Digestive physiology and feeding behaviour of equids – a comparative approach

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Gent 2013

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Vetsuisse Faculty

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of Zoo Animals, Exotic Pets and Wildlife


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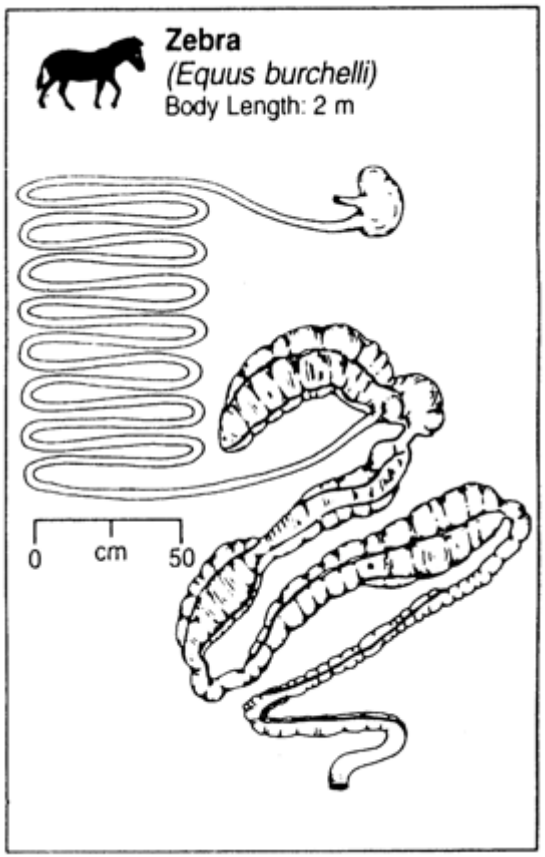
Przewalski Horsese used for grazing (Foto: M. Neubert)

Large herbivore diversity: Equids

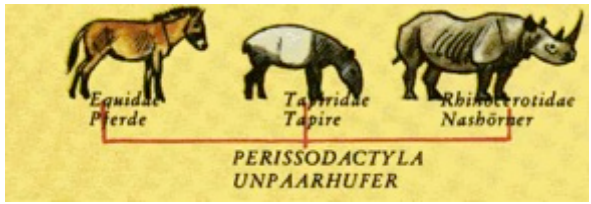
≈ 8 species

Digestive tract: Equids



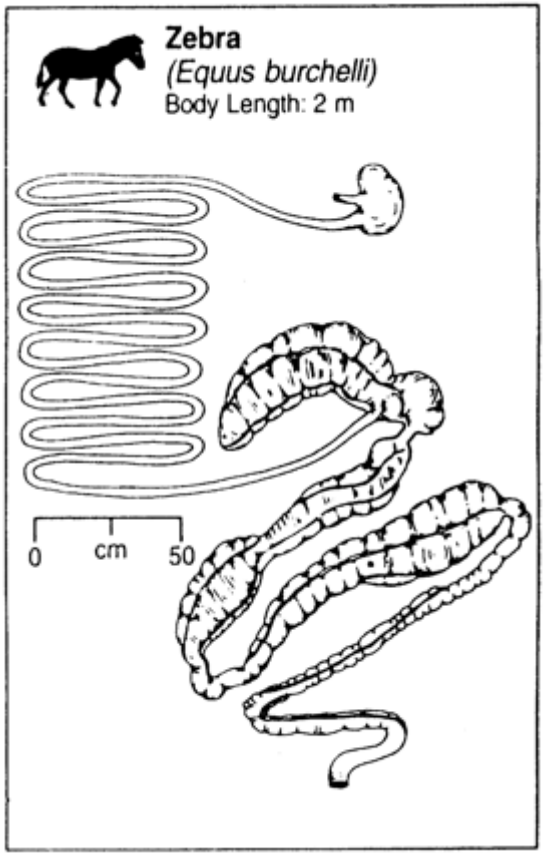
from Stevens und Hume (1995), Clauss et al. (2008)

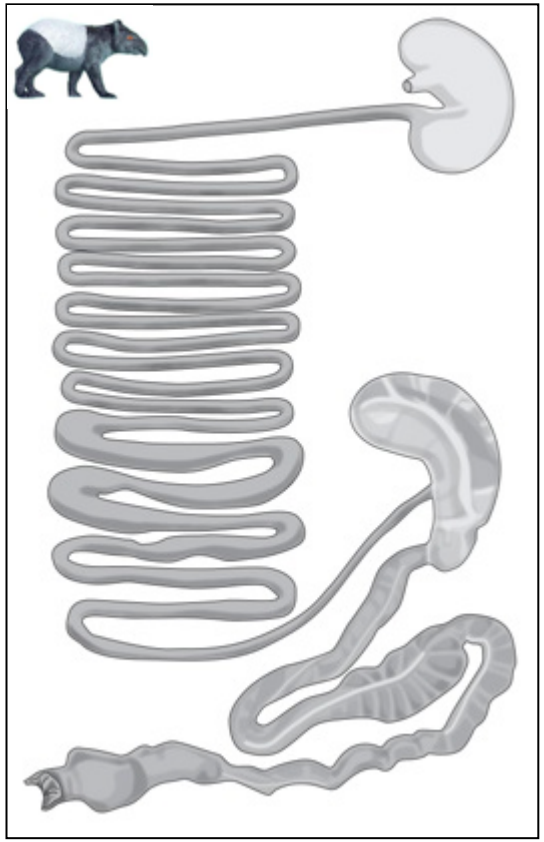
Large herbivore diversity: Perissodactyls

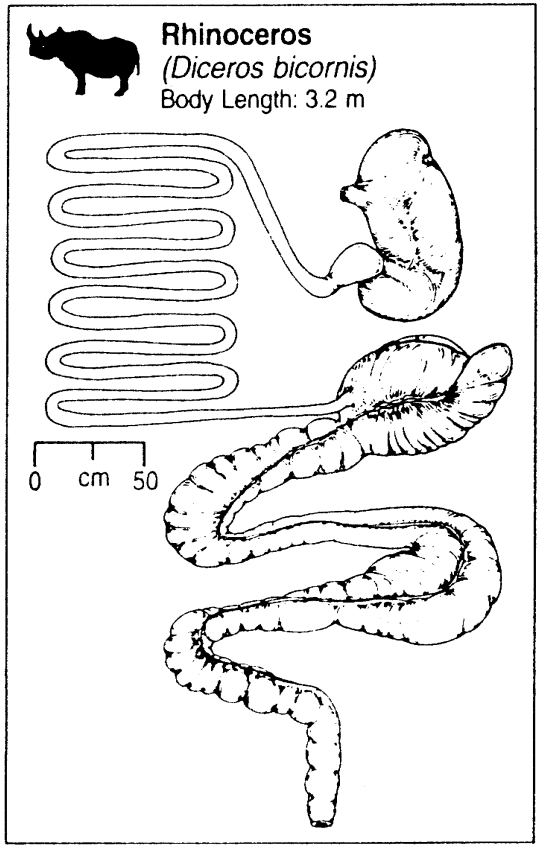


≈ 16 species

Digestive tract: Perissodactyls







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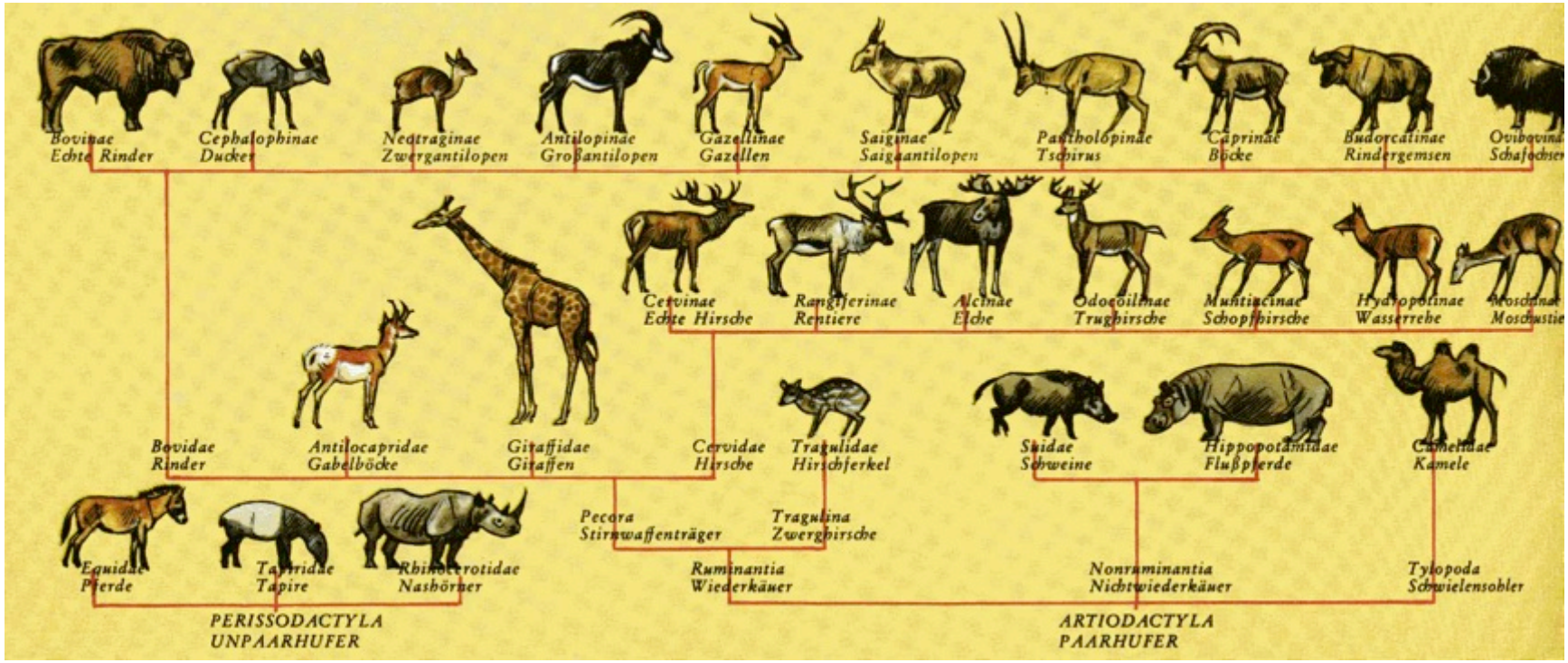
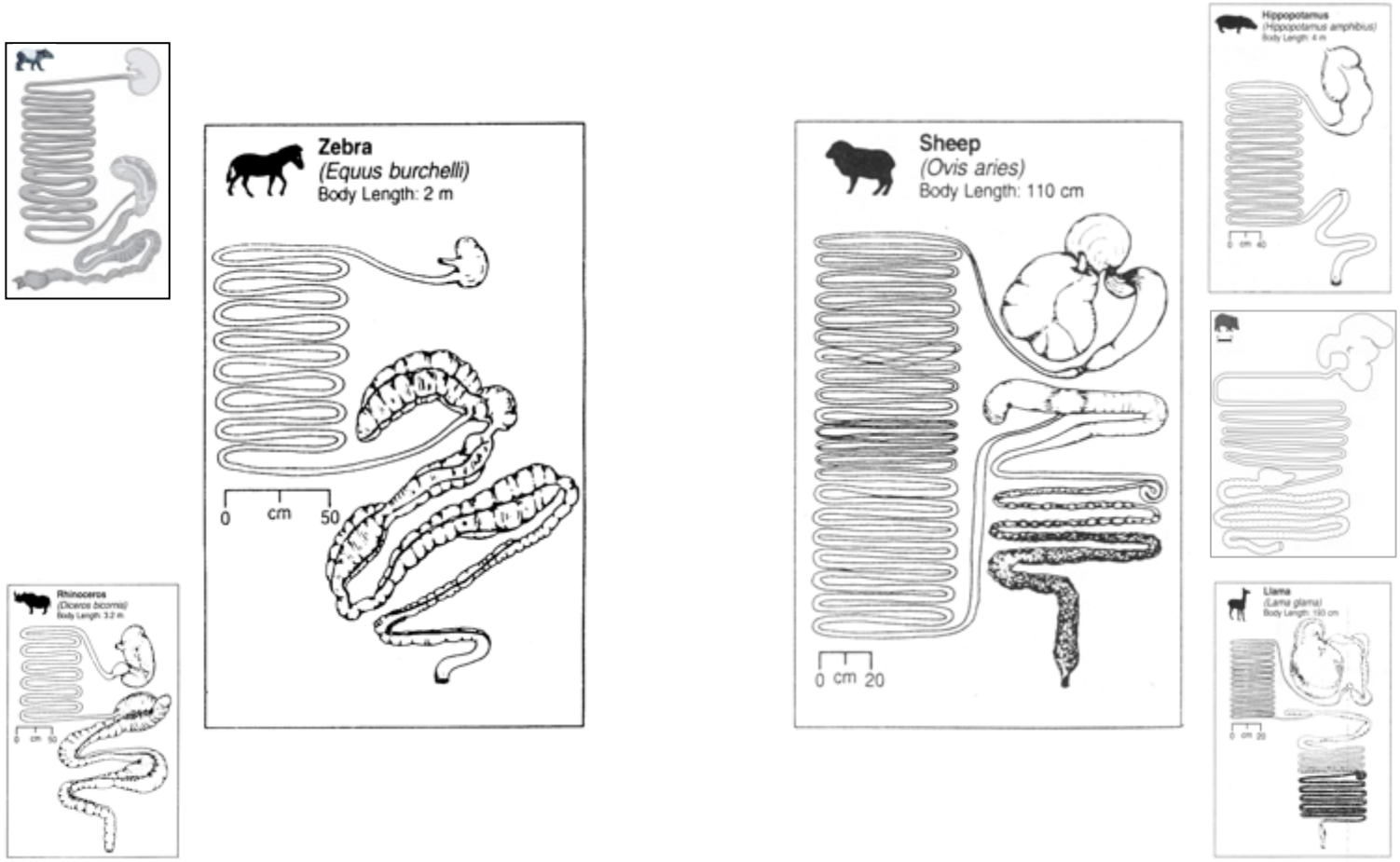
Large herbivore diversity: hoofed mammals



≈ 16 species

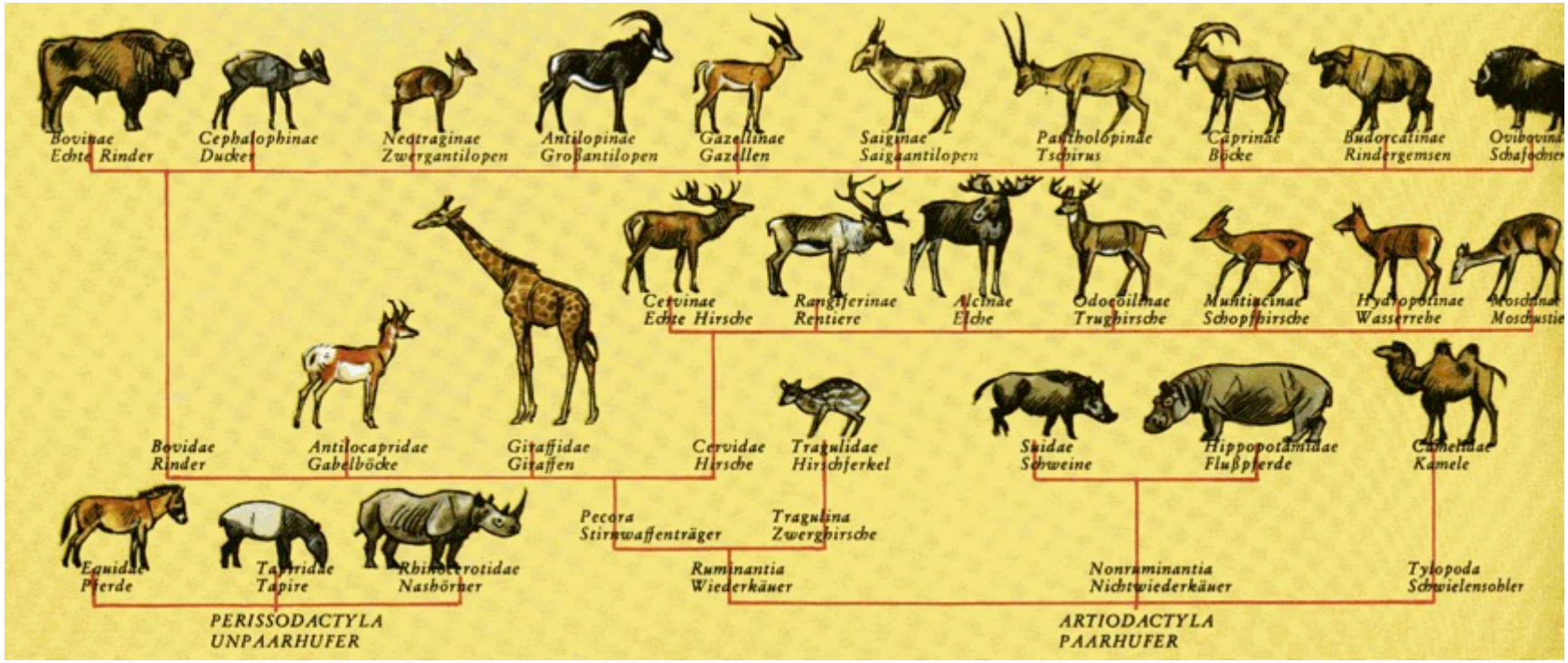
> 300 species

Digestive tract: Perissodactyls vs. Artiodactyls



Stevens und Hume (1995), Clauss et al. (2008), Schwarm et al. (2010), Müller et al. (in prep.)

Large herbivore diversity: hoofed mammals



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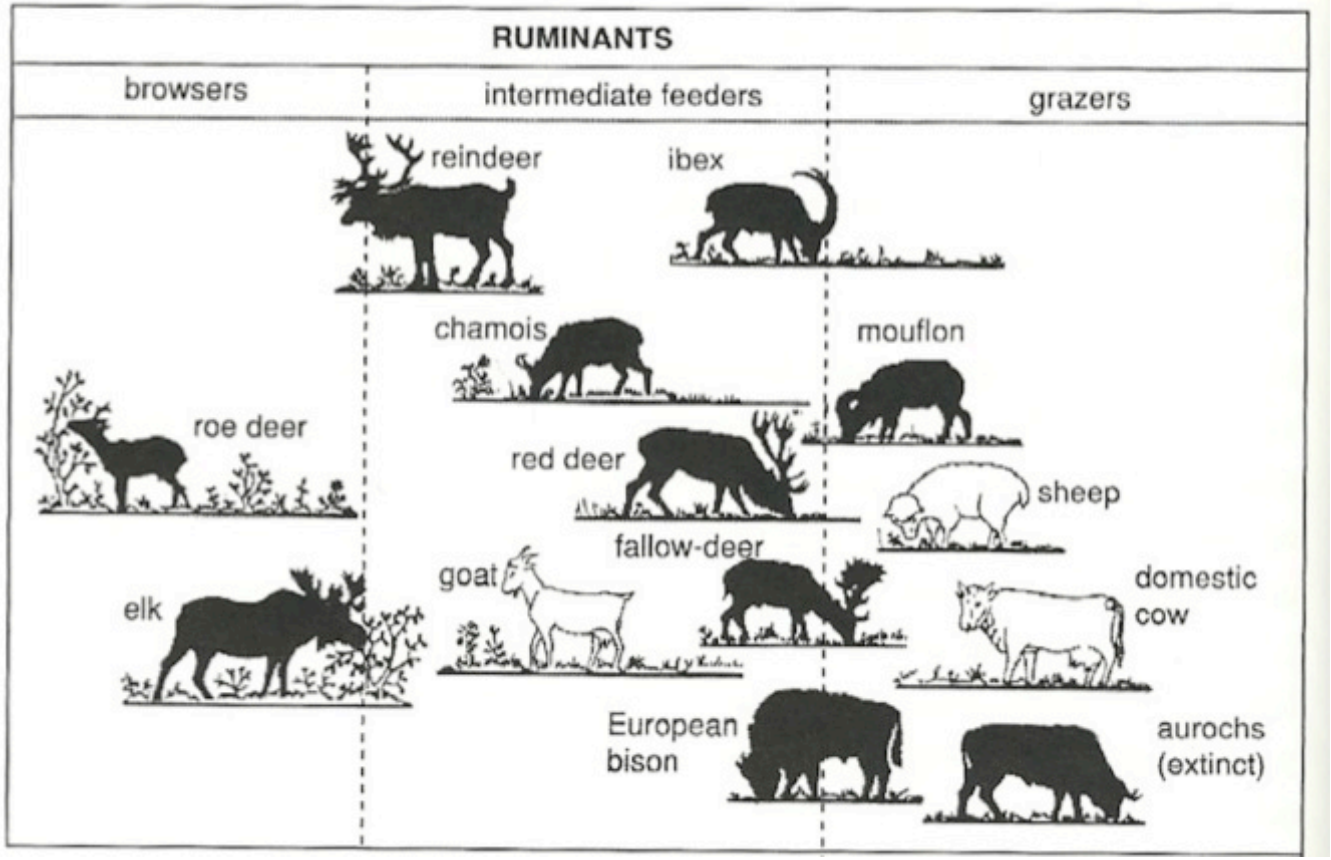
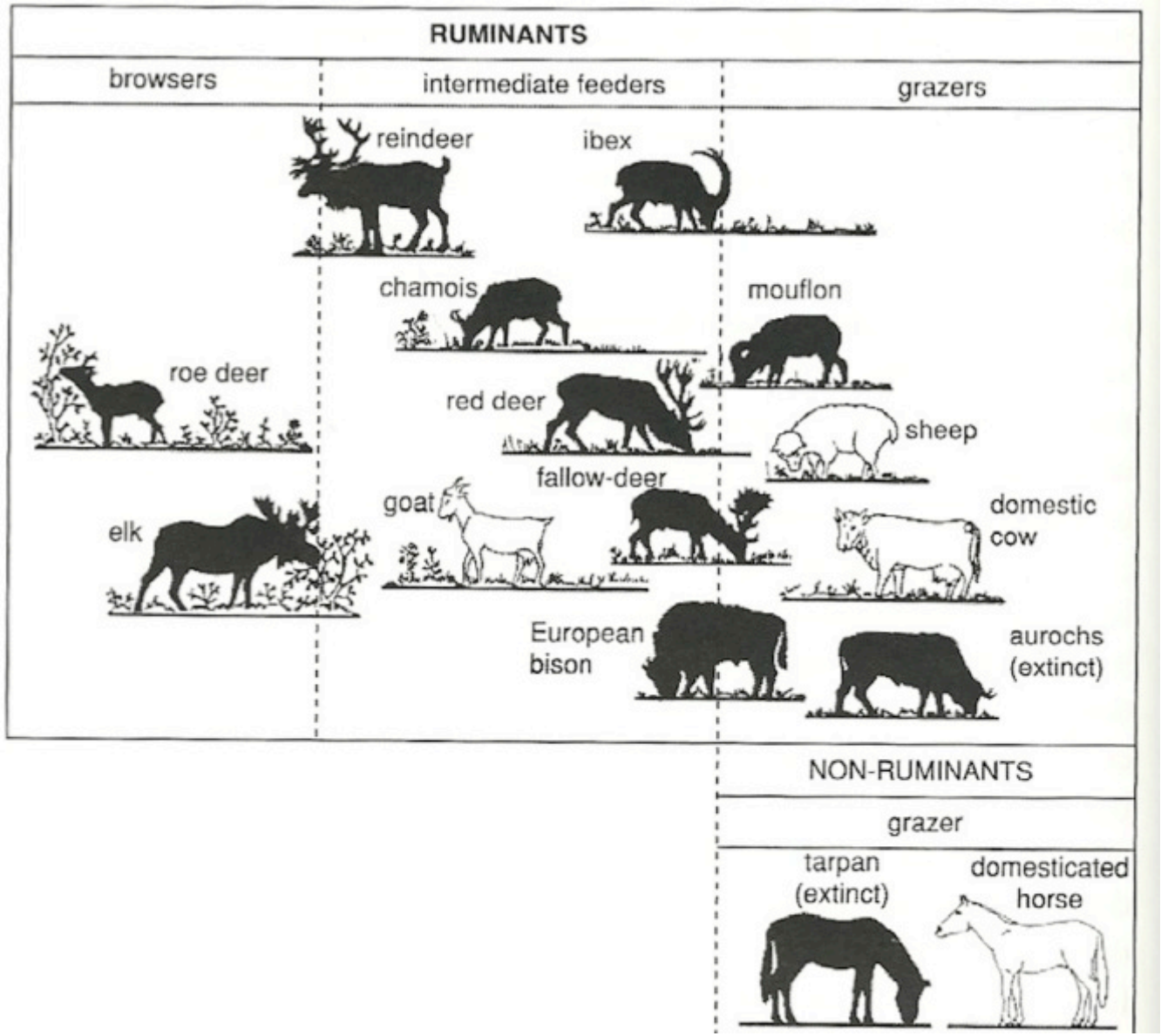
> 300 species

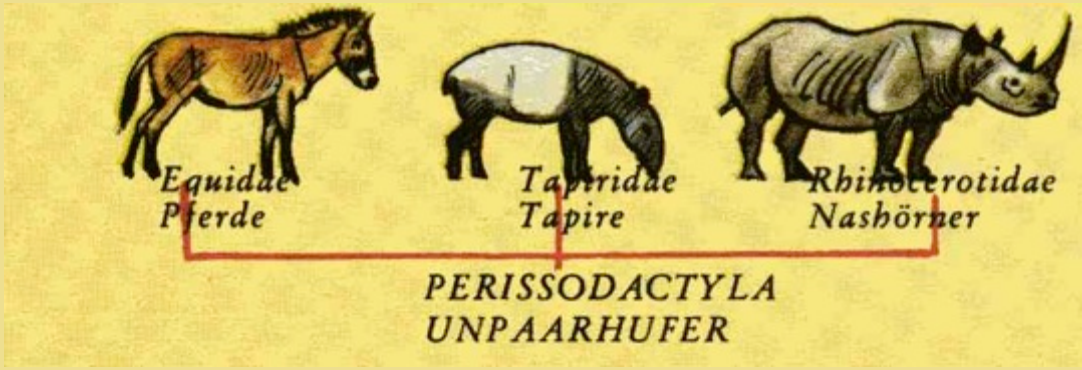
Large herbivore diversity: Europe



Large herbivore diversity: Europe

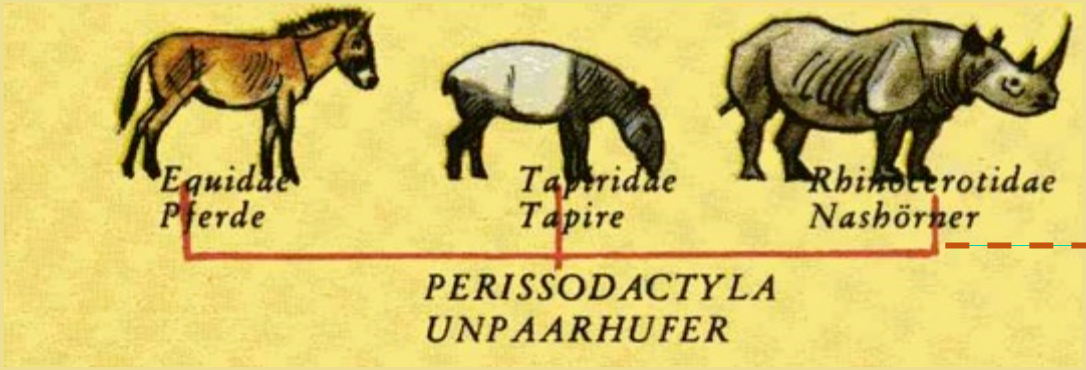


Large herbivore diversity in deep time: Perissodactyls



Large herbivore diversity in deep time: Perissodactyls

Chalicotheres



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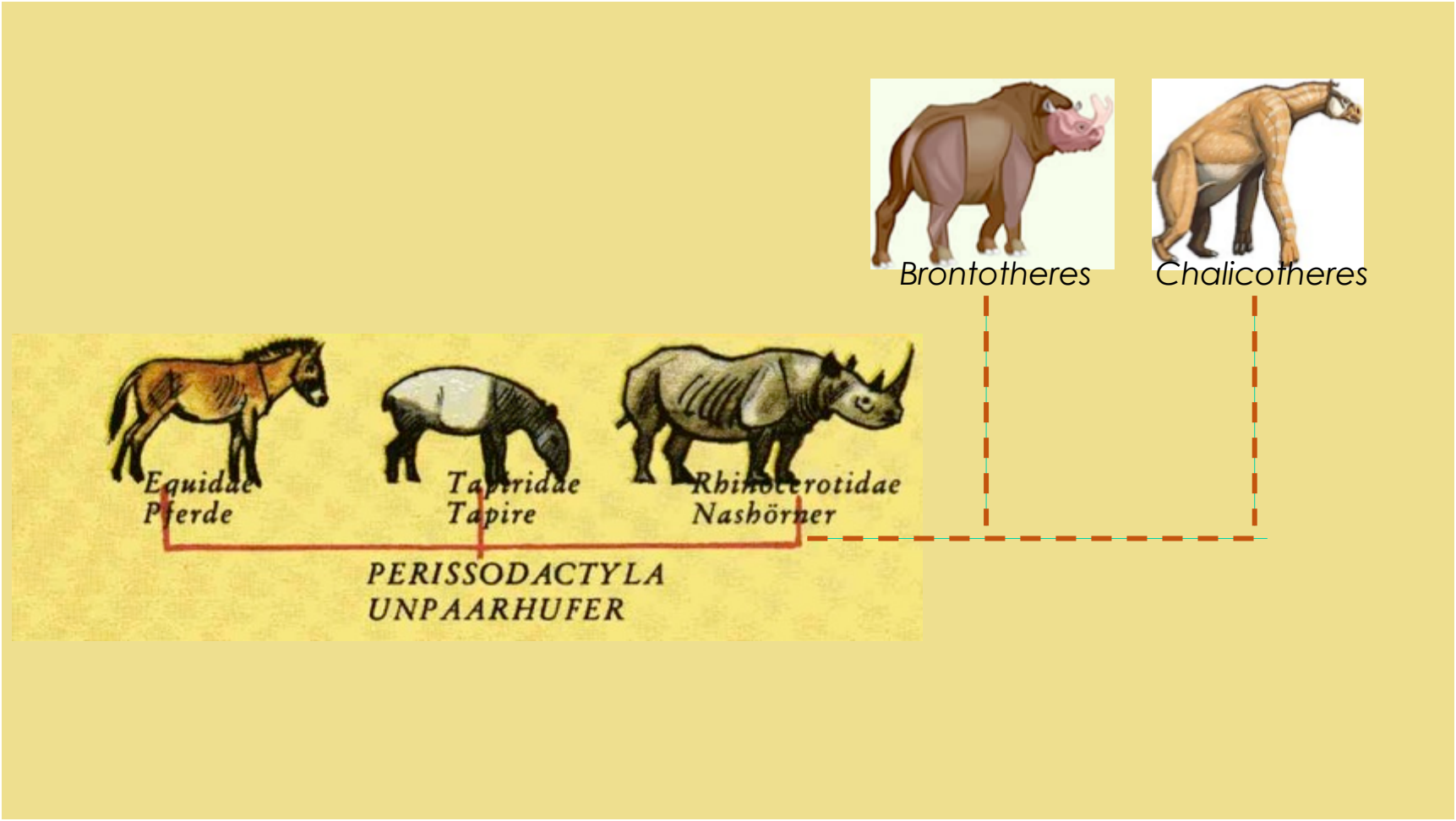

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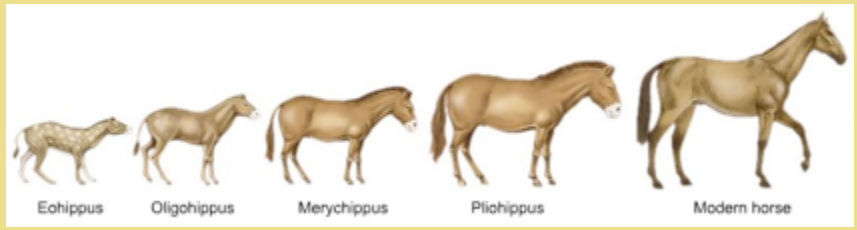
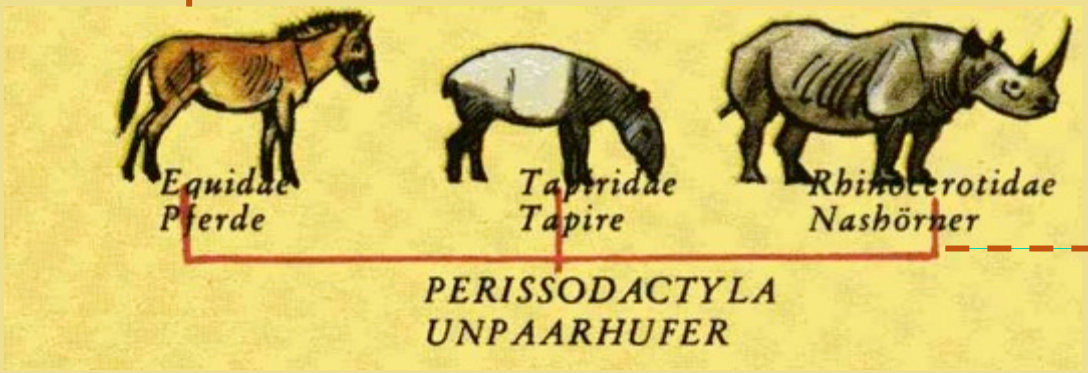


Brontotheres

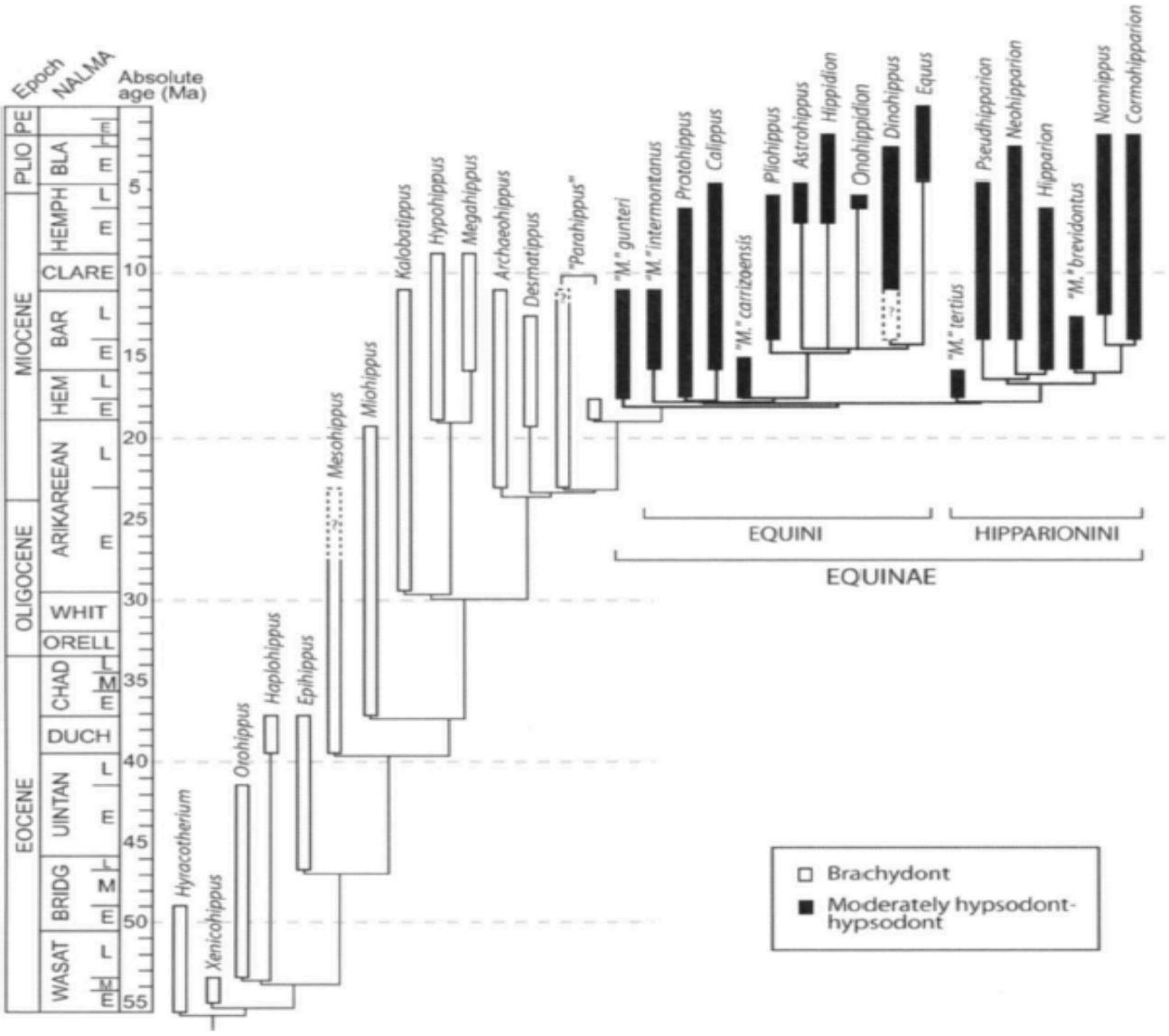
Chalicotheres



Evolution of hypsodonty in equids: testing a hypothesis of adaptation

Caroline A. E. Strömberg

Paleobiology, 32(2), 2006, pp. 236–258



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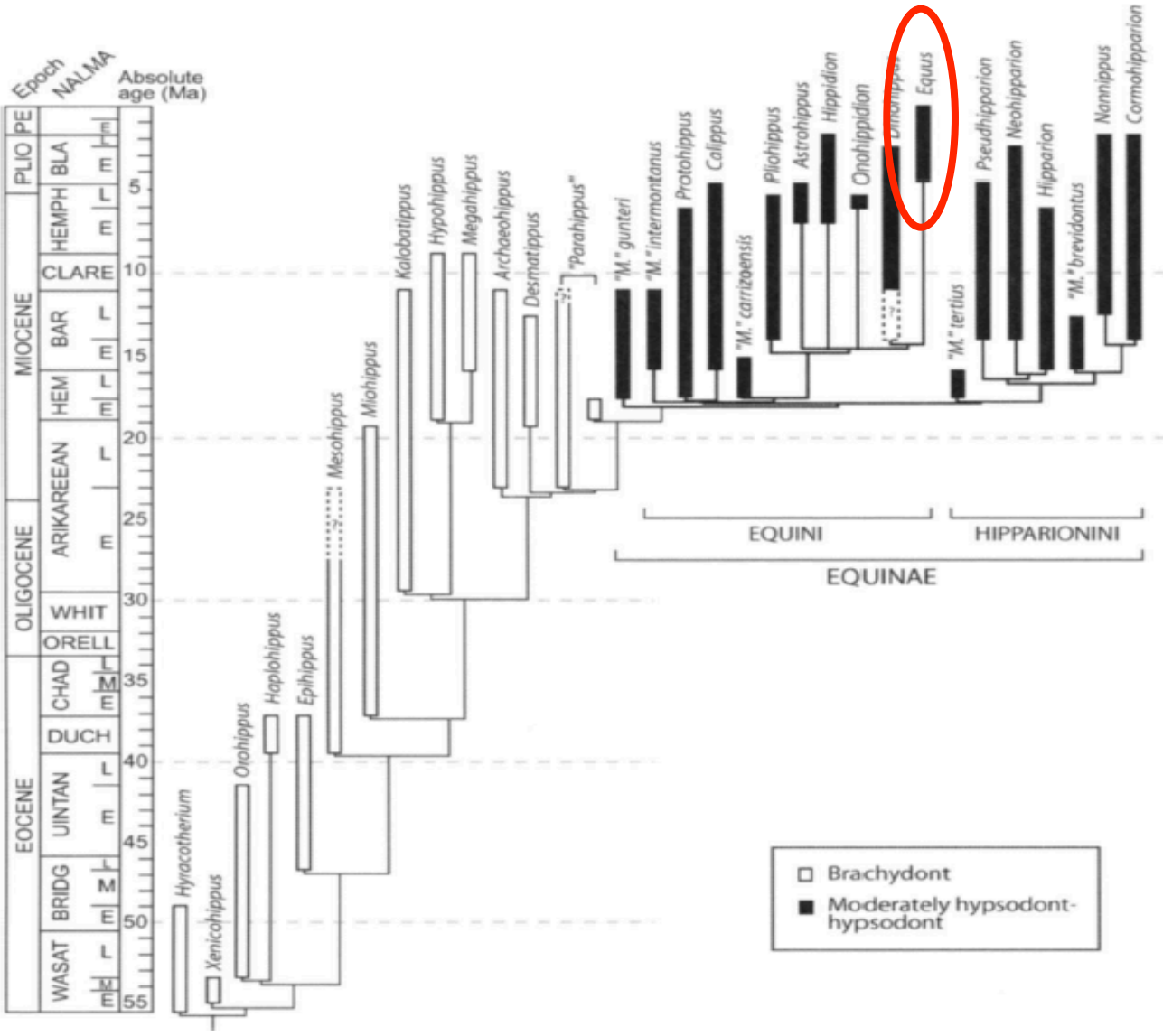

