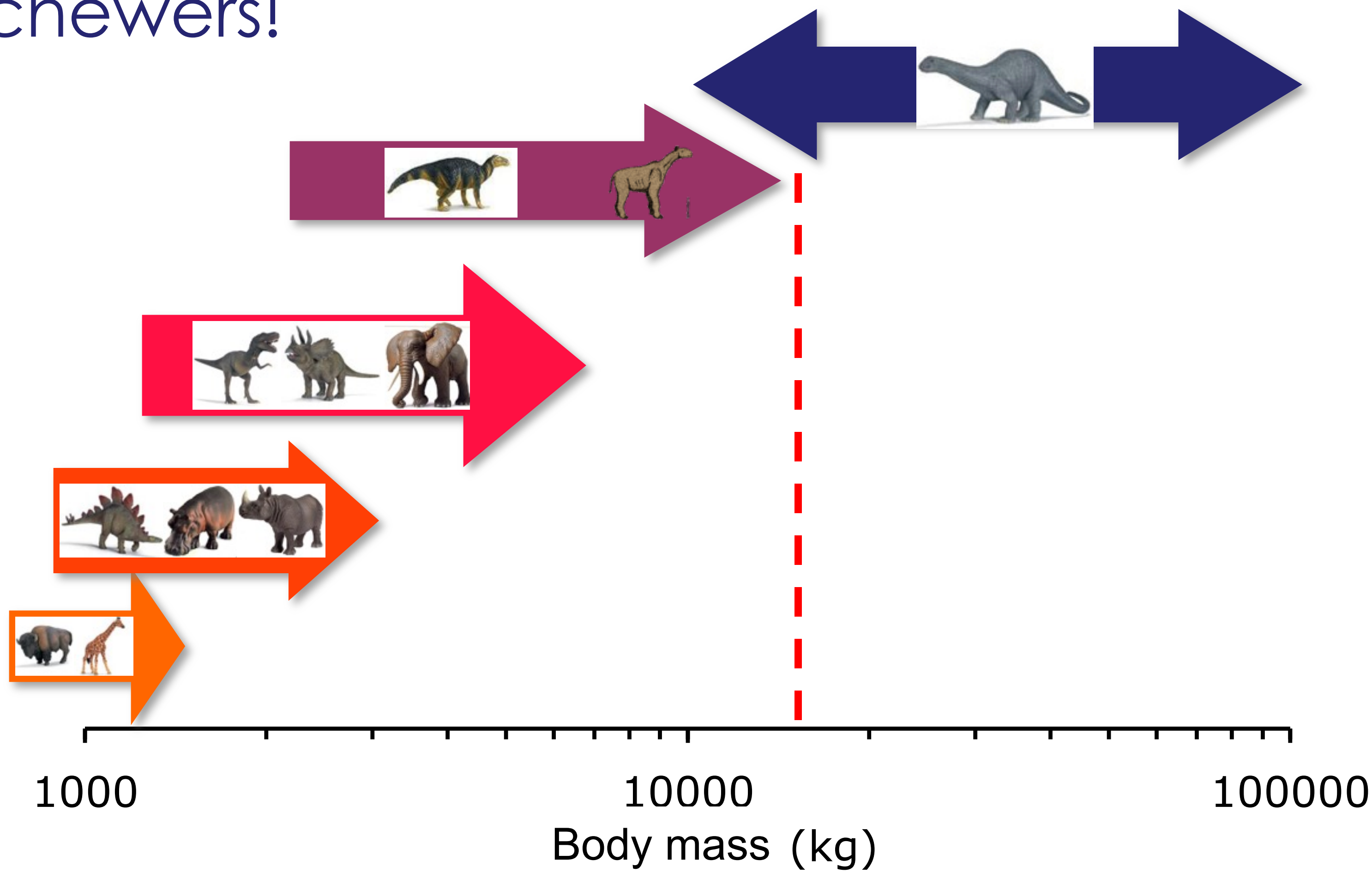
Chewing constrains the time available for feeding and therefore ultimately limits the body size of chewers.

Feeding time (in % day) = 19 Body mass$^{0.17}$

from app. 18 tons onwards, herbivores would have to feed more than 24 hours per day!

Sizing up dinosaurs

- Sauropods outgrew the competition of chewers!

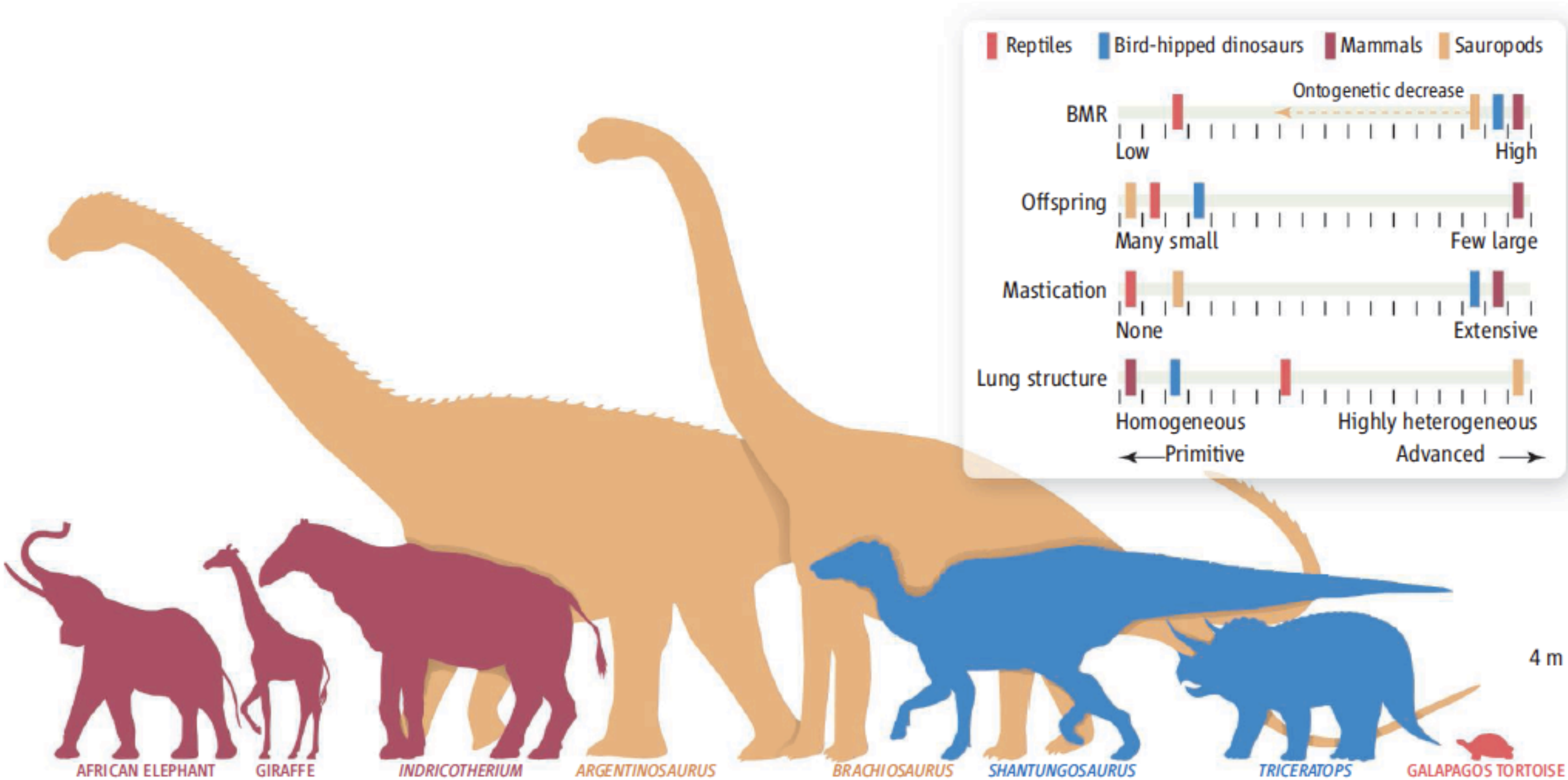


No chewing – no problems with tooth wear

Giant Equisetum

Summary

Absence of mastication is considered a “permissive factor” for sauropod gigantism



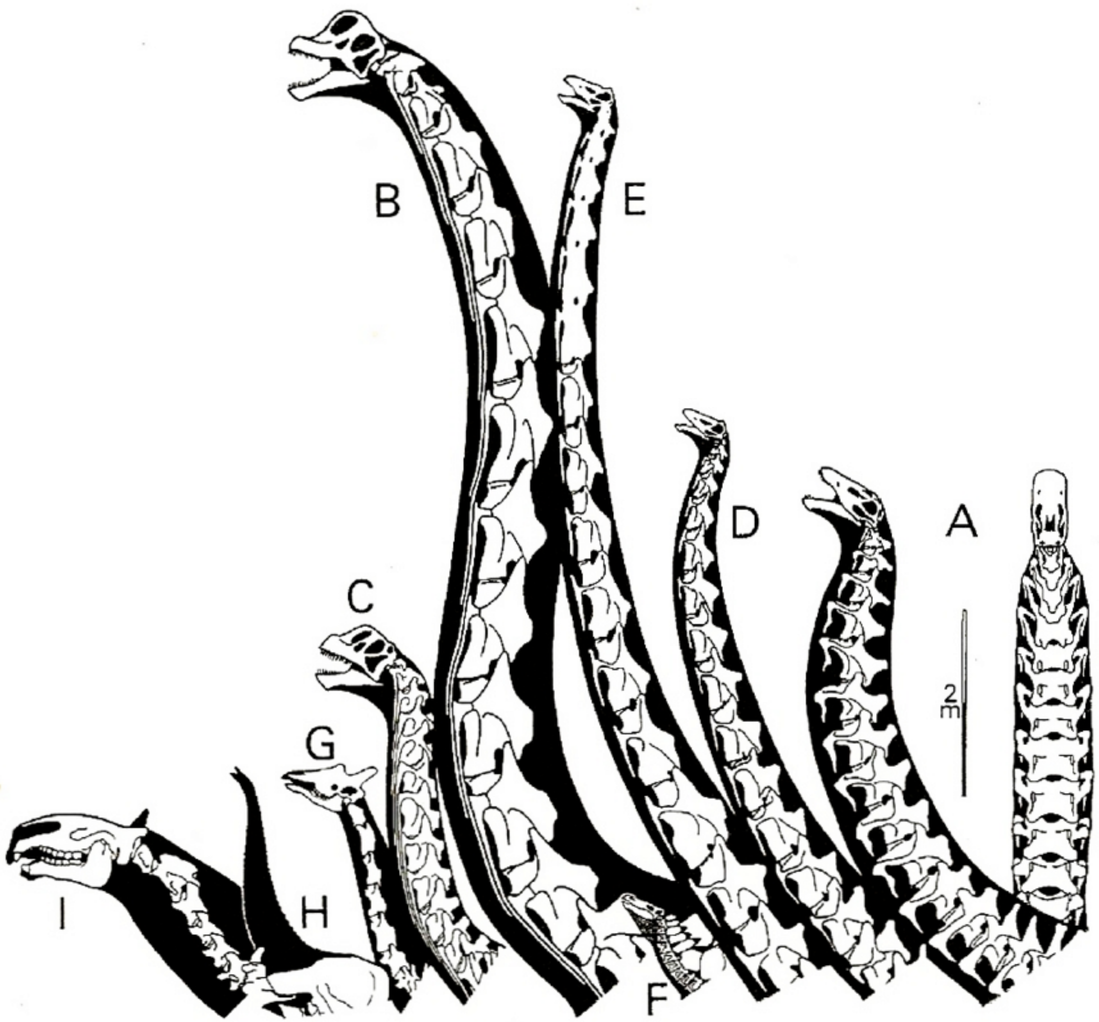
from Sander & Clauss (2008)

Gigantism - Consequences

Being gigantic is good

- Resource accessibility
  - Food (high and low)
  - Migration facilitates use of different habitats
  - More body reserves

Niche differentiation



from Paul (1998)

Niche differentiation

BBC (1998)

Niche differentiation

BBC (1998)

Signs of the past

Easter Island

Signs of the past

Araucaria

Signs of the past

Araucaria forest, Patagonia

Being gigantic is good

- Resource accessibility
  - Food (high and low)
  - Migration facilitates use of different habitats
  - More body reserves
- Less enemies

Size protects against predation

Size protects against predation

Journal of Animal Ecology 2008, 77, 173–183
doi: 10.1111/j.1365-2656.2007.01314.x

Predator–prey size relationships in an African large-mammal food web

Norman Owen-Smith[1]* and M. G. L. Mills[2]

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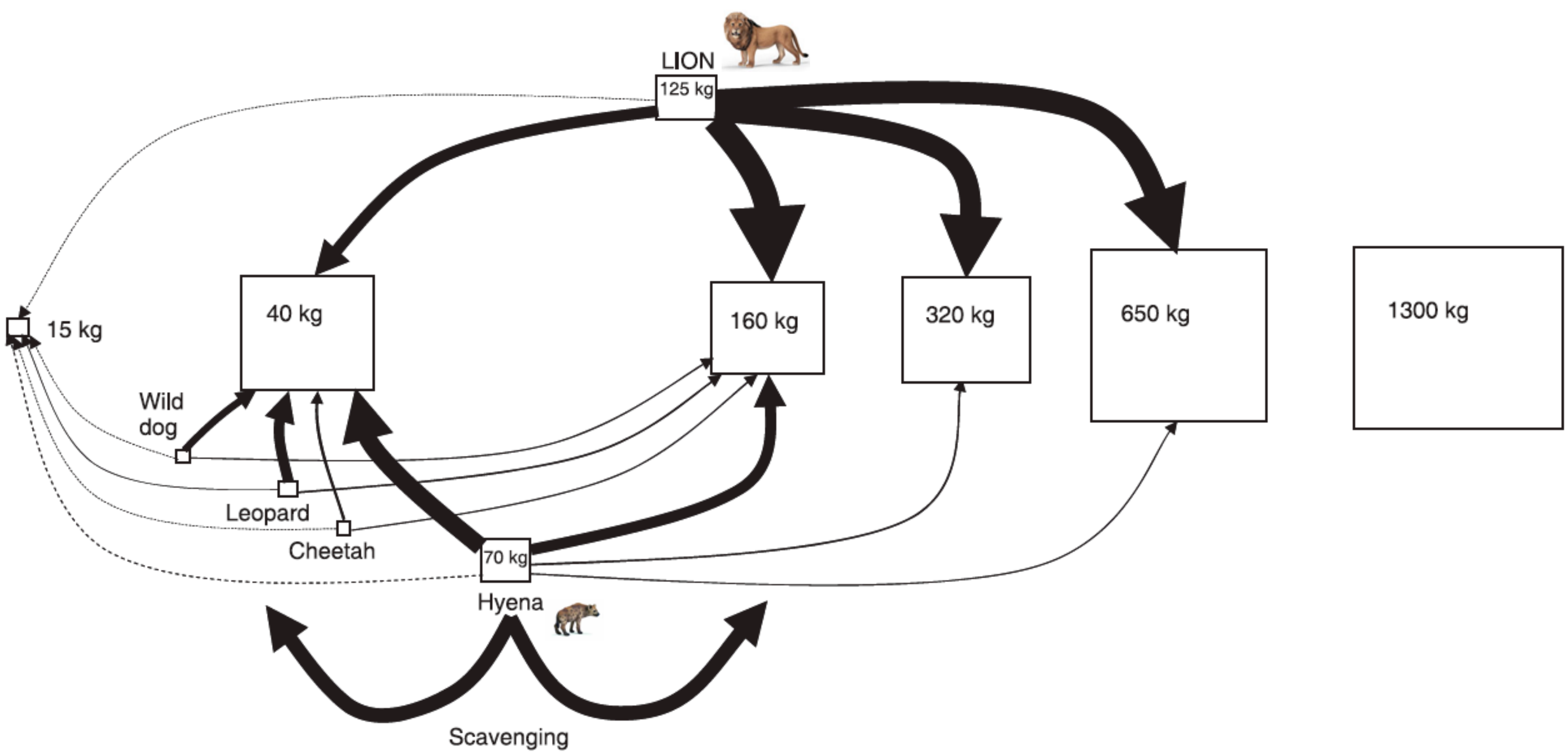

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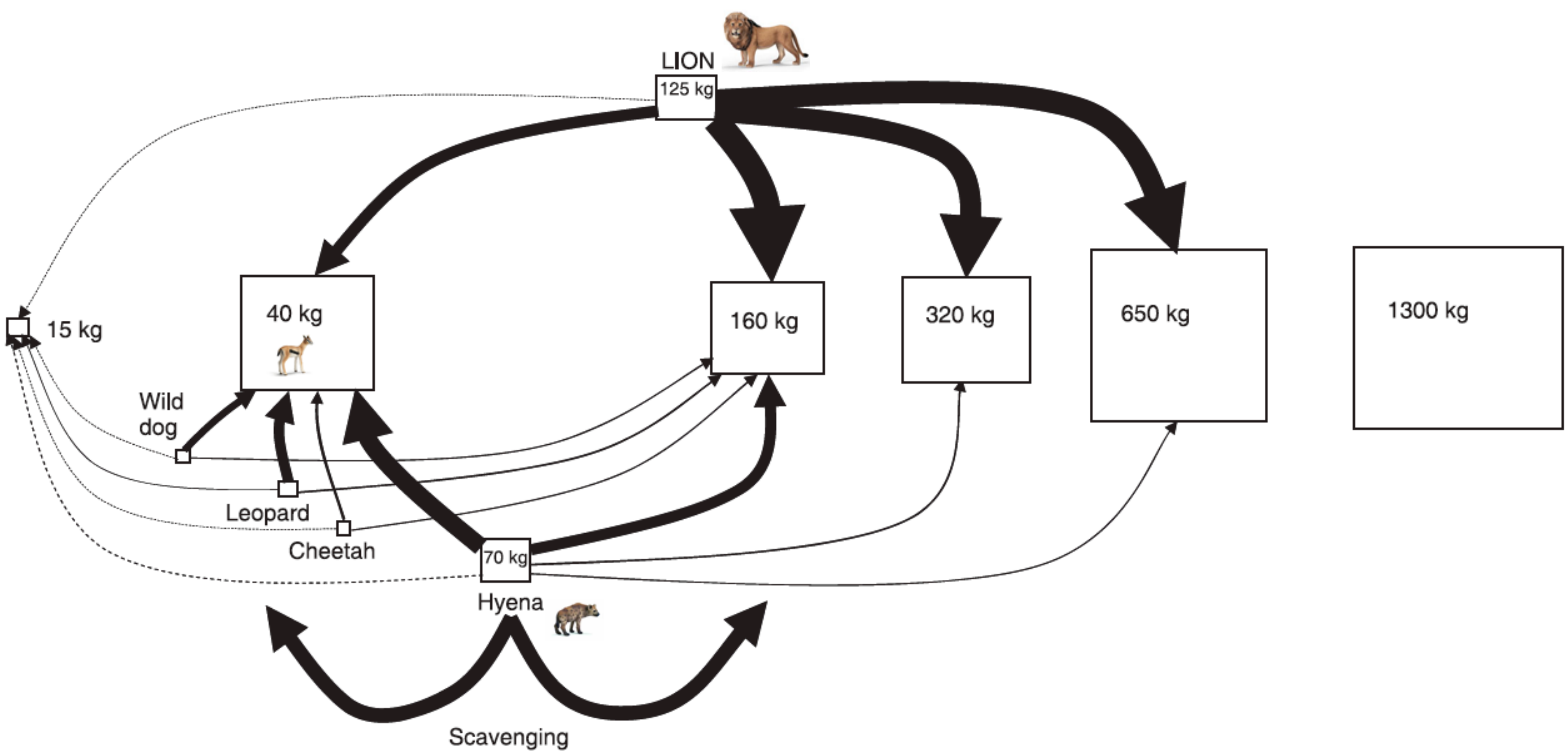

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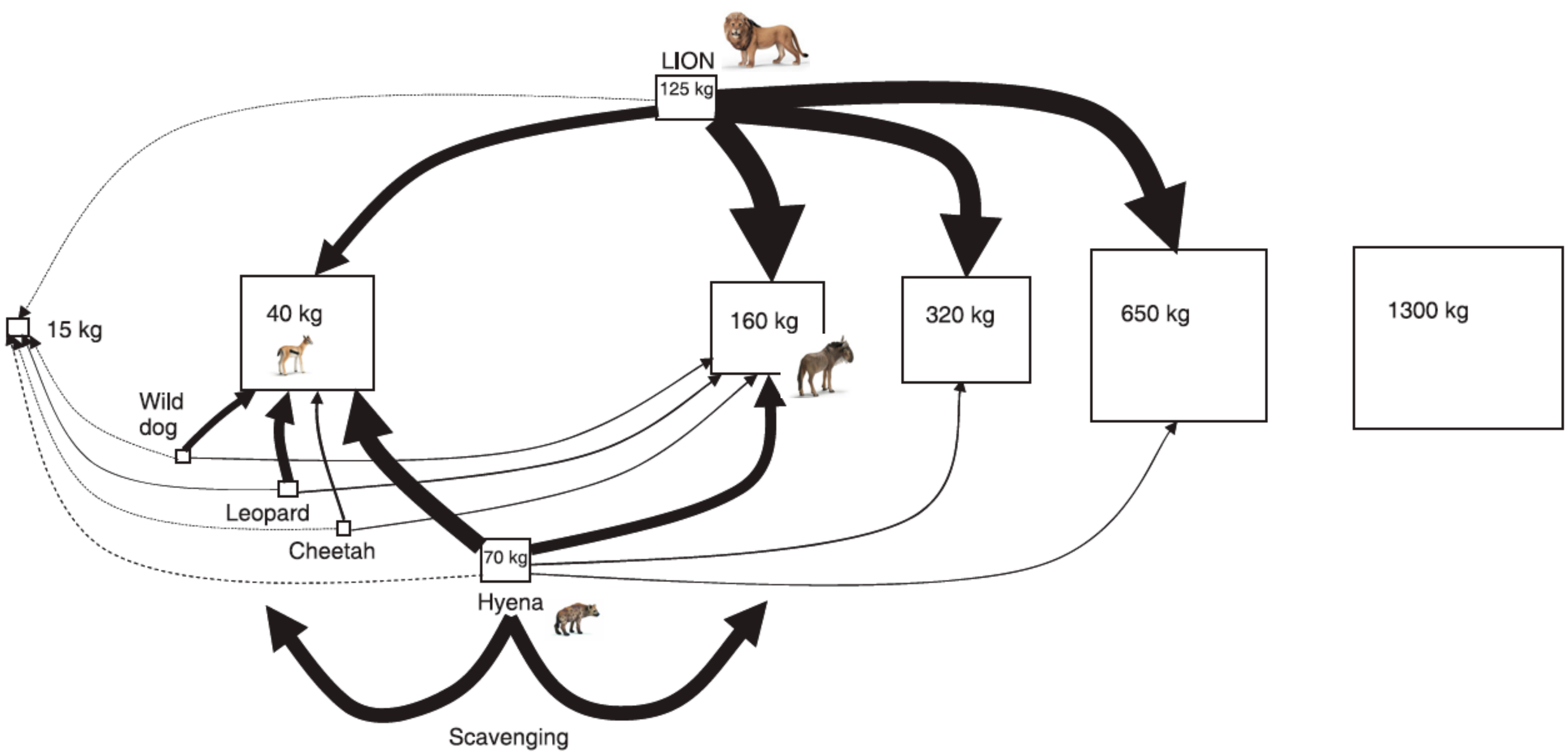

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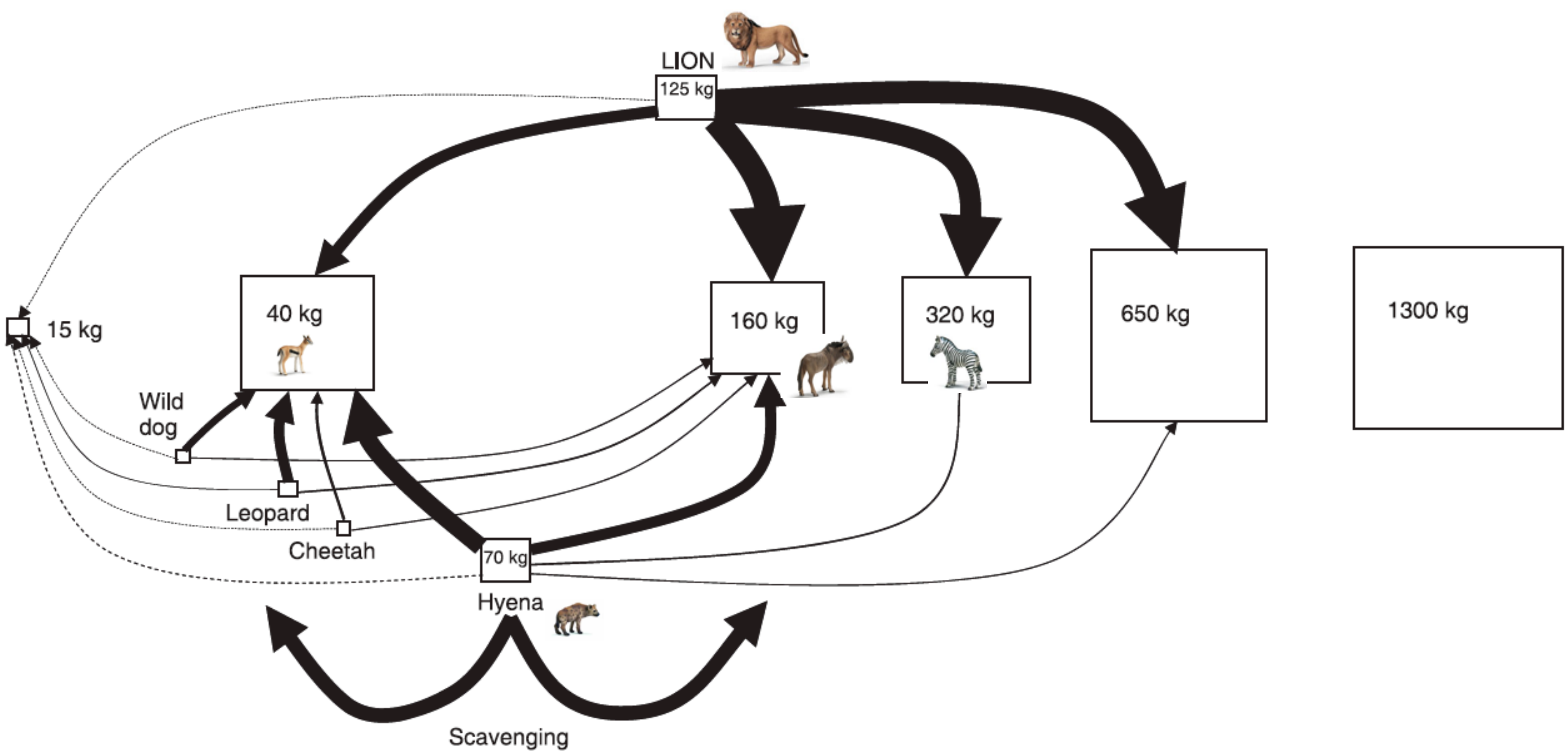

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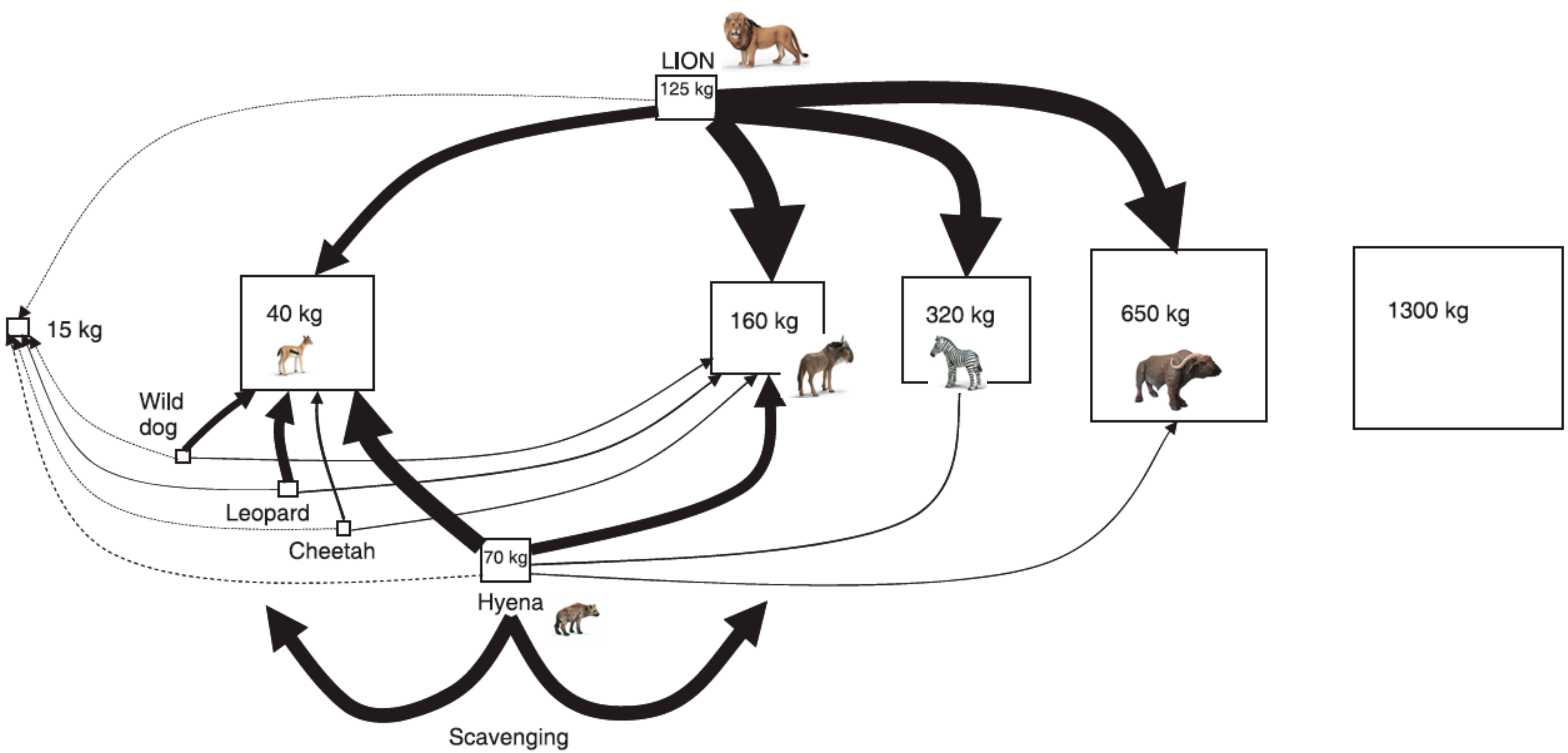

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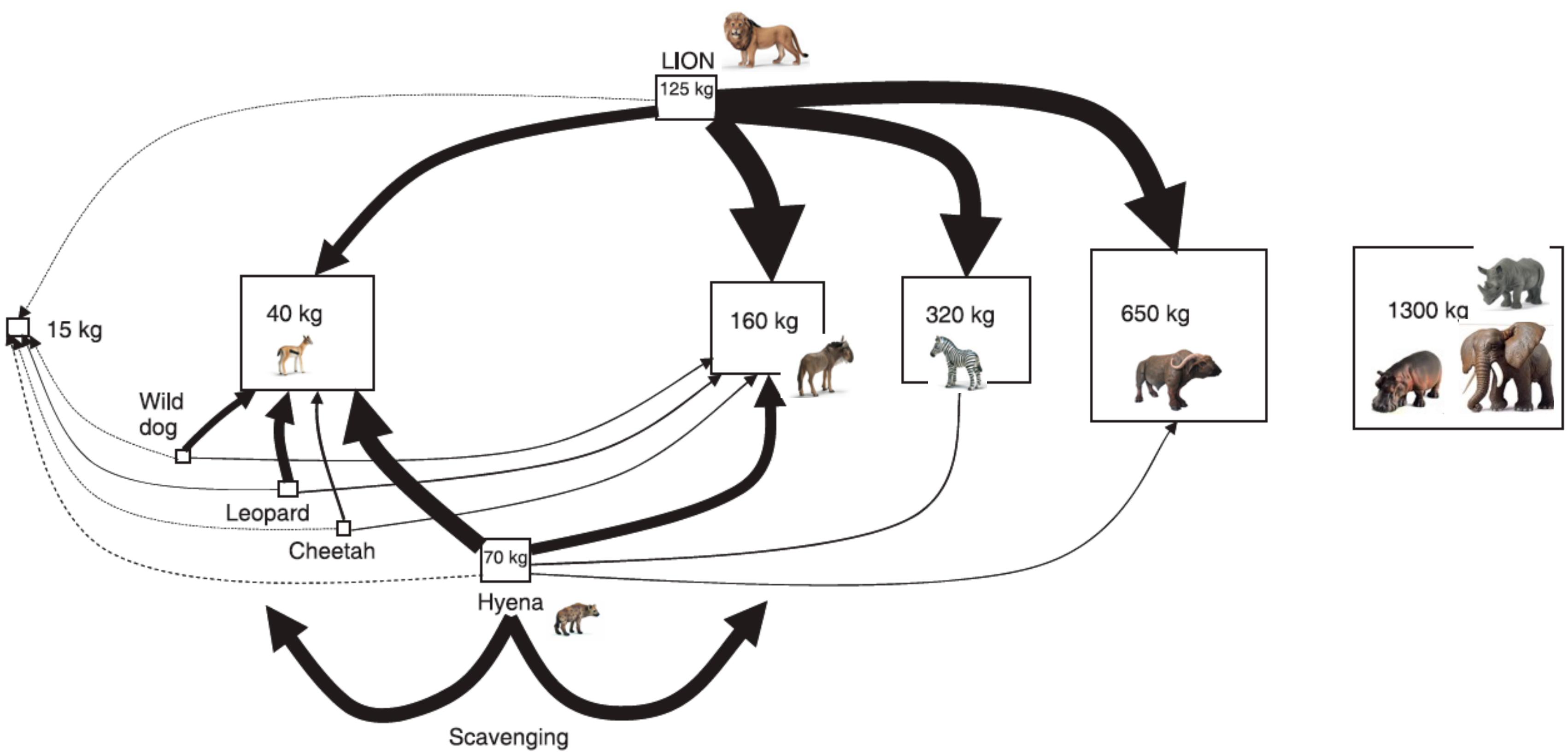

How much does a sauropod eat?

from Spielberg et al. (1993)

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from Spielberg et al. (1993)

... and how much does it defecate?

from Spielberg et al. (1993)

... and how much does it defecate?

