Equid nutritional physiology and behavior – an evolutionary perspective

Marcus Clauss
(Daryl Codron & Jürgen Hummel)

Clinic for Zoo Animals, Exotic Pets and Wildlife, Vetsuisse Faculty, University of Zurich, Switzerland

Texas 2023

University of Zurich
Vetsuisse Faculty

Clinic
of Zoo Animals, Exotic Pets and Wildlife

Equid nutritional physiology and behavior – an evolutionary perspective

… or
how horseshit
was replaced by bullshit
in evolutionary time

Marcus Clauss
(Daryl Codron & Jürgen Hummel)

Clinic for Zoo Animals, Exotic Pets and Wildlife, Vetsuisse Faculty, University of Zurich, Switzerland

Texas 2023

University of Zurich
Vetsuisse Faculty

Clinic
of Zoo Animals, Exotic Pets and Wildlife

Journal of Equine Veterinary Science 124 (2023) 104265

Contents lists available at ScienceDirect

Journal of Equine Veterinary Science

journal homepage: www.j-evs.com

Review Article

Equid Nutritional Physiology and Behavior: An Evolutionary Perspective

Marcus Clauss[a,*], Daryl Codron[b], Jürgen Hummel[c]

[a] Clinic for Zoo Animals, Exotic Pets and Wildlife, Vetsuisse Faculty, University of Zurich, Zurich, Switzerland
[b] Department of Zoology and Entomology, University of the Free State, Bloemfontein, South Africa
[c] Ruminant Nutrition, Department of Animal Sciences, University of Goettingen, Goettingen, Germany

ARTICLE INFO

Article history:
Received 5 January 2023
Received in revised form 18 February 2023
Accepted 23 February 2023
Available online 8 March 2023

Keywords:
Equids
Ruminants
Bovids
Digestion
Ingestion
Chewing

ABSTRACT

Like other members of the odd-toed ungulates (the perissodactyls), equids once had a higher species diversity in the fossil record than they have today. This is generally explained in comparison to the enormous diversity of bovid ruminants. Theories on putative competitive disadvantages of equids include the use of a single toe as opposed to two toes per leg, the lack of a specific brain cooling (and hence water-saving) mechanism, longer gestation periods that delay reproductive output, and in particular digestive physiology. To date, there is no empirical support for the theory that equids fare better on low-quality forage than ruminants. In contrast to the traditional juxtaposition of hindgut and foregut fermenters, we suggest that it is more insightful to sketch the evolution of equid and ruminant digestive physiology as a case of convergence: both evolved a particularly high chewing efficacy in their respective groups, which facilitates comparatively high feed and hence energy intakes. But because the ruminant system, less based on tooth anatomy but more on a forestomach sorting mechanism, is more effective, equids depend more on high feed intakes than ruminants and may well be more susceptible to feed shortages. Arguably, the most underemphasized characteristic of equids may be that in contrast to many other herbivores including ruminants and coprophageous hindgut fermenters, equids do not use the microbial biomass growing in their gastrointestinal tract. Equids display behavioral and morphophysiological adaptations to high feed intakes, and their cranial anatomy that facilitates the cropping of forage while performing grinding chewing at the same time might be unique. Rather than looking for explanations how equids are better adapted to their present niches than other organisms, considering them remnants of a different morphophysiological solution may be more appropriate.

1. Introduction

Many of us deal with living animals, whether for professional reasons as veterinarians and farmers, or for leisure as pet owners or animal enthusiasts. Although we have learned of evolution and fossils during our various forms of education, many of us are usually unaware in our daily business that the extant (living) fauna was preceded by an array of "endless forms" [1] that are now extinct. For many practical day-to-day decisions, knowledge of the evolutionary background of a species may not be critical. By contrast, when it comes to understanding patterns of species diversity, and understanding anatomical, physiological and behavioral differences between species or taxa, evolutionary narratives are paramount.

As any other knowledge system, evolutionary biology is in constant development, and narratives that have previously been in circulation may not necessarily stand the test of time. This is often the case when new fossil discoveries are made, or when theories are freshly tested with empirical evidence, whether from fossil or extant animals. In this review, we present various current theories on characteristics evolved by equids over evolutionary time. In doing so, we have tried to use an accessible language that uses colloquial idioms for the sake of clarity, without disrespect for the

Conflict of interest statement: The authors declare having no known competing financial interests or personal relationship that could have appeared to influence the work reported in this article.

Animal welfare/ethical statement: No animal experiments were performed for the writing of this review article.

* Corresponding author at: Marcus Clauss, Clinic for Zoo Animals, Exotic Pets and Wildlife, Vetsuisse Faculty, University of Zurich, Zurich 8057, Switzerland.
E-mail address: mclauss@vetclinics.uzh.ch (M. Clauss).

https://doi.org/10.1016/j.jevs.2023.104265

Equid diversity and evolution

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

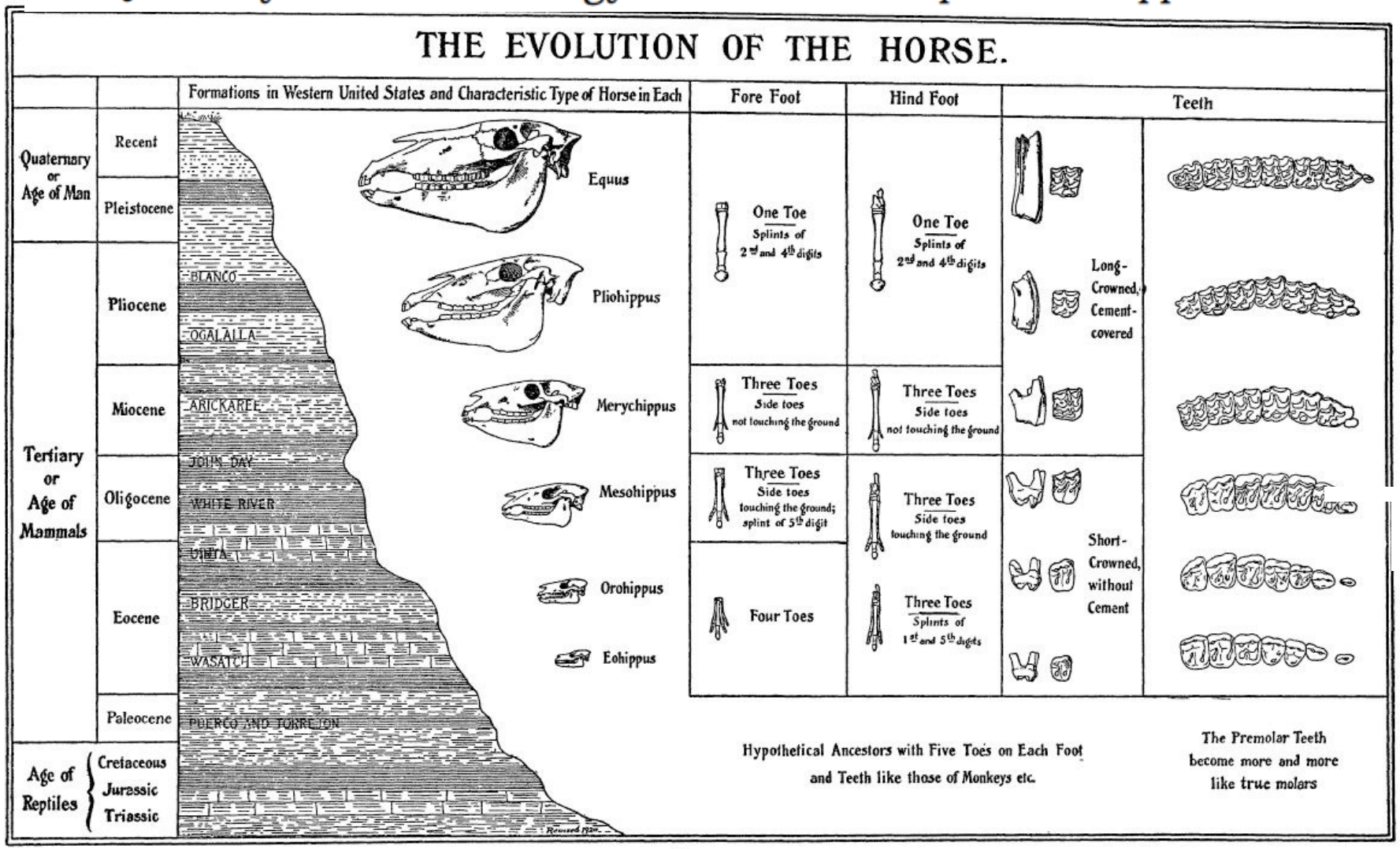


FIG. 27

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

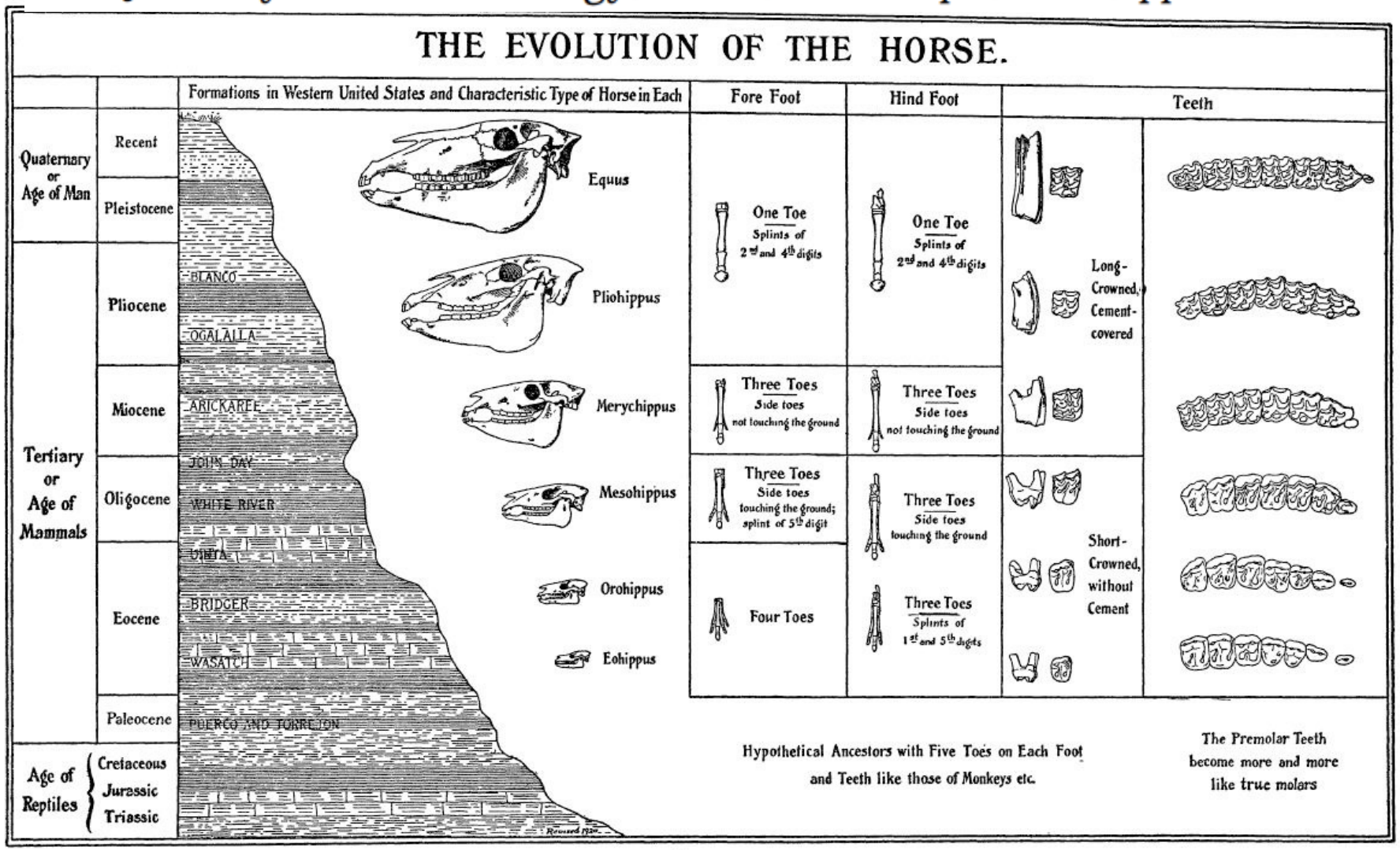
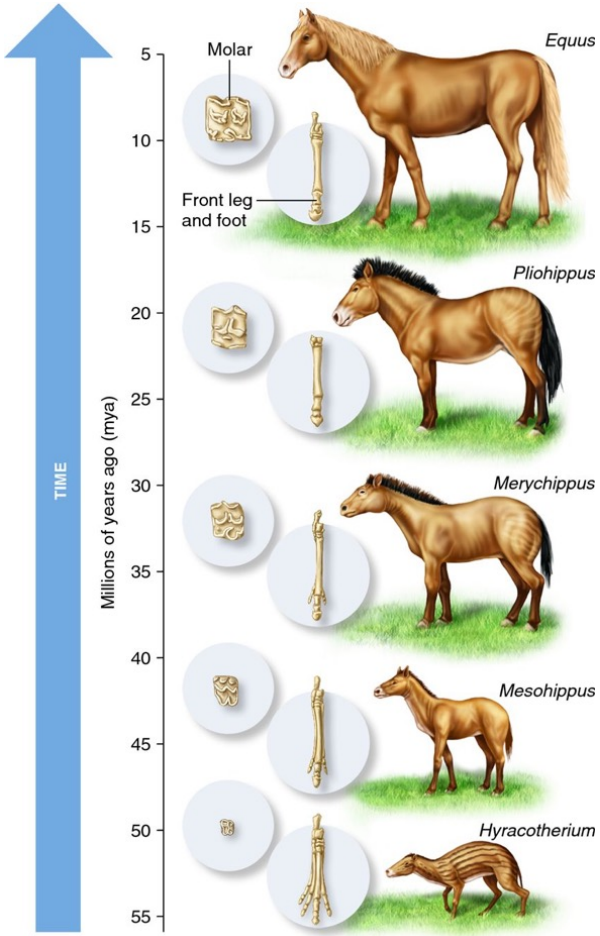
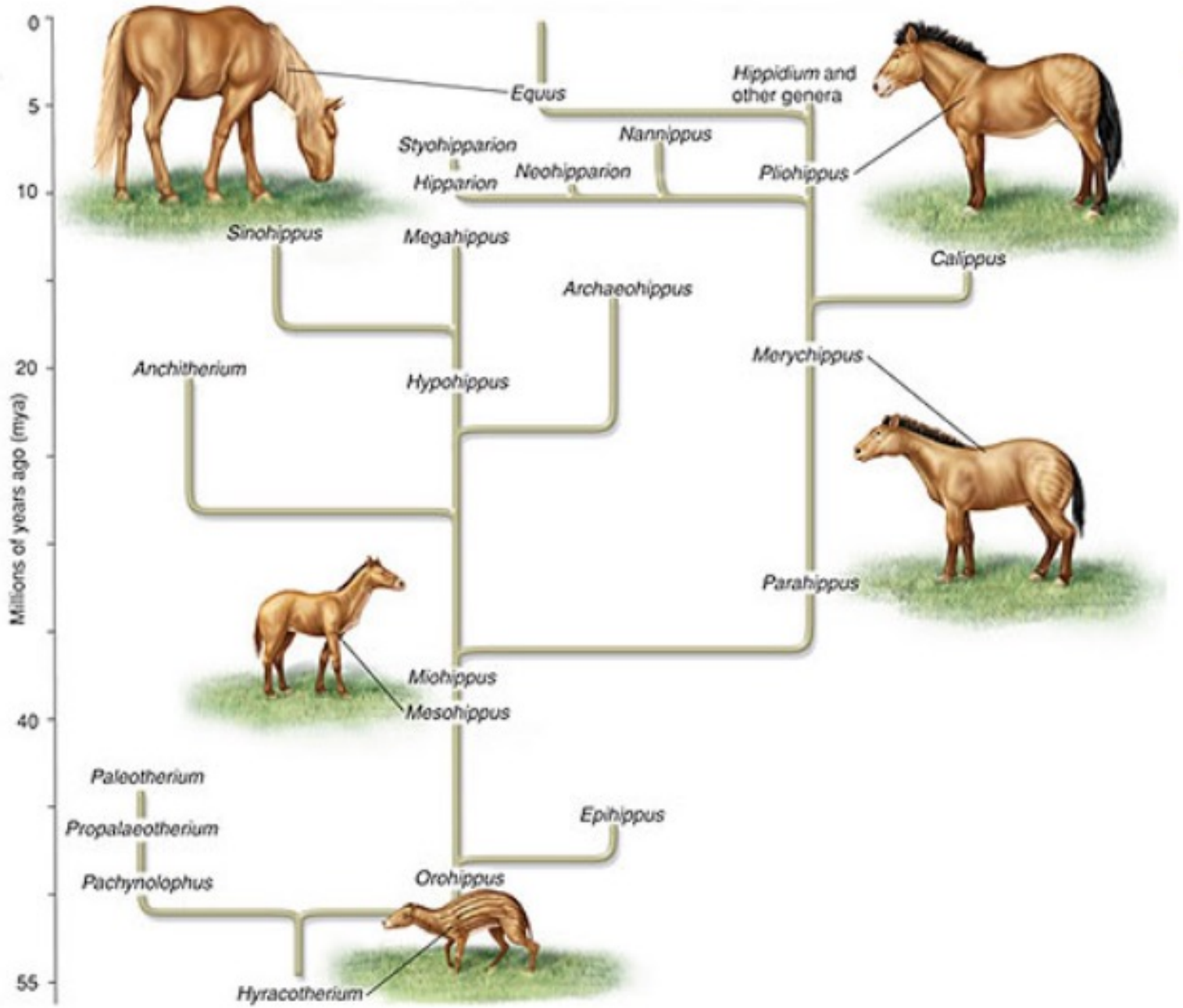
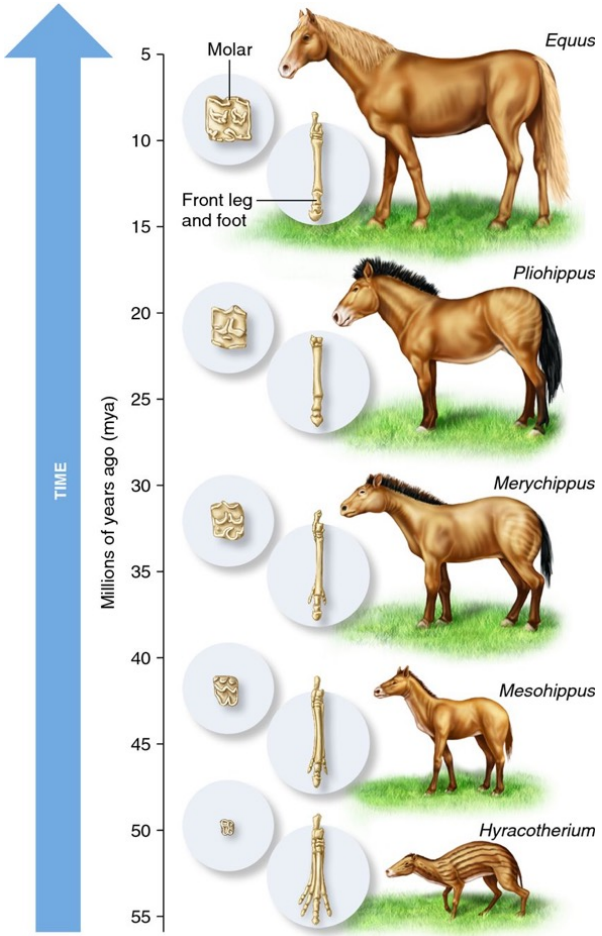


FIG. 27

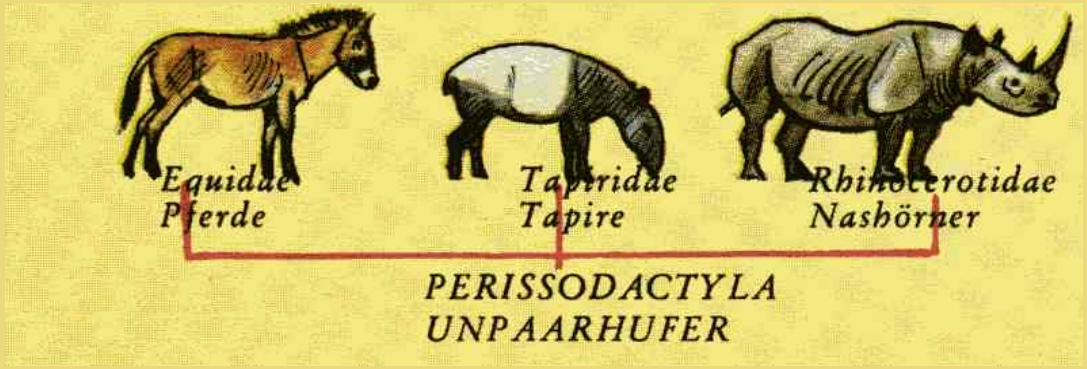



Millions of years ago (mya)
0
5
10
20
40
55
Equus
Hippidium and other genera
Nannippus
Stylohipparion
Hipparion
Neohipparion
Pliohippus
Sinohippus
Megahippus
Calippus
Archaeohippus
Anchitherium
Hypohippus
Merychippus
Parahippus
Miohippus
Mesohippus
Paleotherium
Propalaeotherium
Pachynolophus
Epihippus
Orohippus
Hyracotherium


TIME
Millions of years ago (mya)
5
10
15
20
25
30
35
40
45
50
55
Molar
Front leg and foot
Equus
Pliohippus
Merychippus
Mesohippus
Hyracotherium

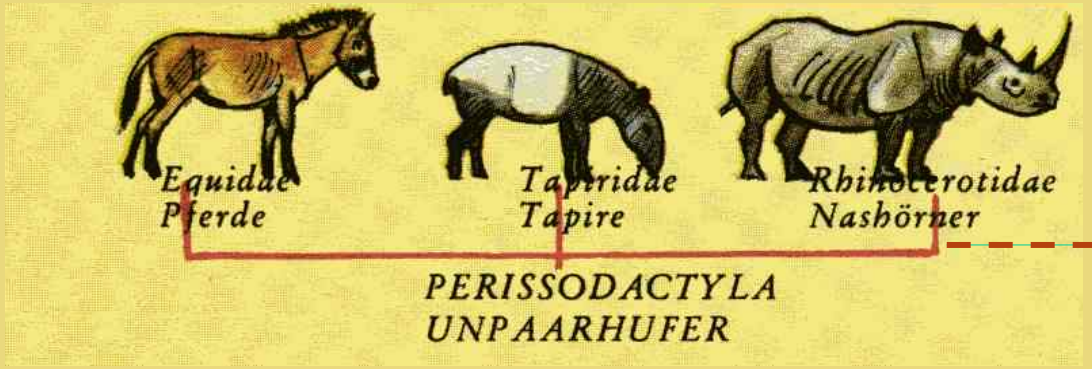
Large herbivore diversity in deep time: Perissodactyls

Large herbivore diversity in deep time: Perissodactyls



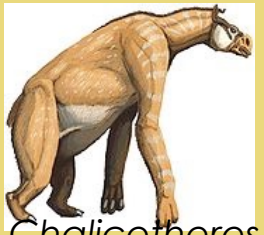
Large herbivore diversity in deep time: Perissodactyls