THE EVOLUTION OF THE HORSE. A RECORD AND ITS INTERPRETATION

By W. D. MATTHEW

The Quarterly Review of Biology, Vol. 1, No. 2 (Apr., 1926), pp. 139-185

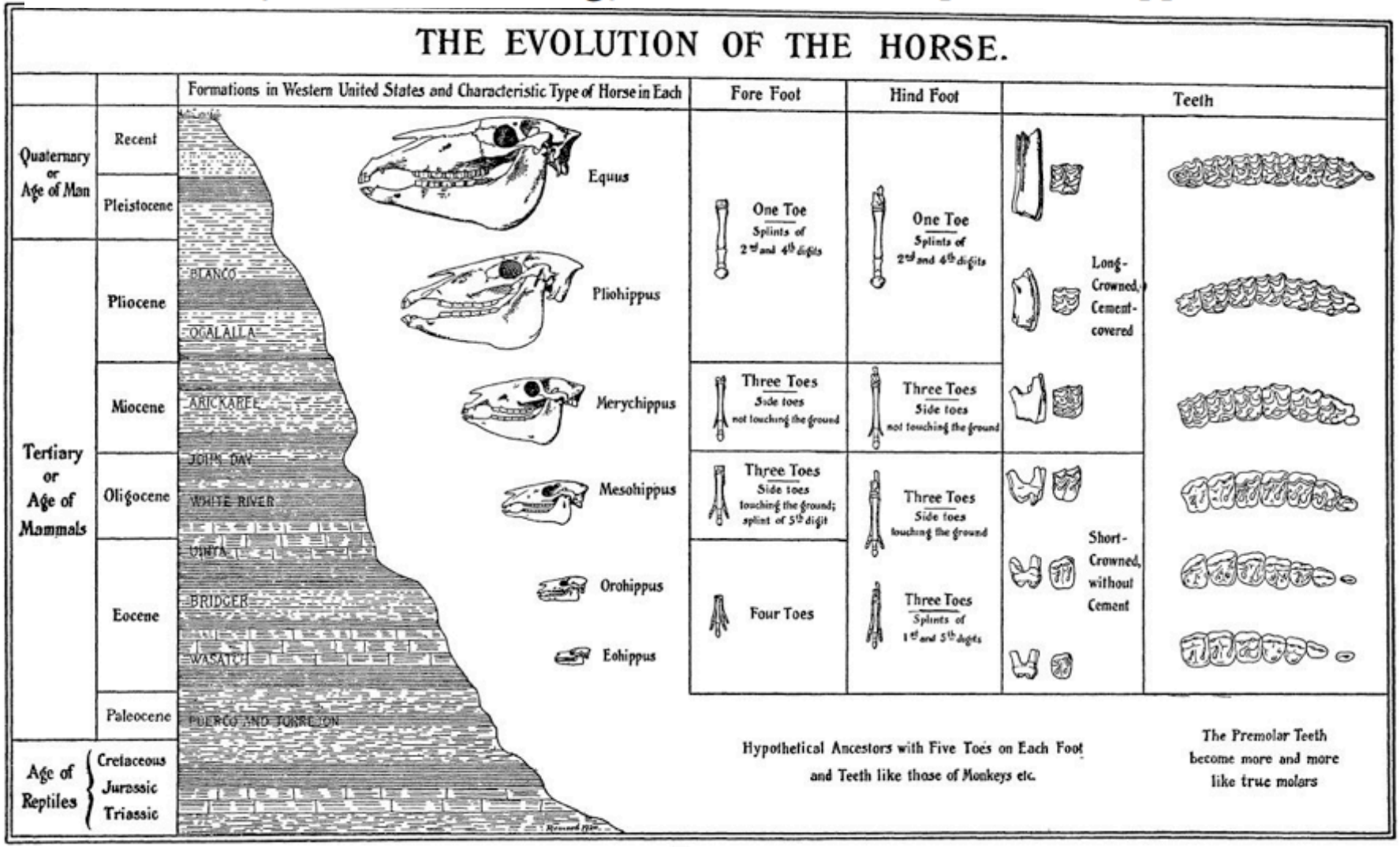

FIG. 27

Evolution of hypsodonty in equids: testing a hypothesis of adaptation

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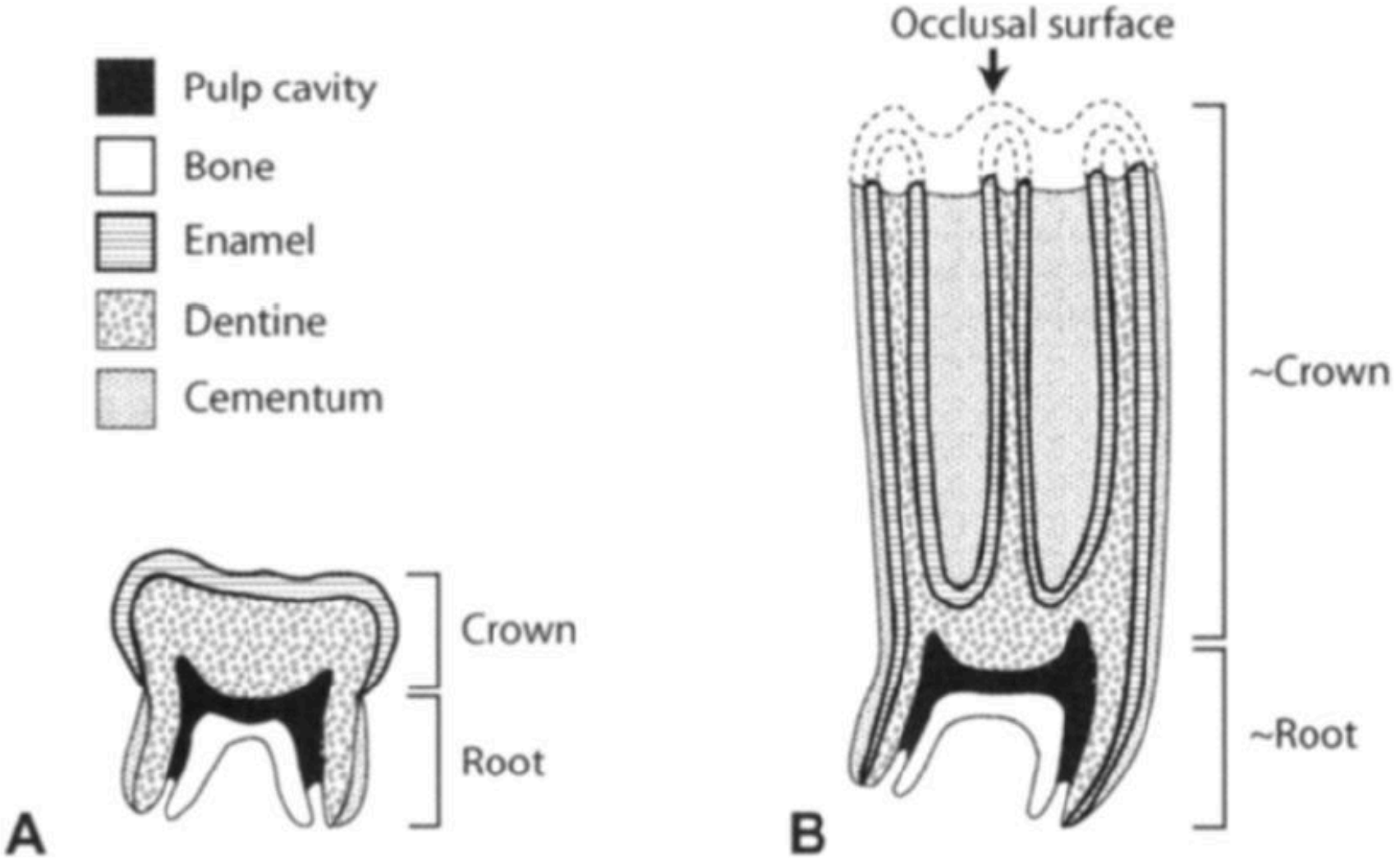

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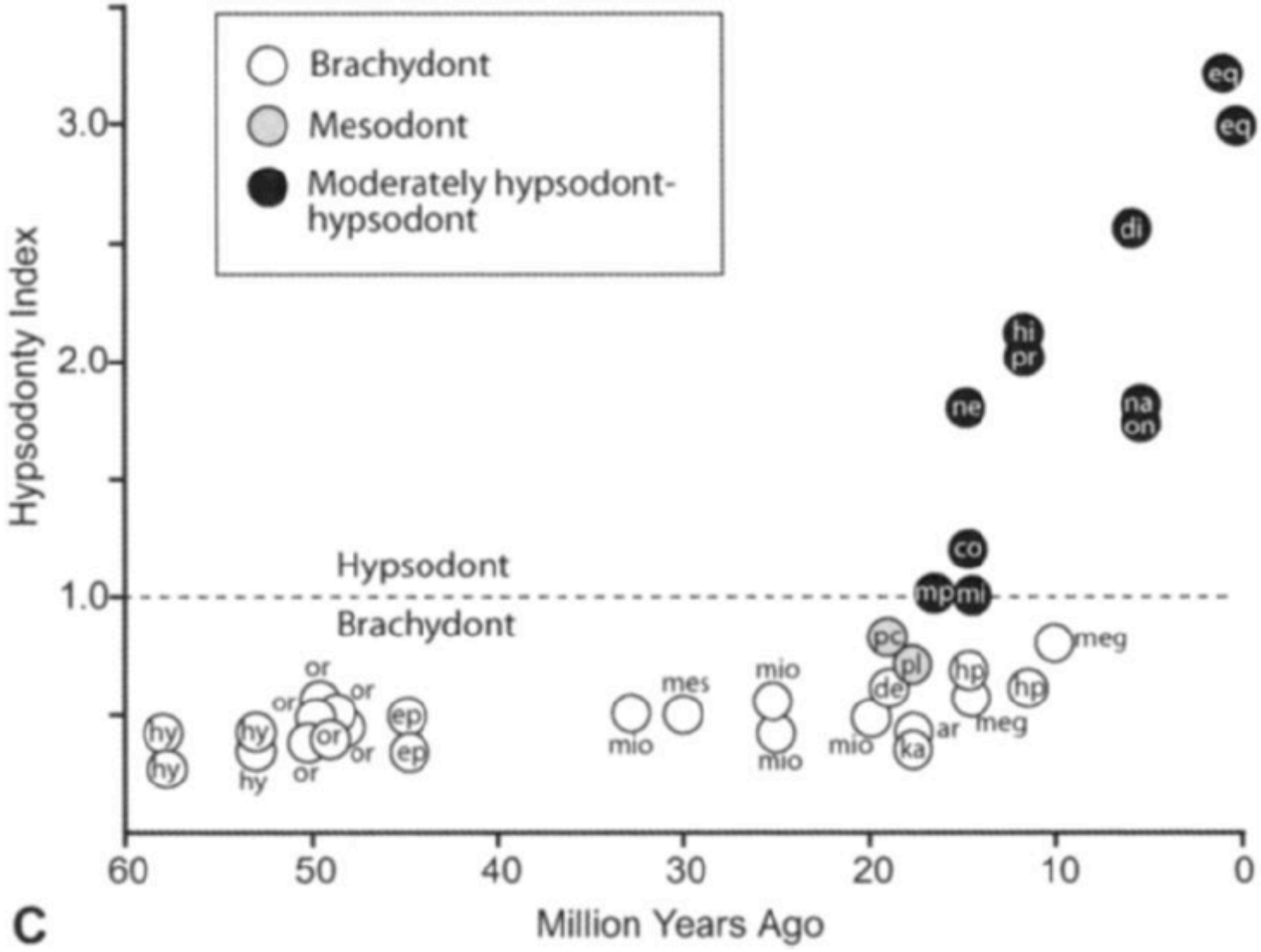

Fossil horses and carbon isotopes: new evidence for Cenozoic dietary, habitat, and ecosystem changes in North America

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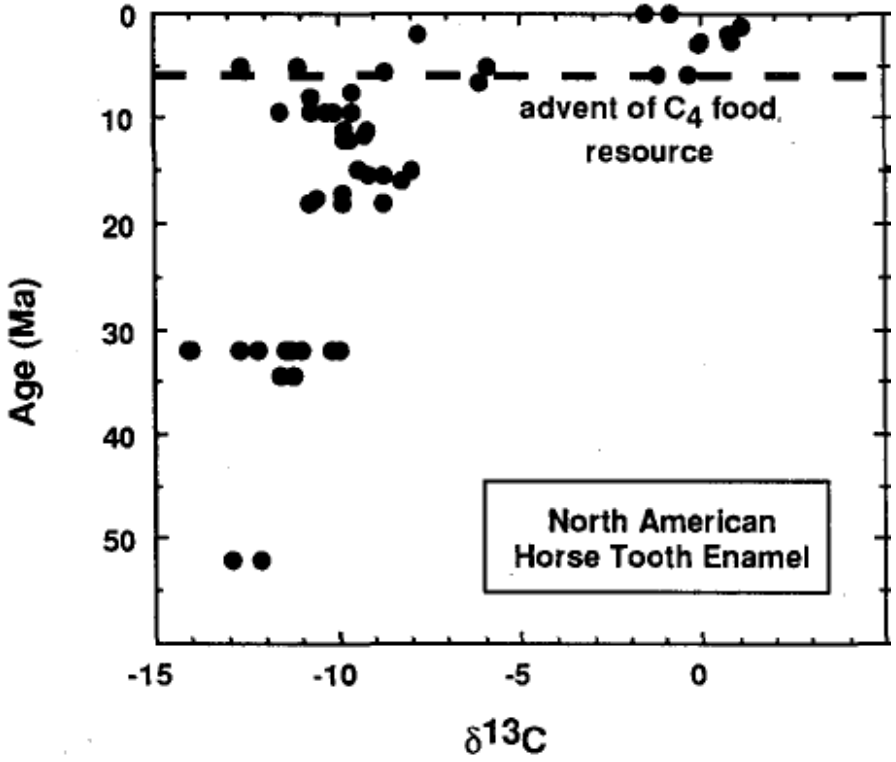

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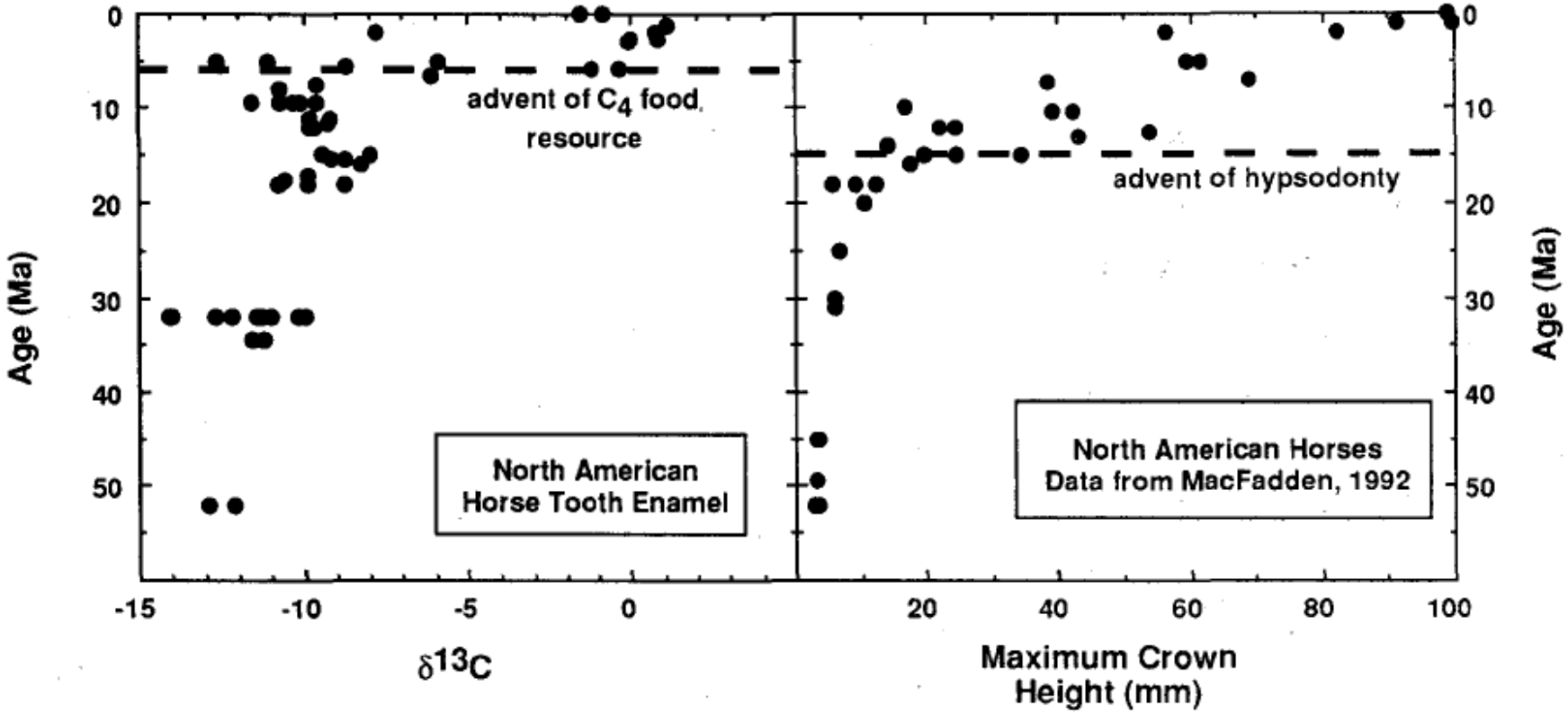

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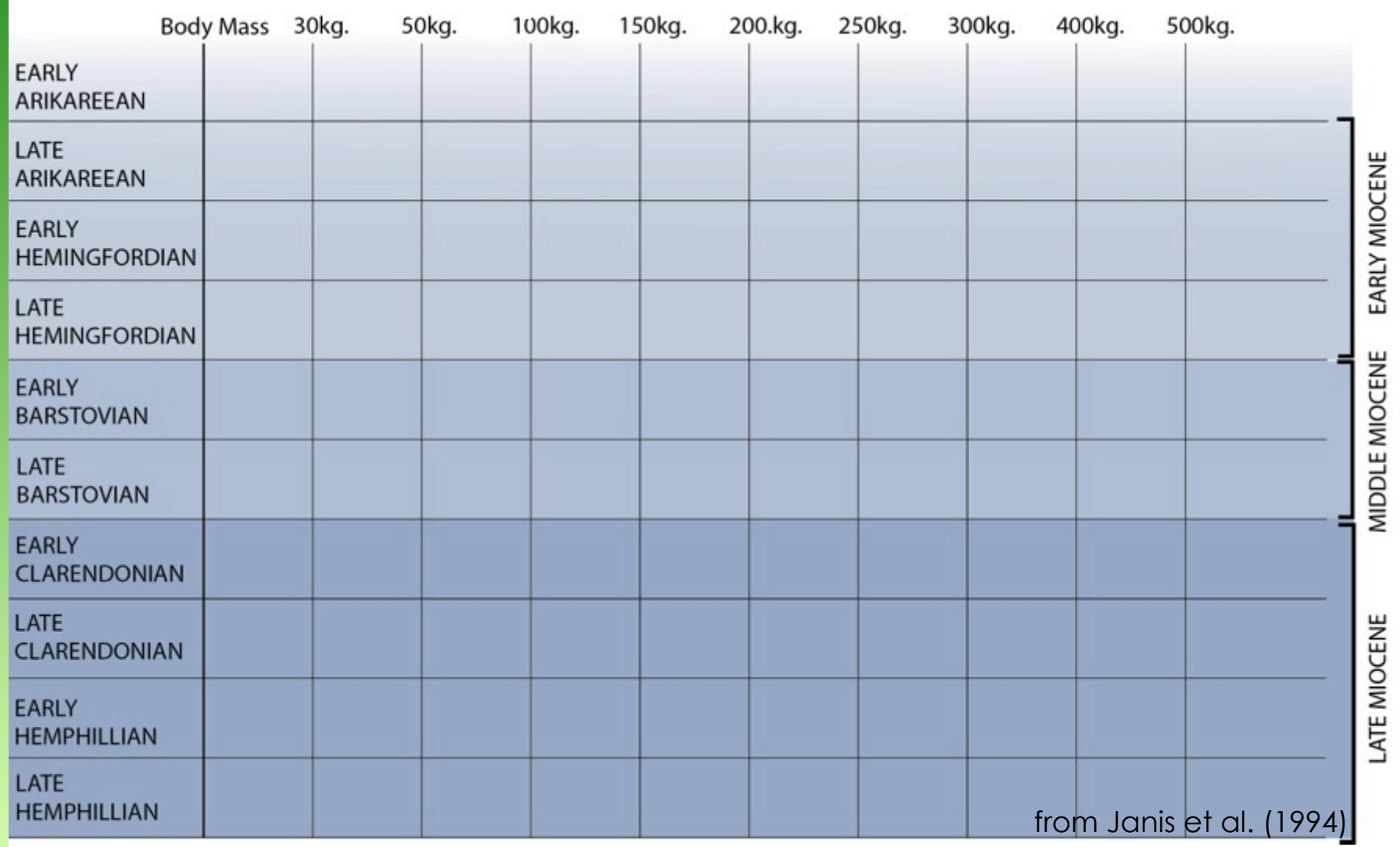

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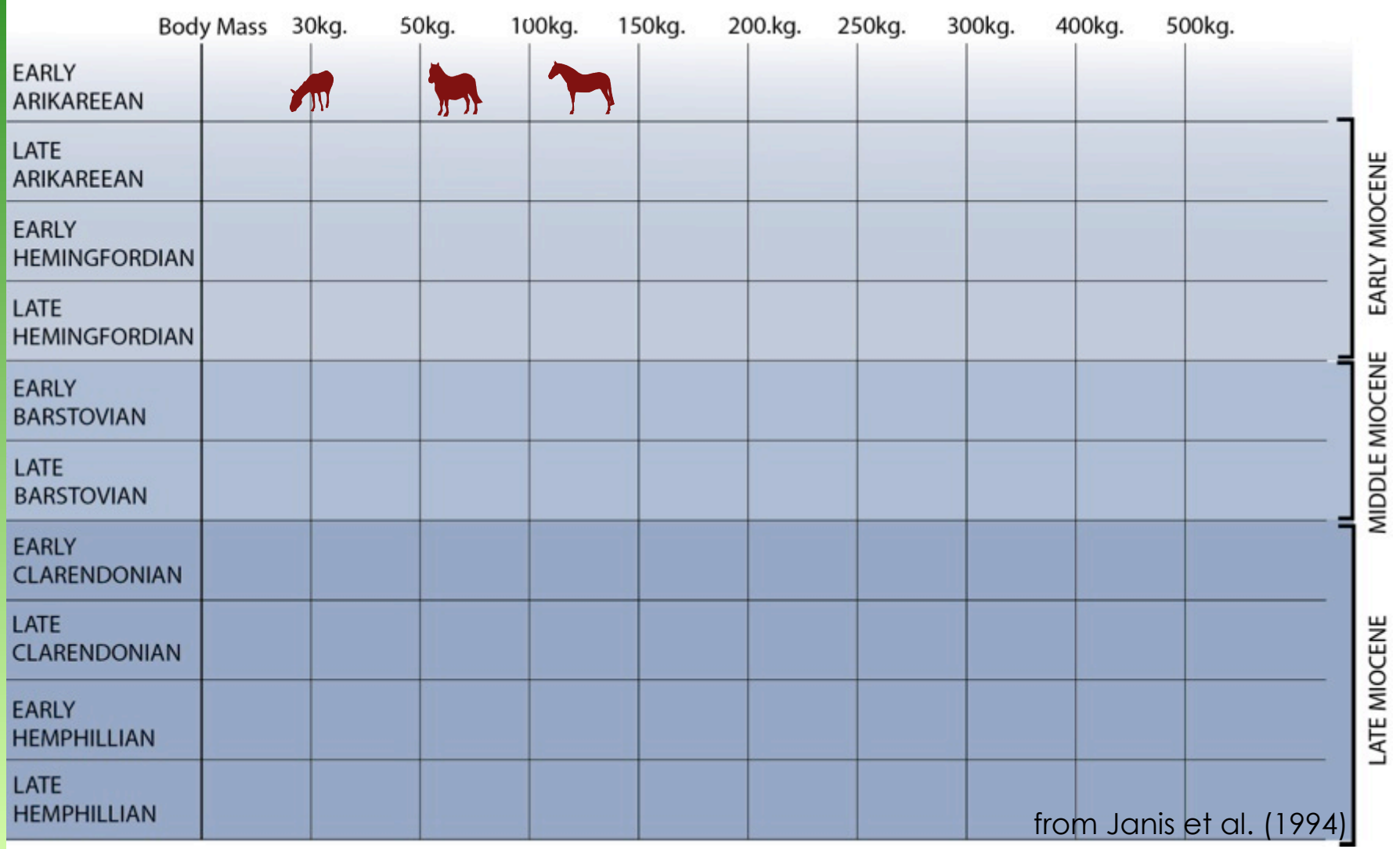

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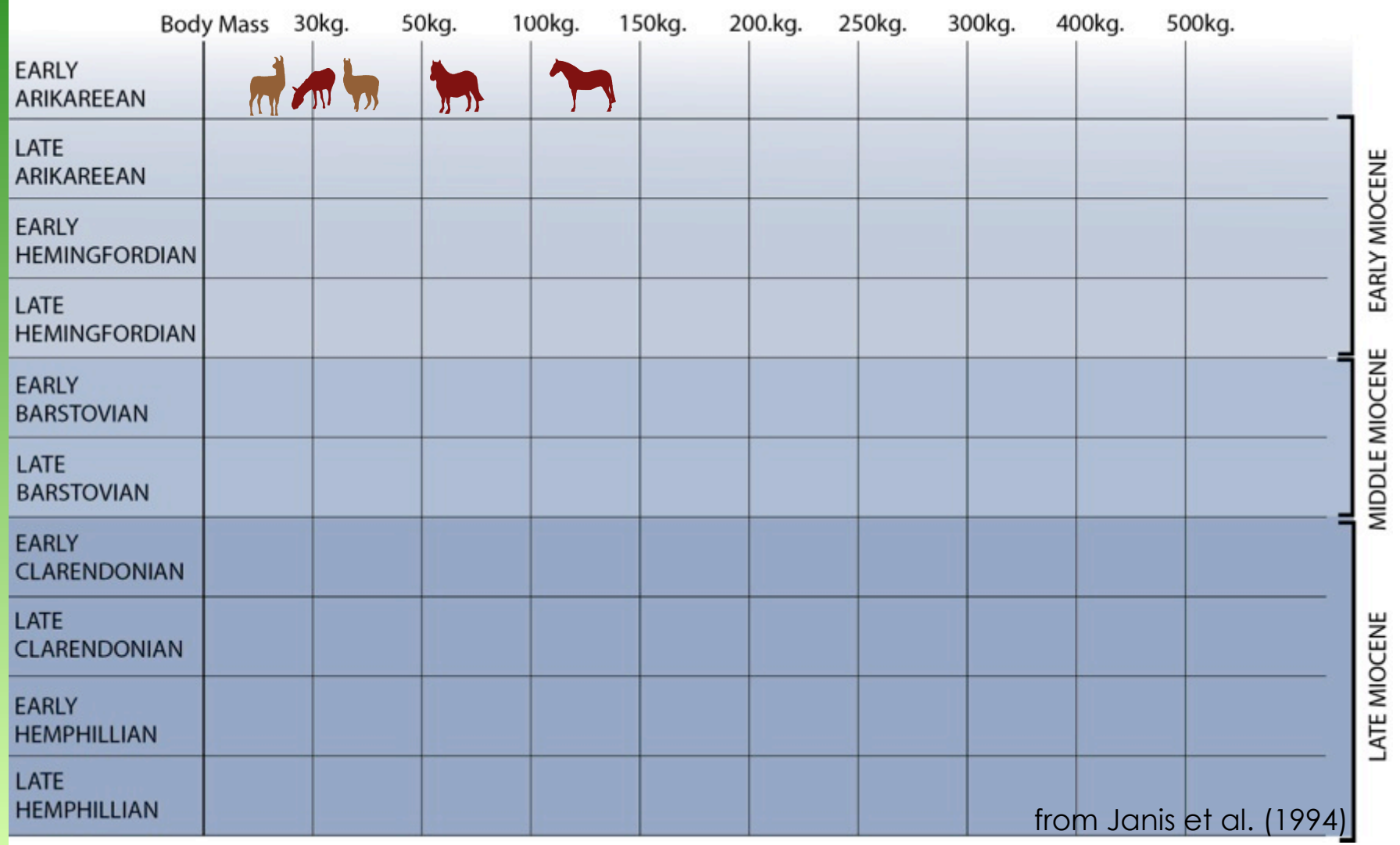

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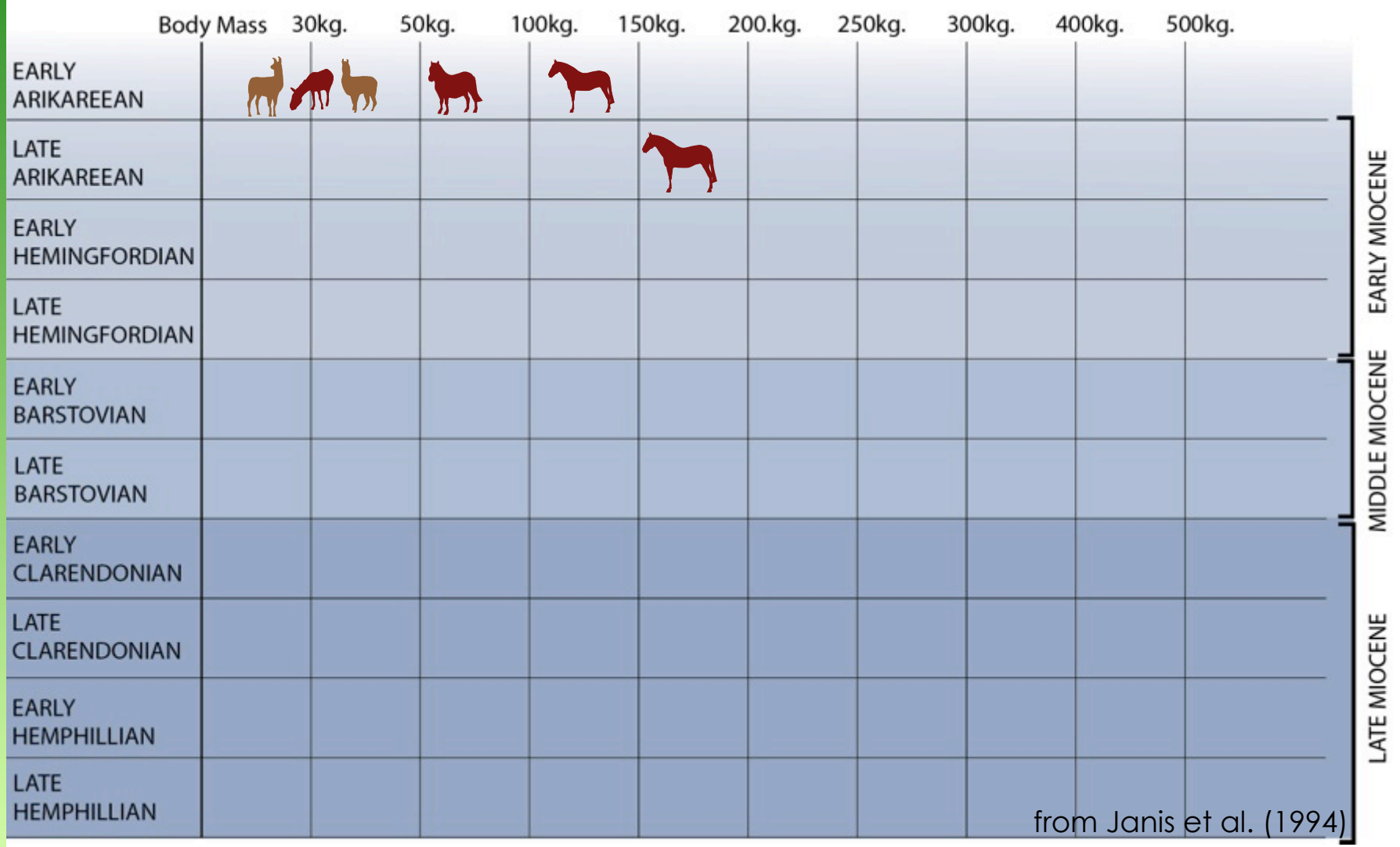

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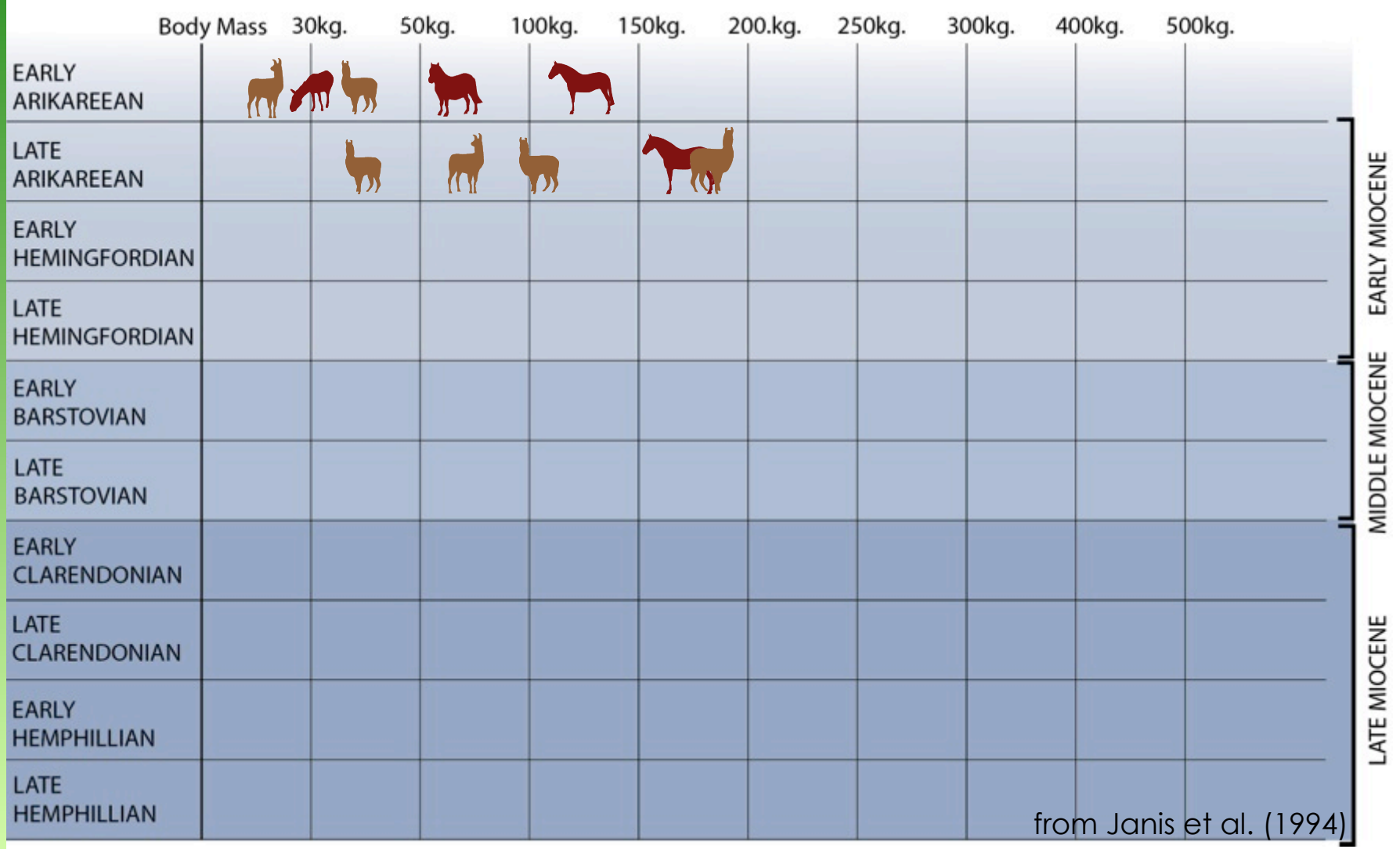

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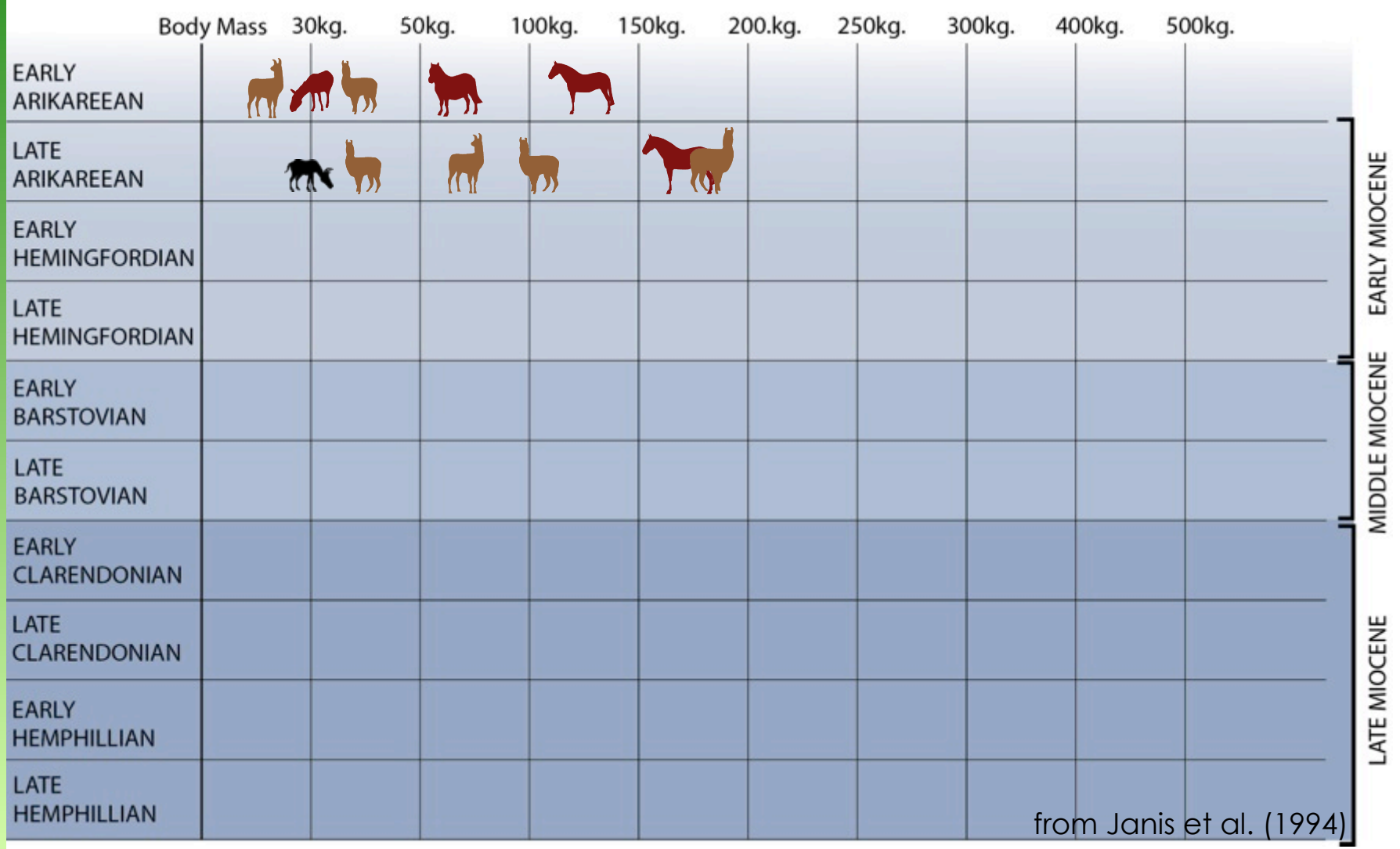