BBC (1998)

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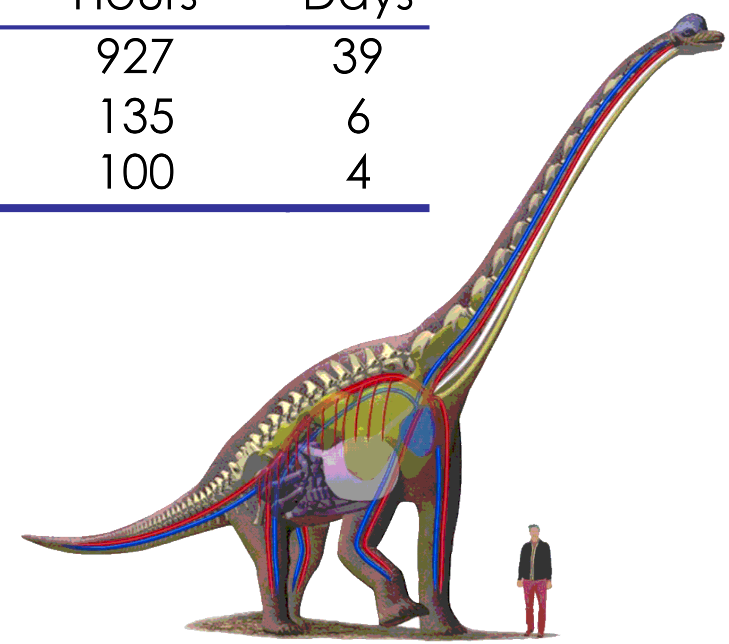
BBC (1998)

Reconstructing digestive physiology

38 ton Brachiosaurus – body cavity ~32 m^3

Estimated gut capacity ~4000 kg

Metabolism	Food intake	Faeces	Digesta passage	
	kg/d	kg/d	Hours	Days
Reptile	67	37	927	39
Intermediate	467	260	135	6
Mammal	627	347	100	4



from Gunga et al. & Hummel et al. (2008), Franz et al. (2009)

A case of notariophagy

from Spielberg et al. (1993)
Brett-Surman & Farlow (1997)

How many notaries does a *T. rex* need per year?

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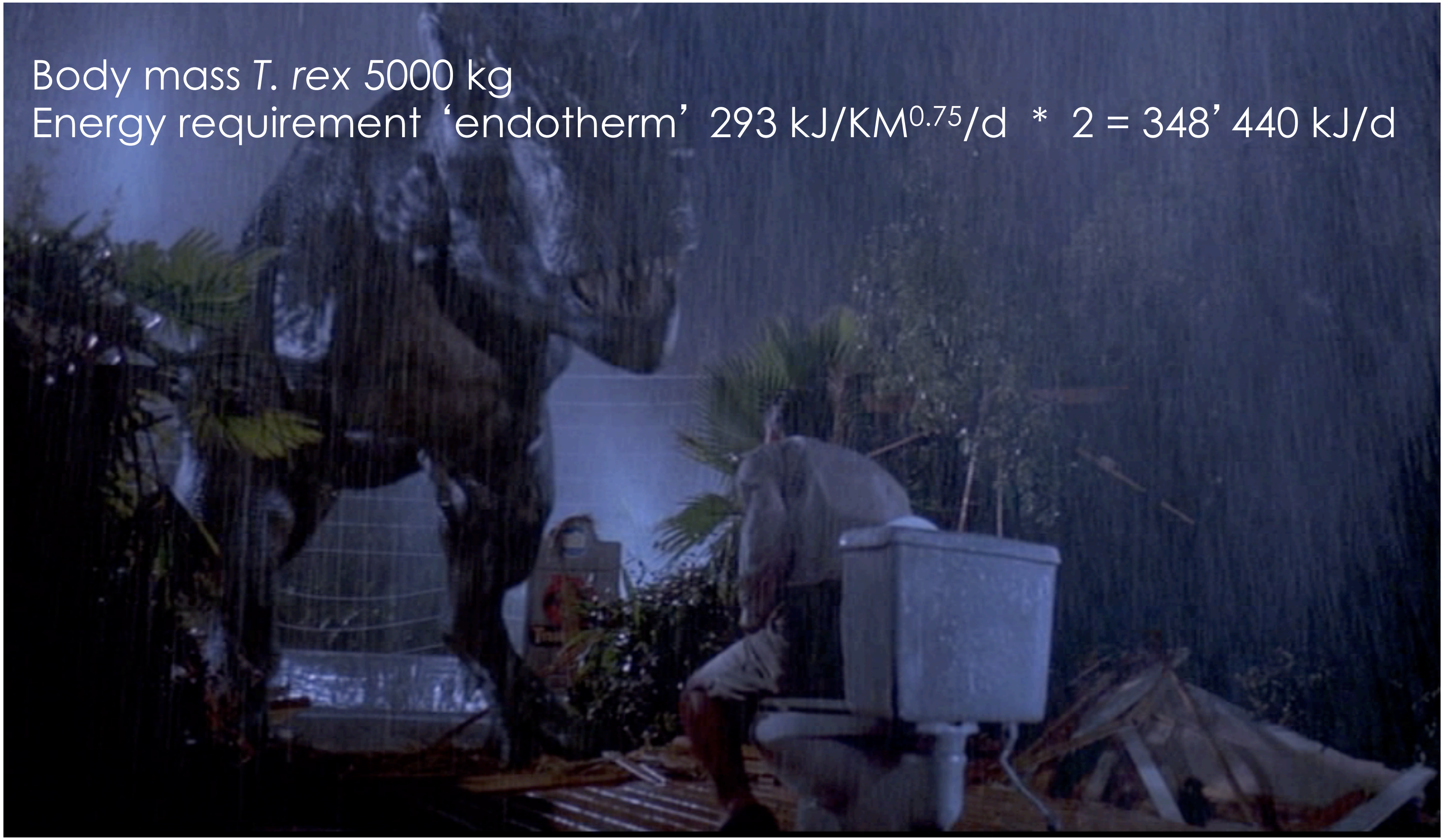

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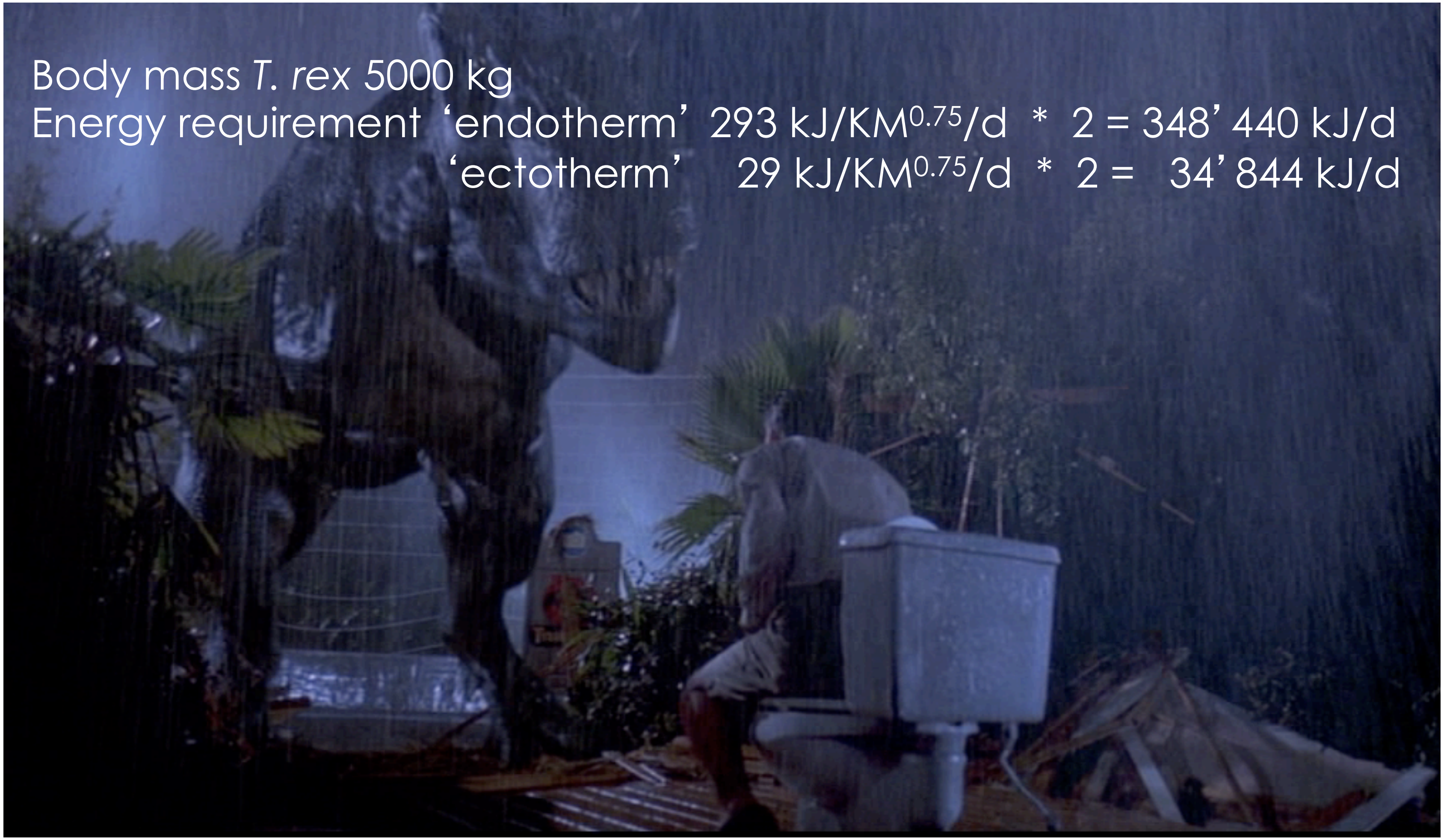

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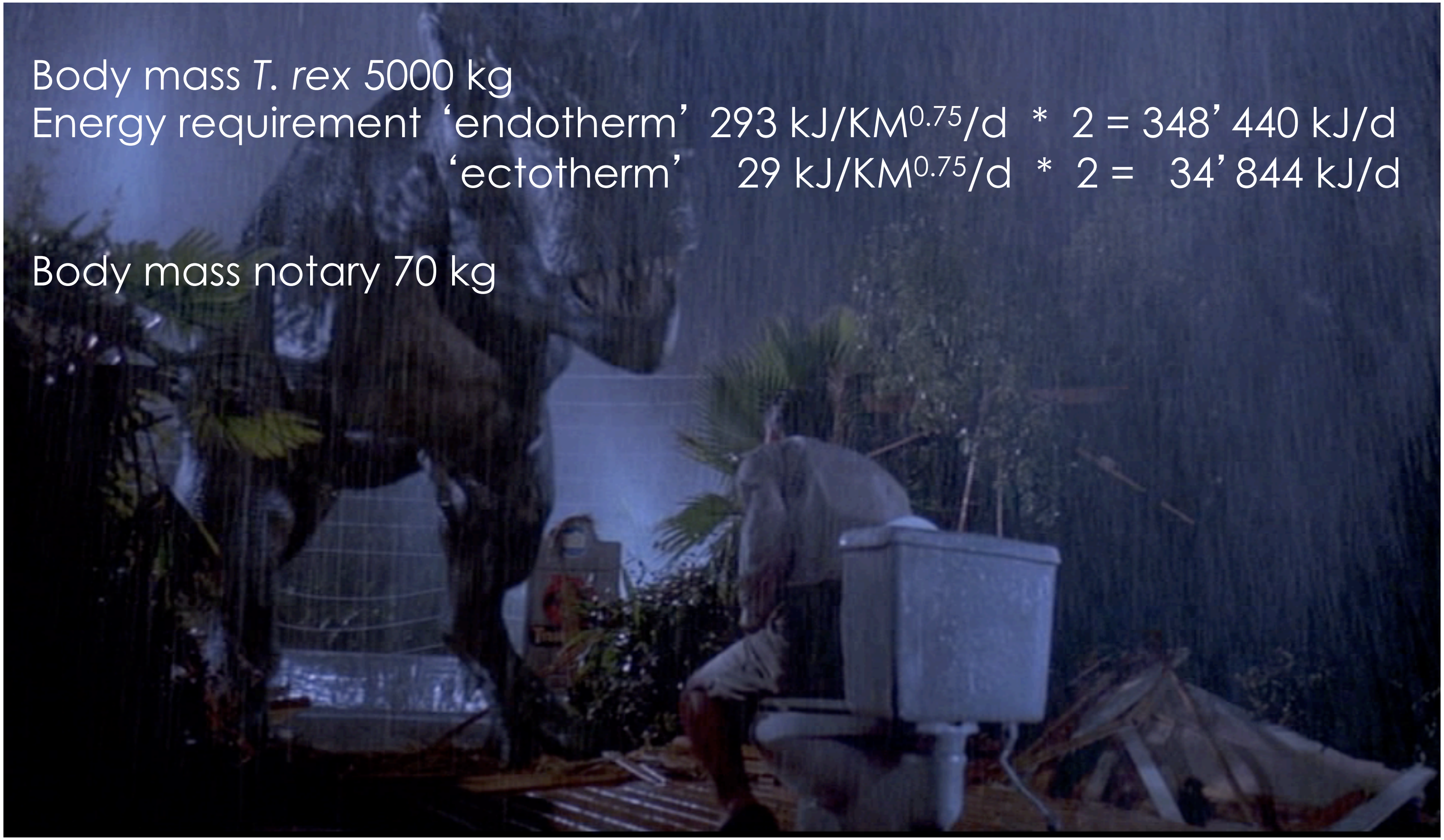

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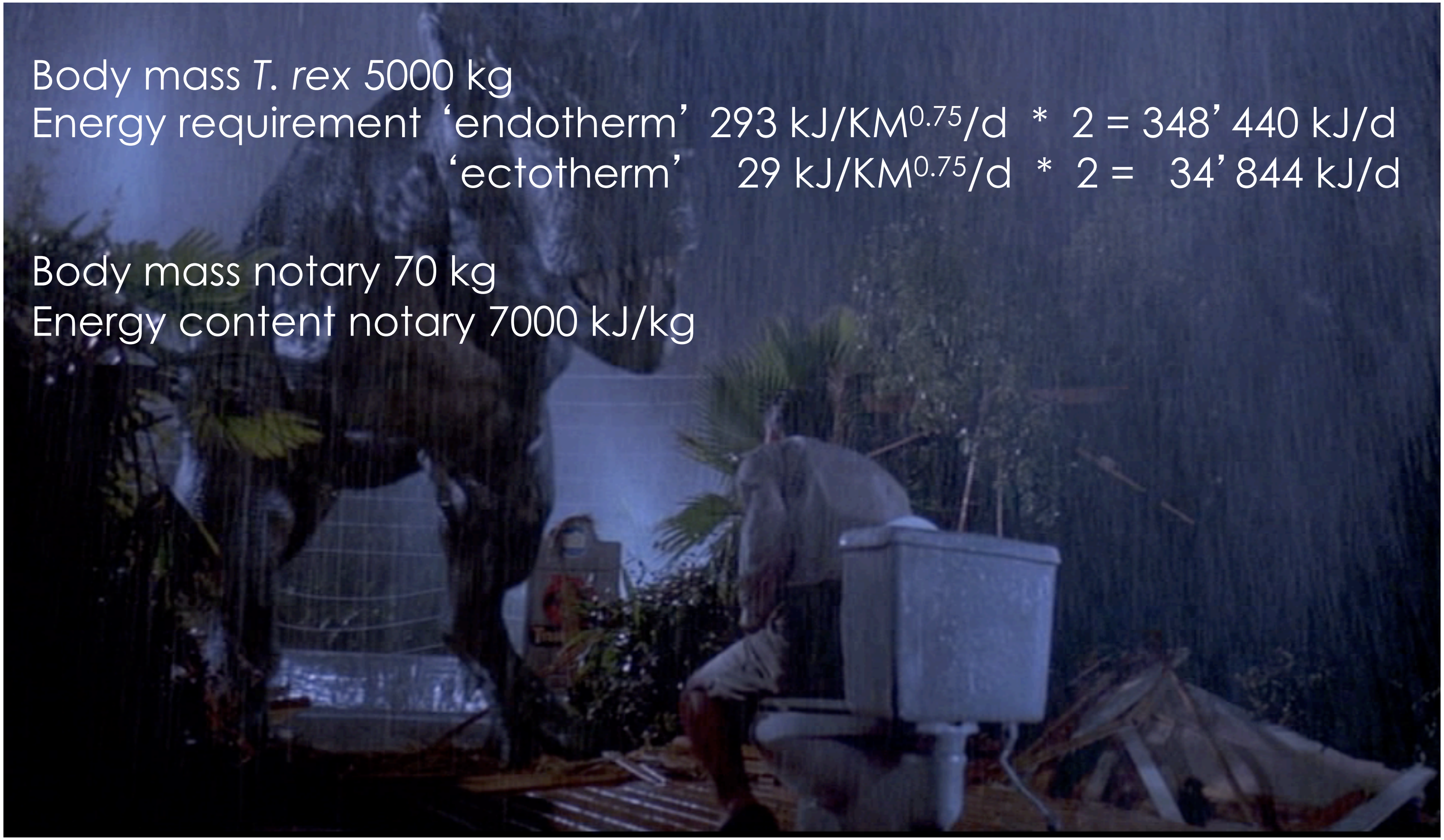


Body mass *T. rex* 5000 kg

Energy requirement ‘endotherm’ 293 $kJ/KM^{0.75}/d$ * 2 = 348’ 440 kJ/d

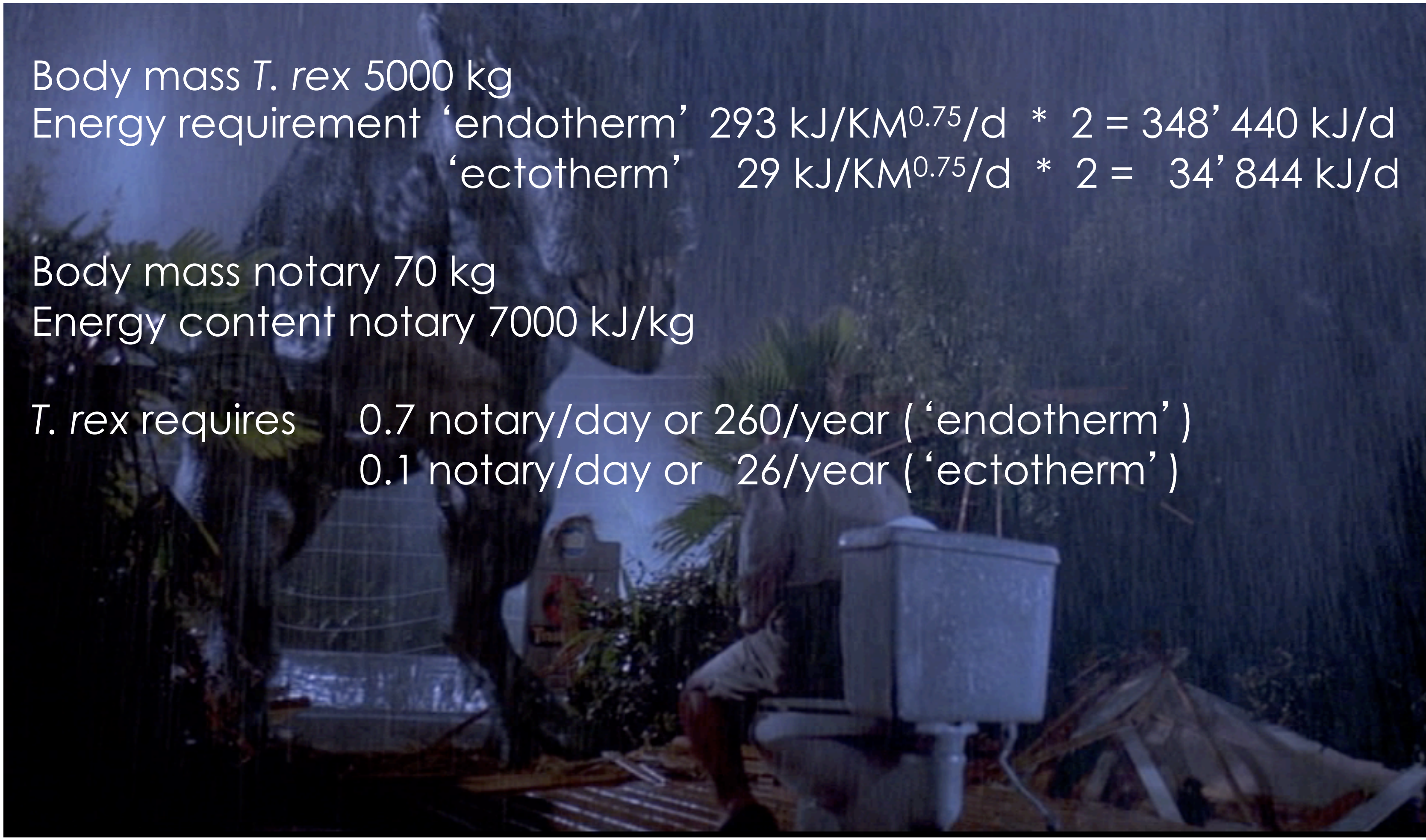
‘ectotherm’ 29 $kJ/KM^{0.75}/d$ * 2 = 34’ 844 kJ/d

Body mass notary 70 kg

Energy content notary 7000 kJ/kg

from Spielberg et al. (1993)
Brett-Surman & Farlow (1997)

How many notaries does a *T. rex* need per year?



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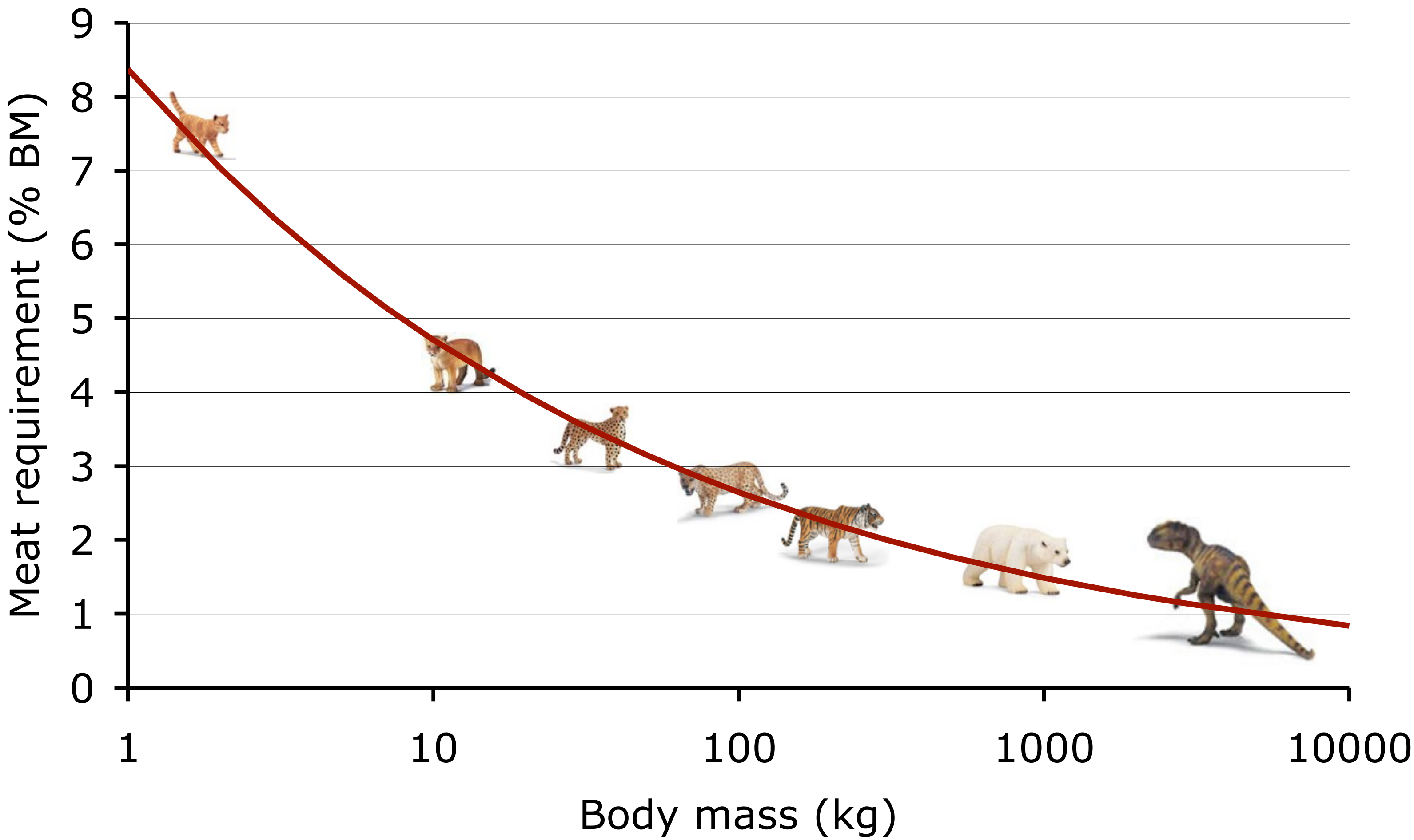
Body mass notary 70 kg
Energy content notary 7000 kJ/kg

T. rex requires 0.7 notary/day or 260/year (‘endotherm’)
0.1 notary/day or 26/year (‘ectotherm’)

from Spielberg et al. (1993)
Brett-Surman & Farlow (1997)

Food requirements of carnivores



Hunting food or glory ?

BBC (1998)

Hunting food !

BBC (1998)

Hunting food !

BBC (1998)

Hunting food !

BBC (1998)

Growing up

Growing up

BBC (1998)

Growing up

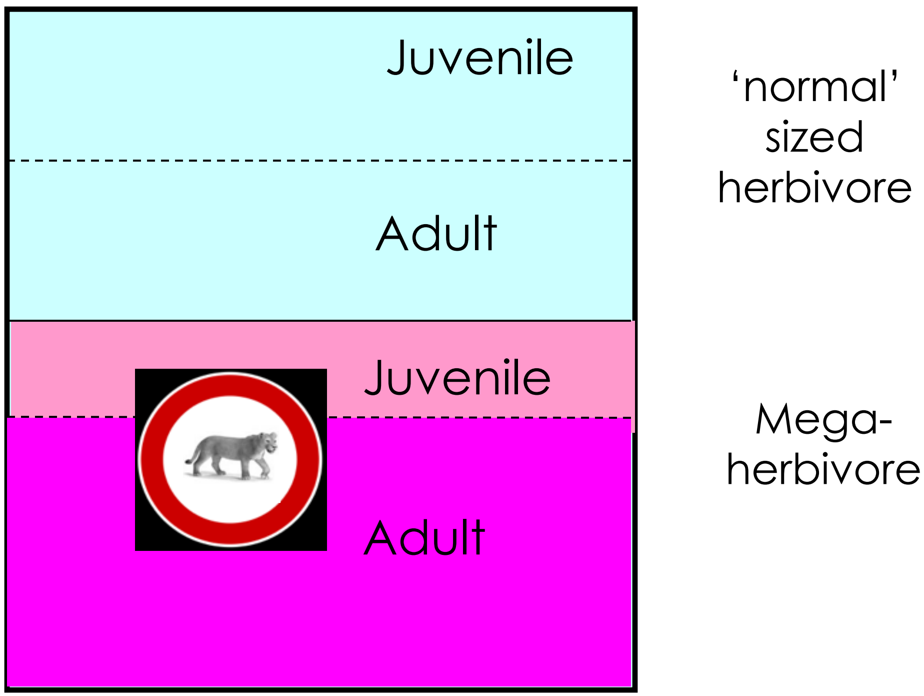
BBC (1998)

Growing up

BBC (1998)

Prey availability

Mammal Herbivores

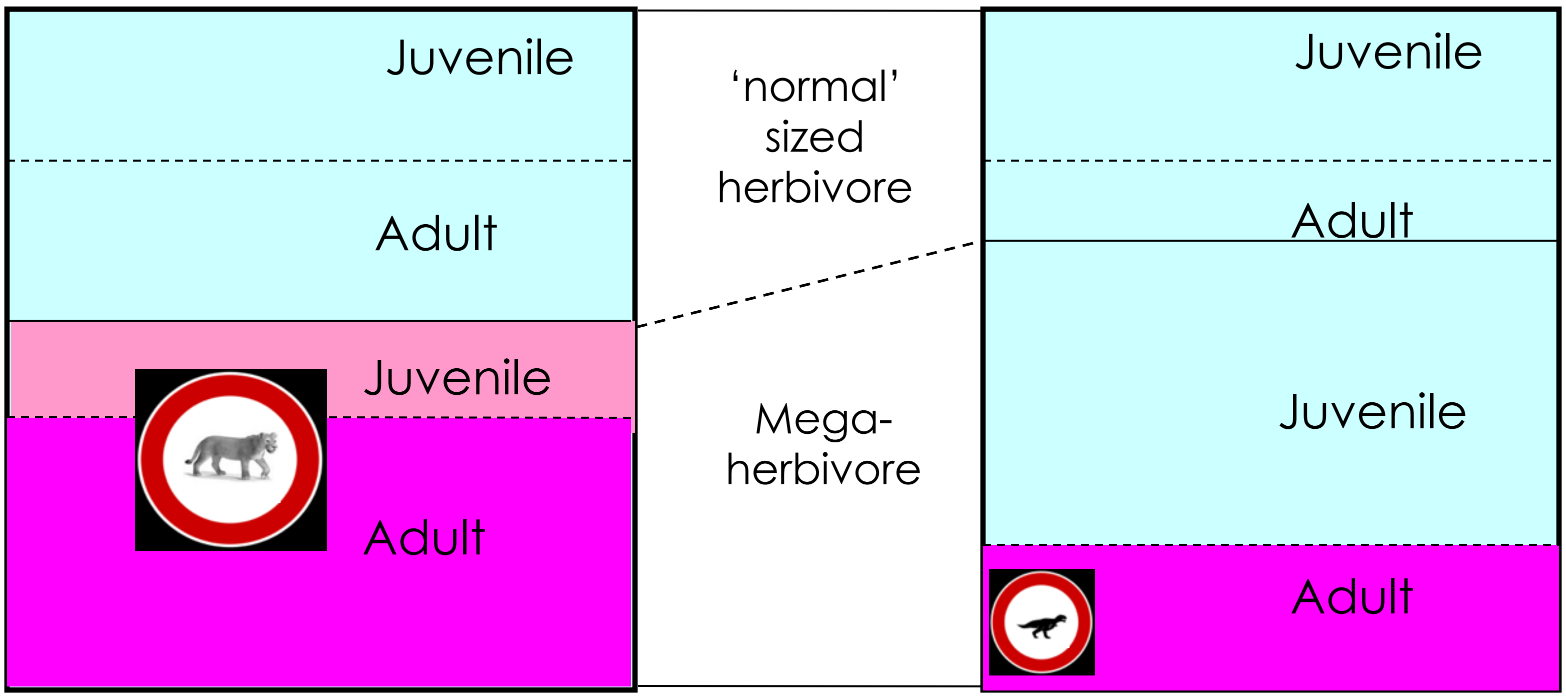


from Hummel & Clauss (2008)

Prey availability

Mammal Herbivores

Dinosaur Herbivores



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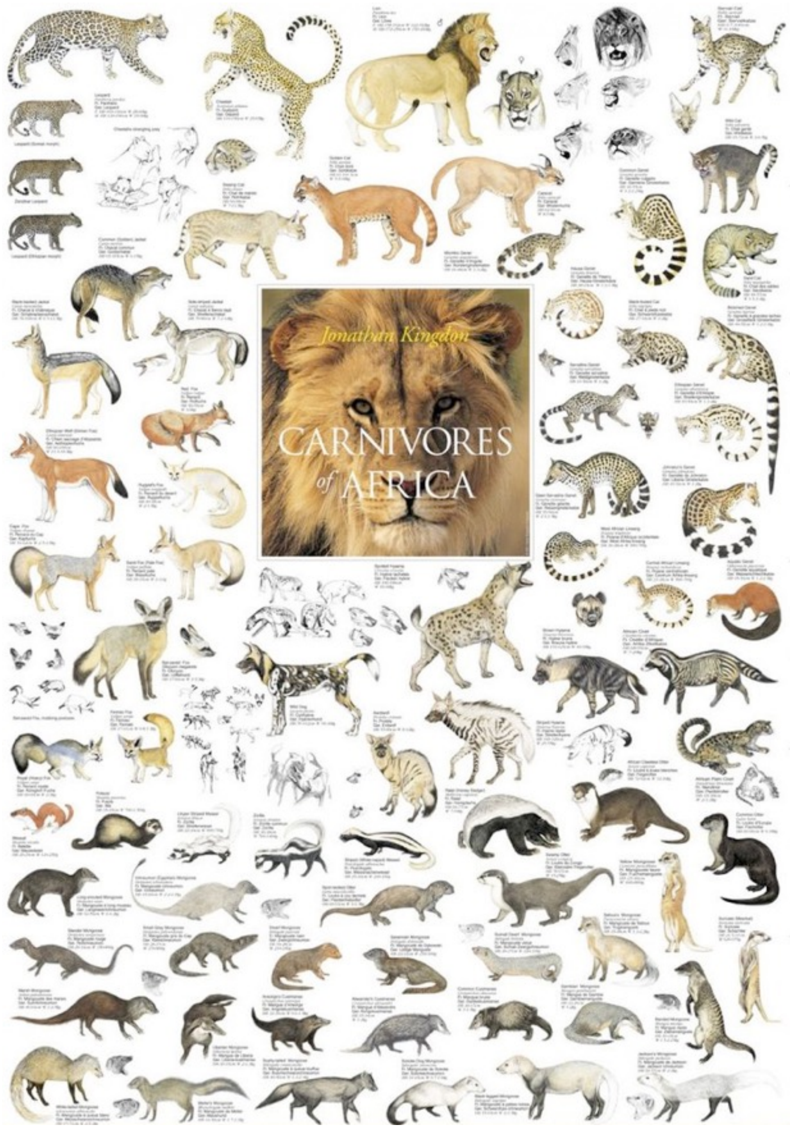
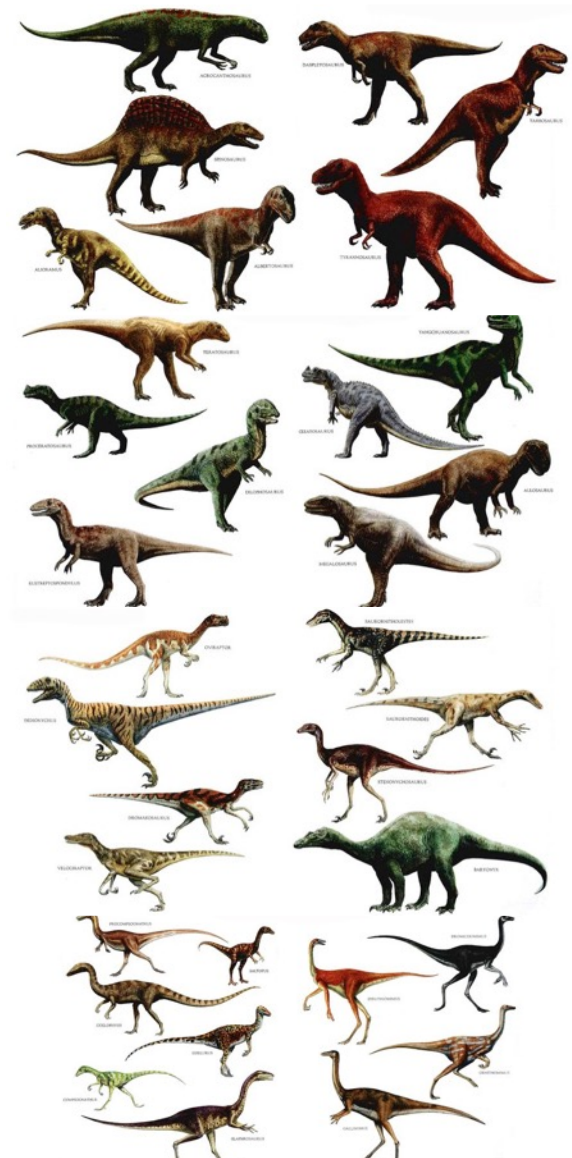
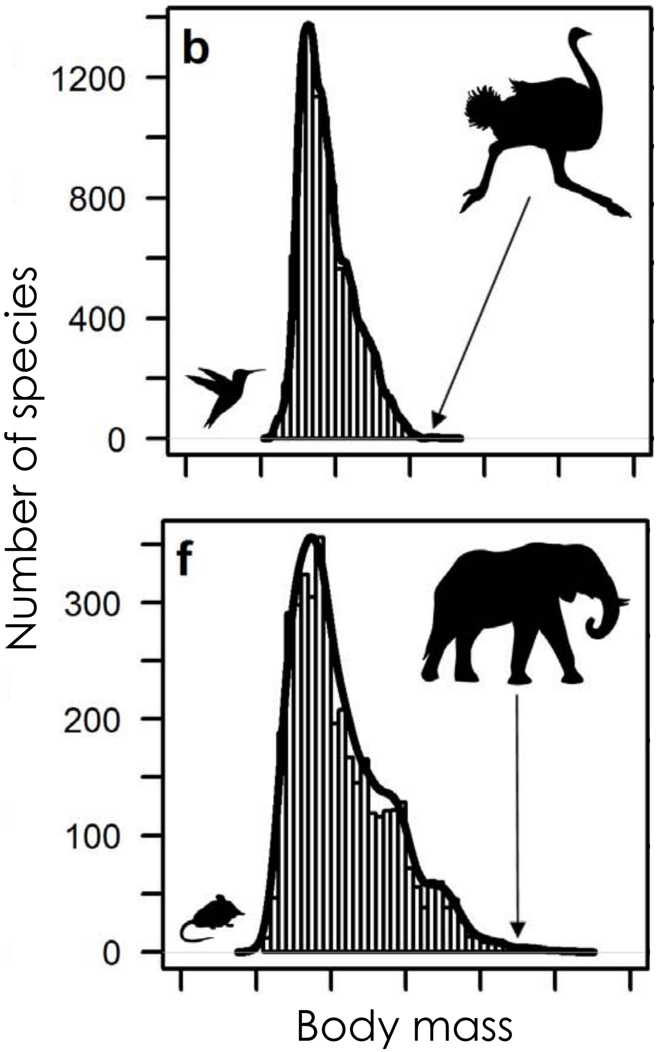
Carnivore faunas