Chalicotheres

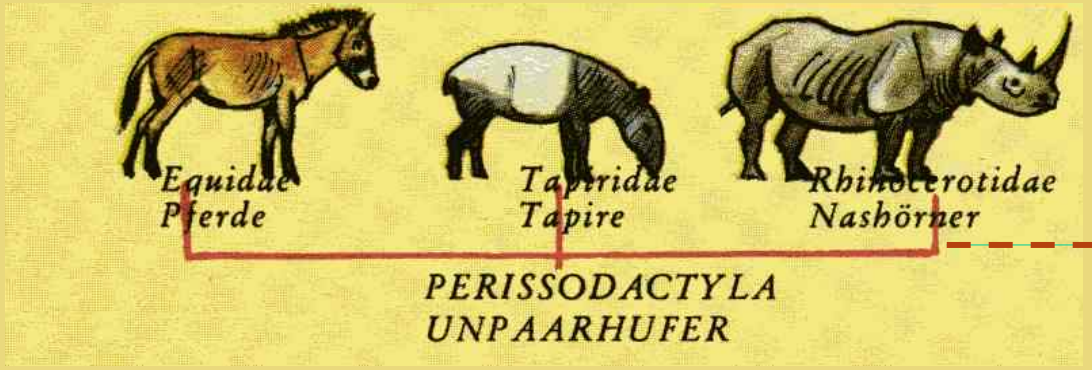


Large herbivore diversity in deep time: Perissodactyls

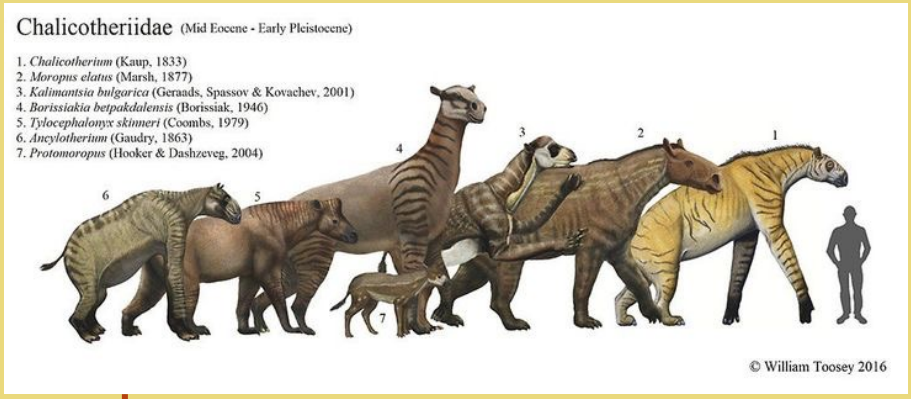
Brontotheres



Chalicotheres

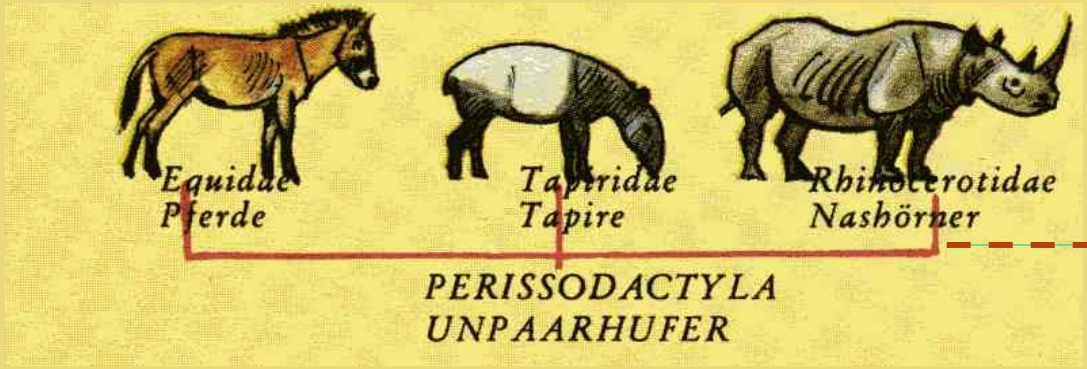


Large herbivore diversity in deep time: Perissodactyls

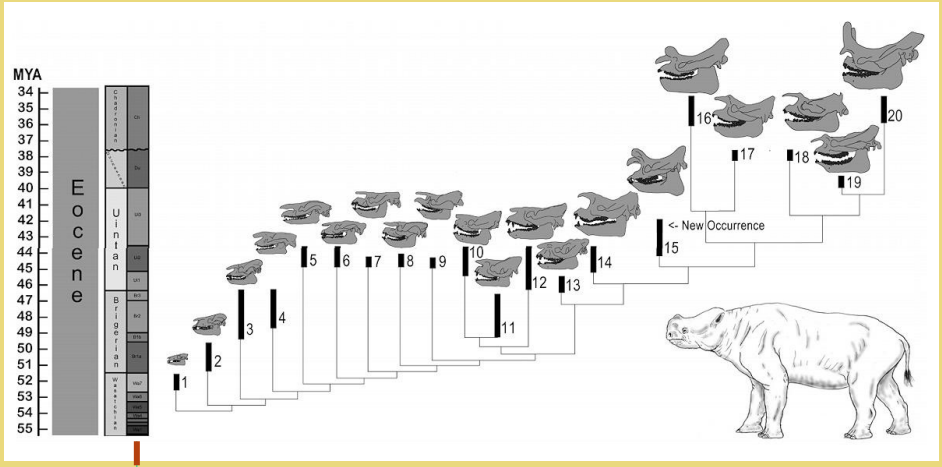


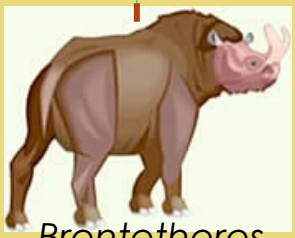
Brontotheres

Chalicotheres

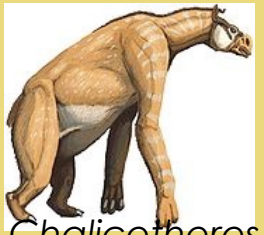


Large herbivore diversity in deep time: Perissodactyls

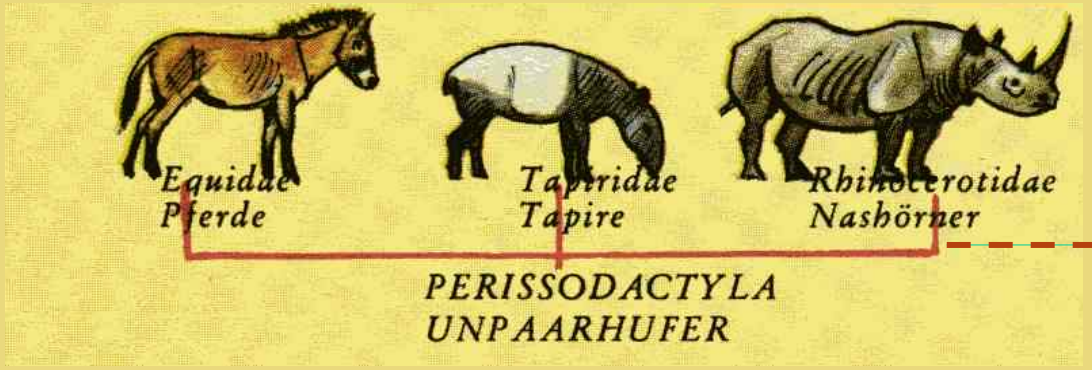




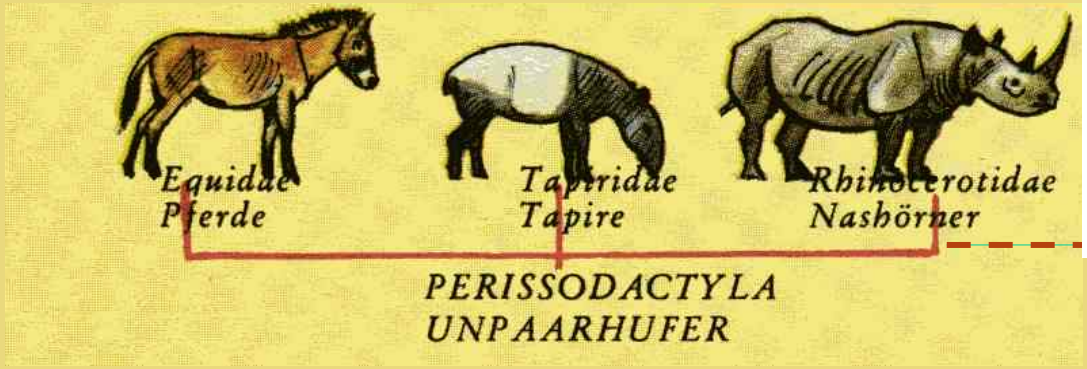
Brontotheres

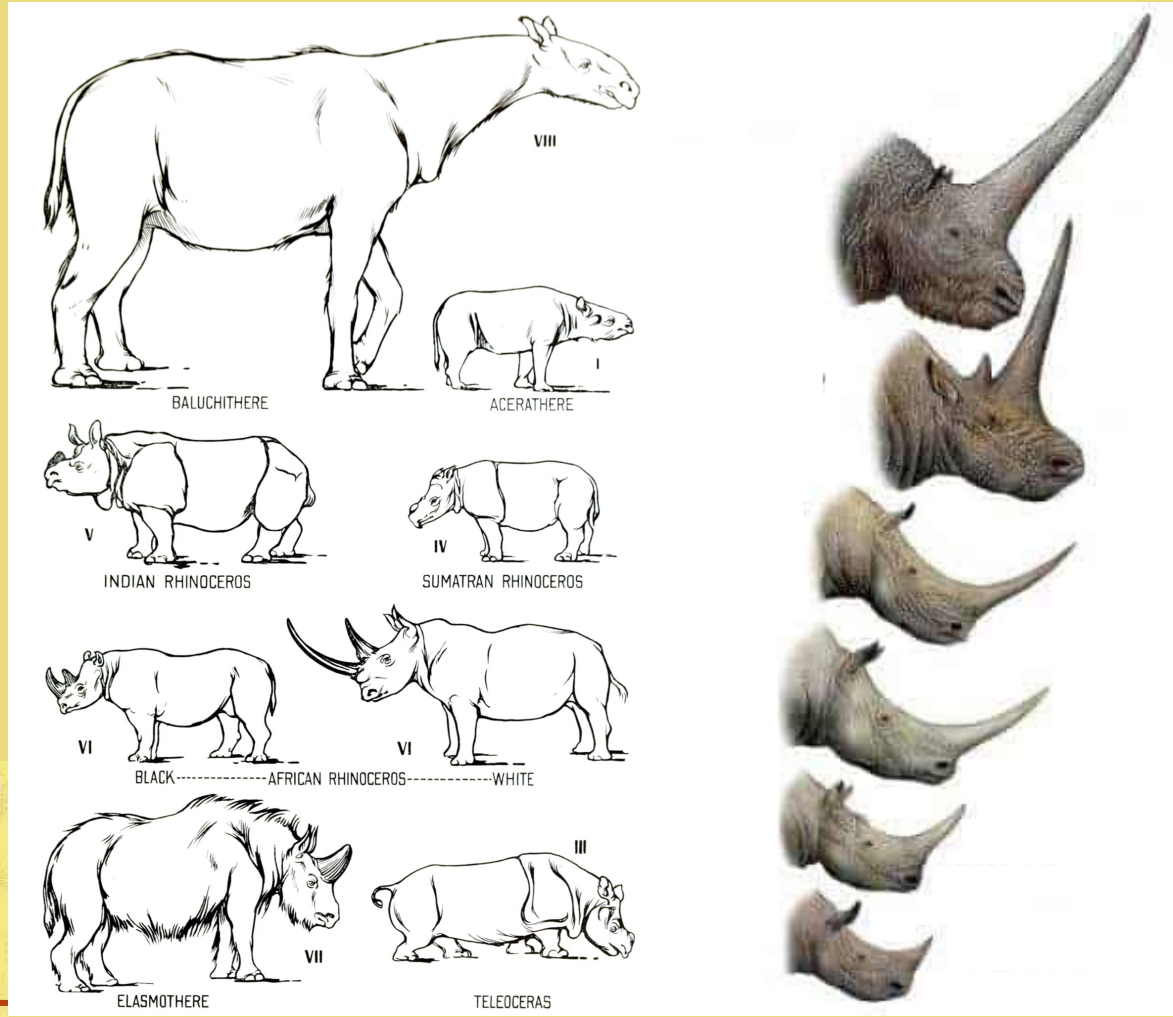


Chalicotheres

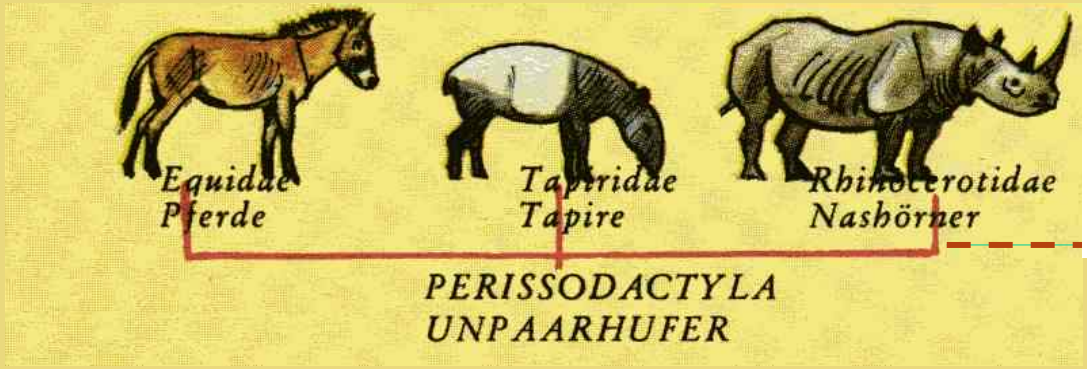


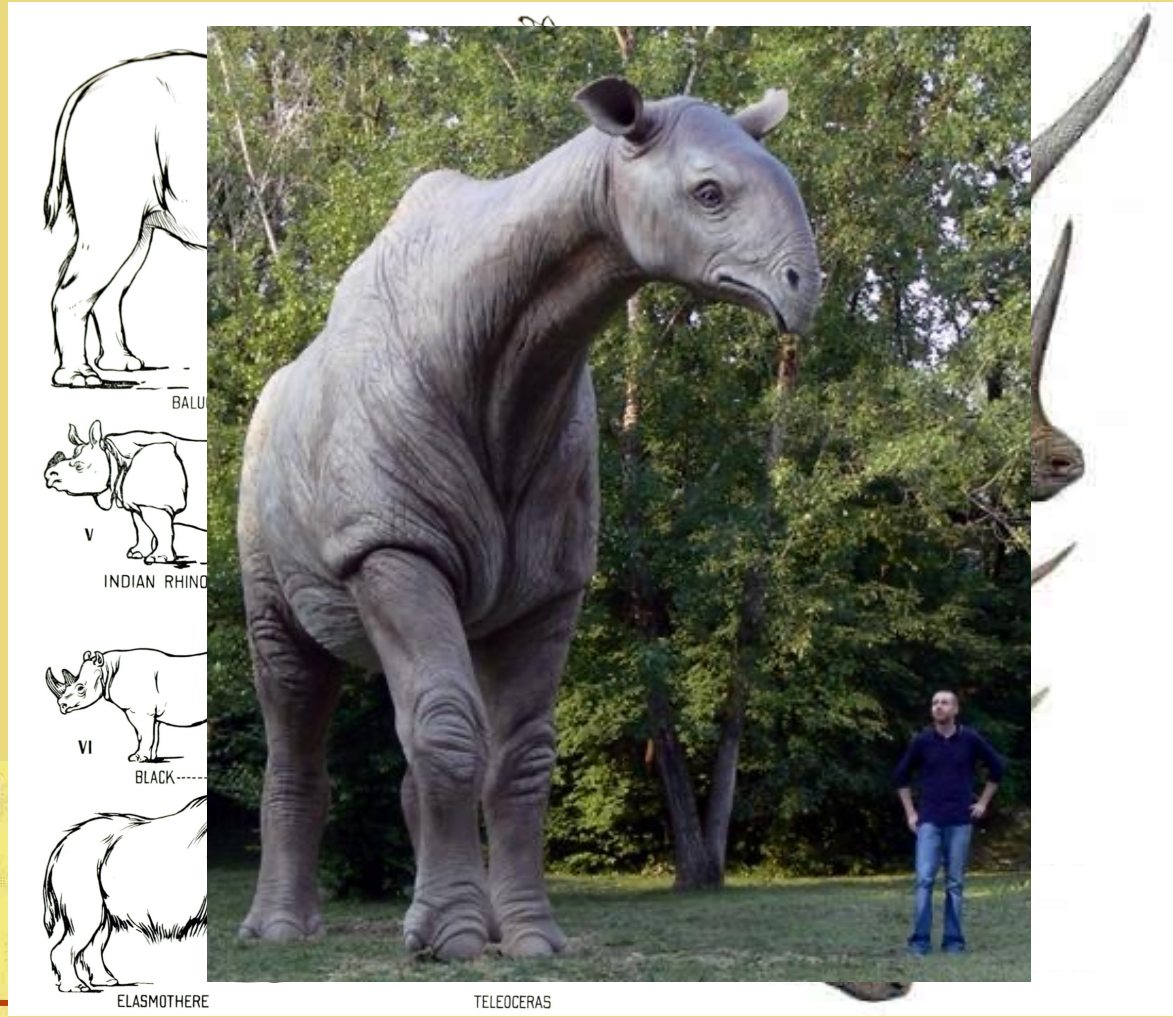
Large herbivore diversity in deep time: Perissodactyls



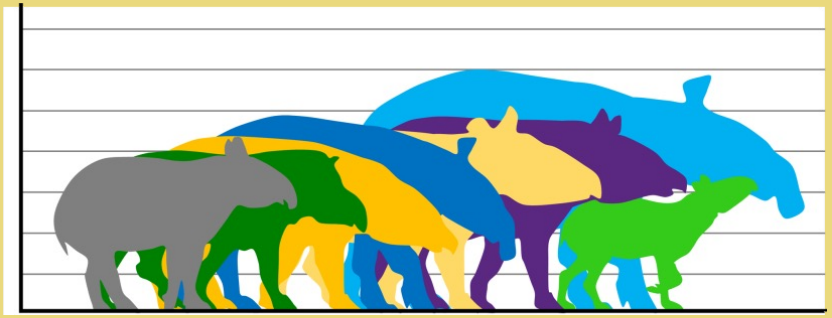


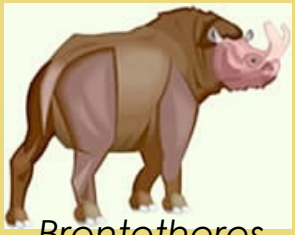
Large herbivore diversity in deep time: Perissodactyls



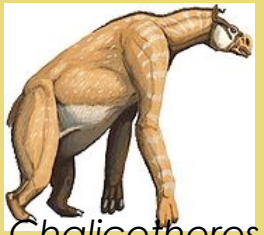


Large herbivore diversity in deep time: Perissodactyls

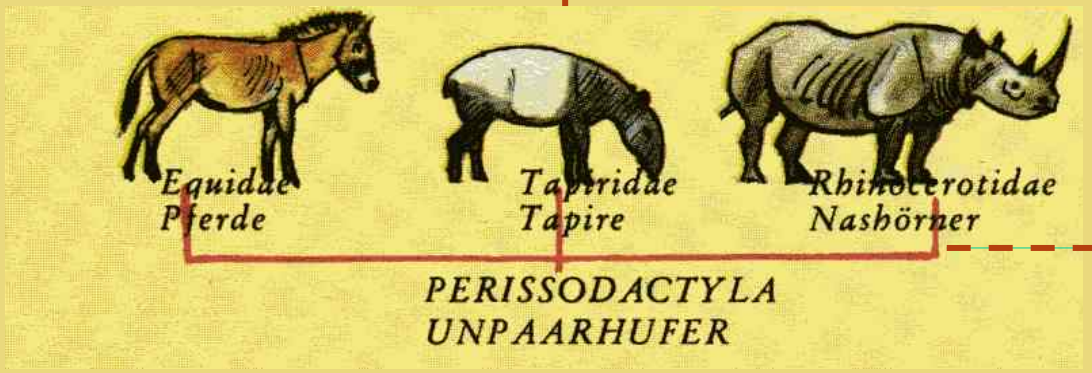




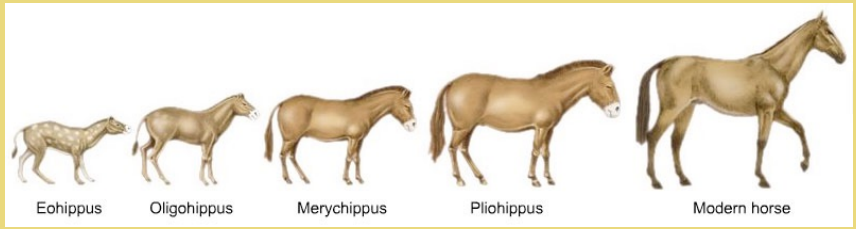
Brontotheres



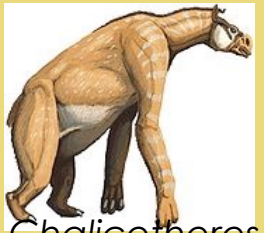
Chalicotheres



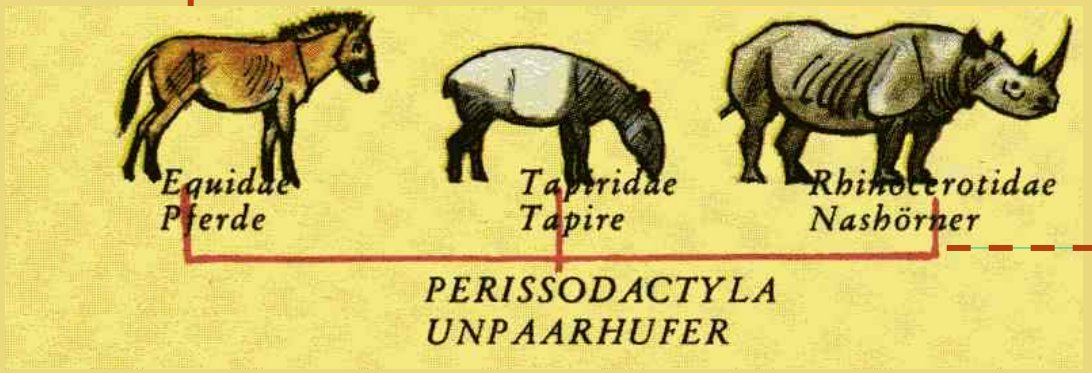
Large herbivore diversity in deep time: Perissodactyls



Brontotheres



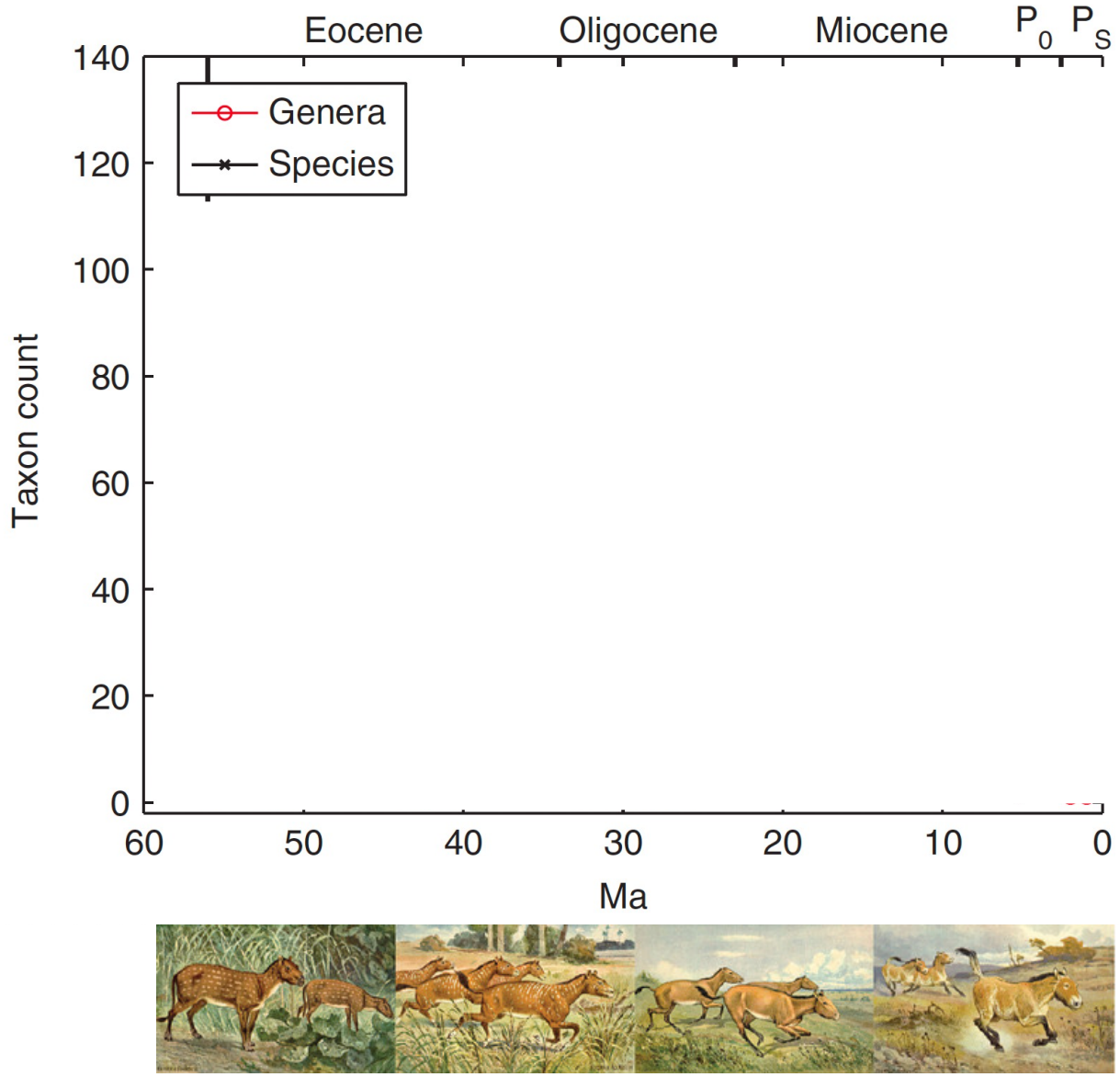
Chalicotheres



Body mass evolution and diversification within horses (family Equidae)

Ecology Letters, (2014) **17**: 211–220

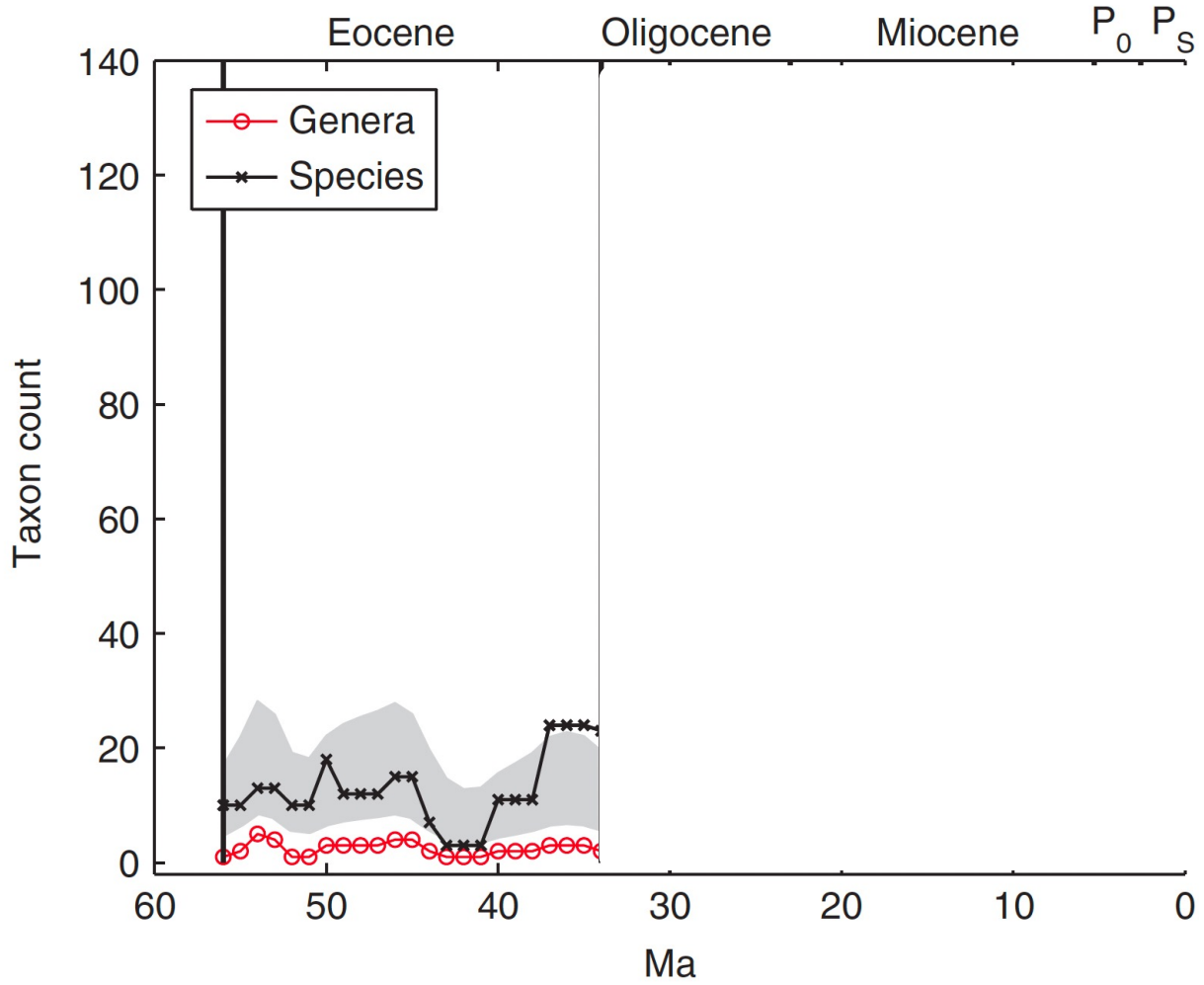
Lauren Shoemaker[1,2] **and Aaron Clauset**[2,3,4]*



Body mass evolution and diversification within horses (family Equidae)

Ecology Letters, (2014) **17**: 211–220

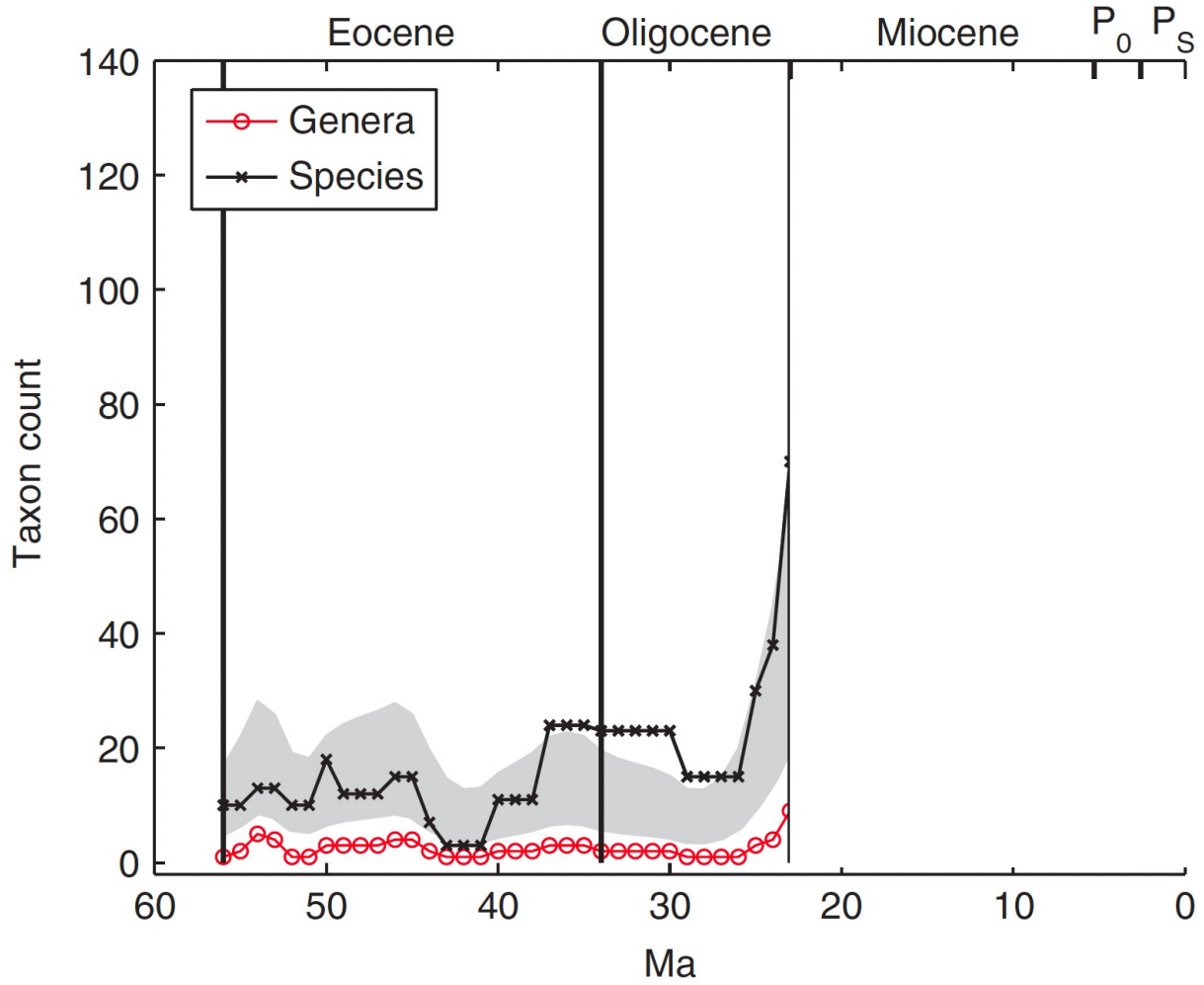
Lauren Shoemaker[1,2] **and Aaron Clauset**[2,3,4]*



Body mass evolution and diversification within horses (family Equidae)

Ecology Letters, (2014) **17**: 211–220

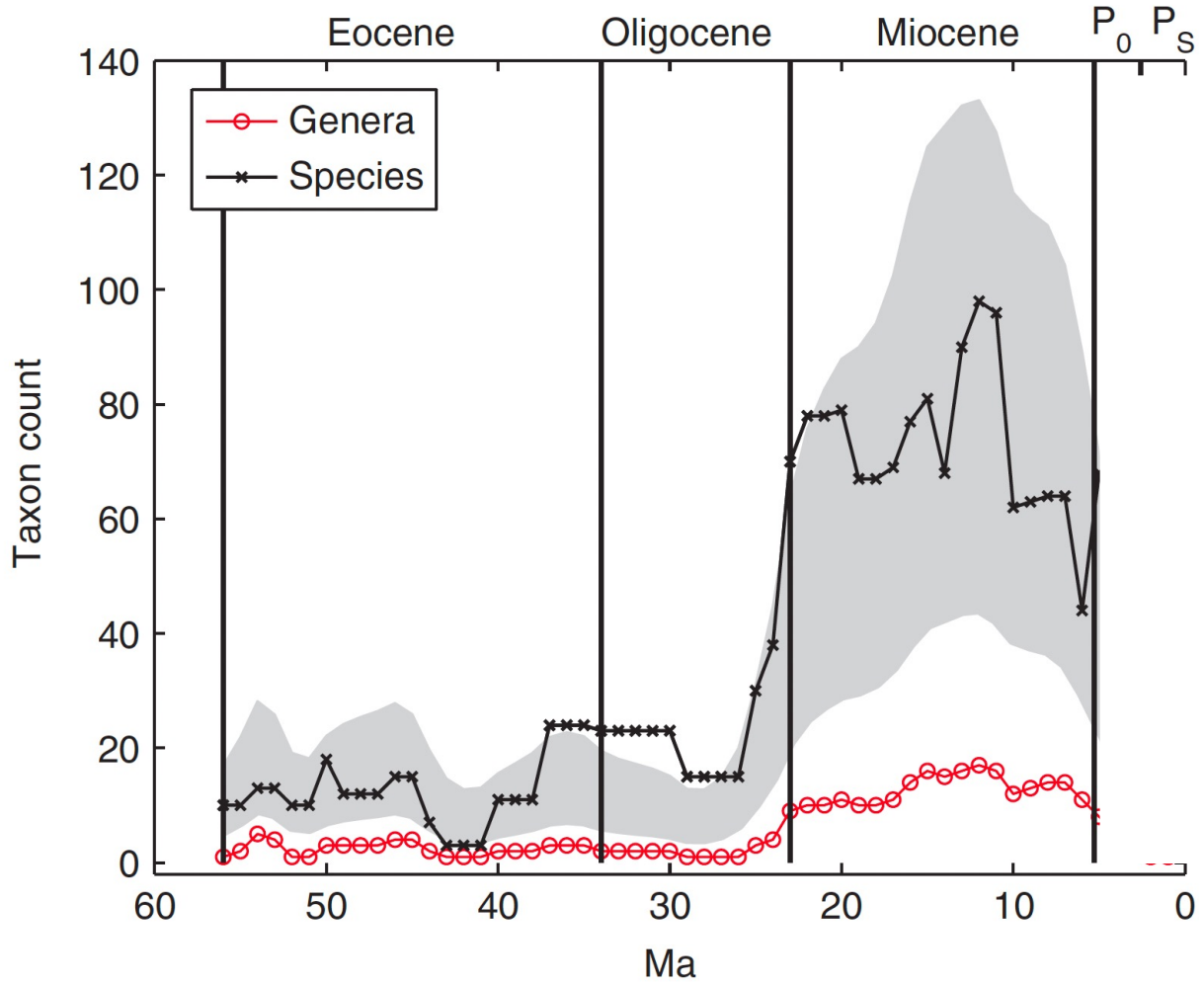
Lauren Shoemaker[1,2] **and Aaron Clauset**[2,3,4]*



Body mass evolution and diversification within horses (family Equidae)