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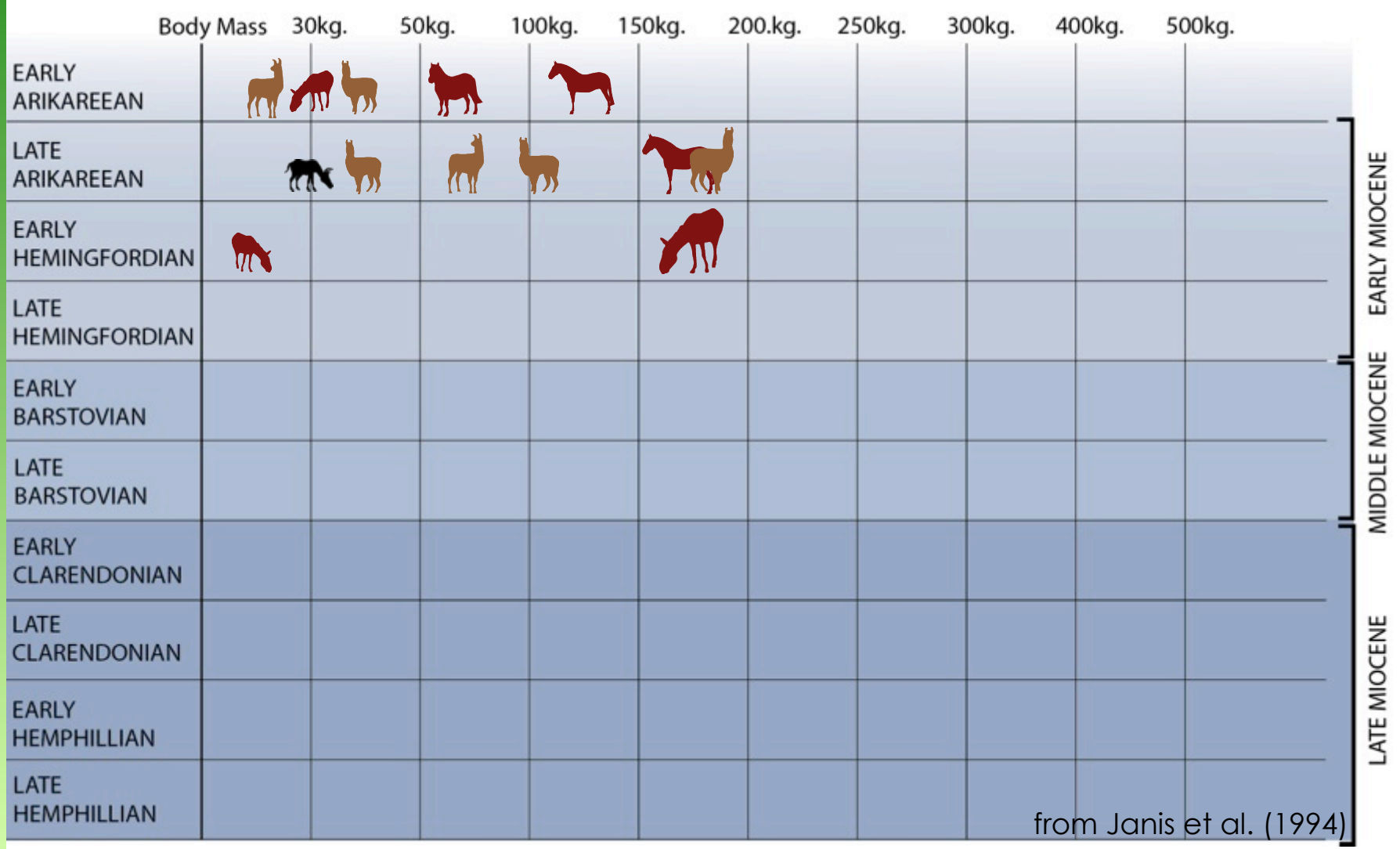

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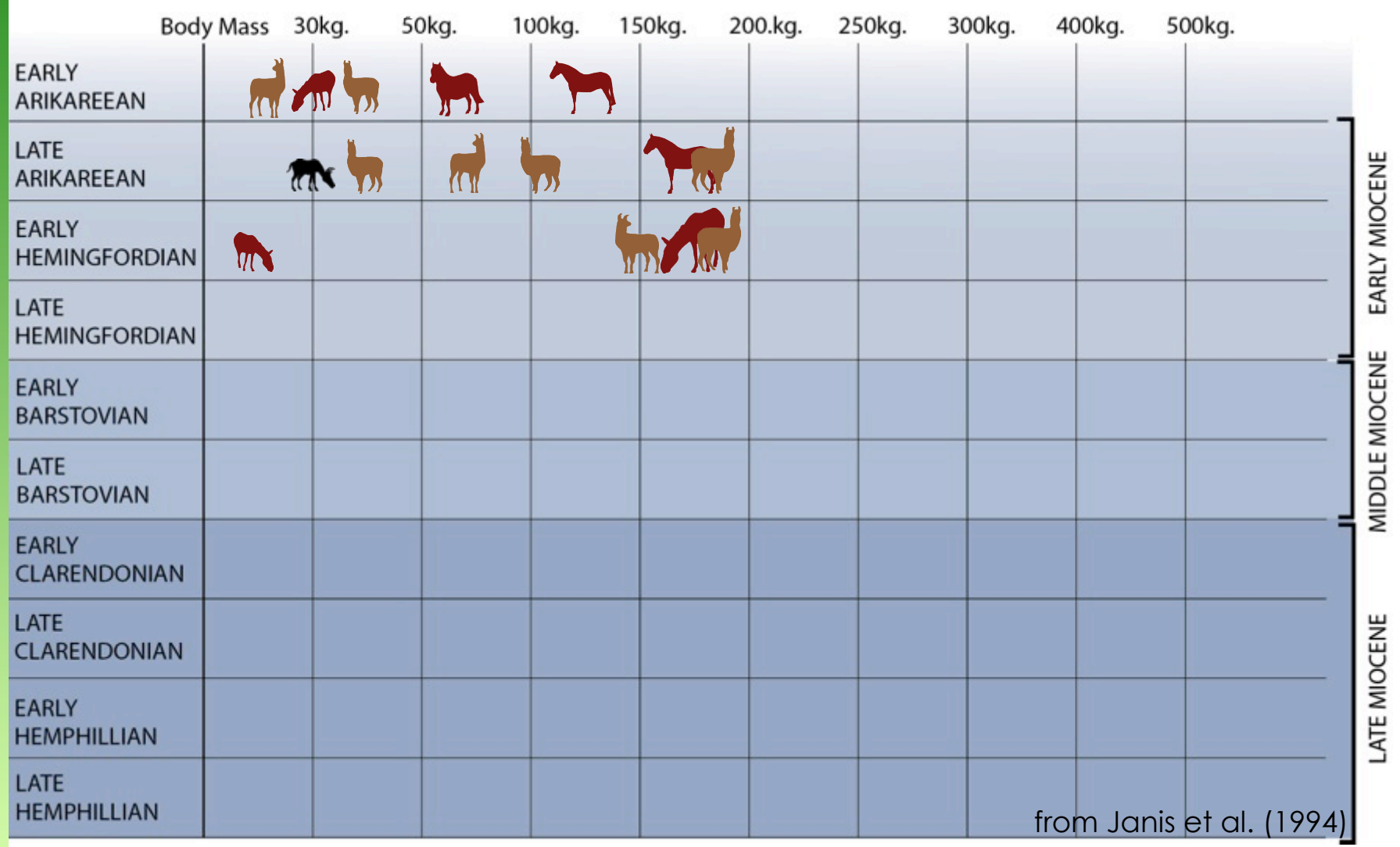

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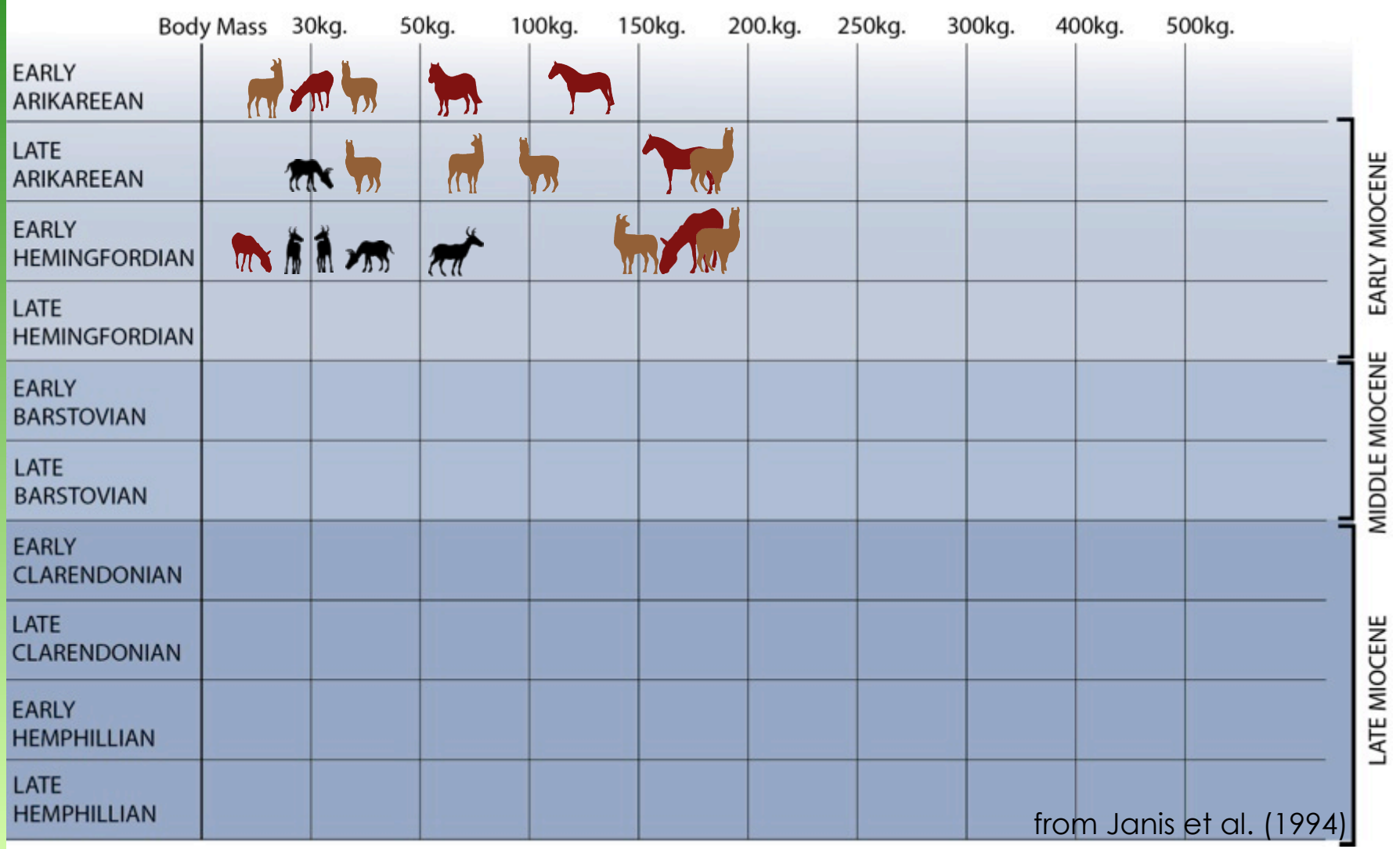

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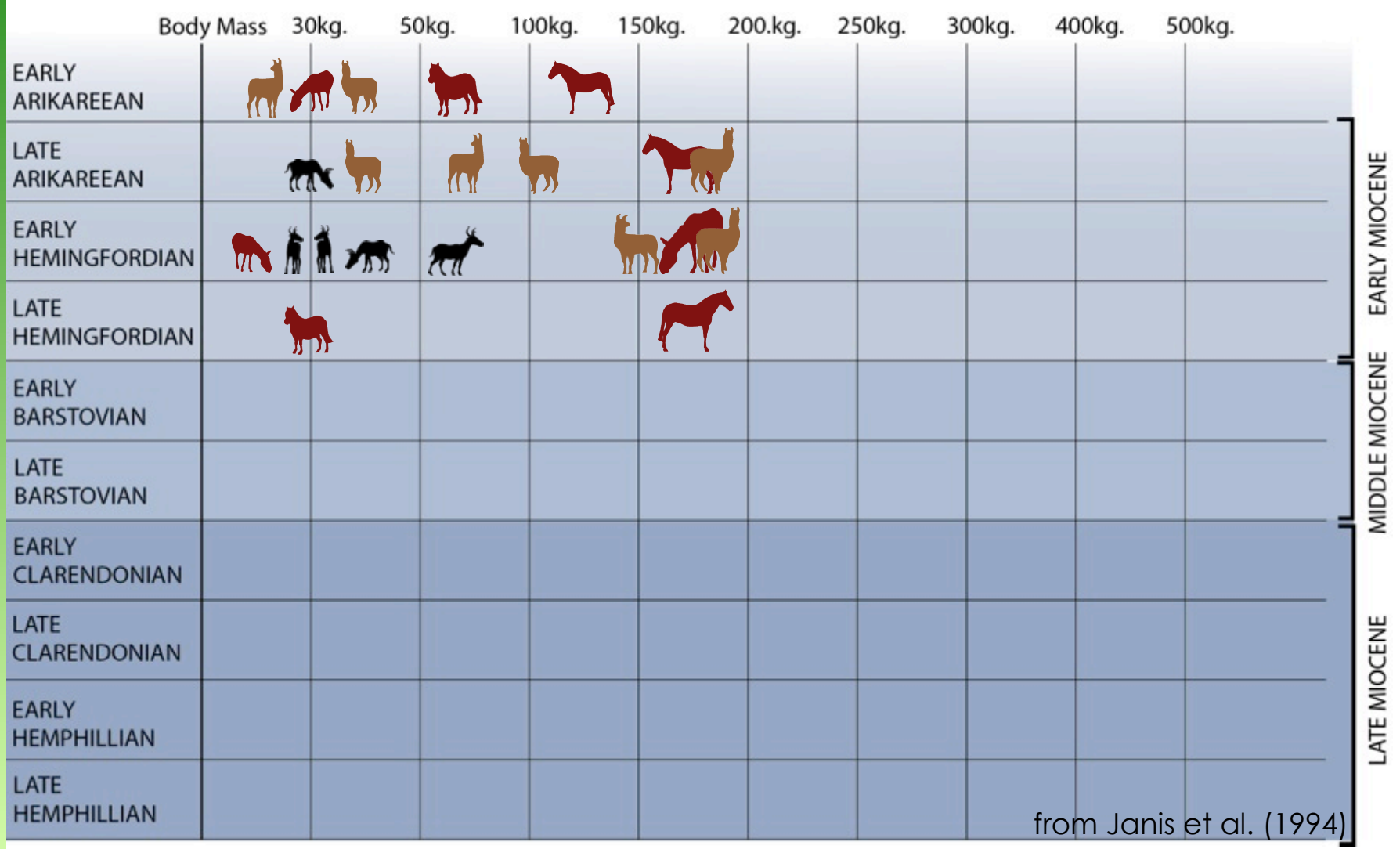

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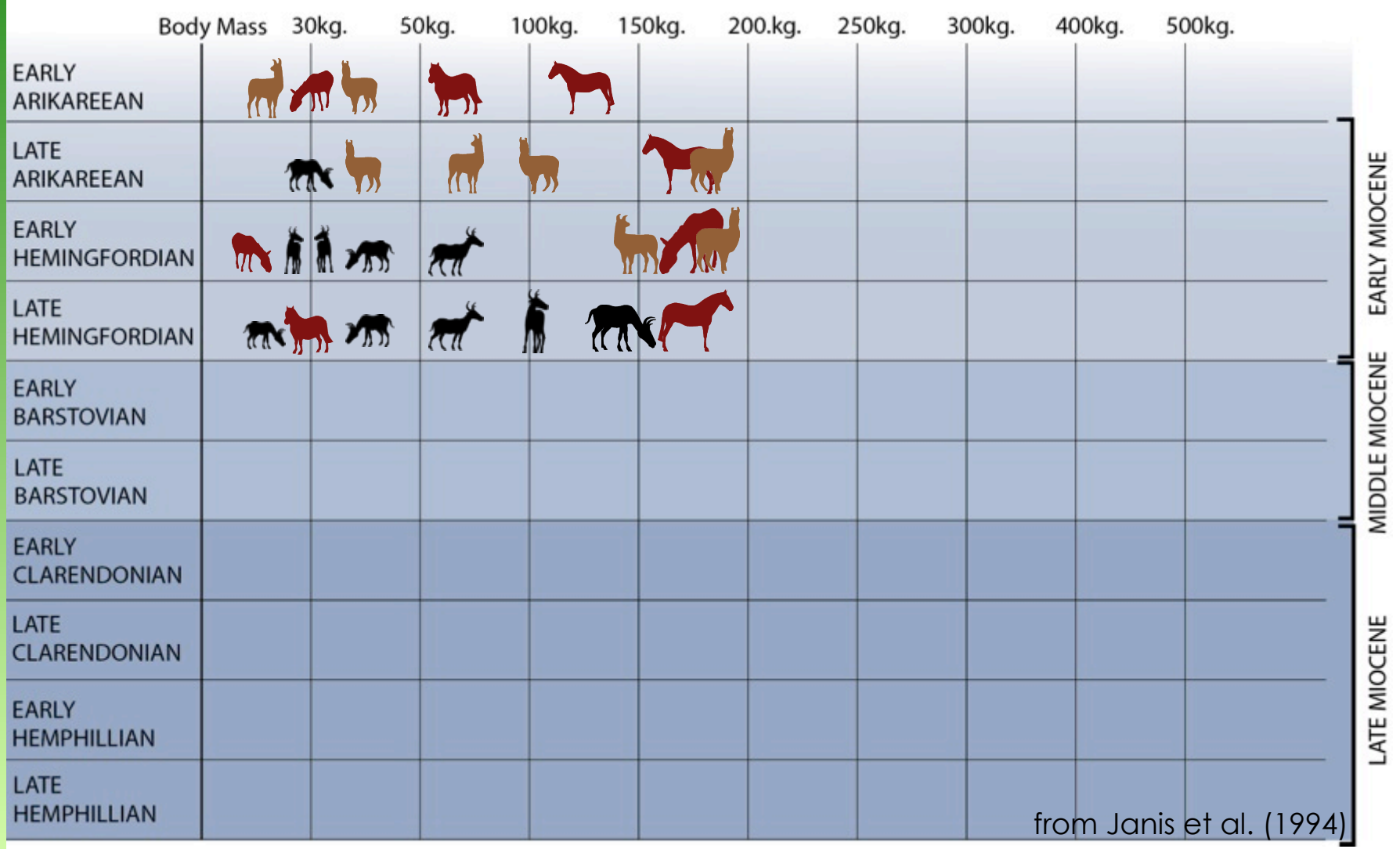

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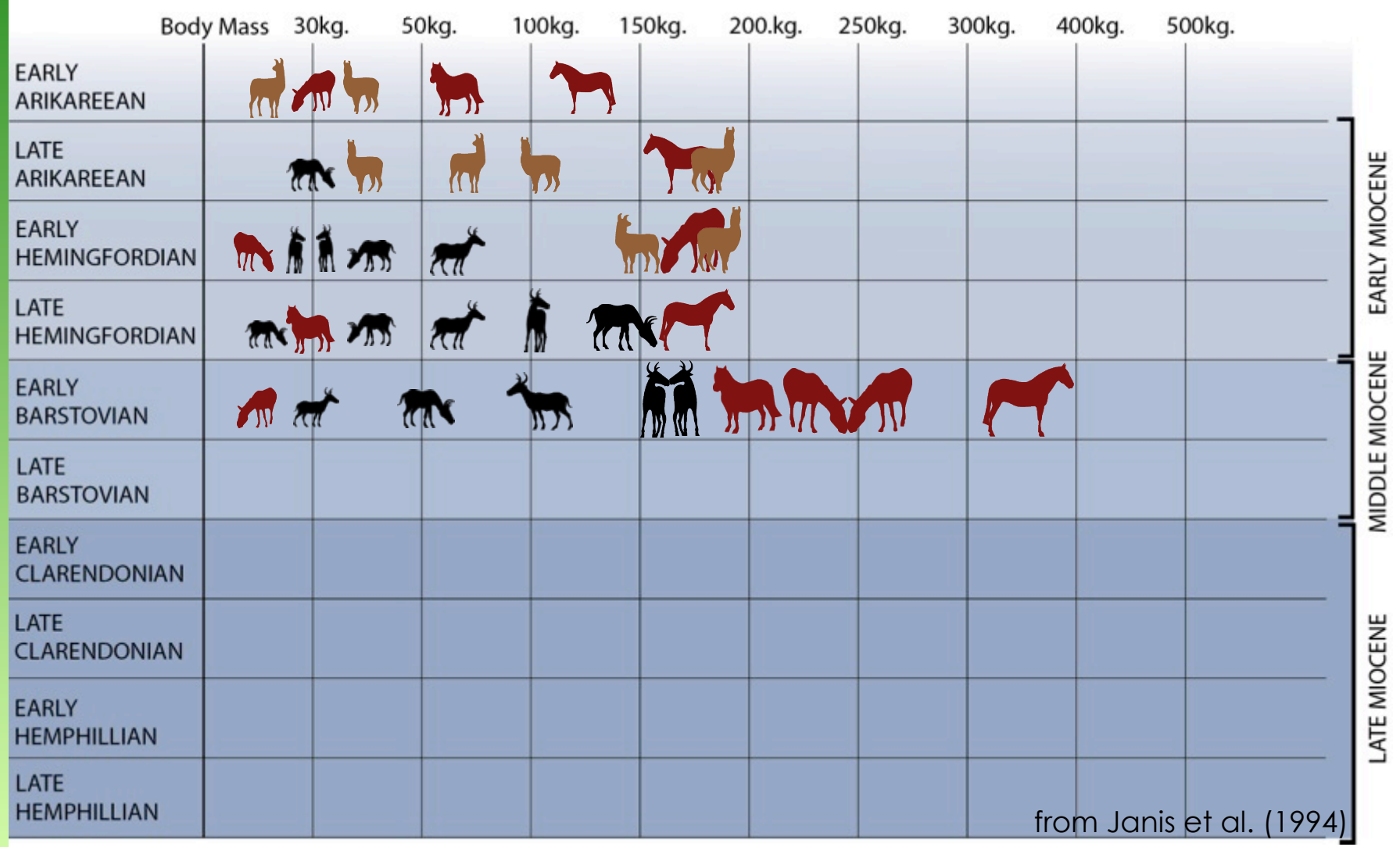

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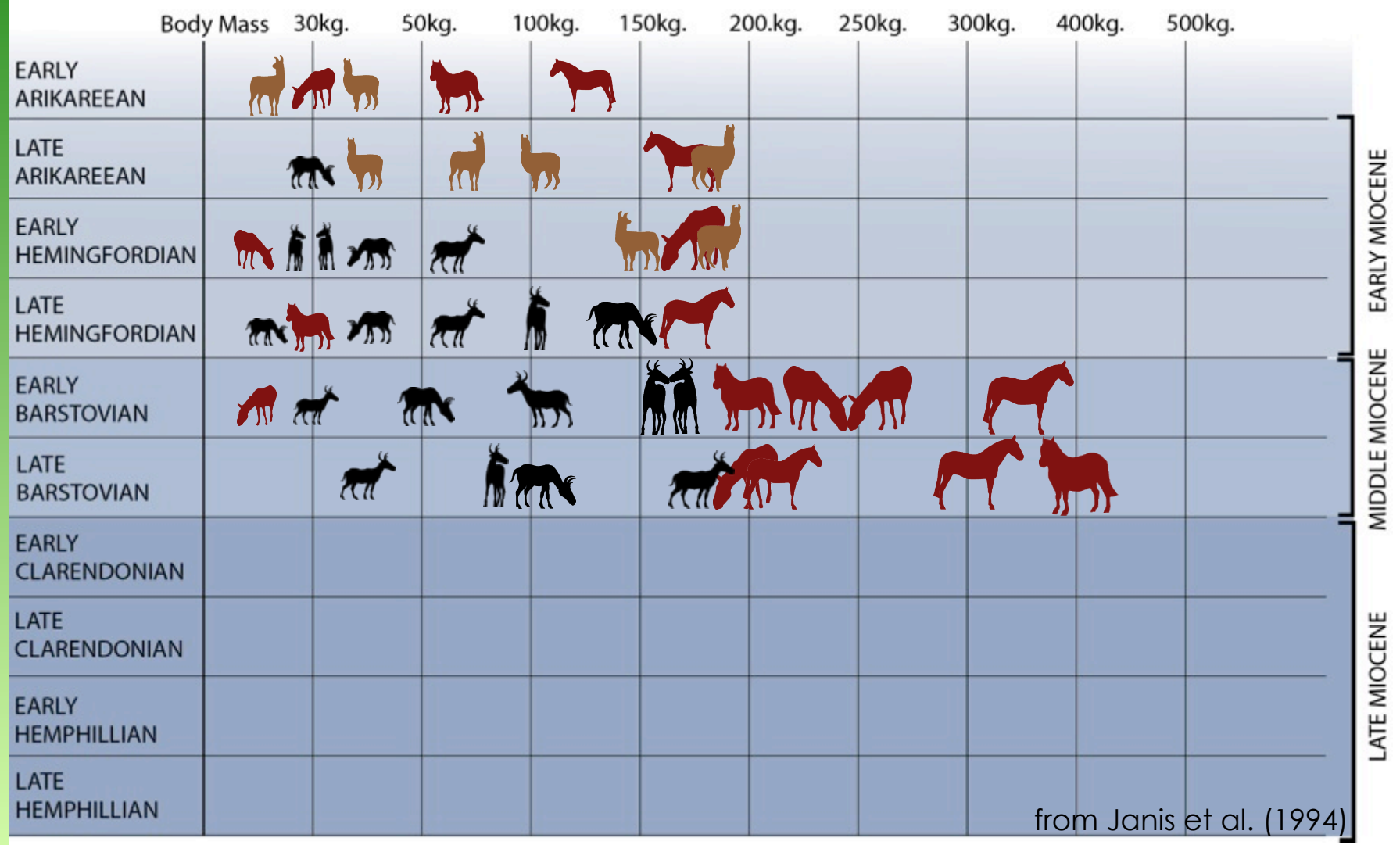

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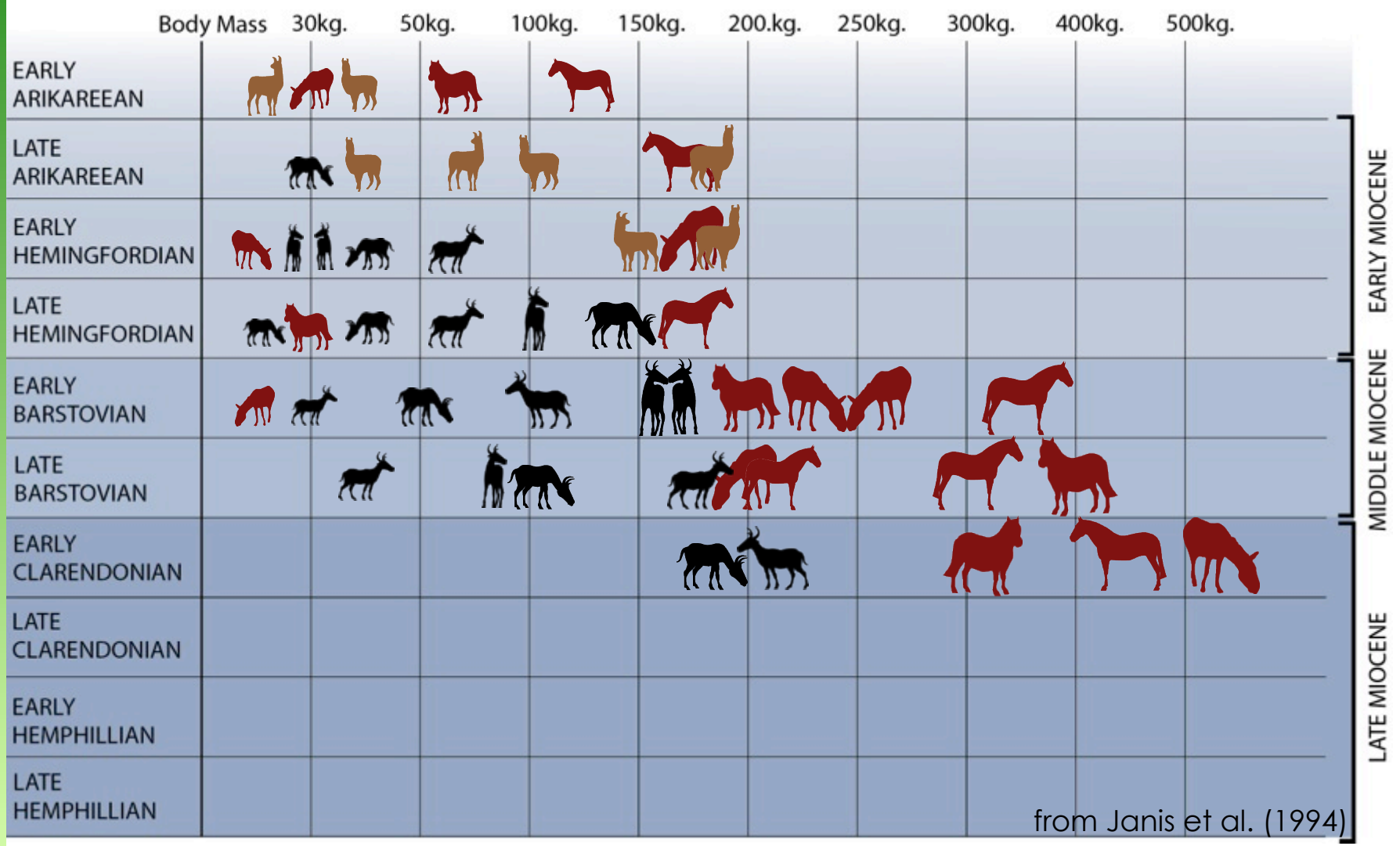

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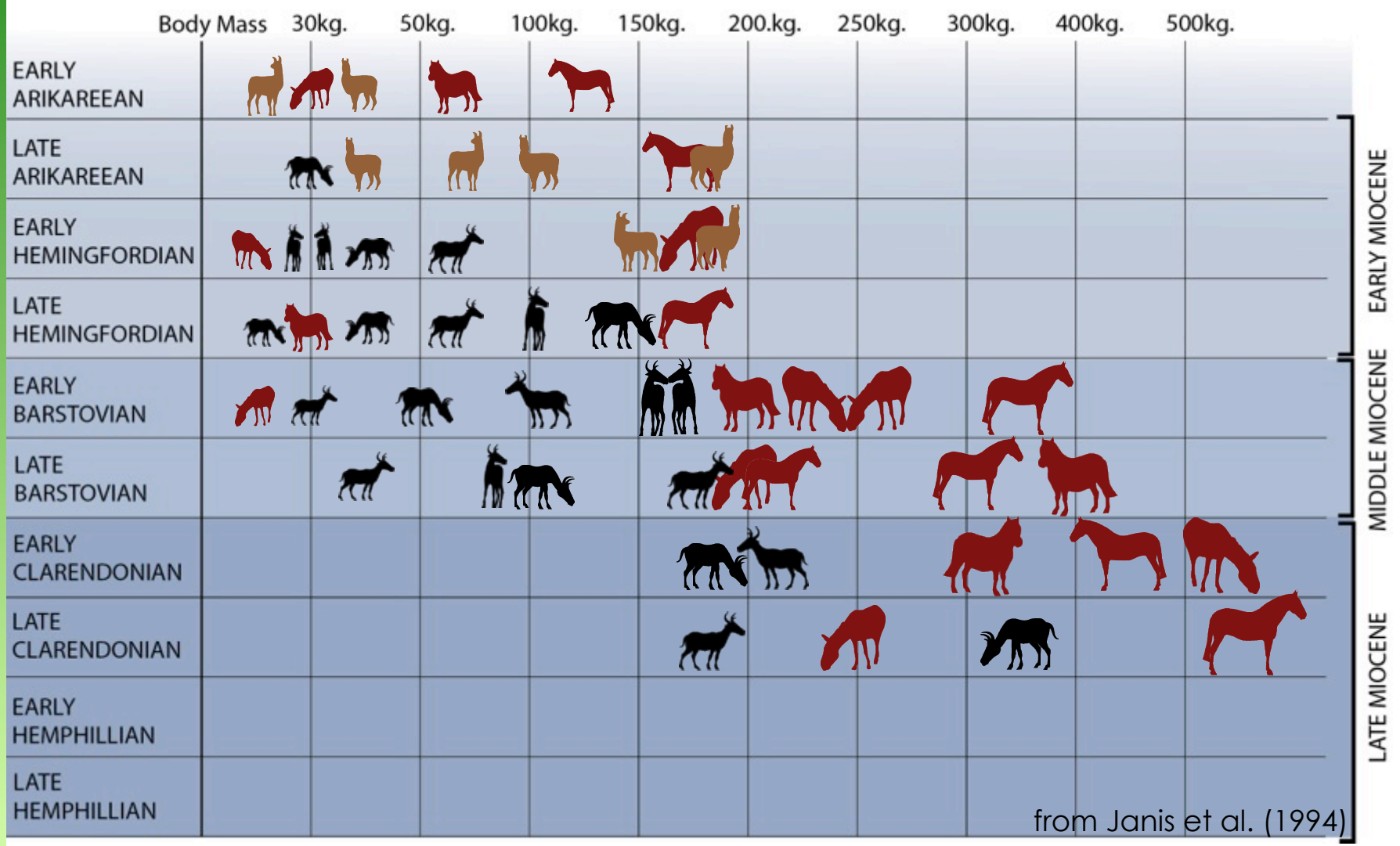

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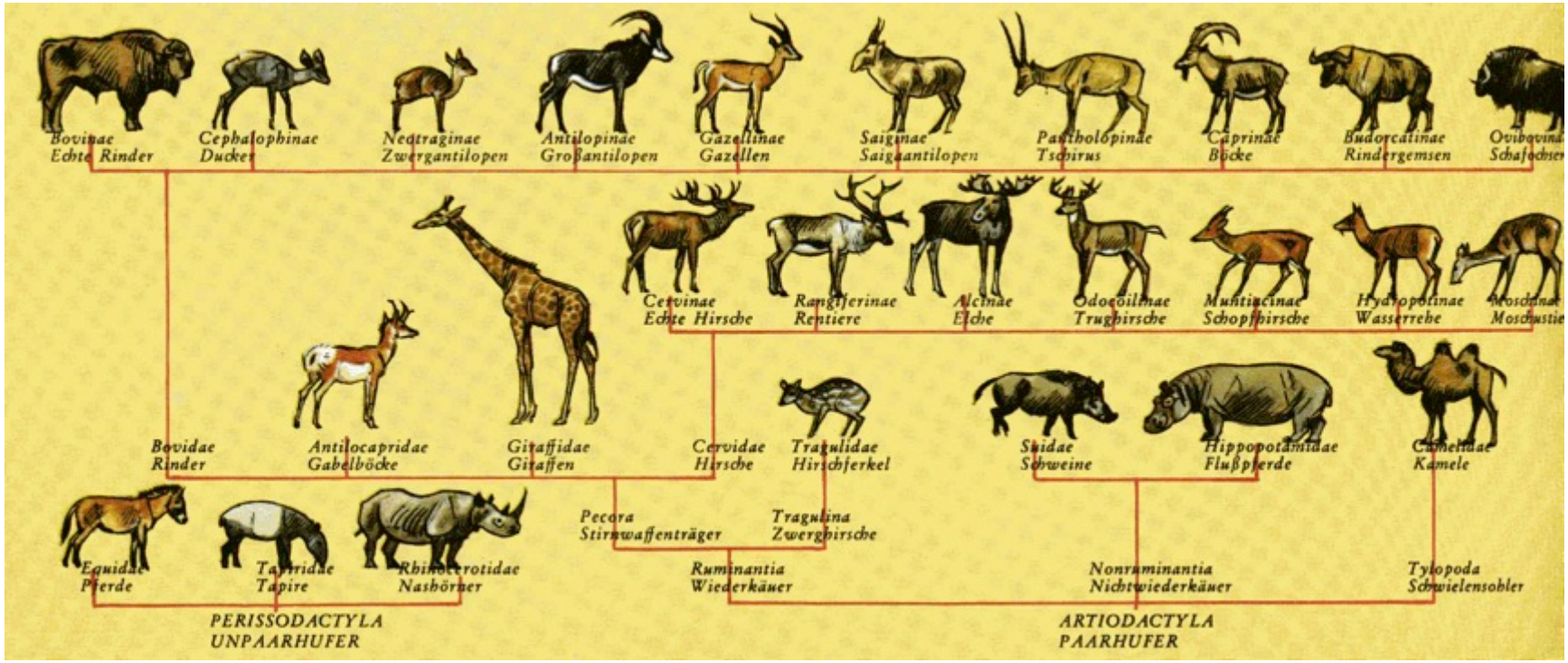
Large herbivore diversity: hoofed mammals



≈ 16 species

> 300 species

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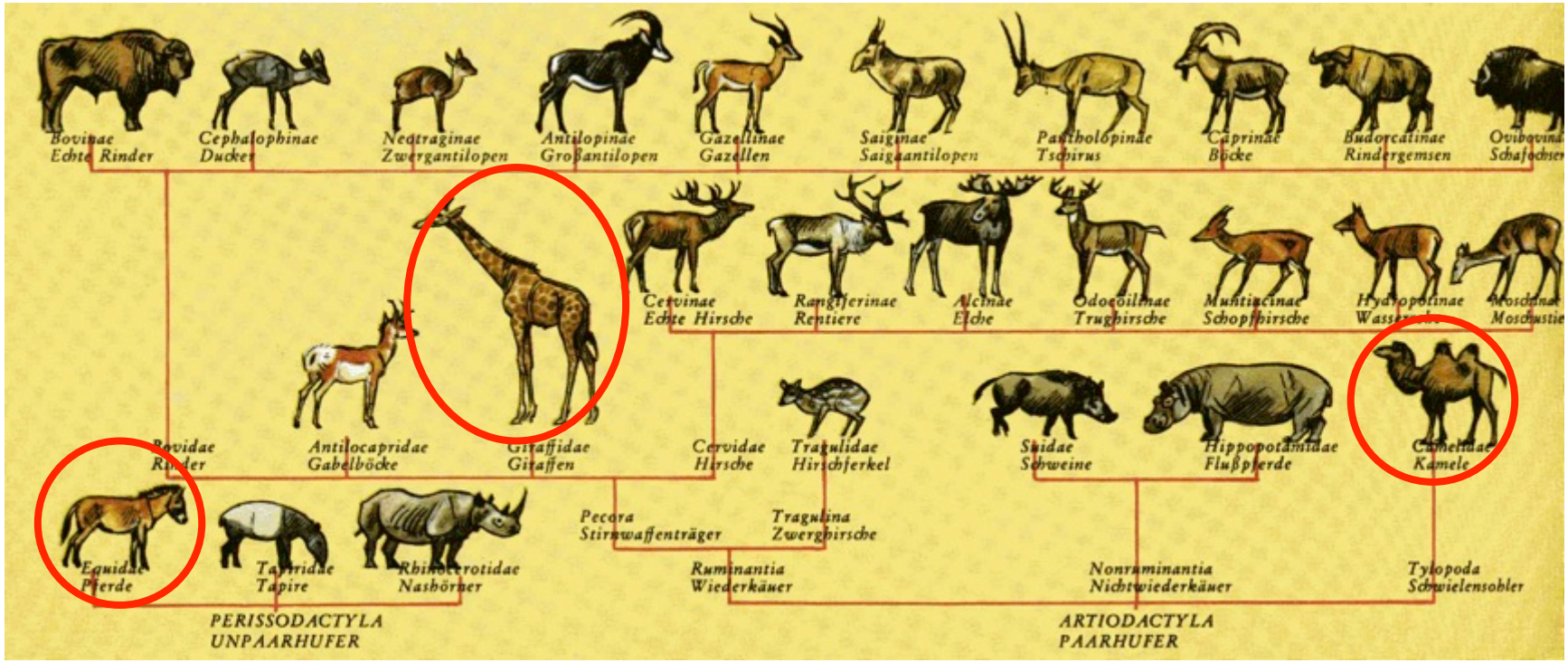

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Mammal gestation period

For any mammal, achieving the same degree of neonatal development in a shorter gestation period – if not associated with higher costs – should be advantageous (higher fecundity due to shorter generation times).

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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

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The difference cannot be due to body size!

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nearly extinct in a very limited geographical range

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only in extreme, resource-poor habitats

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rule the world !!