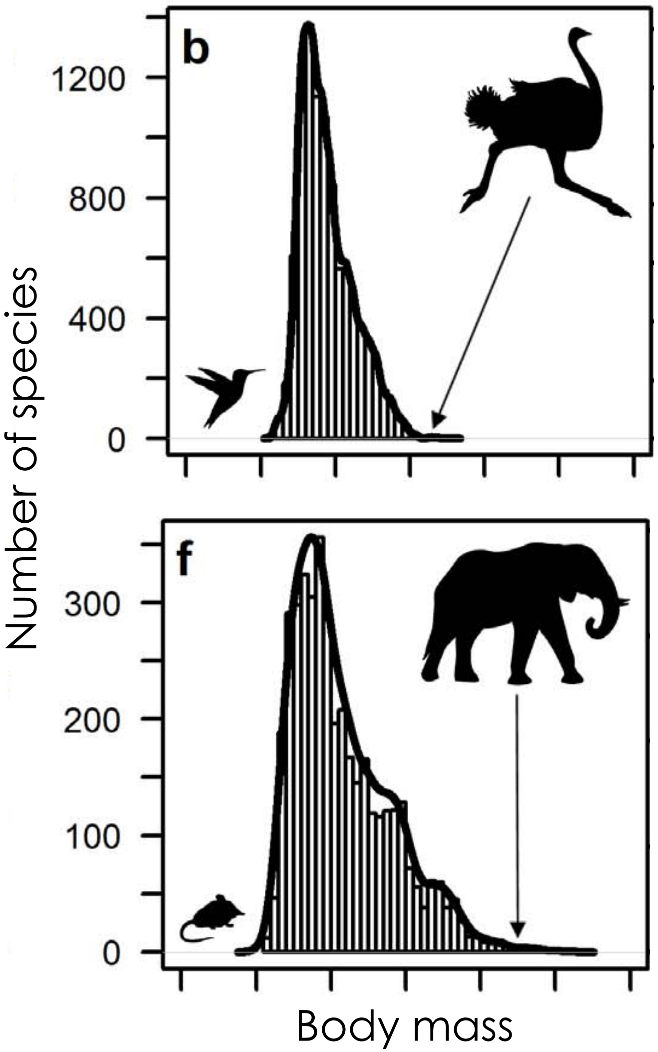


Species distributions - mammals/birds



O'Gorman & Hone (2012)

Species distributions - mammals/birds



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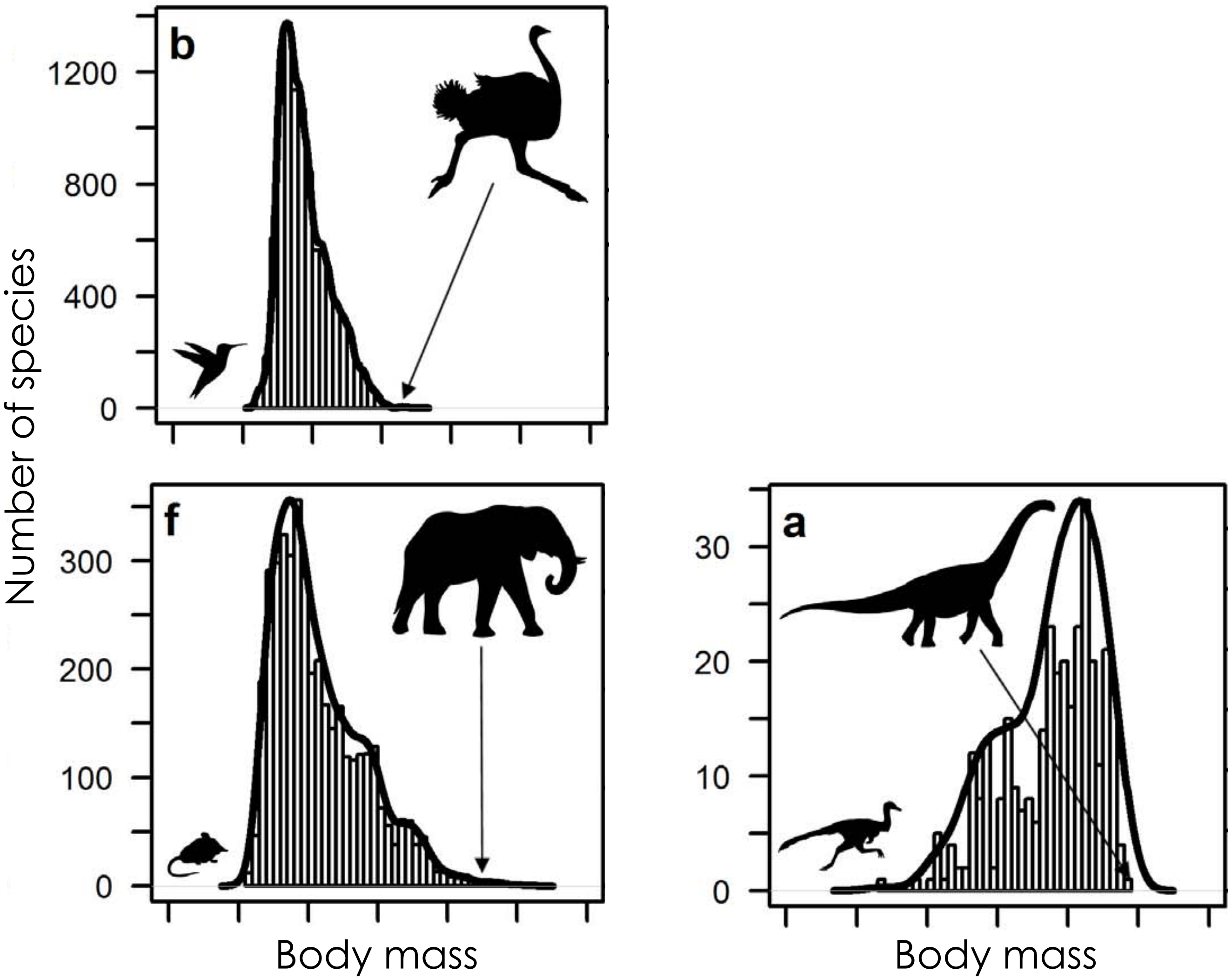
Species distributions - dinosaurs



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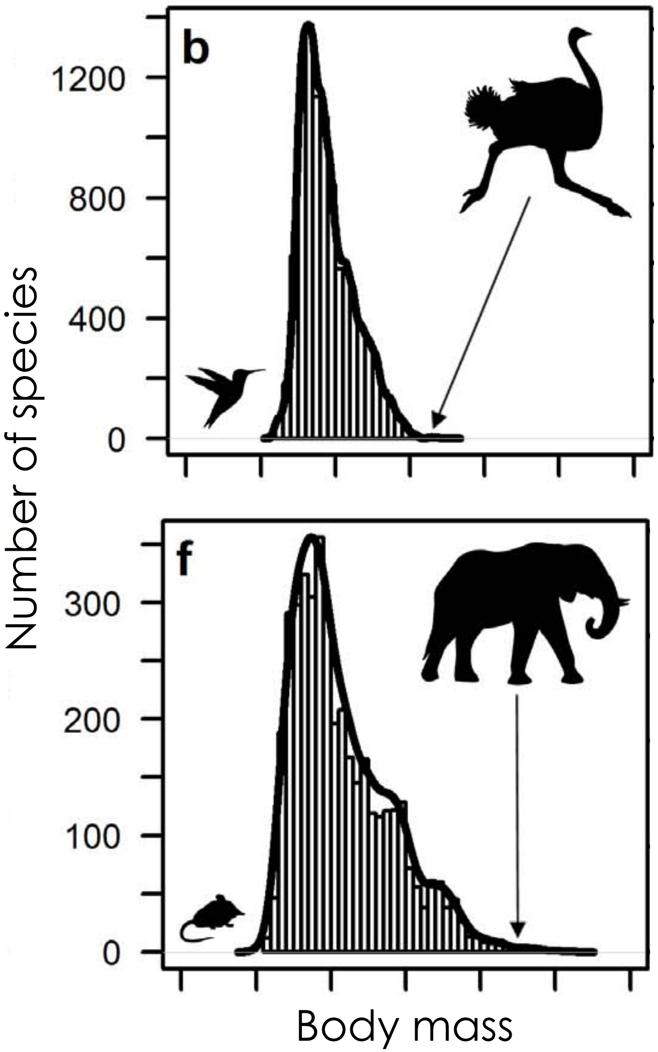

O'Gorman & Hone (2012)

Start assumptions

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- Niche stratification according to body size (=body mass)

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- Eggs cannot increase endlessly in size because of physical constraints on egg shell thickness (stronger shells needed for larger eggs) and diffusion (thicker shells prevent diffusion of oxygen)

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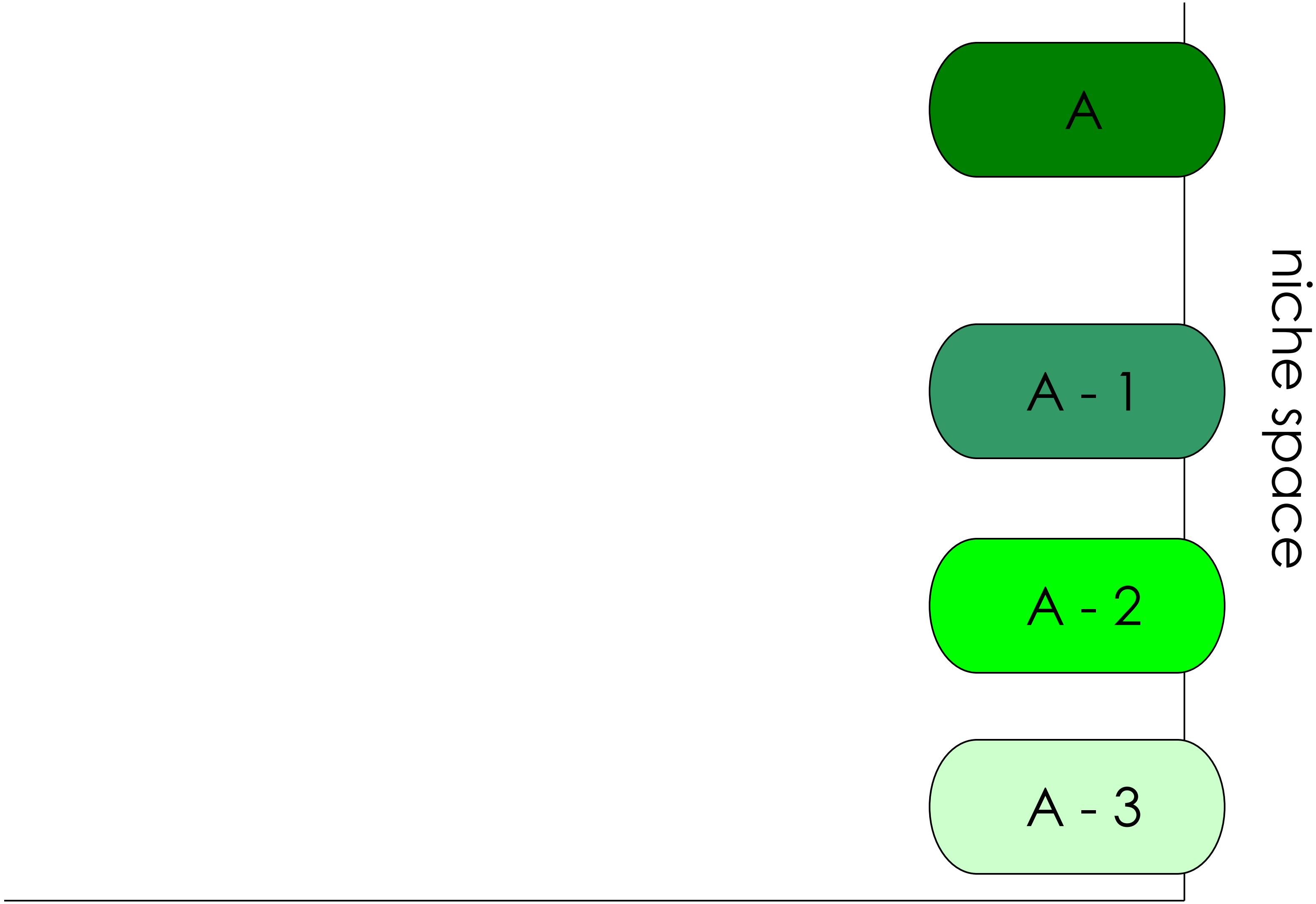
- Niche stratification according to body size (=body mass)
- Eggs cannot increase endlessly in size because of physical constraints on egg shell thickness (stronger shells needed for larger eggs) and diffusion (thicker shells prevent diffusion of oxygen)
- The K-T extinction event affected all animals above a certain body size threshold

Niches of parent and offspring



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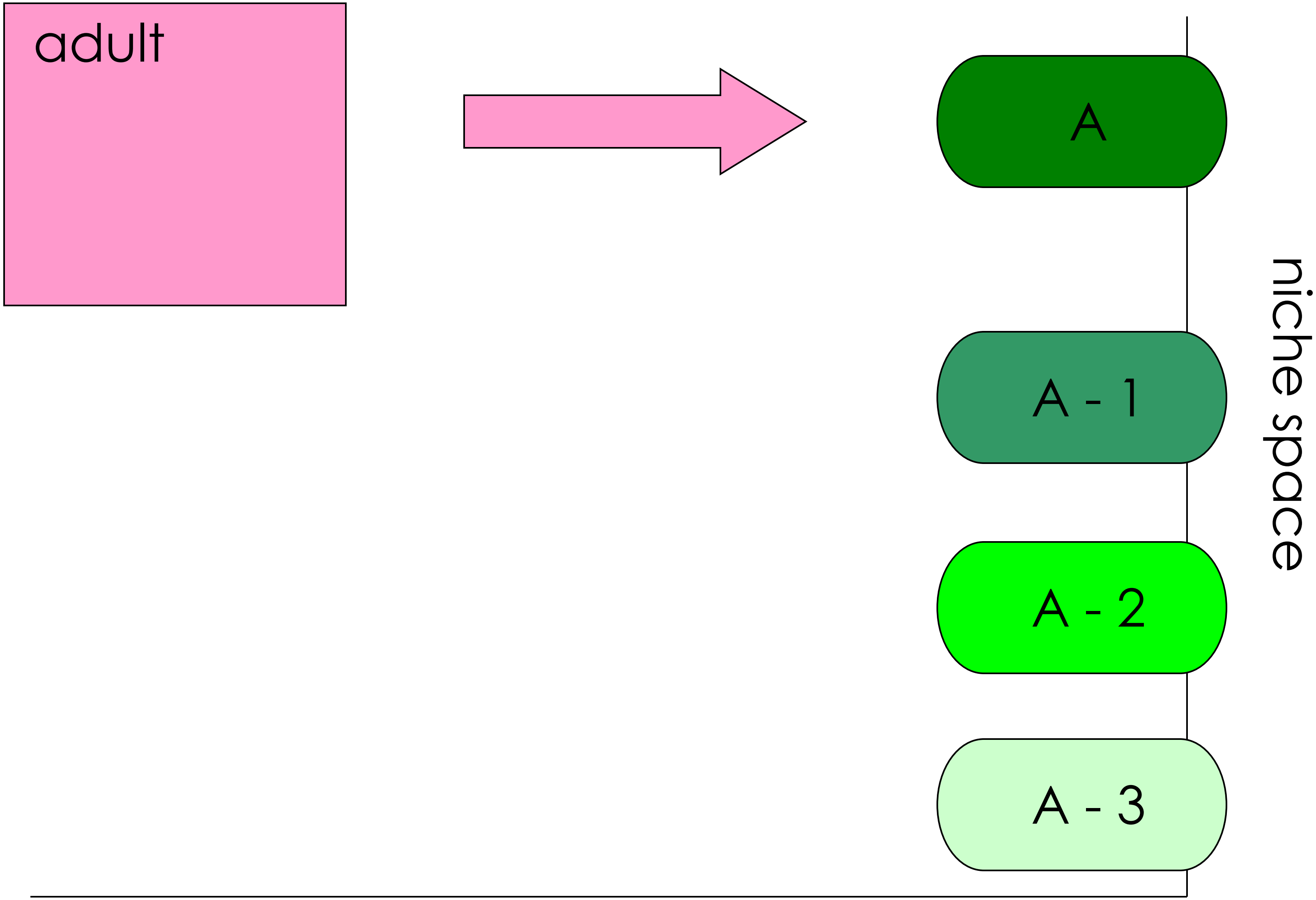

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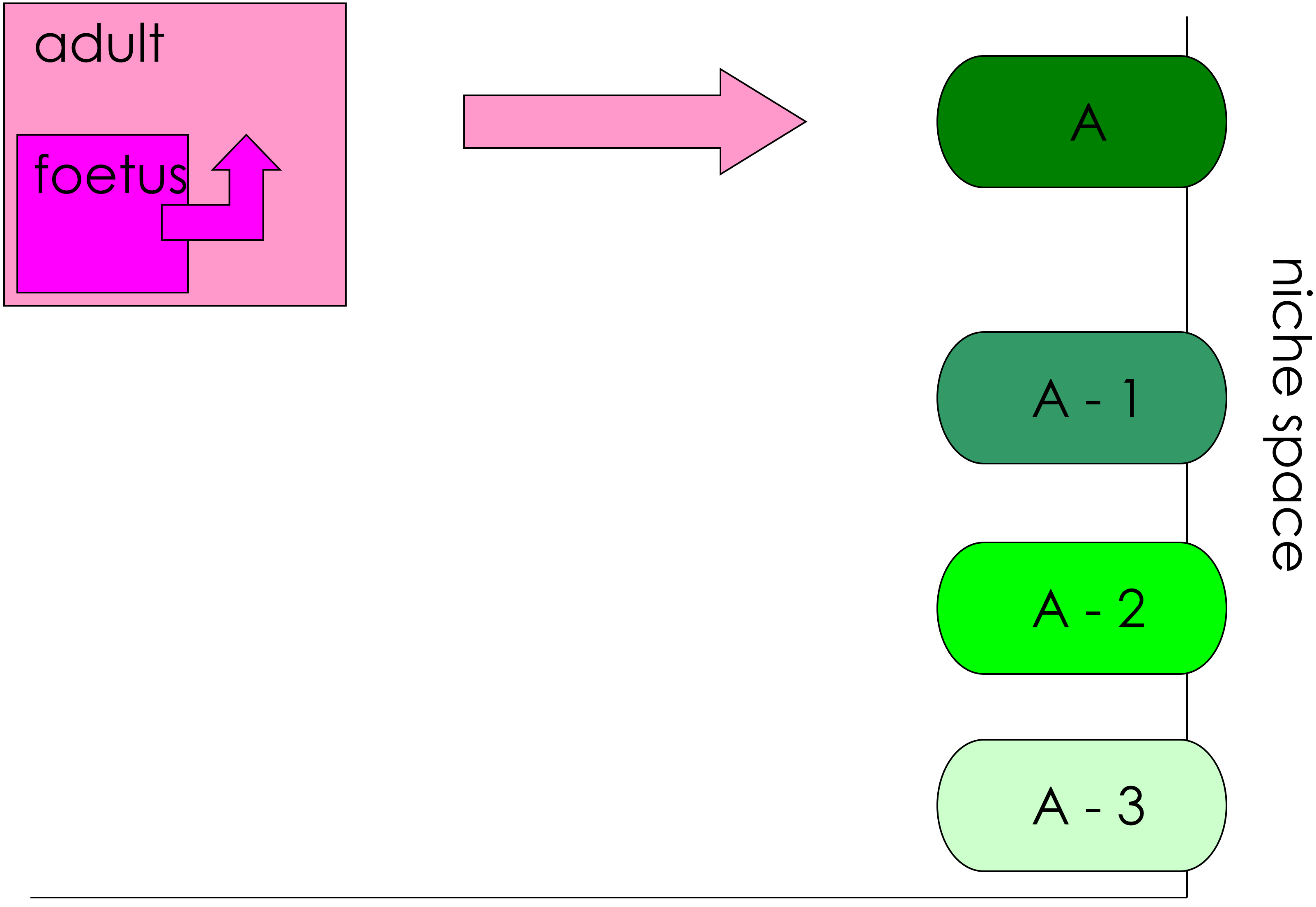

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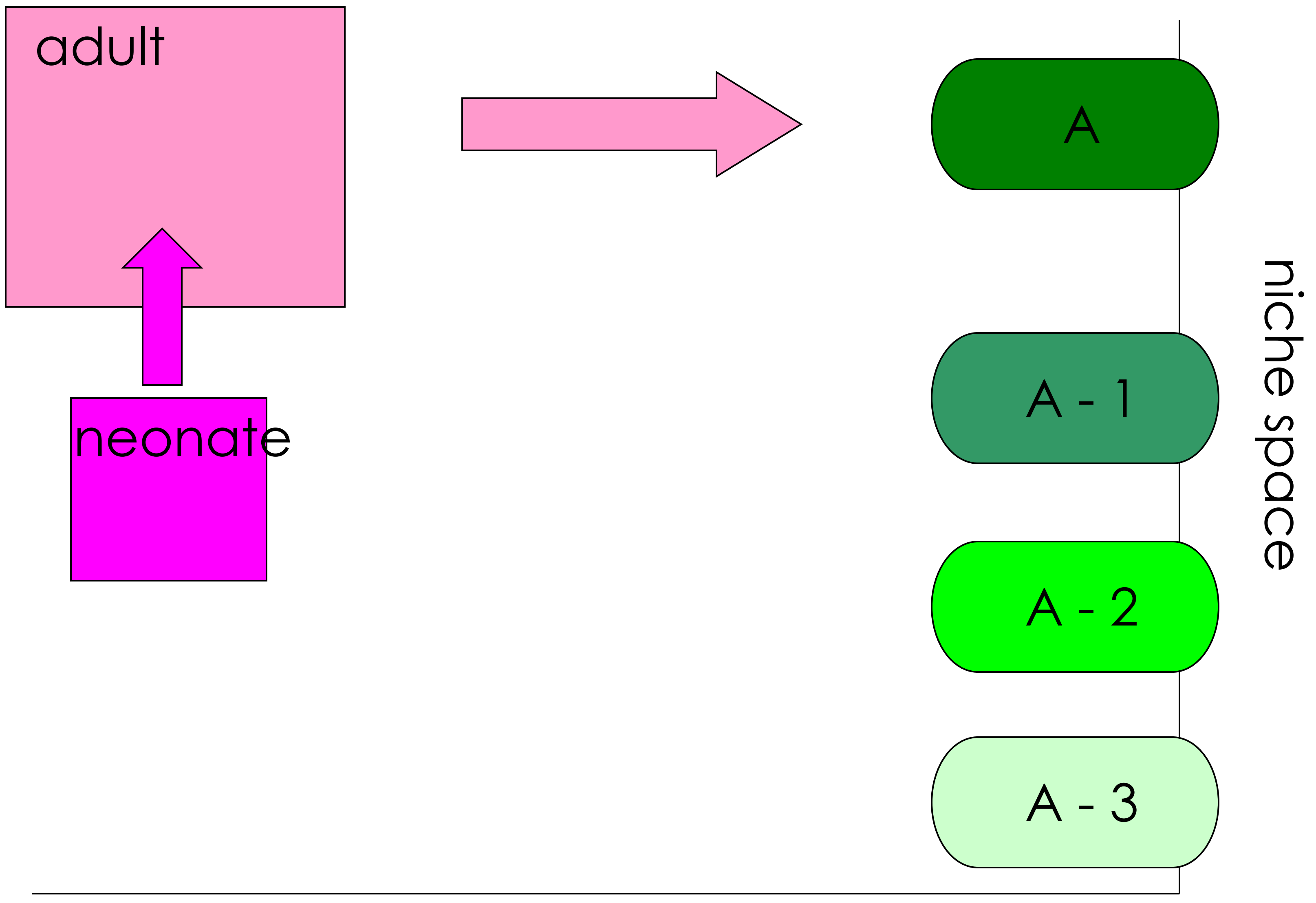

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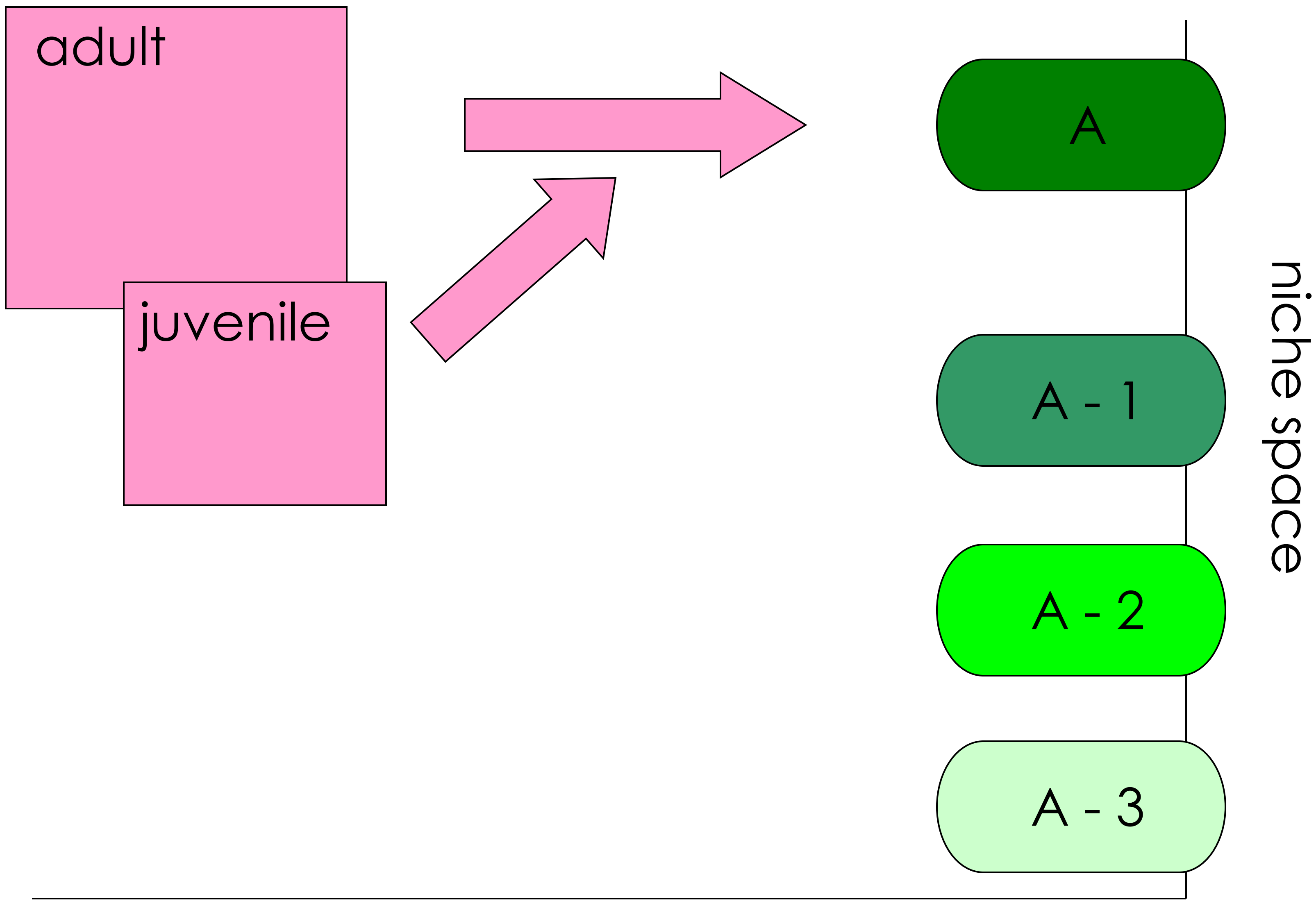

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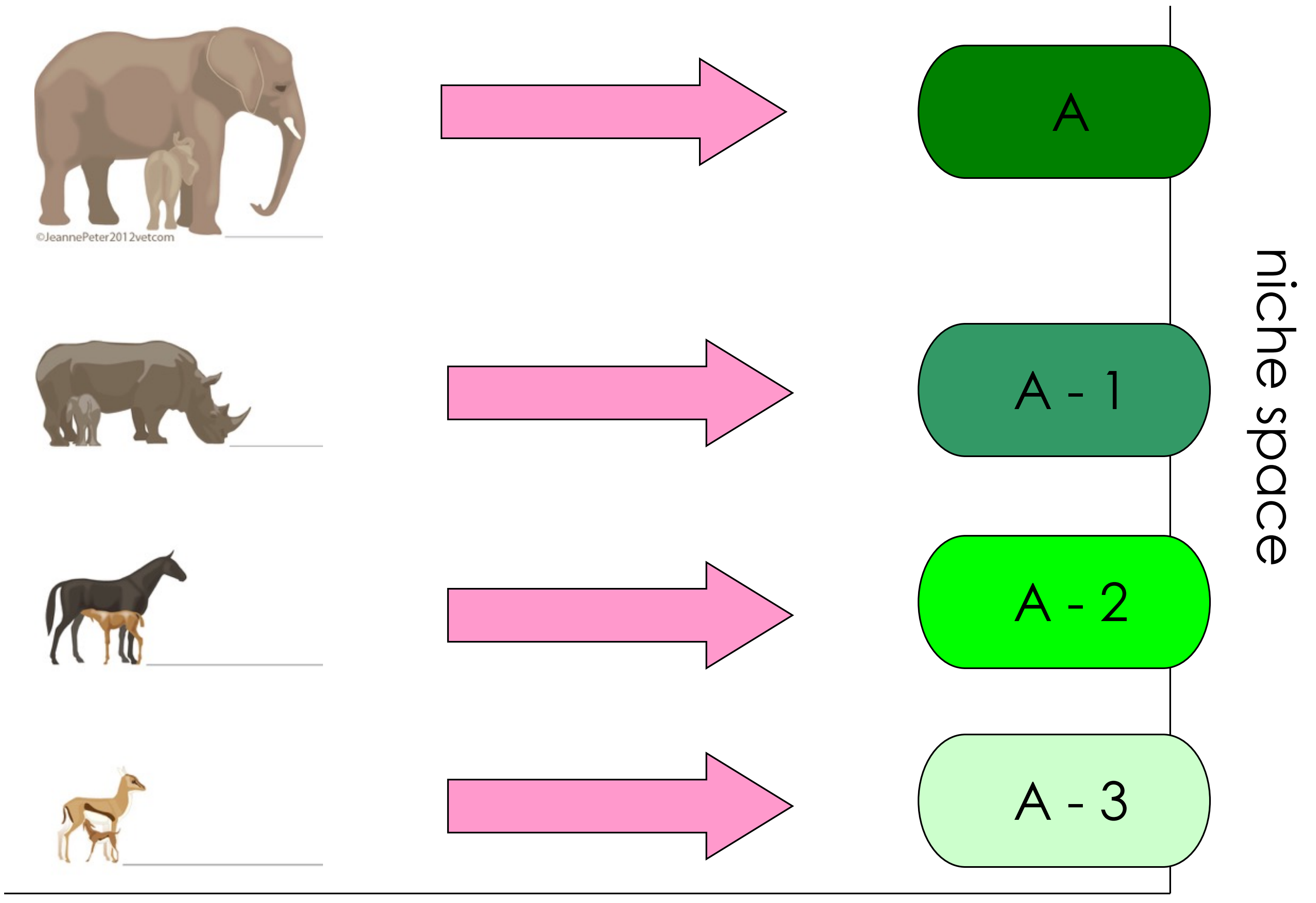