Ecology Letters, (2014) **17**: 211–220

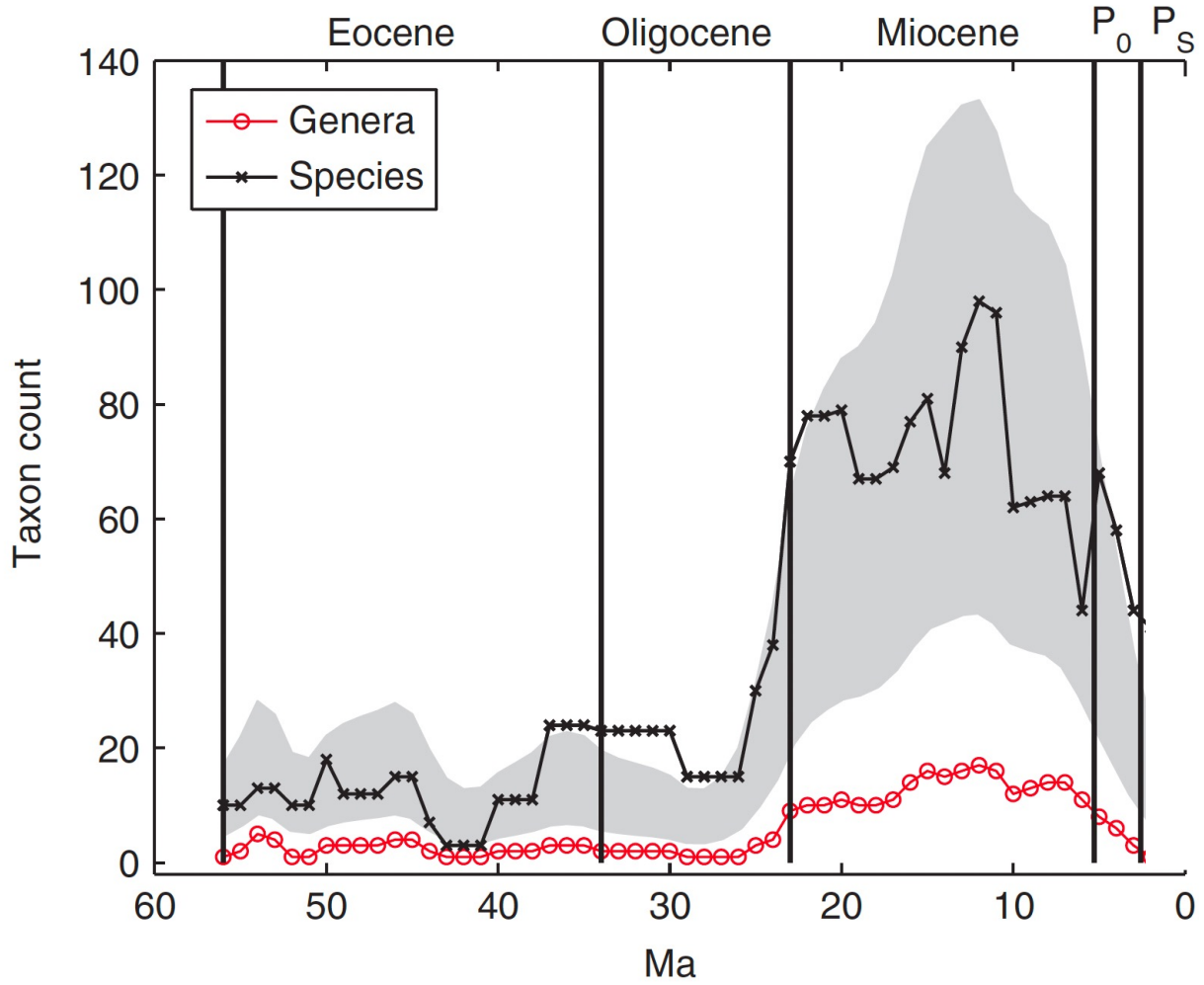
Lauren Shoemaker[1,2] **and Aaron Clauset**[2,3,4]*



Body mass evolution and diversification within horses (family Equidae)

Ecology Letters, (2014) **17**: 211–220

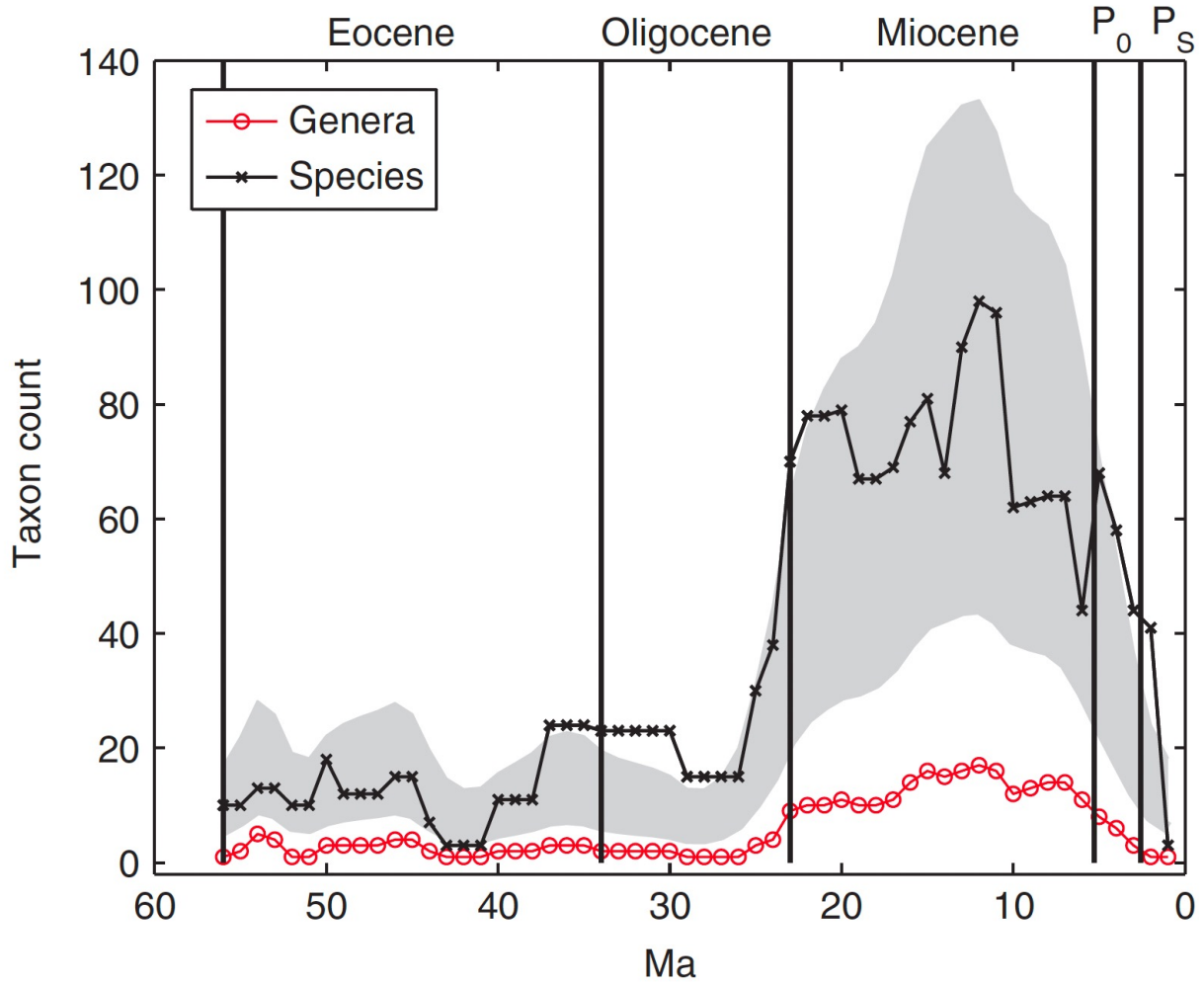
Lauren Shoemaker[1,2] **and Aaron Clauset**[2,3,4]*



Body mass evolution and diversification within horses (family Equidae)

Ecology Letters, (2014) **17**: 211–220

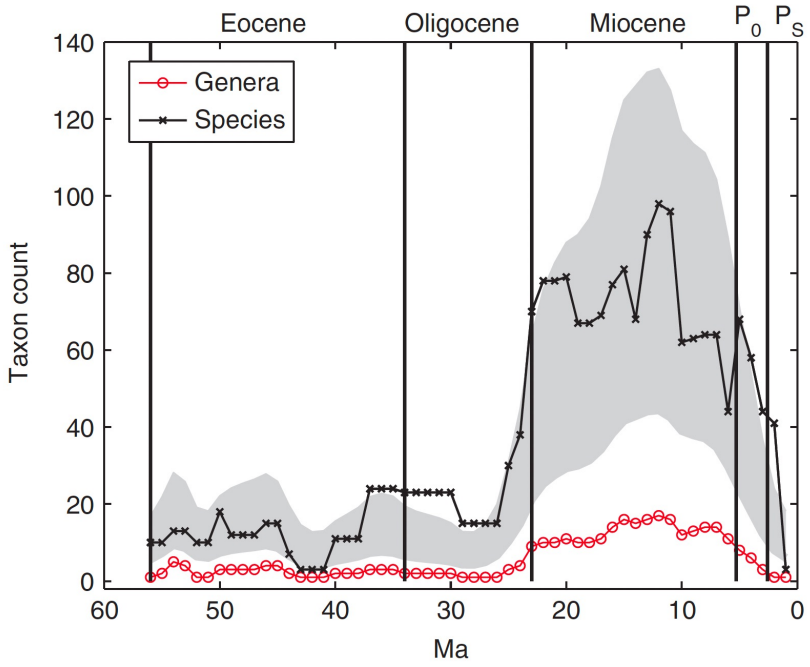
Lauren Shoemaker[1,2] **and Aaron Clauset**[2,3,4]*

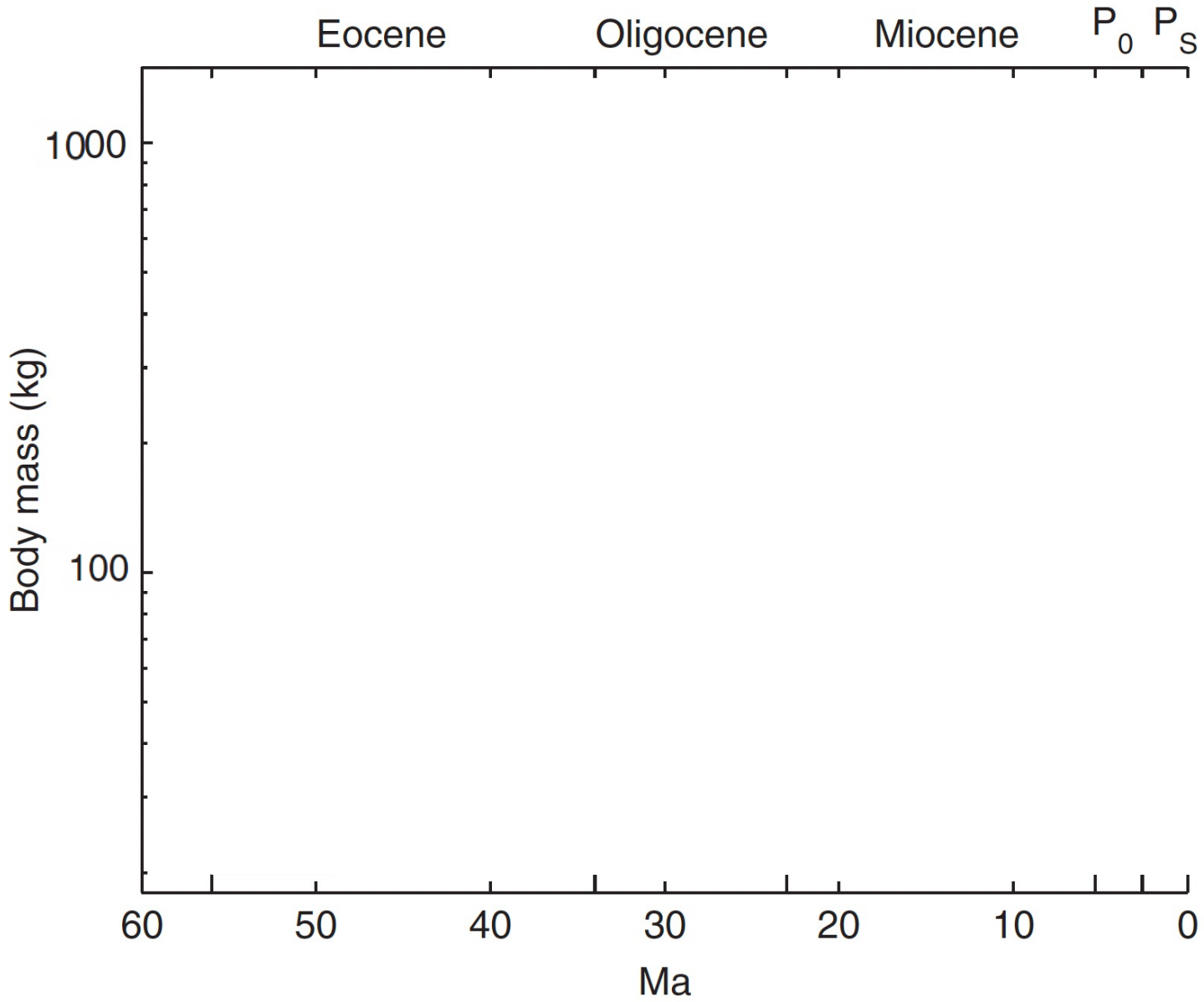


Body mass evolution and diversification within horses (family Equidae)

Ecology Letters, (2014) **17**: 211–220

Lauren Shoemaker[1,2] **and**
Aaron Clauset[2,3,4]*

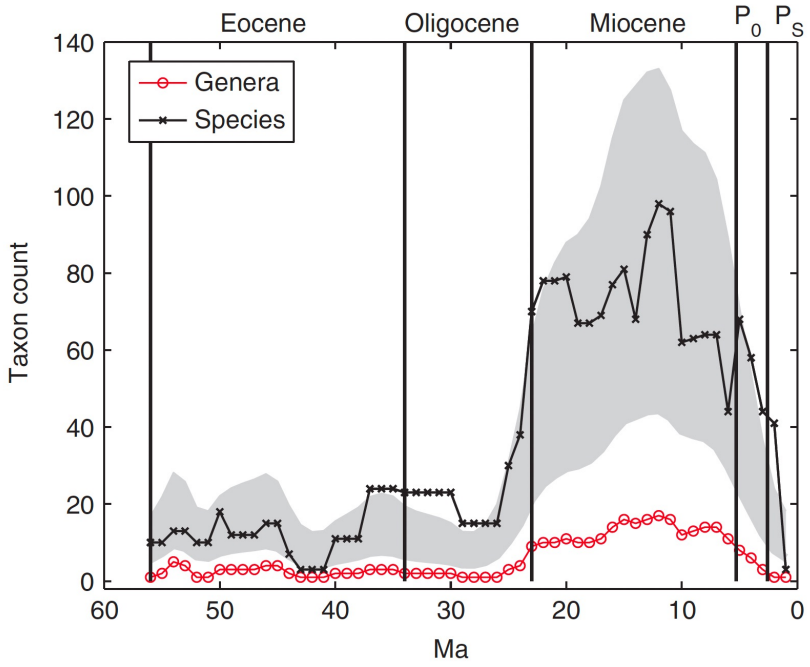


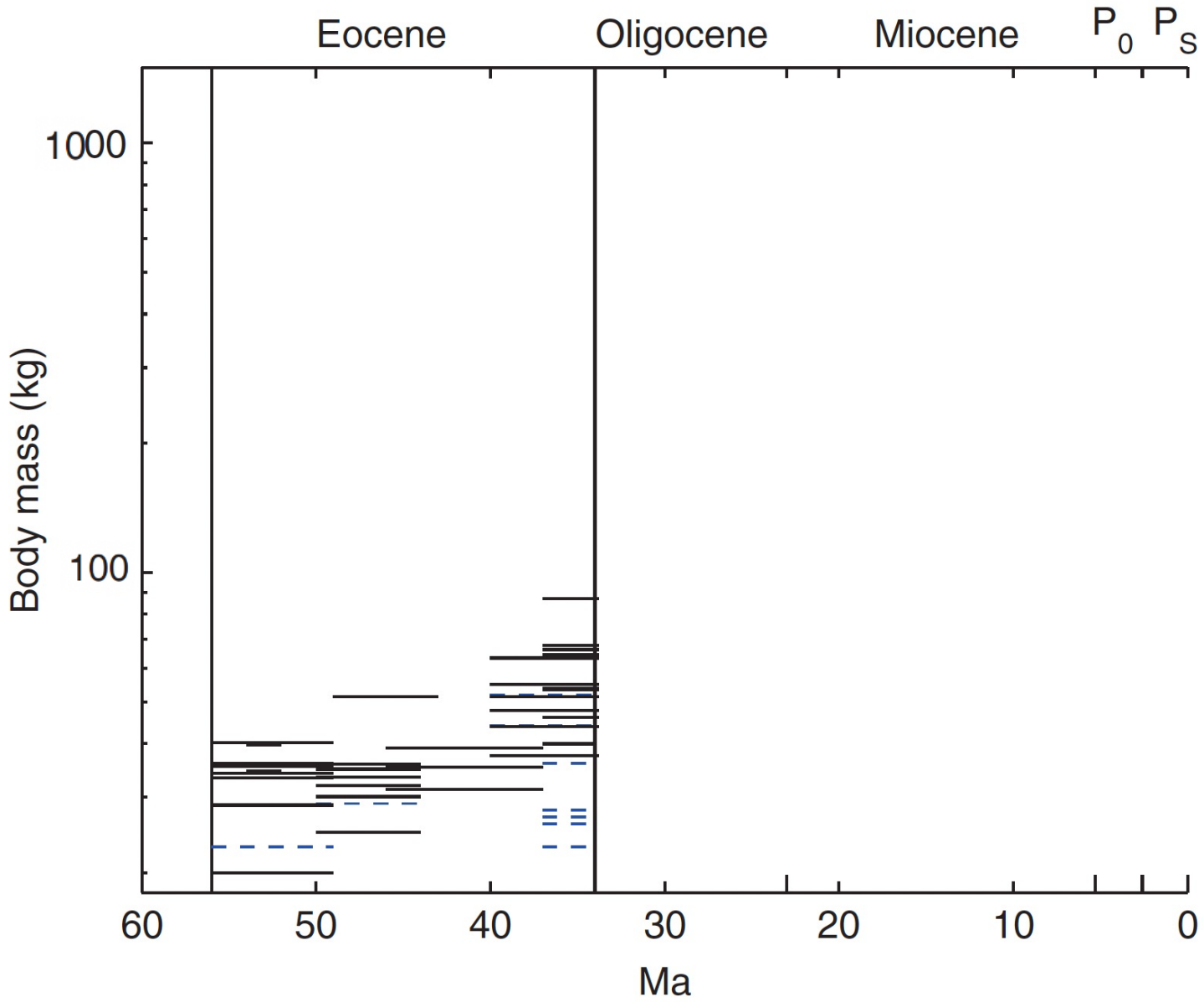


Body mass evolution and diversification within horses (family Equidae)

Ecology Letters, (2014) **17**: 211–220

Lauren Shoemaker[1,2] **and**
Aaron Clauset[2,3,4]*

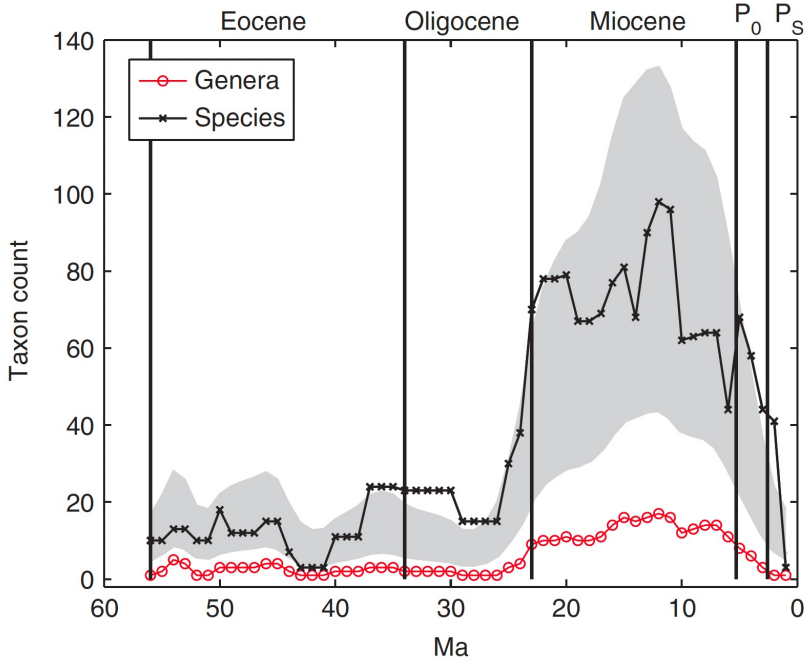


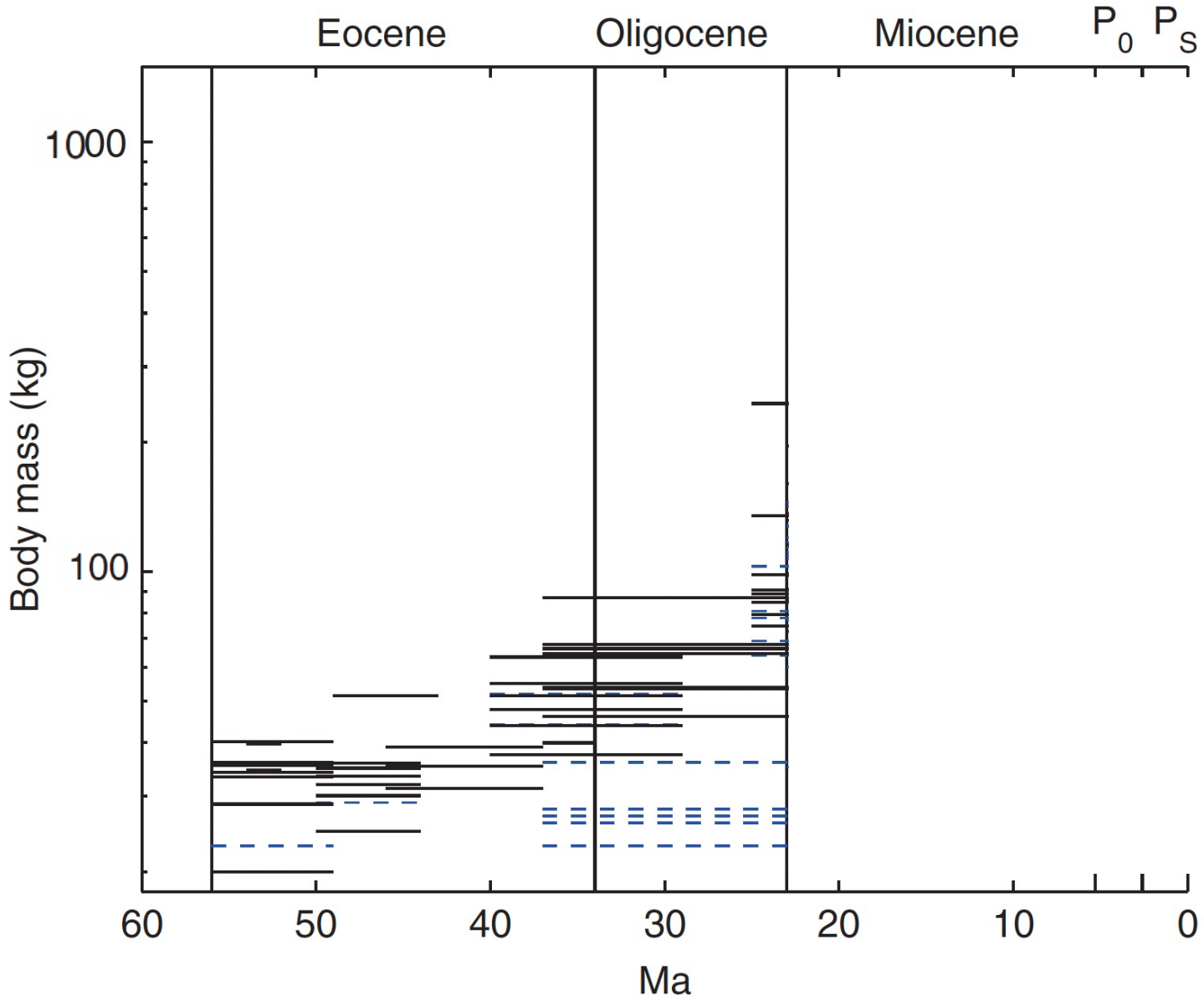


Body mass evolution and diversification within horses (family Equidae)

Ecology Letters, (2014) **17**: 211–220

Lauren Shoemaker[1,2] **and**
Aaron Clauset[2,3,4]*

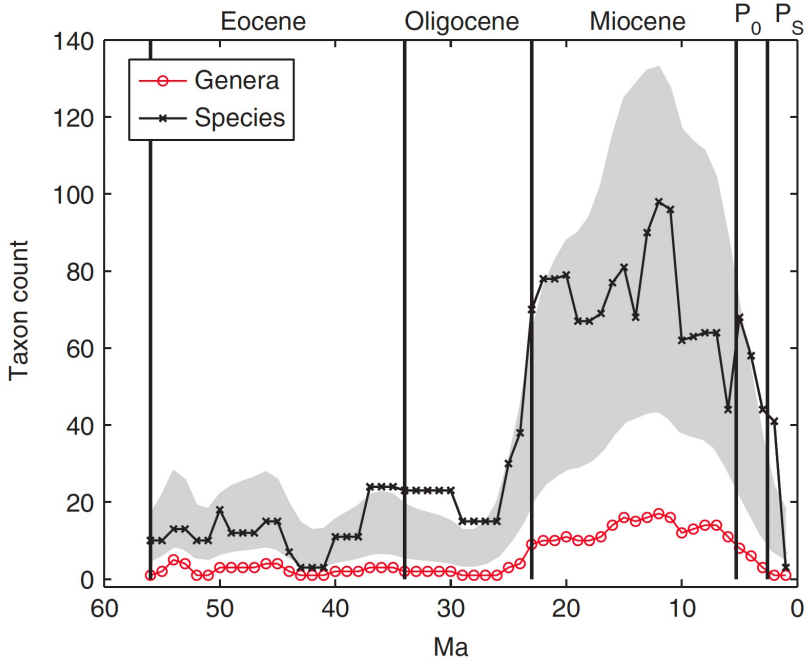


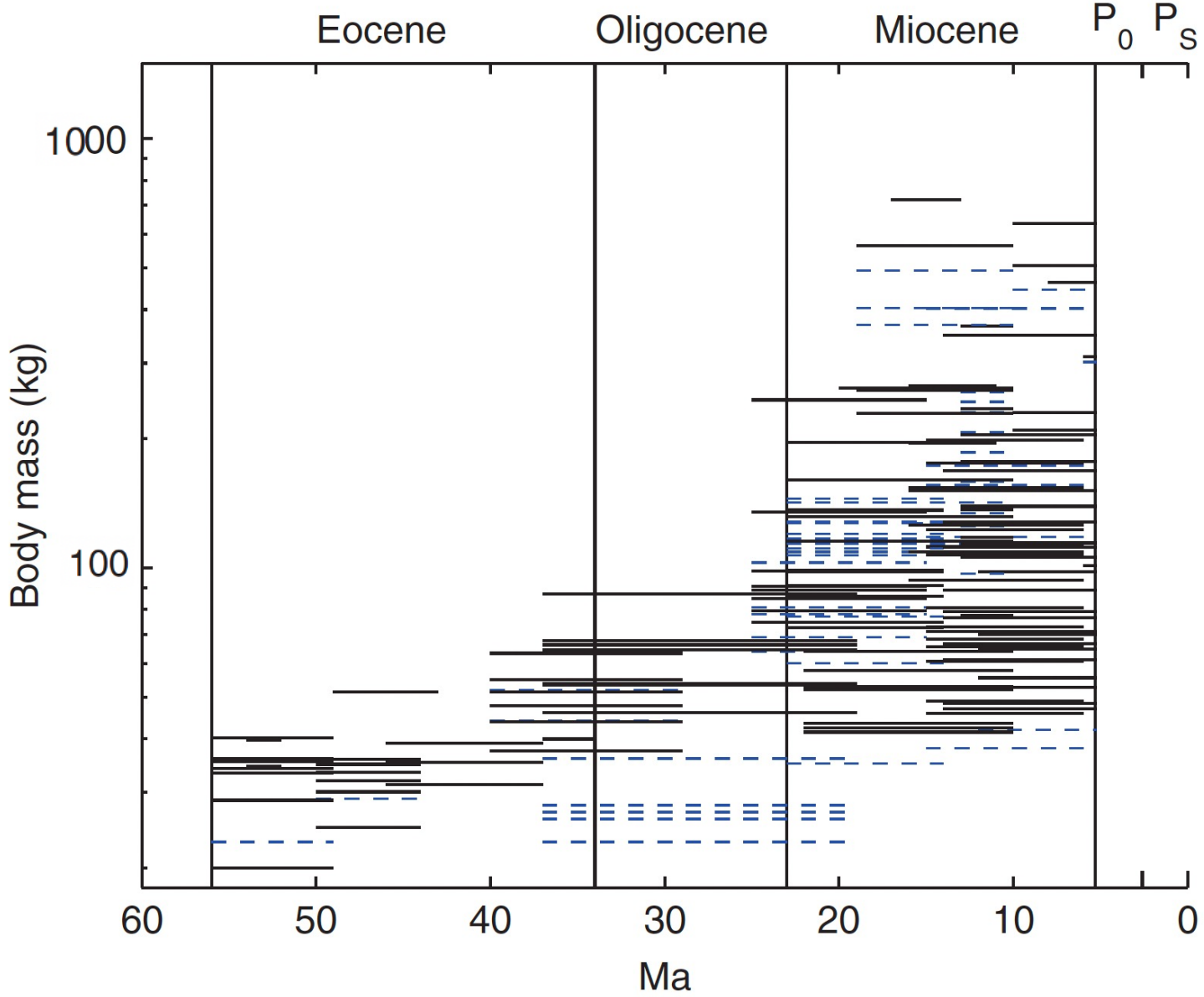


Body mass evolution and diversification within horses (family Equidae)