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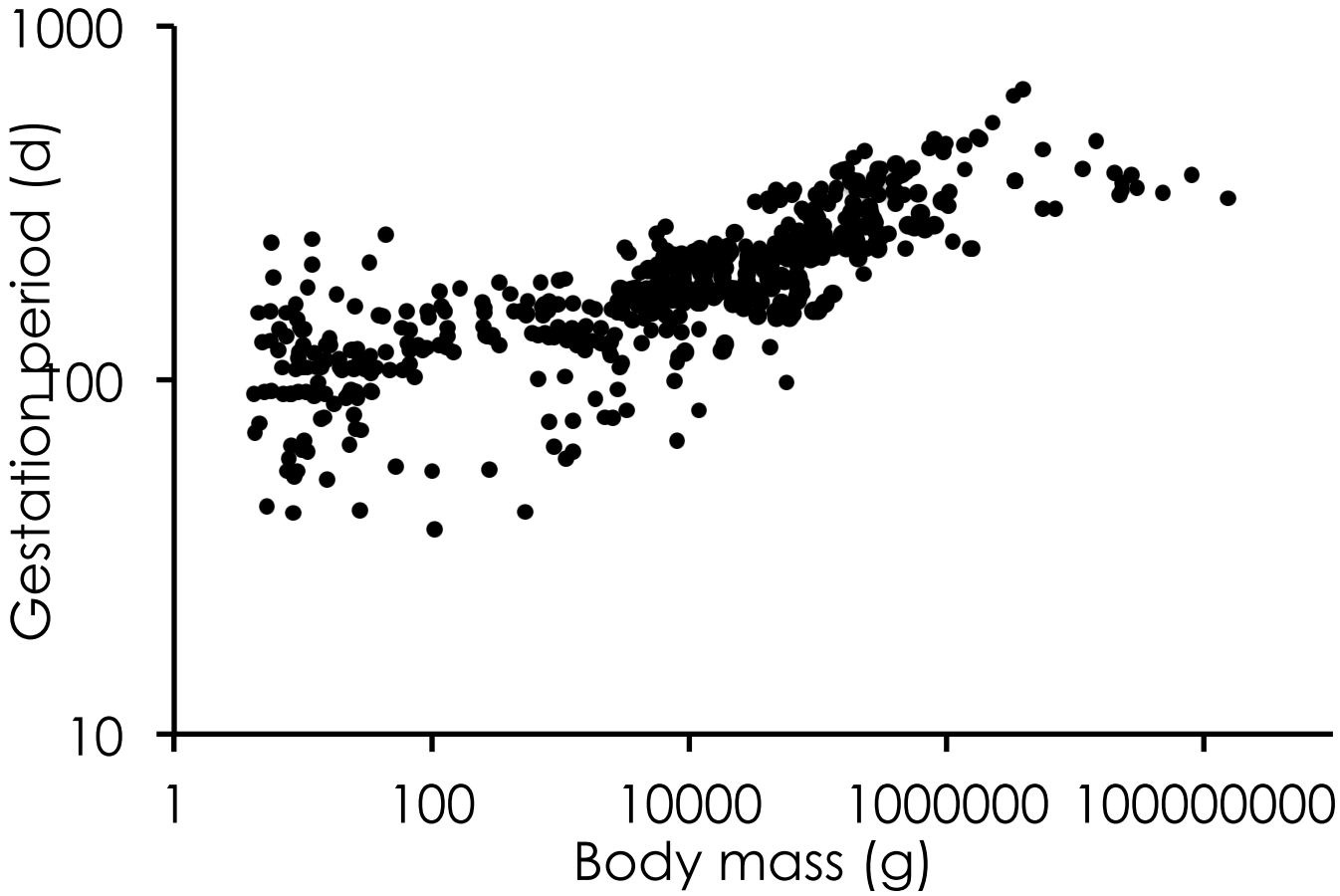
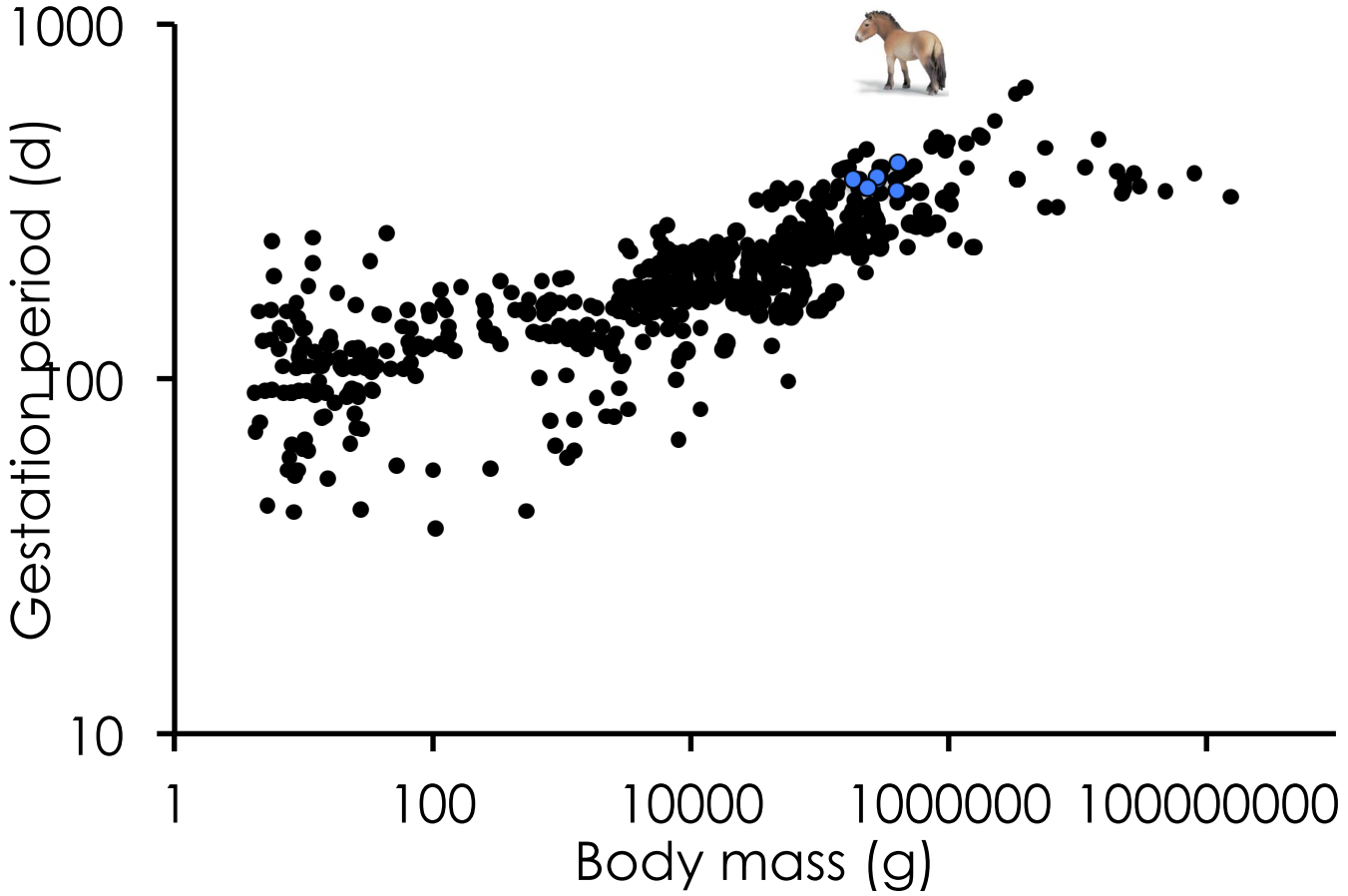
We would predict that animals with a shorter gestation period should be particularly 'successful' (e.g. in terms of species diversity).

(Precocial) Mammal gestation period



from Clauss et al. (2013)

(Precocial) Mammal gestation period



from Clauss et al. (2013)

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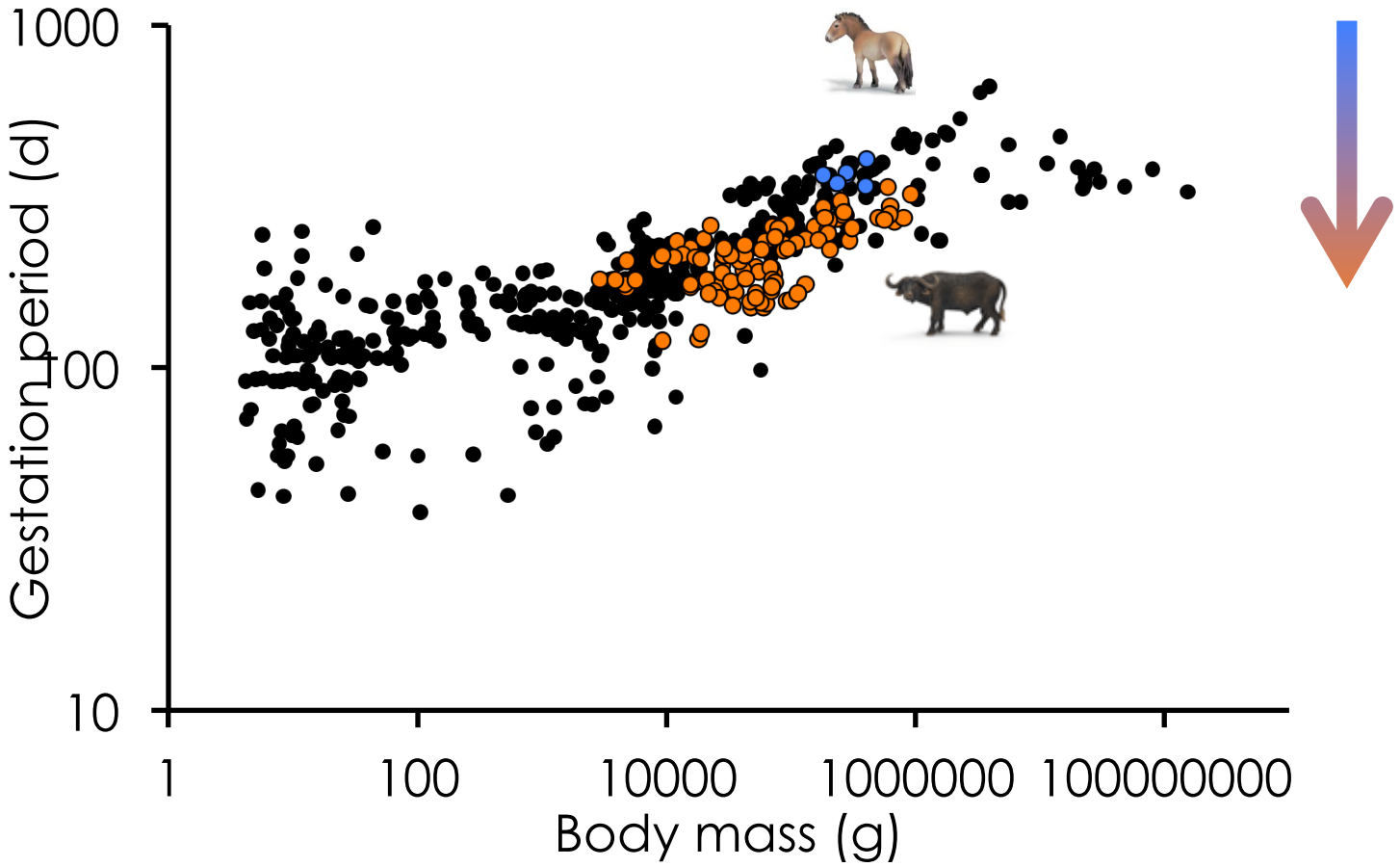

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Mammal chewing efficiency

For any herbivore, increasing chewing efficiency – if not associated with higher costs – should be advantageous (higher feeding efficiency due to higher digestibility) because there is …

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Evidence for a tradeoff between retention time and chewing efficiency in large mammalian herbivores

Marcus Clauss [a,*], Charles Nunn [b,c], Julia Fritz [d], Jürgen Hummel [e]

Comparative Biochemistry and Physiology, Part A 154 (2009) 376–382

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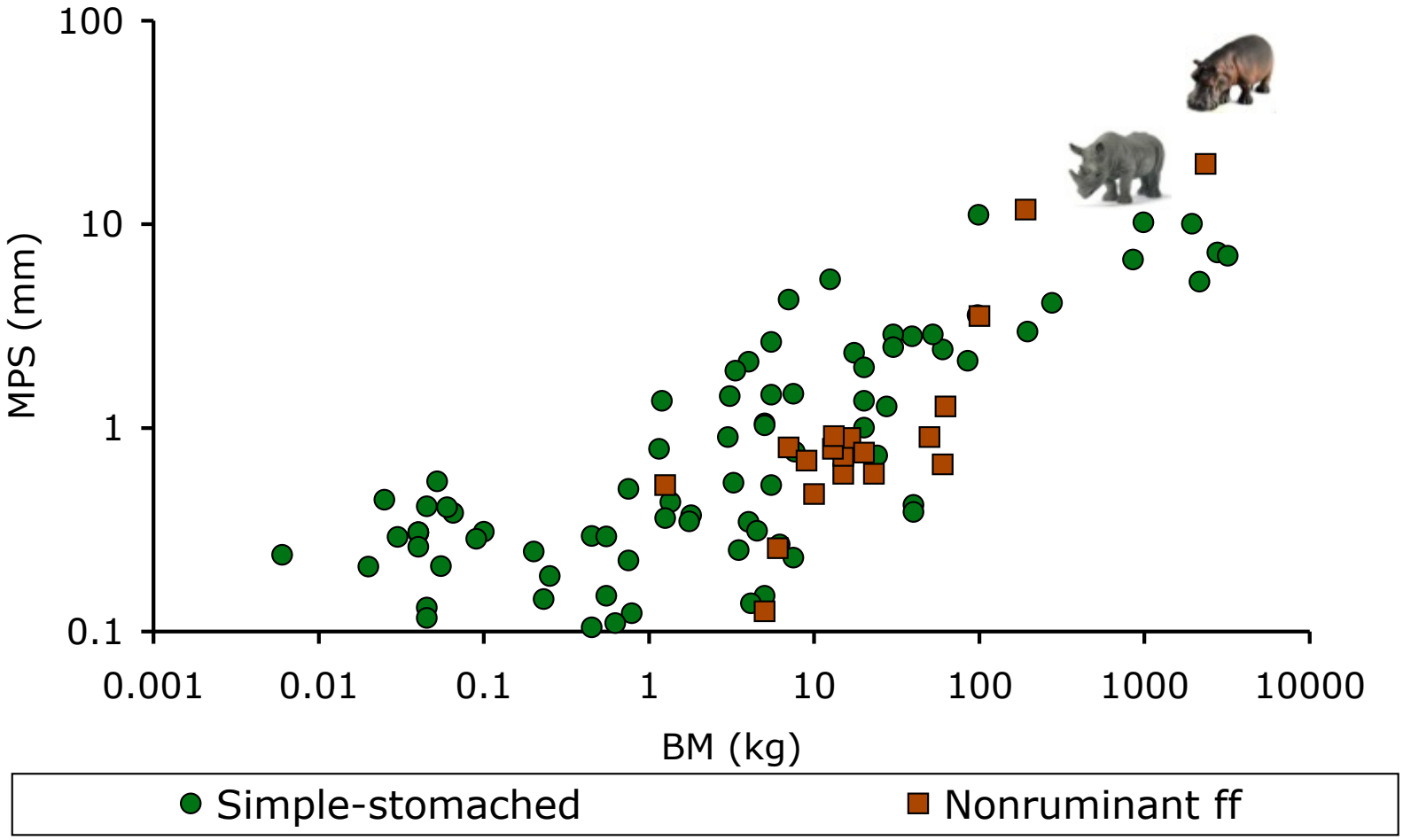
More efficient mastication allows increasing intake without compromising digestibility or necessitating a larger gut: Comparative feeding trials in banteng (*Bos javanicus*) and pygmy hippopotamus (*Hexaprotodon liberiensis*)

Angela Schwarm [a,b,*], Sylvia Ortmann [a], Christian Wolf [c], W. Jürgen Streich [a], Marcus Clauss [d]

Comparative Biochemistry and Physiology, Part A 152 (2009) 504–512

Mammal chewing efficiency



from Fritz et al. (2009)

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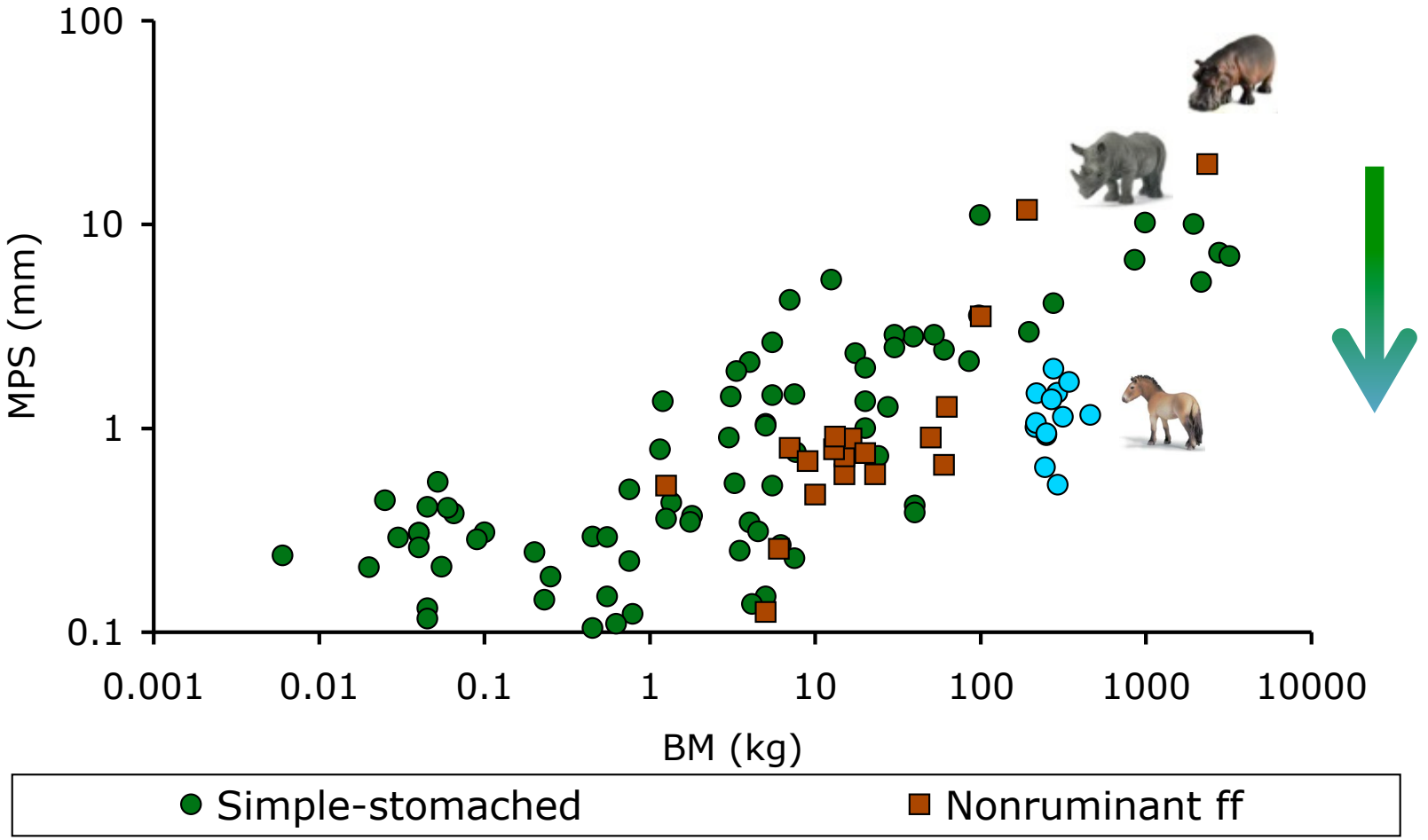

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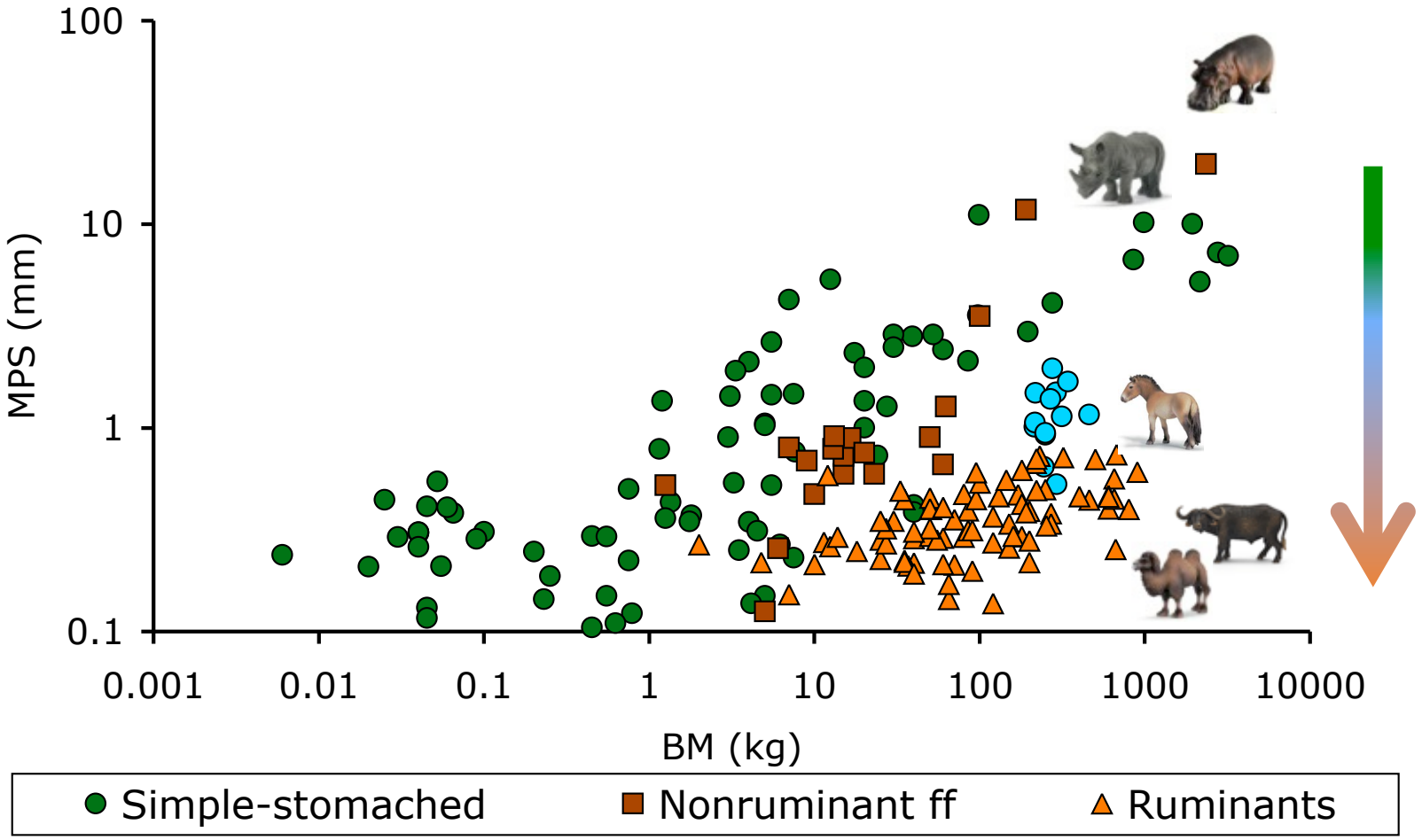
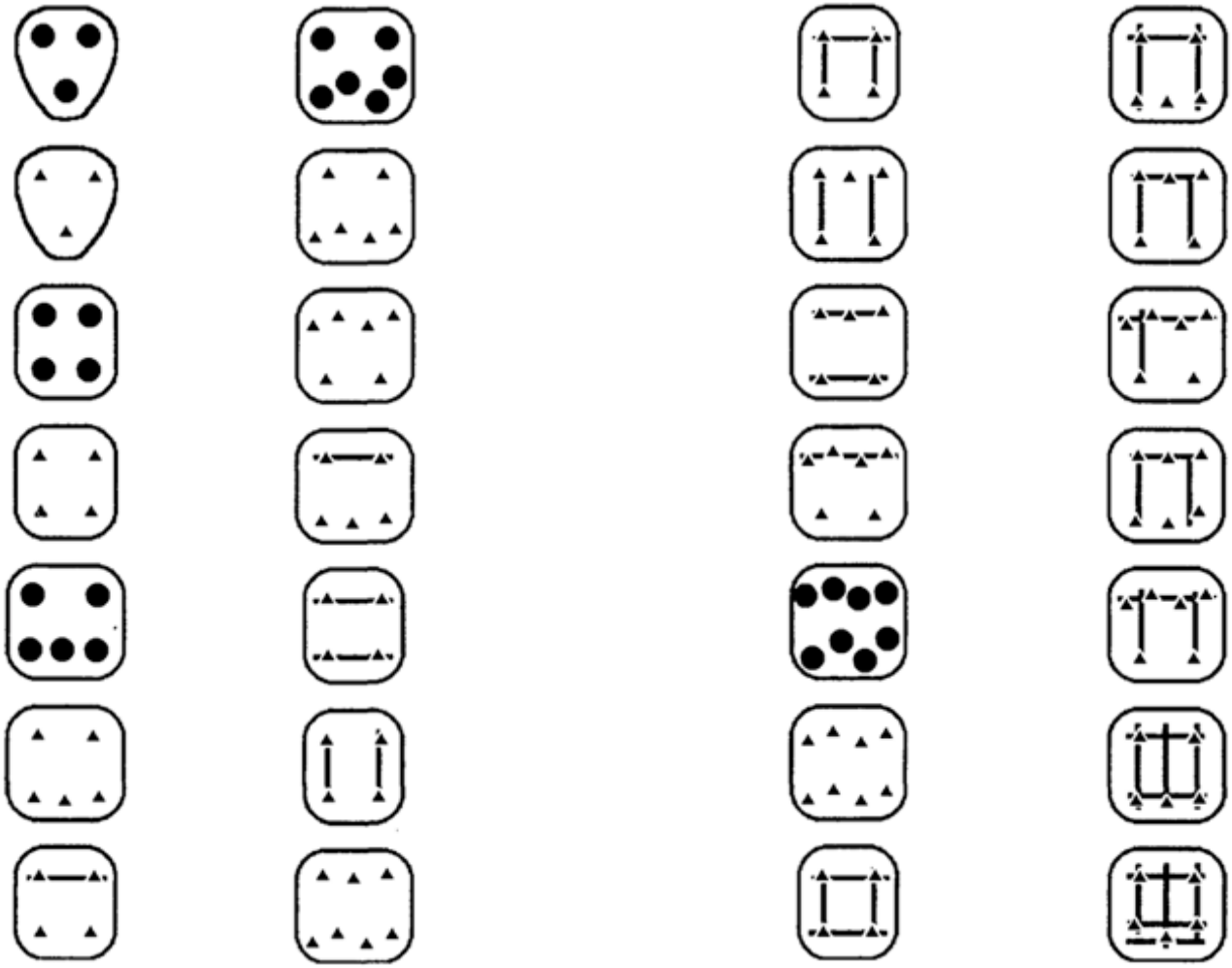


from Fritz et al. (2009)

Large mammal molar surfaces



from Jernvall et al. (1996)

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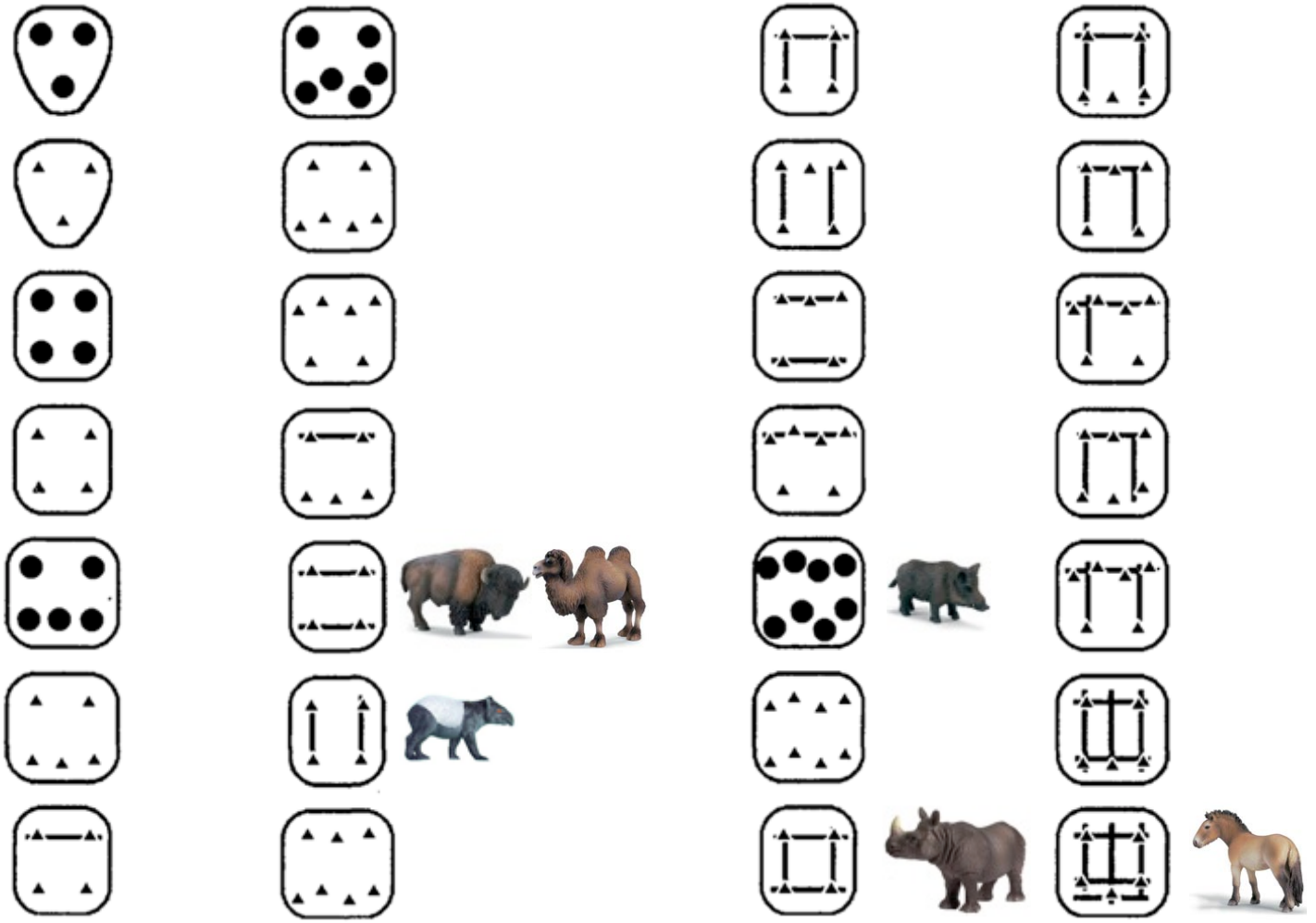

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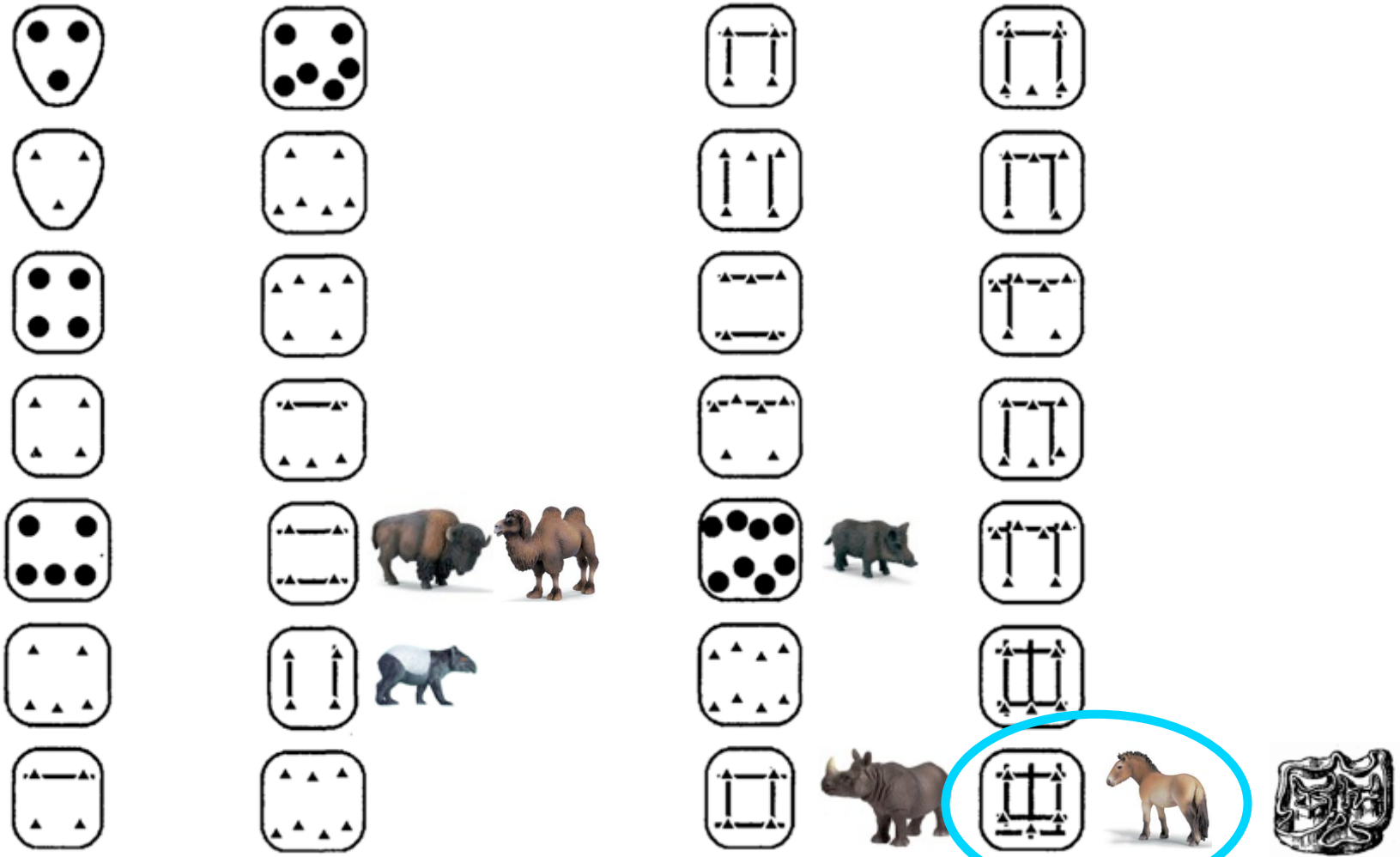

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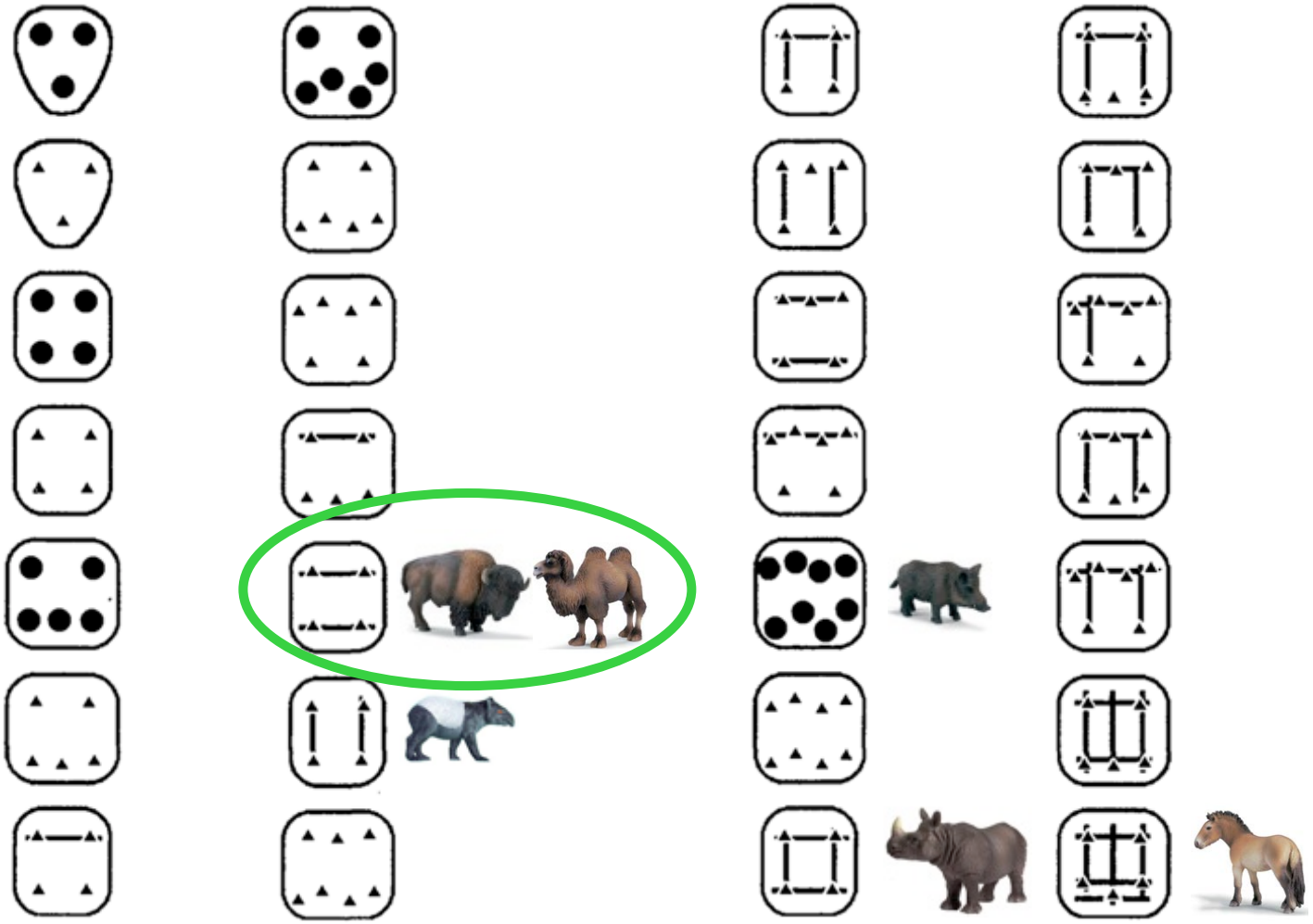
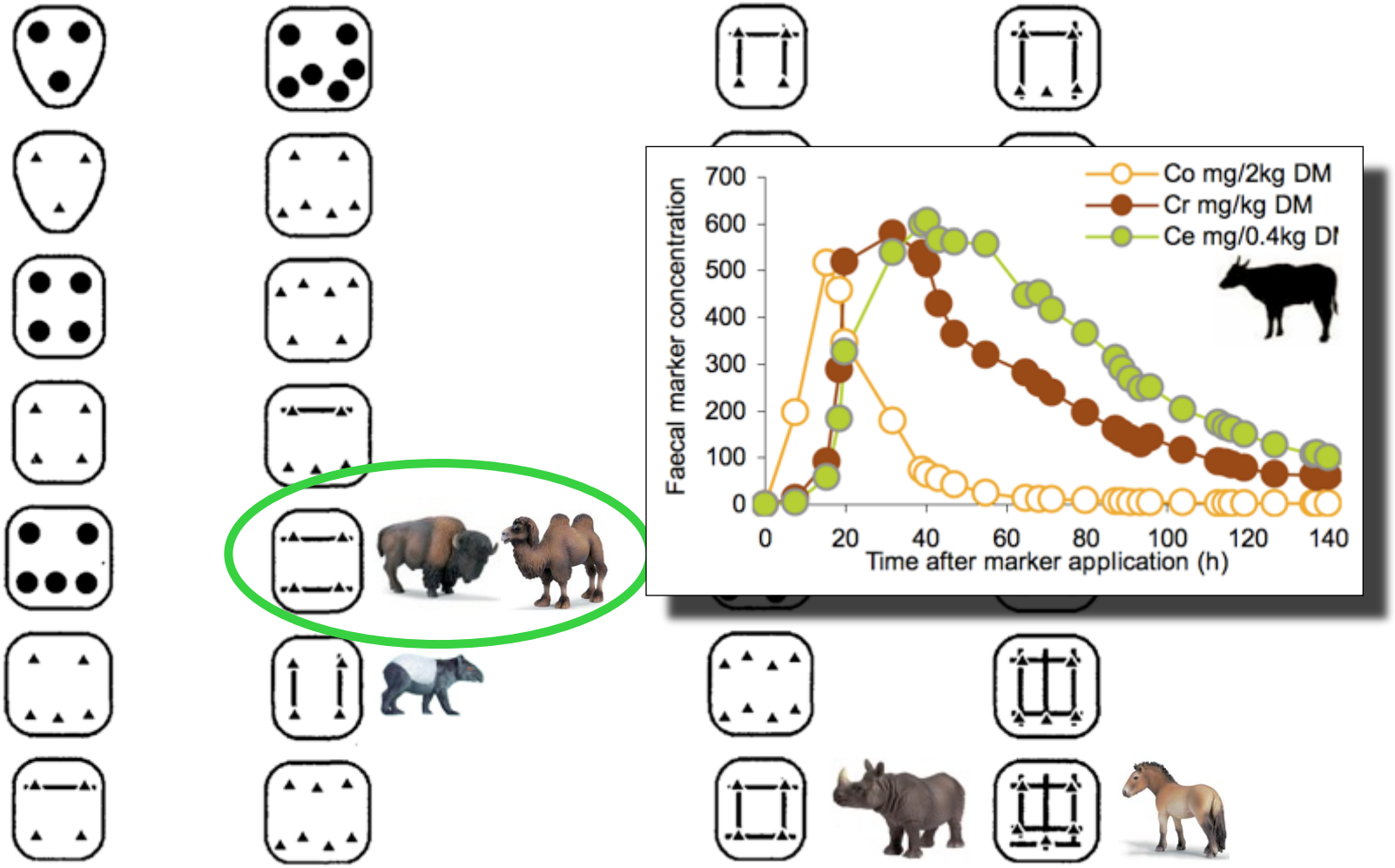


from Jernvall et al. (1996),
Schwarm et al. (2008)

Ruminant sorting mechanism



from Jernvall et al. (1996), Schwarm et al. (2008)

Parallel evolution?