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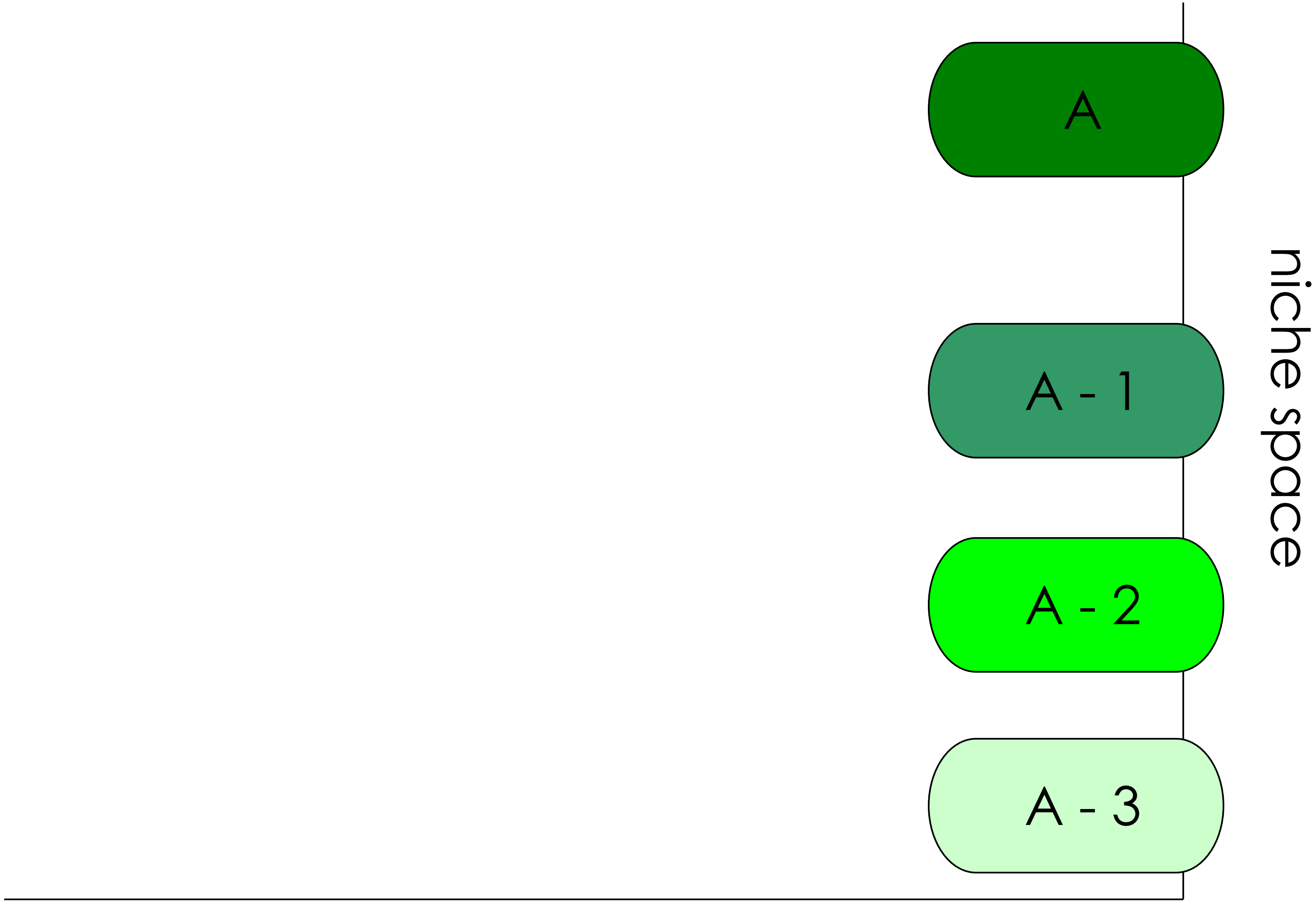

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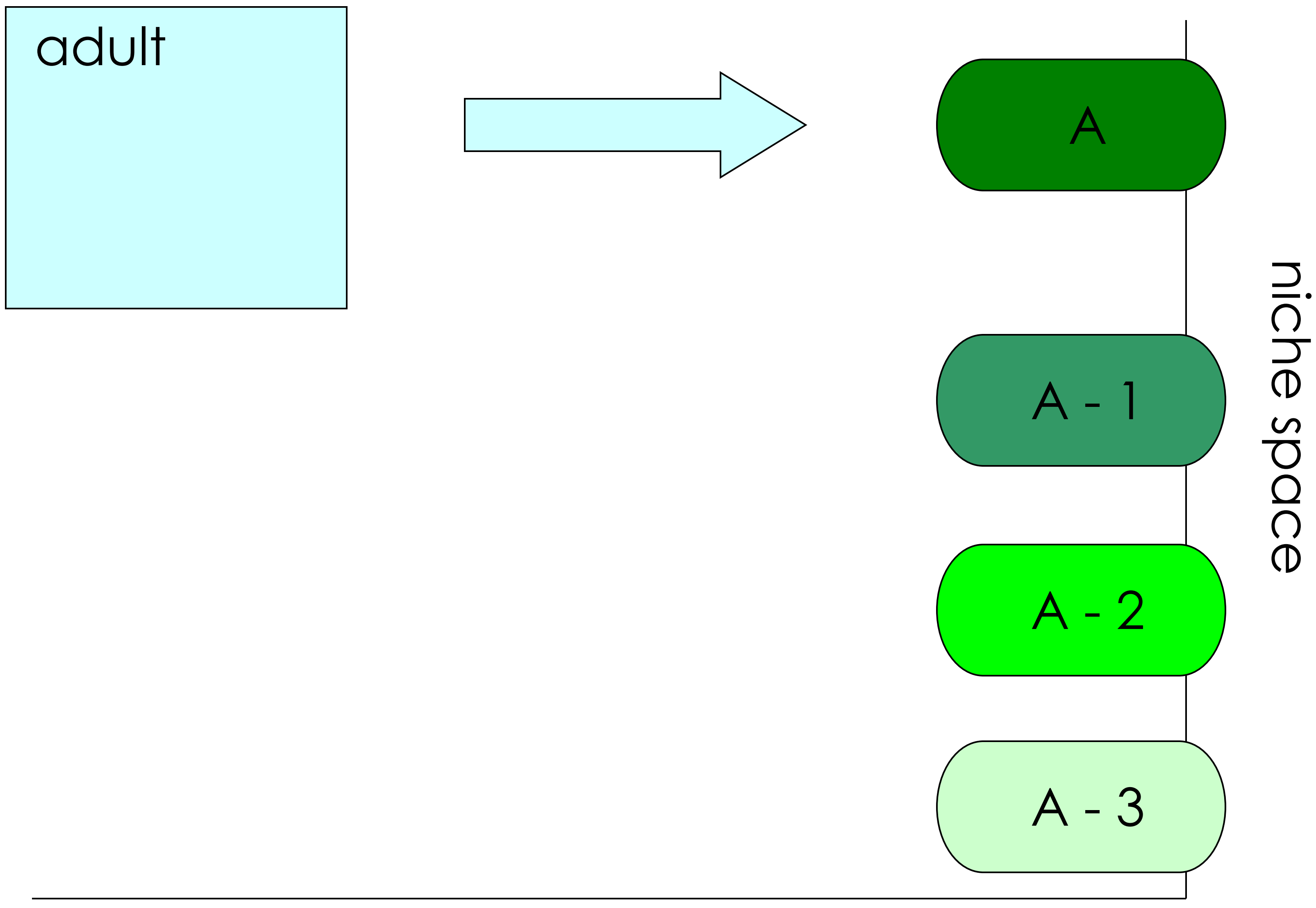

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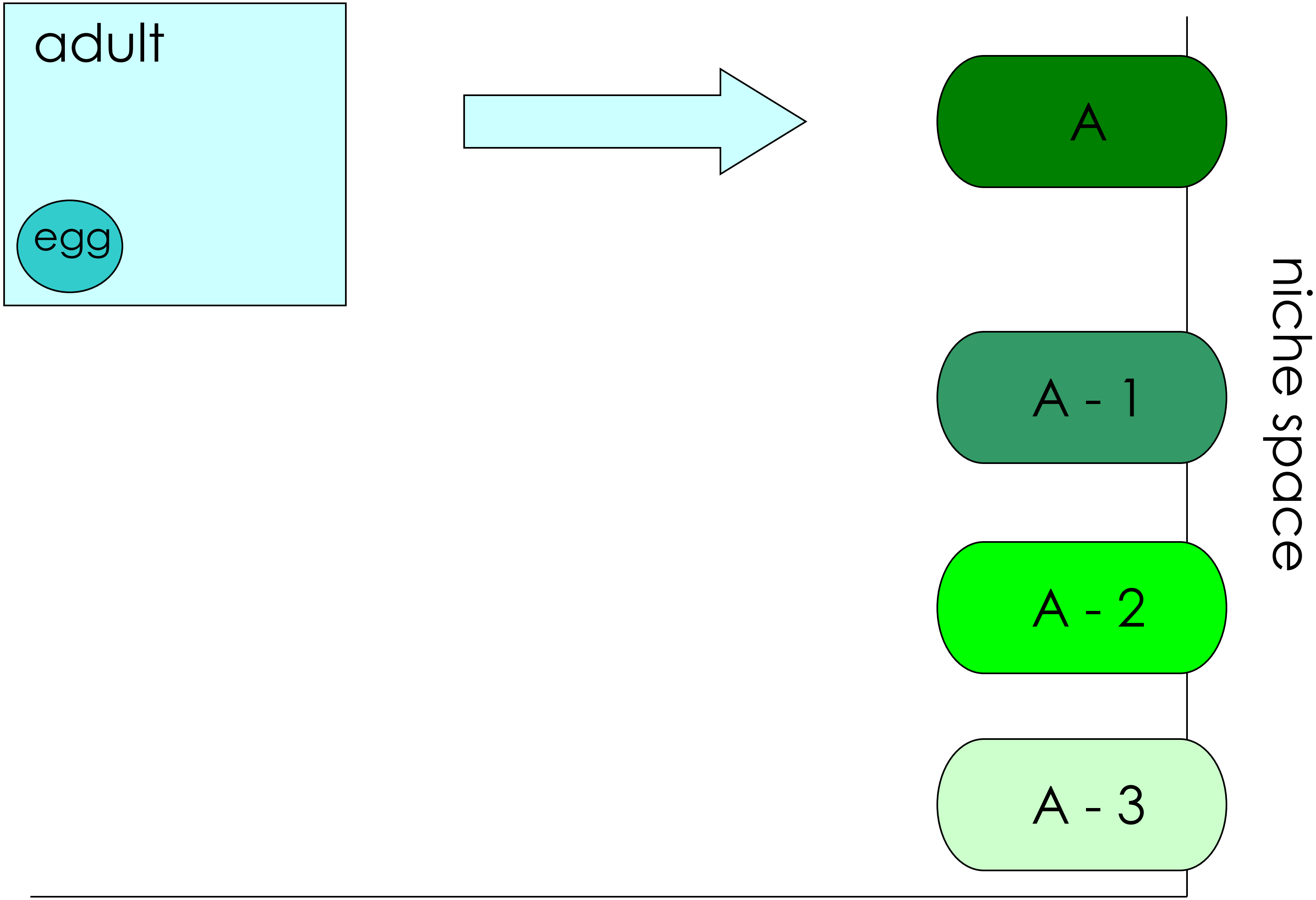

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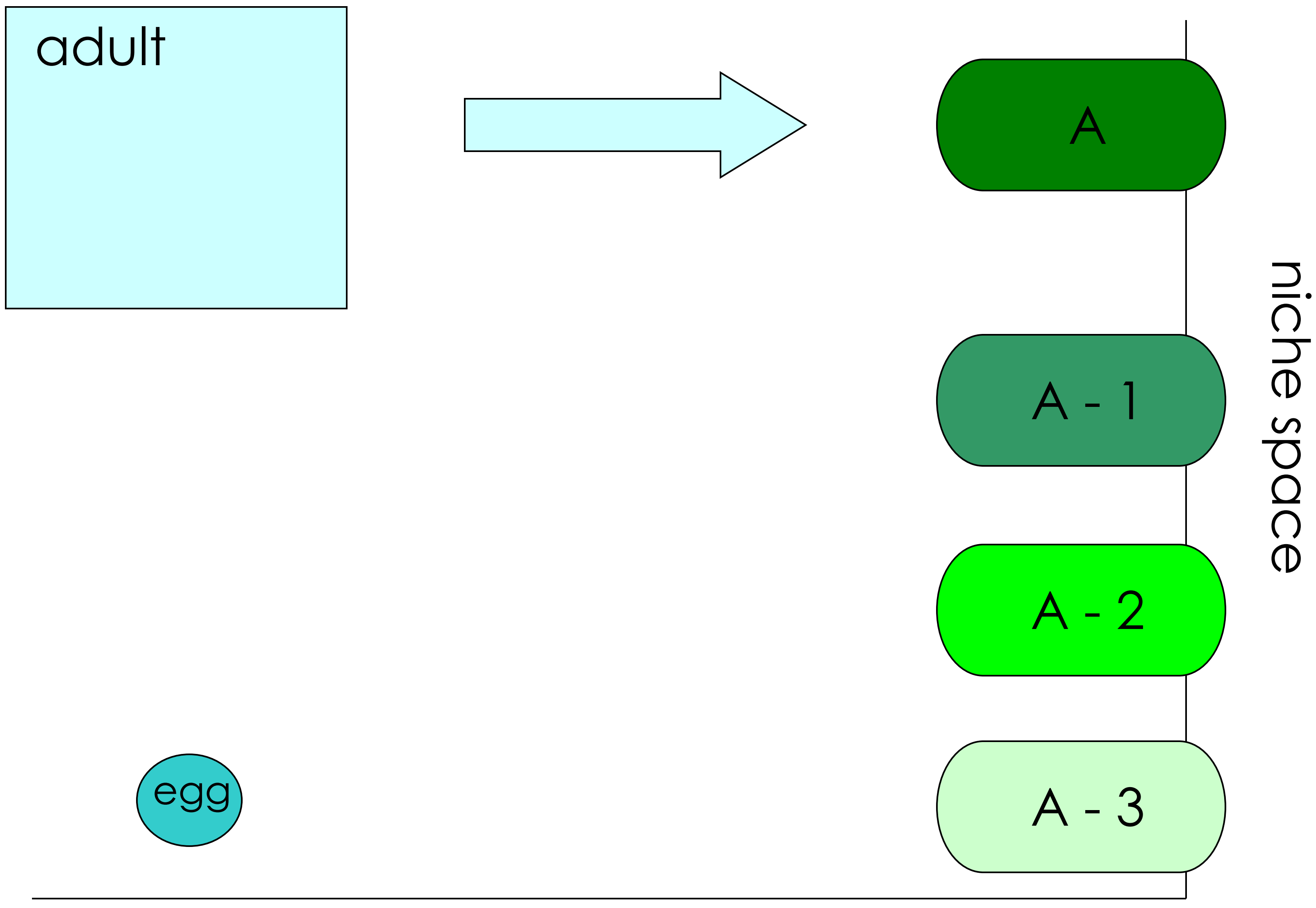

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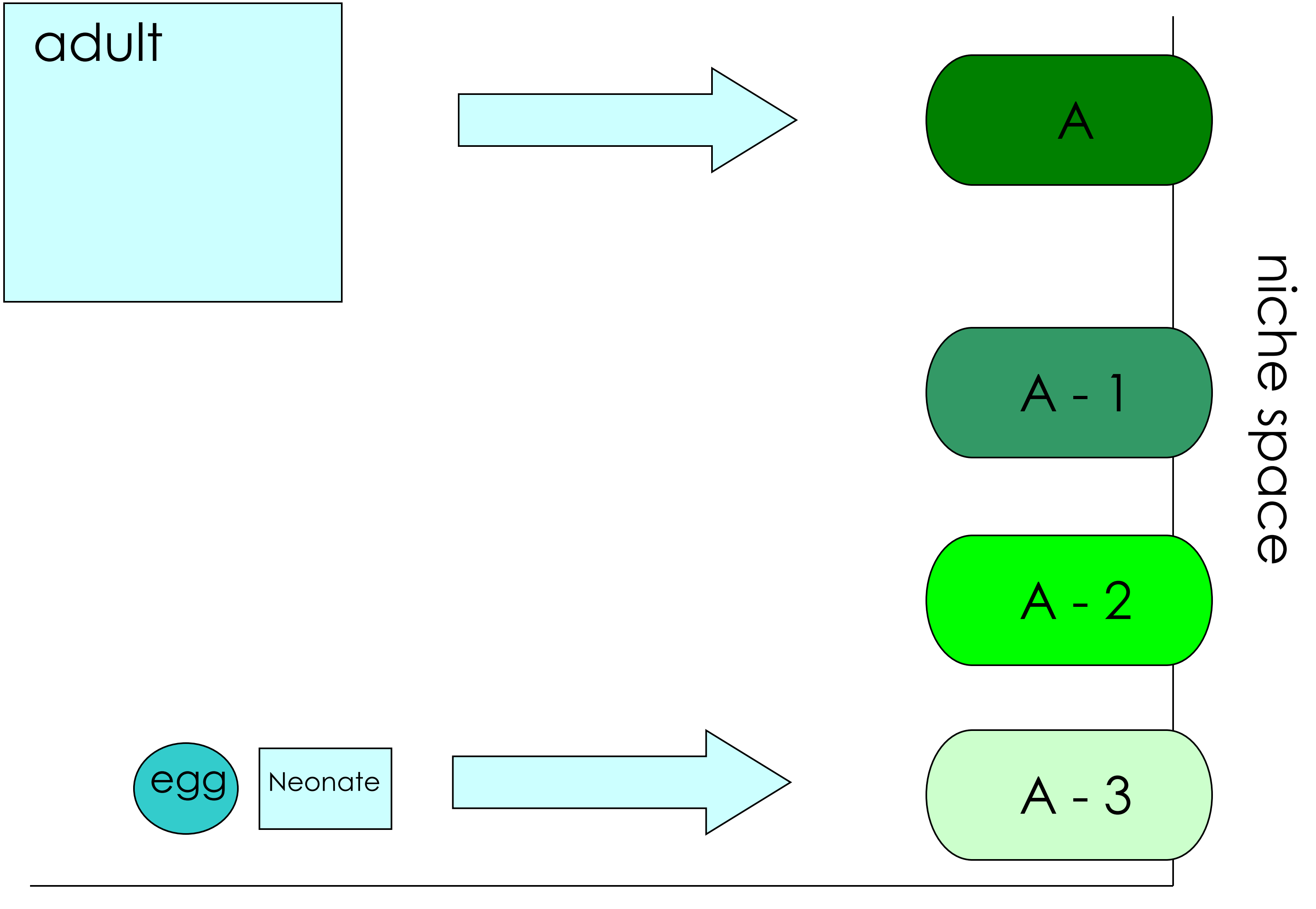

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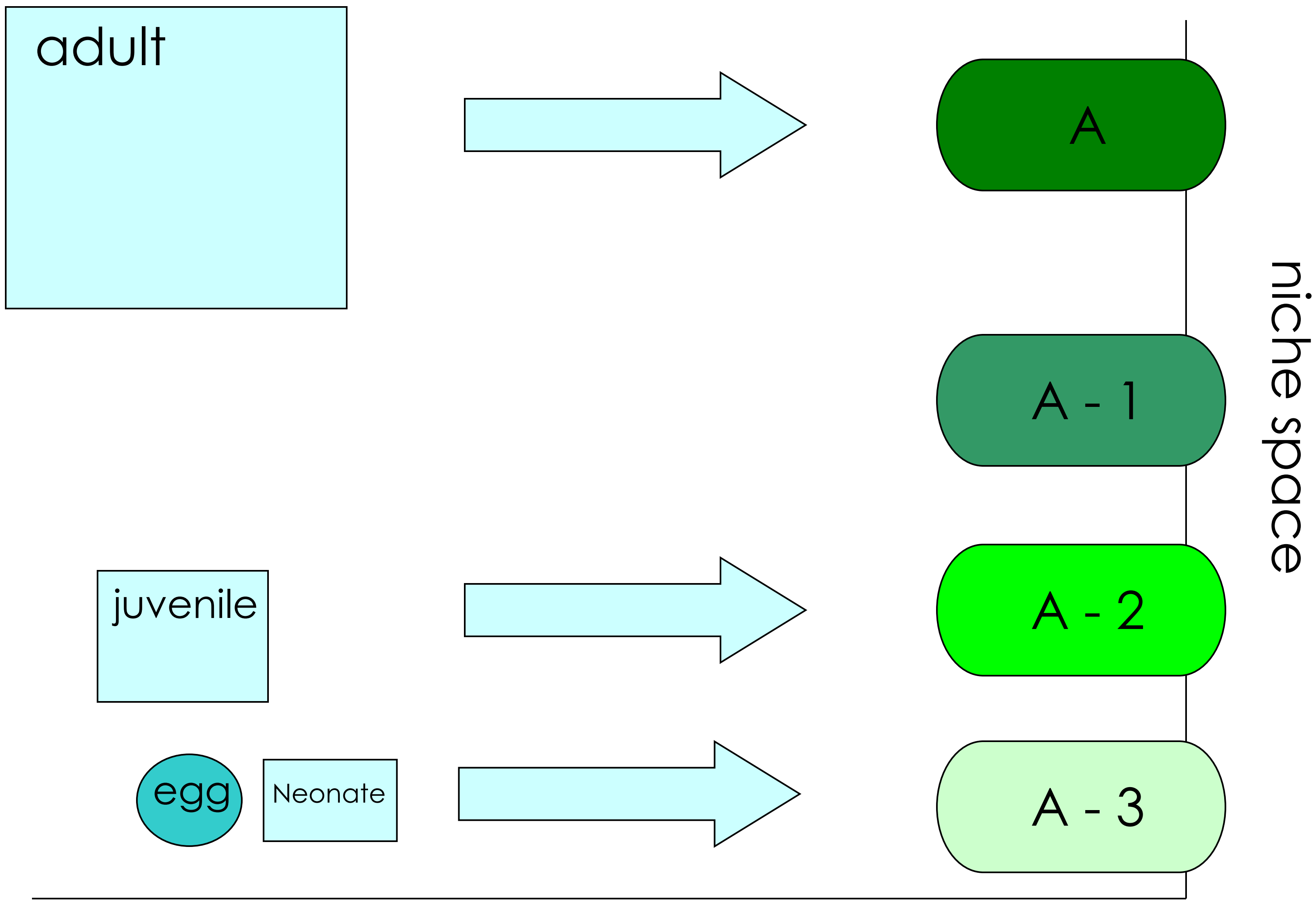

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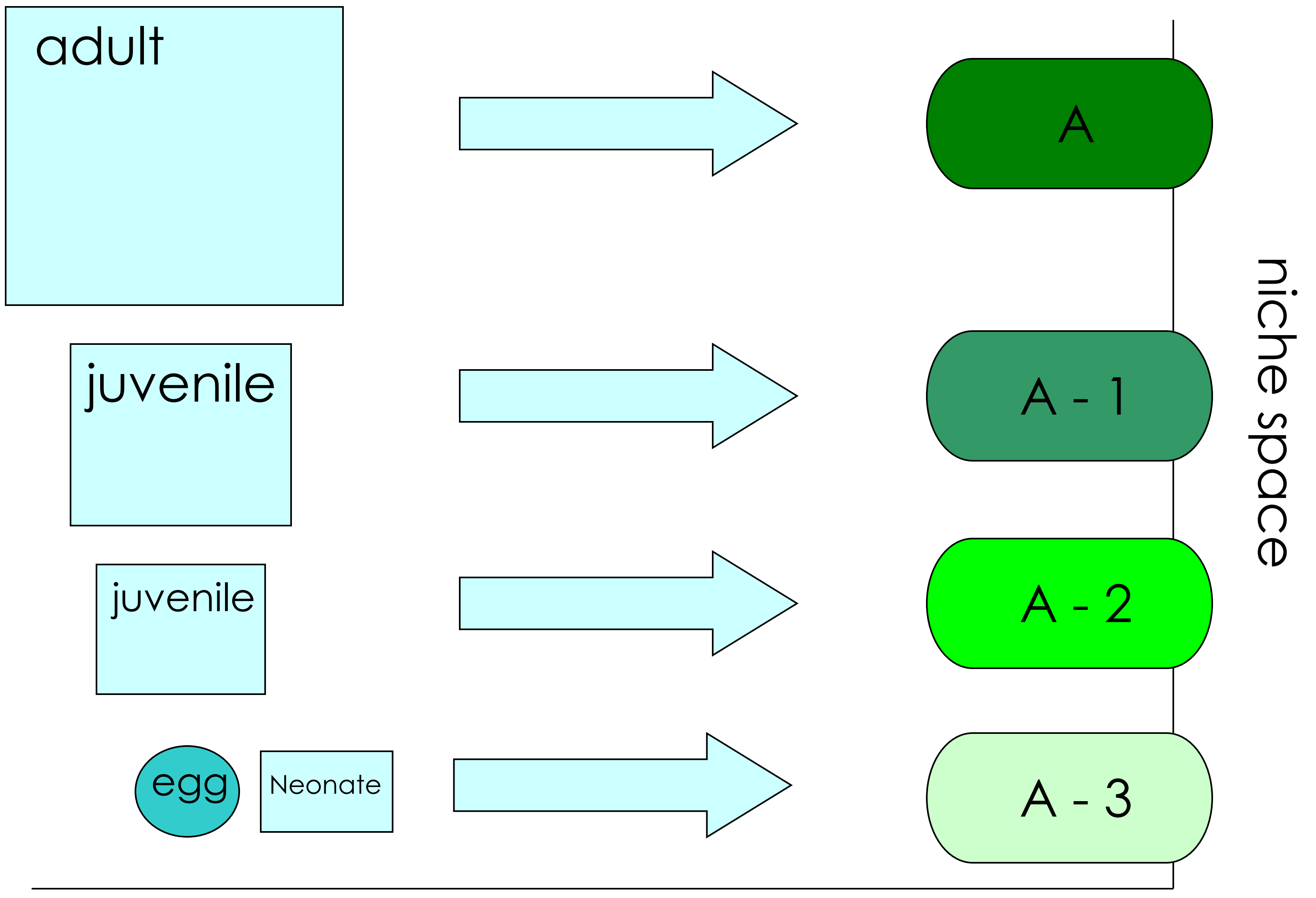

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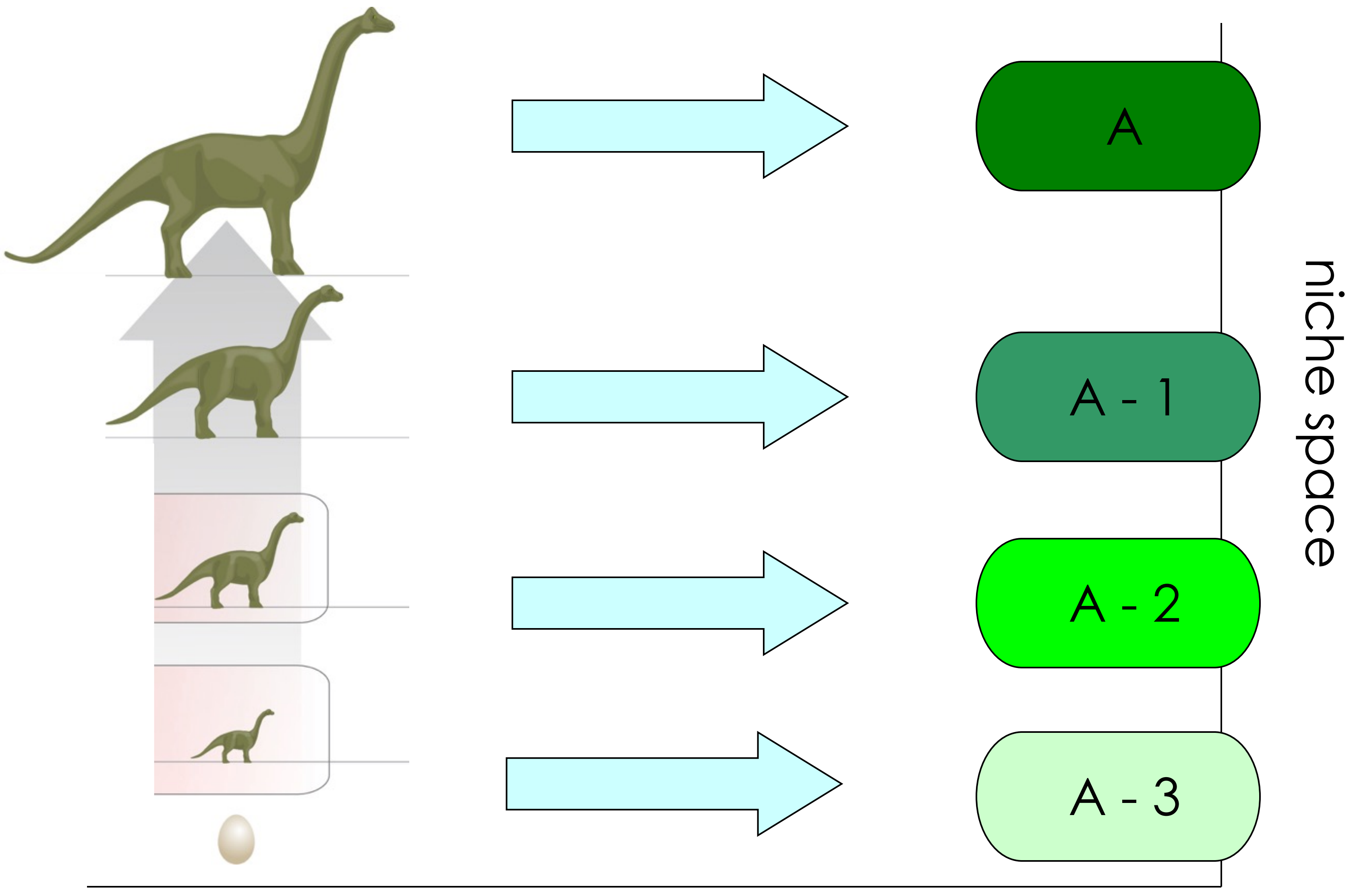

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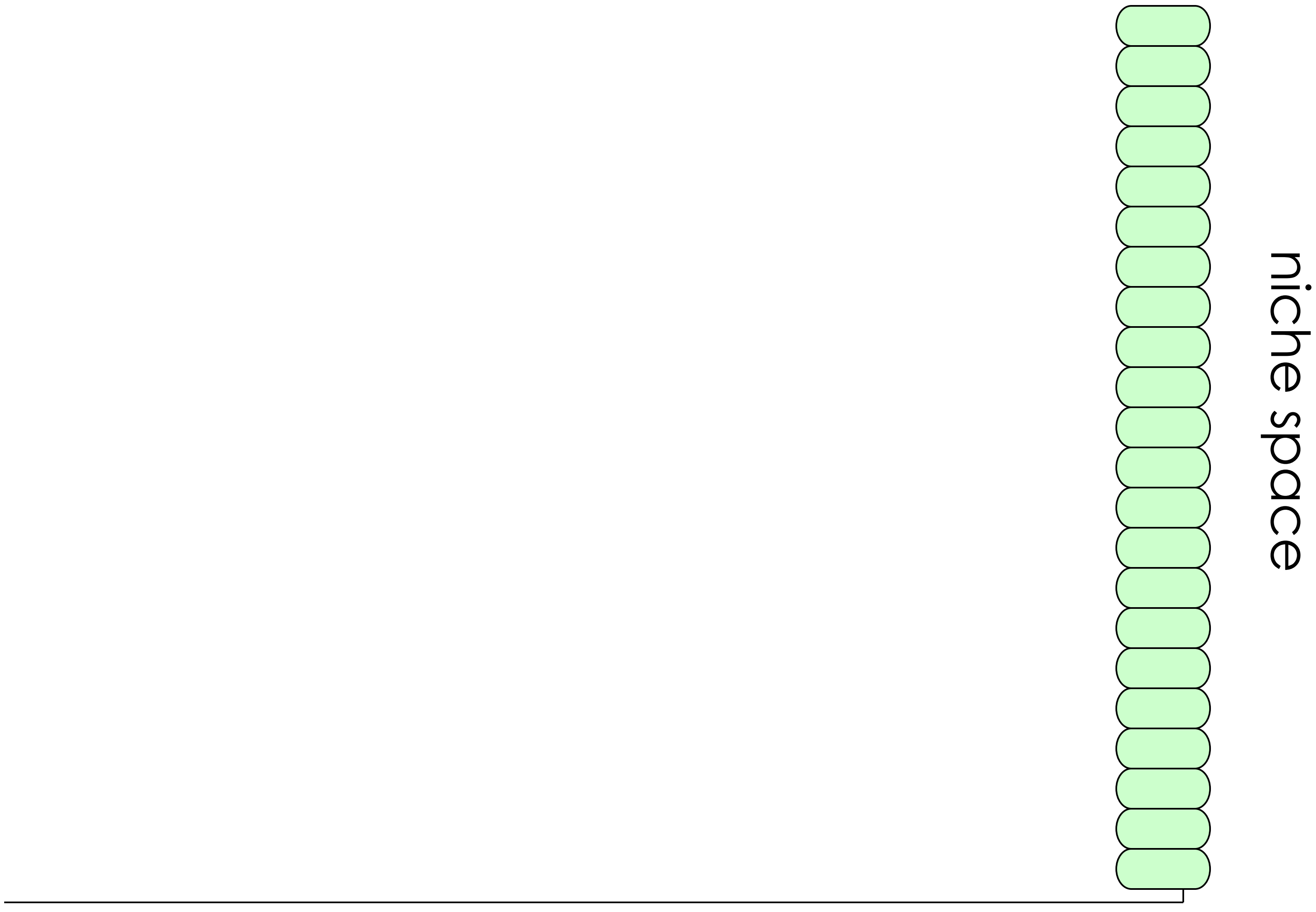