Ecology Letters, (2014) **17**: 211–220

Lauren Shoemaker[1,2] **and**
Aaron Clauset[2,3,4]*

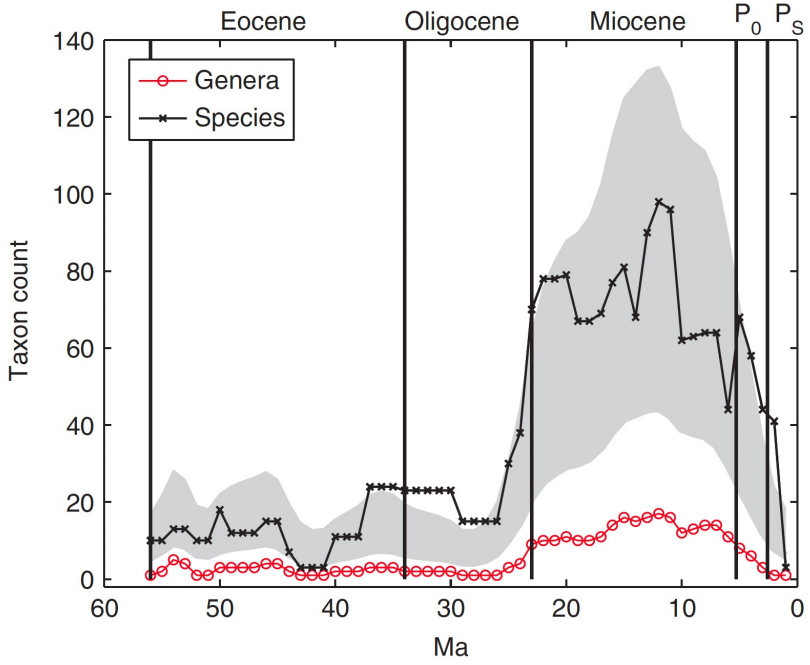


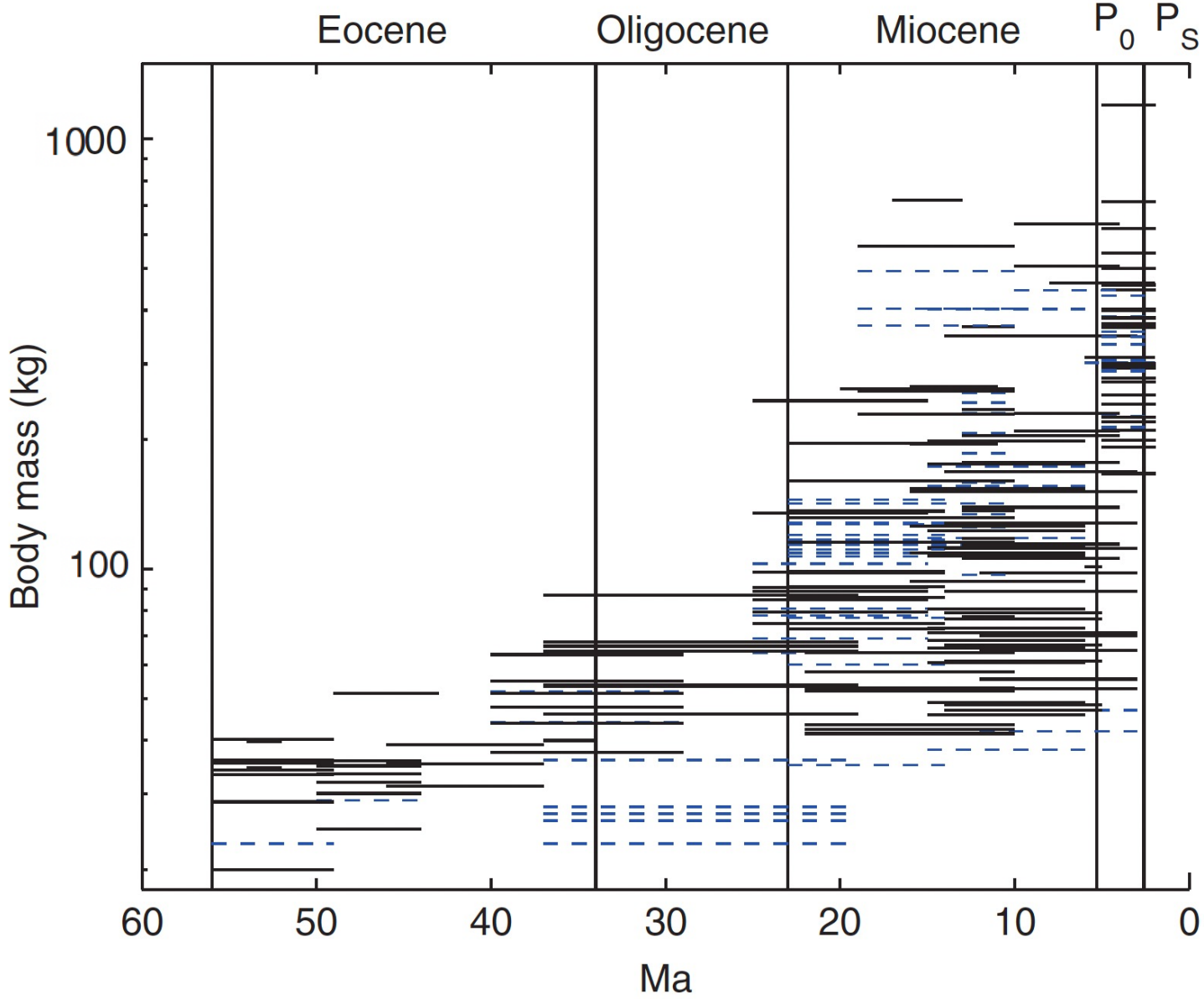


Body mass evolution and diversification within horses (family Equidae)

Ecology Letters, (2014) **17**: 211–220

Lauren Shoemaker[1,2] **and**
Aaron Clauset[2,3,4]*

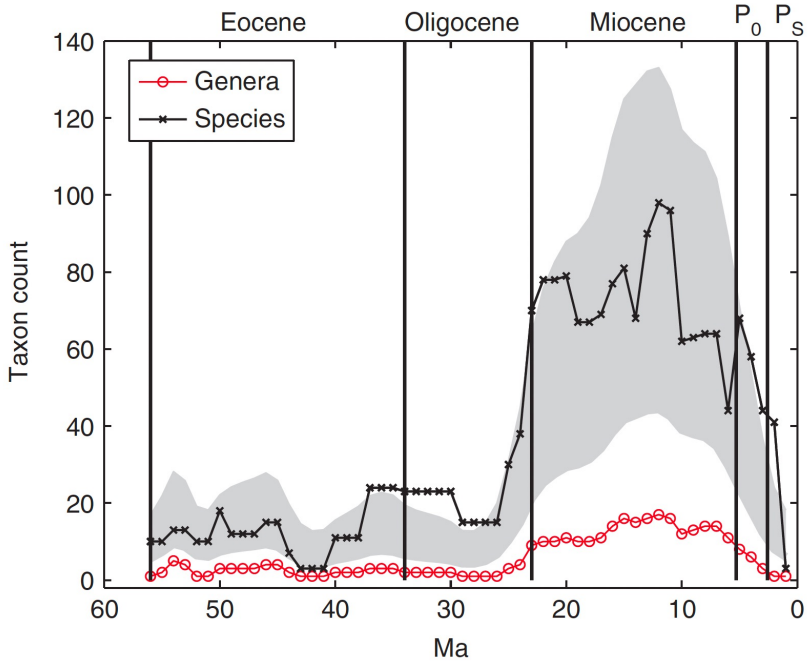


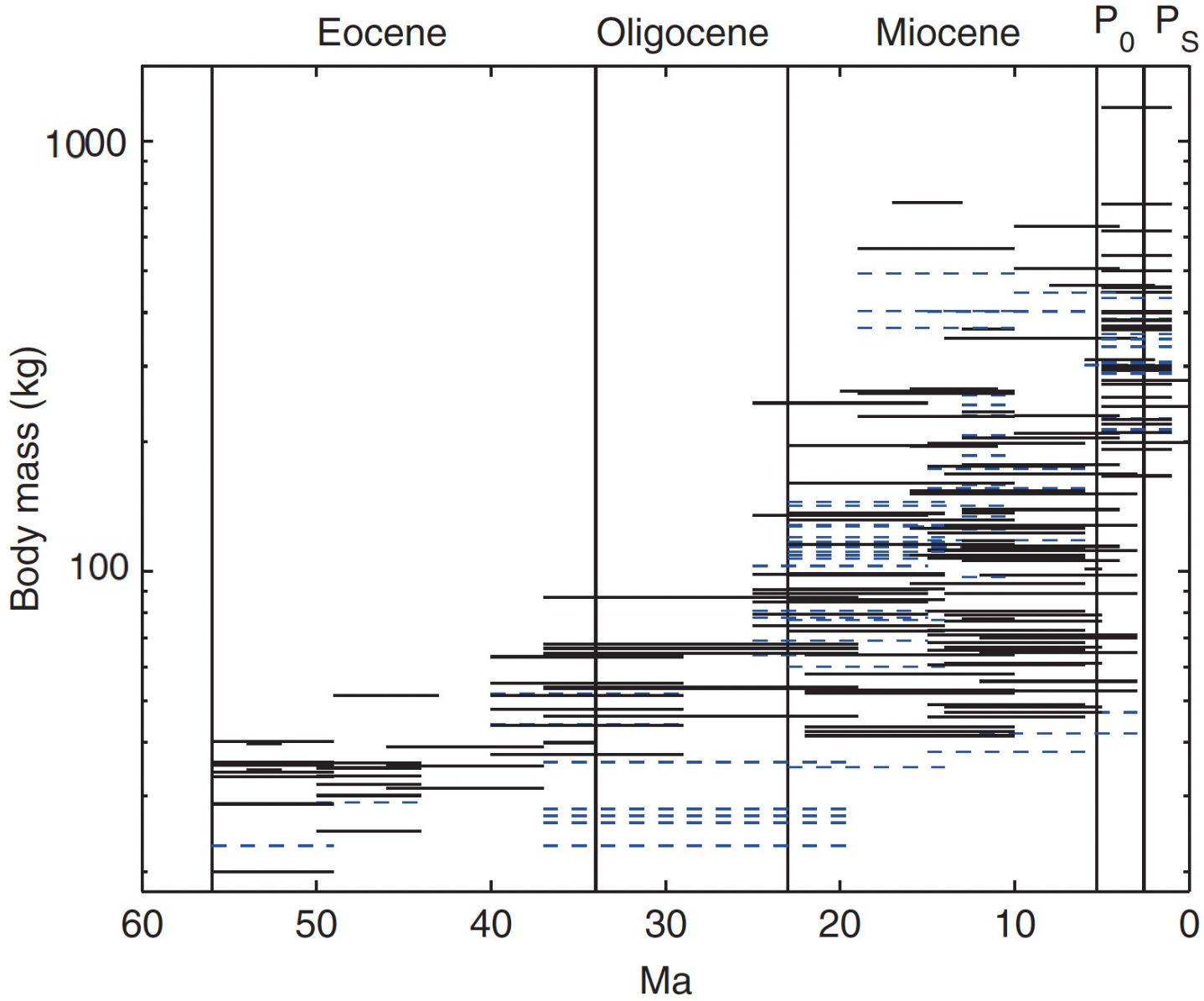


Body mass evolution and diversification within horses (family Equidae)

Ecology Letters, (2014) **17**: 211–220

Lauren Shoemaker[1,2] **and**
Aaron Clauset[2,3,4]*

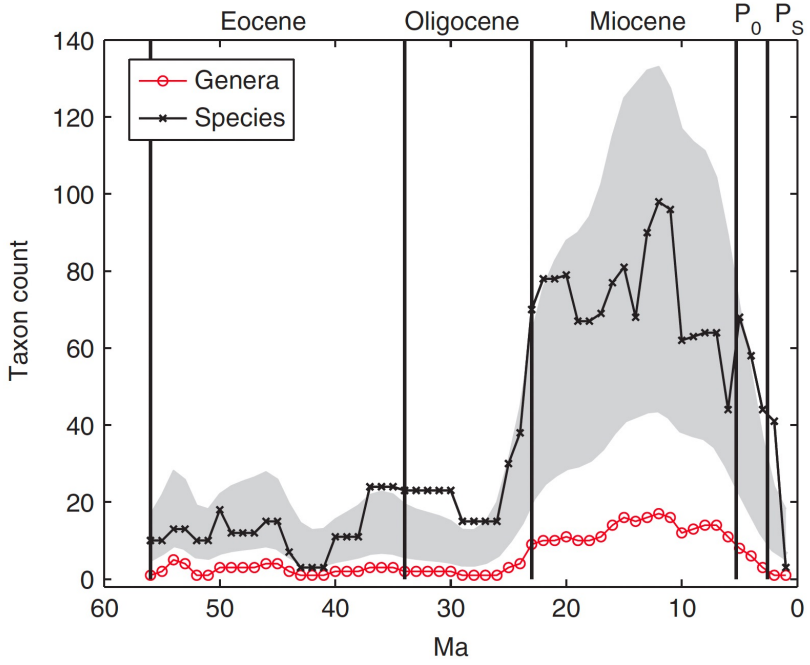


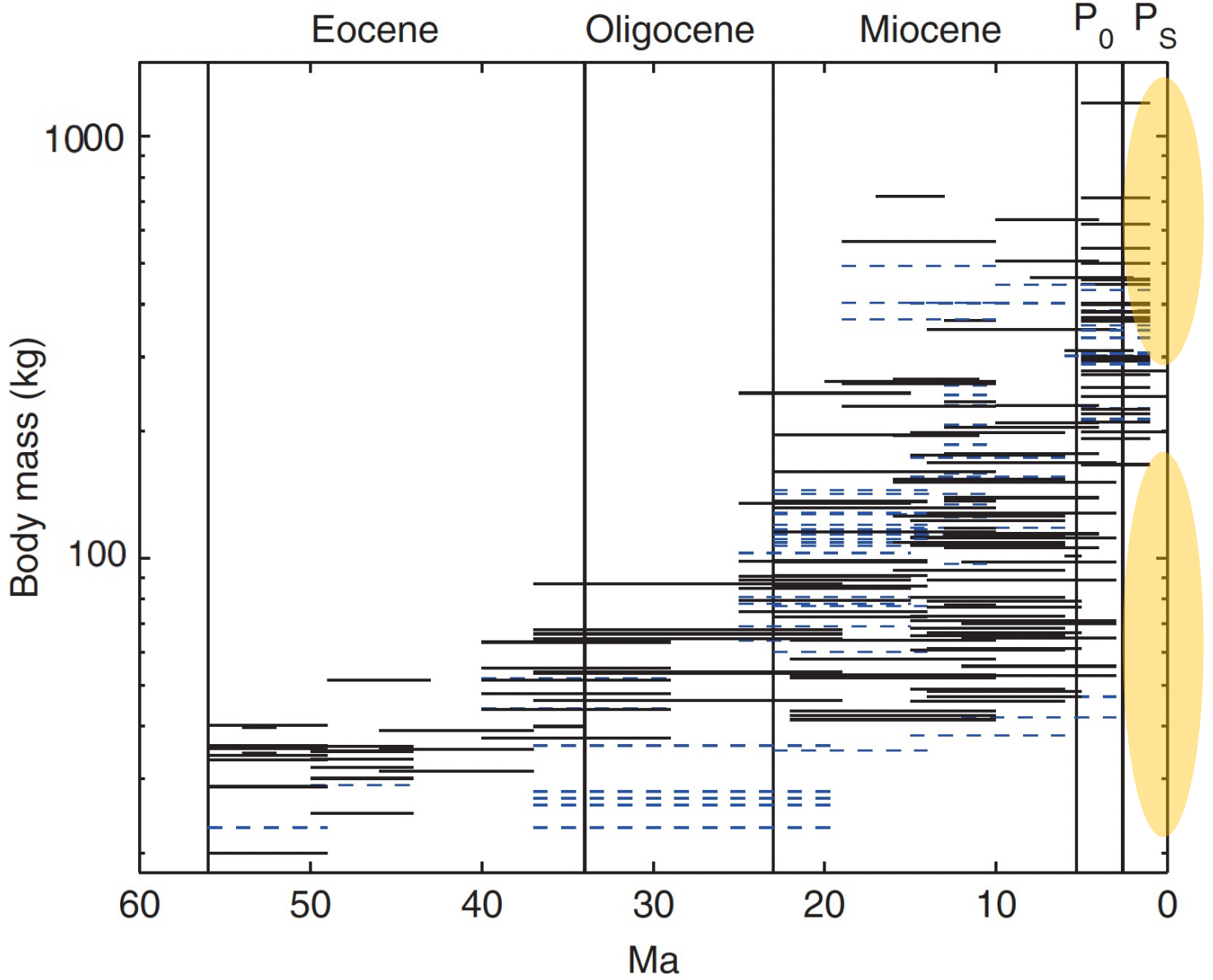


Body mass evolution and diversification within horses (family Equidae)

Ecology Letters, (2014) **17**: 211–220

Lauren Shoemaker[1,2] **and**
Aaron Clauset[2,3,4]*





What led to the decline of equid diversity ?

MODELLING EQUID/RUMINANT COMPETITION IN THE FOSSIL RECORD

CHRISTINE M. JANIS[1], IAIN J. GORDON[2] and ANDREW W. ILLIUS[3]

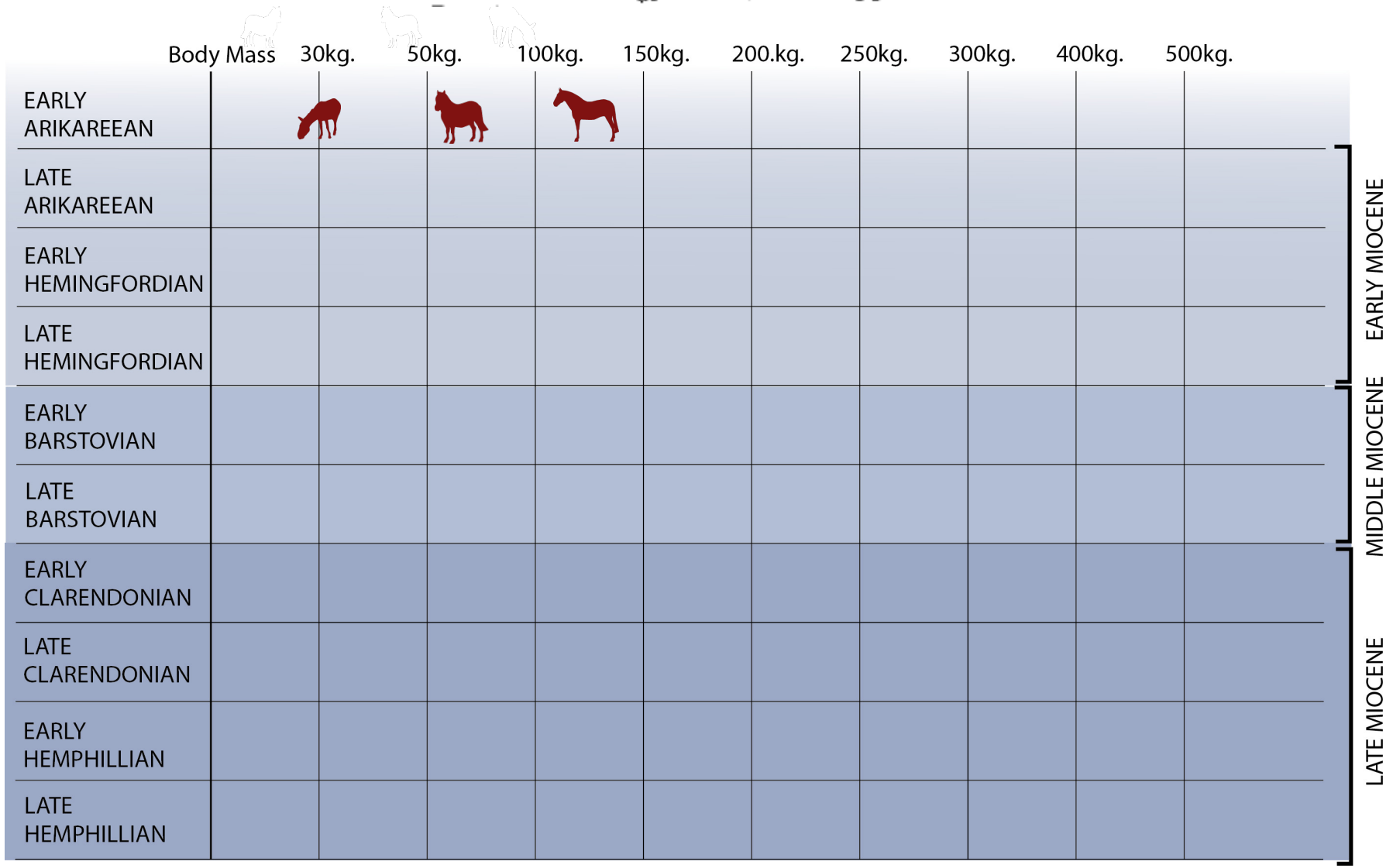
Historical Biology, 1994, Vol. 8, pp. 15–29

Body Mass	30kg.	50kg.	100kg.	150kg.	200.kg.	250kg.	300kg.	400kg.	500kg.	
EARLY ARIKAREEAN										
LATE ARIKAREEAN										EARLY MIOCENE
EARLY HEMINGFORDIAN										
LATE HEMINGFORDIAN										
EARLY BARSTOVIAN										MIDDLE MIOCENE
LATE BARSTOVIAN										
EARLY CLARENDONIAN										LATE MIOCENE
LATE CLARENDONIAN										
EARLY HEMPHILLIAN										
LATE HEMPHILLIAN										

MODELLING EQUID/RUMINANT COMPETITION IN THE FOSSIL RECORD

CHRISTINE M. JANIS[1], IAIN J. GORDON[2] and ANDREW W. ILLIUS[3]

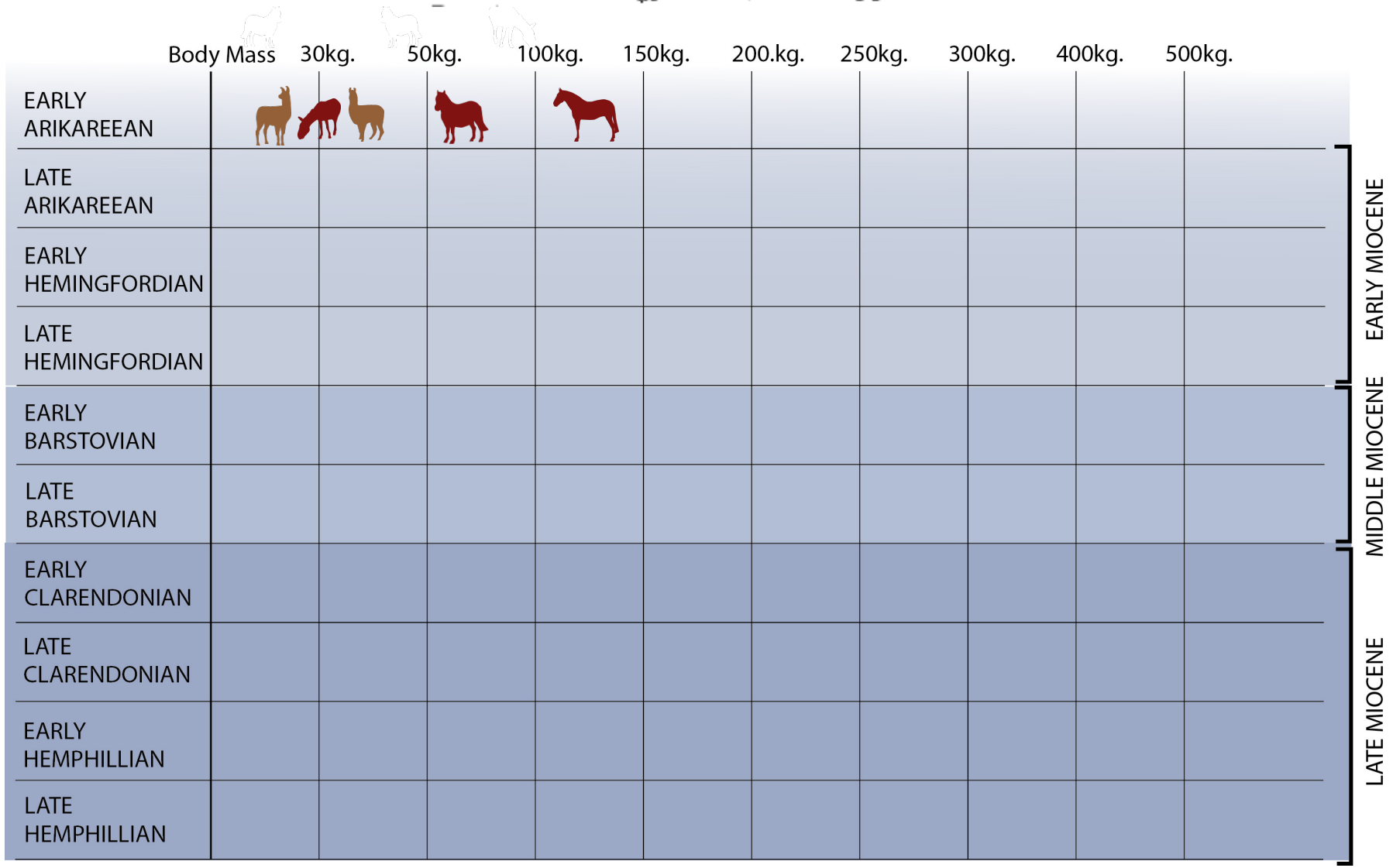
Historical Biology, 1994, Vol. 8, pp. 15–29



MODELLING EQUID/RUMINANT COMPETITION IN THE FOSSIL RECORD

CHRISTINE M. JANIS[1], IAIN J. GORDON[2] and ANDREW W. ILLIUS[3]

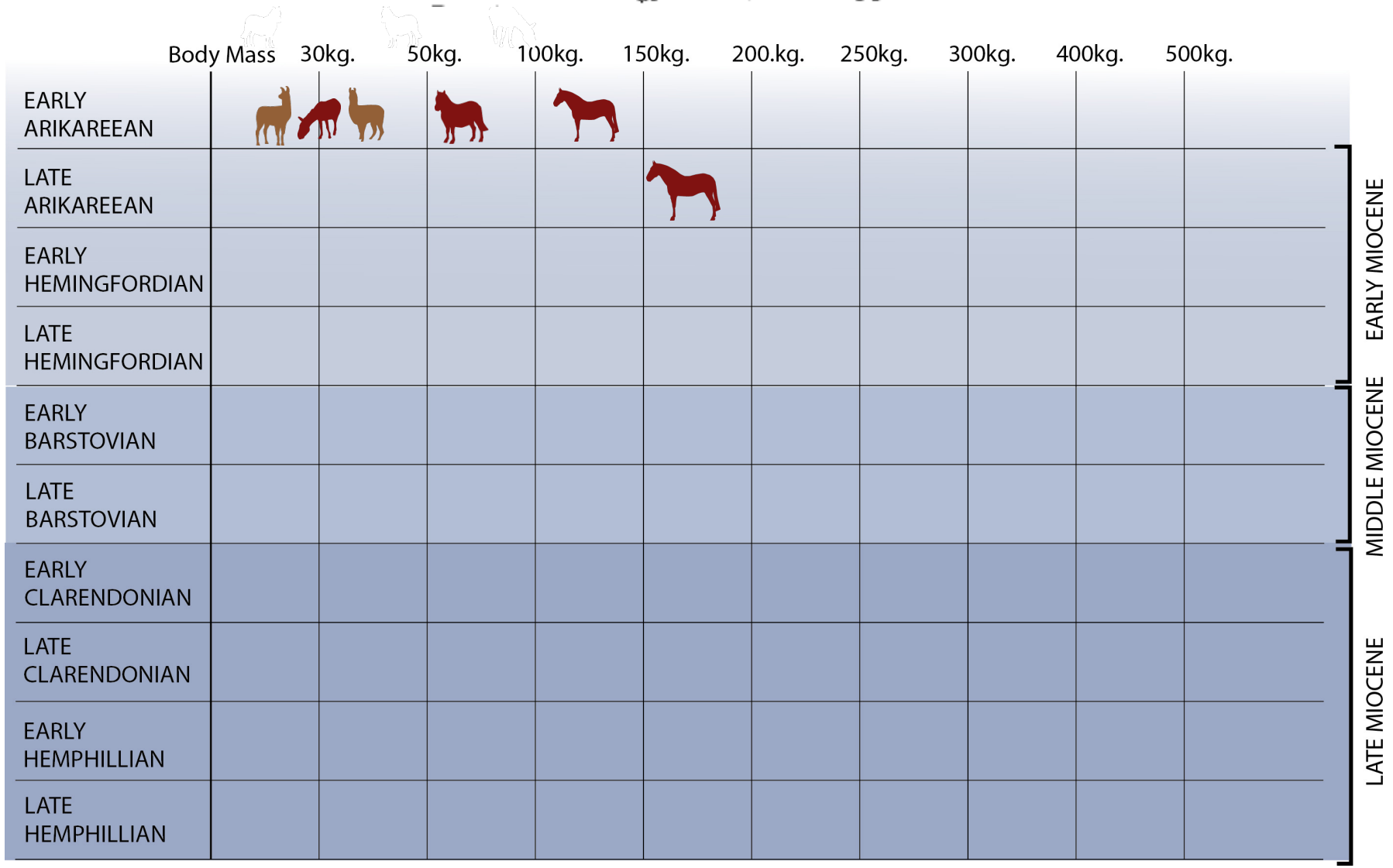
Historical Biology, 1994, Vol. 8, pp. 15–29



MODELLING EQUID/RUMINANT COMPETITION IN THE FOSSIL RECORD

CHRISTINE M. JANIS[1], IAIN J. GORDON[2] and ANDREW W. ILLIUS[3]

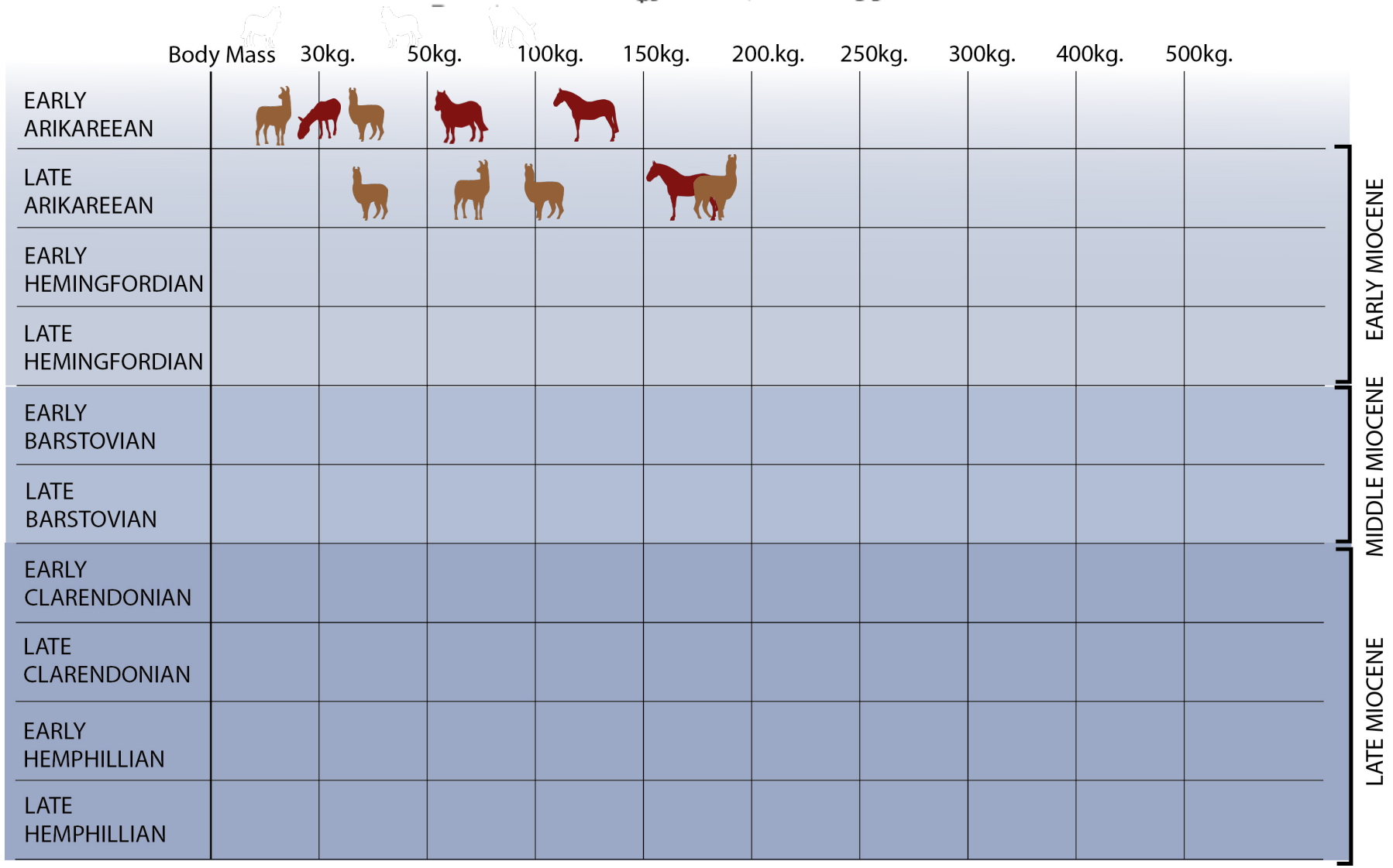
Historical Biology, 1994, Vol. 8, pp. 15–29