Perissodactyls

Artiodactyls

Parallel evolution?

among

Perissodactyls

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Parallel evolution?

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Equids

Ruminants

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achieve

comparatively high
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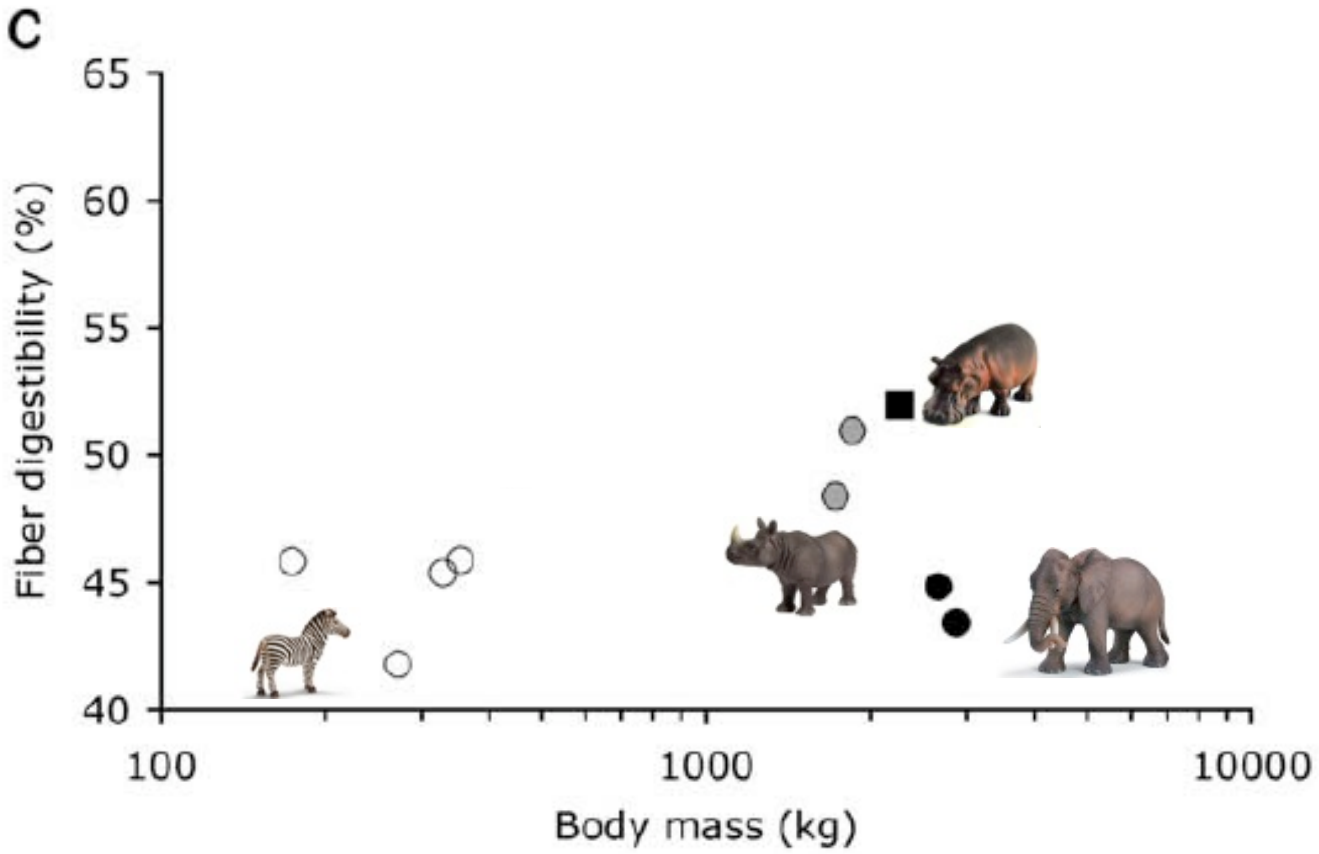
and food intakes

but …

Advantage ruminants?

Due to their superior chewing efficiency, ruminants achieve higher digestibilities ...



from Clauss et al. (2009; data from Foose 1982)

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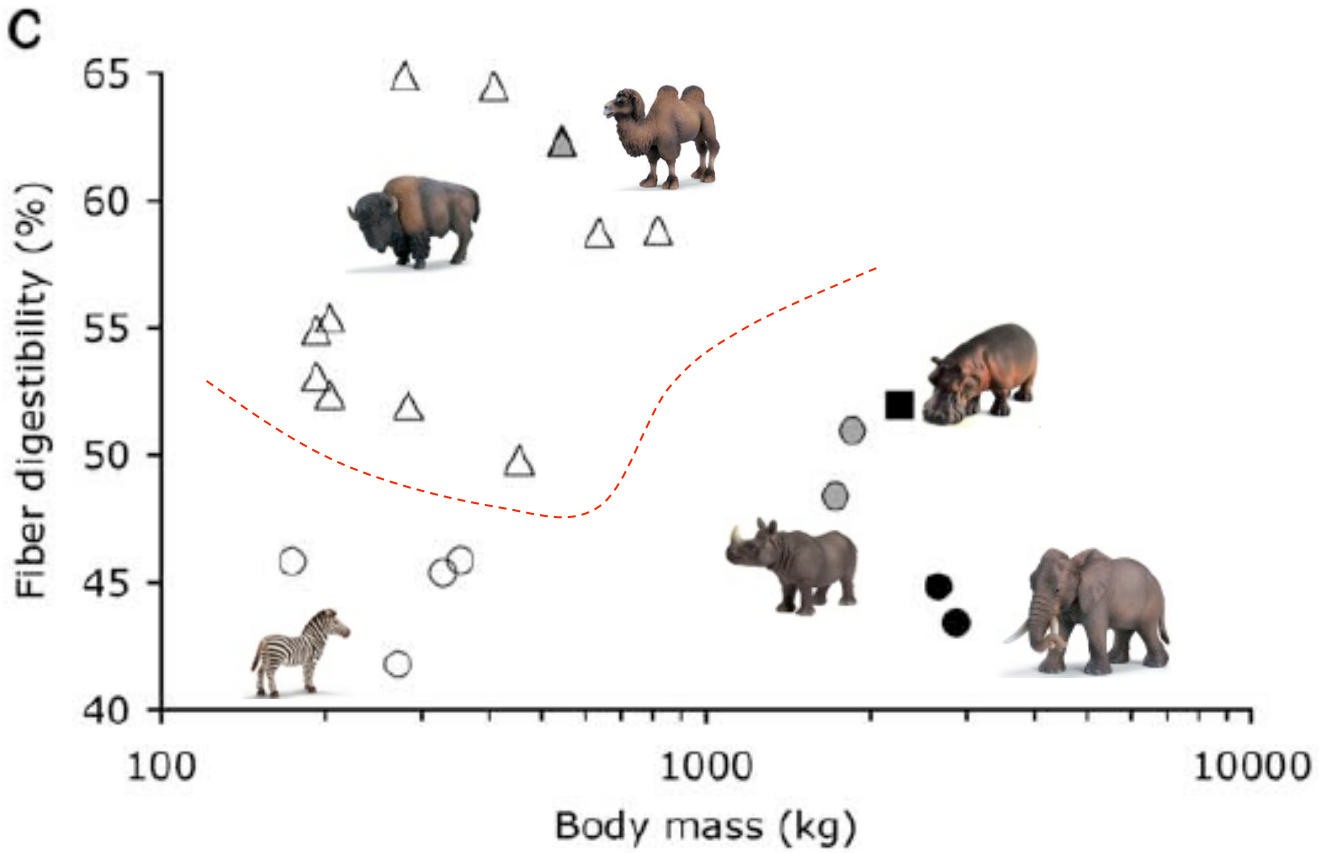


from Clauss et al. (2009; data from Foose 1982)

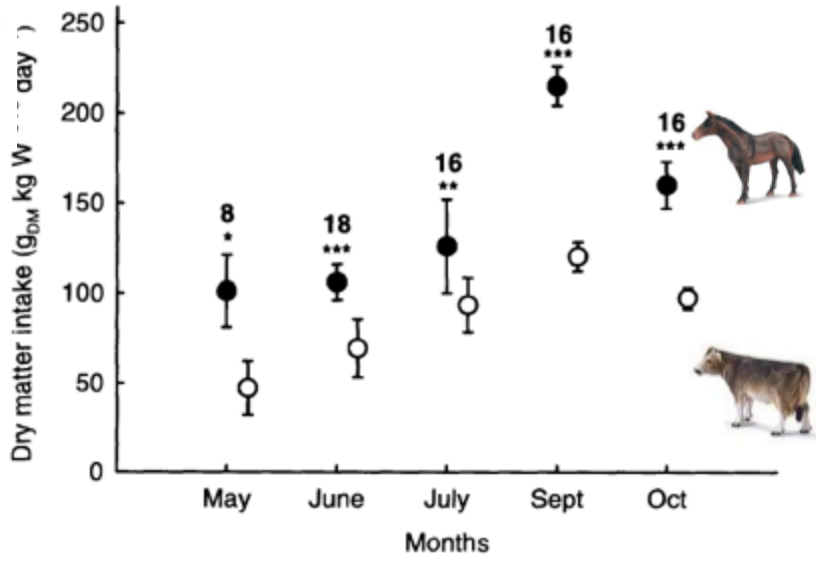
Advantage ruminants?

Due to their superior chewing efficiency, ruminants achieve higher digestibilities ... and therefore do not require as high a food intake.

Comparative foraging and nutrition of horses and cattle in European wetlands

CATHERINE MENARD*, PATRICK DUNCAN*†, GERALDINE FLEURANCE*‡, JEAN-YVES GEORGES* and MARC LILA§

Journal of Applied Ecology 2002
39, 120–133



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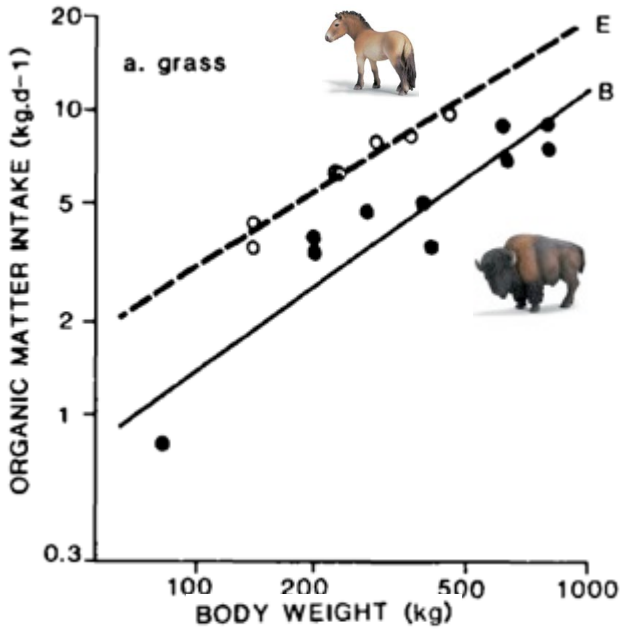
Oecologia (1990) 84:411–418

Patrick Duncan[1], T.J. Foose[2], I.J. Gordon[1,*], C.G. Gakahu[3], and Monte Lloyd[4]



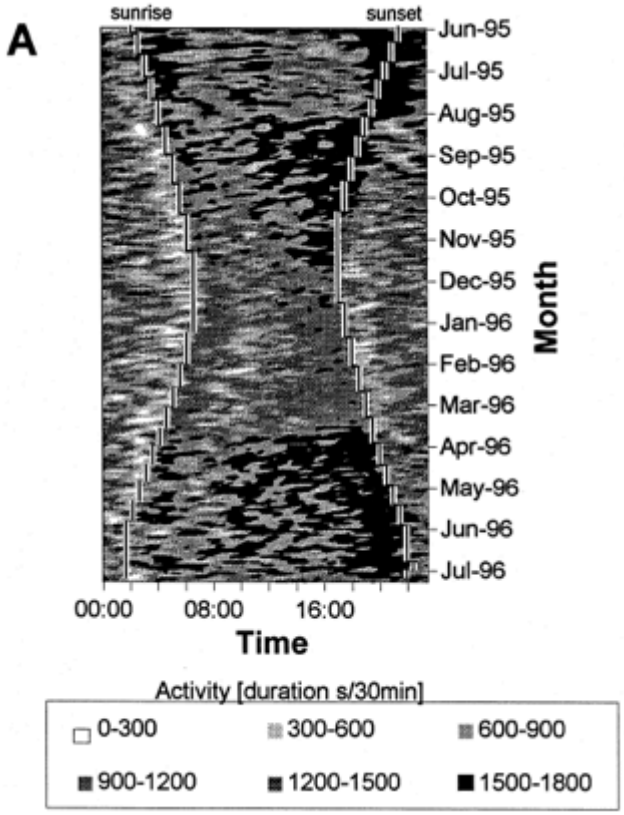
Advantage ruminants?

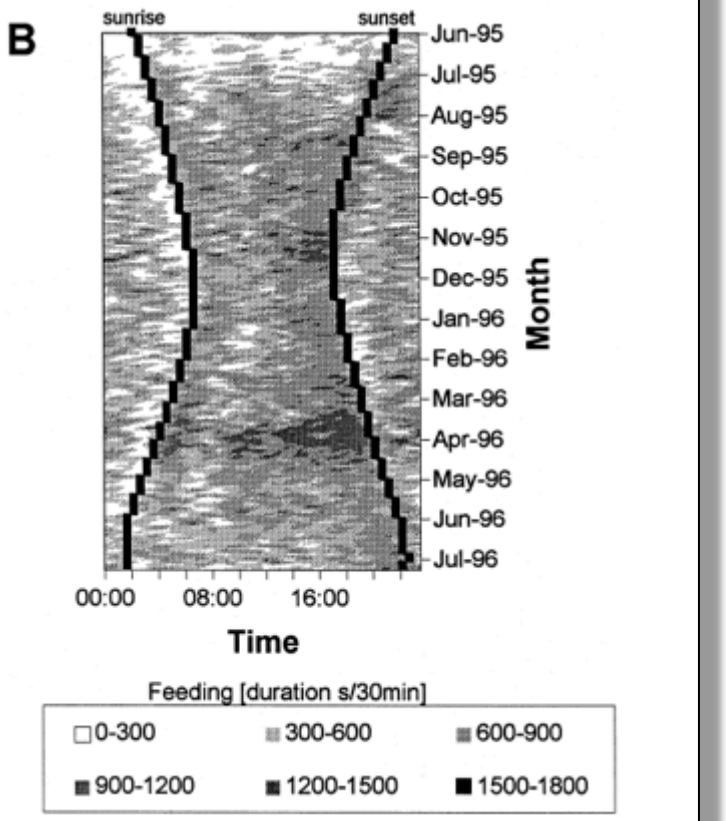
Because they need to feed more (and do not have 'rumination breaks'), equids nearly feed continuously.

Diurnal and ultradian rhythms of behaviour in a mare group of Przewalski horse (*Equus ferus przewalskii*), measured through one year under semi-reserve conditions

Anne Berger *,1, Klaus-M. Scheibe, Knut Eichhorn, Annemarie Scheibe, Jürgen Streich

Applied Animal Behaviour Science 64 (1999) 1–17





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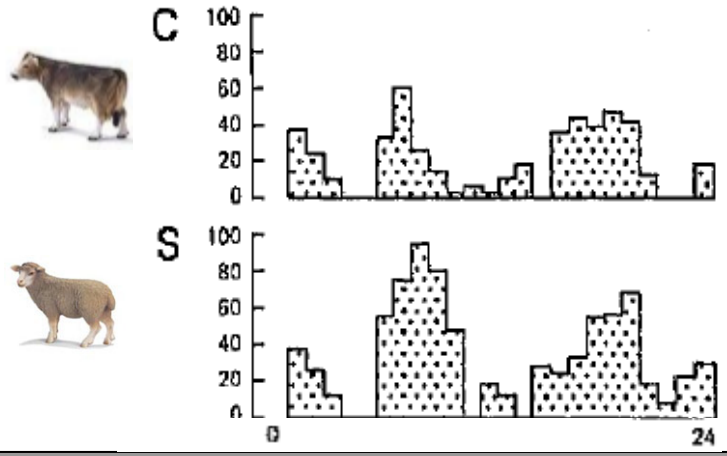
COMPARISON OF THE TIME BUDGETS AND CIRCADIAN PATTERNS OF MAINTENANCE ACTIVITIES IN SHEEP, CATTLE AND HORSES GROUPED TOGETHER

G.W. ARNOLD

Applied Animal Behaviour Science, 13 (1984/85) 19—30

Grazing



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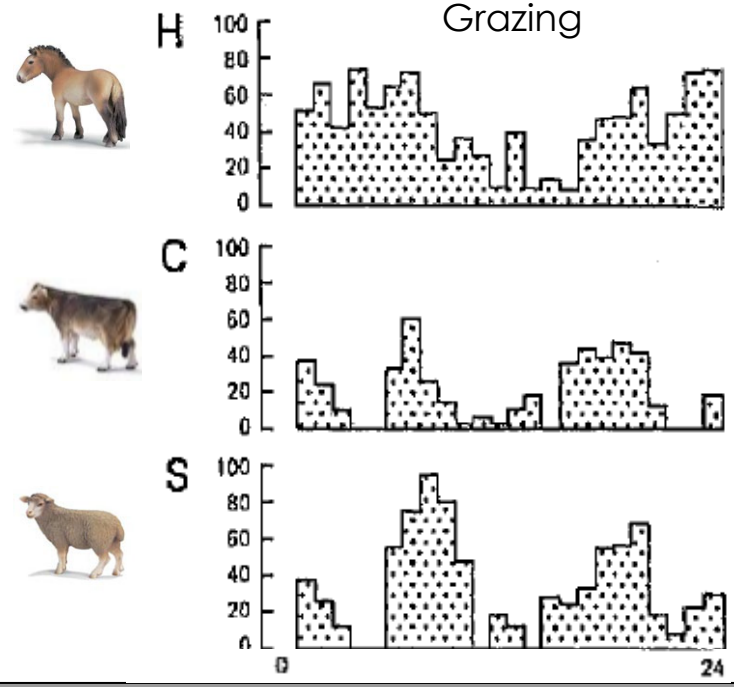


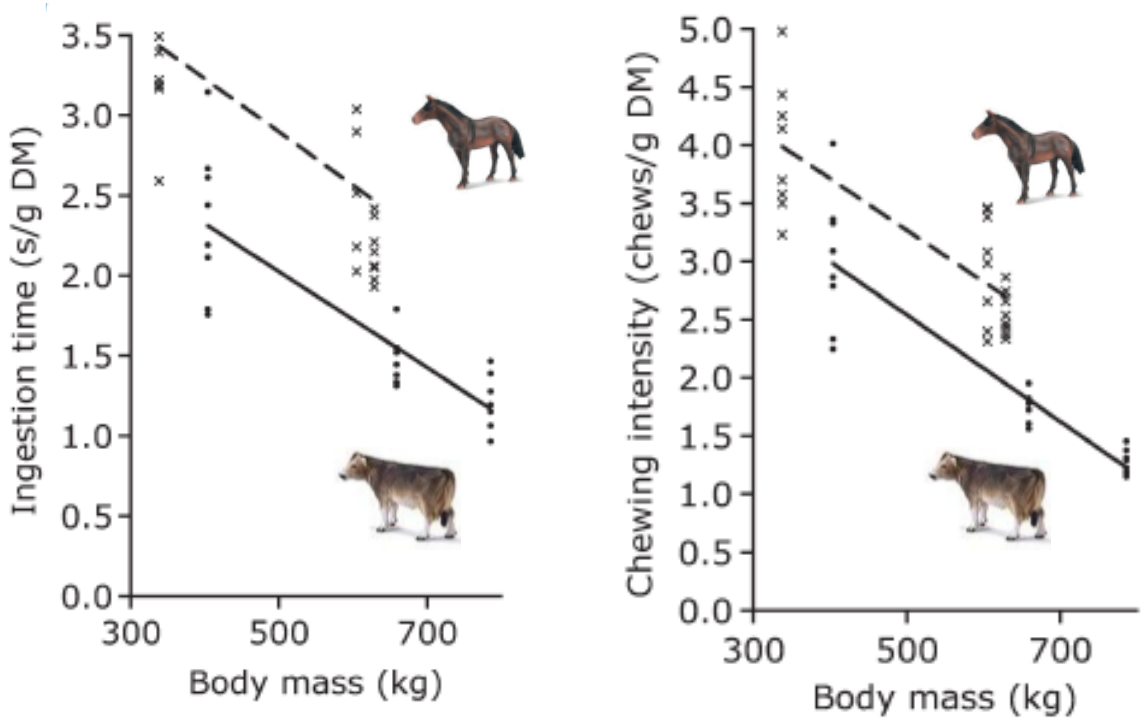
Advantage ruminants?

Because do not have 'rumination breaks', equids have higher ingestive mastication activity.

Comparative ingestive mastication in domestic horses and cattle: a pilot investigation

C. M. Janis[1], E. C. Constable[1,2], K. A. Houpt[3], W. J. Streich[4] and M. Clauss[5]

Journal of Animal Physiology and Animal Nutrition **94** (2010) e402–e409



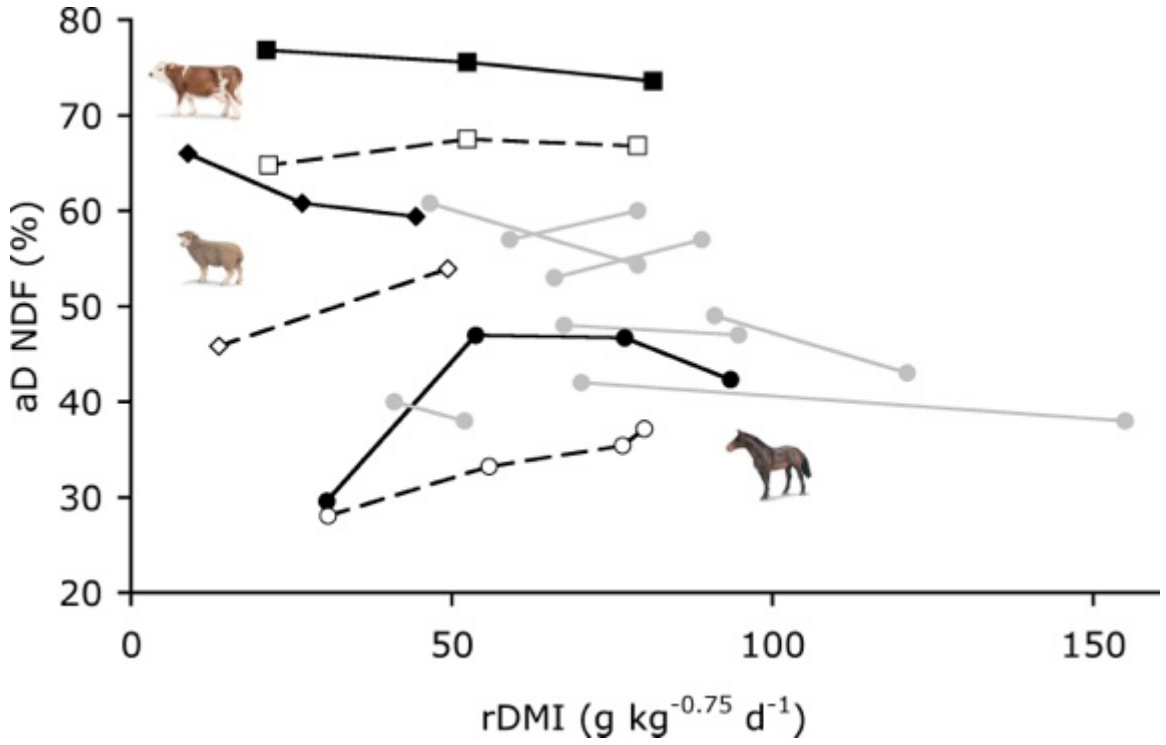
Advantage ruminants?

Are horses more susceptible to low food intake than ruminants?

The effect of very low food intake on digestive physiology and forage digestibility in horses

M. Clauss[1], K. Schiele[2], S. Ortmann[3], J. Fritz[2], D. Codron[1], J. Hummel[4] and E. Kienzle[2]

Journal of Animal Physiology and Animal Nutrition © 2013



Advantage ruminants?

Horses cannot achieve the difference between particle and fluid retention (SF selectivity factor) as observed in ruminants.

The effect of very low food intake on digestive physiology and forage digestibility in horses

M. Clauss[1], K. Schiele[2], S. Ortmann[3], J. Fritz[2], D. Codron[1], J. Hummel[4] and E. Kienzle[2]

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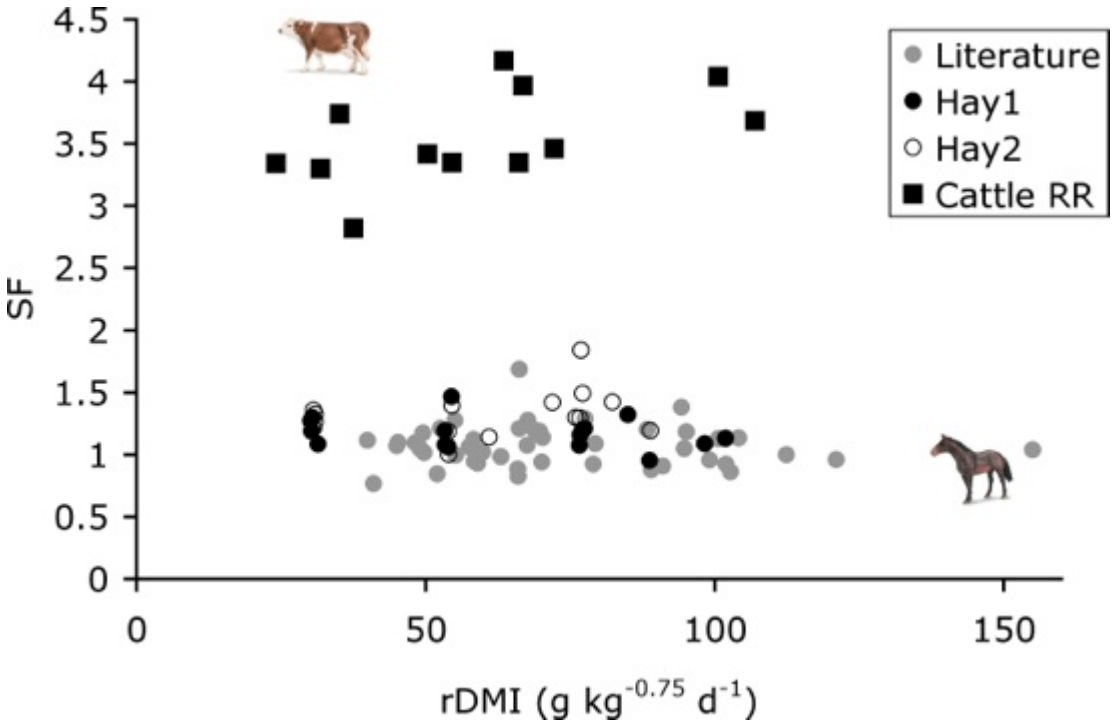


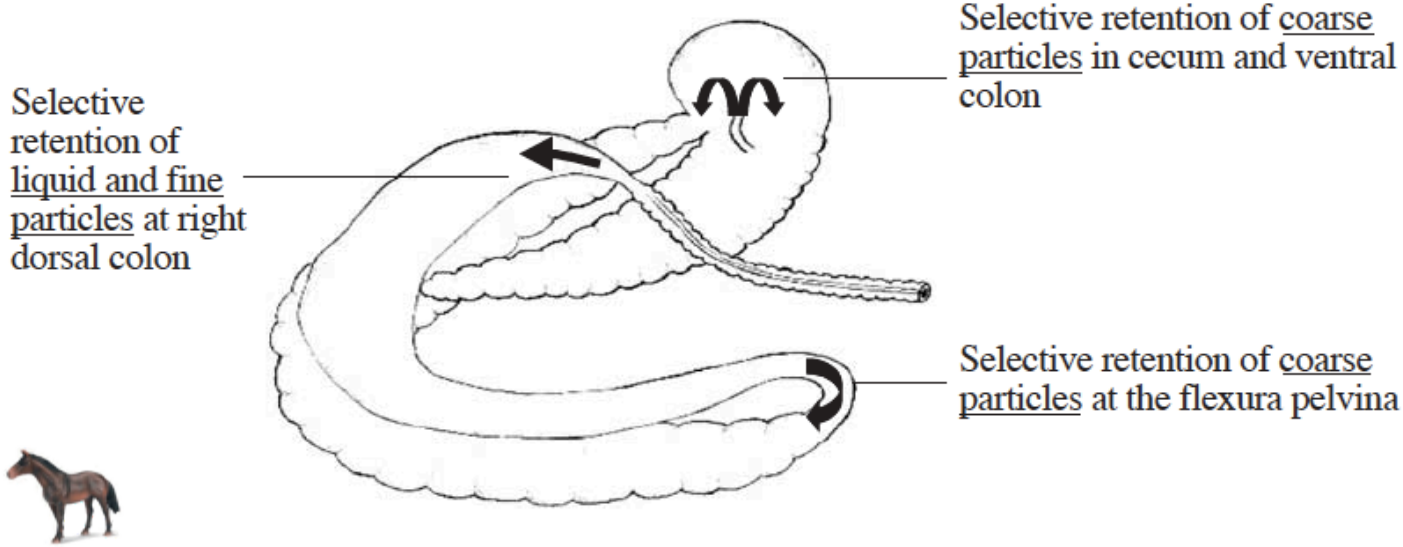
Advantage ruminants?

In spite of theoretical concept …

Passage rate of digesta through the equine gastrointestinal tract: A review

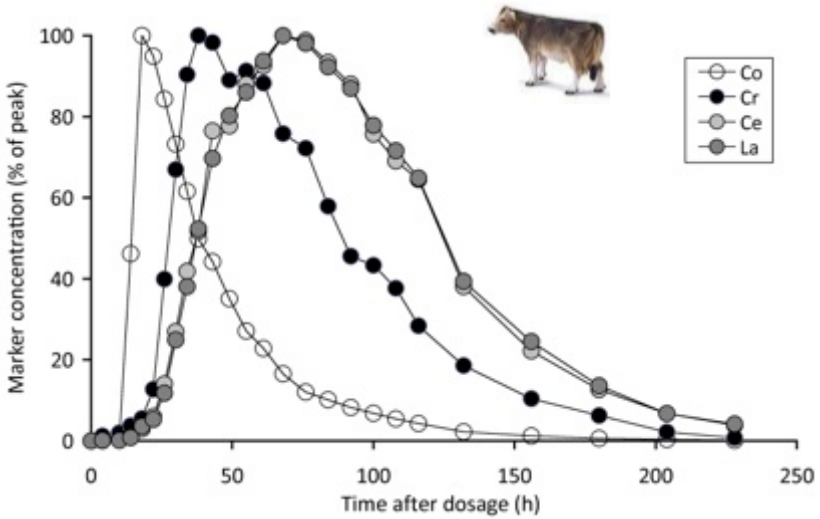
S. Van Weyenberg *, J. Sales, G.P.J. Janssens

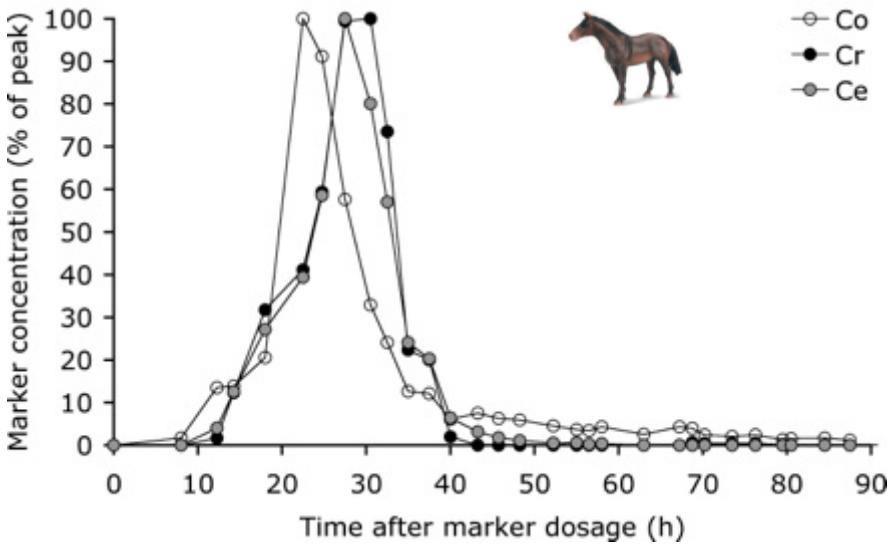
Livestock Science 99 (2006) 3–12



Advantage ruminants?

In spite of theoretical concept … no net empirical indication for differentiated passage in horses.





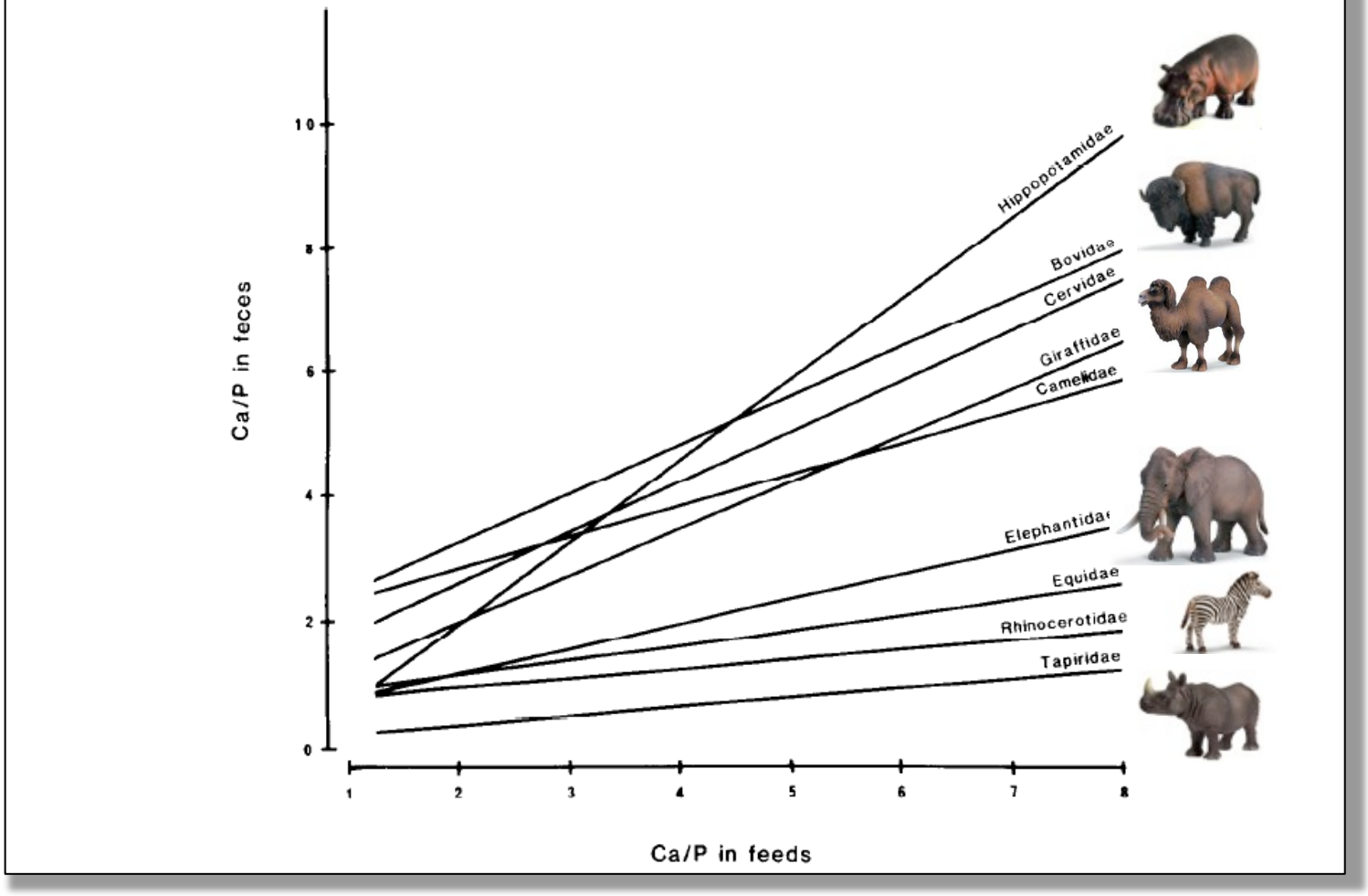
from Lechner et al. (2010), Clauss et al. (pers. obs.)