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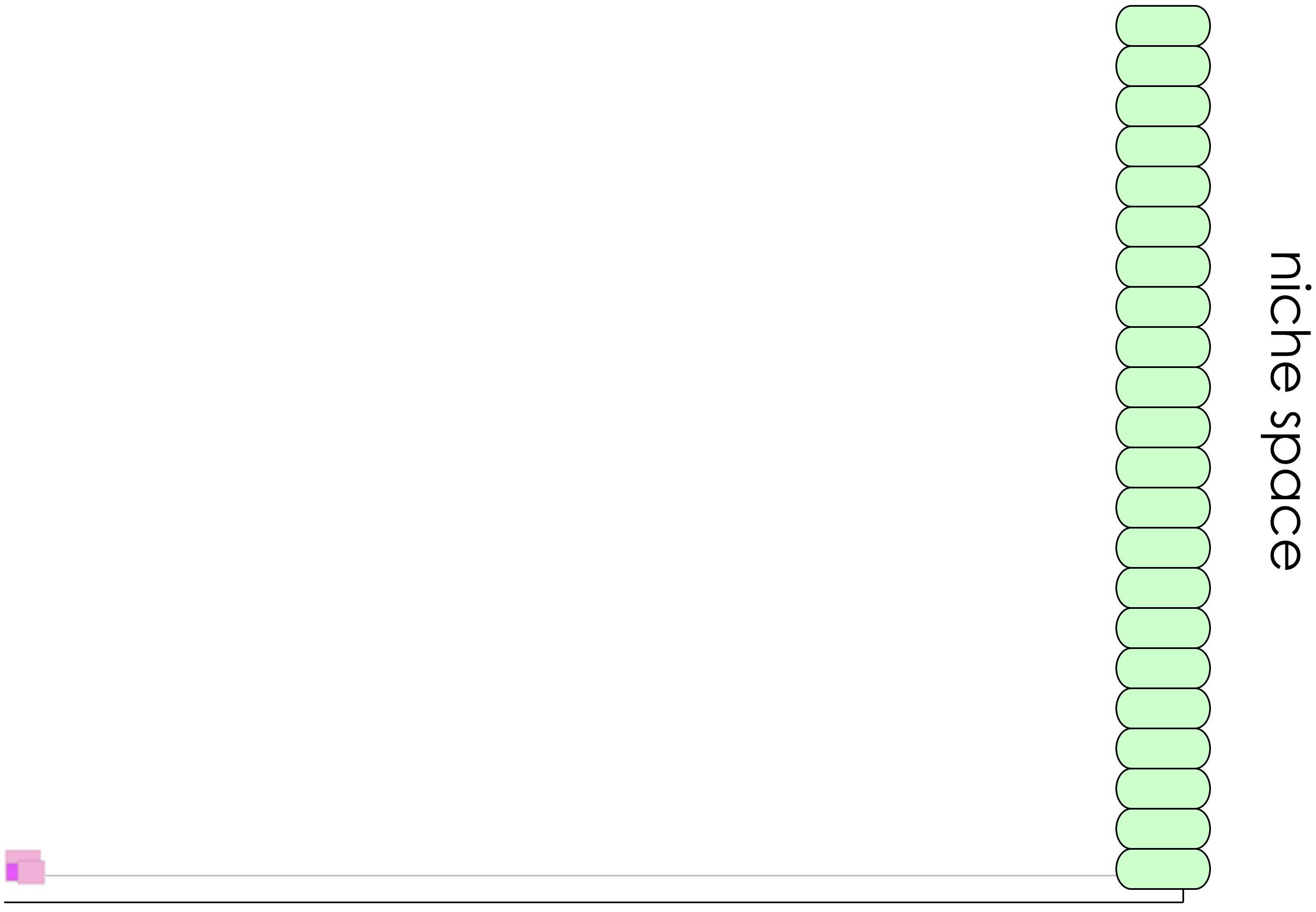

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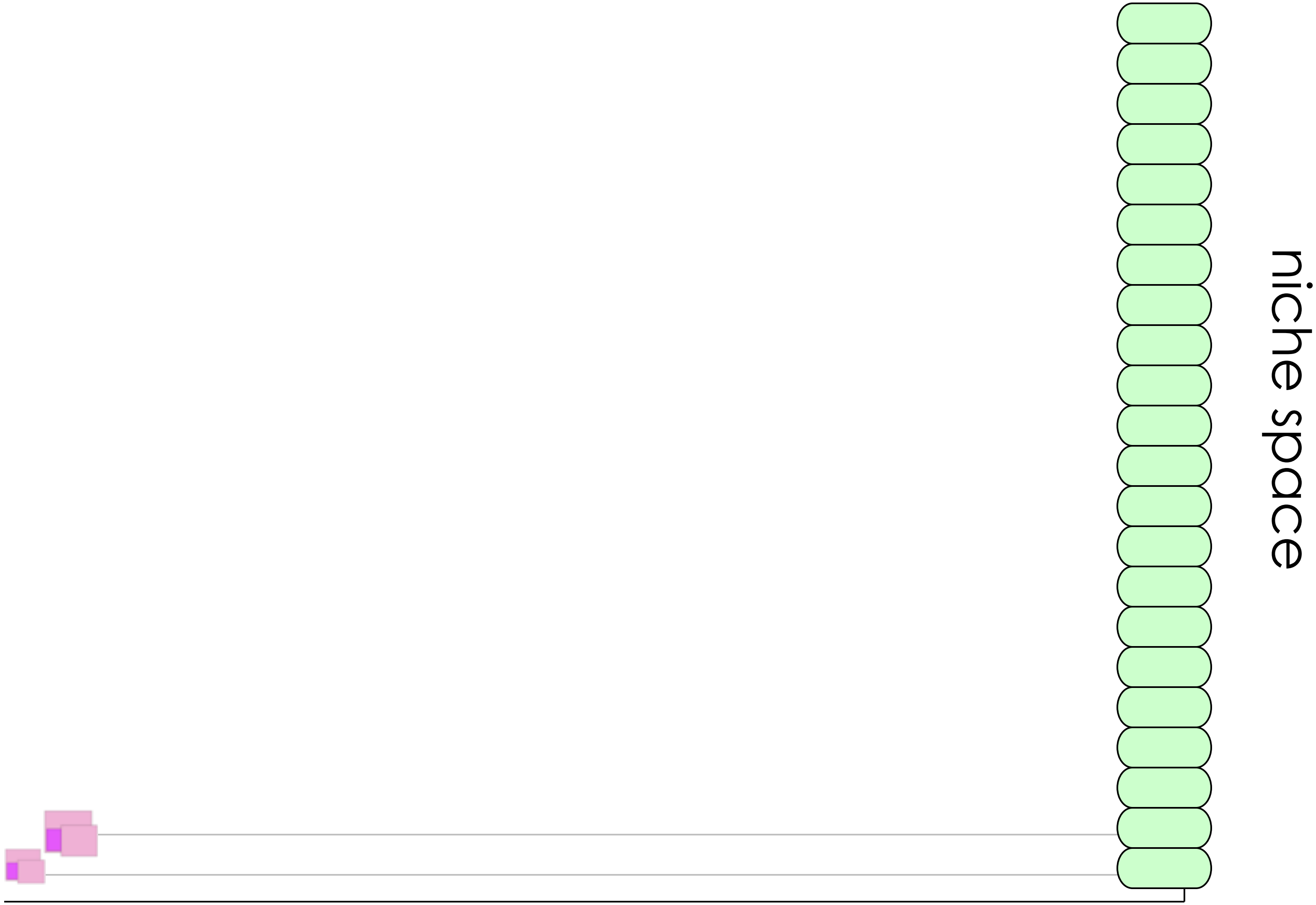

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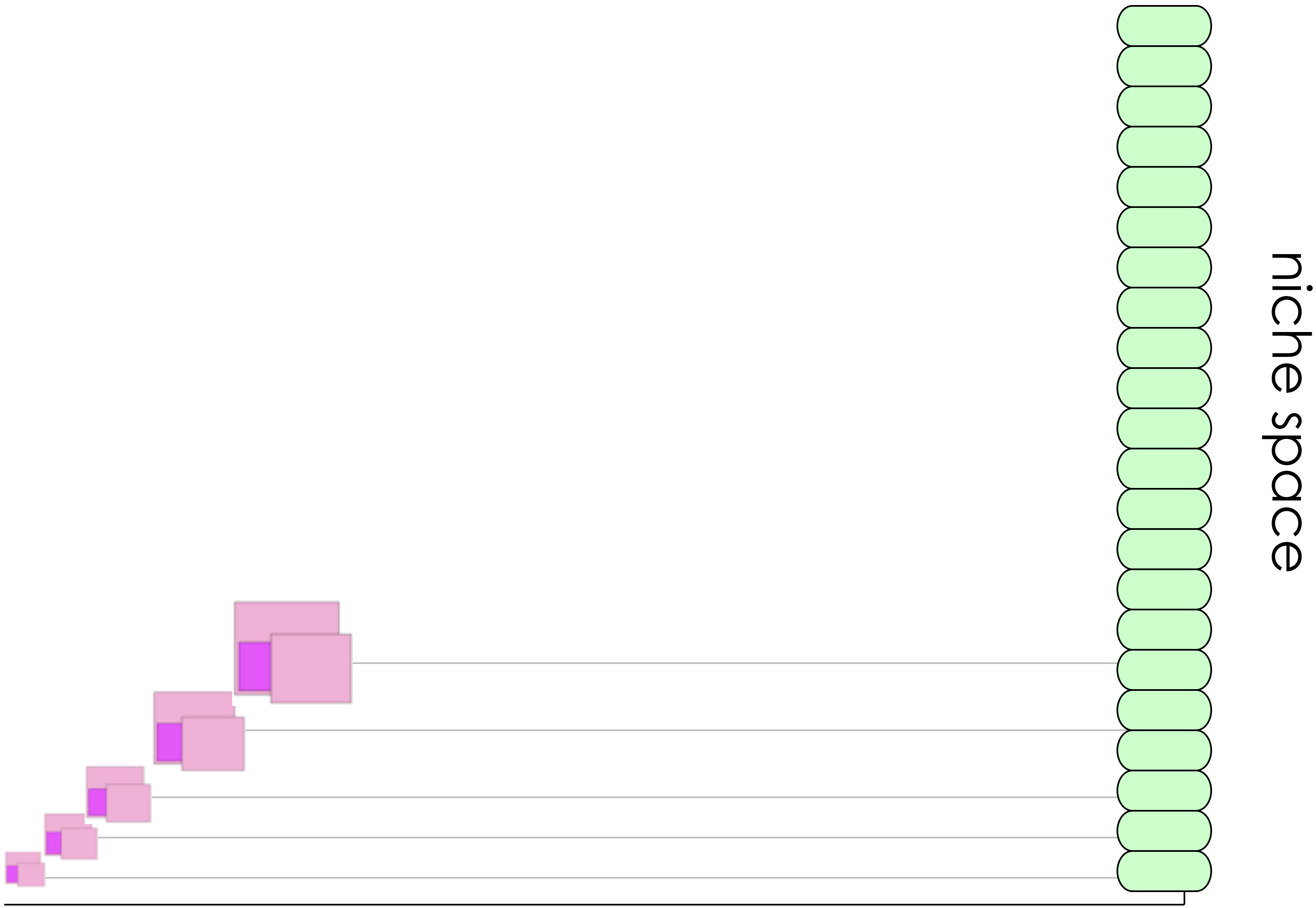

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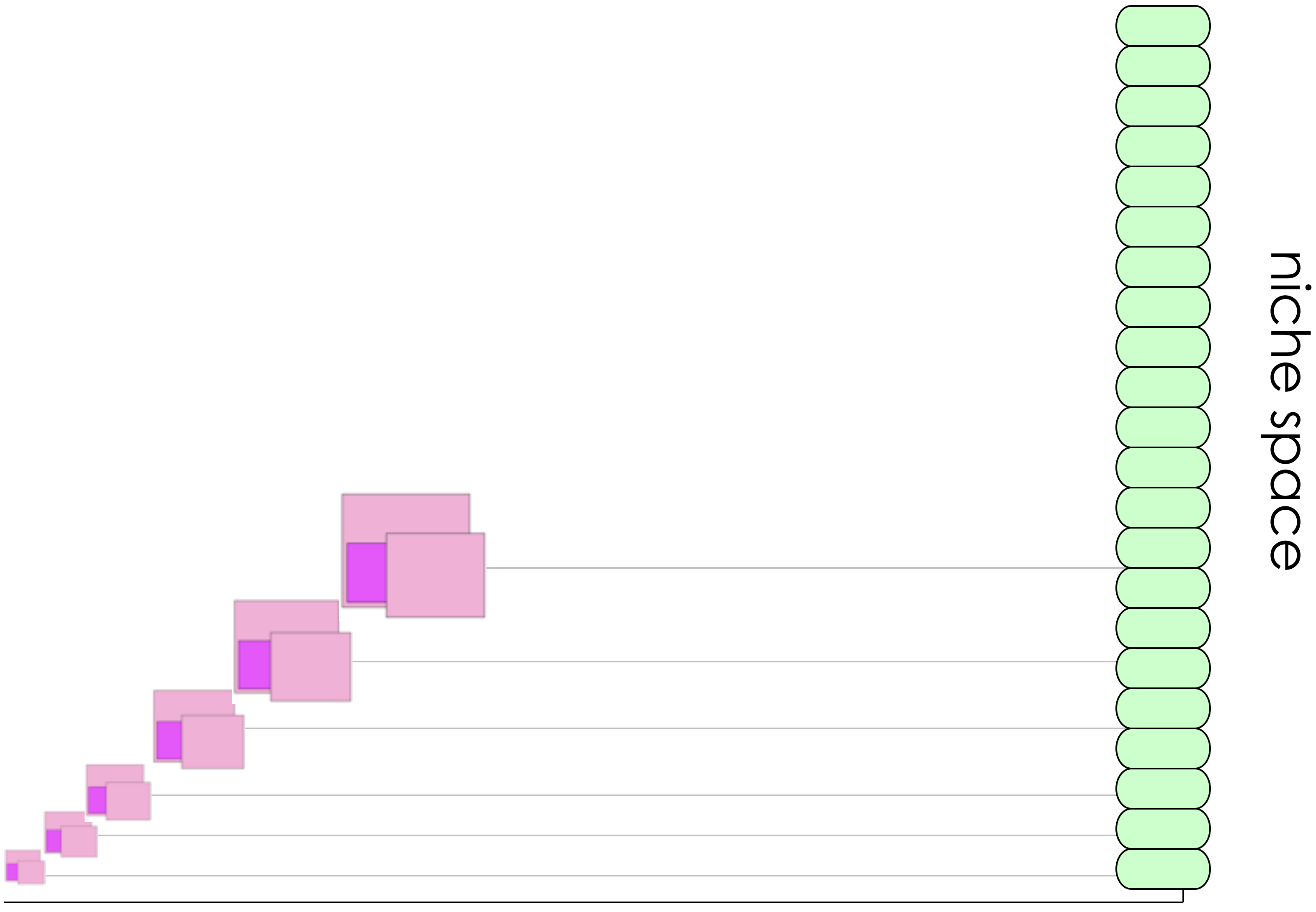

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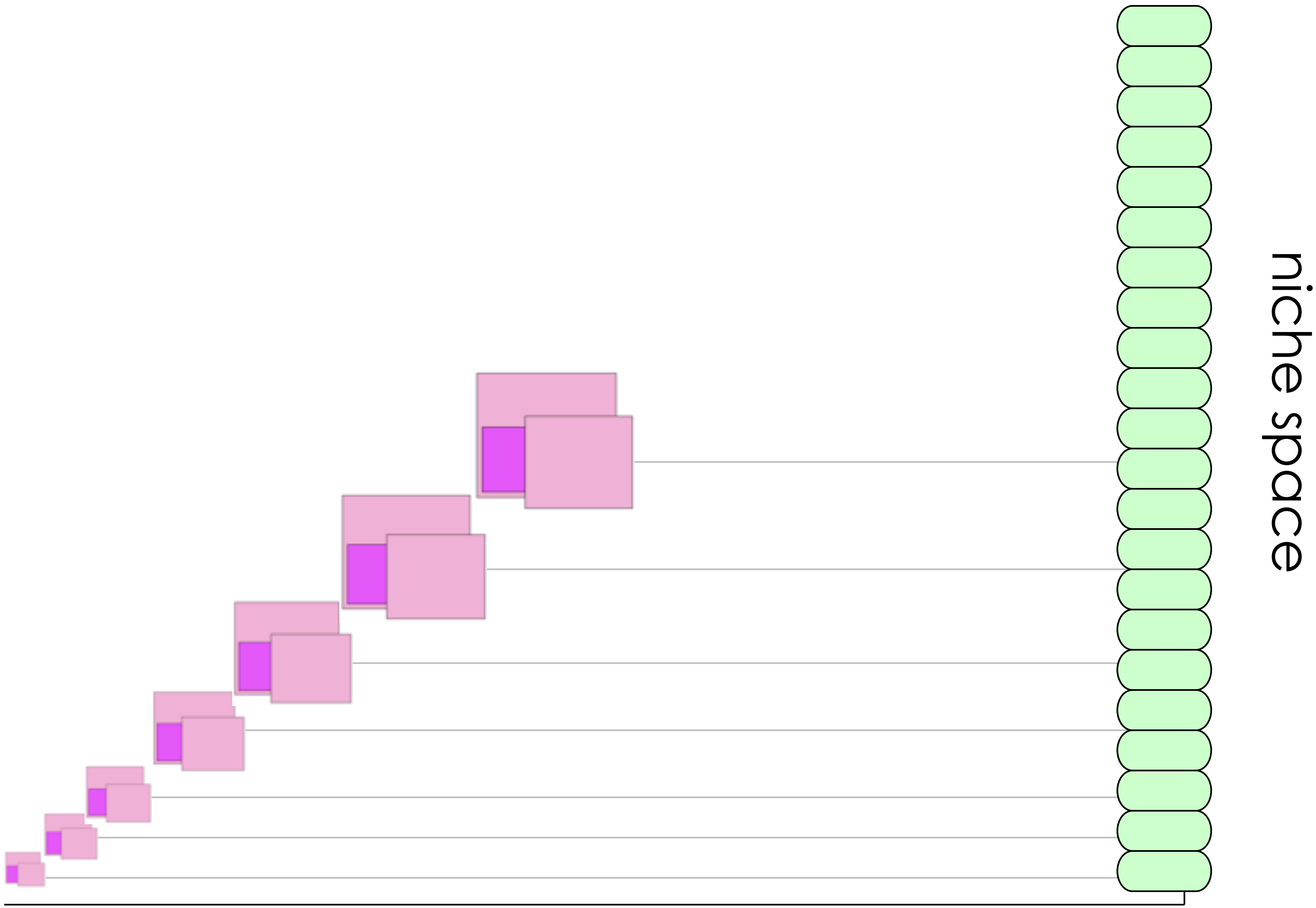

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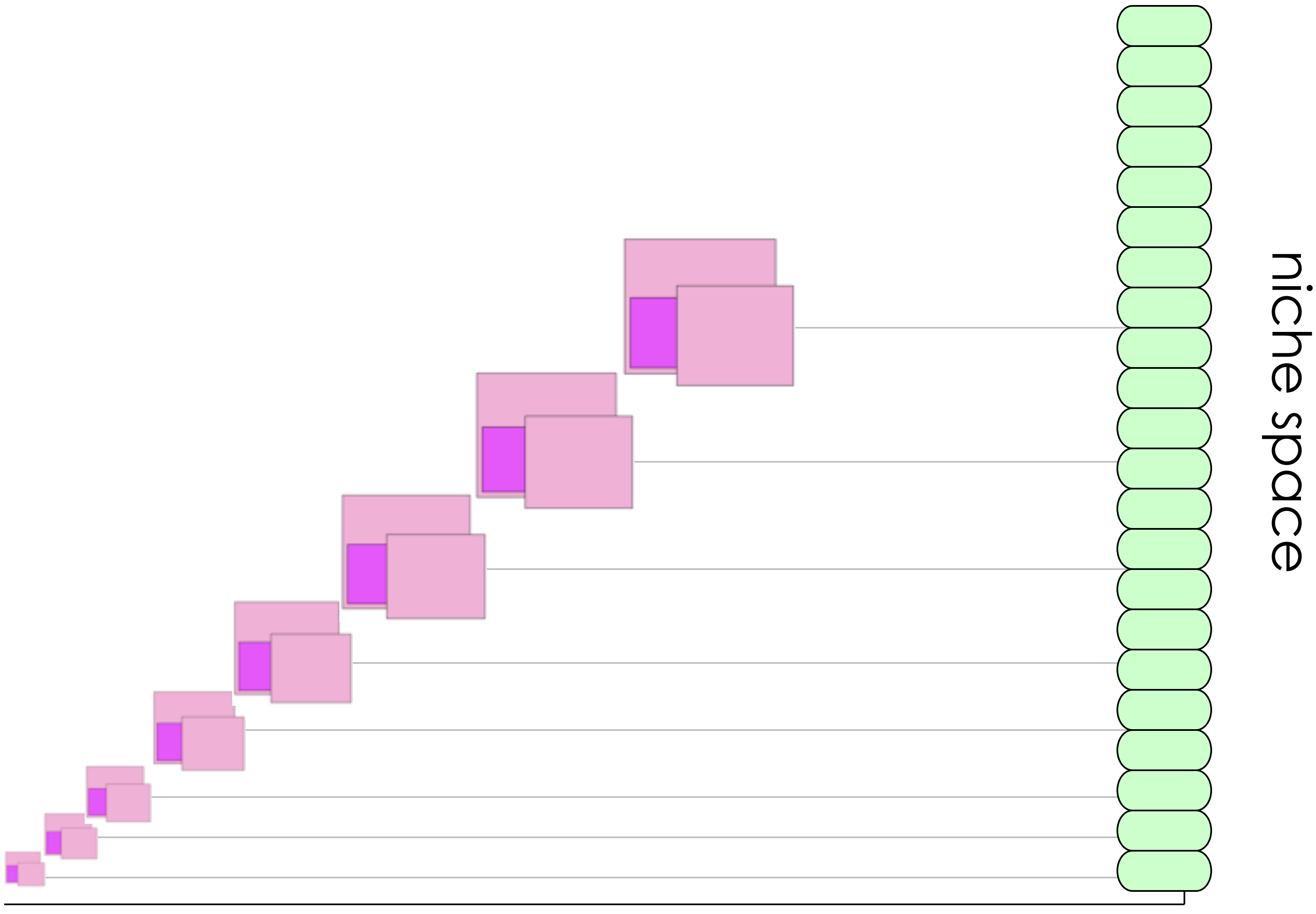

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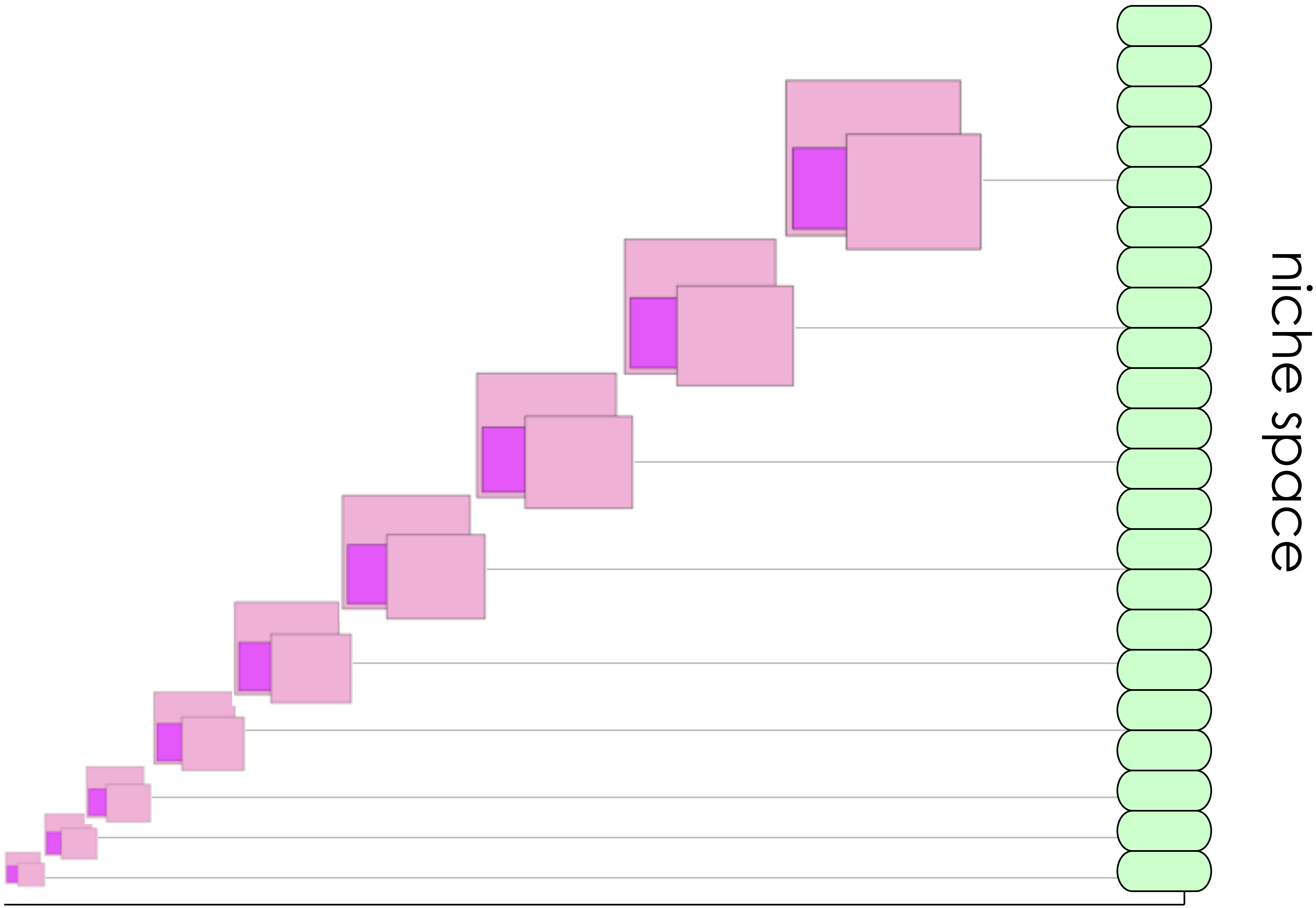

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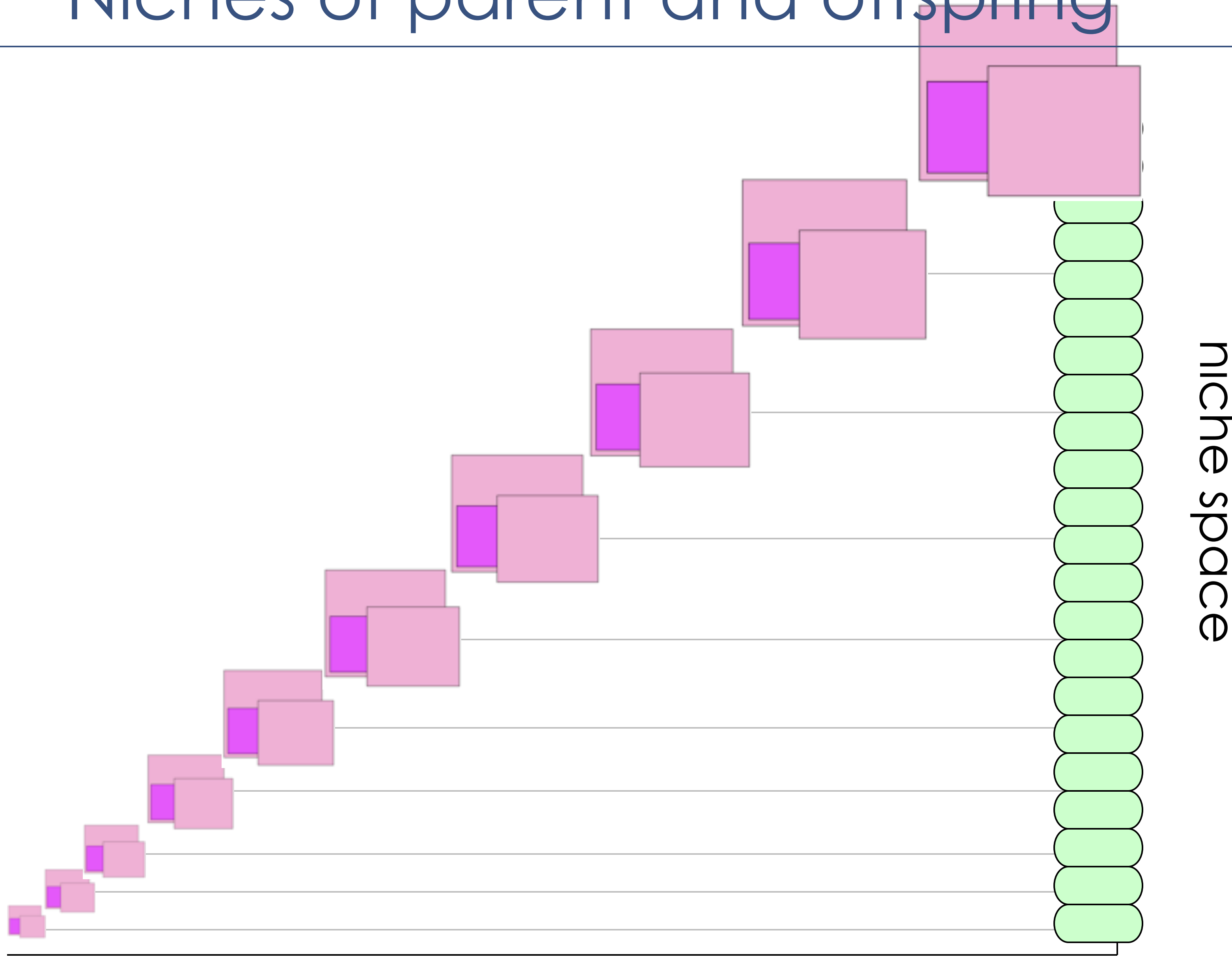

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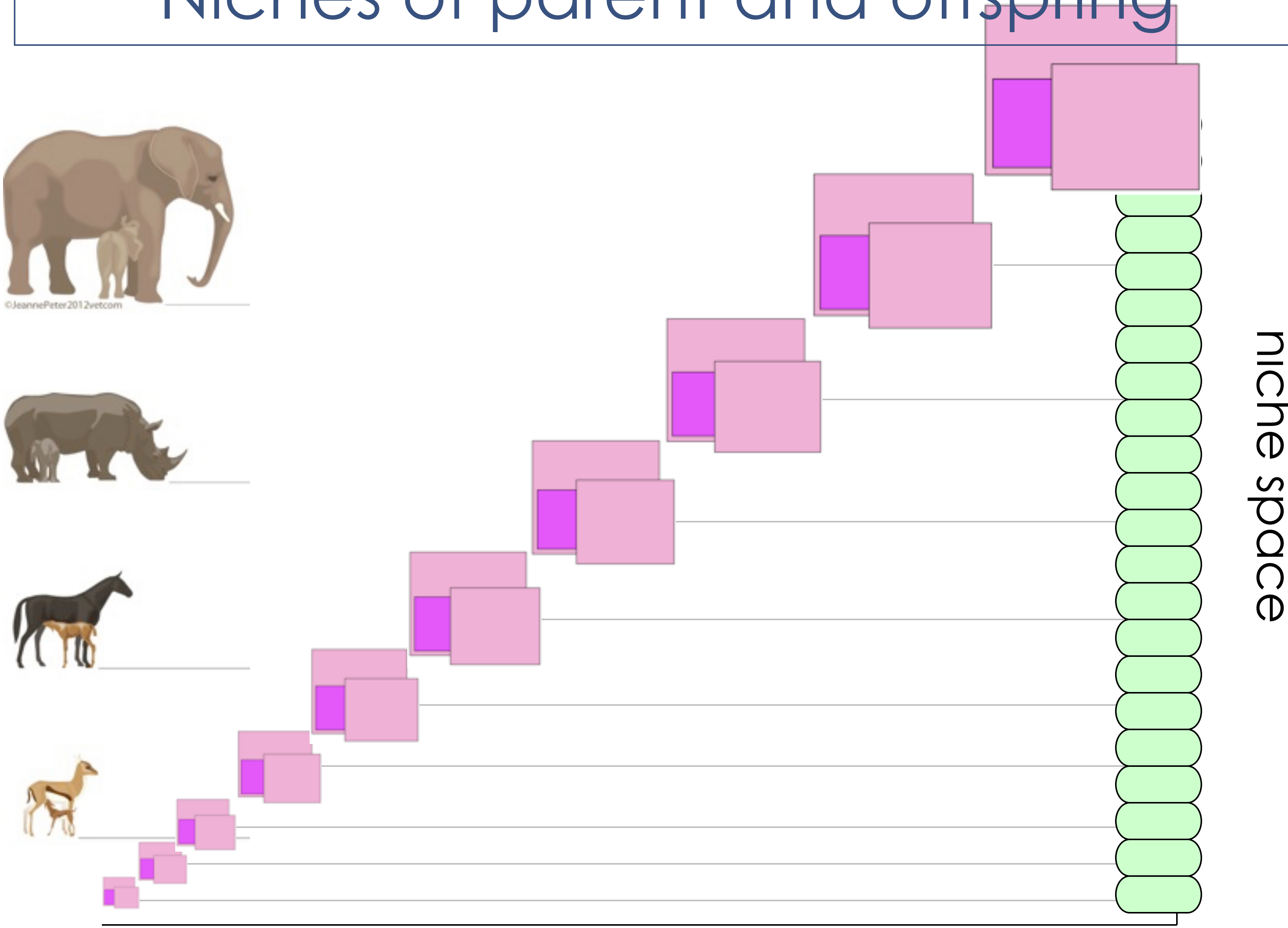

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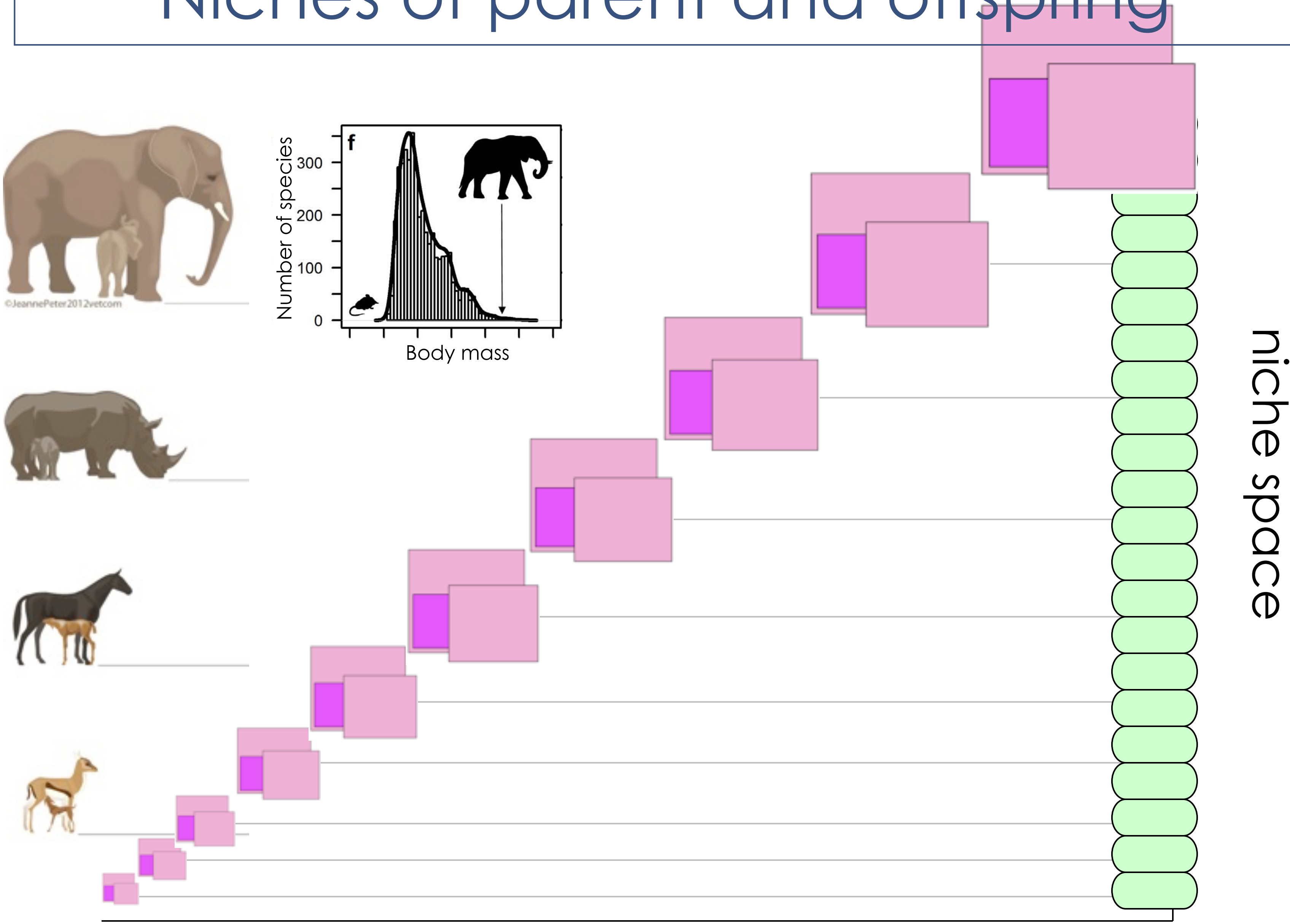