MODELLING EQUID/RUMINANT COMPETITION IN THE FOSSIL RECORD

CHRISTINE M. JANIS[1], IAIN J. GORDON[2] and ANDREW W. ILLIUS[3]

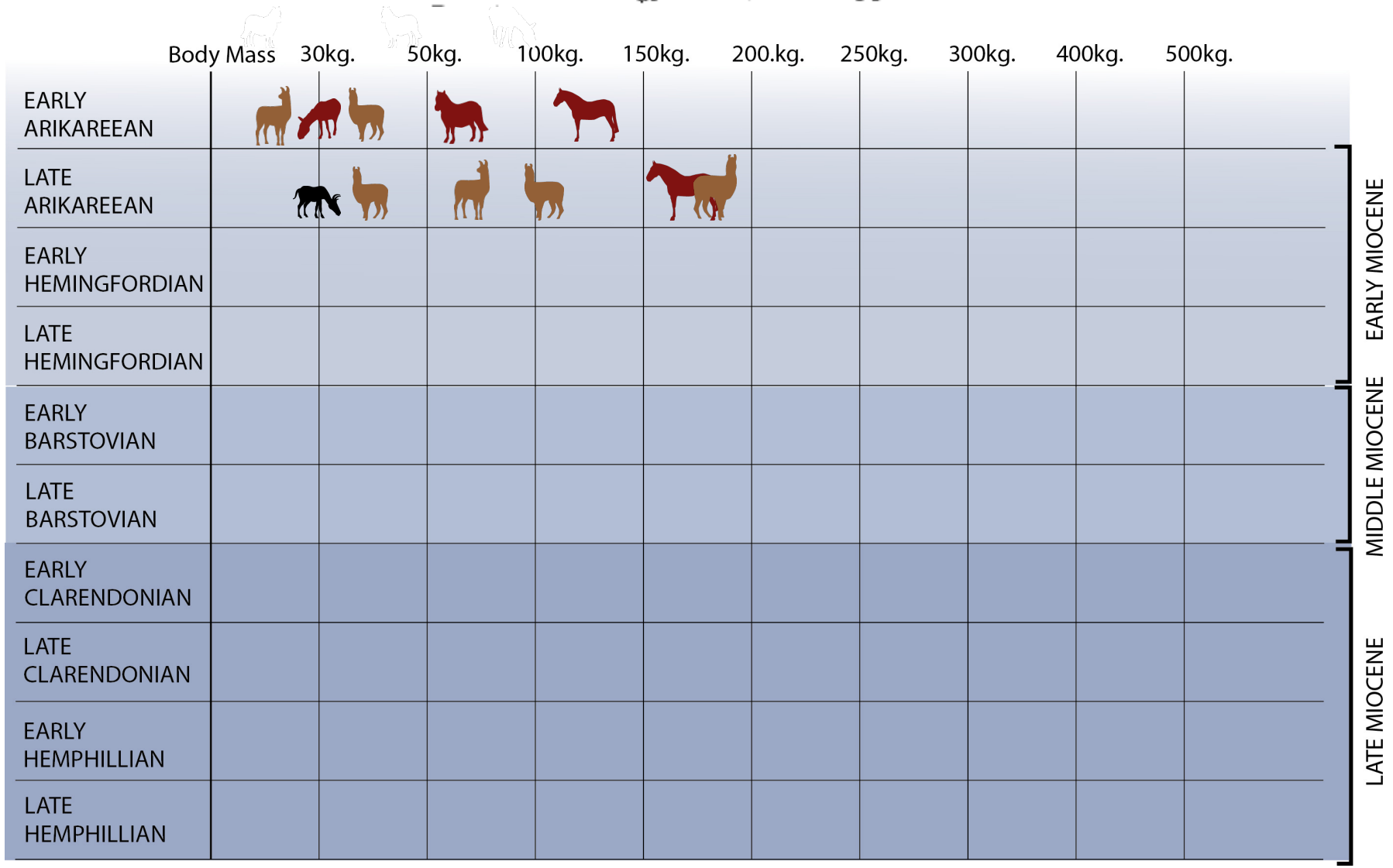
Historical Biology, 1994, Vol. 8, pp. 15–29



MODELLING EQUID/RUMINANT COMPETITION IN THE FOSSIL RECORD

CHRISTINE M. JANIS[1], IAIN J. GORDON[2] and ANDREW W. ILLIUS[3]

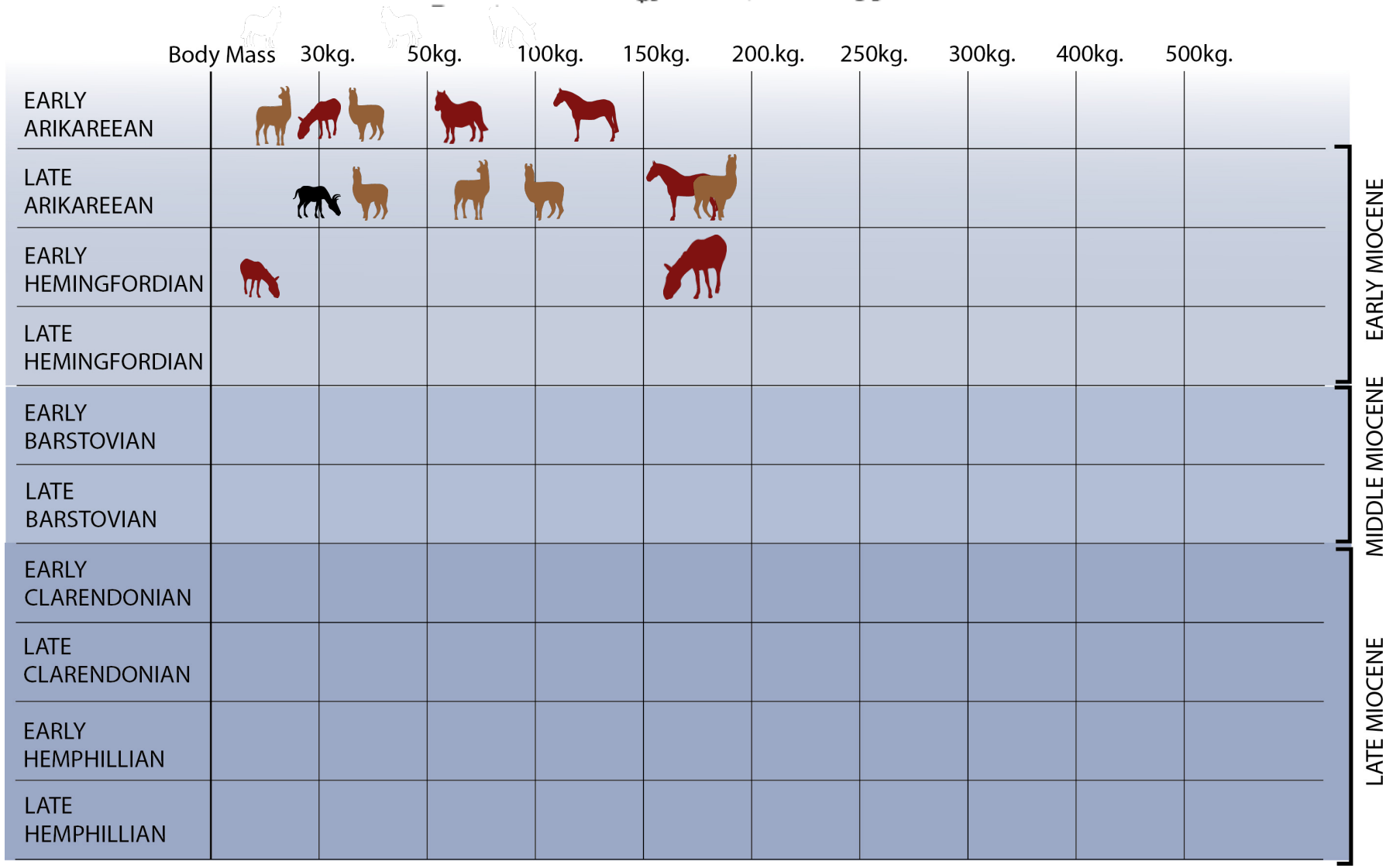
Historical Biology, 1994, Vol. 8, pp. 15–29



MODELLING EQUID/RUMINANT COMPETITION IN THE FOSSIL RECORD

CHRISTINE M. JANIS[1], IAIN J. GORDON[2] and ANDREW W. ILLIUS[3]

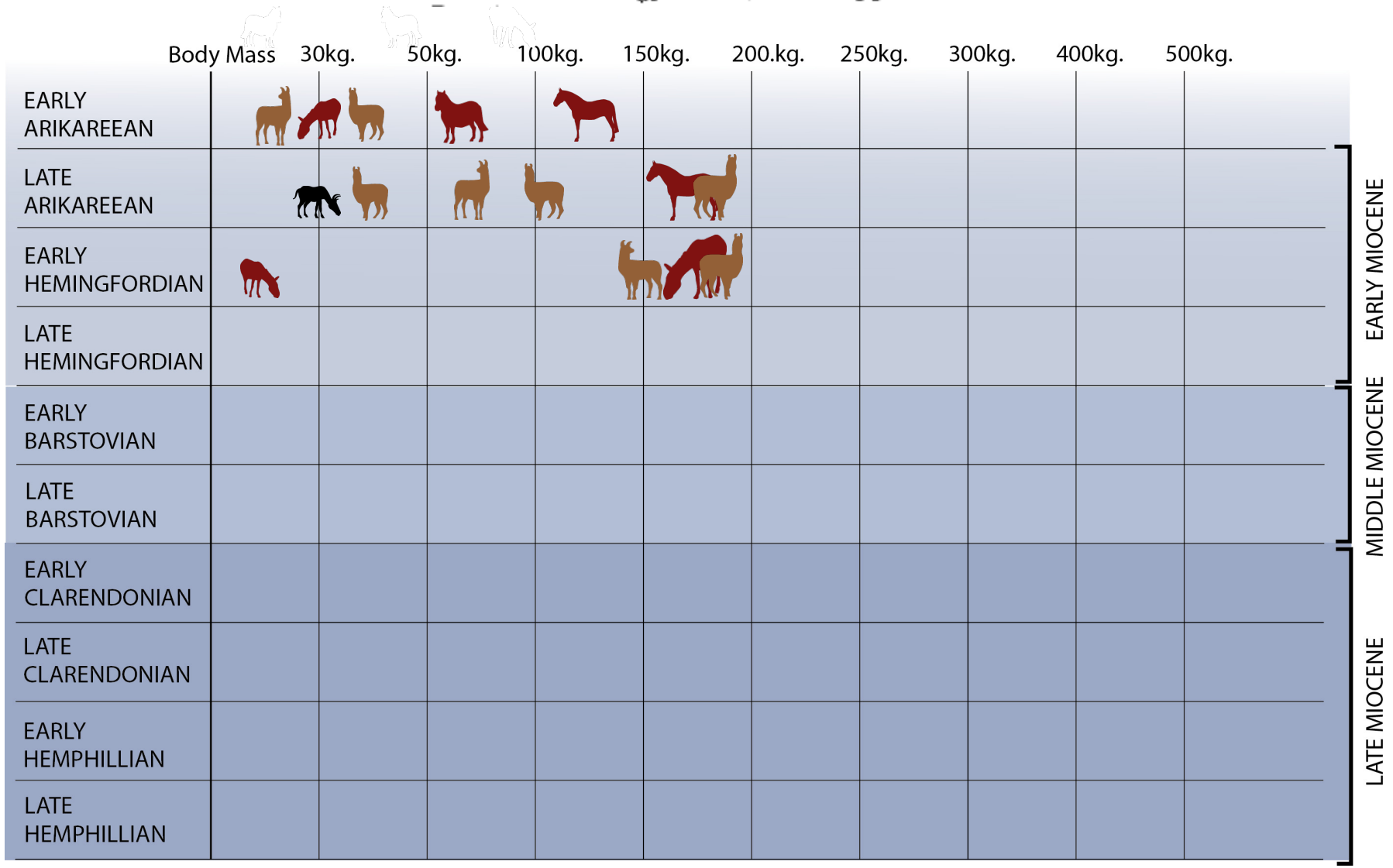
Historical Biology, 1994, Vol. 8, pp. 15–29



MODELLING EQUID/RUMINANT COMPETITION IN THE FOSSIL RECORD

CHRISTINE M. JANIS[1], IAIN J. GORDON[2] and ANDREW W. ILLIUS[3]

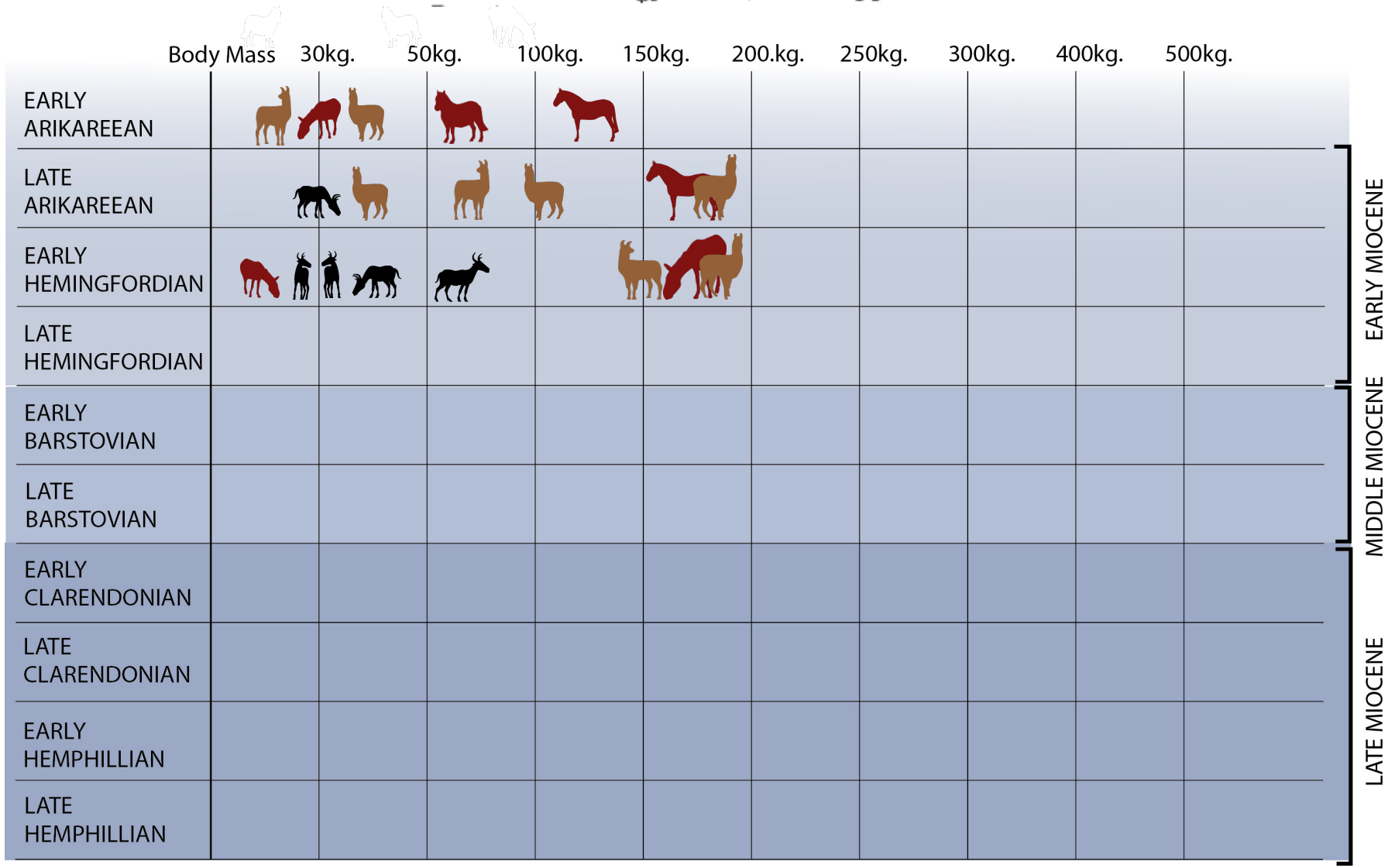
Historical Biology, 1994, Vol. 8, pp. 15–29



MODELLING EQUID/RUMINANT COMPETITION IN THE FOSSIL RECORD

CHRISTINE M. JANIS[1], IAIN J. GORDON[2] and ANDREW W. ILLIUS[3]

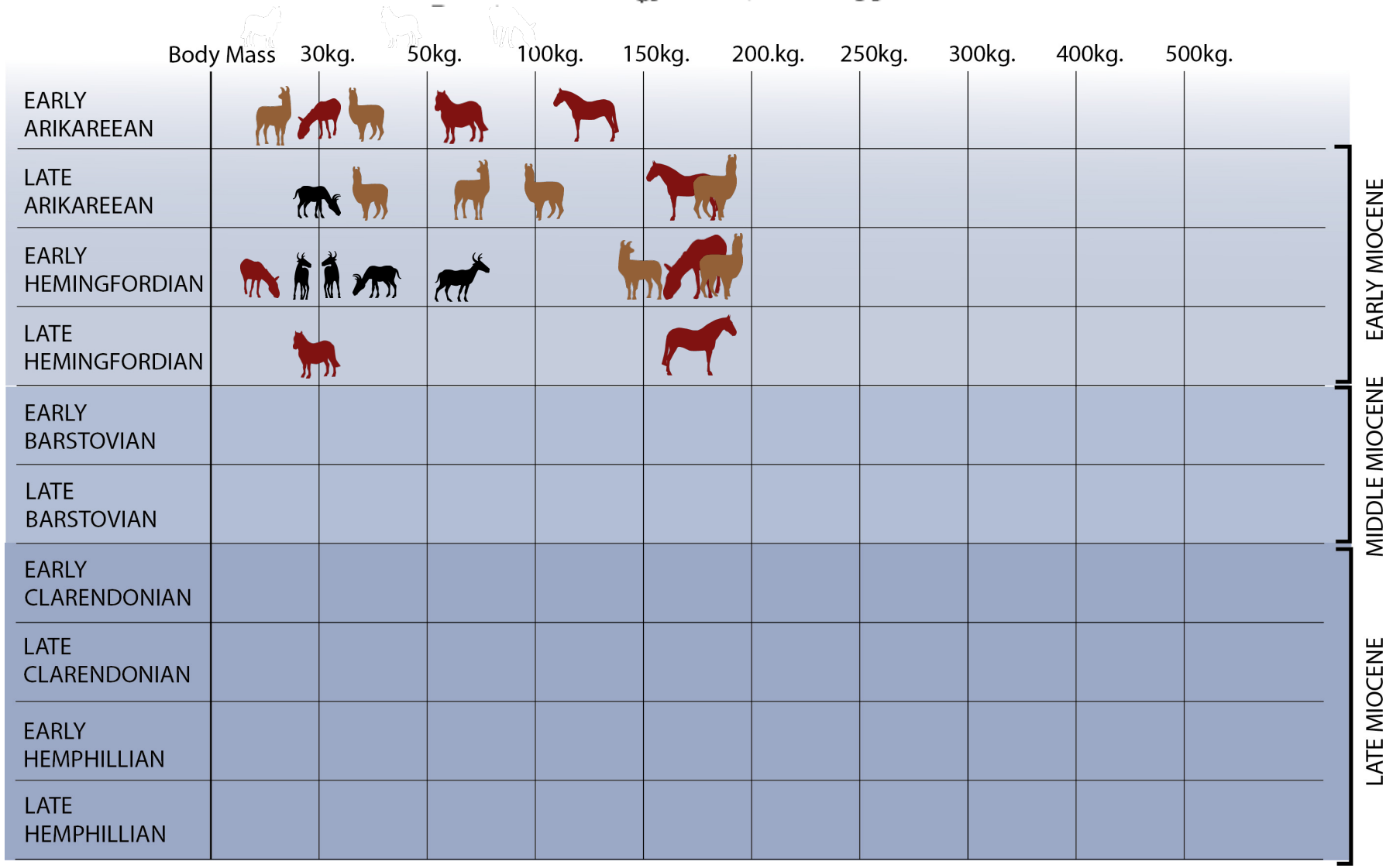
Historical Biology, 1994, Vol. 8, pp. 15–29



MODELLING EQUID/RUMINANT COMPETITION IN THE FOSSIL RECORD

CHRISTINE M. JANIS[1], IAIN J. GORDON[2] and ANDREW W. ILLIUS[3]

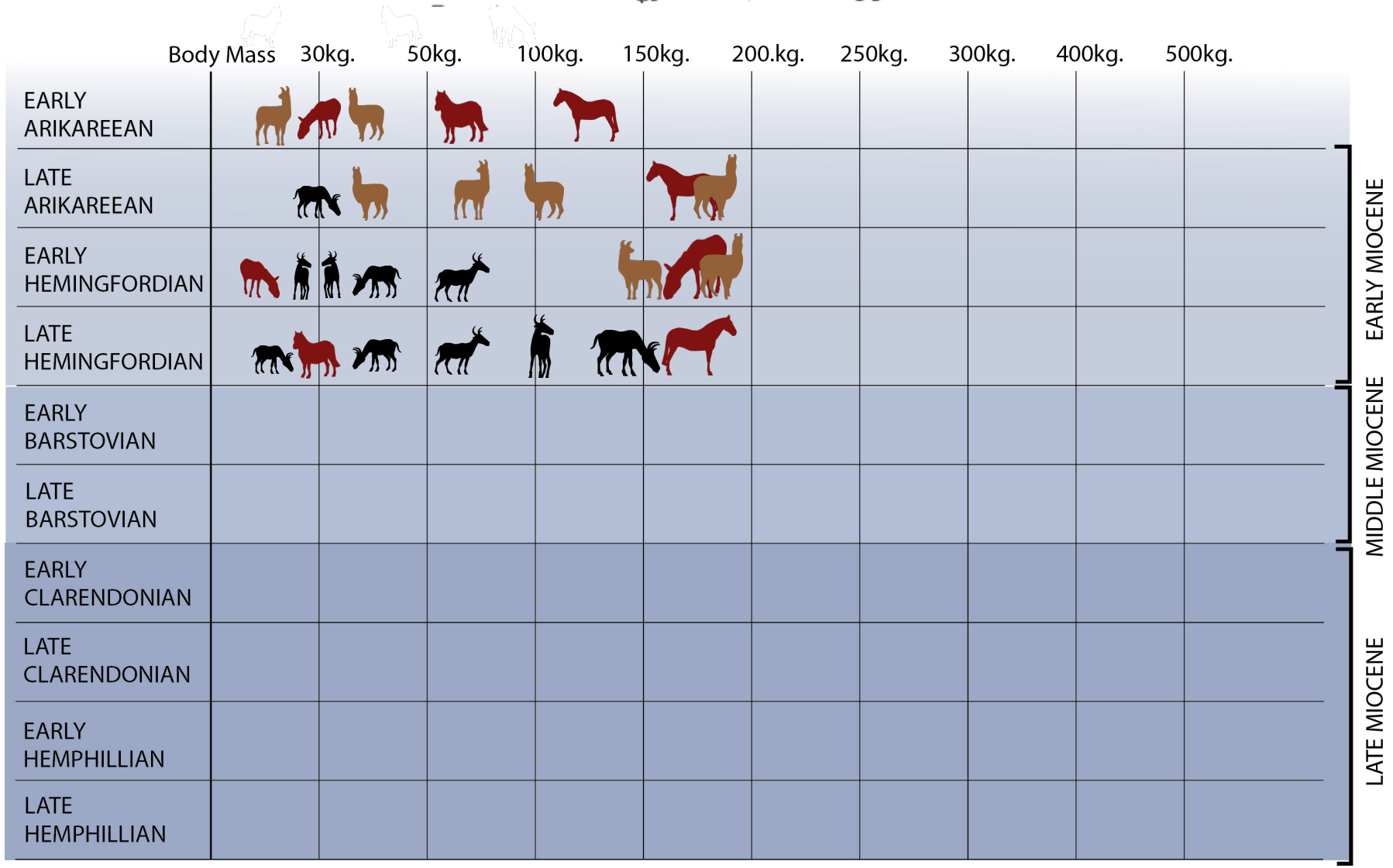
Historical Biology, 1994, Vol. 8, pp. 15–29



MODELLING EQUID/RUMINANT COMPETITION IN THE FOSSIL RECORD

CHRISTINE M. JANIS[1], IAIN J. GORDON[2] and ANDREW W. ILLIUS[3]

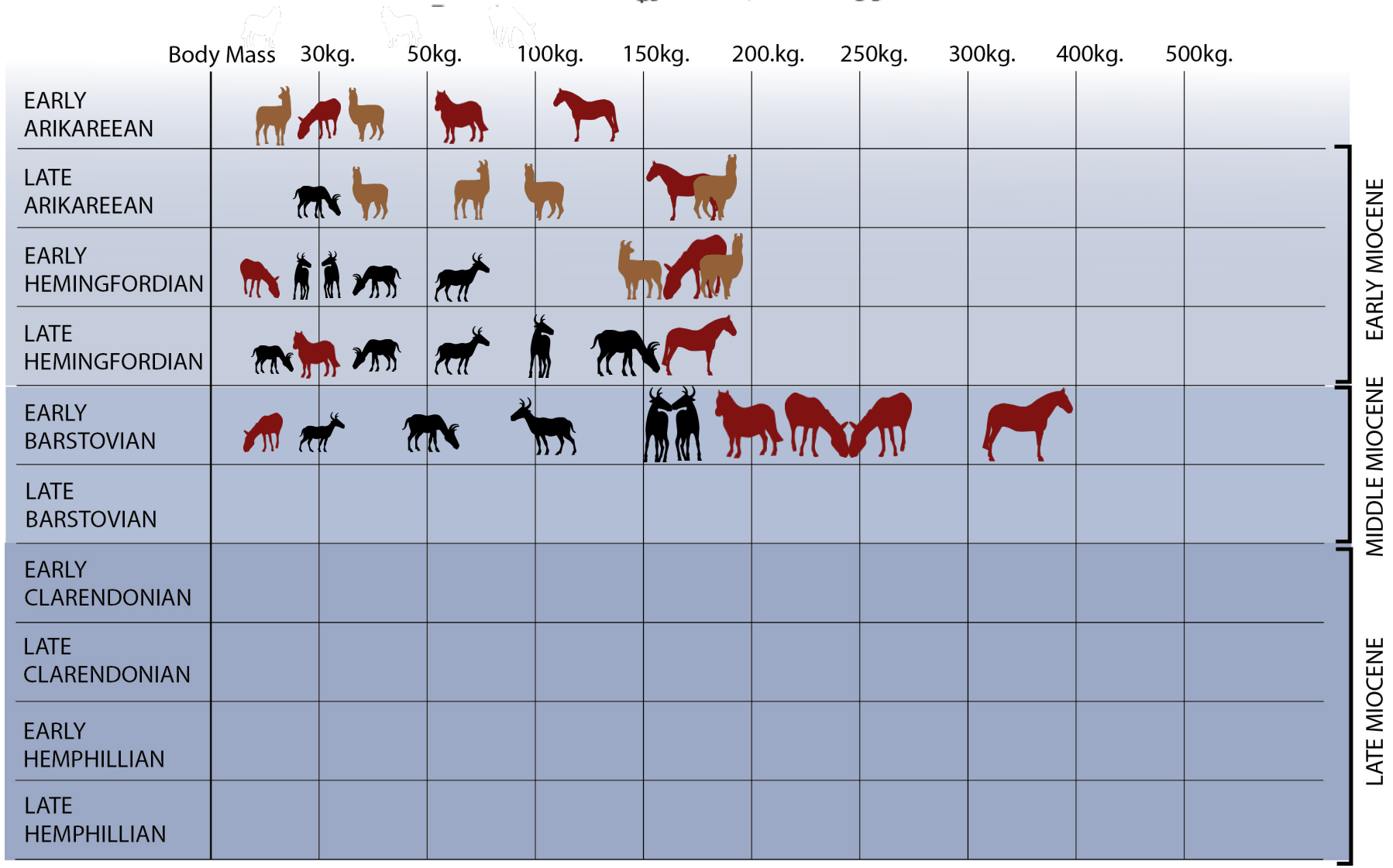
Historical Biology, 1994, Vol. 8, pp. 15–29



MODELLING EQUID/RUMINANT COMPETITION IN THE FOSSIL RECORD

CHRISTINE M. JANIS[1], IAIN J. GORDON[2] and ANDREW W. ILLIUS[3]

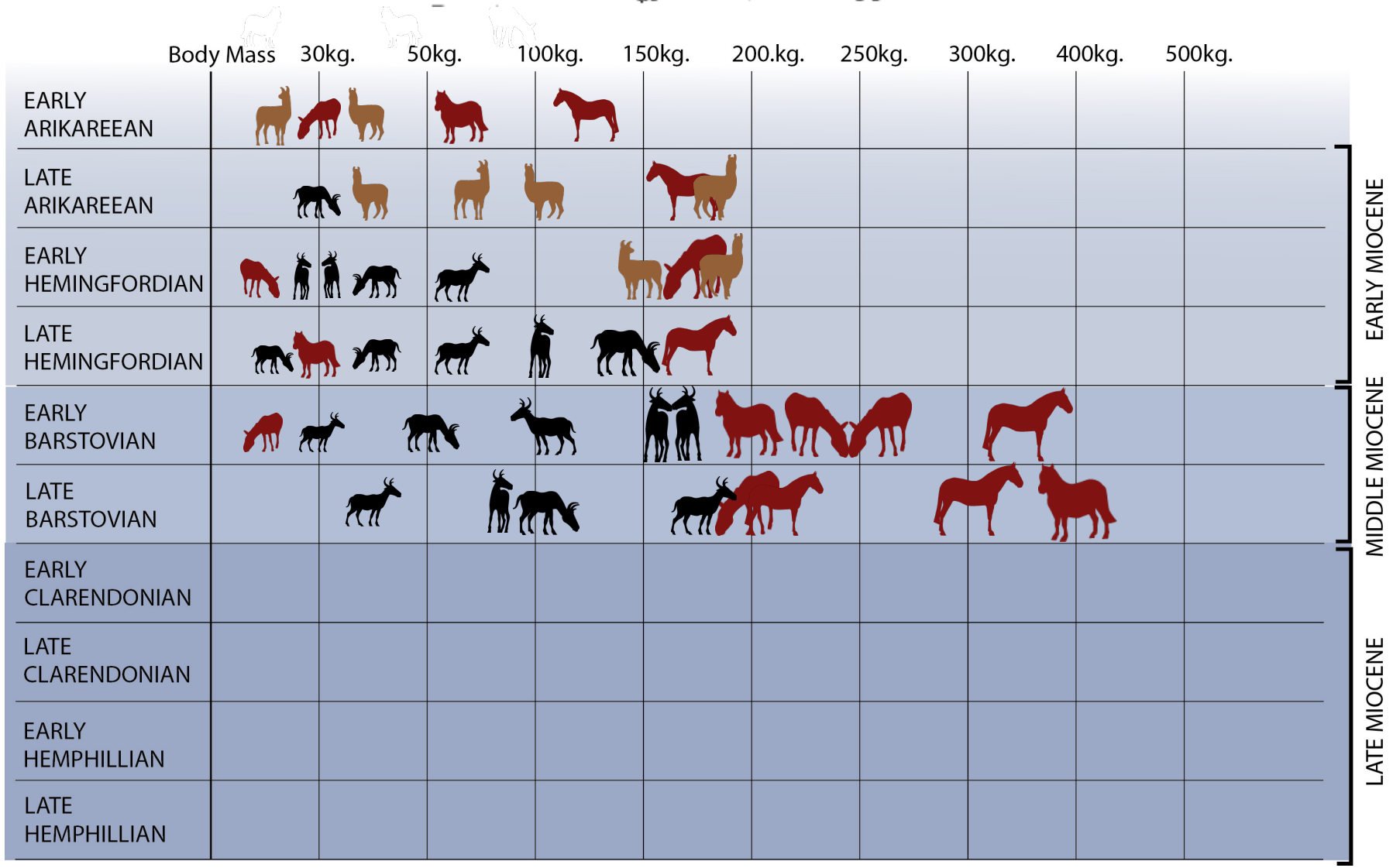
Historical Biology, 1994, Vol. 8, pp. 15–29