Other differences: Calcium digestibility

CALCIUM EXCRETION IN FECES OF UNGULATES

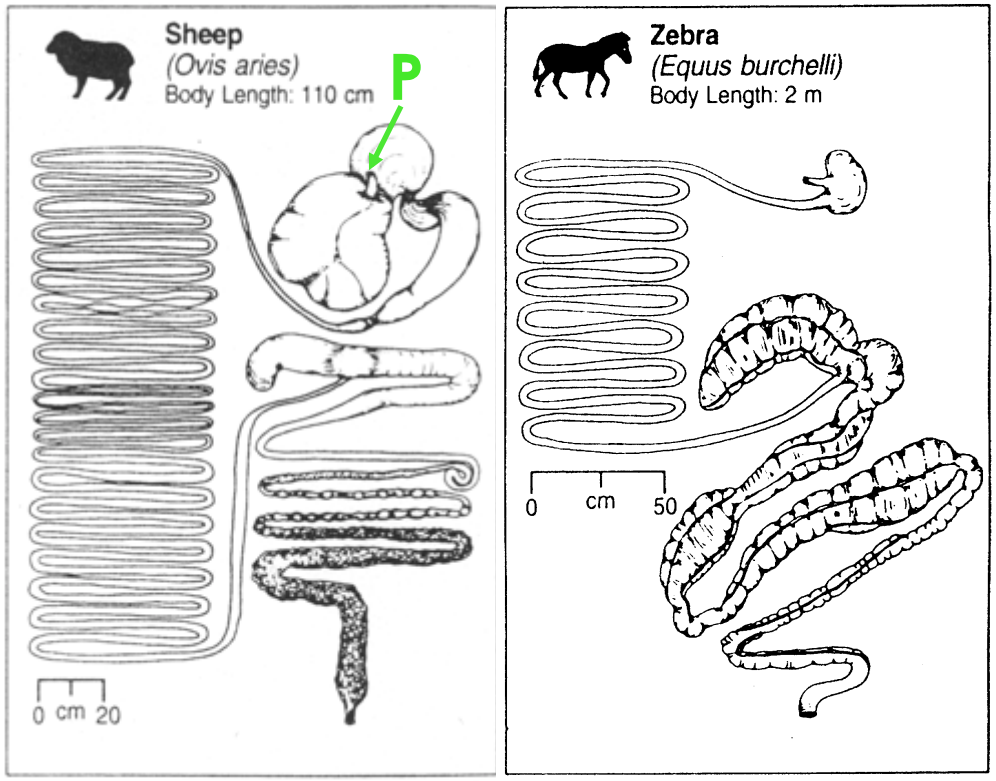
H. F. SCHRYVER, T. J. FOOSE*, J. WILLIAMS and H. F. HINTZ

Comp. Biochem. Physiol. Vol. 74A, No. 2, pp. 375 to 379, 1983



Other differences: Calcium digestibility

Phosphorus is supplied directly to microbes via saliva



from Stevens & Hume (1995)

Other differences: Calcium digestibility

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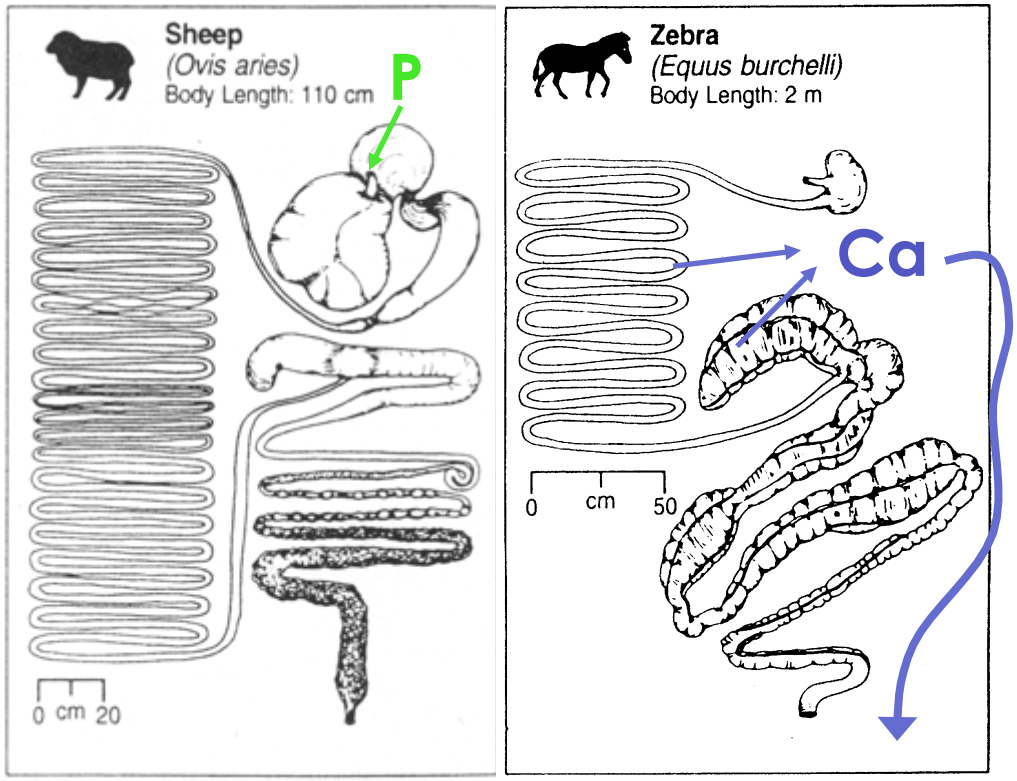


In order to guarantee **phosphorus** availability in the hindgut, **calcium** is actively absorbed from ingesta and excreted via urine

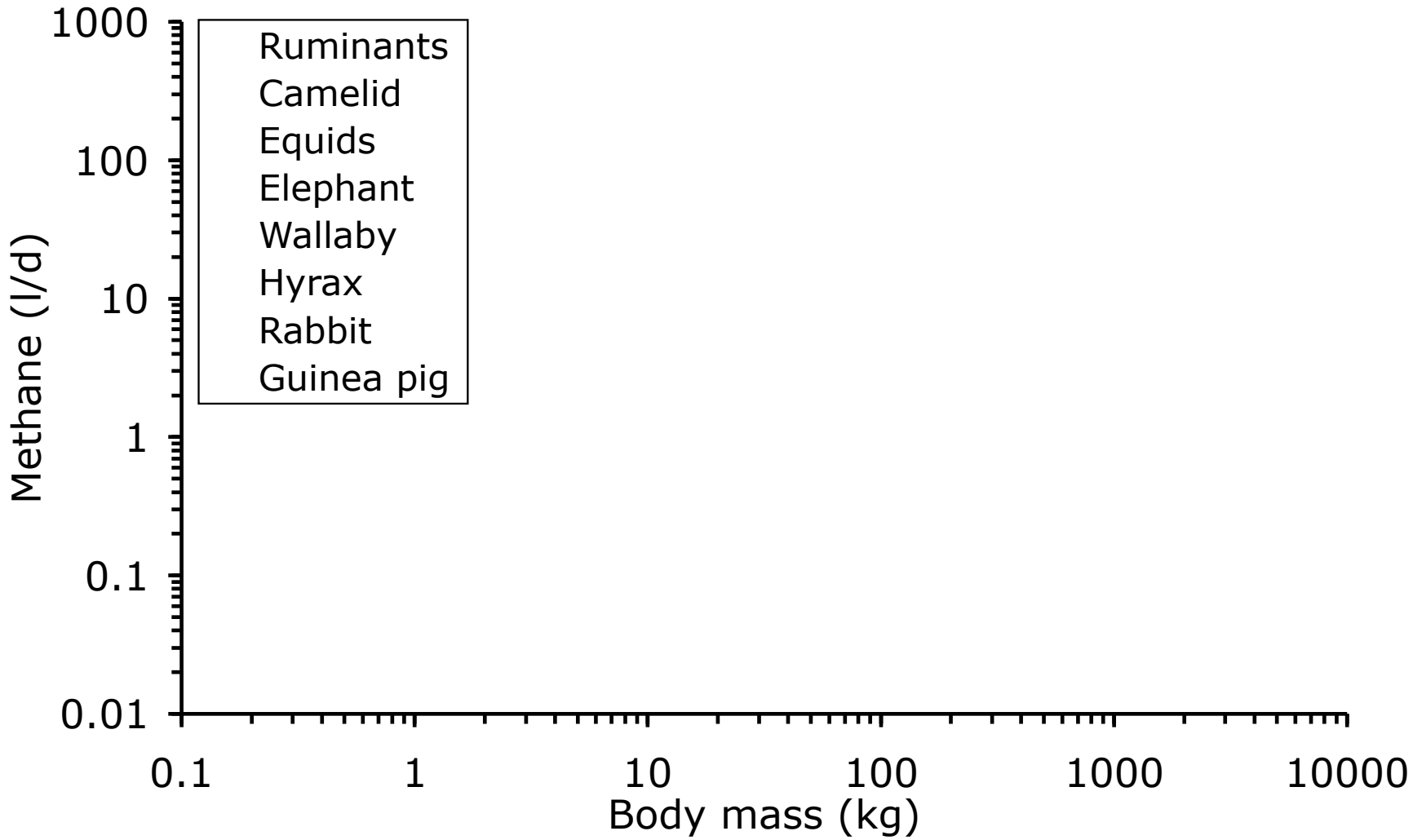
from Stevens & Hume (1995)
hypothesis by Clauss & Hummel (2008)

Why equids?

Other perissodactyls survive in body size ranges beyond the ruminant range (rhinos) or in absence of ruminant competition (tapirs).

Why / how do equids survive (only in the upper ruminant body size range, and only in the grazing niche)?

Other differences: Methane production?



from Franz et al. (2010)

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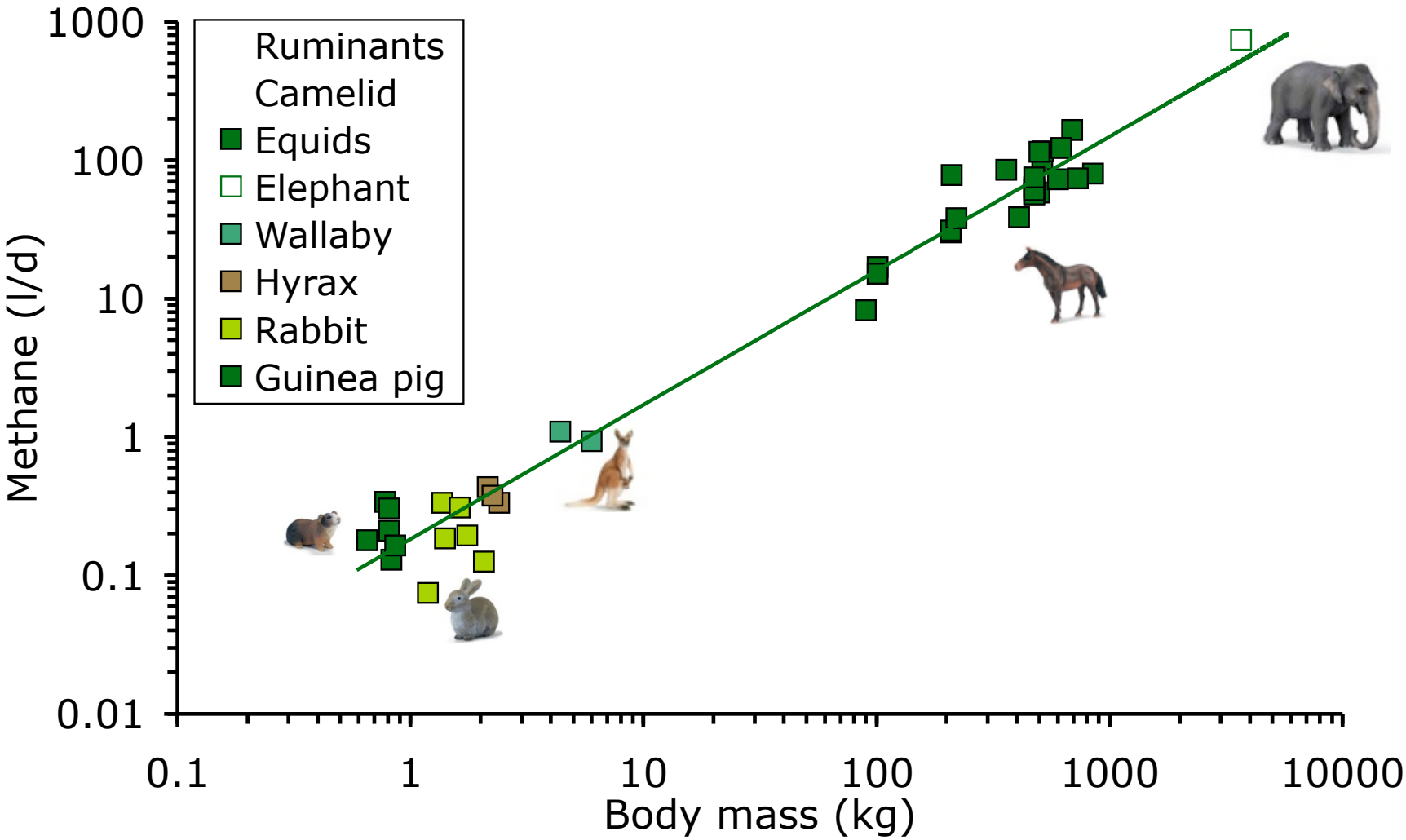

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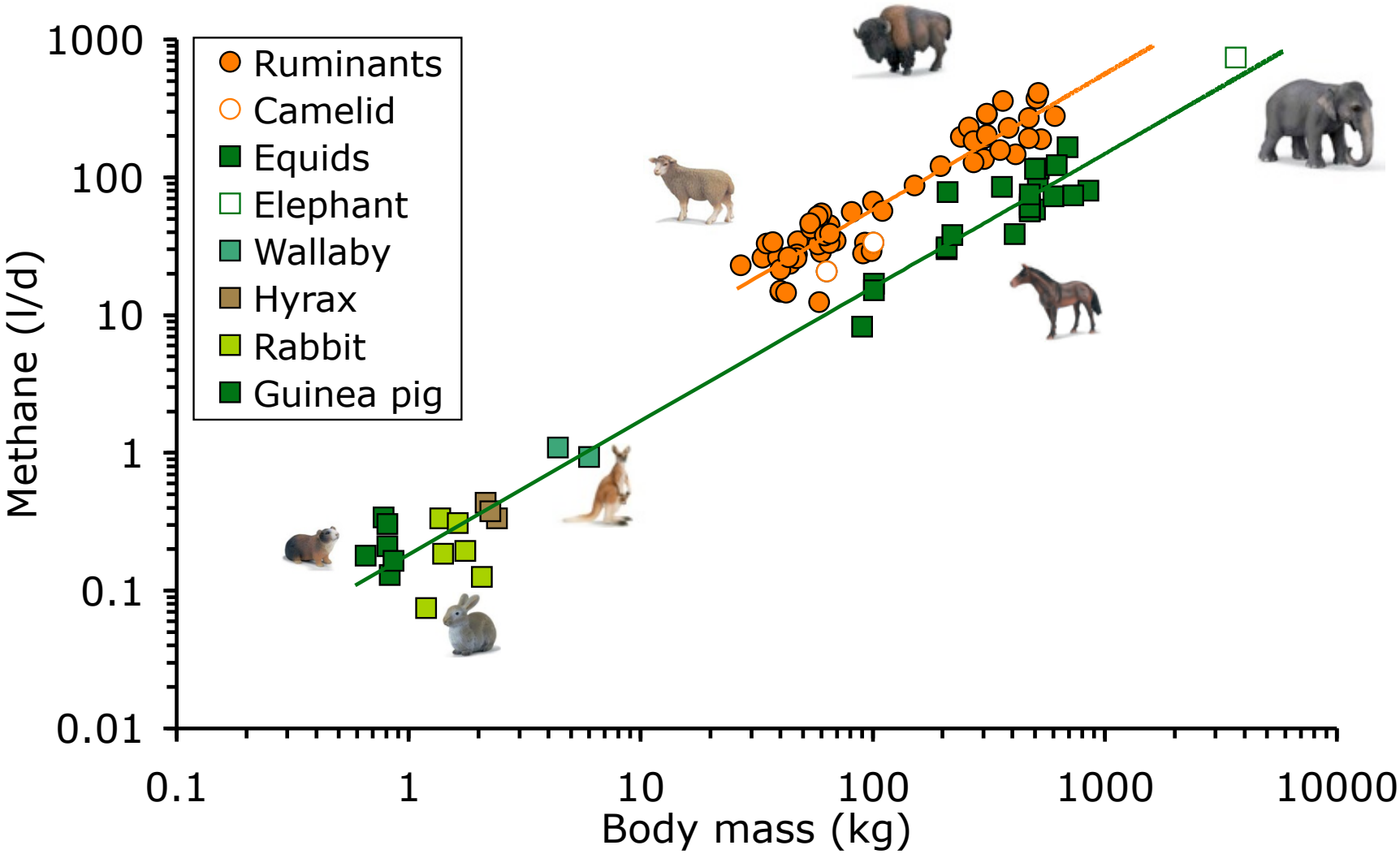

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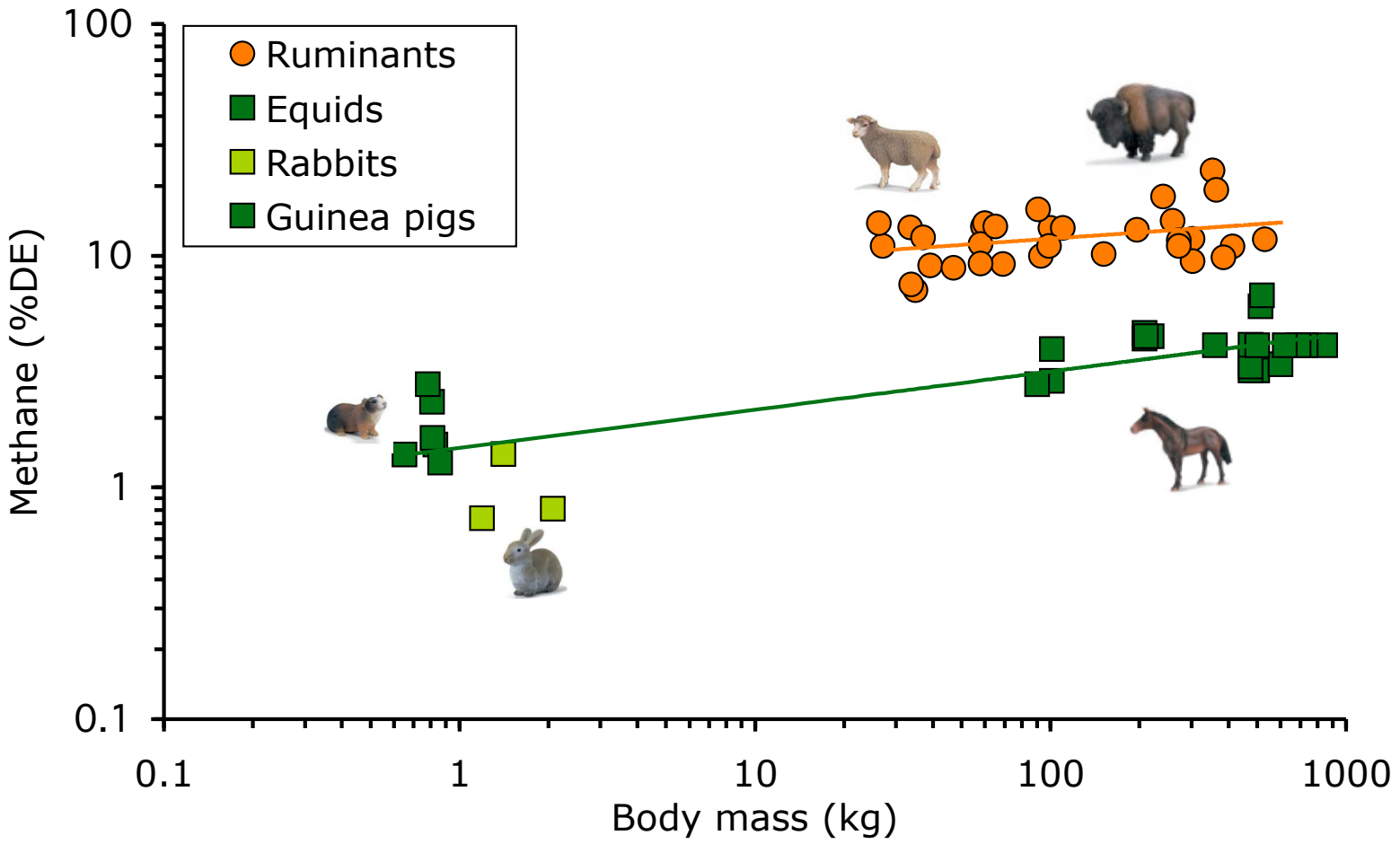


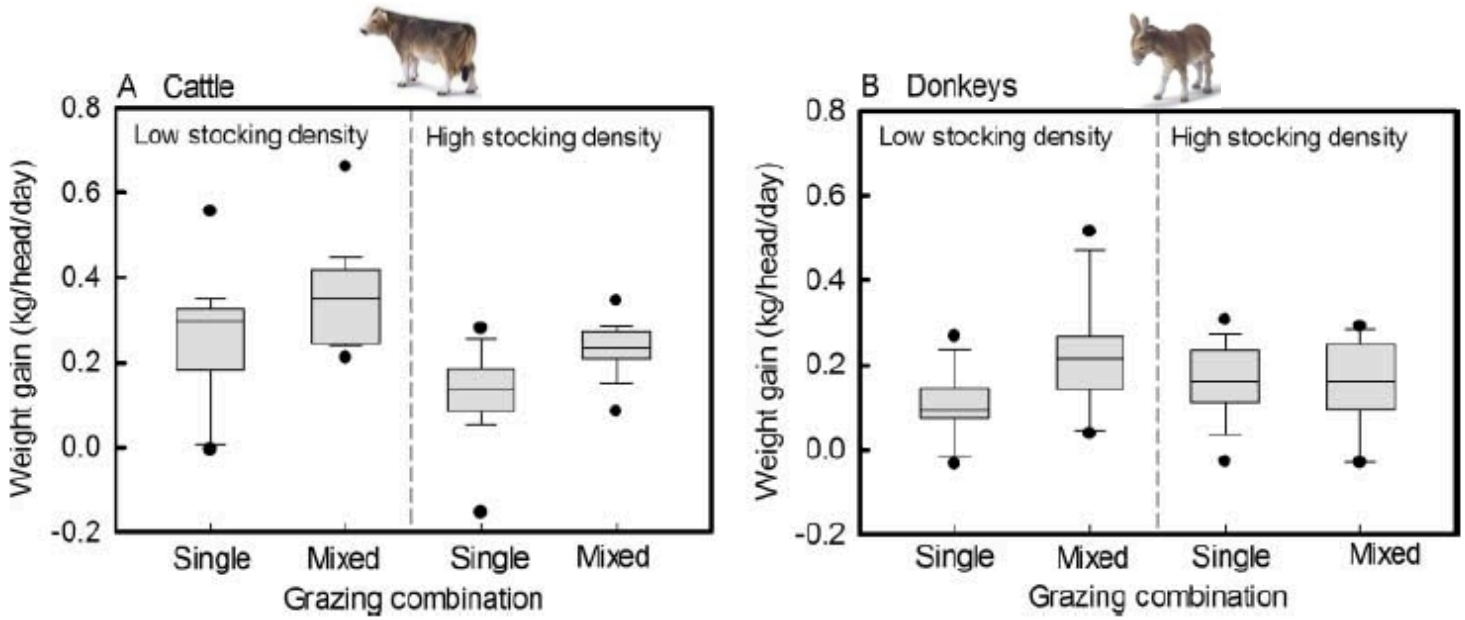
from Franz et al. (2010)

Equid-ruminant facilitation?

Facilitation between bovids and equids on an African savanna

Wilfred O. Odadi[1,2,3], Meha Jain[1,4], Sipke E. Van Wieren[5], Herbert H.T. Prins[5] and Daniel I. Rubenstein[1,2]

Evolutionary Ecology Research, 2011, **13**: 237–252



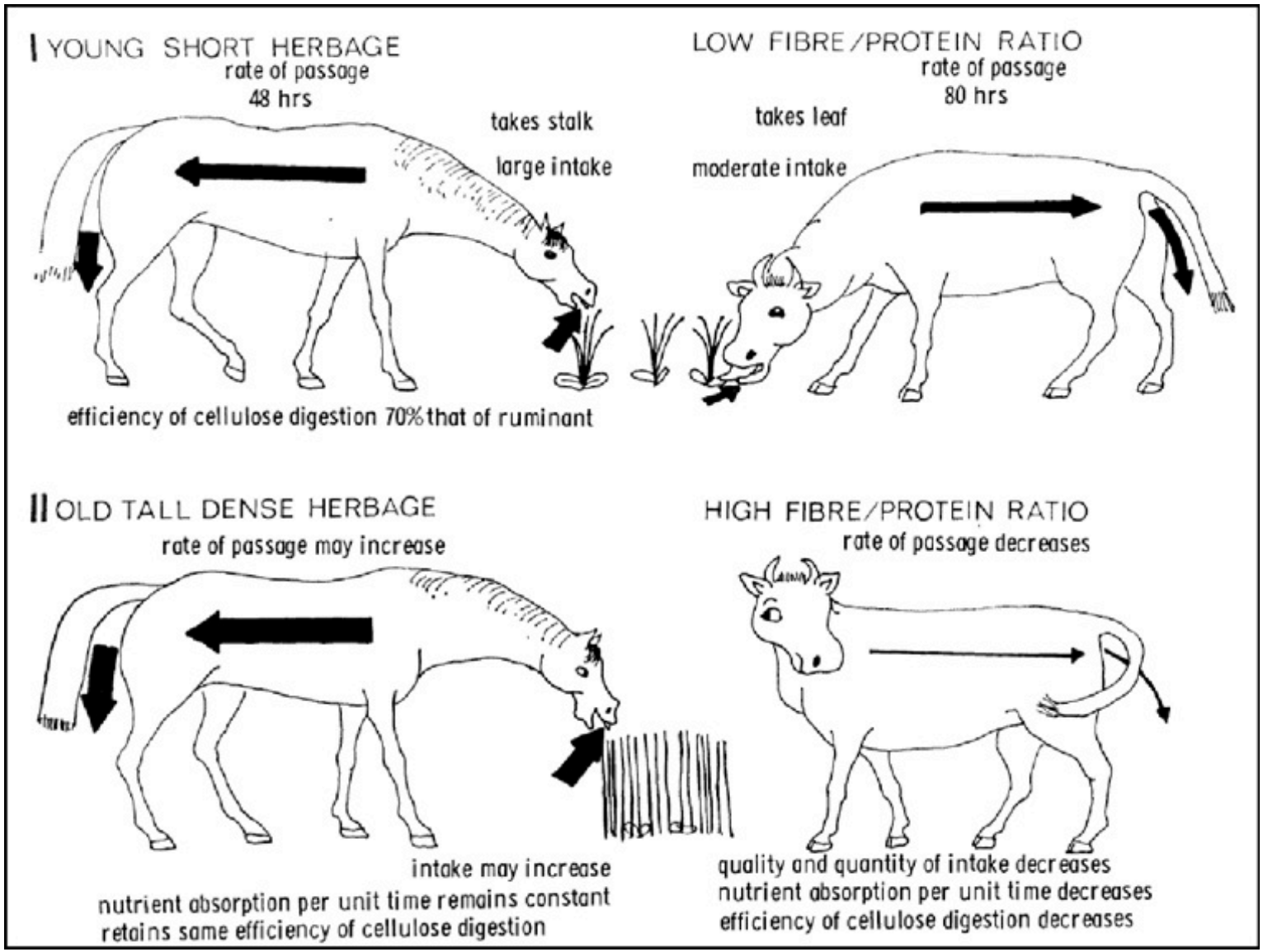
Digestive advantage for equids?

When resources are scarce on African game farms, the ruminants lose condition first …

… but it is when the zebras lose condition that you need to start to worry.

(Adrian Shrader, pers. comm.)

The traditional view of foregut vs. hindgut fermentation



Janis (1976)

Do you believe it?

"if diet quality gets lower, a horse simply eats more"

The Effects of Caloric Dilution on Meal Patterns and Food Intake of Ponies

JANE E. LAUT, KATHERINE A. HOUPT,[1] HAROLD F. HINTZ AND T. RICHARD HOUPT

Physiology & Behavior, Vol 35, pp 549–554

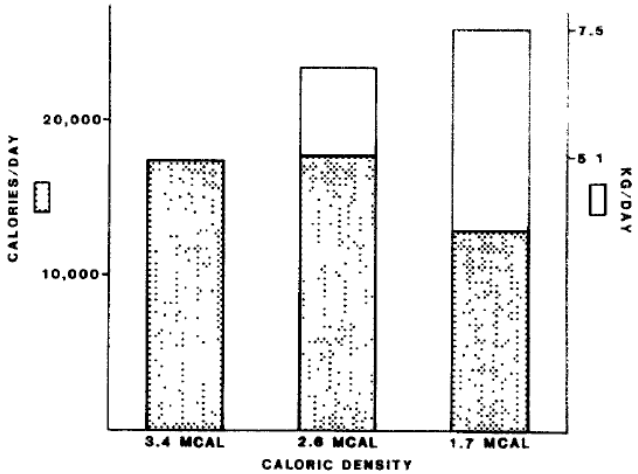


FIG 1. The intake of ponies on 3 diets varying in caloric density The total height of the column indicates the mean weight of feed eaten per day (left ordinate) The dark portion of the column indicates the mean calories consumed per day (right ordinate)

Data in sheep

SYMPOSIUM ON FACTORS INFLUENCING THE VOLUNTARY INTAKE OF HERBAGE BY RUMINANTS: VOLUNTARY INTAKE IN RELATION TO CHEMICAL COMPOSITION AND DIGESTIBILITY [1]

P. J. VAN SOEST

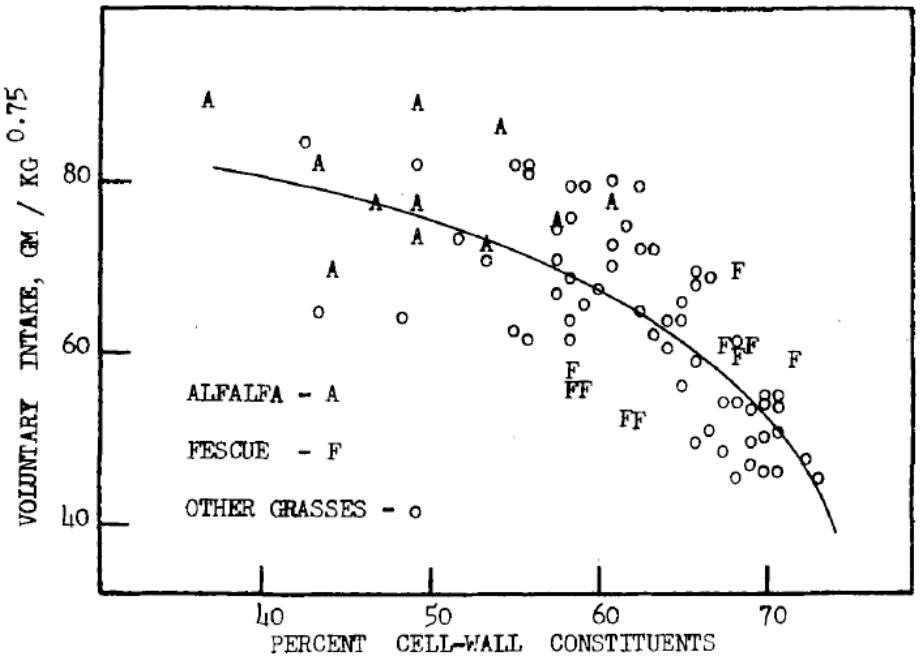


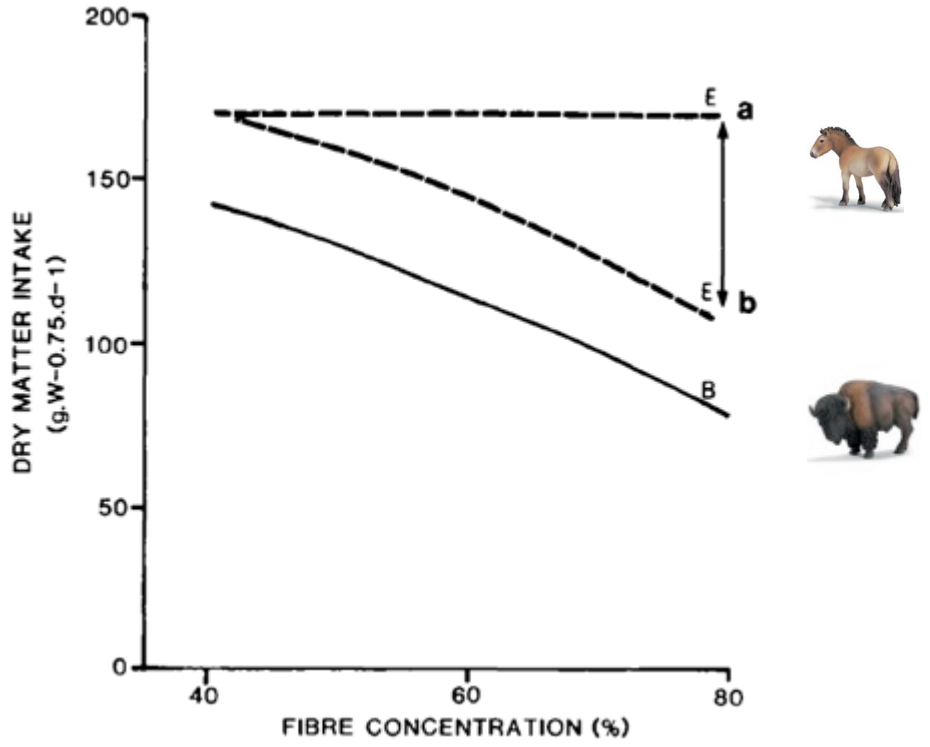
Figure 2. Relationship between voluntary intake and cell-wall constituents of 83 forages from West Virginia. Regression equation: Y=110.4 —1716/(100—X).

The traditional view of foregut vs. hindgut fermentation

Comparative nutrient extraction from forages by grazing bovids and equids: a test of the nutritional model of equid/bovid competition and coexistence

Oecologia (1990) 84:411–418

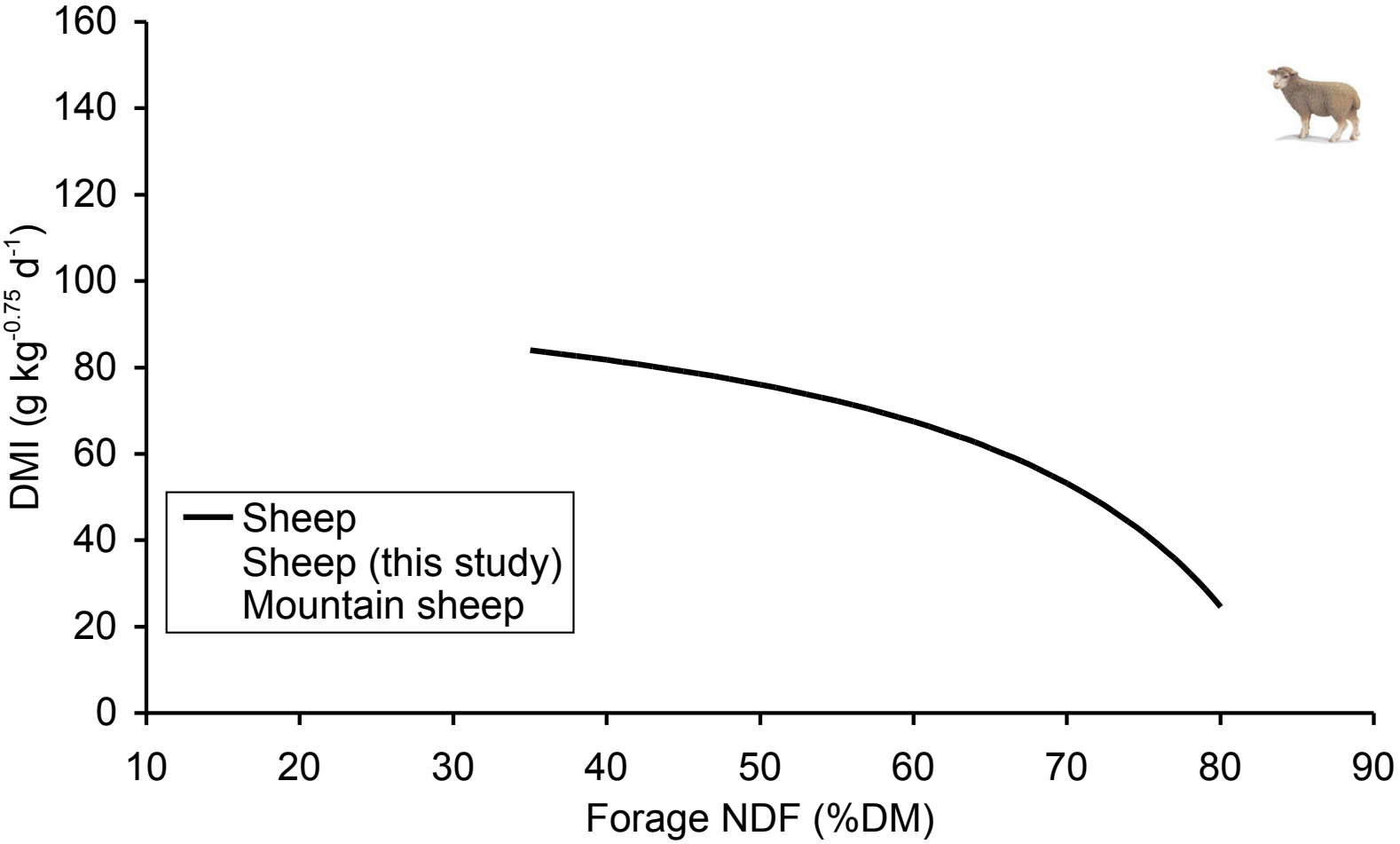
Patrick Duncan[1], T.J. Foose[2], I.J. Gordon[1,*], C.G. Gakahu[3], and Monte Lloyd[4]



The relationship between forage cell wall content and voluntary food intake in mammalian herbivores

Kerstin MEYER Jürgen HUMMEL Marcus CLAUSS*

Mammal Rev. 2010, Volume 40, No. 3, 221–245



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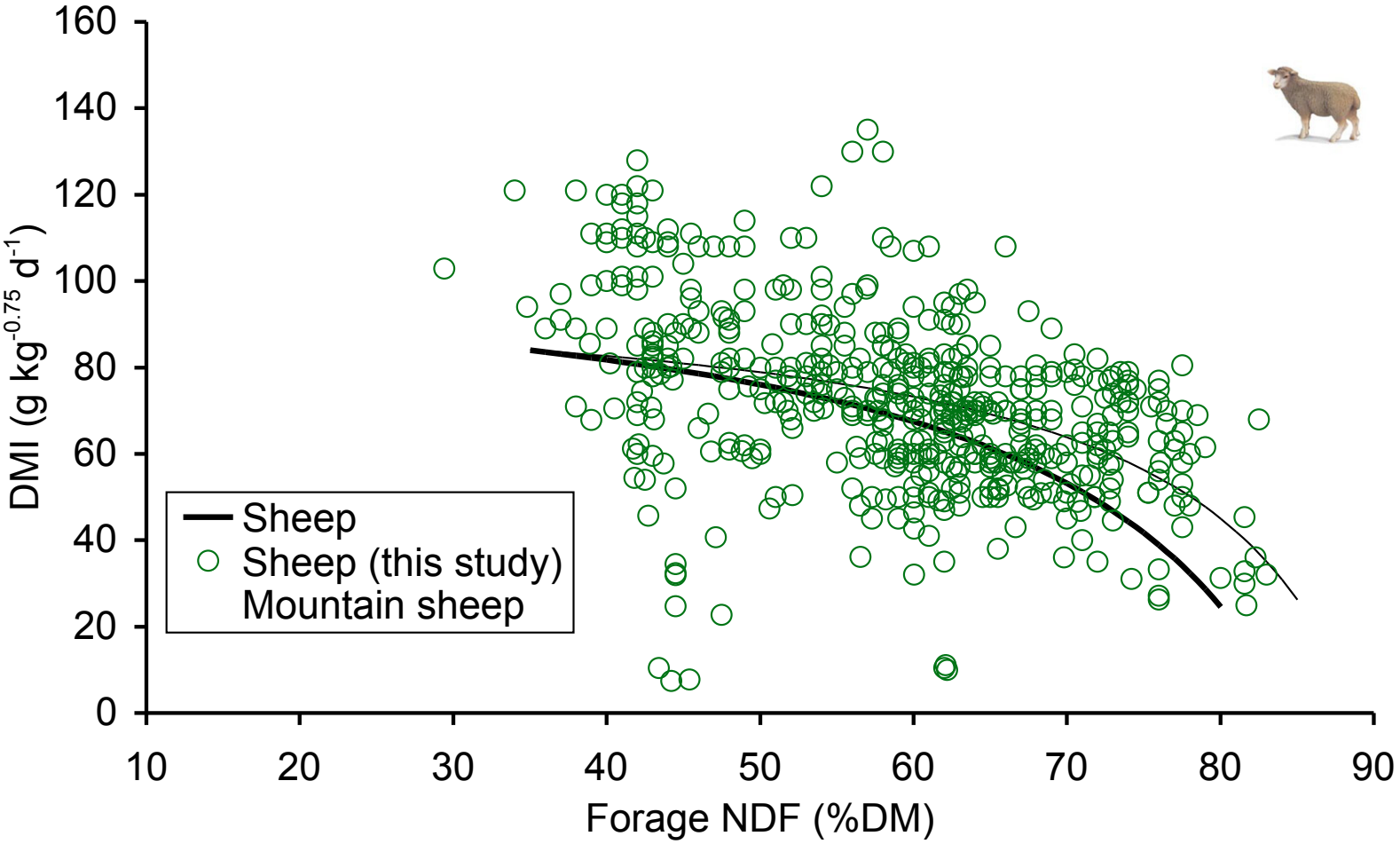