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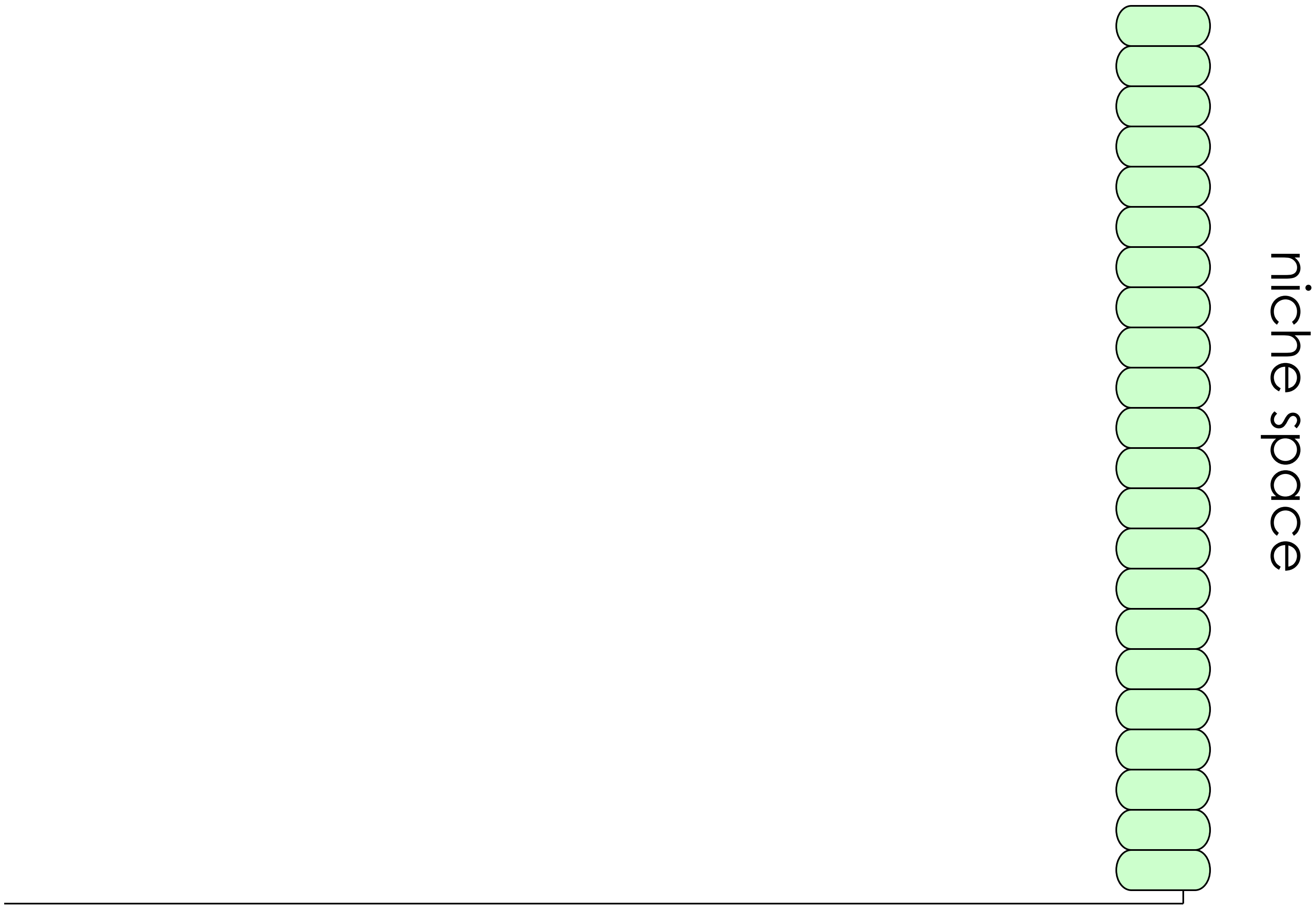

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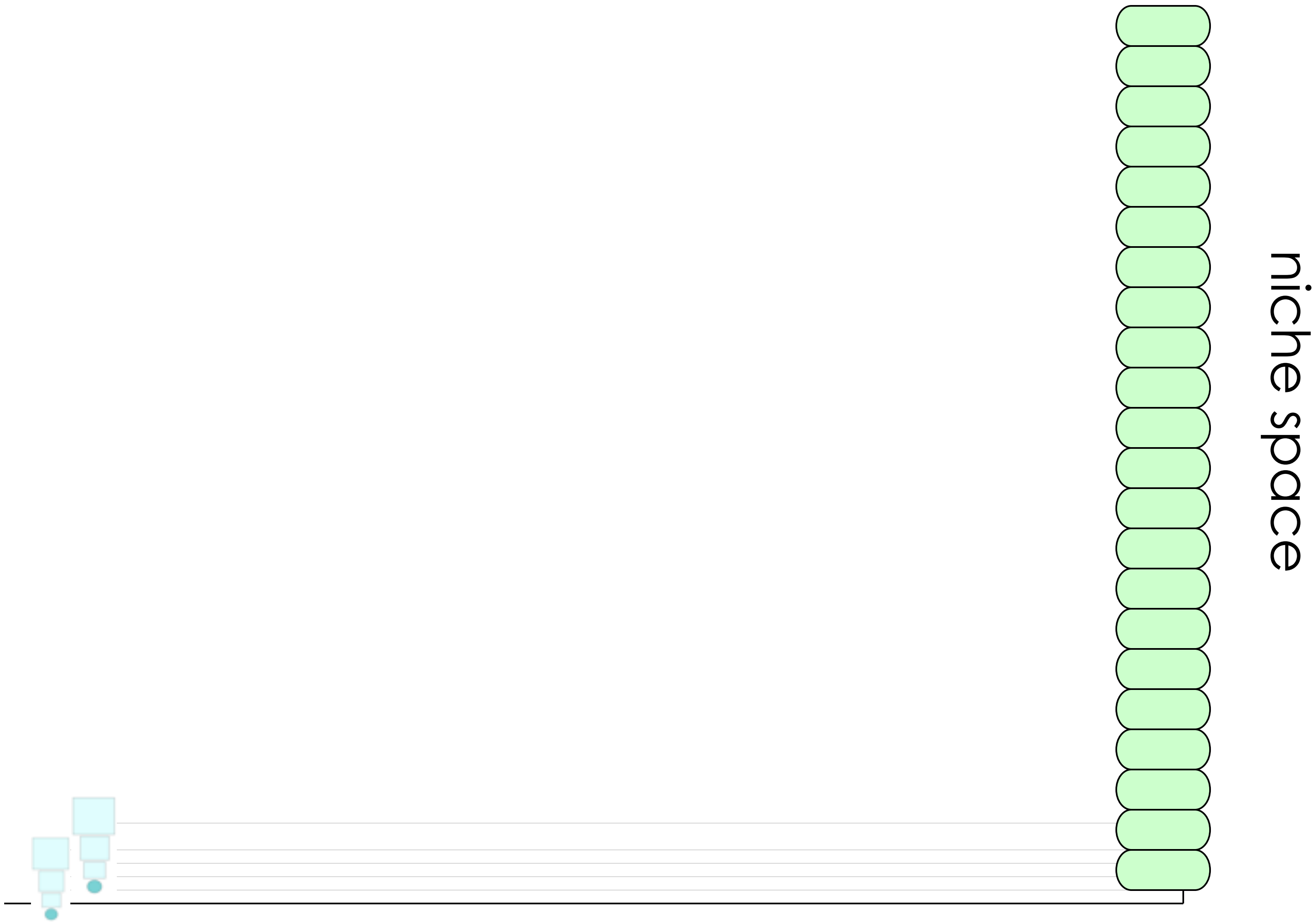

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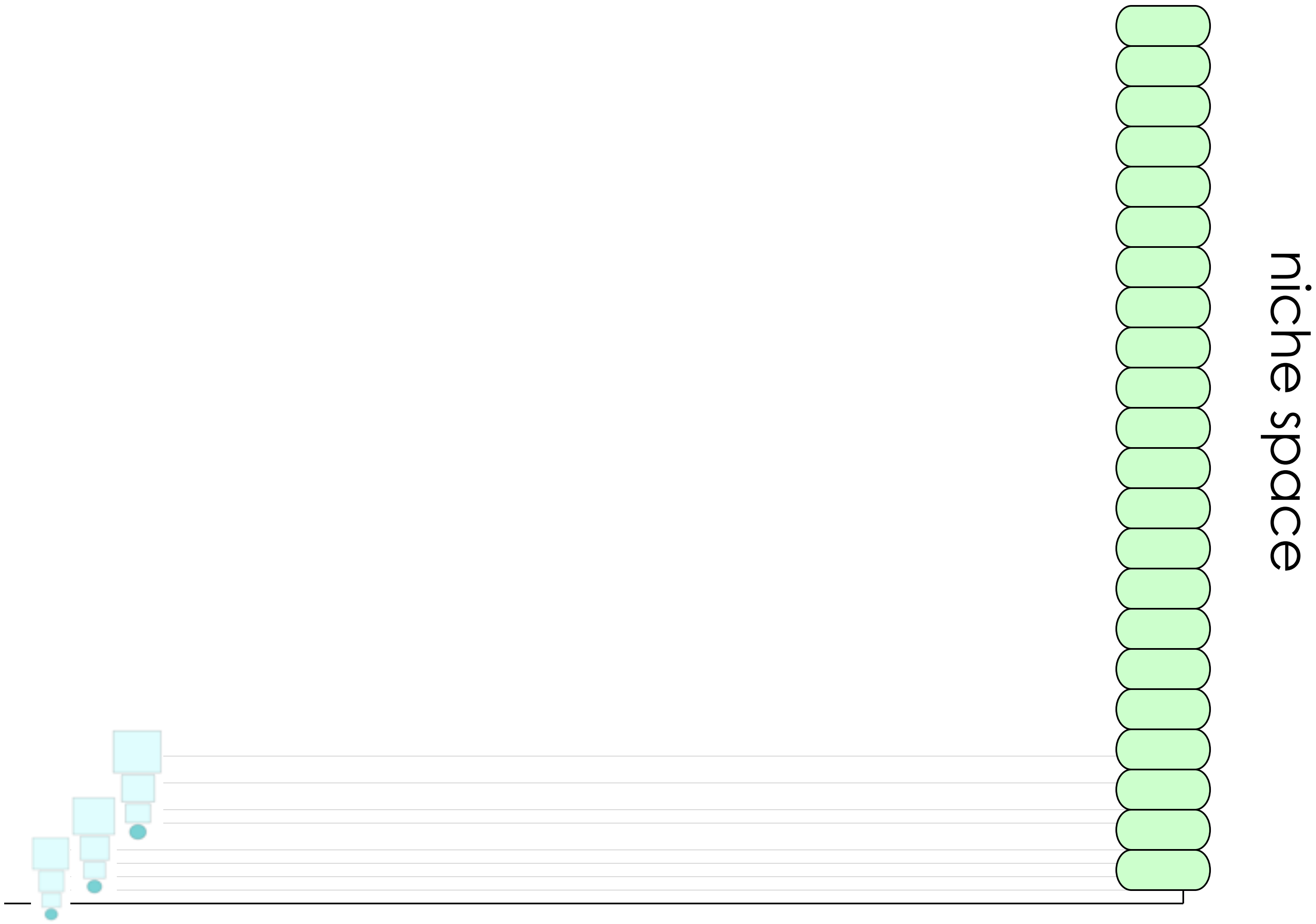

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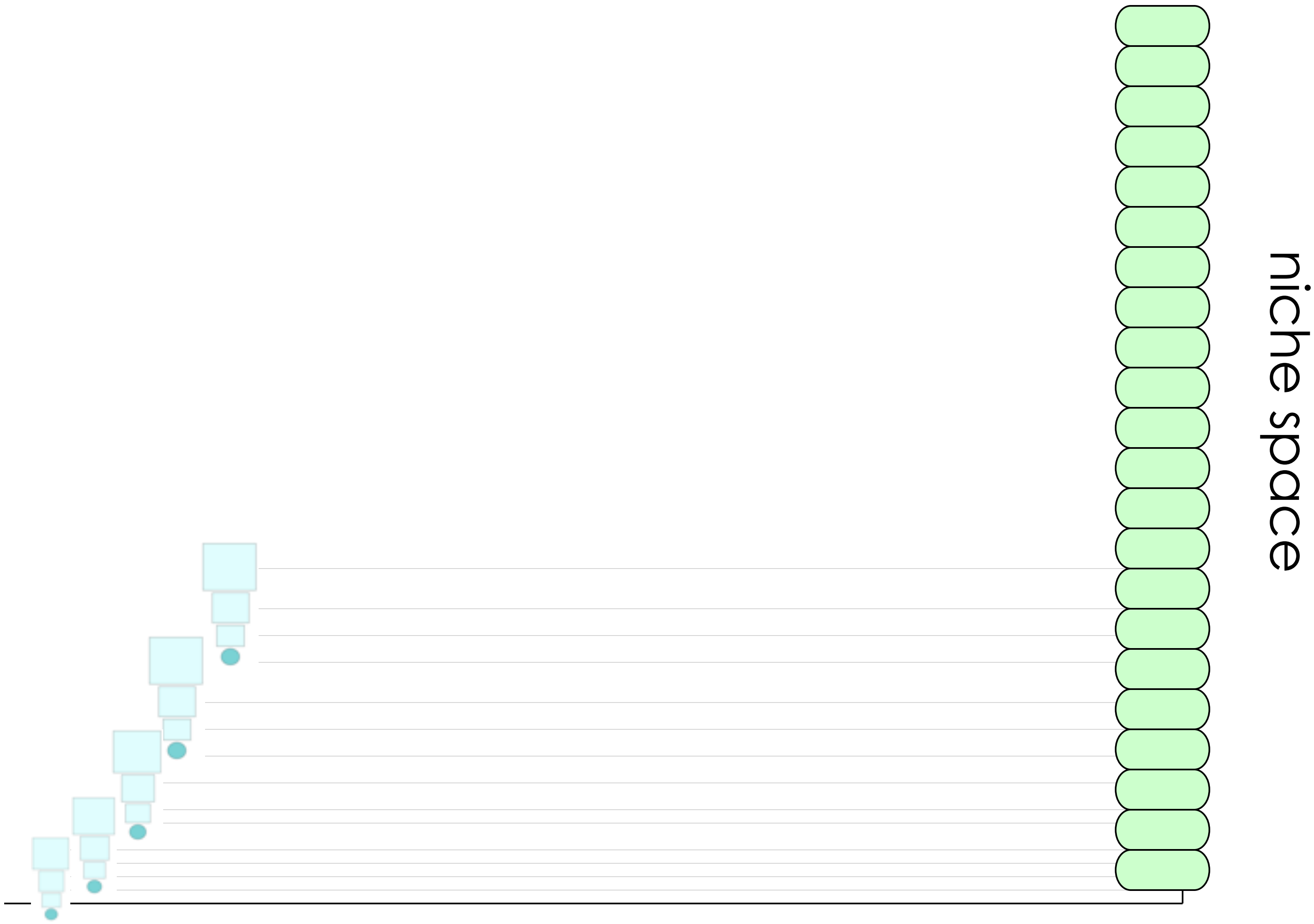

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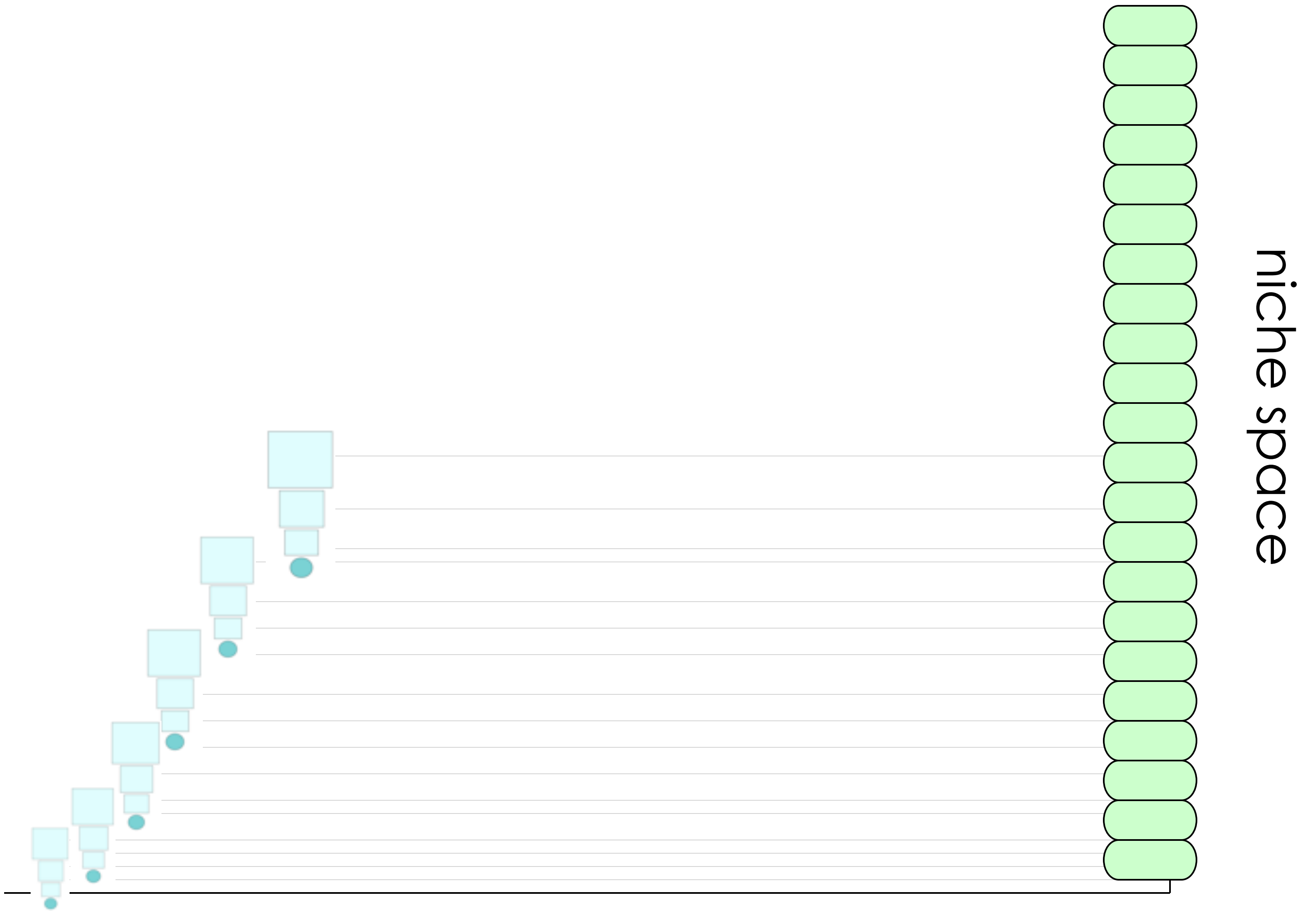

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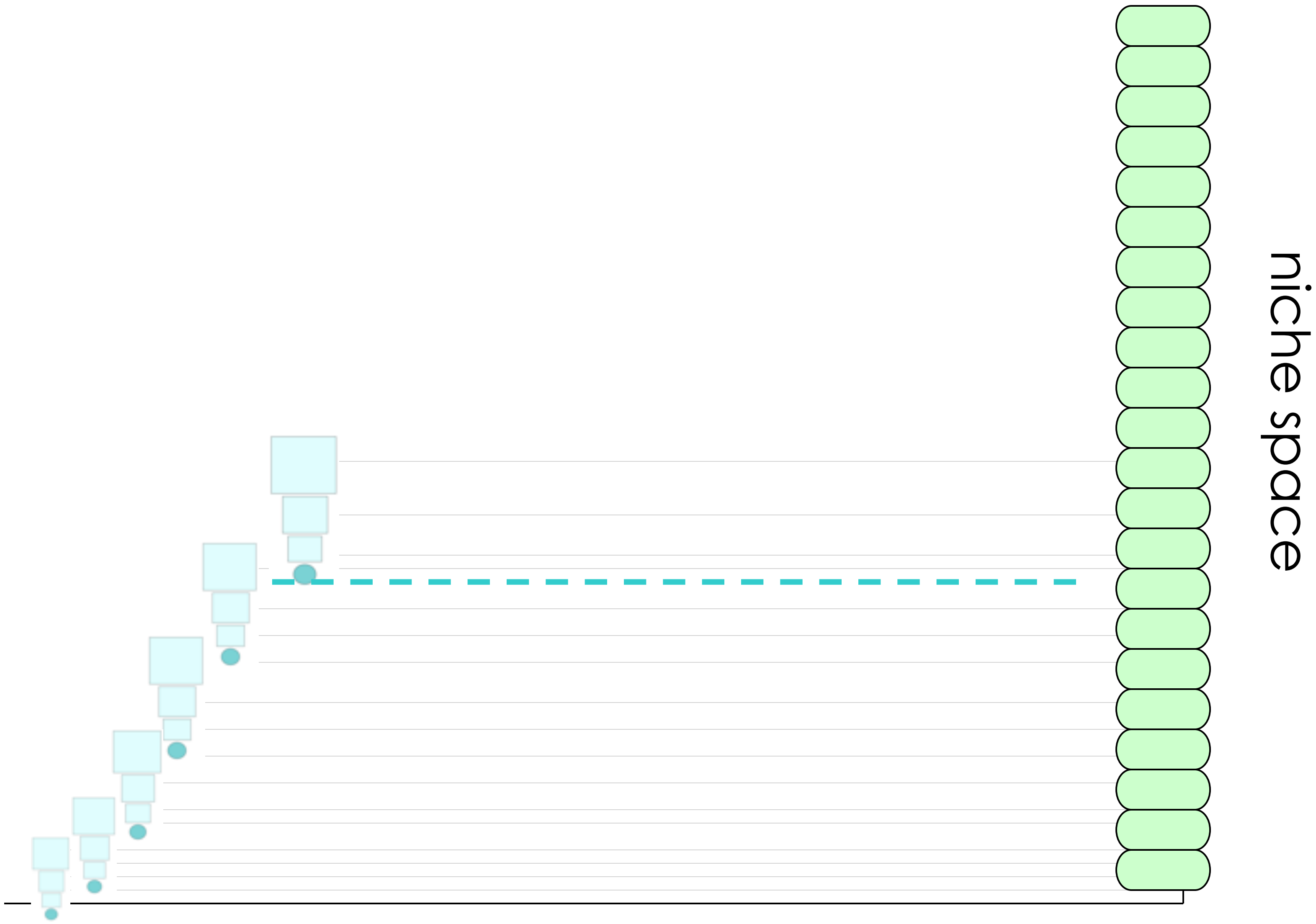

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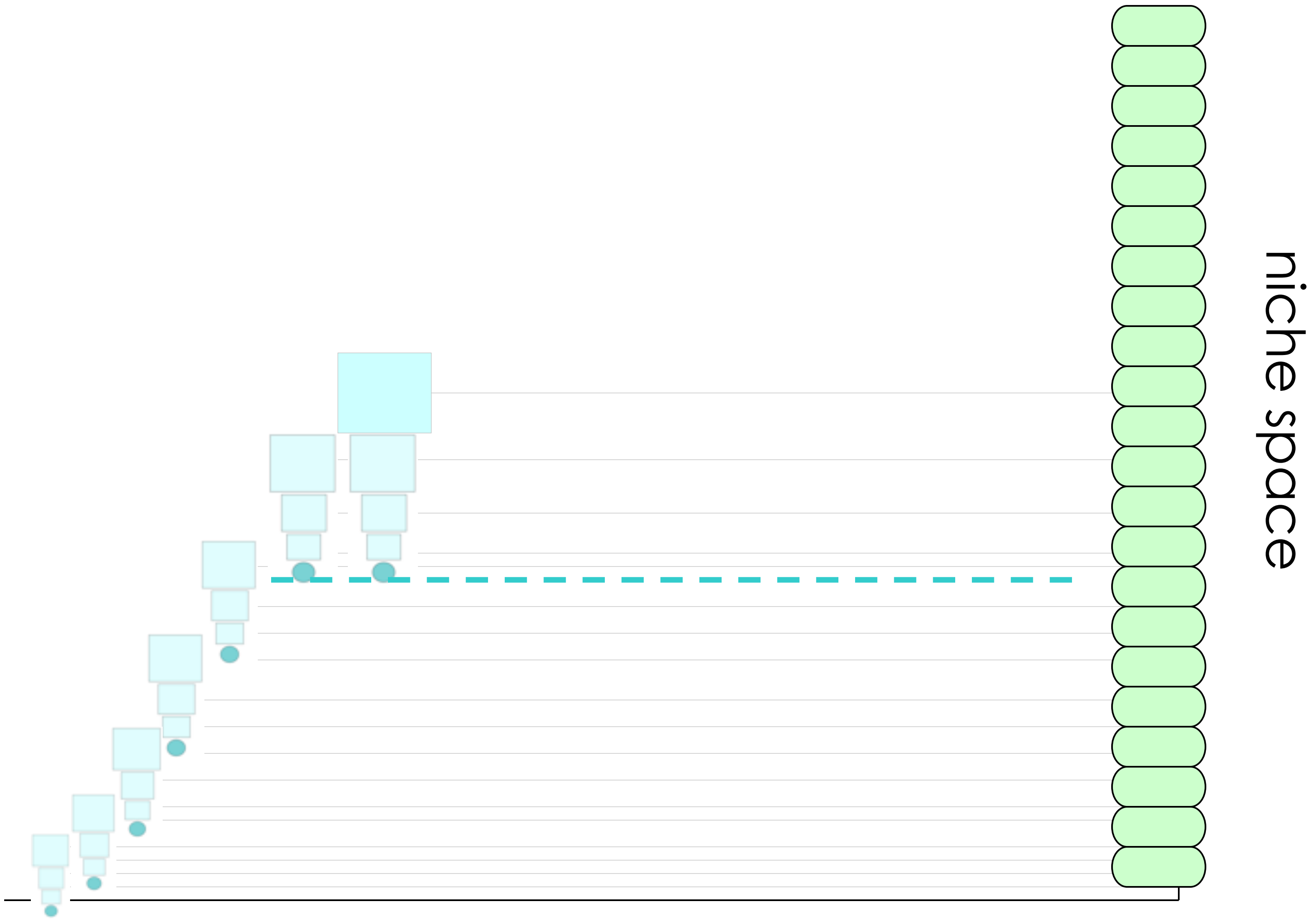

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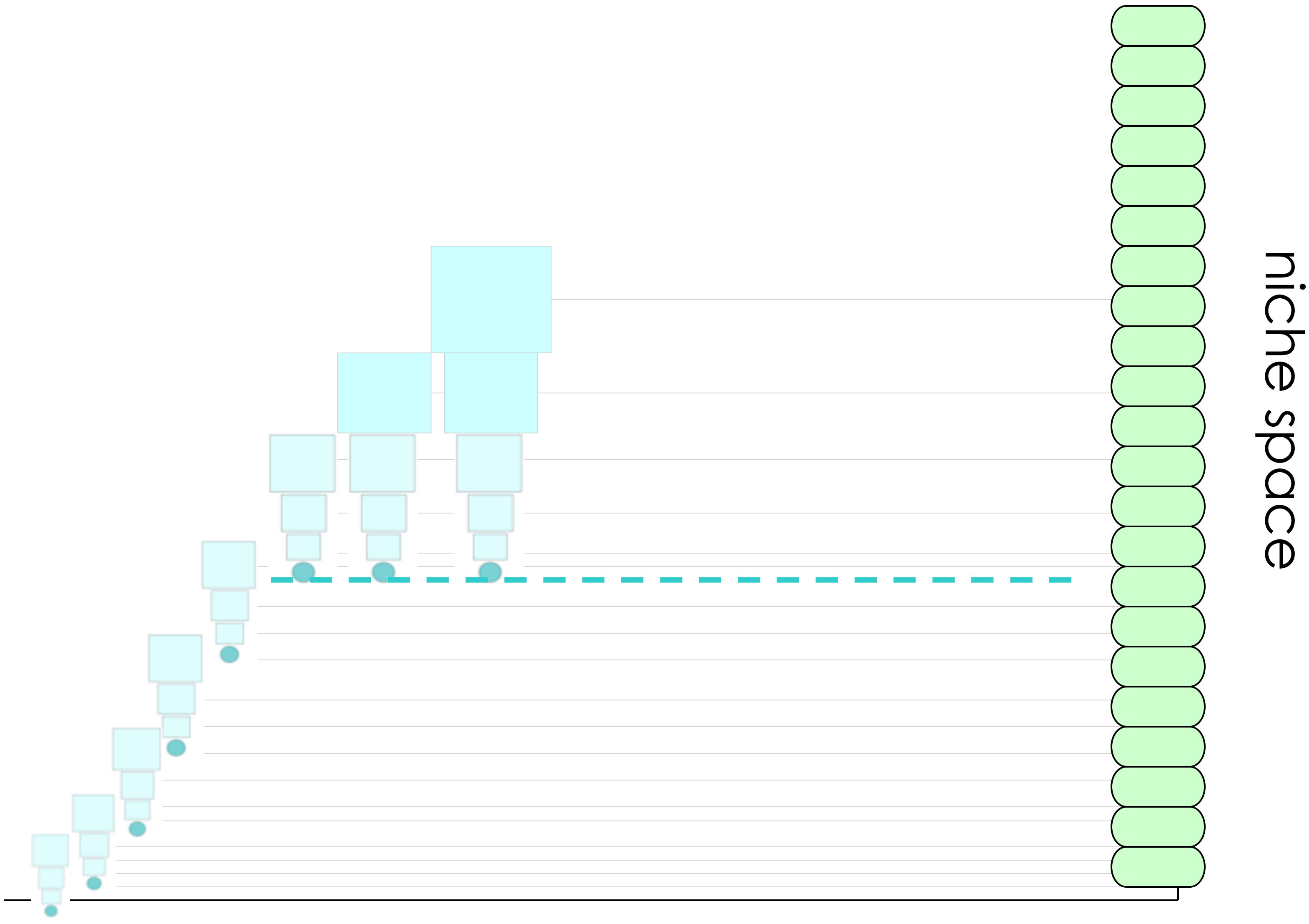

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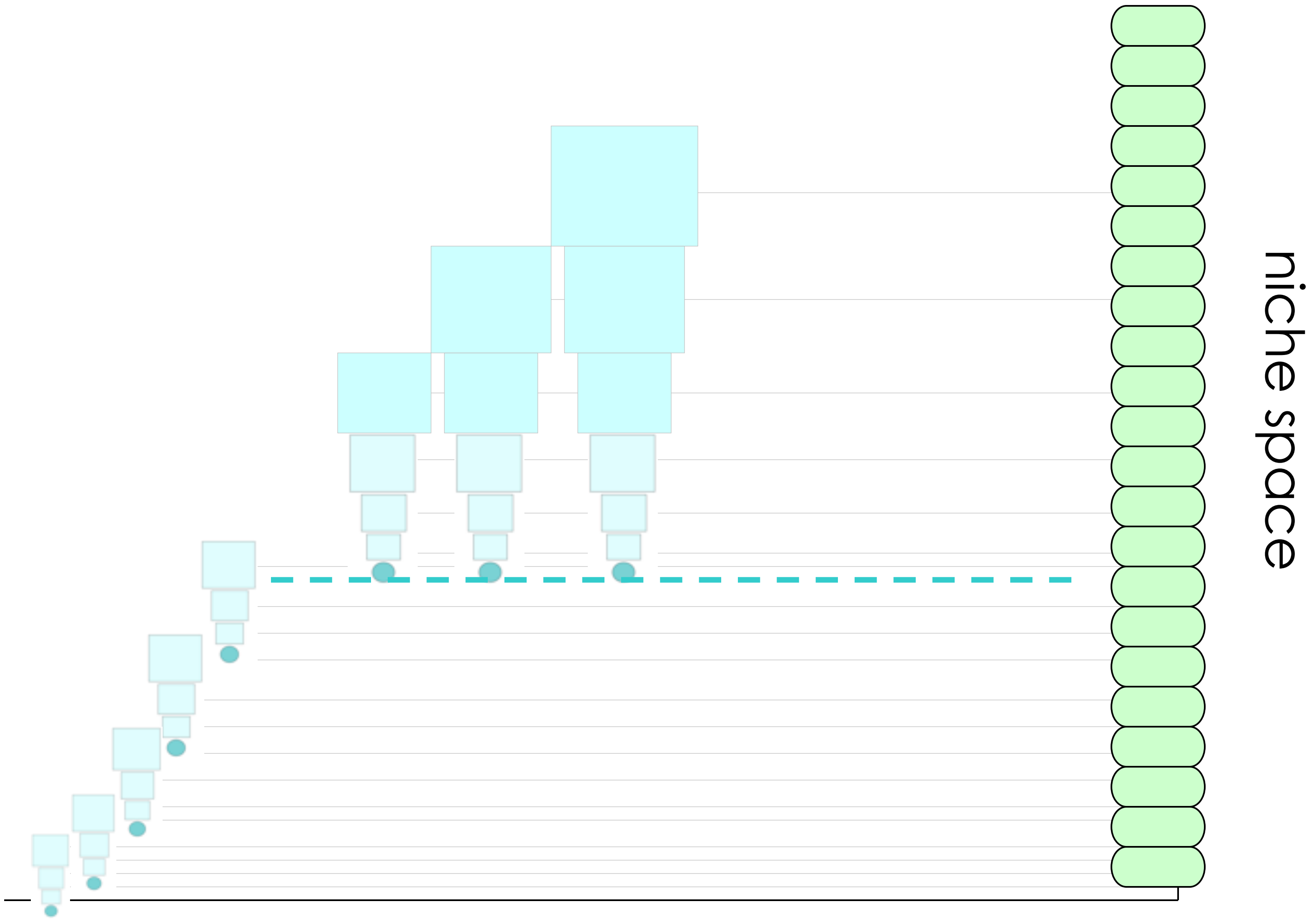