MODELLING EQUID/RUMINANT COMPETITION IN THE FOSSIL RECORD

CHRISTINE M. JANIS[1], IAIN J. GORDON[2] and ANDREW W. ILLIUS[3]

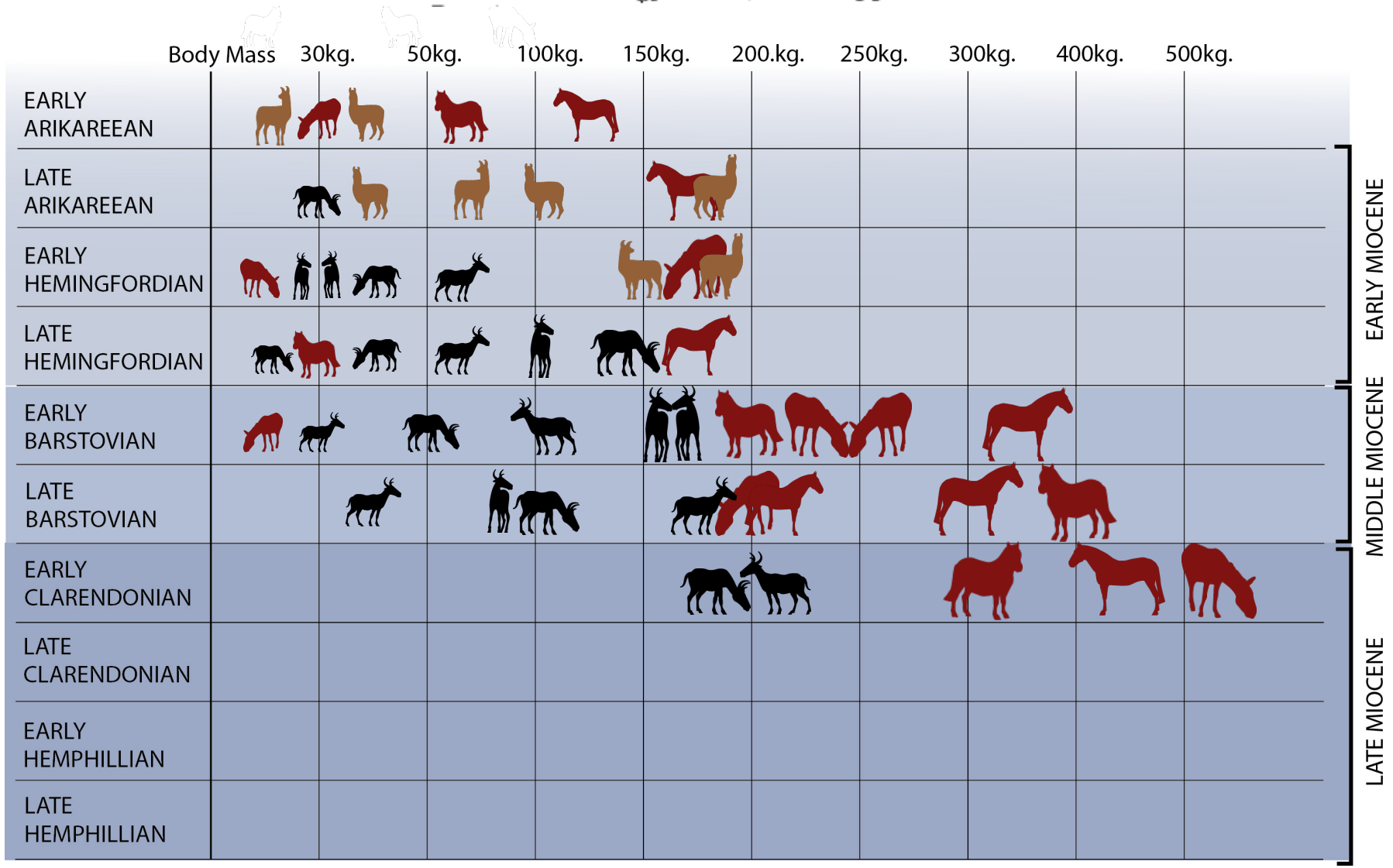
Historical Biology, 1994, Vol. 8, pp. 15–29



MODELLING EQUID/RUMINANT COMPETITION IN THE FOSSIL RECORD

CHRISTINE M. JANIS[1], IAIN J. GORDON[2] and ANDREW W. ILLIUS[3]

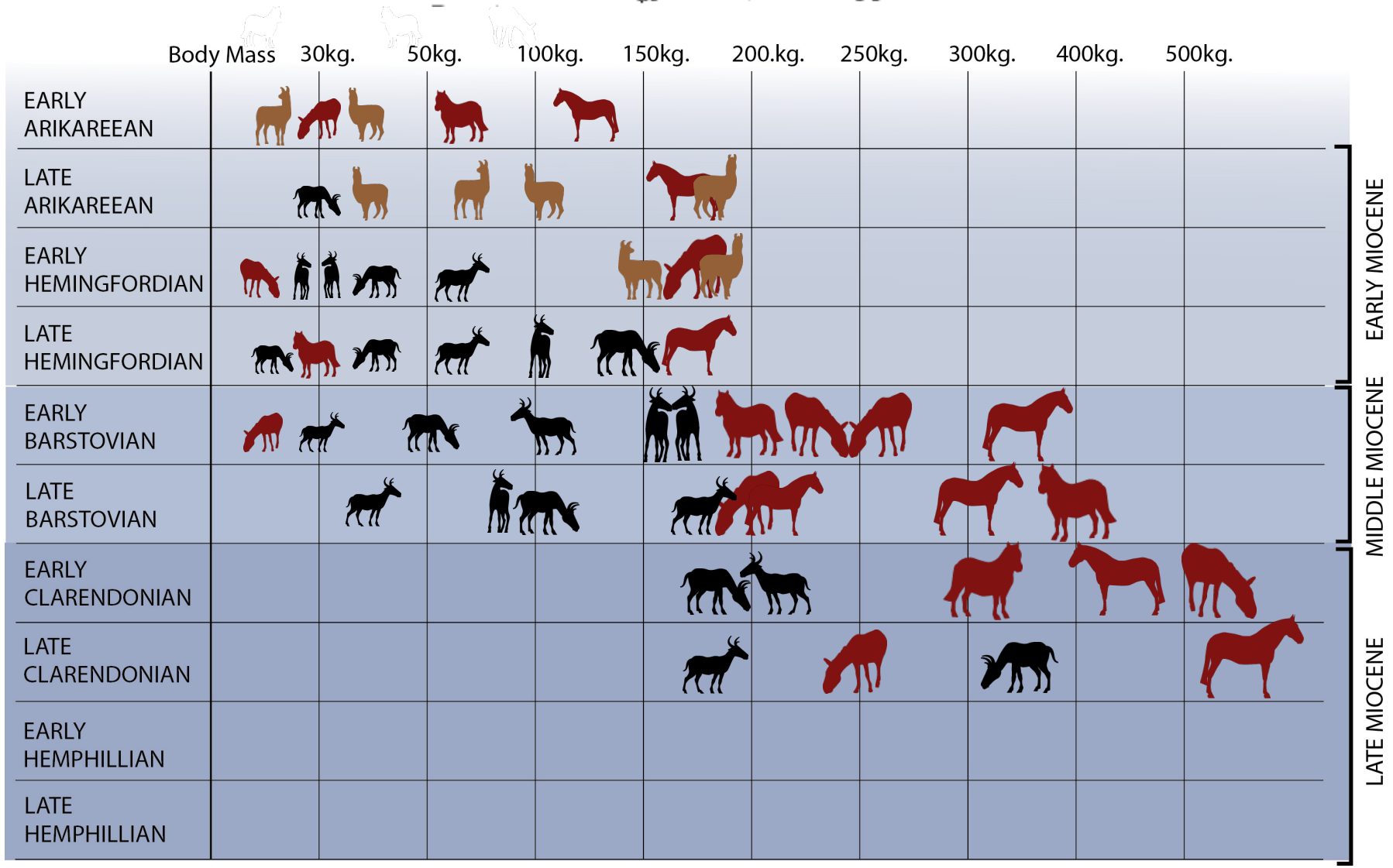
Historical Biology, 1994, Vol. 8, pp. 15–29



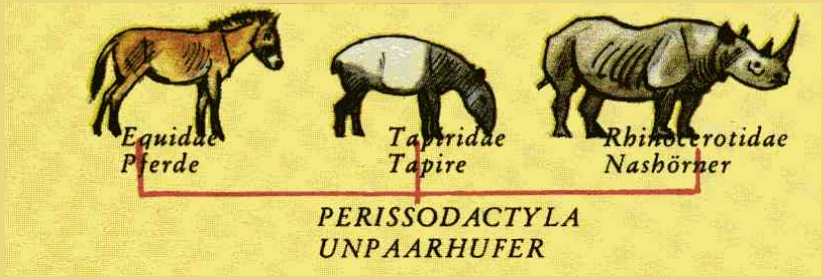
MODELLING EQUID/RUMINANT COMPETITION IN THE FOSSIL RECORD

CHRISTINE M. JANIS[1], IAIN J. GORDON[2] and ANDREW W. ILLIUS[3]

Historical Biology, 1994, Vol. 8, pp. 15–29

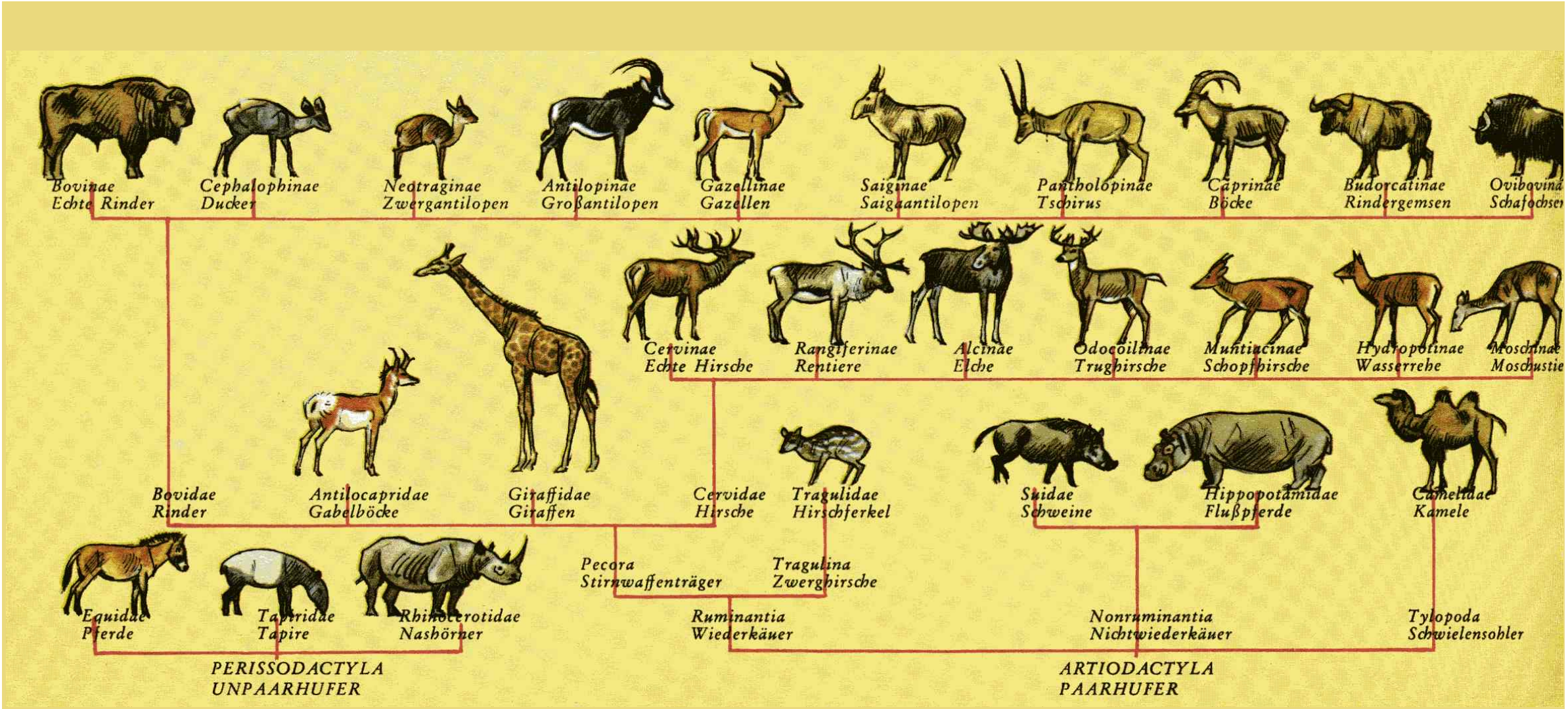


Large herbivore diversity in deep time: hoofed mammals



≈ 16 species

Large herbivore diversity in deep time: hoofed mammals



≈ 16 species

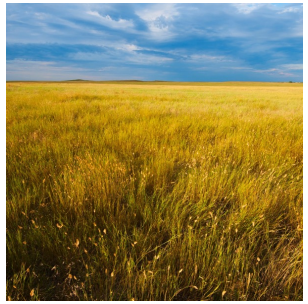
> 300 species

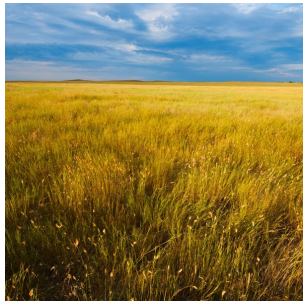
What are possible reasons for an evolutionary advantage of ruminants ?

Differences in hoof function ?

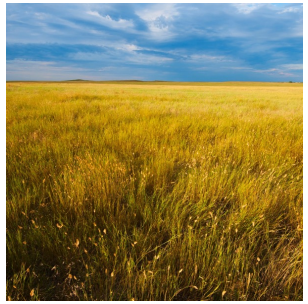
Differences in hoof function ?

Differences in hoof function ?

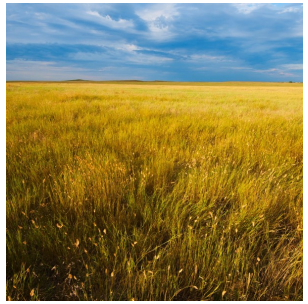




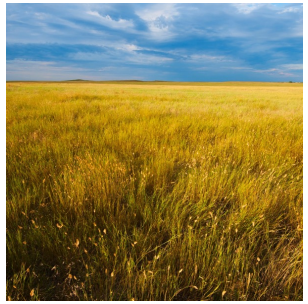
Differences in hoof function ?

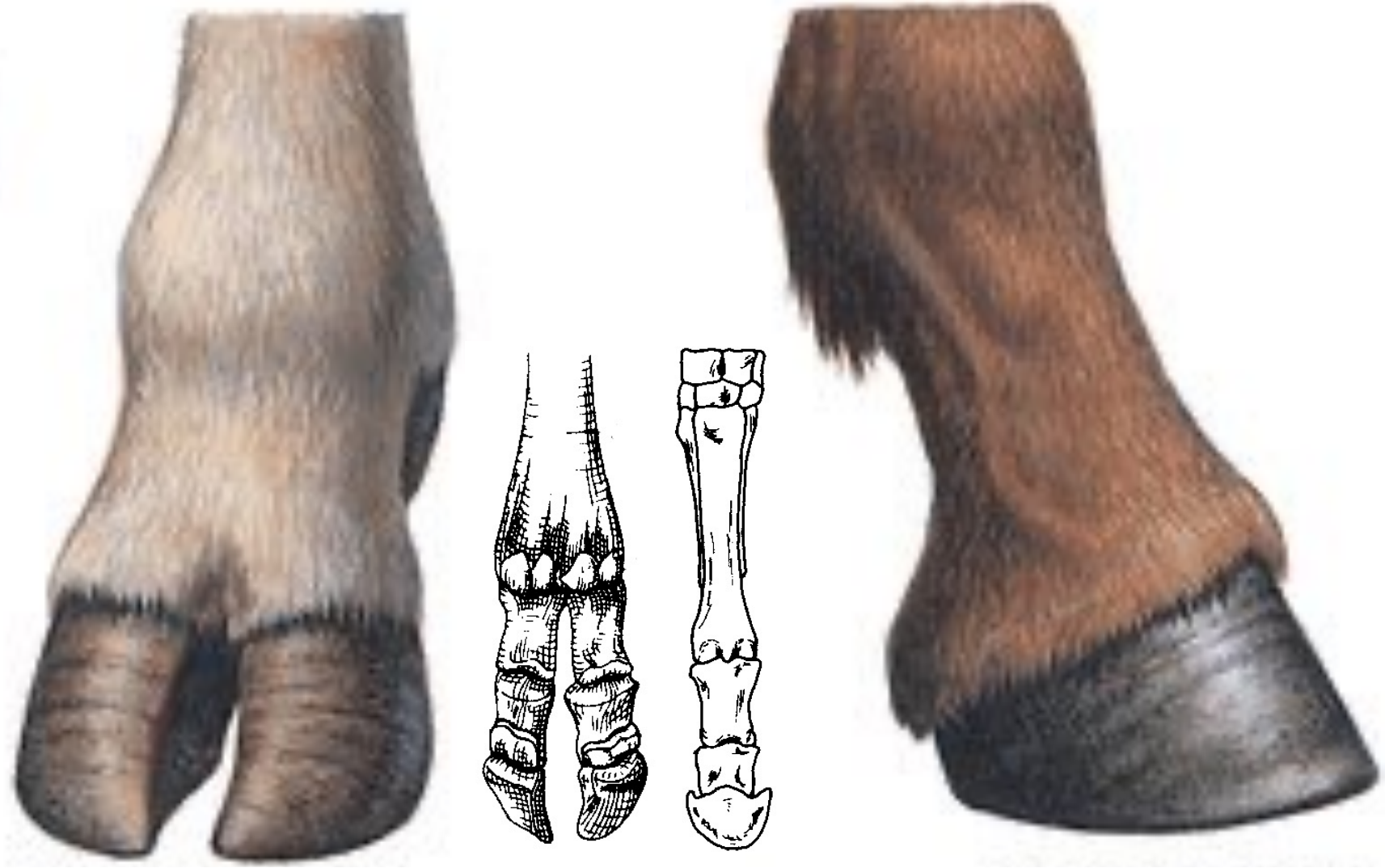


Differences in hoof function ?

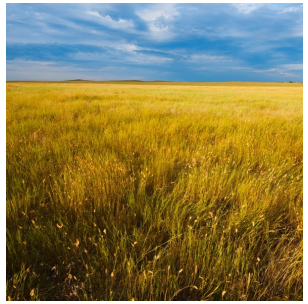


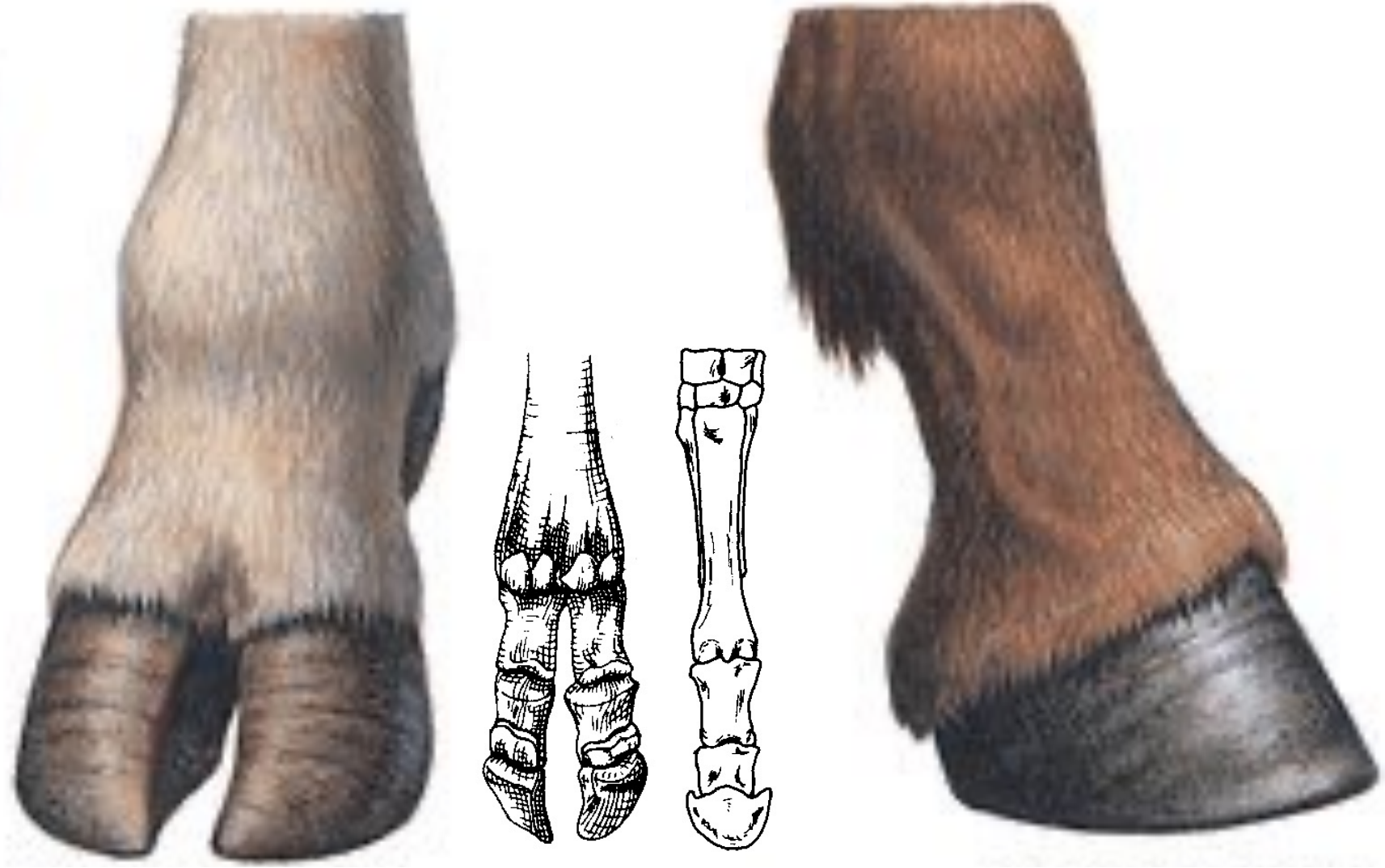
Differences in hoof function ?





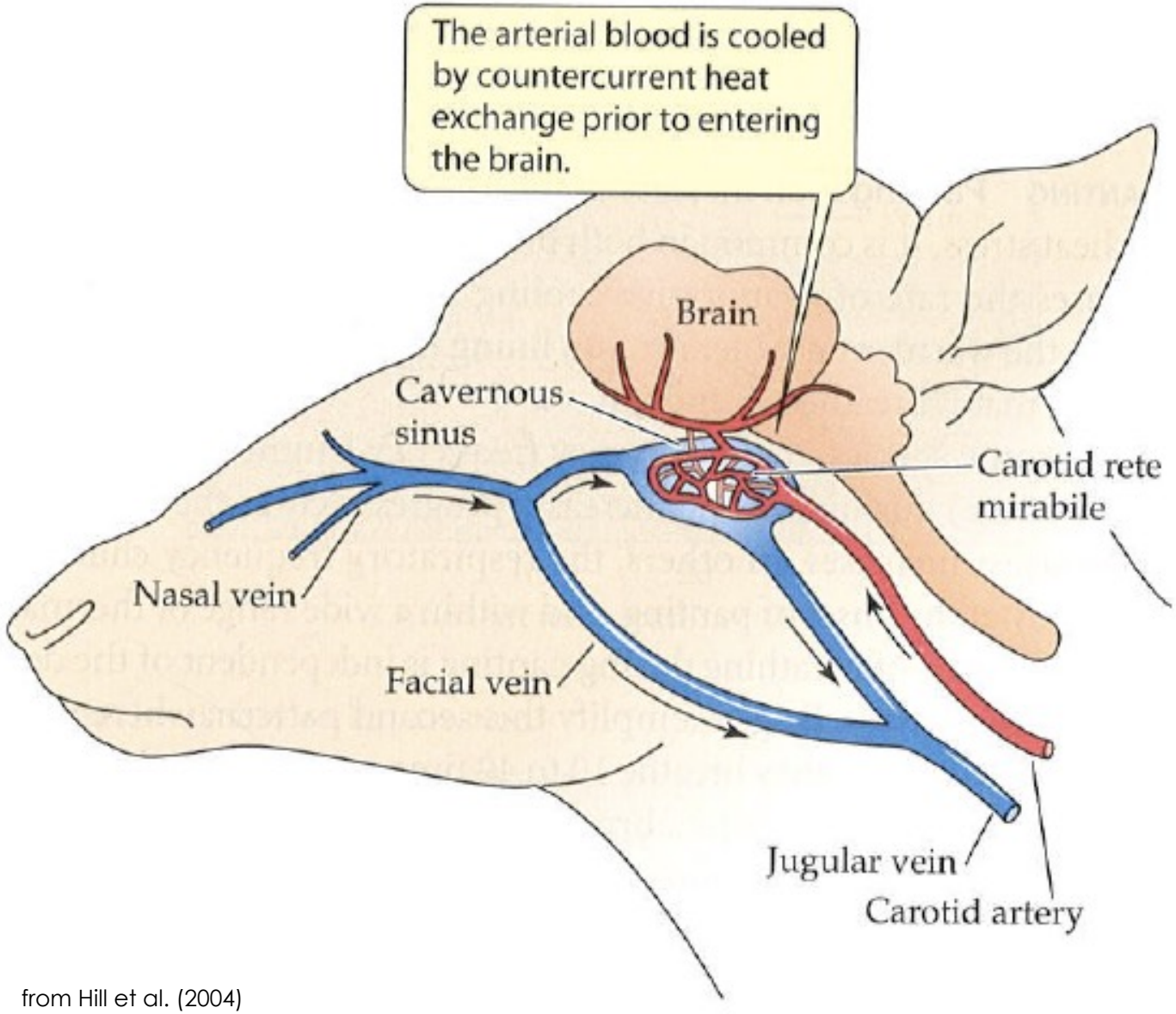
Differences in hoof function ?





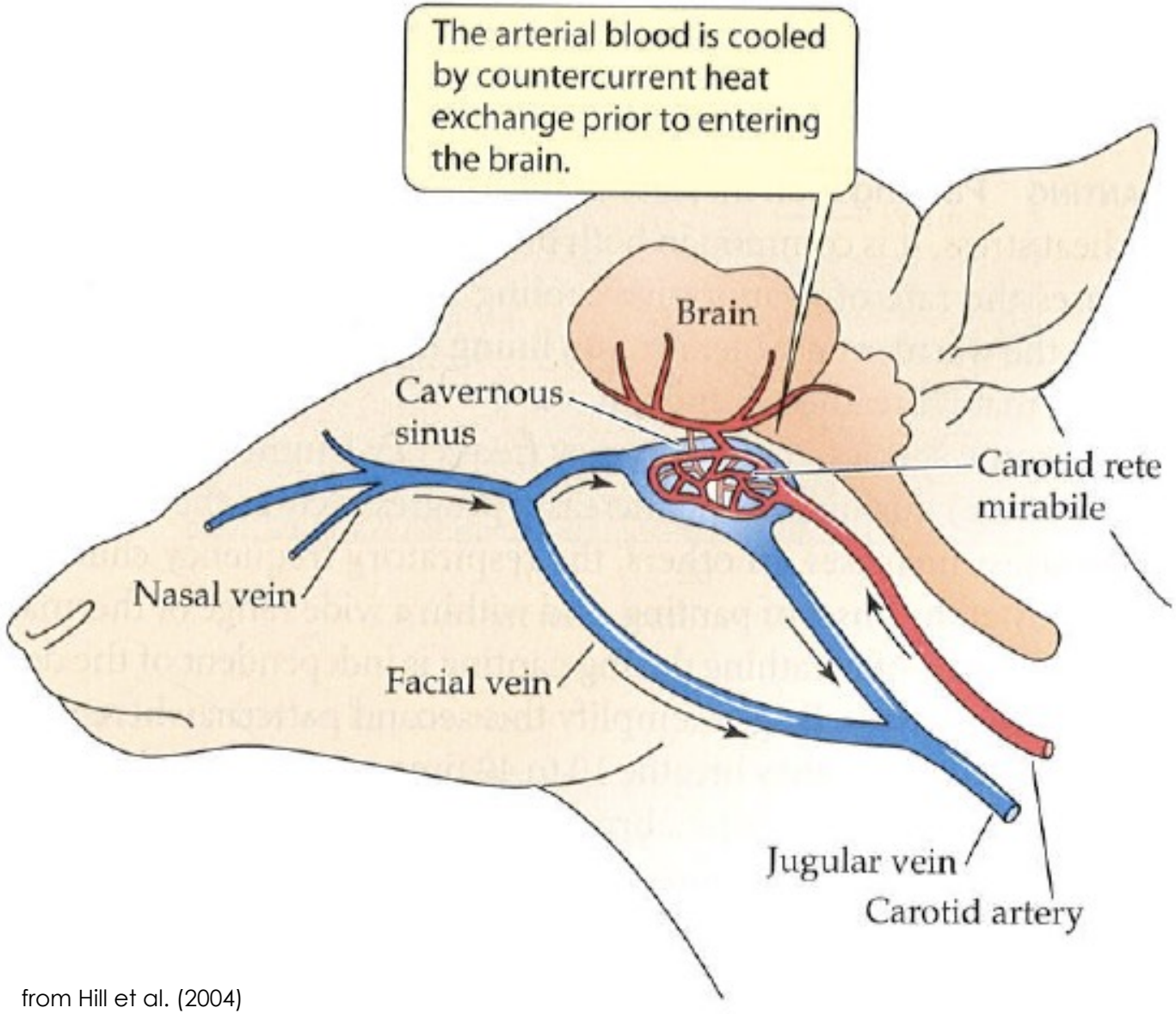
Differences in water dependence flexibility ?