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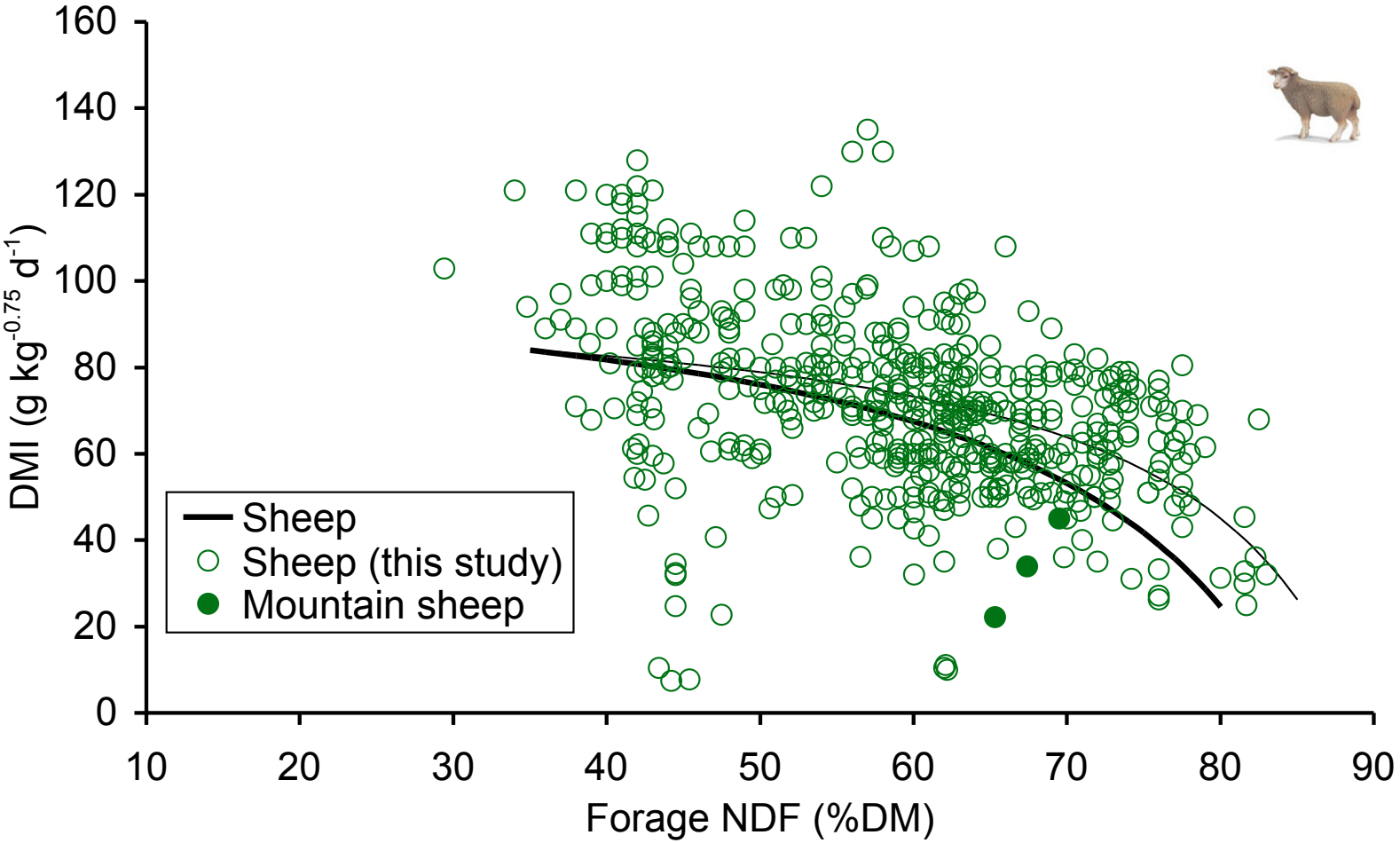

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The relationship between forage cell wall content and voluntary food intake in mammalian herbivores

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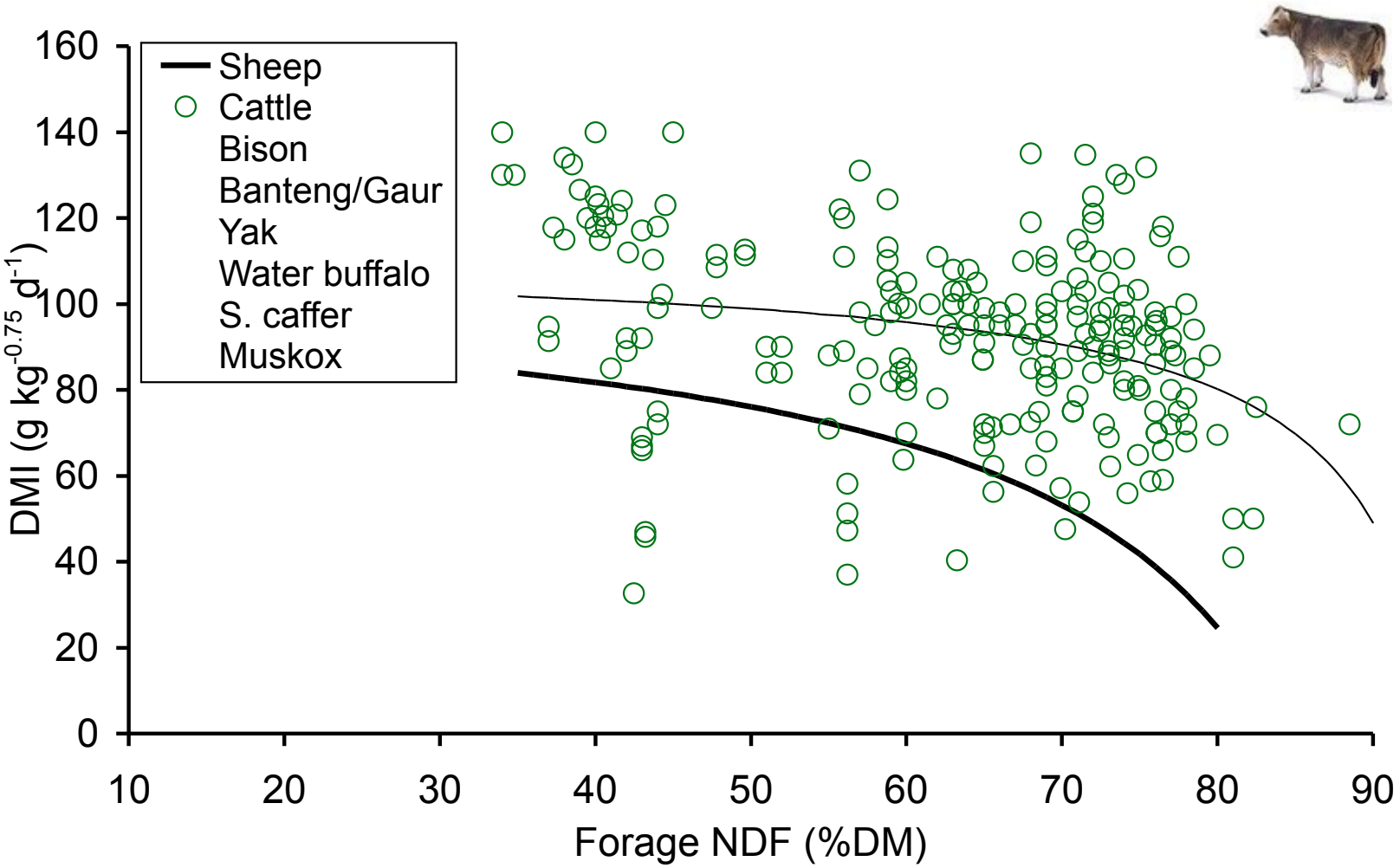

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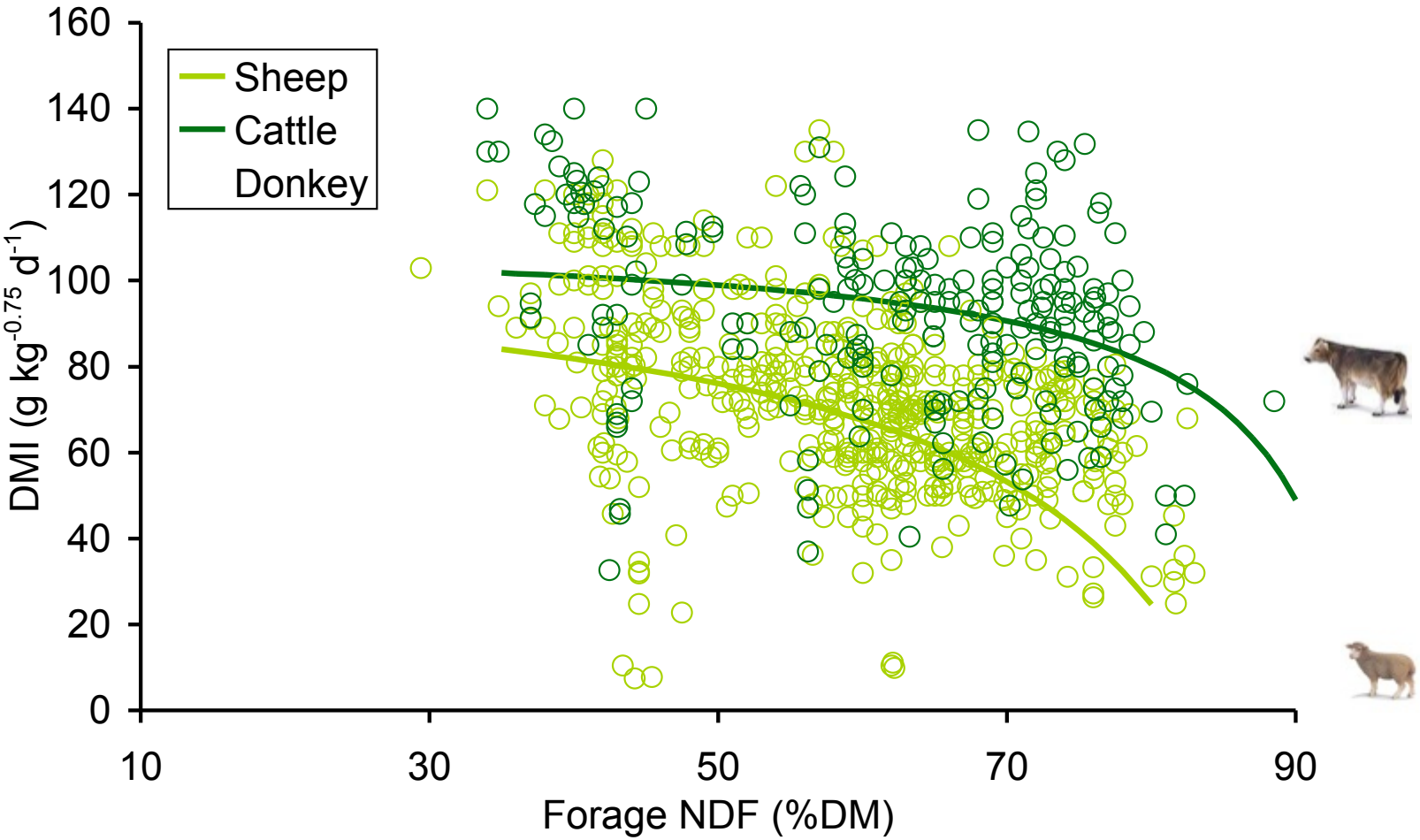

Meyer et al. (2010)

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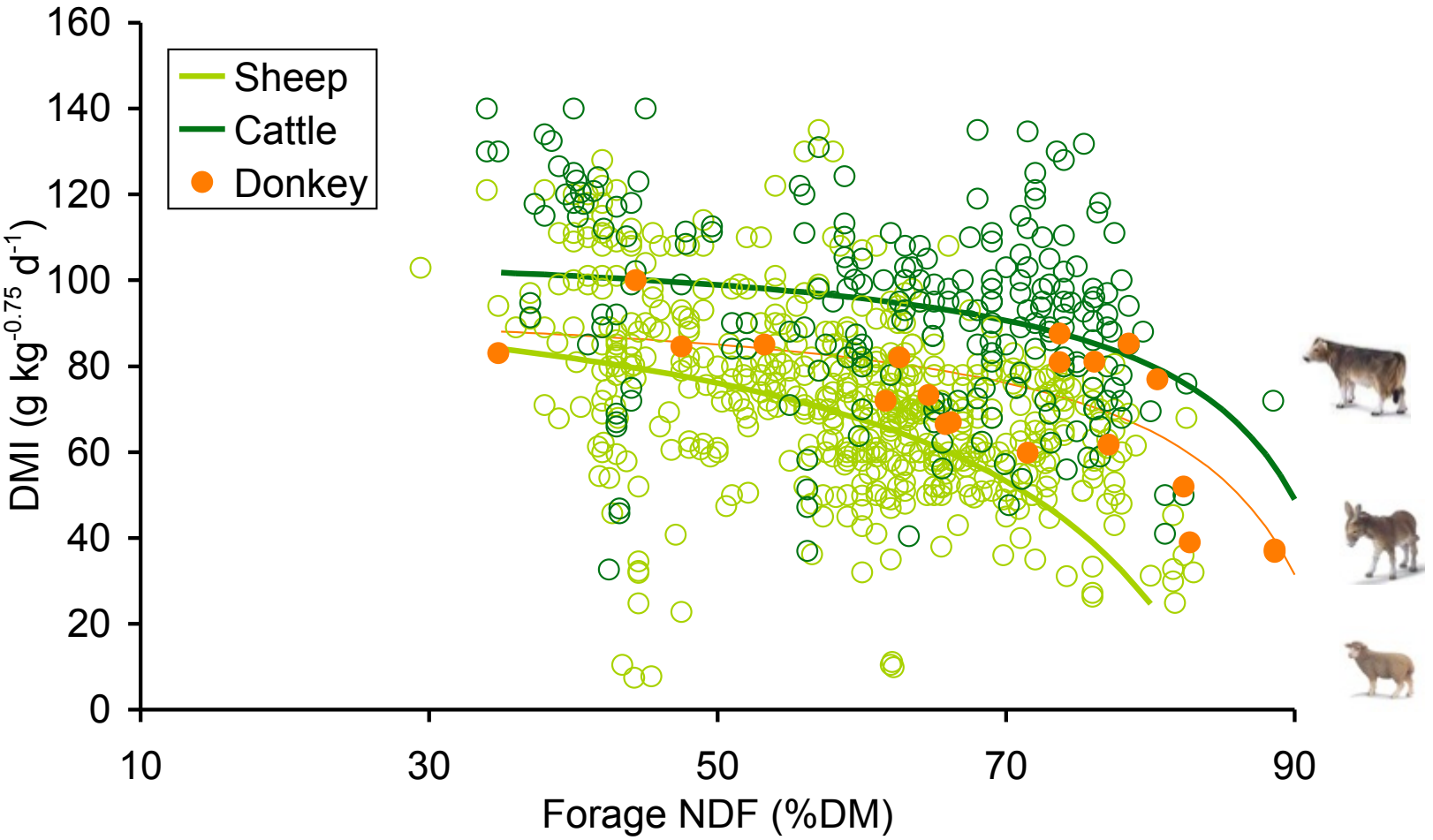

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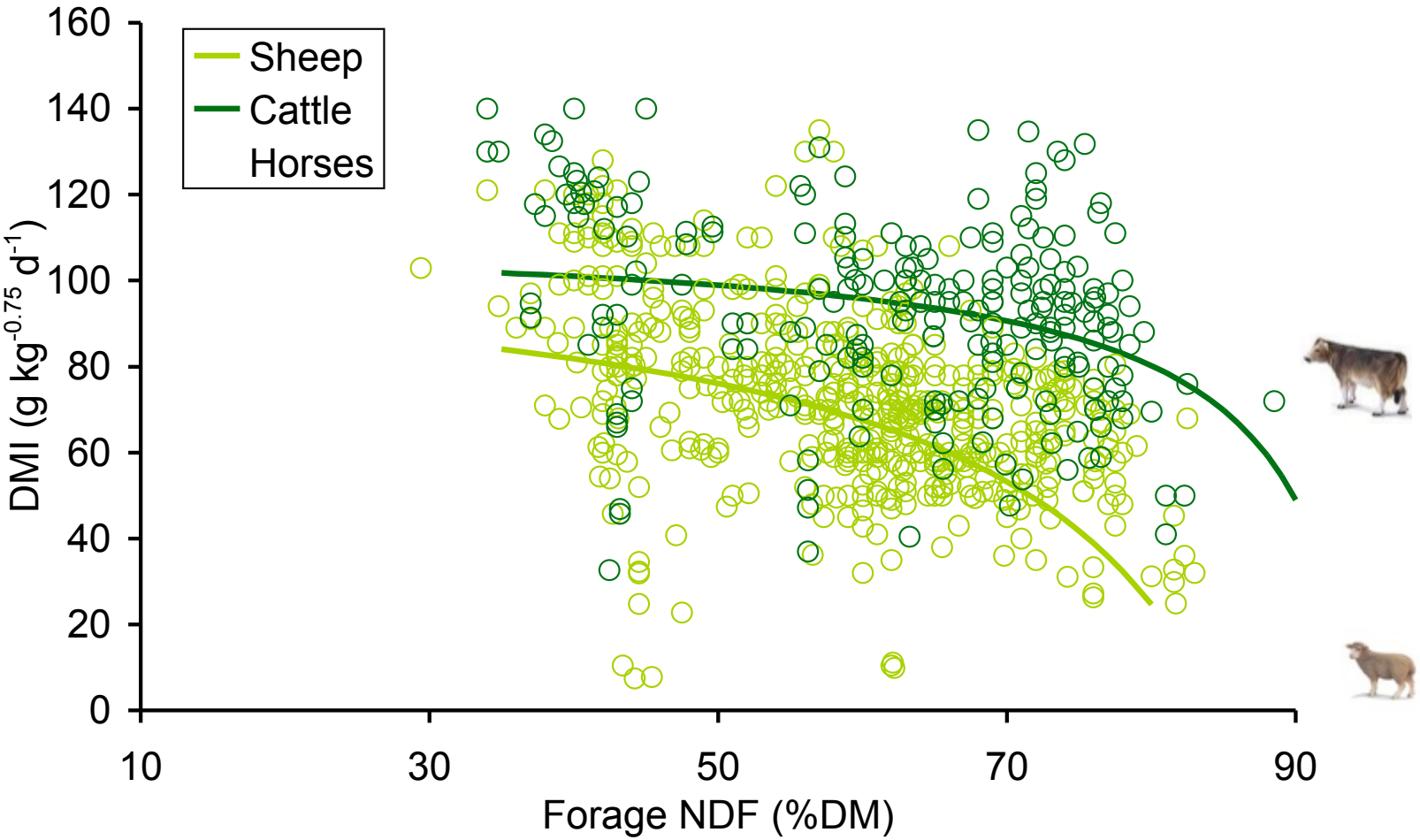

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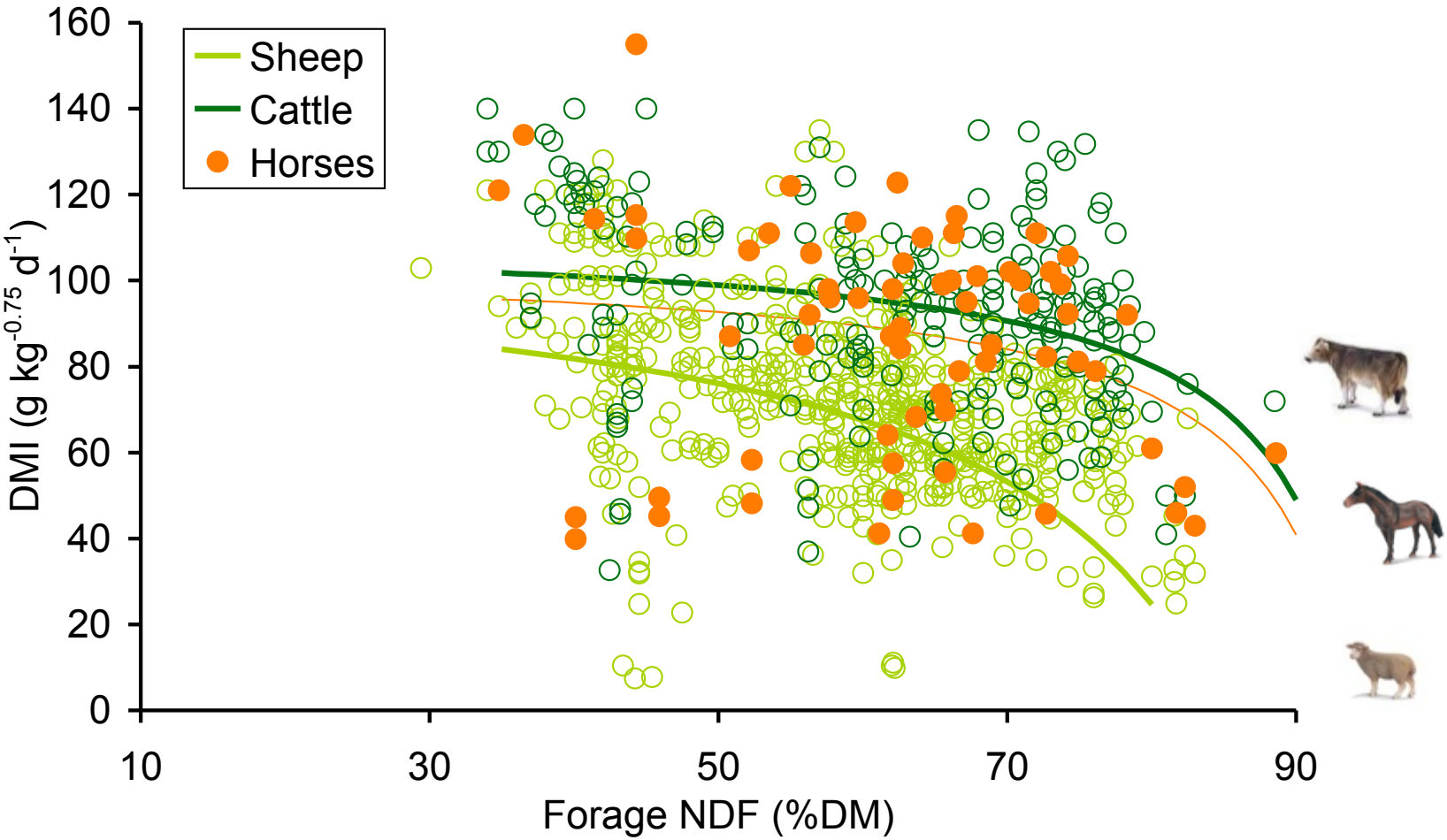

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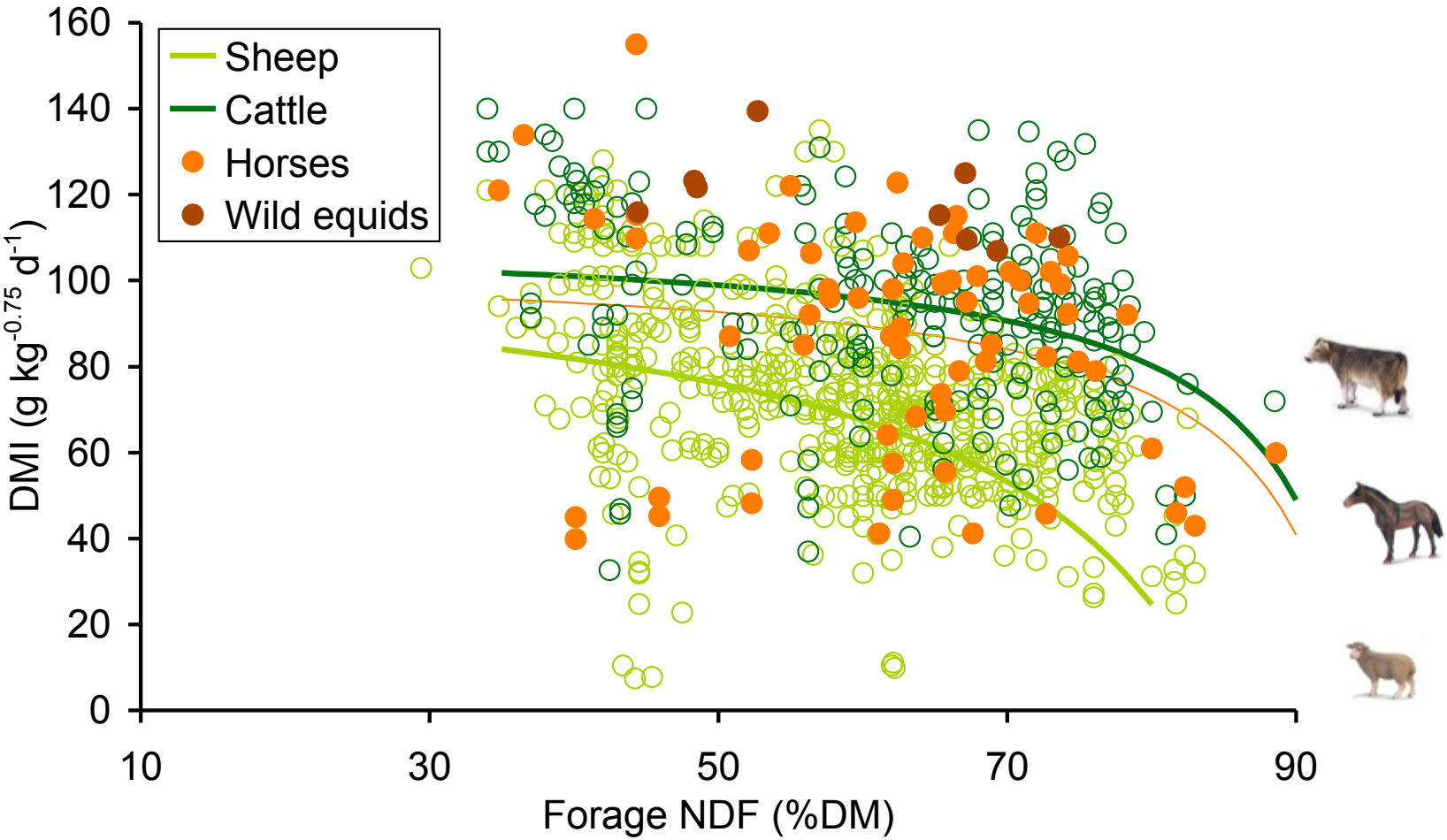

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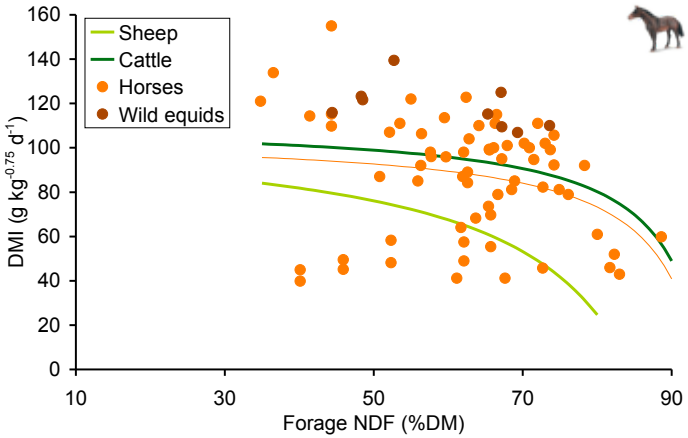

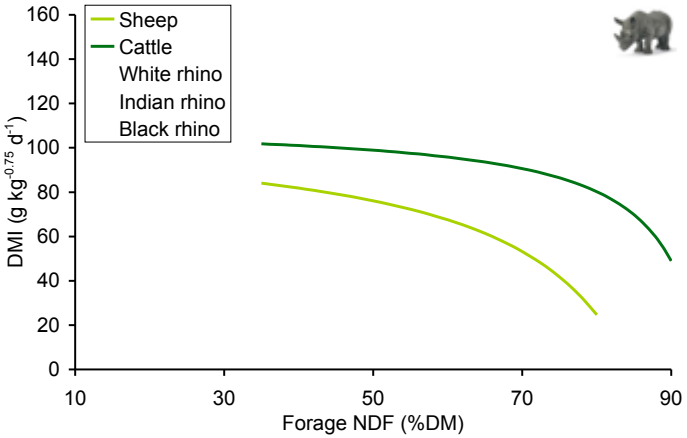

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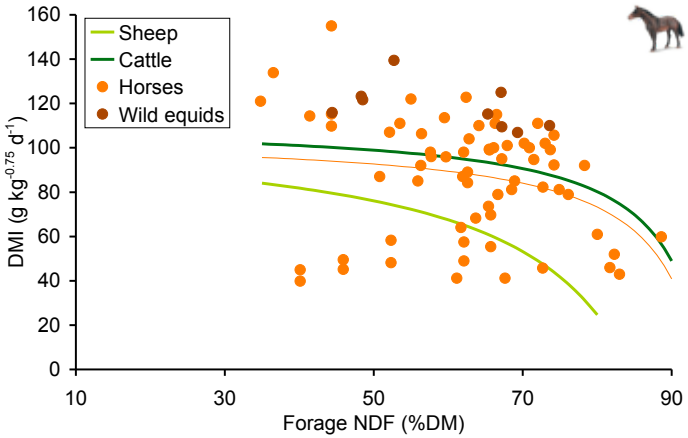

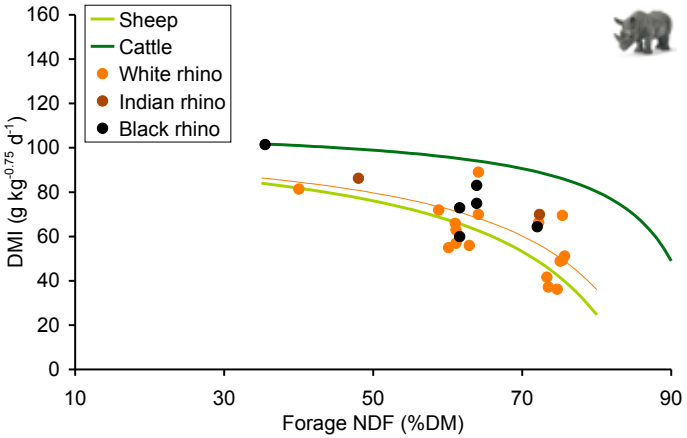

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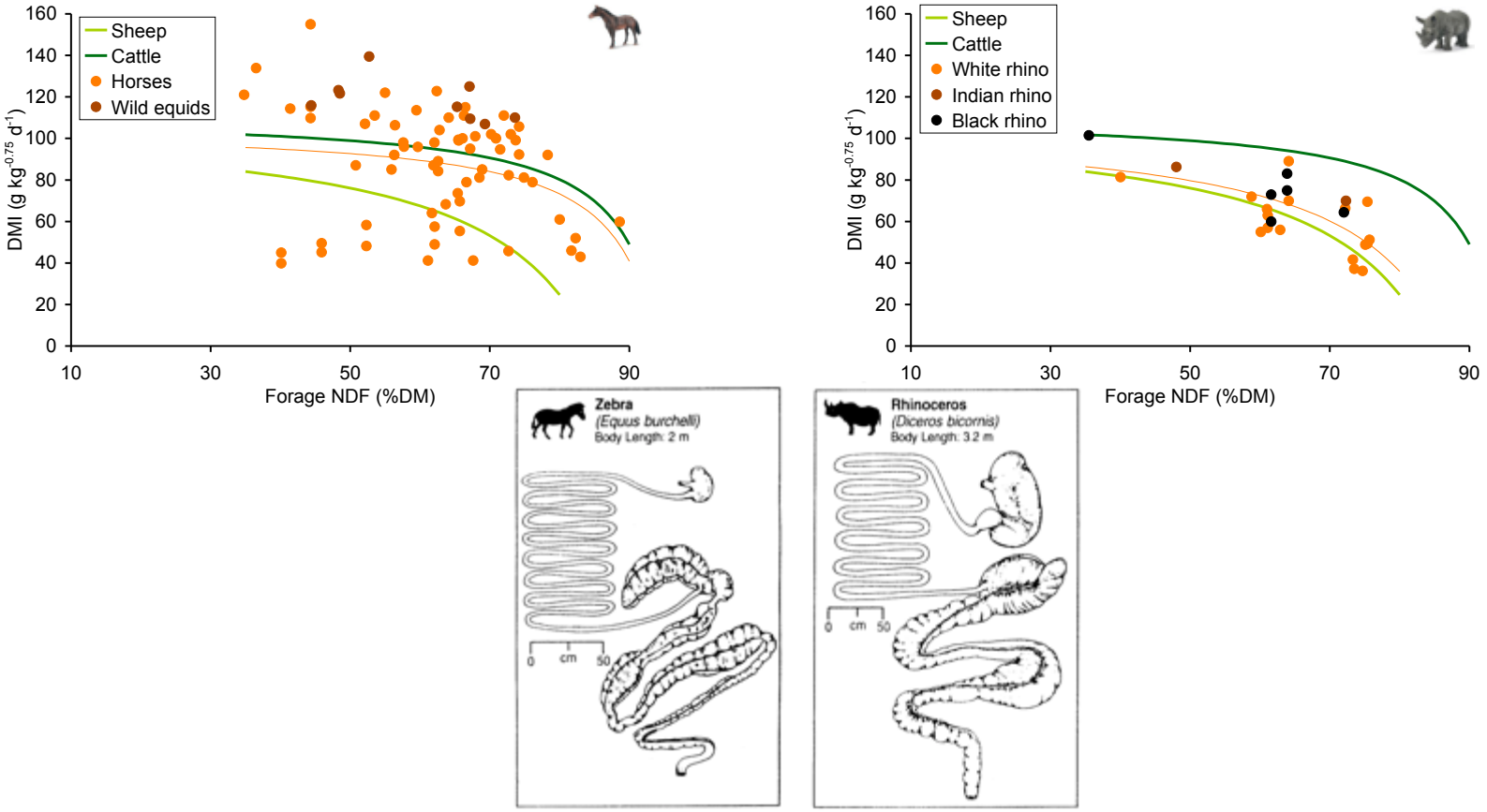
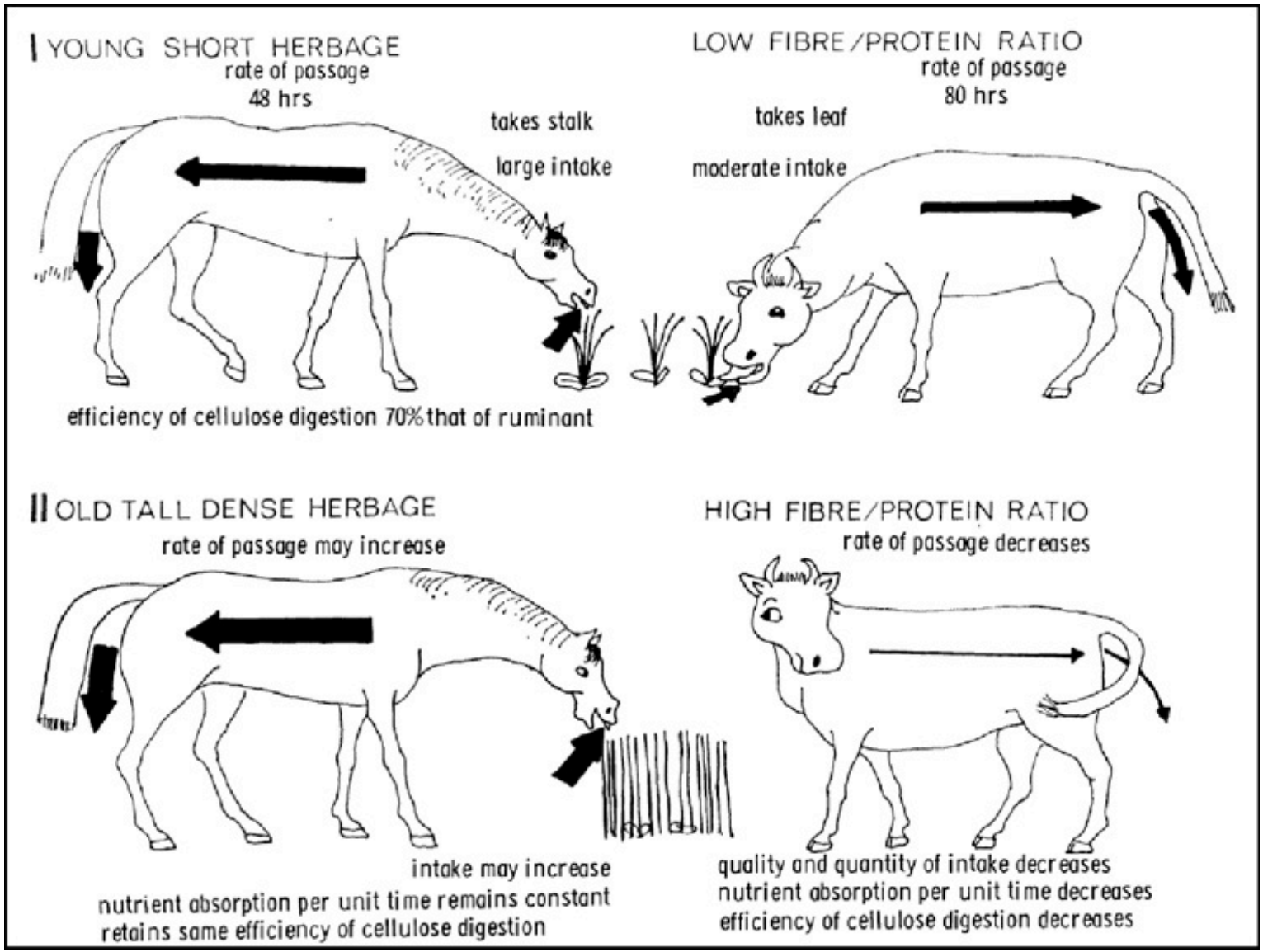
Misinterpretation of anatomical features?