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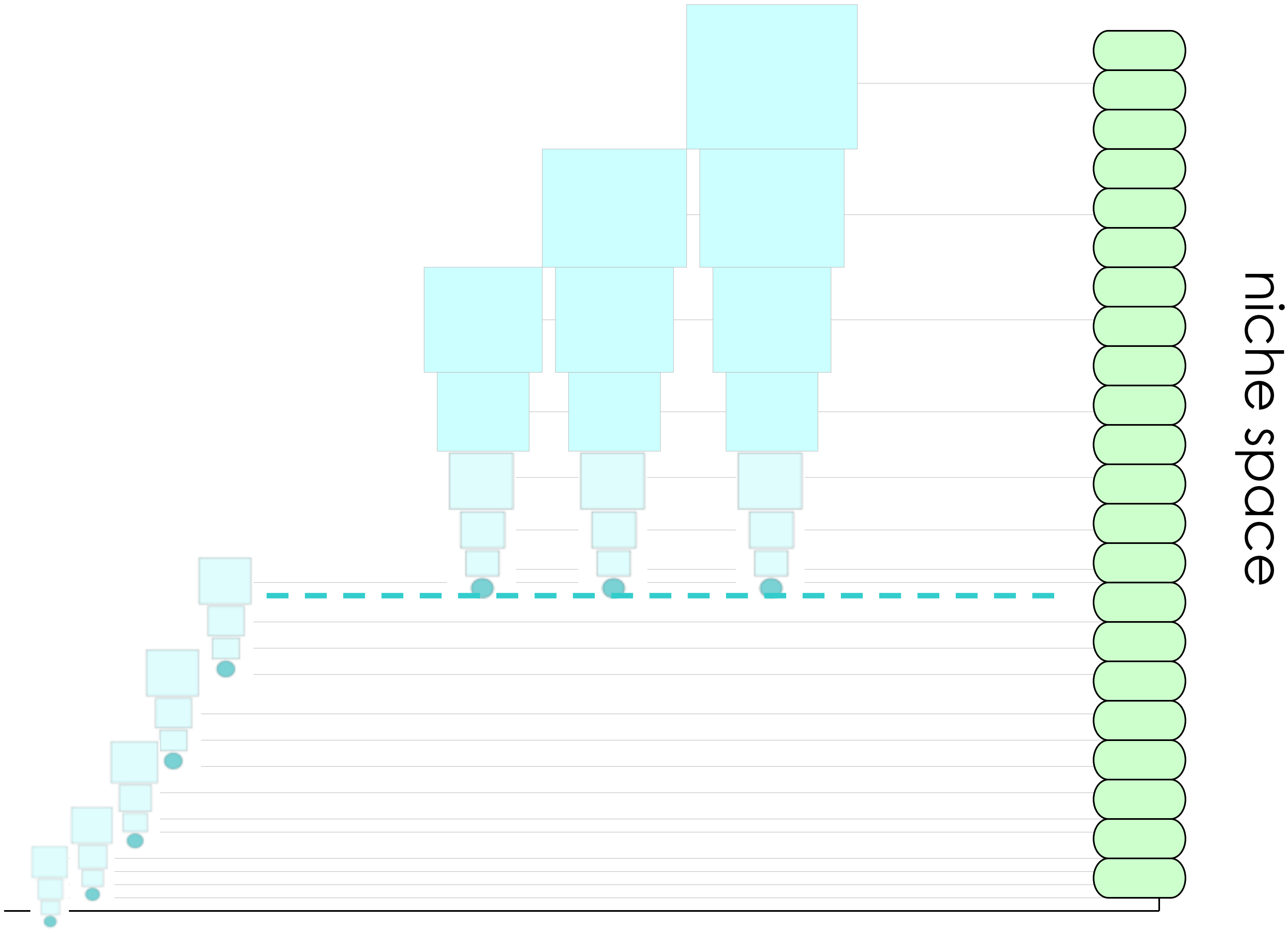

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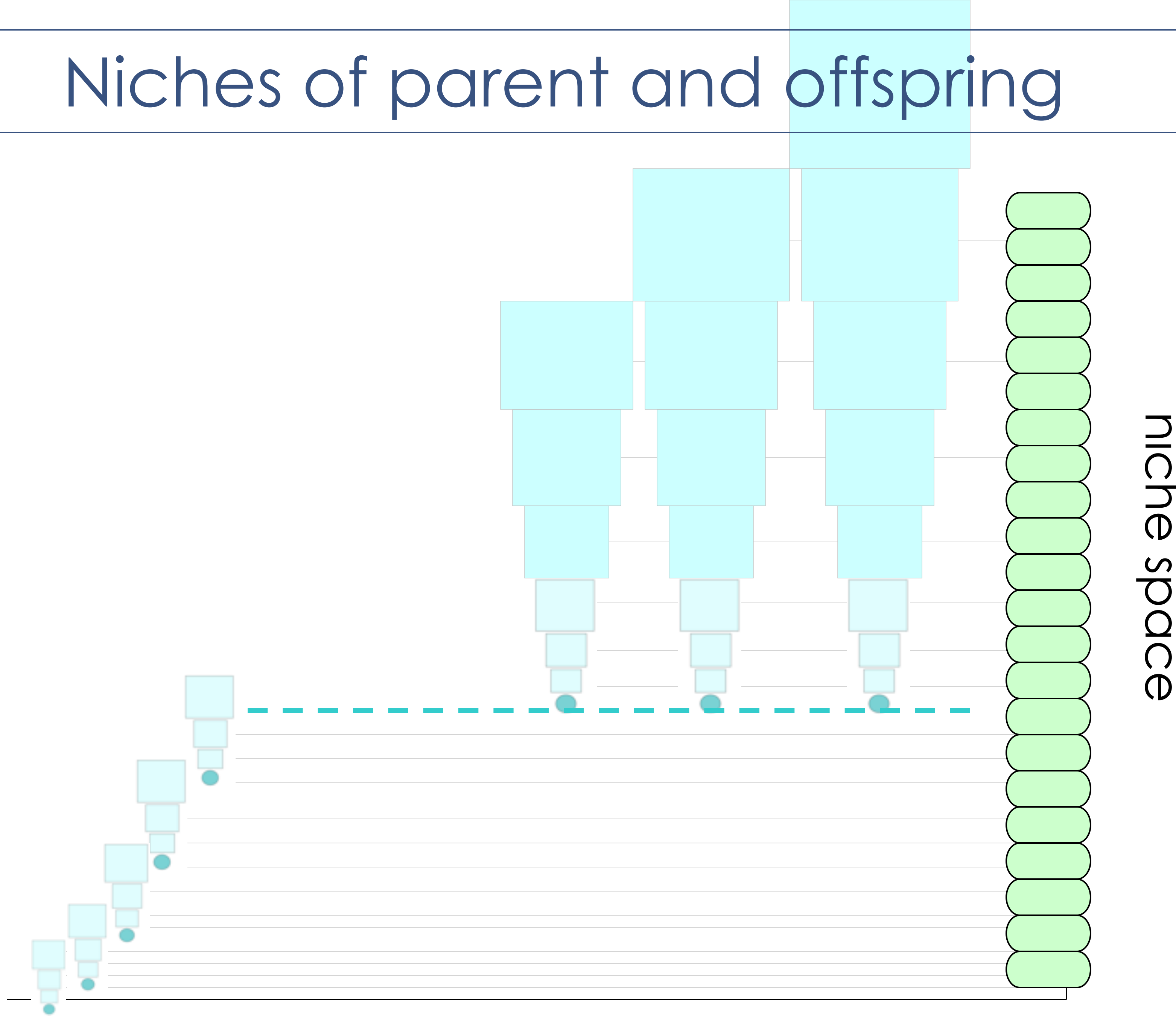

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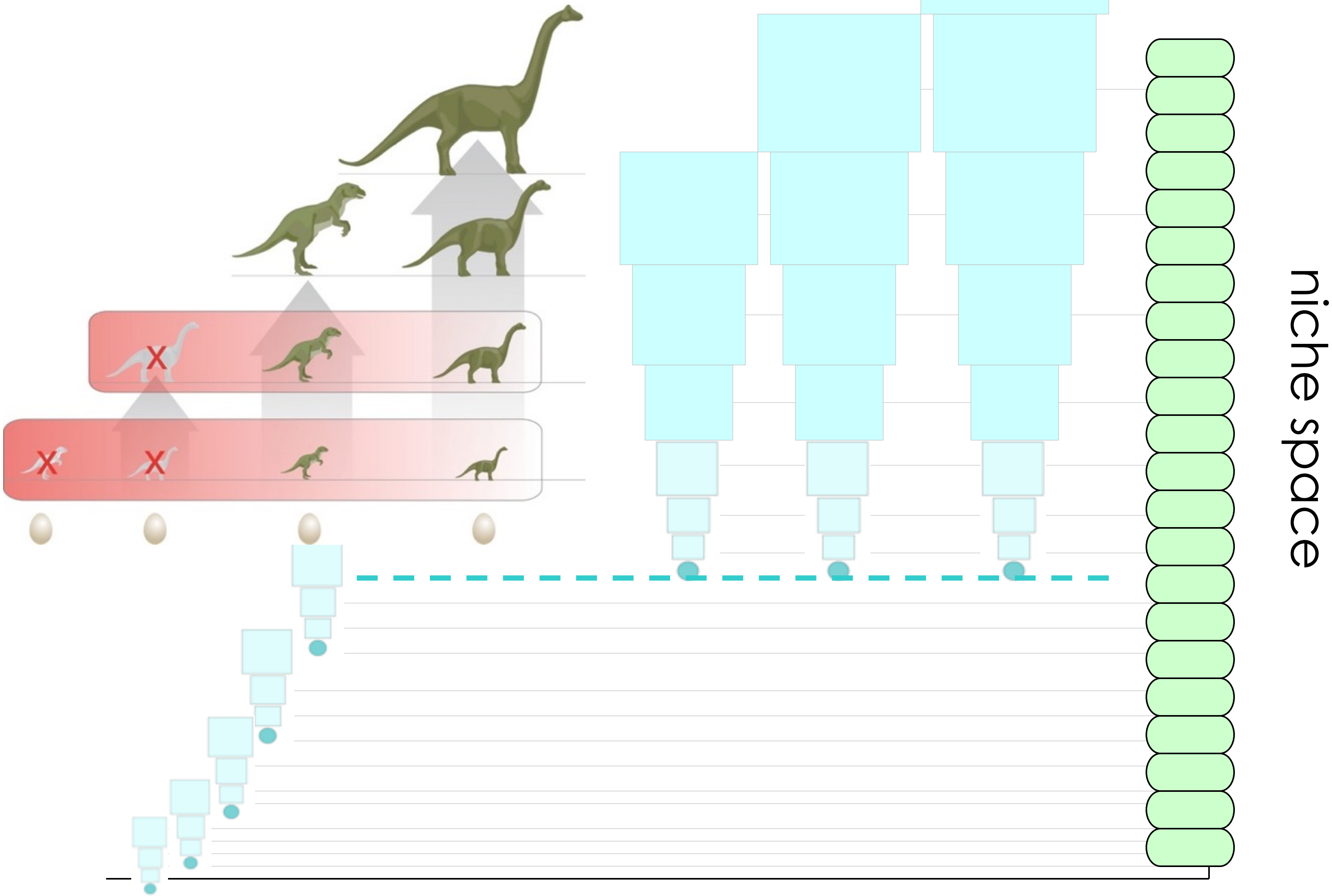
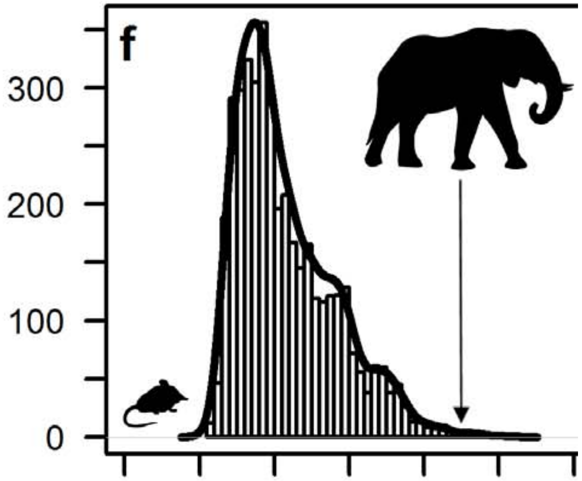
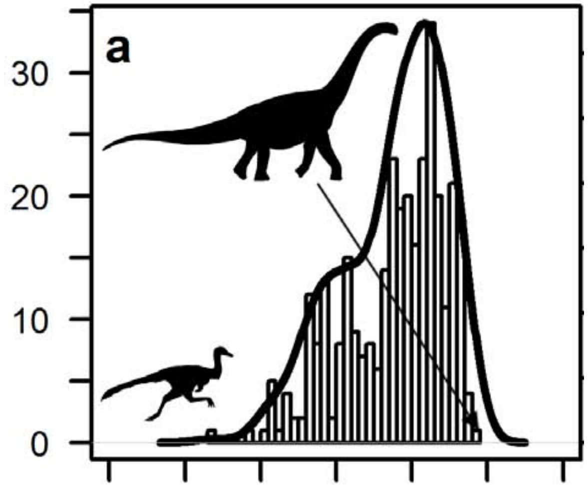


Species distributions





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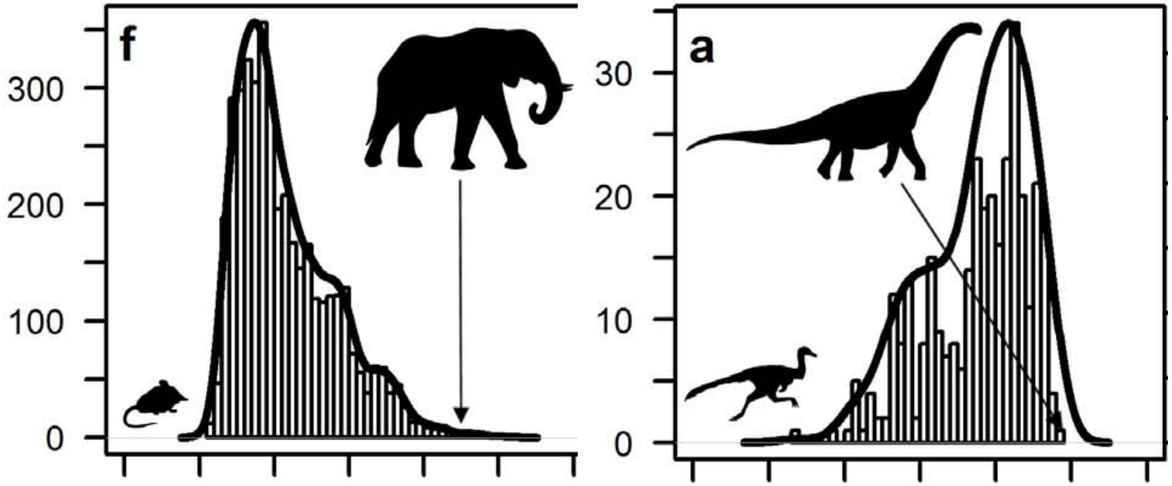

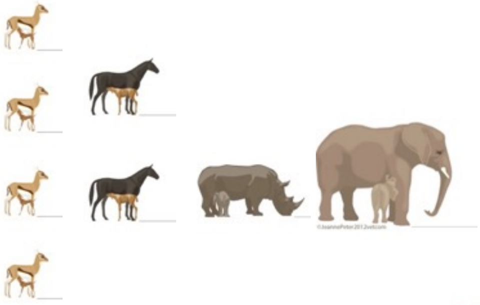

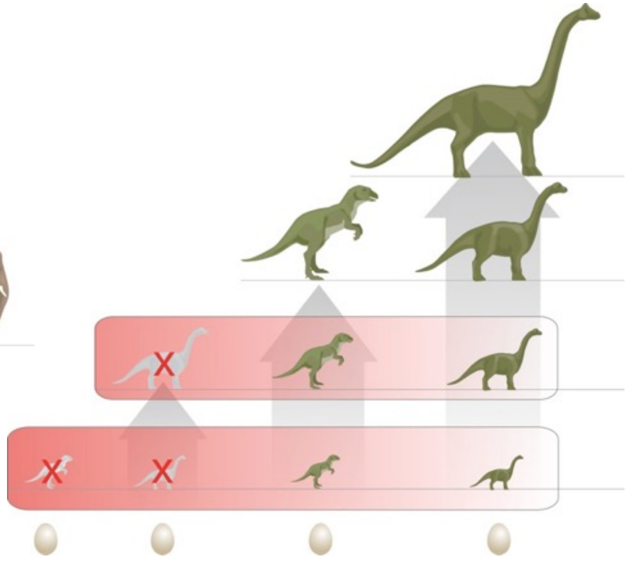

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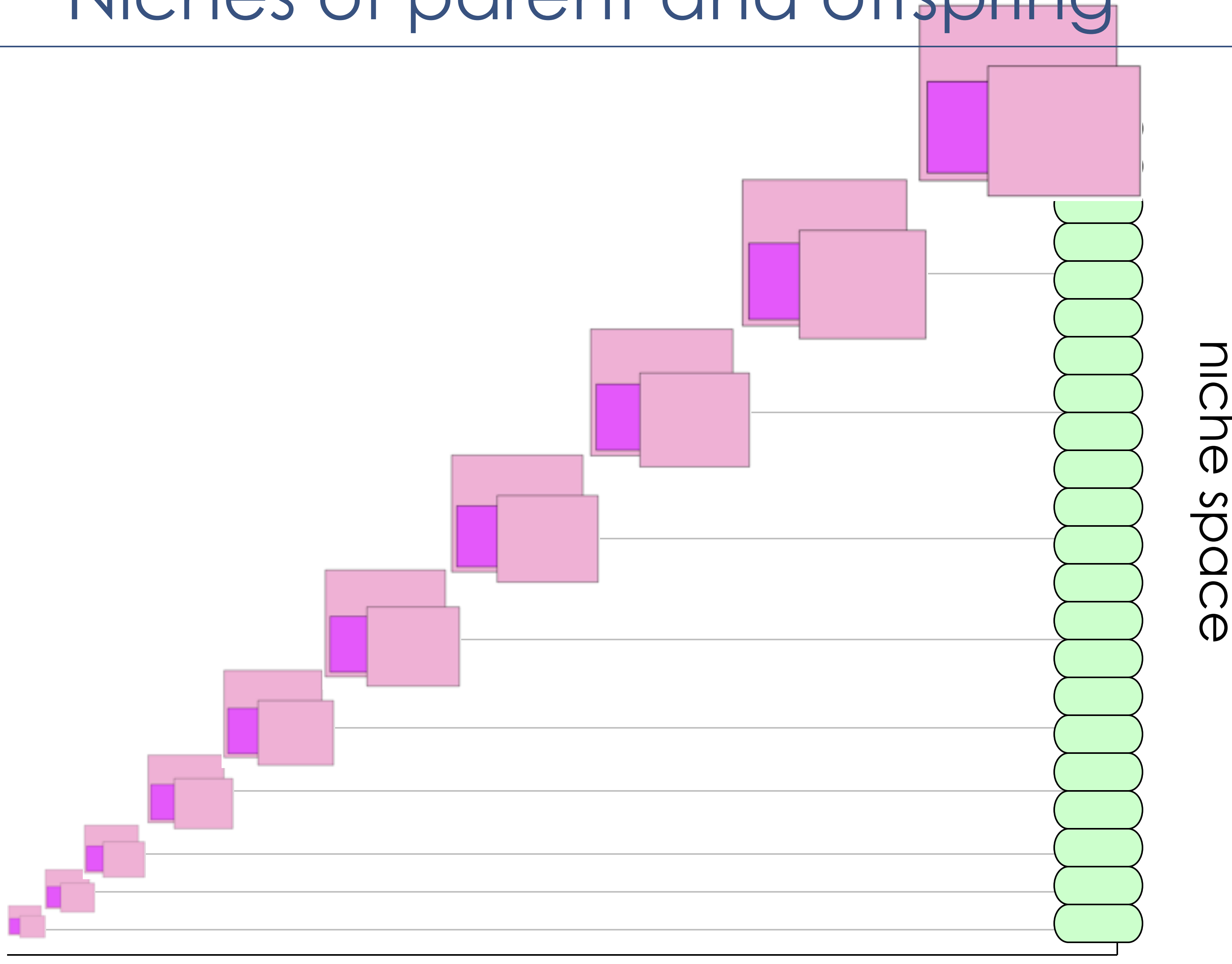

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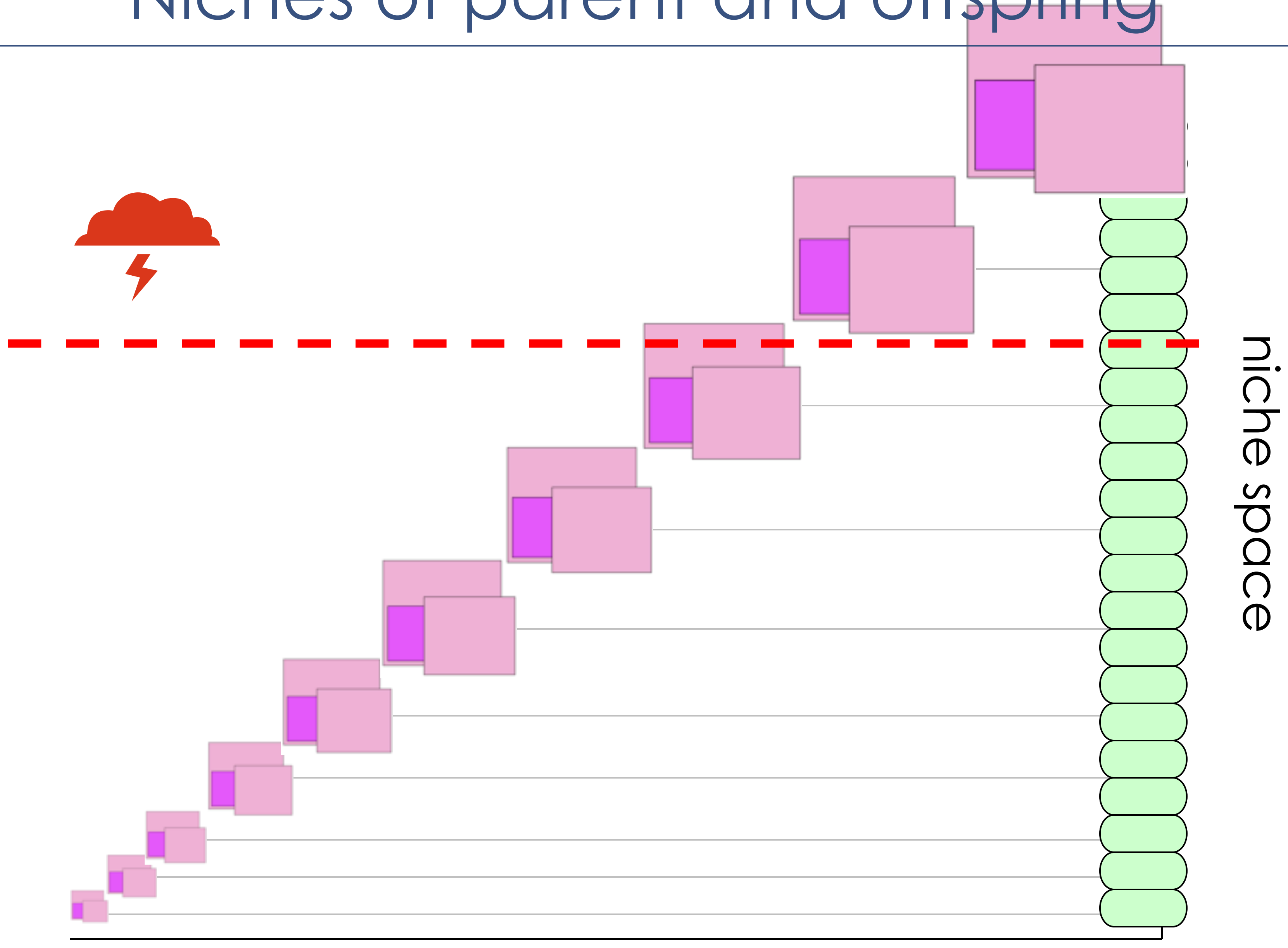

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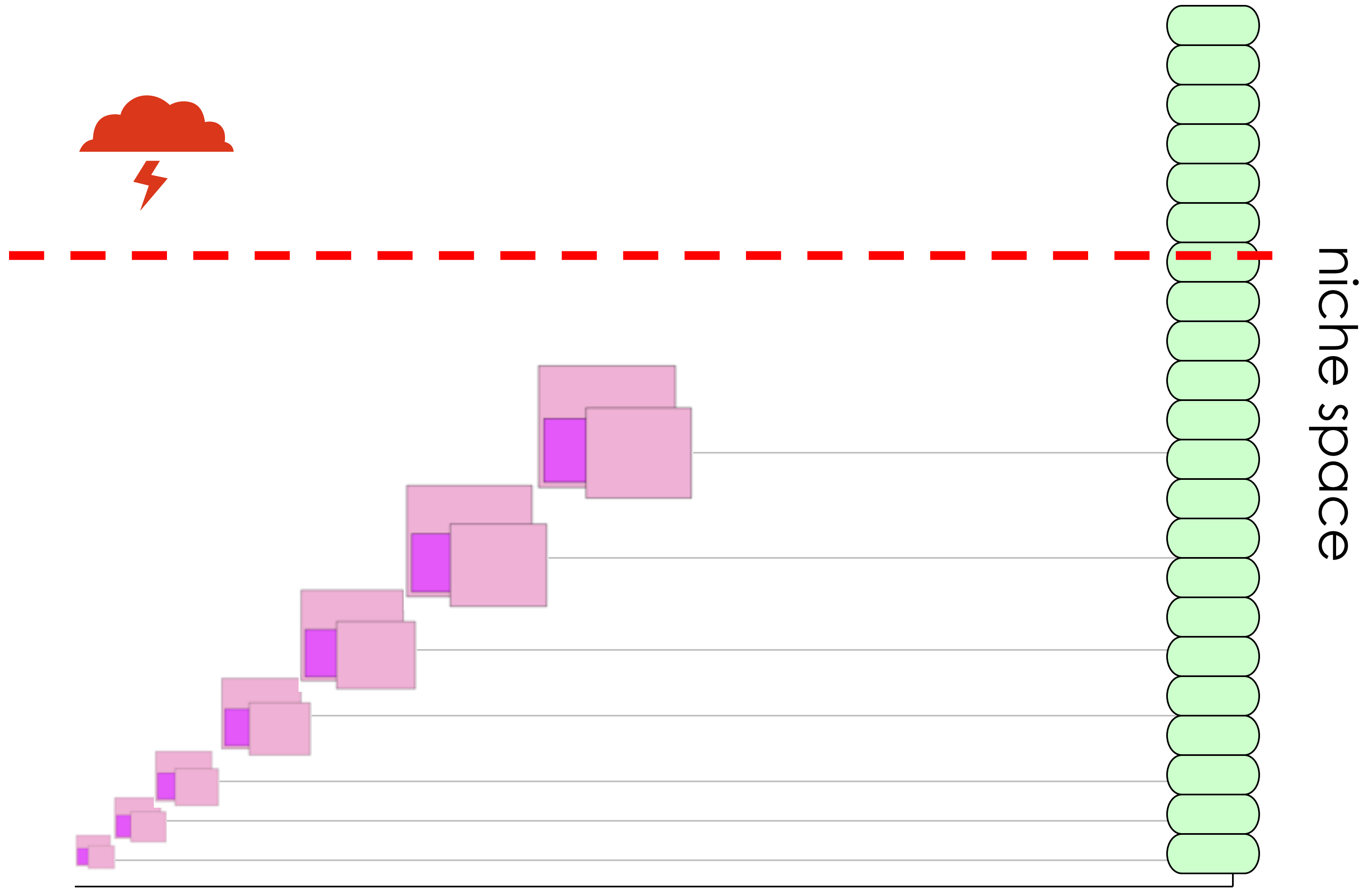


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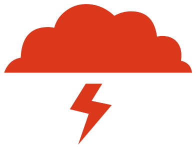

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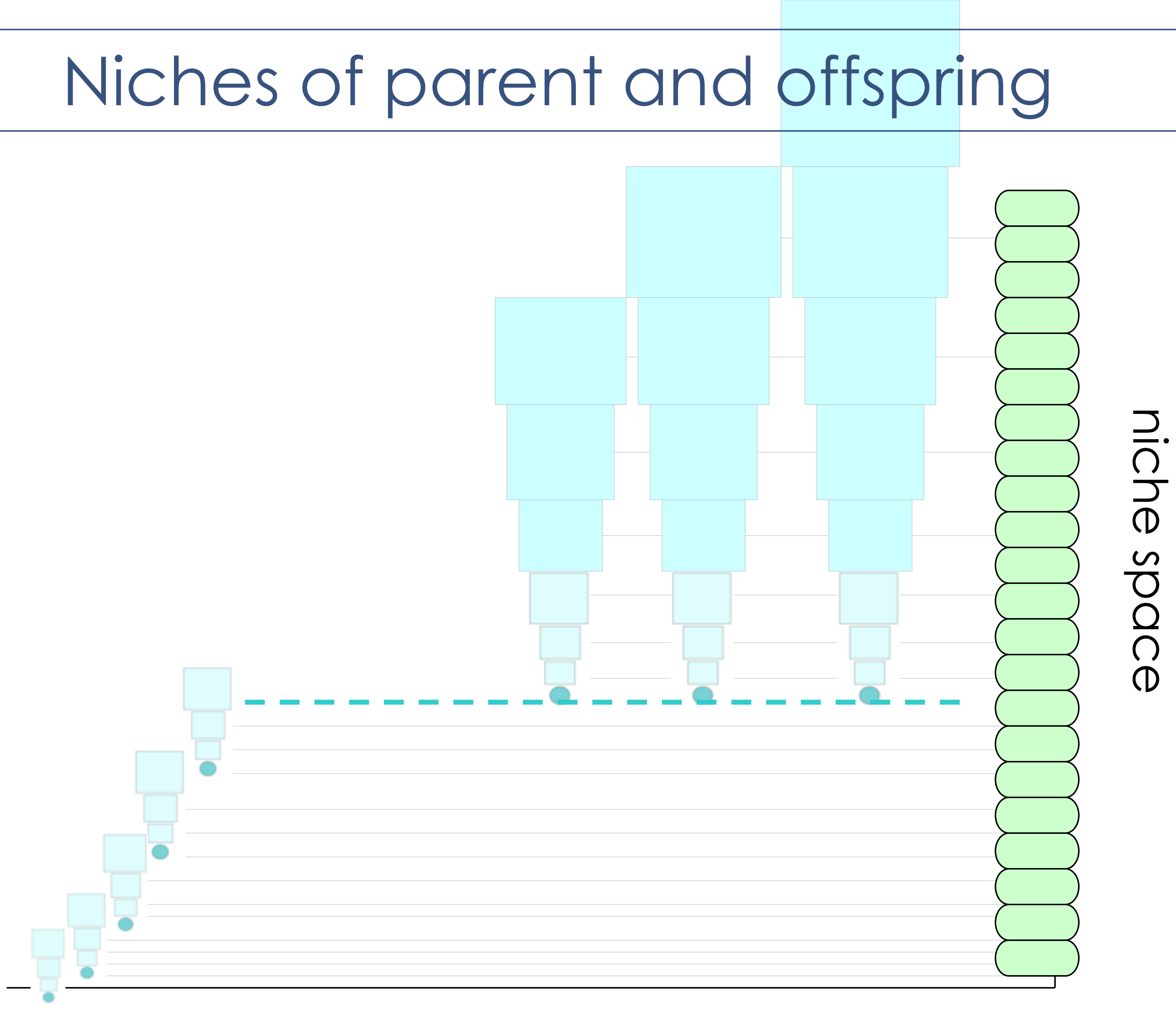

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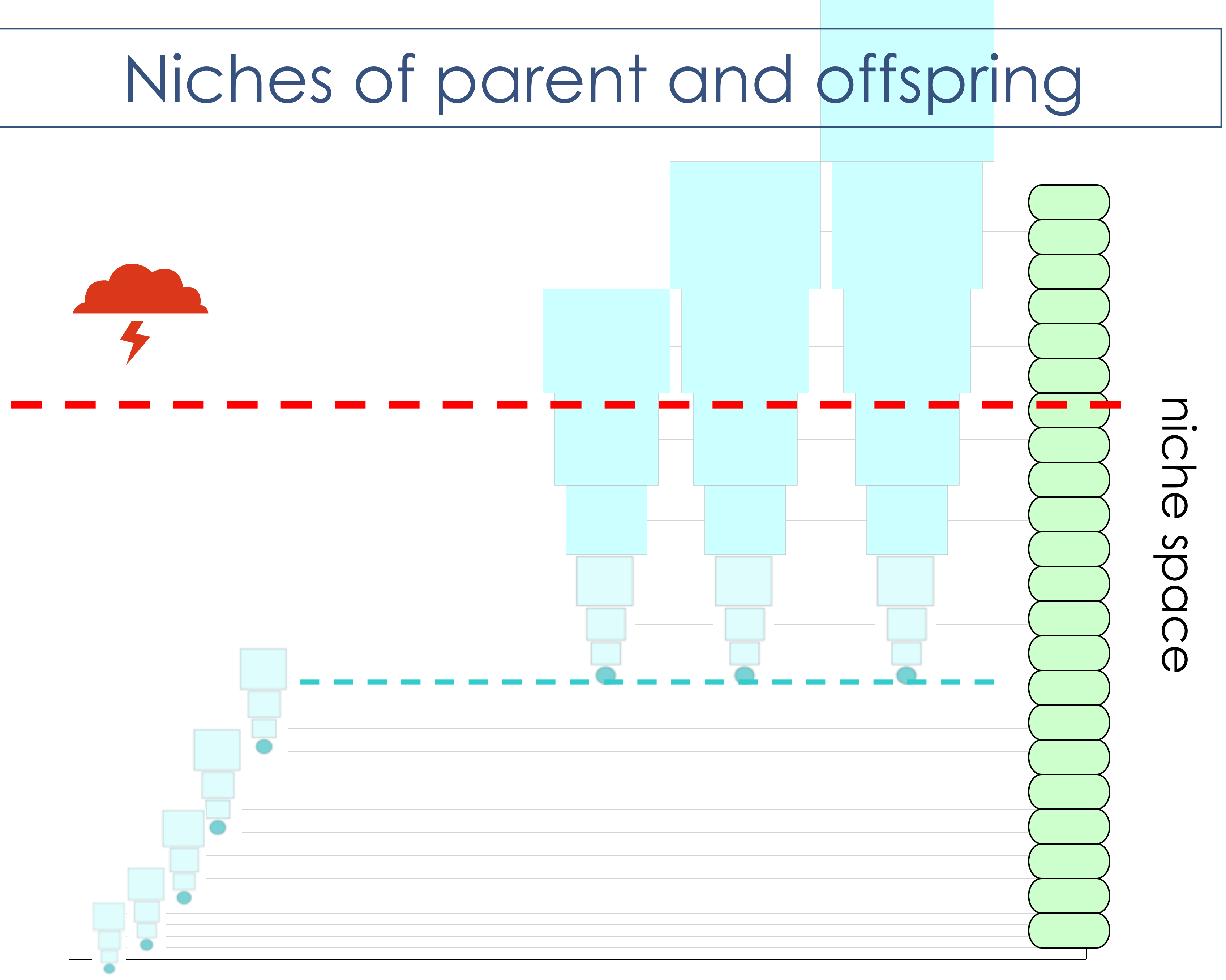