Differences in water dependence flexibility ?

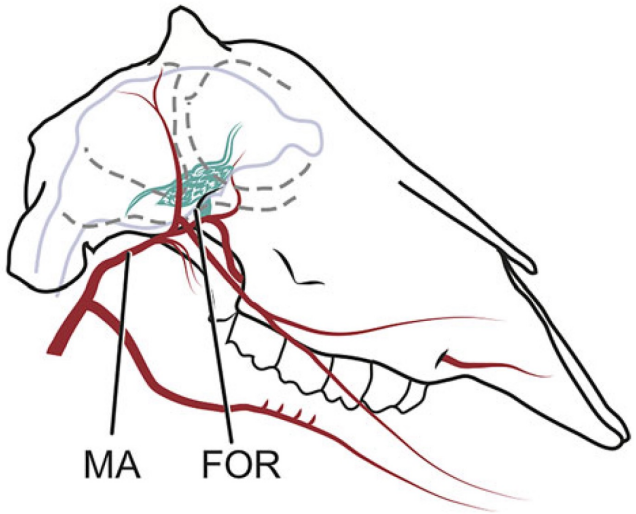


from Hill et al. (2004)

Differences in water dependence flexibility ?

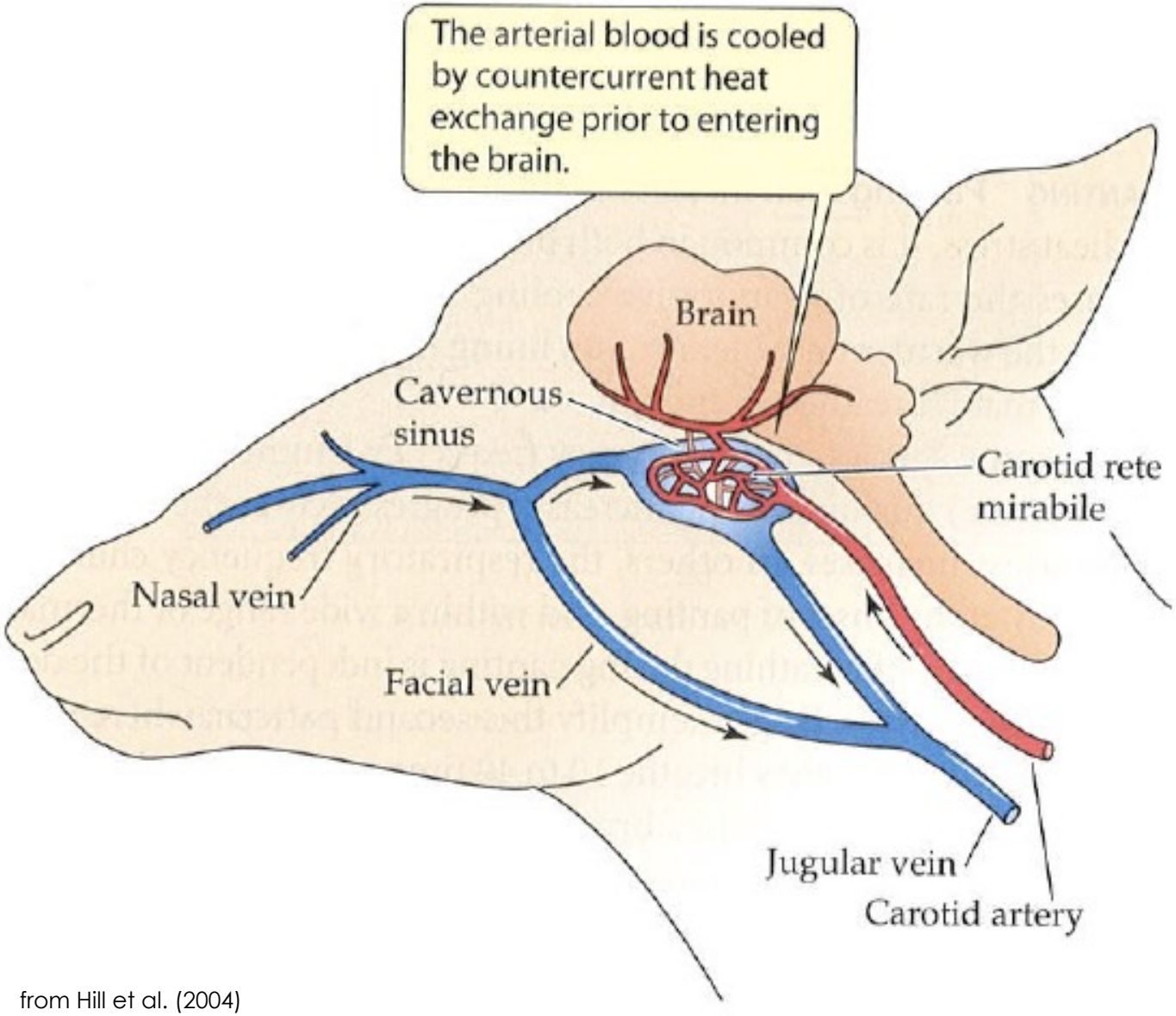


from Hill et al. (2004)

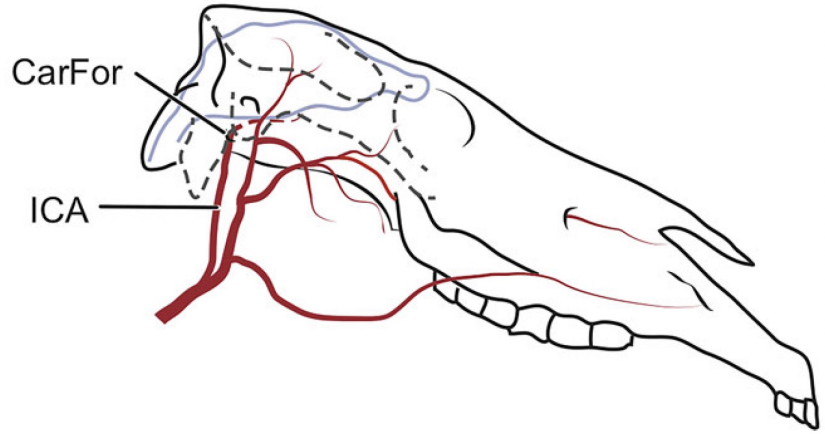


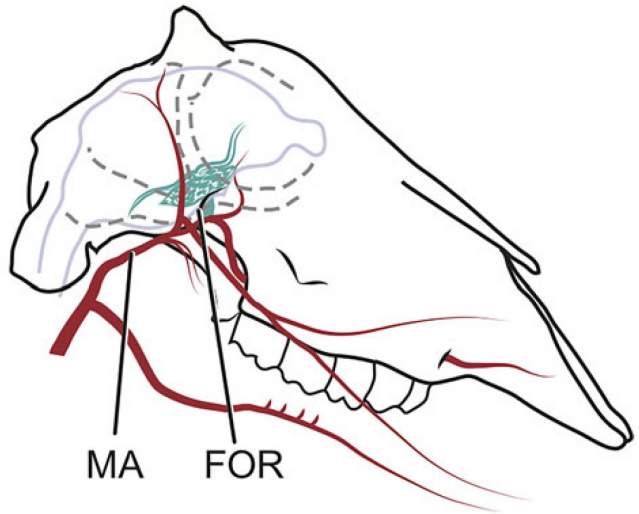
from O'Brian (2020)

Differences in water dependence flexibility ?



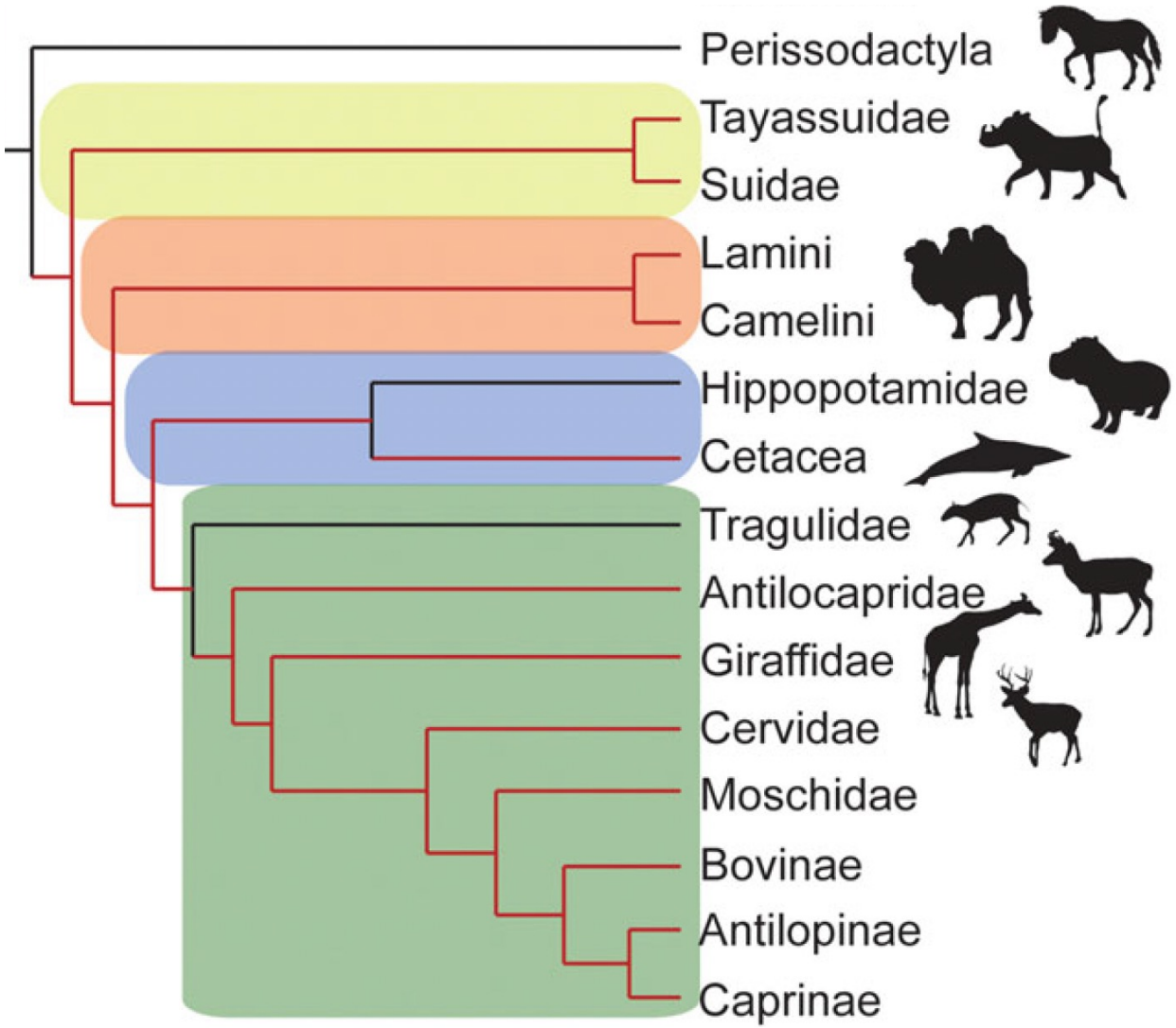
from Hill et al. (2004)



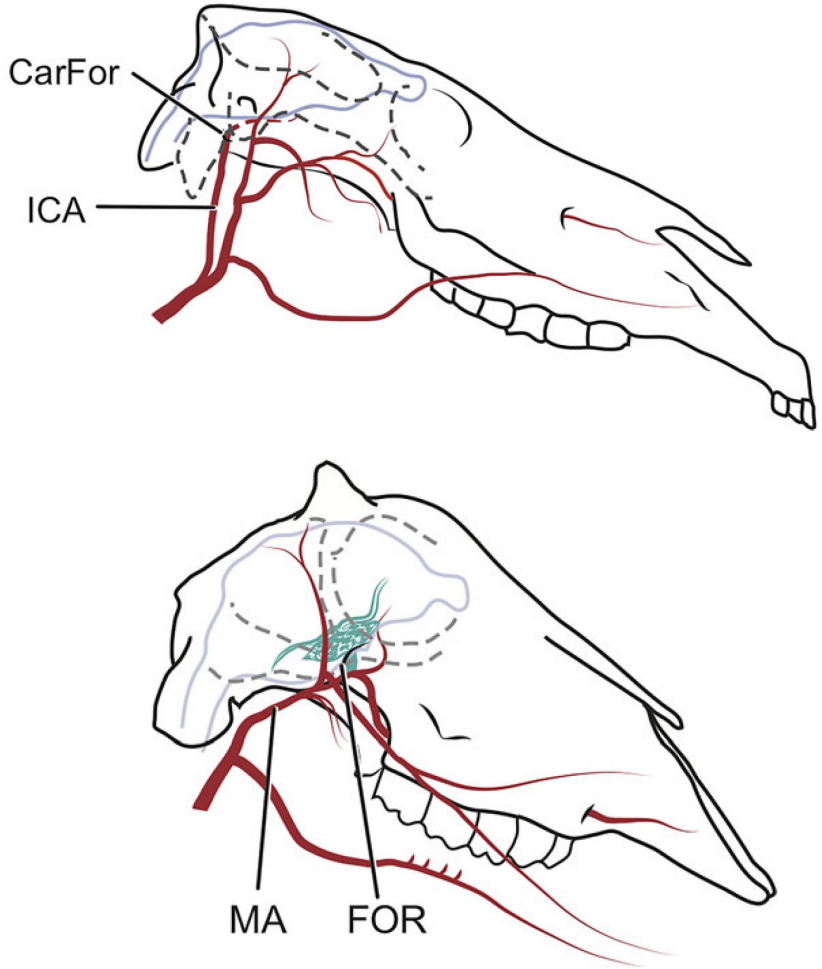


from O'Brian (2020)

Differences in water dependence flexibility ?

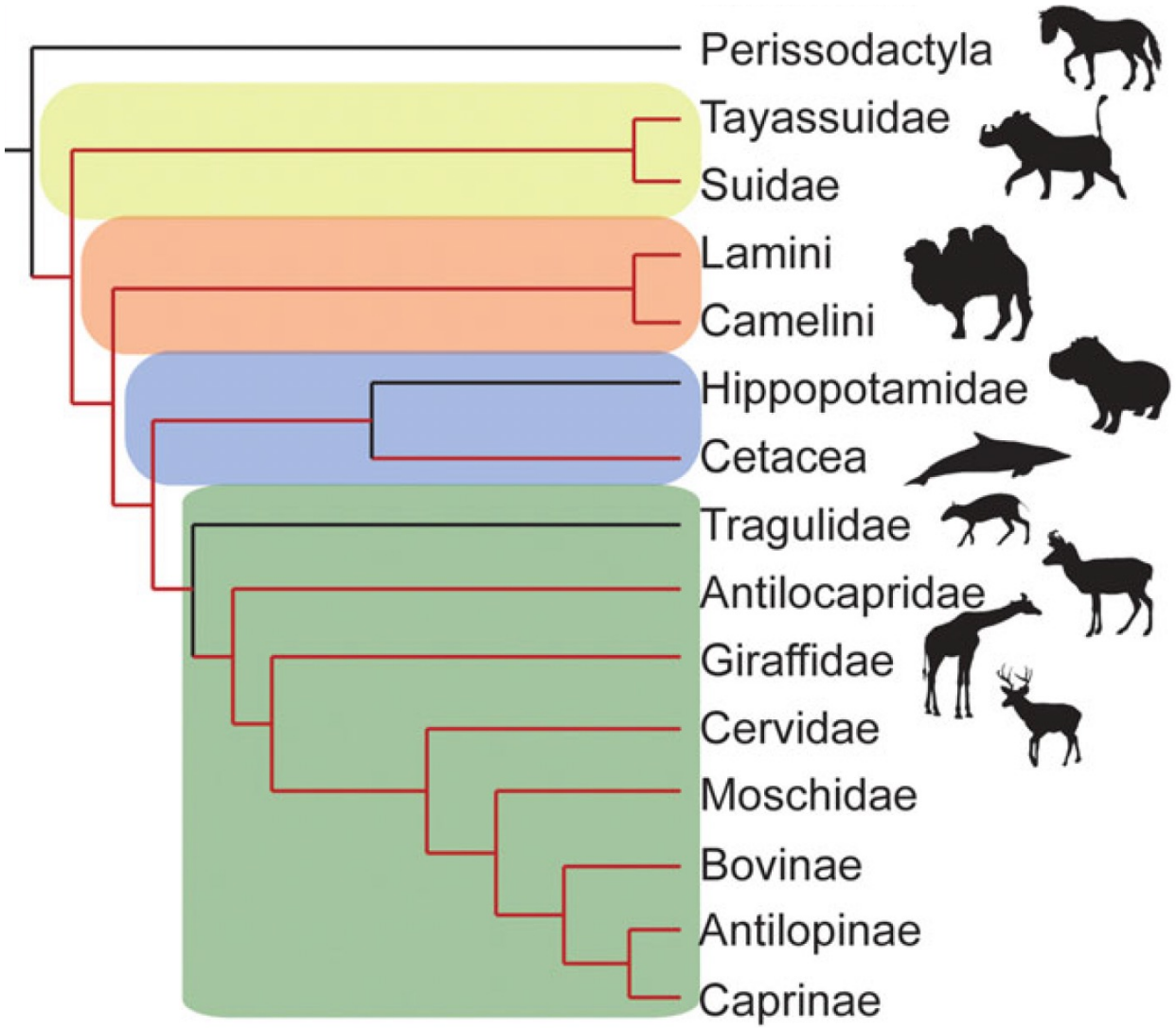


from Strauss et al. (2017)

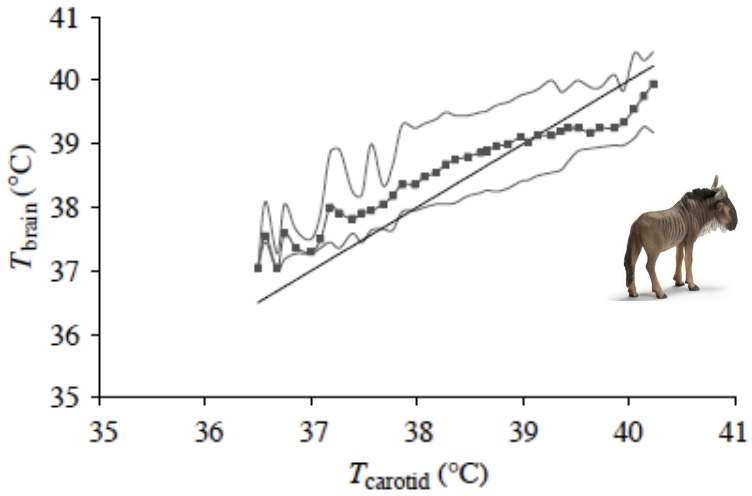


from O'Brian (2020)

Differences in water dependence flexibility ?

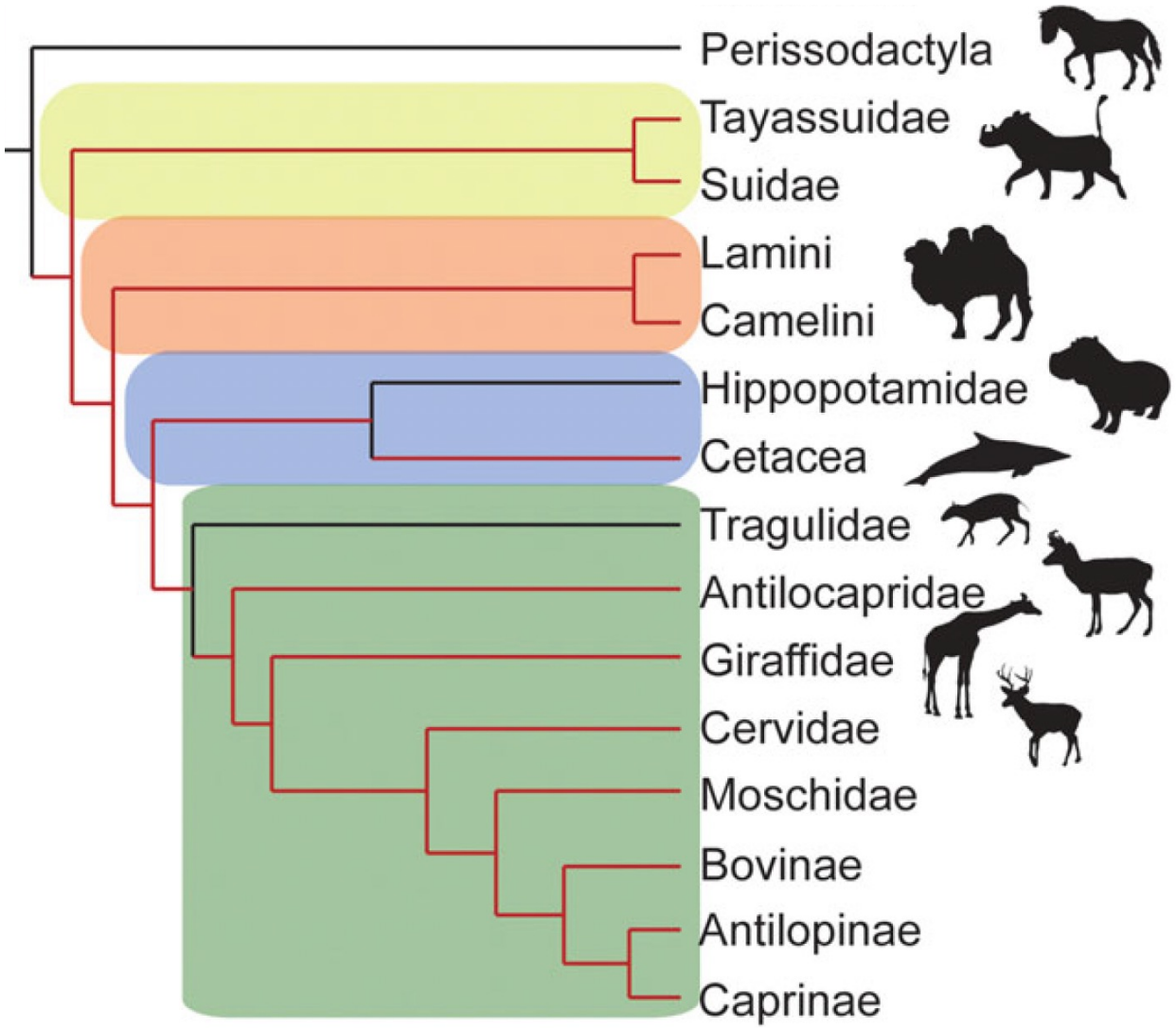


from Strauss et al. (2017)

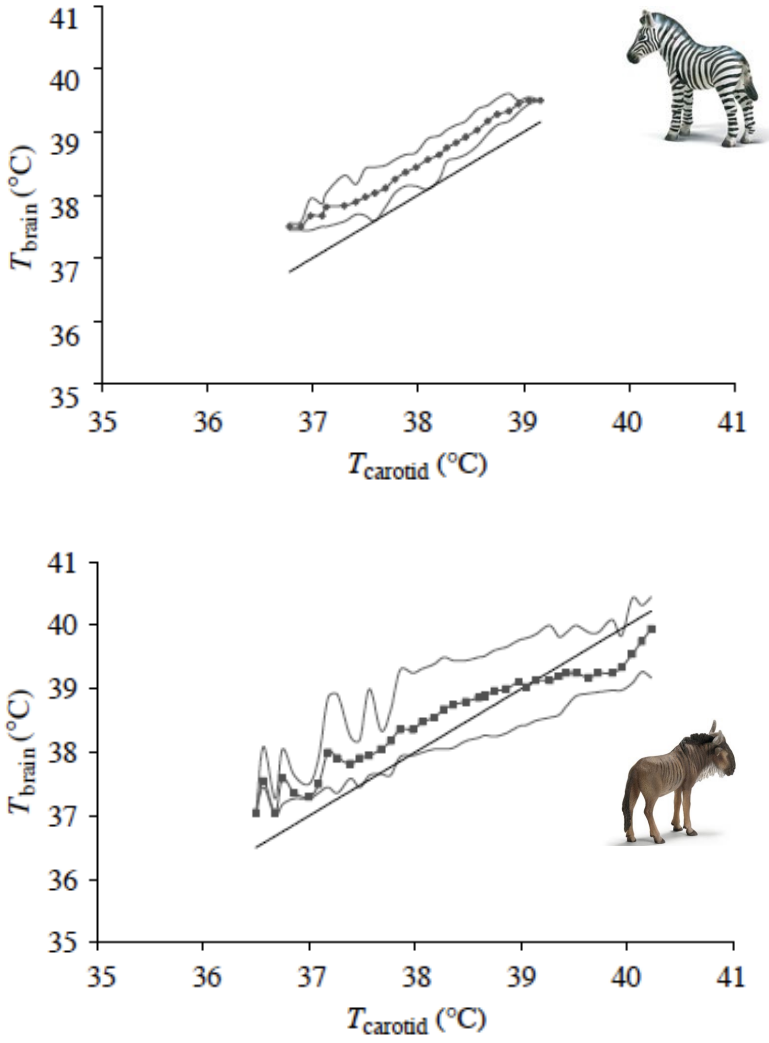


from Mitchell & Lust (2008)

Differences in water dependence flexibility ?

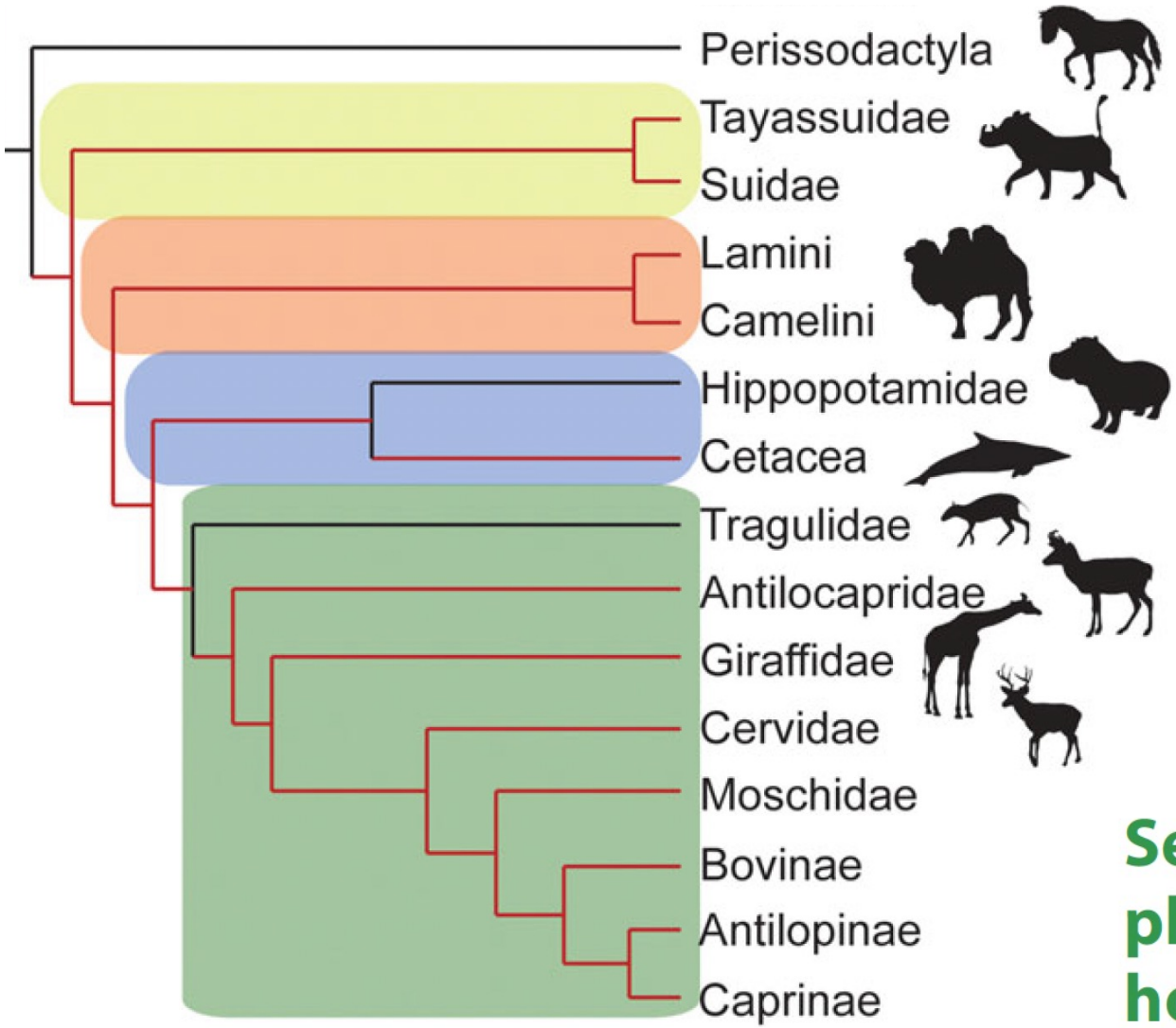


from Strauss et al. (2017)



from Mitchell & Lust (2008)

Differences in water dependence flexibility ?



Selective brain cooling as a physiological feature for surviving hotter and drier environments

from Strauss et al. (2017)

Differences in reproductive ***rate*** ?

Differences in reproductive ***rate*** ?

Gestation period

280 days

340 days

390 days

440 days

from Clauss et al. (2014)

Differences in reproductive ***rate*** ?