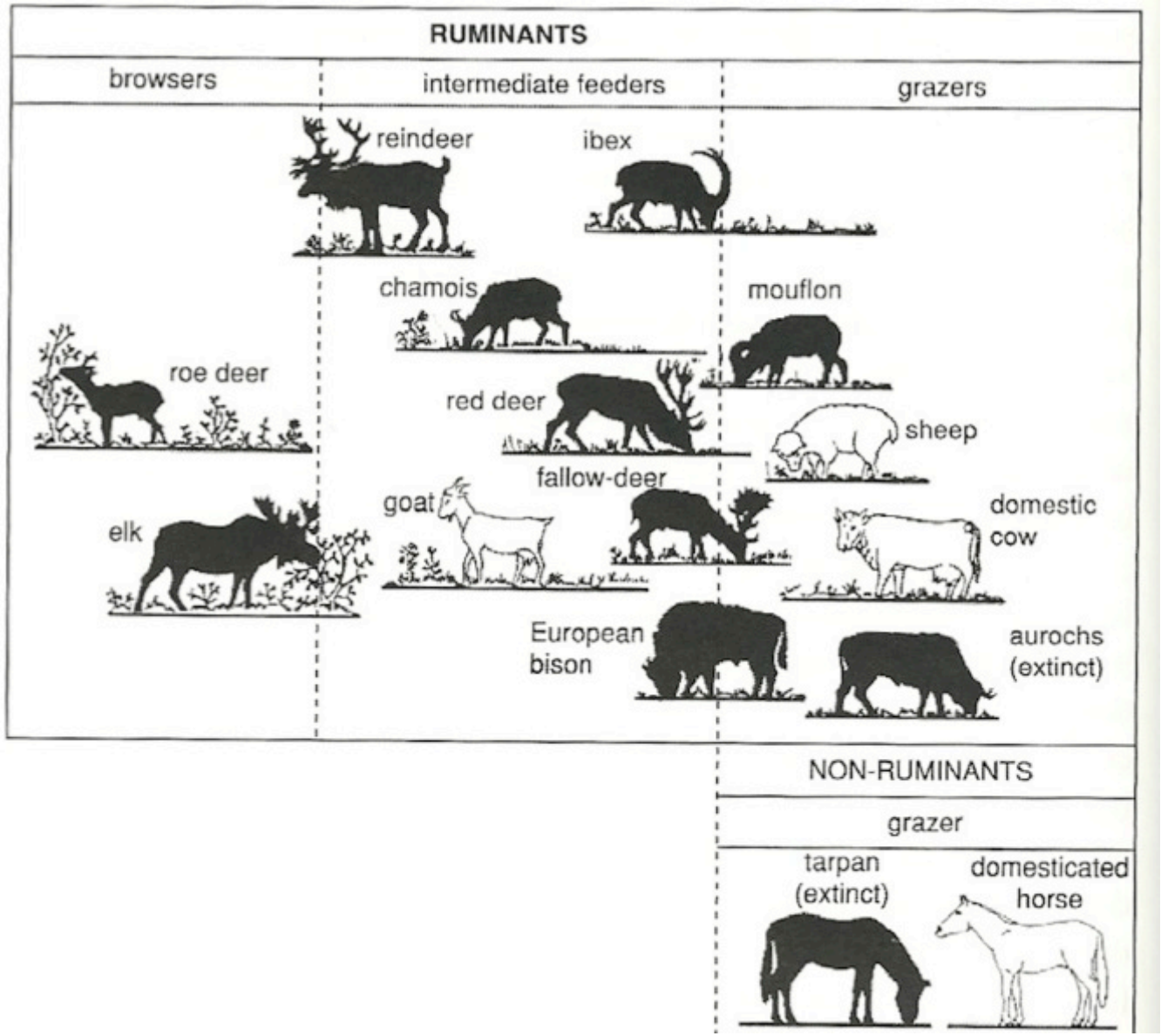
from Stevens und Hume (1995), Clauss et al. (2008)

The traditional view of foregut vs. hindgut fermentation

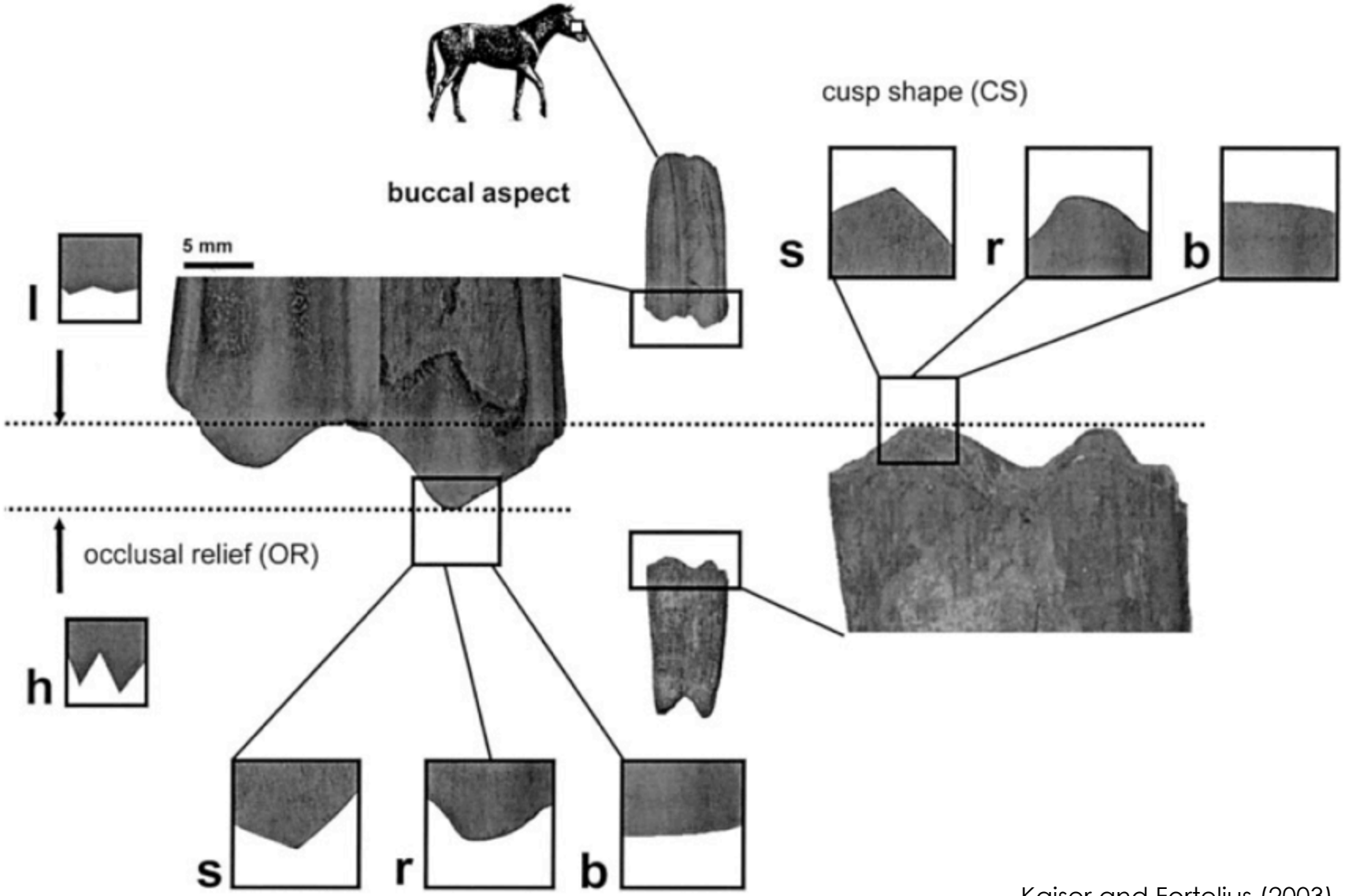


Janis (1976)

Extant horses are grazers



Diet and mesowear



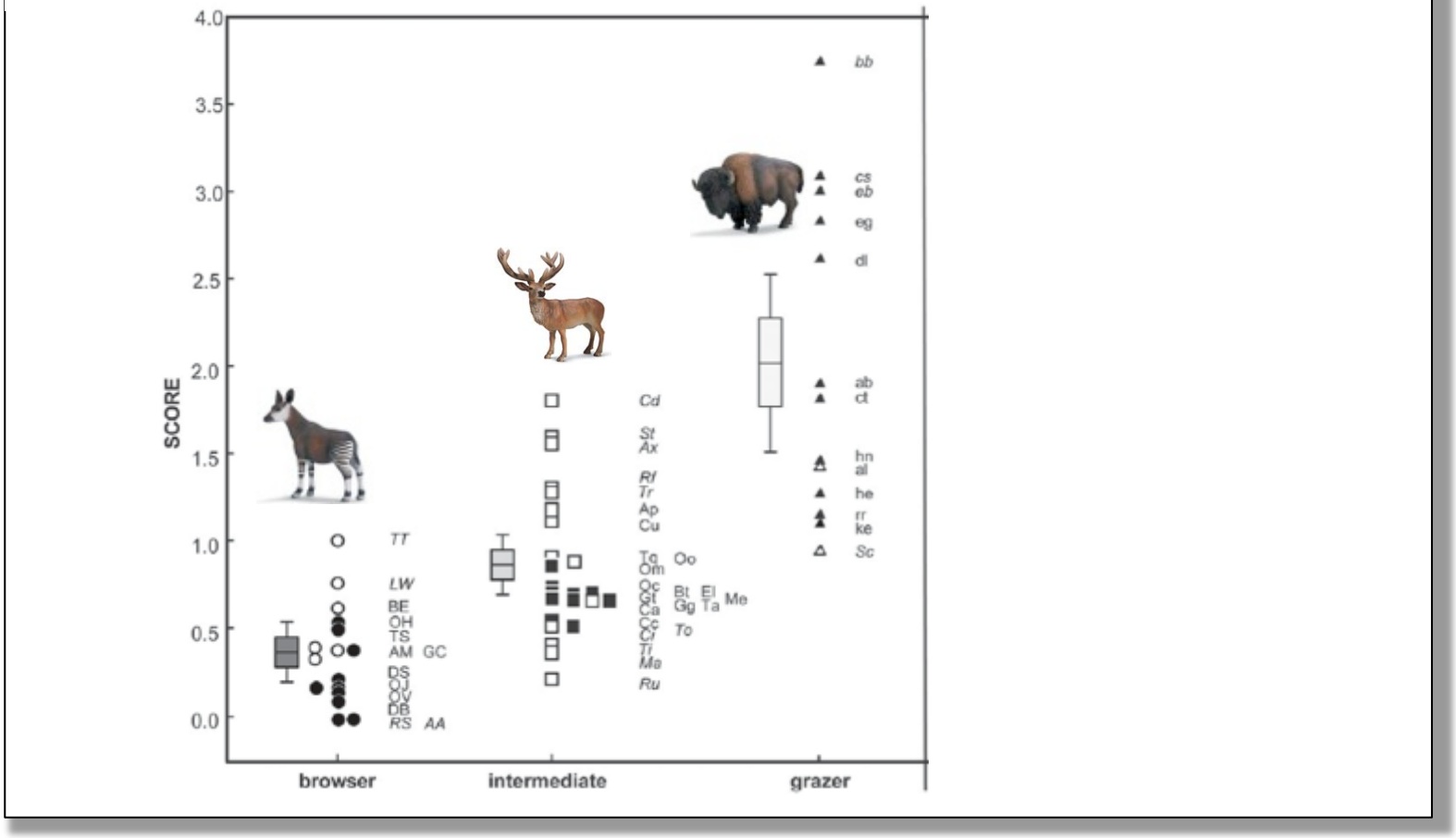
Kaiser and Fortelius (2003)

Diet and mesowear

Historical distribution, habitat requirements and feeding ecology of the genus *Equus* (Perissodactyla)

Ellen SCHULZ* Thomas M. KAISER

Mammal Review **43** (2013) 111–123



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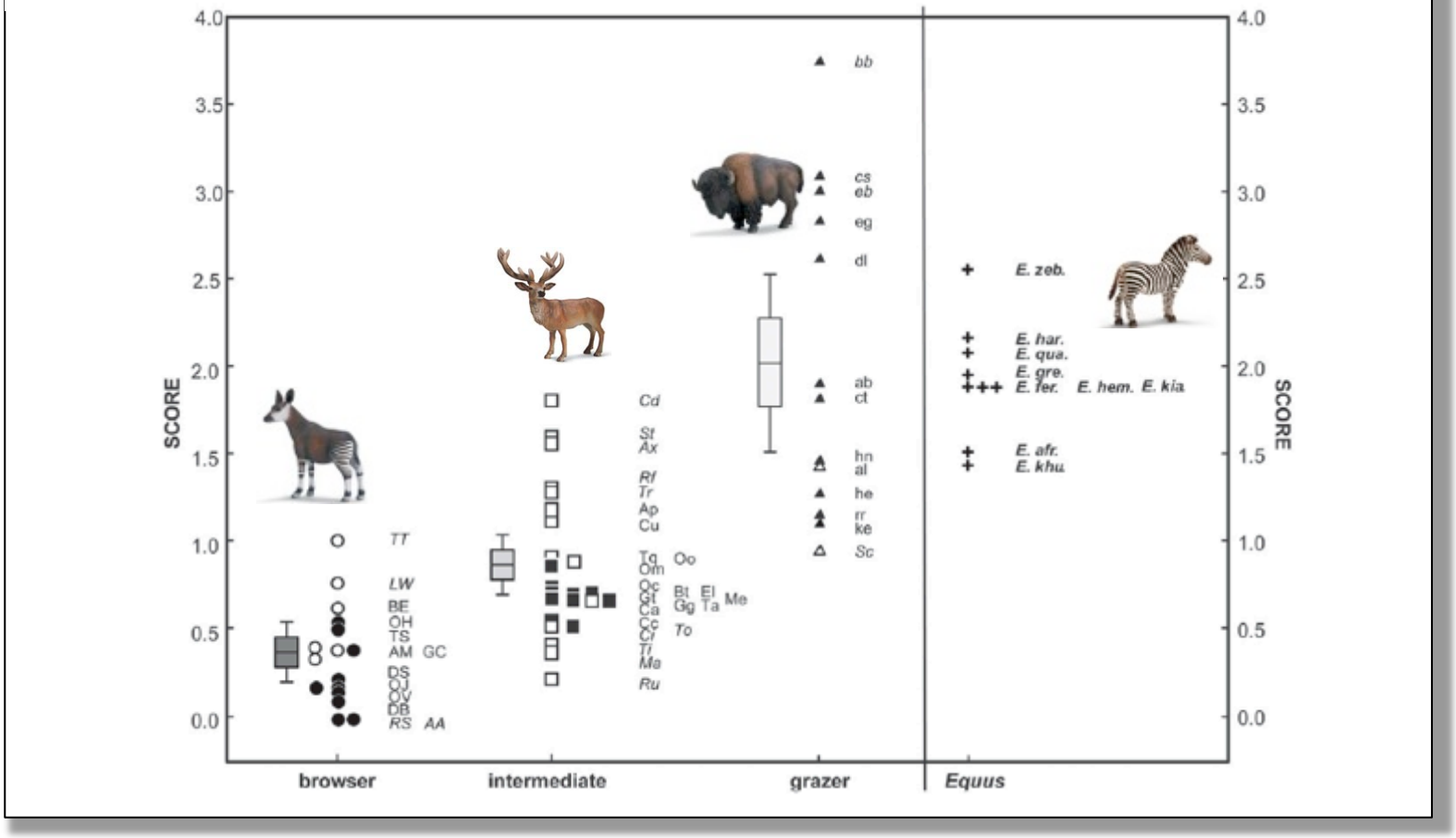
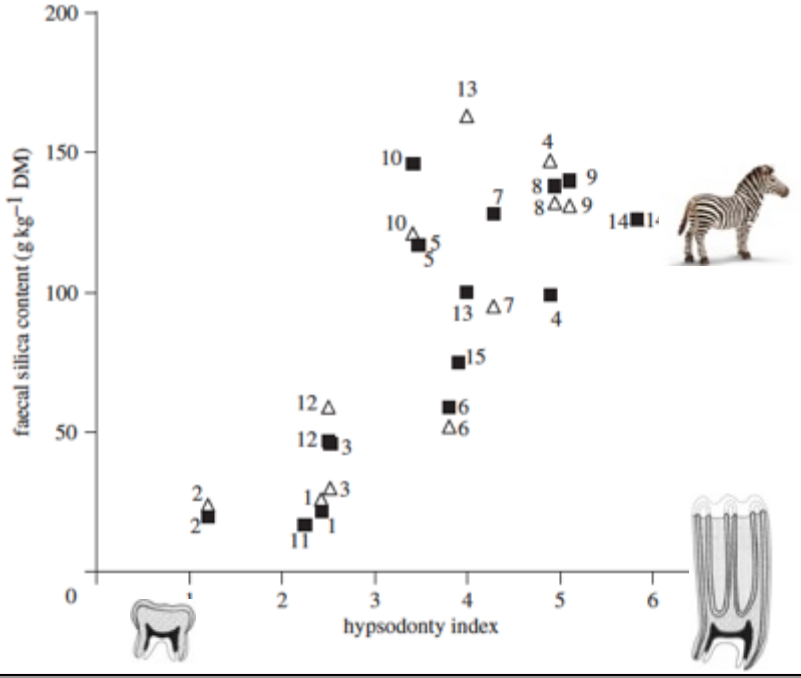


Adapted to abrasive diets

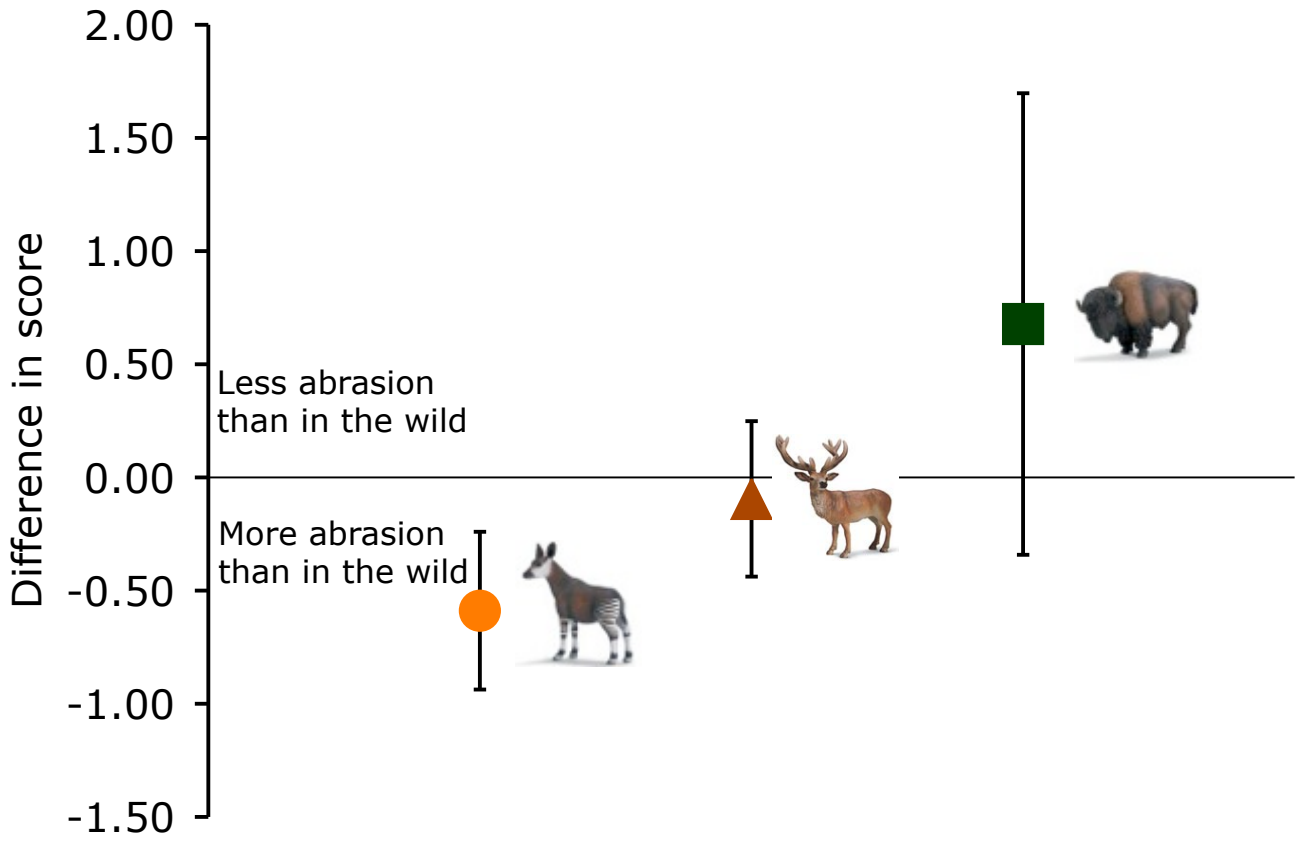
Another one bites the dust: faecal silica levels in large herbivores correlate with high-crowned teeth

Jürgen Hummel[1,*], Eva Findeisen[1], Karl-Heinz Südekum[1], Irina Ruf[2], Thomas M. Kaiser[3], Martin Bucher[4], Marcus Clauss[5] and Daryl Codron[5]

Proc. R. Soc. B (2011) 278, 1742–1747



Diet and mesowear: zoo vs. wild



from Kaiser et al. (2009)

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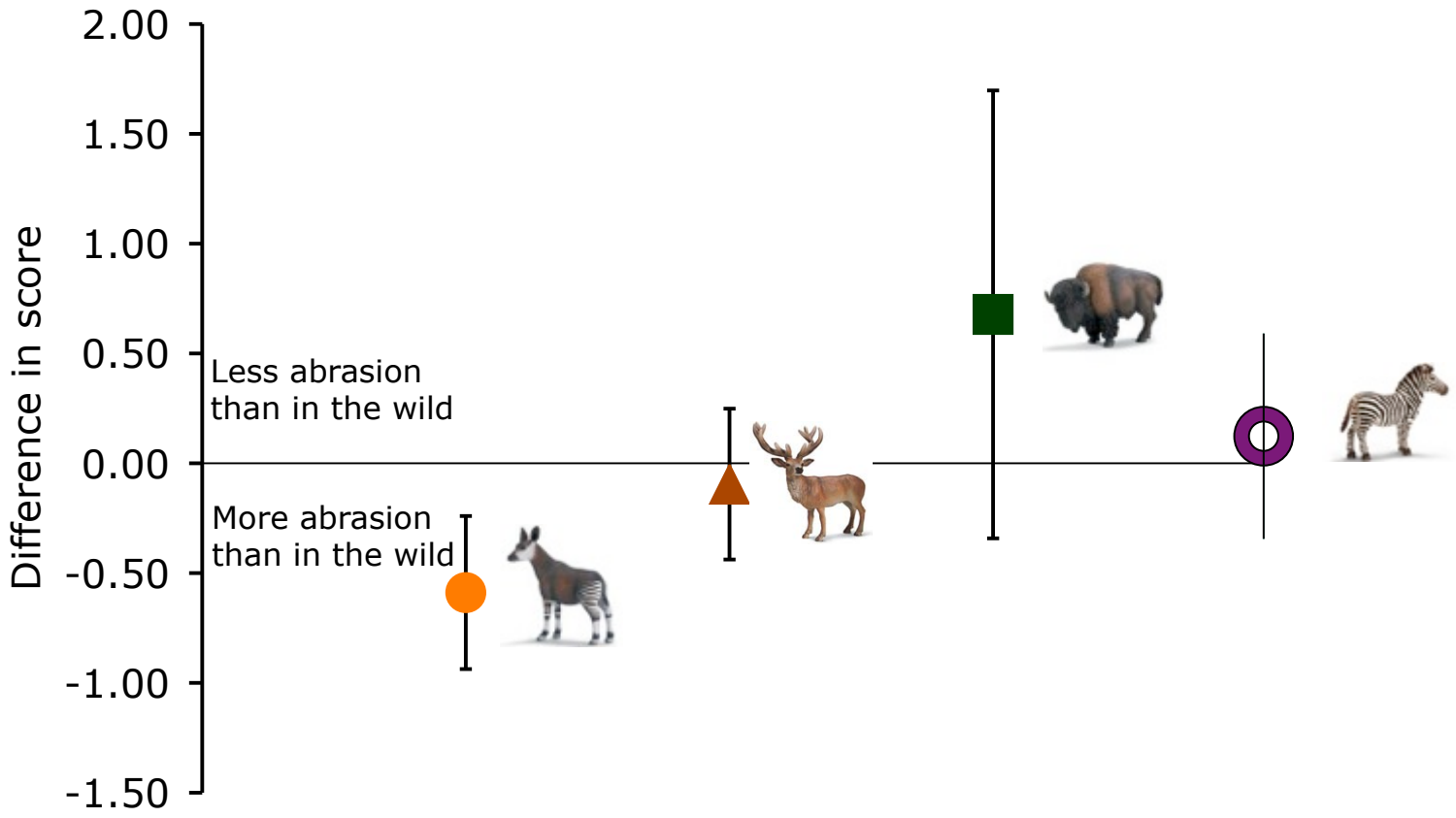

from Kaiser et al. (2009), Taylor et al. (in prep.)

Wild equids in captivity

Similar as in grazing ruminants, few health problems related to nutrition in captive wild equids (because zoo diets are typically more forage dominated?)

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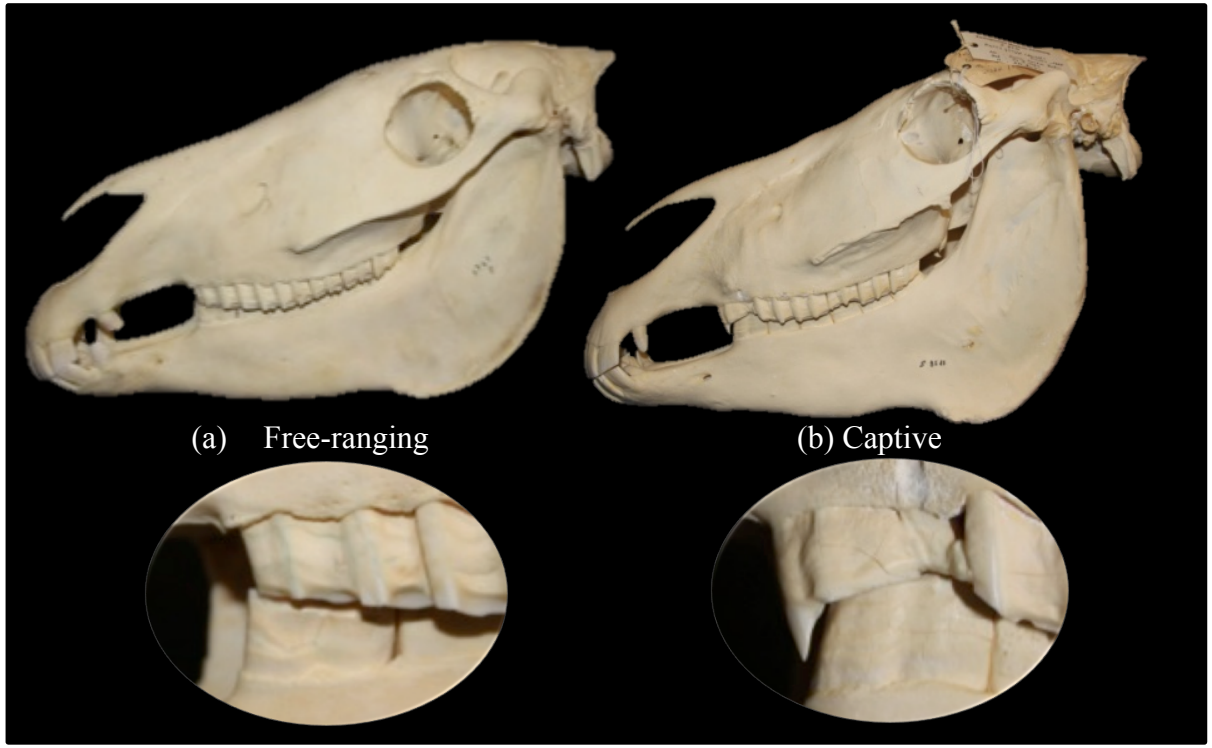
- *Incidents of dental abnormalities*



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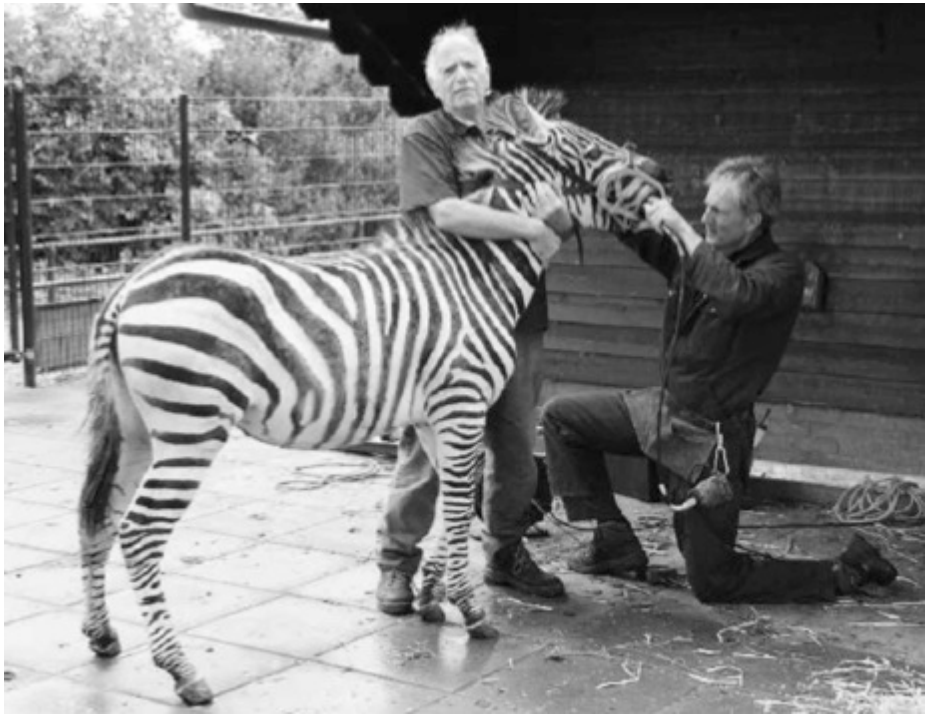

Hoyer et al. (2012)

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- *Incidents of dental abnormalities*

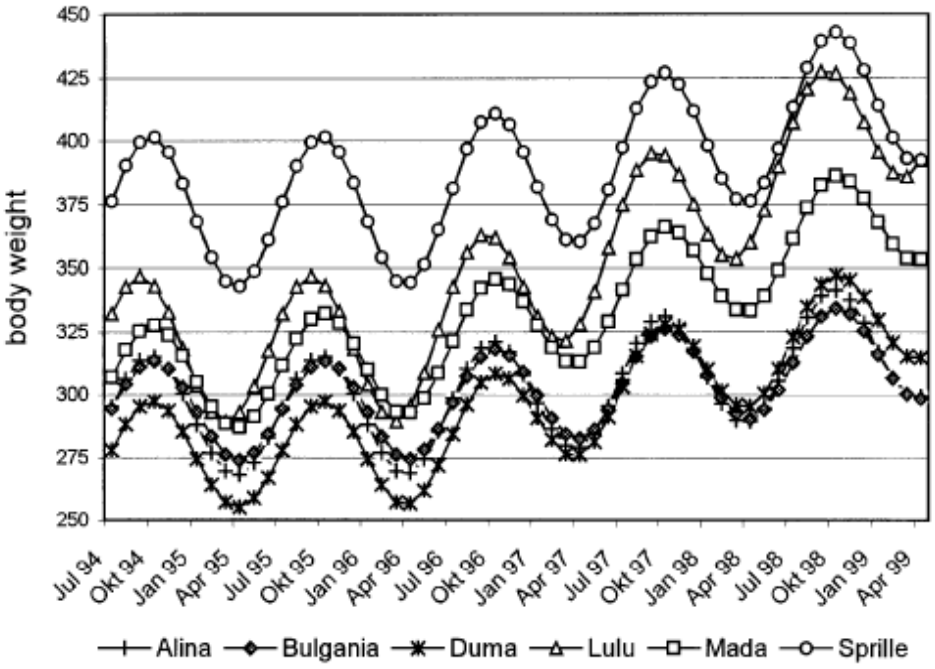
- *Hoof overgrowth/laminitis*

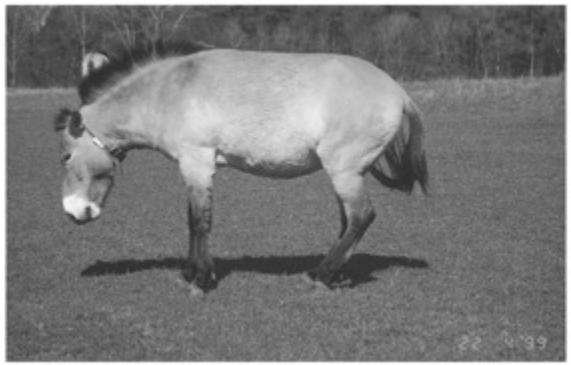
Equid seasonality

Laminitis in Przewalski horses kept in a semireserve

Klaus-Dieter Budras*, Klaus Scheibe[1], Bianca Patan, Wolf J. Streich[1] and Kabsu Kim[2]

J. Vet. Sci. (2001), **2**(1), 1–7





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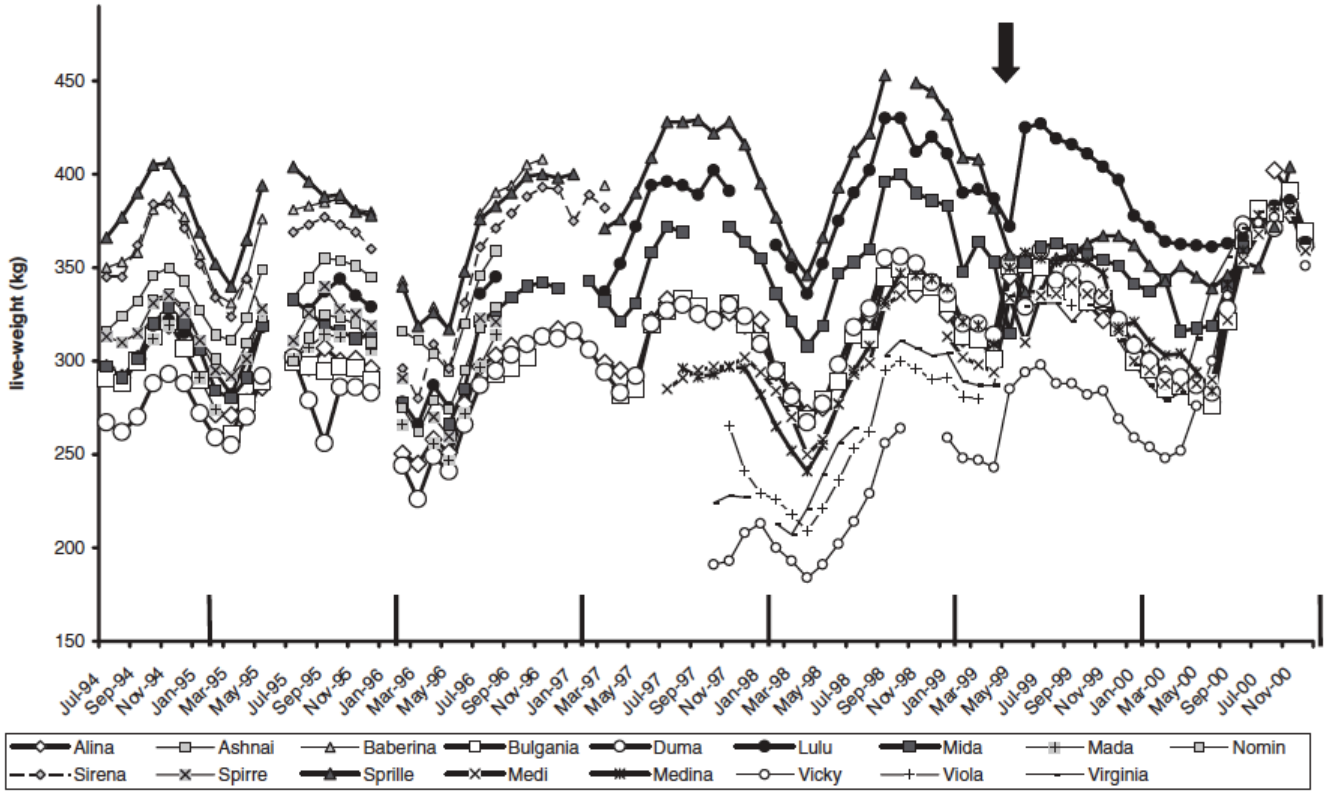
- *Obesity*

Equid seasonality

Annual Rhythm of Body Weight in Przewalski Horses (*Equus ferus przewalskii*)

Klaus M. Scheibe and Wolf J. Streich

Biological Rhythm Research
2003, Vol. 34 No. 4. pp. 383–395



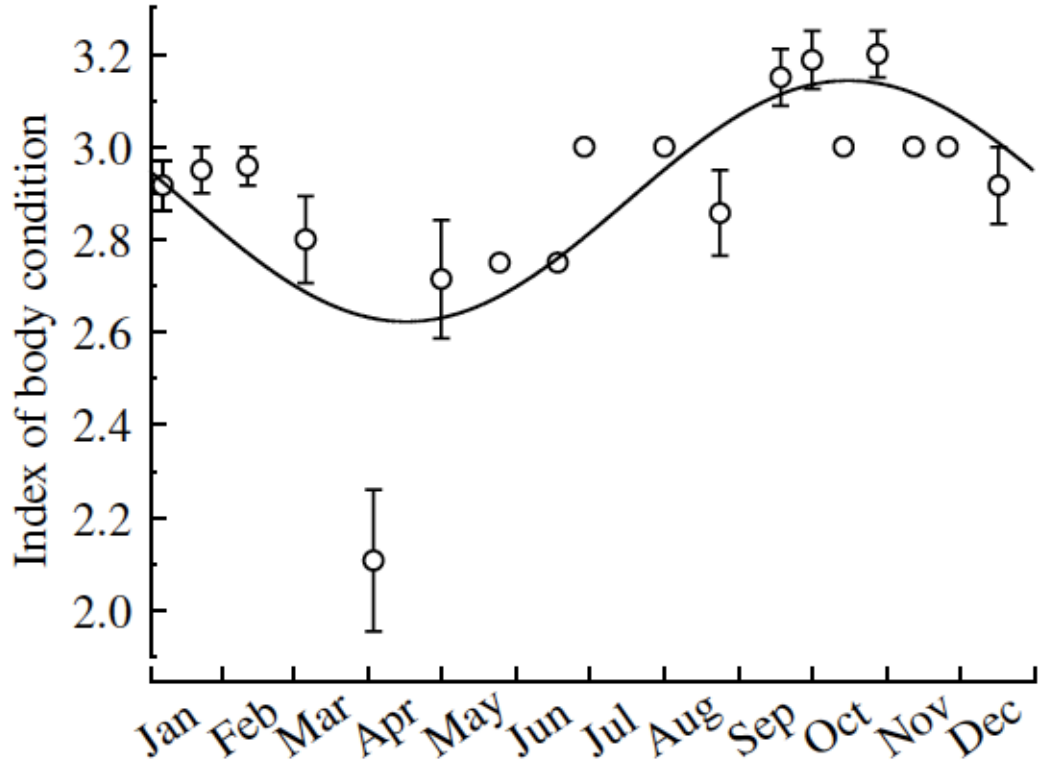
Equid seasonality

Seasonal adjustment of energy budget in a large wild mammal, the Przewalski horse (*Equus ferus przewalskii*)

I. Energy intake

Regina Kuntz, Christina Kubalek, Thomas Ruf, Frieda Tataruch and Walter Arnold*

The Journal of Experimental Biology 209, 4557-4565

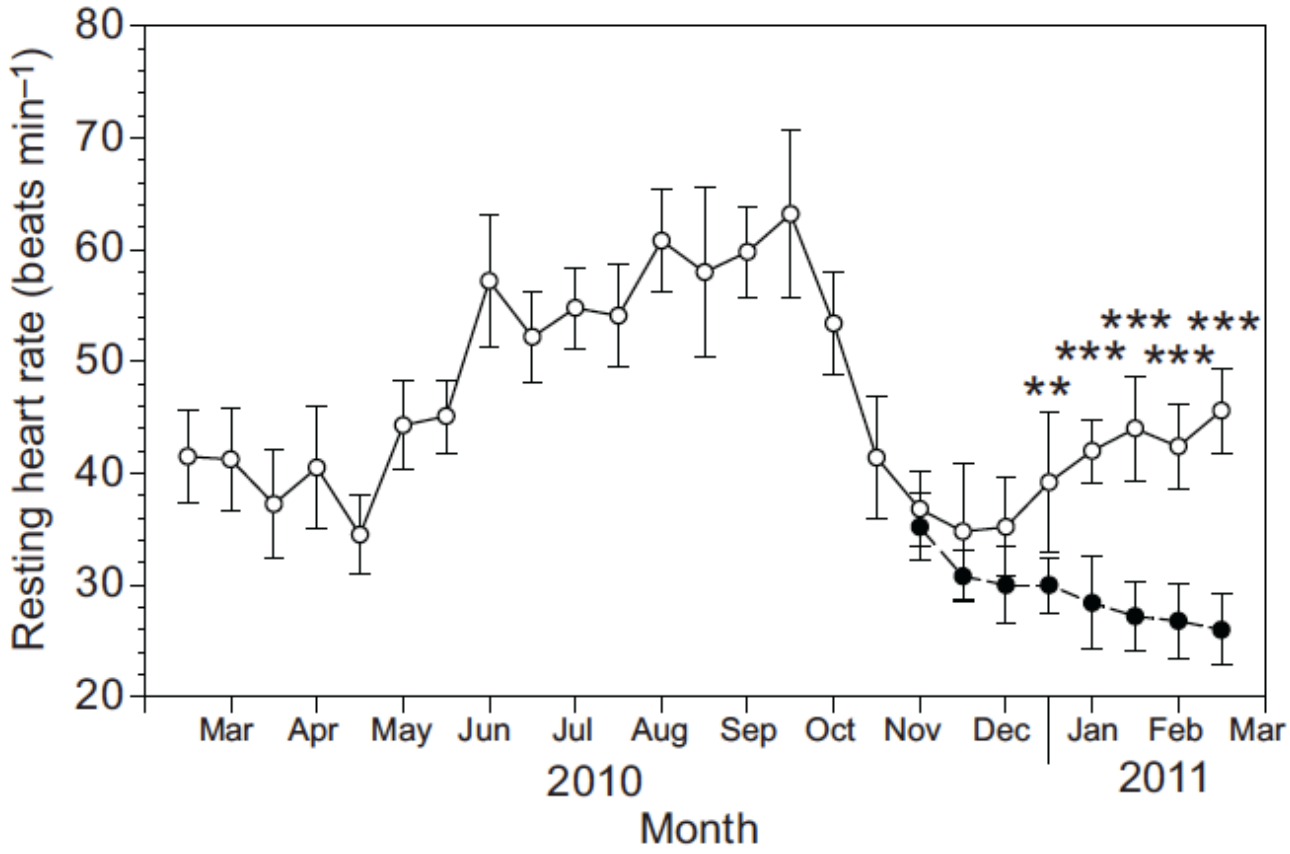


Equid seasonality

Adaptation strategies to seasonal changes in environmental conditions of a domesticated horse breed, the Shetland pony (*Equus ferus caballus*)

Lea Brinkmann, Martina Gerken and Alexander Riek*

The Journal of Experimental Biology 215, 1061-1068



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- *Incidents of dental abnormalities*
- *Hoof overgrowth/laminitis*
- *Obesity*
- *Colic*
- *Vitamin E deficiency*

Conclusion

From a nutritional point of view, wild equids appear well understood: (grass) forage diets available at all times, ideally with mimicking seasonal patterns in the wild.

How the digestive physiology of equids differs from that of ruminants, especially in terms of minimum intake tolerable and differential digesta movements, remain to be investigated.

The sequence, and the mechanisms, of the equid-ruminant diversification and competition in evolution remain to be explained in a way that matches empirical data.

thank you
for your attention

Iron Deficiency in Stabled Dutch Warmblood Foals

H. Brommer and Marianne M. Sloet van Oldruitenborgh-Oosterbaan

J Vet Intern Med 2001;15:482–485