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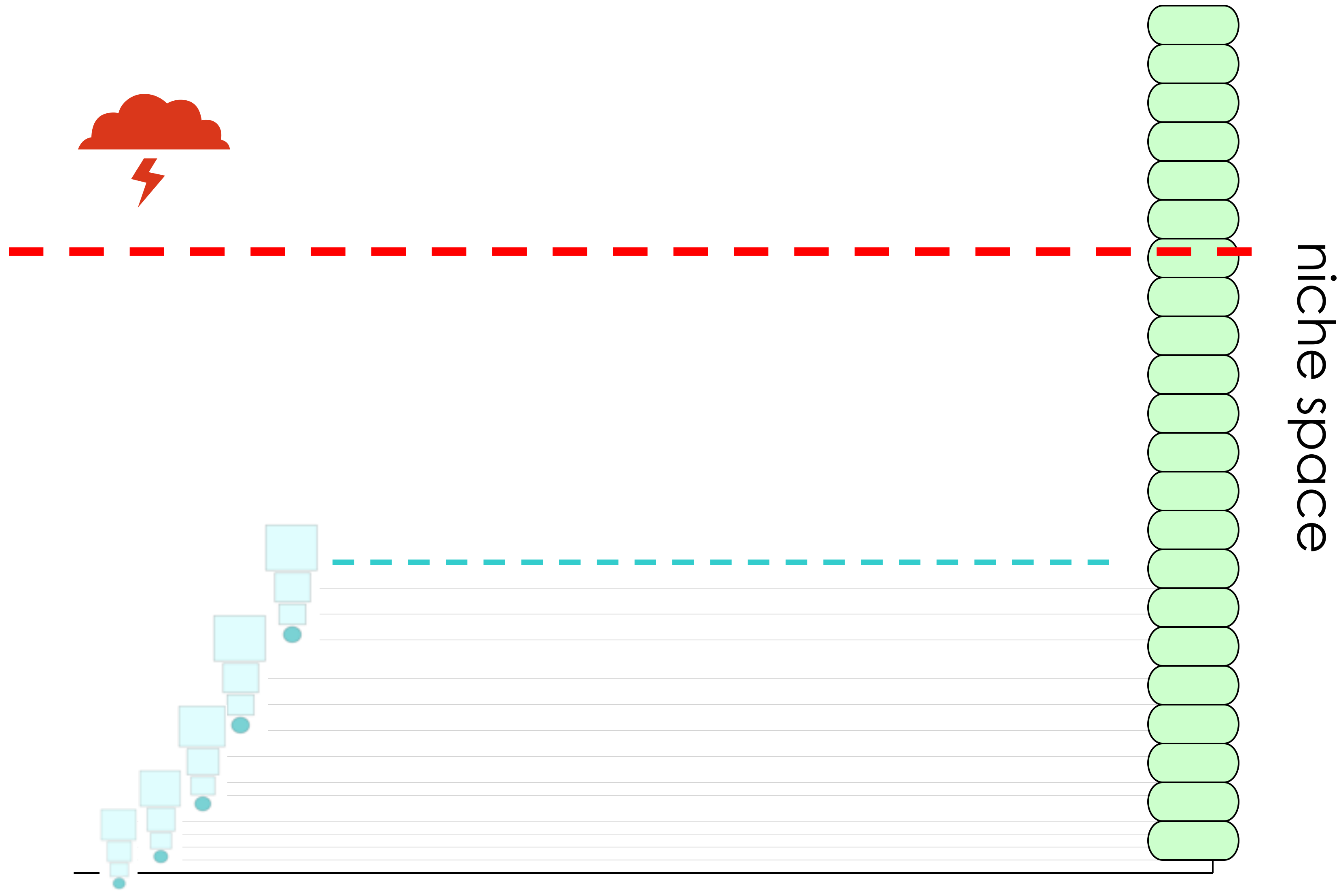

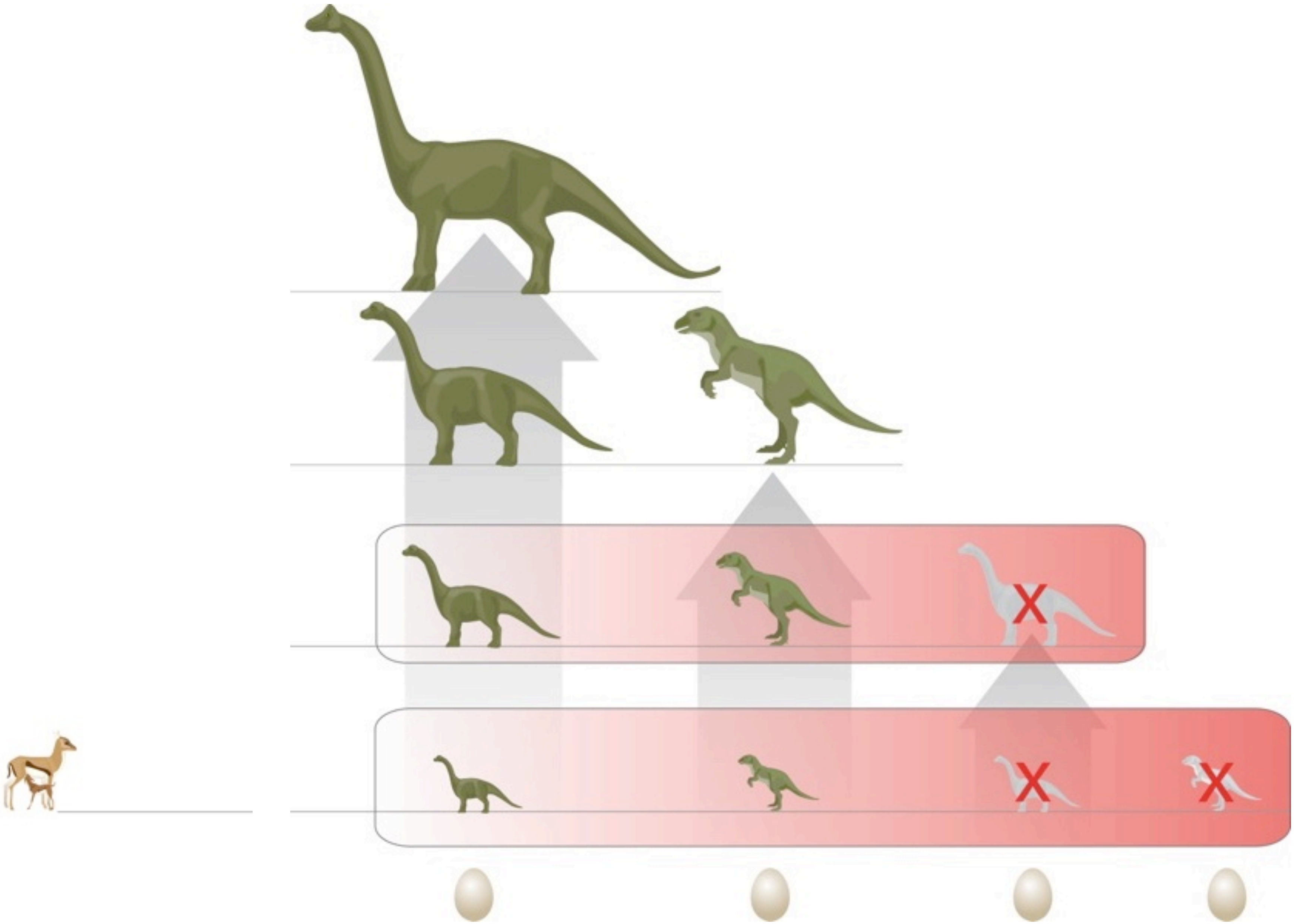

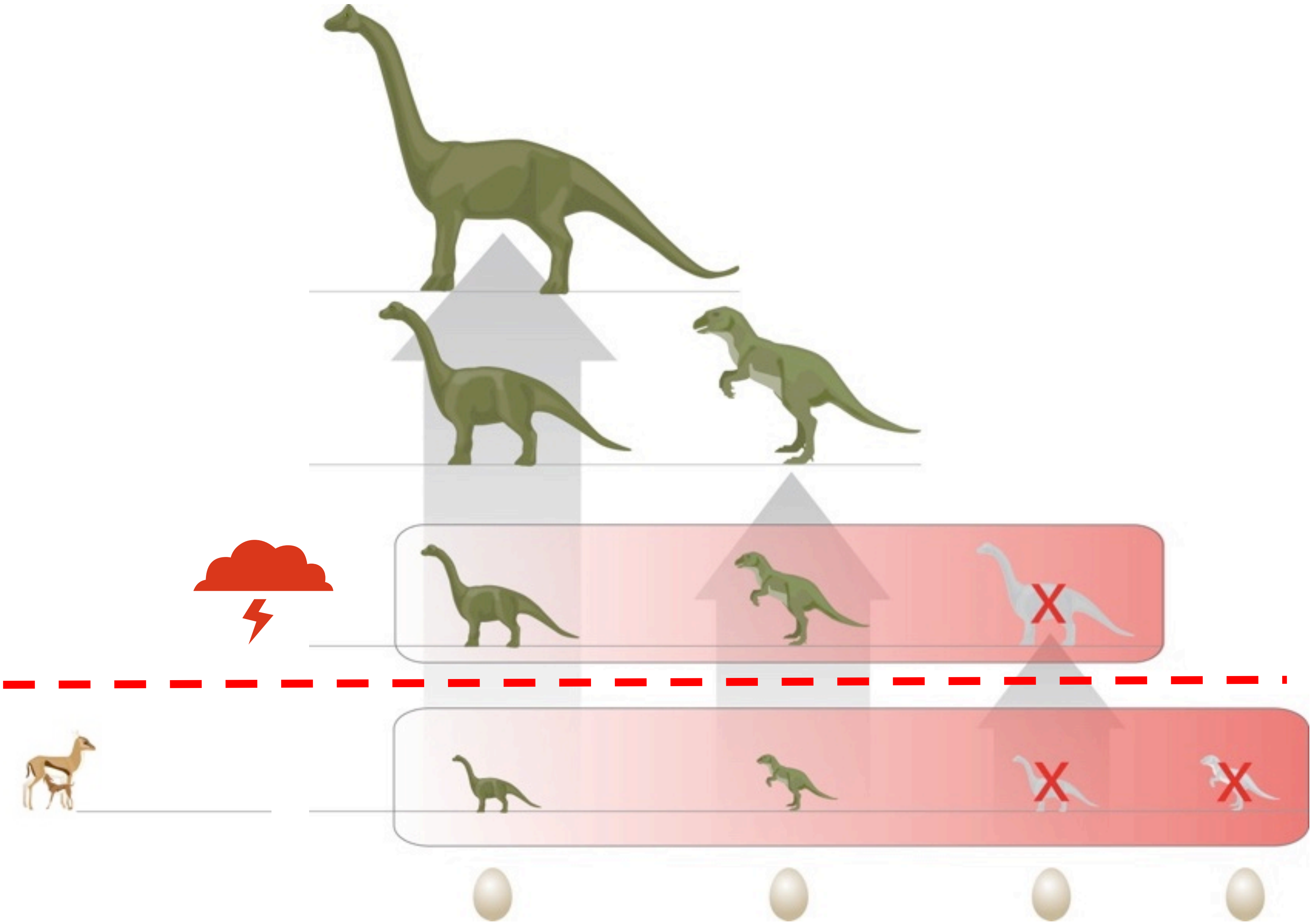

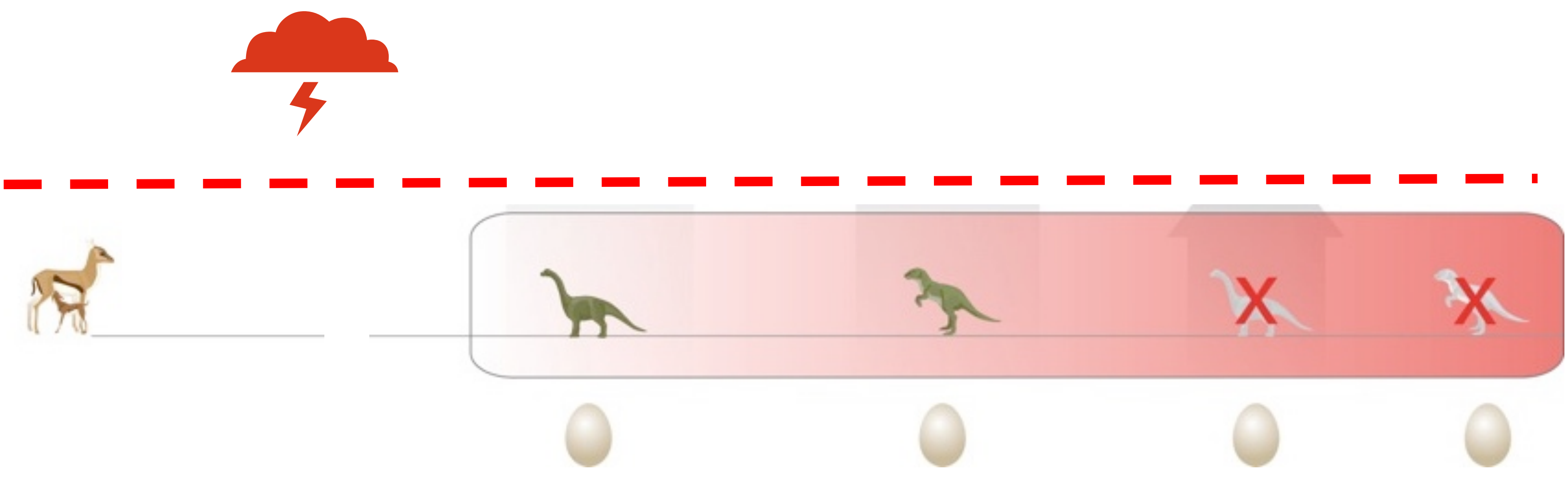

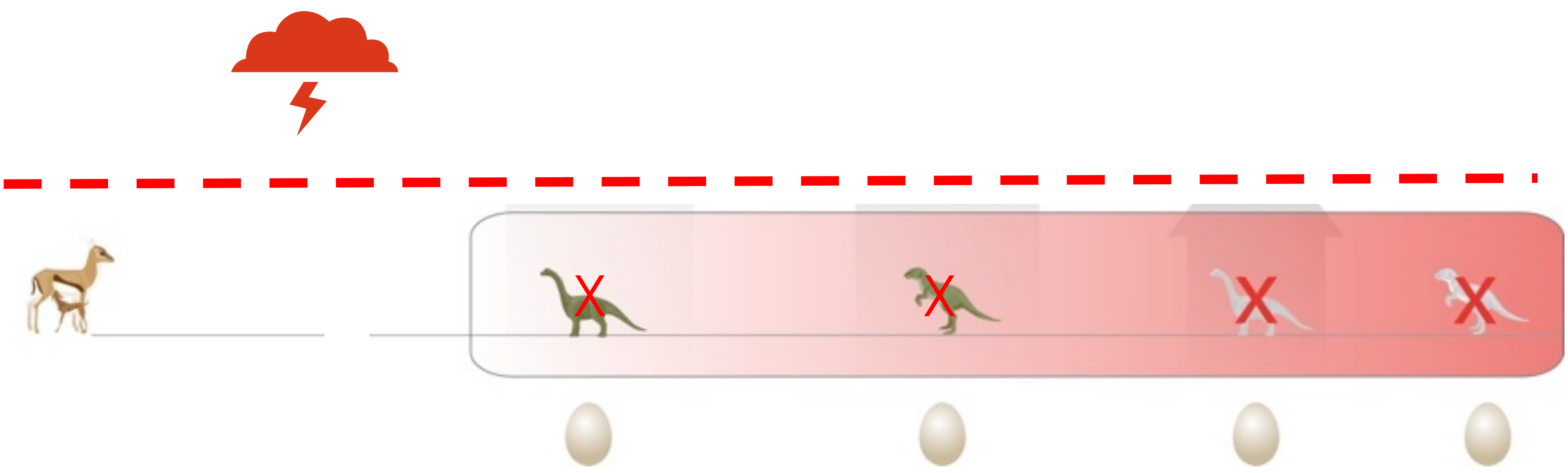

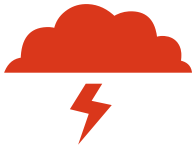

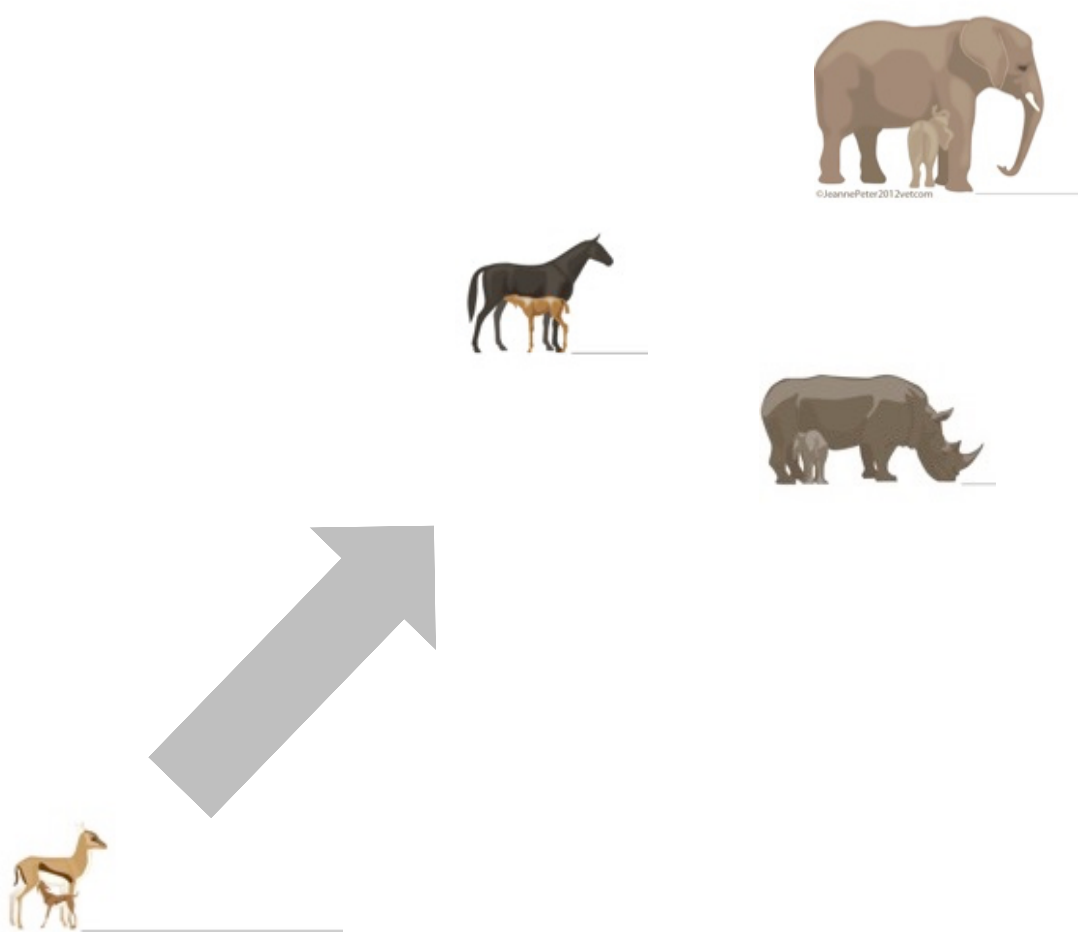
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Gigantic dinosaurs ...

- ... could use the gigantism niche due to a combination of opportunity, large habitats, lightweight construction, oviparity, and (in sauropods) a lack of mastication

Gigantic dinosaurs ...

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Gigantic dinosaurs ...

- ... most likely grew very fast
- Reasons for differences in growth speed between breeds of a species, or between species groups (e.g. insular dwarfs) remain to be studied ...
- ... maybe based on the knowledge from human endicronology and genetics?

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Gigantic dinosaurs ...

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- ... had large numbers of offspring,
  - providing copious resources for carnivores
  - leaving little niche space for medium-sized dinosaur species (which was a decisive disadvantage after the K-T-extinction)

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Medienmitteilung vom 18.04.2012

Das Eierlegen war der Anfang vom Ende der Dinosaurier

Sie legten Eier, besetzten mit nur einer Art viele ökologische Nischen, und sie standen in Konkurrenz auch untereinander. Forscher der Universität Zürich haben die Kette der Ereignisse enthüllt, die zum Aussterben der Dinosaurier geführt haben.

Der Anfang vom Ende liegt in ihrer Fortpflanzungsstrategie: Daraus, dass sie Eier legen, erwächst den Dinosauriern gegenüber den lebend gebärenden Säugetieren ein entscheidender Nachteil. Warum und wie dies letztendlich zu ihrem Aussterben geführt hat, haben Daryl Codron und Marcus Clauss von der Universität Zürich zusammen mit Kollegen der Zoological Society of London erforscht und in der Zeitschrift «Biology Letters» veröffentlicht.

Das Ei des Dinosauriers und das winzige Dino-Baby

2'500-mal schwerer ist das vier Tonnen schwere Muttertier als ihr neugeschlüpftes Dinosaurierbaby. Im Vergleich dazu: Die gleich schwere Elefantenmutter wiegt lediglich etwa 22-mal so viel wie ihr Neugeborenes. Bei den grossen Arten der Säugetiere sind also bereits die Neugeborenen gross.

Der gigantische Grössenunterschied zwischen neugeschlüpften Dinosauriern und

Kontakte

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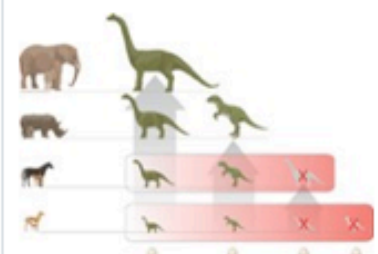

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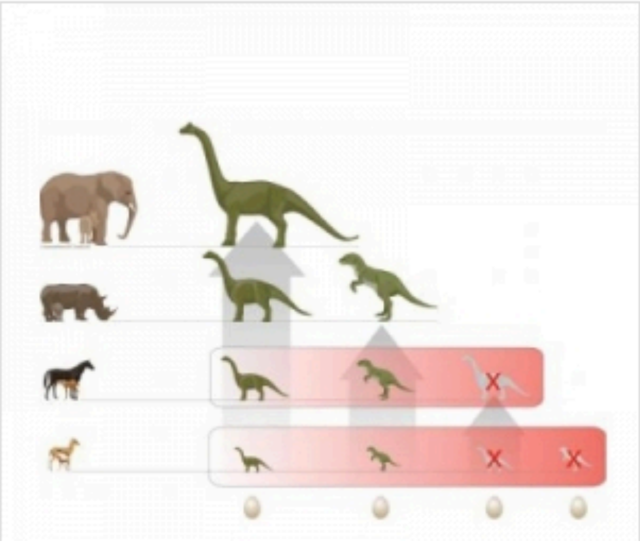
News

Eggs failed the dinosaurs

Agence France Presse

Wednesday, 18 April 2012



PARIS: Their reproductive strategy spelled the beginning of the end: The fact that land-bound dinosaurs laid eggs is what sealed their fate of mass extinction while live birthing mammals went on to thrive, scientists said.

The fact that dinosaurs laid eggs put them at a considerable disadvantage compared to viviparous mammals. Together with colleagues from the Zoological Society of London, Daryl Codron and Marcus Clauss from the University of Zurich investigated why and how this ultimately led to the extinction of the dinosaurs and published their findings in the journal *Biology Letters* today.

WHY HUGE DINOSAURS HAD SUCH TINY BABIES

In the end, dinosaurs were no match for mammals and the main issue was their egg-laying.

By Jennifer Viegas
Tue Apr 17, 2012 07:00 PM ET
(5) Comments | Leave a Comment

Egg-laying may have helped dinosaurs get big.

THE GIST

- Larger mammals can have larger babies, but dinosaurs could not due to the physical limitations of laying eggs.
- Most dinosaurs were either large or small, but mammals can fill all body size niches in the ecosystem.
- When a catastrophic event wiped out larger species 65.5 million years ago, mammals were better able to recover.

A new study may explain many mysteries about dinosaurs, such as why enormous species had such small offspring, why non-flying dinos went extinct, and why today's birds fly.

The paper, published in the journal Biology Letters,

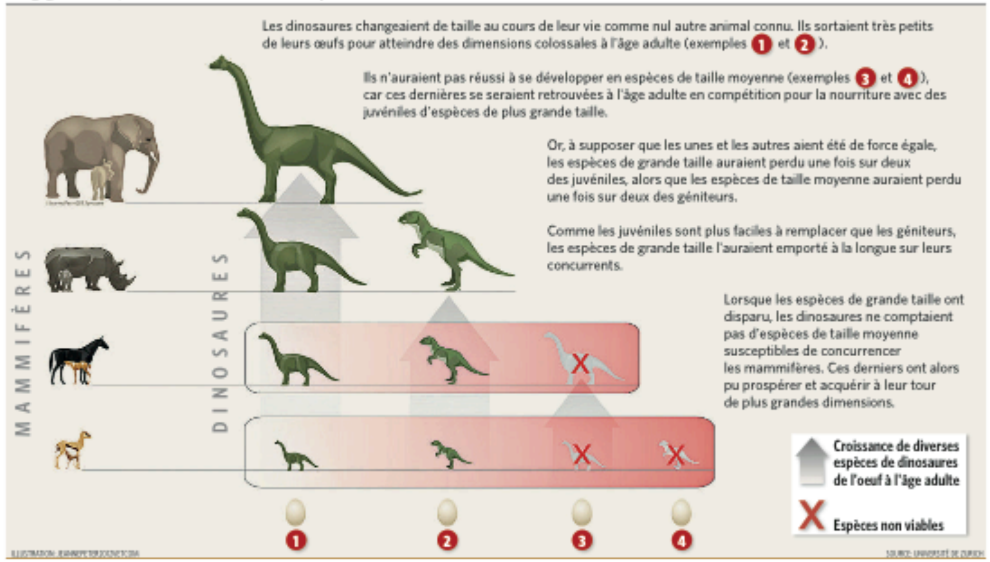
Le Temps
Mercredi 18 avril 2012

Les dinosaures trahis par leurs œufs

> Paléontologie Diplodocus et autres tyrannosaures passaient d'une minuscule à une gigantesque taille

> Cette particularité aurait fini par avantager les mammifères

Le gigantisme, un atout devenu handicap



Etienne Dubuis

Les dinosaures ont perdu leur suprématie sur la faune terrestre parce qu'ils pondaient des œufs. Ce mode de reproduction, qui leur a permis de régner sans partage pendant plus de 150 millions d'années, s'est subitement retourné contre eux. Telle est l'hypothèse originale avancée ce mercredi dans la revue *Biology Letters* par une équipe internationale de chercheurs, composée notamment de vétérinaires de l'Université de Zurich.

Les auteurs de l'article ont tenté de refaire l'histoire sur la base d'un modèle. Ils ont composé des populations de mammifères et de dinosaures dotés de différents poids – de quelques grammes à 16 tonnes pour les premiers, de quelques grammes à 130 tonnes pour les seconds. Puis ils les ont mis en concurrence lorsqu'ils possédaient une taille approchante et ont comparé leur évolution avant et après la grande extinction des espèces de la fin du crétacé, il y a 65 millions d'années.

Les chercheurs expliquent la domination des dinosaures par deux facteurs: la taille bien sûr, mais aussi une extraordinaire croissance entre le moment où ces bêtes sortaient de leurs œufs et celui où elles arrivaient à maturité. Alors qu'un éléphant est 22 fois plus lourd à l'âge adulte qu'à la naissance, un sauropode comme le titanosaure possédait un poids 2500 fois supérieur. Une telle caractéristique avait pour effet que ces animaux occupaient au cours de leur existence une très large gamme de niches écologiques, ce qui les amenait à entrer en compétition avec des espèces de tailles très diverses et à faire le vide autour d'eux à de nombreux «étages».

Pareil écart pouvait difficilement être évité. «Les dinosaures étaient forcément petits à la naissance puisqu'ils étaient mis au monde dans des œufs et que les œufs ne peuvent pas abriter un animal de grande taille sans se casser, explique l'un des auteurs de l'étude, Marcus Clauss, vétérinaire à l'Université de Zurich et spécialiste des fonctions digestives des mammifères. Les plus grands œufs jamais découverts, ceux de l'oiseau-éléphant de Madagascar (disparu il y a 500 ans), pesaient ainsi une dizaine de kilos. Et ceux des dinosaures restaient compris entre 5 et 7 kilos.»

Quant à la croissance des dinosaures, elle était favorisée par la compétition entre espèces. «Des espèces de taille moyenne avaient peu de chances de survivre puisque leurs adultes auraient été en conflit direct pour la nourriture avec des juvéniles d'espèces de grande taille, poursuit Marcus Clauss. A supposer qu'à dimension égale les uns et les autres aient été de force égale, les espèces de grande taille auraient perdu une fois sur deux des juvéniles, alors que les espèces de taille moyenne auraient perdu une fois sur deux des géniteurs. Comme les juvéniles sont plus faciles à remplacer que les géniteurs, les espèces de grande taille se seraient inéluctablement imposées à la longue et les espèces de taille moyenne auraient fatalement disparu.»

> La quasi-totalité des survivants ont dû voler ou se réfugier sur des îles

Mais l'avantage qu'a longtemps procuré cette croissance physique s'est transformé en inconvénient à la fin du crétacé, poursuivent les chercheurs. Les grandes espèces de dinosaures n'ont pas survécu à la disparition de l'essentiel de la couverture végétale consécutive à la chute d'une énorme météorite ou à l'intensification de l'activité volcanique. Ces grands mangeurs avaient résisté sans mal aux catastrophes naturelles tant qu'elles étaient restées de courte durée, parce que la capacité des femelles à pondre de nombreux œufs permettait à l'espèce de récupérer rapidement. Mais ils se sont retrouvés sans défense face à une crise prolongée. Et une fois ces géants éteints, leur «branche animale» n'a plus compris que de tout petits êtres, faute d'avoir «su» développer des espèces de taille intermédiaire.

«Le champ libre a alors été laissé aux mammifères, parmi lesquels quelques espèces de taille moyenne avaient survécu au cataclysme, assure Marcus Clauss. Concurrencés cette fois par plus gros qu'eux, les dinosaures ne sont jamais parvenus à refaire leur retard de poids et de taille. Ceux qui sont parvenus jusqu'à nous, les oiseaux, ont dû voler pour échapper aux mammifères ou occuper des îles exemptes de prédateurs, comme les kiwis de Nouvelle-Zélande. L'autruche est l'exception qui confirme la règle.»

«La disparition des dinosaures non aviaires s'explique par la rupture des chaînes alimentaires à la fin du crétacé, confirme Lionel Cavin, conservateur du Département de géologie et de paléontologie du Muséum d'histoire naturelle de la ville de Genève. Ceux qui se nourrissaient de végétation et ceux qui se nourrissaient d'espèces végétariennes ont disparu faute de nourriture, alors que les animaux mangeant des insectes ou de la matière en décomposition ont survécu.»

L'article de *Biology Letters* est-il susceptible de compléter les connaissances actuelles sur la suite? «La démarche est originale, comme l'est la spécialité des chercheurs, la biologie et non la paléontologie, poursuit Lionel Cavin. Mais il s'agit d'un modèle très théorique. Il reste à confronter cette hypothèse à la réalité du terrain.»

Panorama

Santé

Implants mammaires fragiles

Les ruptures sur les implants mammaires PIP au gel de silicone «frelaté» pourraient être plus nombreuses que prévu d'après une étude britannique publiée dans le *Journal of plastic, reconstructive and aesthetic surgery* et conduite auprès de 500 femmes dans ce pays. Le taux de rupture serait situé entre 15,9 et 33,8% pour des prothèses vieilles de 7 à 12 ans. «Selon de précédentes études, les taux de rupture rapportés étaient de 2 à 5%», avise Jan Stanek, l'auteur principal de cette étude. (AFP)

Nivologie

Hiver des extrêmes

L'hiver 2011-2012 a été celui des extrêmes en Suisse, selon l'Institut pour l'étude de la neige et des avalanches SLF. Après un début de saison avare en neige, la tendance s'est drastiquement inversée en janvier. Les records de mesures ont même été battus à Ulrichen (VS), qui a enregistré 456 cm de neige, ou Samedan (GR), avec 192 cm. Au final, le total de neige n'a pas dépassé la moyenne. Et si davantage de dégâts matériels ont été enregistrés, les 83 avalanches signalées ont fait moins de victimes (15) qu'en moyenne. (ATS)

Nature

Champignon des pins décrit

Une vaste étude internationale, à laquelle a participé Lassaad Belbahri, biologiste à l'Université de Neuchâtel, a permis de décrypter le génome d'un champignon du genre *Heterobasidion*, un parasite des pins qui provoque des pertes évaluées à quelque 800 millions d'euros par an dans les forêts européennes. Ce résultat, publié dans la revue *New Phytologist*, ouvre de nouvelles perspectives dans la lutte contre cet agent pathogène. (LT)

Ouragans

«Irene» retirée de la liste

L'Organisation météorologique mondiale a annoncé mardi le retrait du prénom «Irene» de la liste des noms des cyclones à la suite des dommages exceptionnels causé par l'ouragan dévastateur *Irene* qui s'était abattu sur les Etats-Unis et les Caraïbes en août 2011. (AFP)