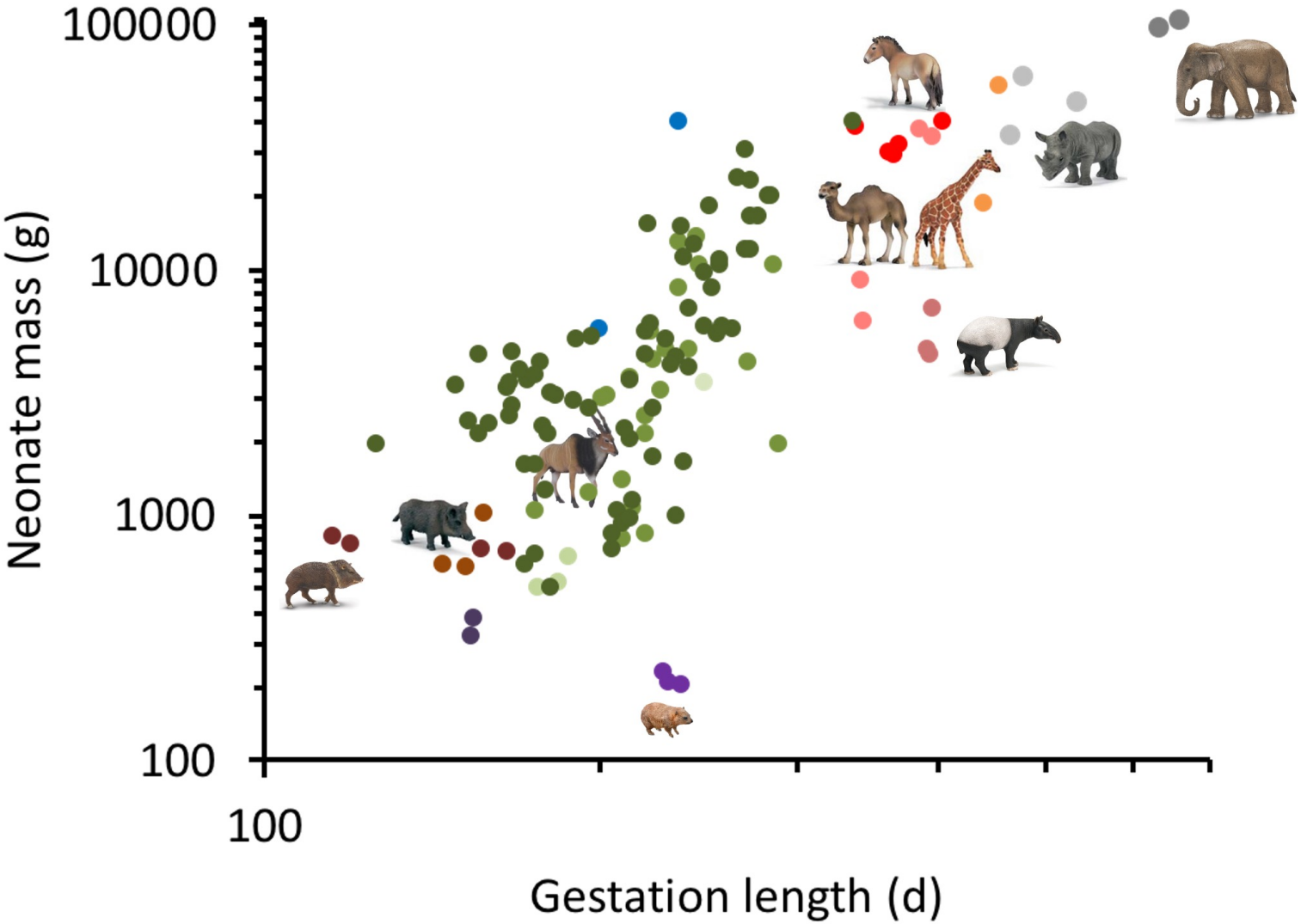
Gestation period

280 days

340 days

390 days

440 days



from Clauss et al. (2014, 2019)

Differences in reproductive ***rate*** ?

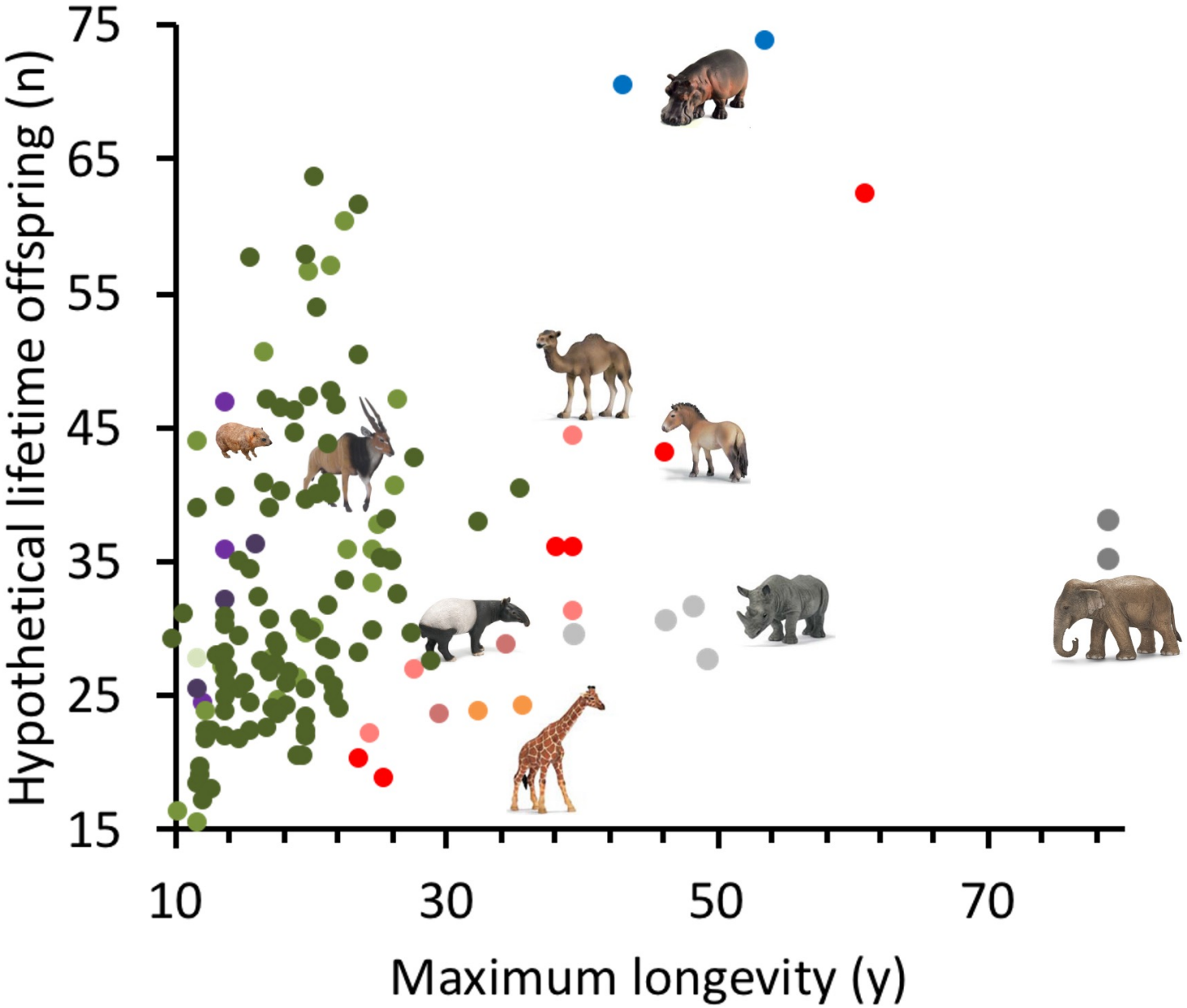
Gestation period

280 days

340 days

390 days

440 days

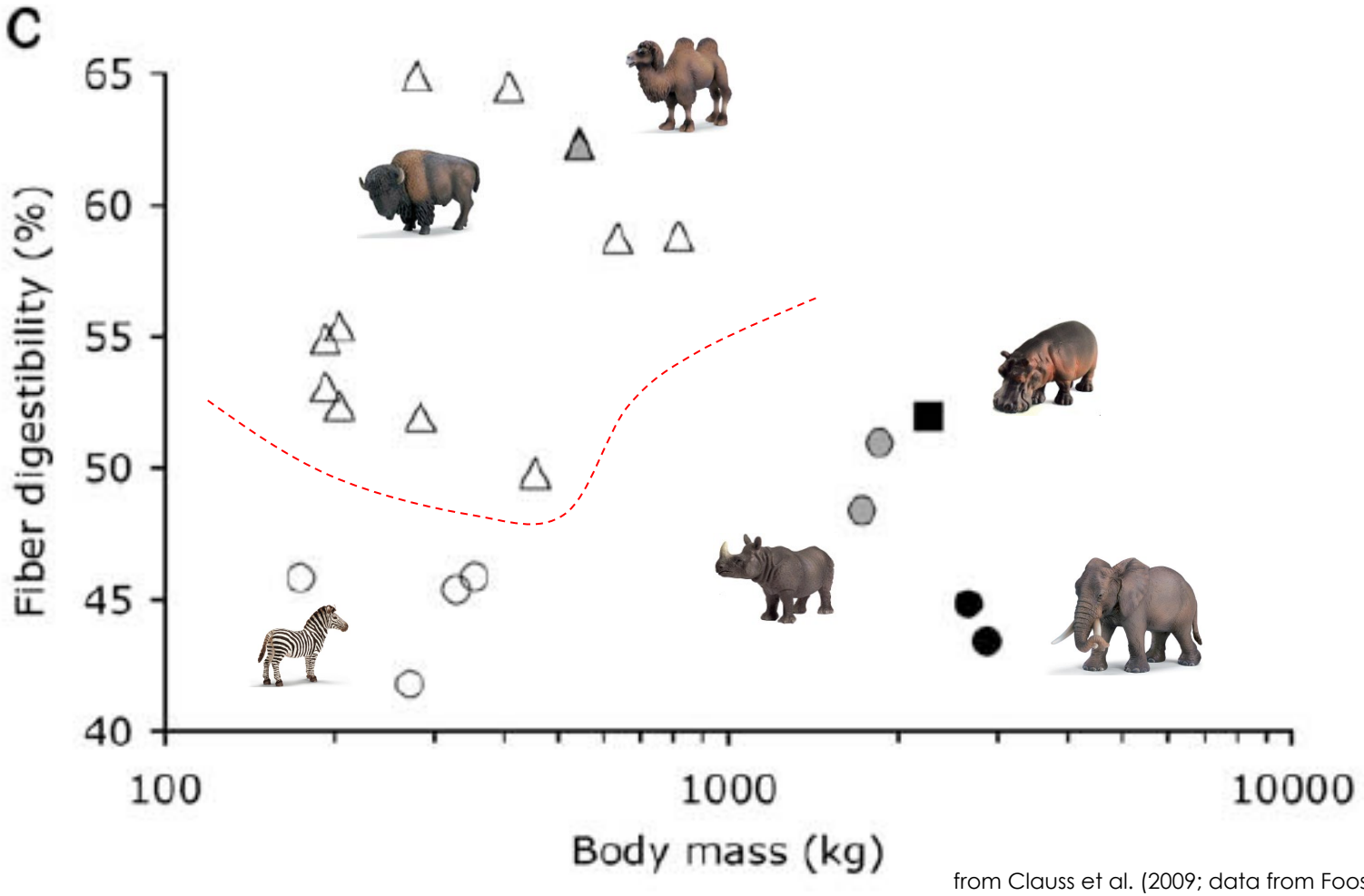


from Clauss et al. (2014, 2019)

Differences in digestive physiology between equids and ruminants: digestive efficiency and intake

Differences in digestive efficiency ?

Ruminants achieve higher digestive efficiencies



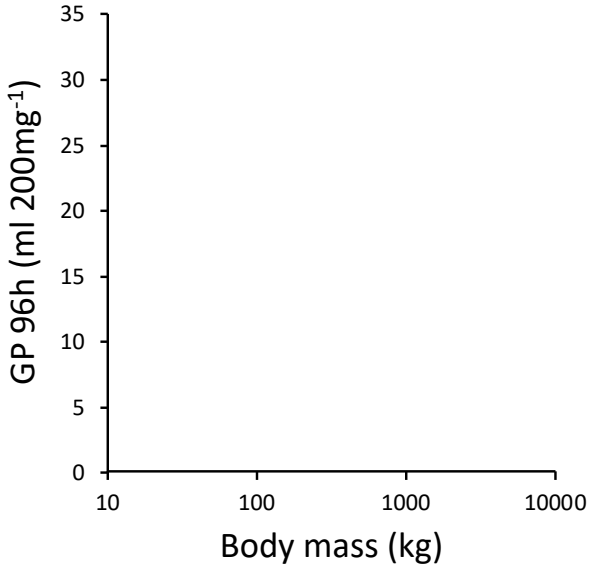
from Clauss et al. (2009; data from Foose 1982)

Digestive physiology meets herbivore diversity

Marcus Clauss [a], Patrick Steuer [b], Kerstin Erlinghagen-Lückerath [b], Jacques Kaandorp [c], Julia Fritz [a], Karl-Heinz Südekum [b,*], Jürgen Hummel [b,d]

Comparative Biochemistry and Physiology, Part A 179 (2015) 182–191

Residual digestibility in faeces

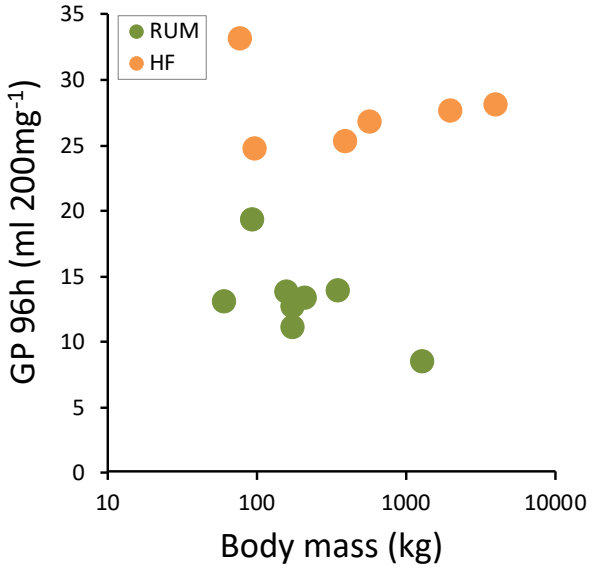


Digestive physiology meets herbivore diversity

Marcus Clauss [a], Patrick Steuer [b], Kerstin Erlinghagen-Lückerath [b], Jacques Kaandorp [c], Julia Fritz [a], Karl-Heinz Südekum [b,*], Jürgen Hummel [b,d]

Comparative Biochemistry and Physiology, Part A 179 (2015) 182–191

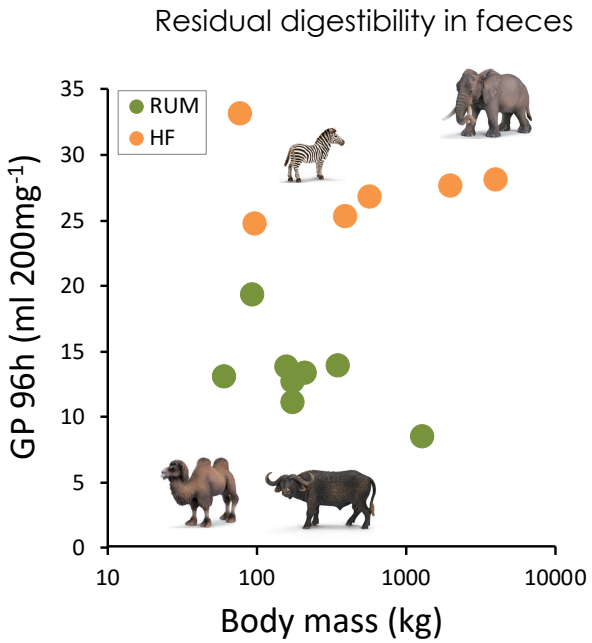
Residual digestibility in faeces



Digestive physiology meets herbivore diversity

Marcus Clauss [a], Patrick Steuer [b], Kerstin Erlinghagen-Lückerath [b], Jacques Kaandorp [c], Julia Fritz [a], Karl-Heinz Südekum [b,*], Jürgen Hummel [b,d]

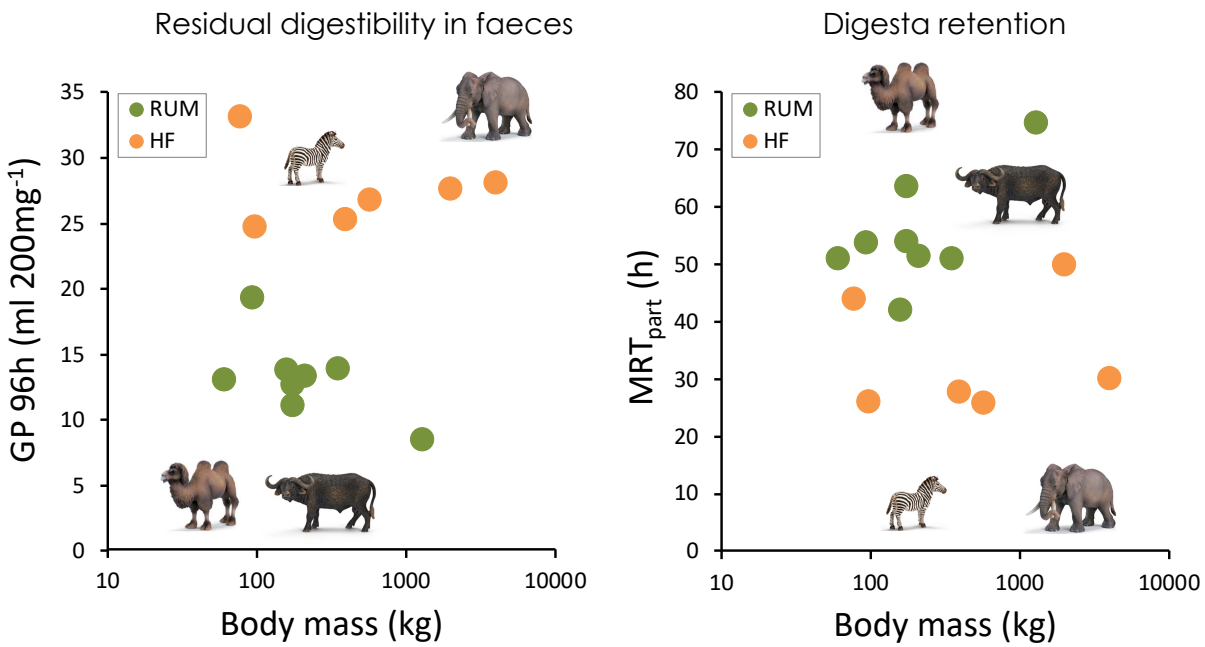
Comparative Biochemistry and Physiology, Part A 179 (2015) 182–191



Digestive physiology meets herbivore diversity

Marcus Clauss [a], Patrick Steuer [b], Kerstin Erlinghagen-Lückerath [b], Jacques Kaandorp [c], Julia Fritz [a], Karl-Heinz Südekum [b,*], Jürgen Hummel [b,d]

Comparative Biochemistry and Physiology, Part A 179 (2015) 182–191

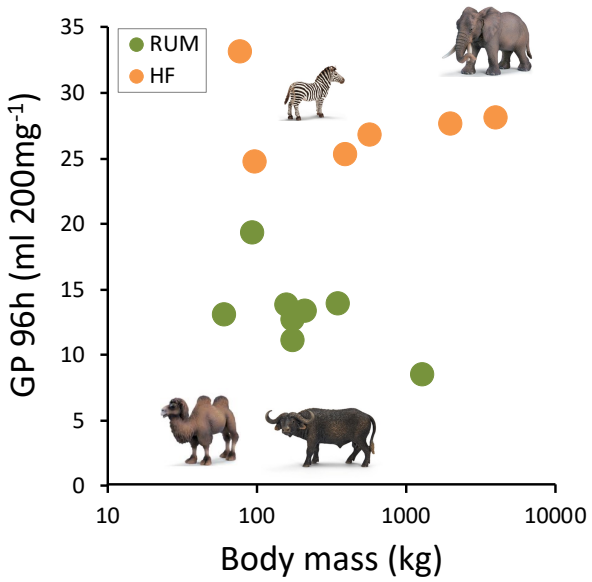


Digestive physiology meets herbivore diversity

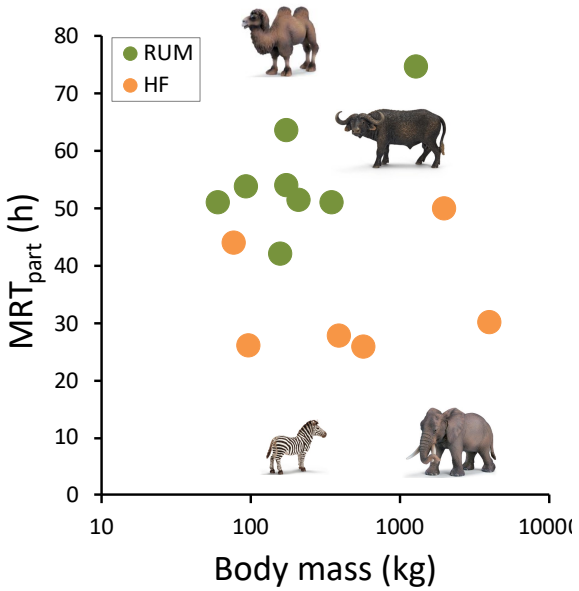
Marcus Clauss [a], Patrick Steuer [b], Kerstin Erlinghagen-Lückerath [b], Jacques Kaandorp [c], Julia Fritz [a], Karl-Heinz Südekum [b,*], Jürgen Hummel [b,d]

Comparative Biochemistry and Physiology, Part A 179 (2015) 182–191

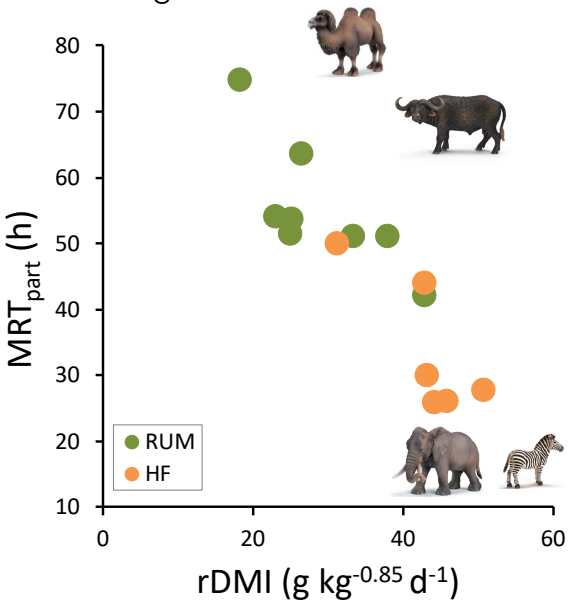
Residual digestibility in faeces



Digesta retention



Digesta retention vs. intake

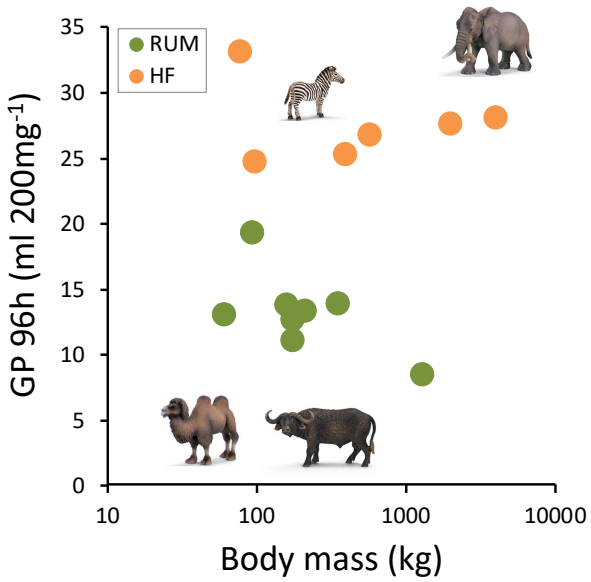


Digestive physiology meets herbivore diversity

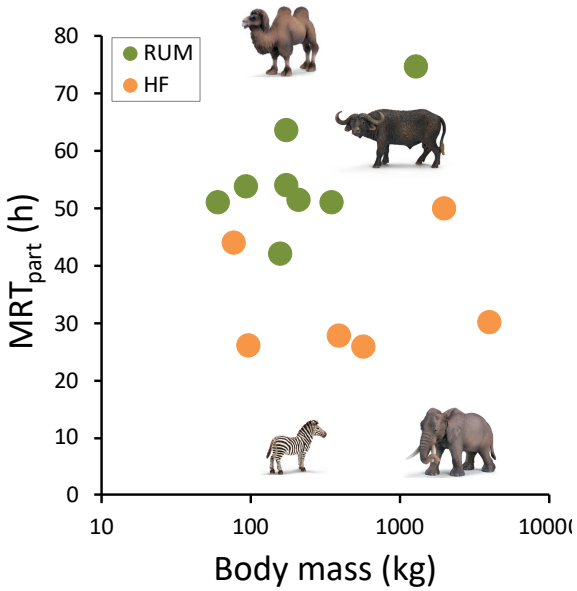
Marcus Clauss [a], Patrick Steuer [b], Kerstin Erlinghagen-Lückerath [b], Jacques Kaandorp [c], Julia Fritz [a], Karl-Heinz Südekum [b,*], Jürgen Hummel [b,d]

Comparative Biochemistry and Physiology, Part A 179 (2015) 182–191

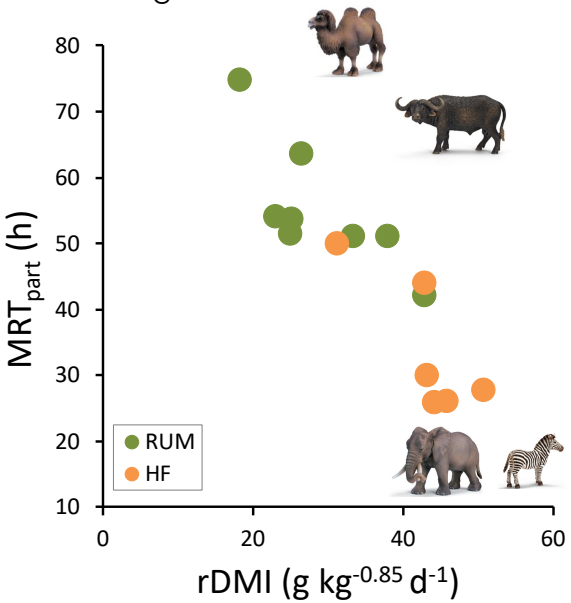
Residual digestibility in faeces



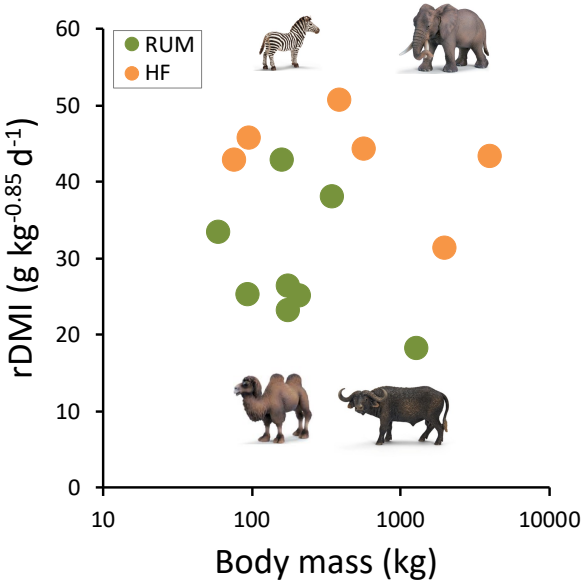
Digesta retention



Digesta retention vs. intake



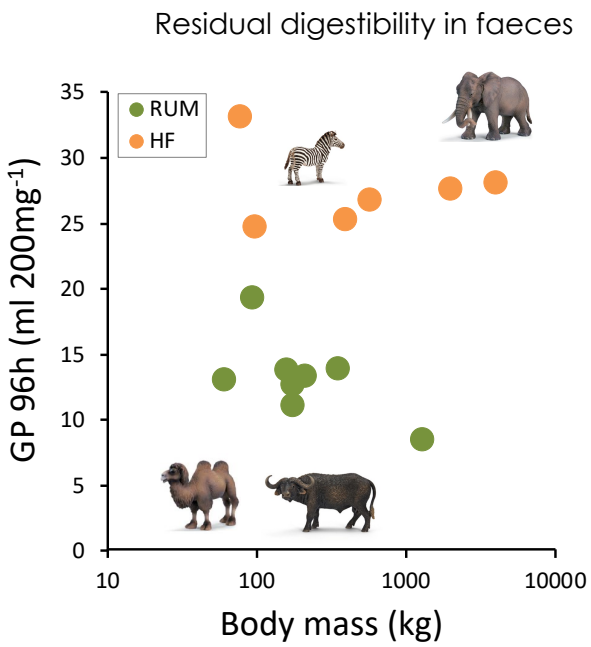
Relative intake

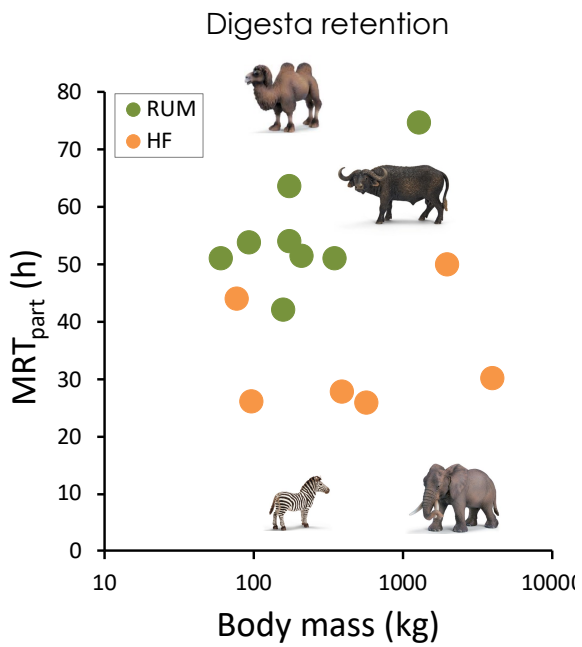


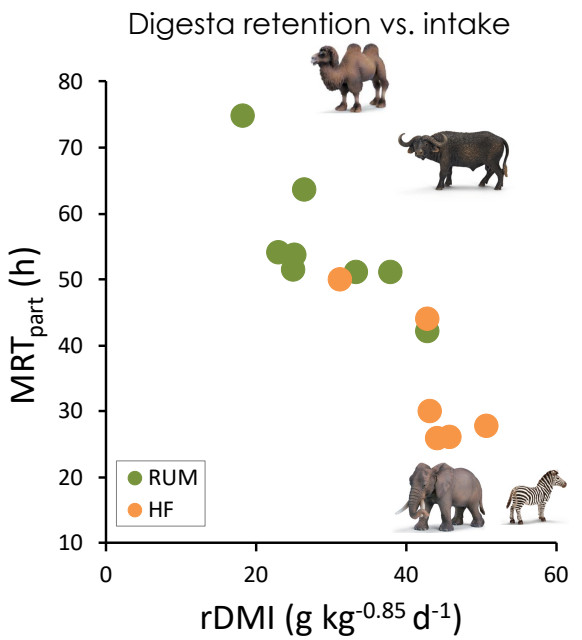
Digestive physiology meets herbivore diversity

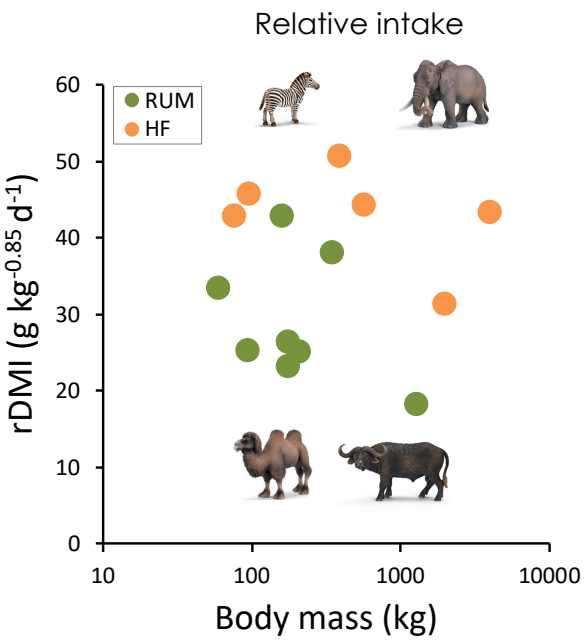
Marcus Clauss [a], Patrick Steuer [b], Kerstin Erlinghagen-Lückerath [b], Jacques Kaandorp [c], Julia Fritz [a], Karl-Heinz Südekum [b,*], Jürgen Hummel [b,d]

Comparative Biochemistry and Physiology, Part A 179 (2015) 182–191







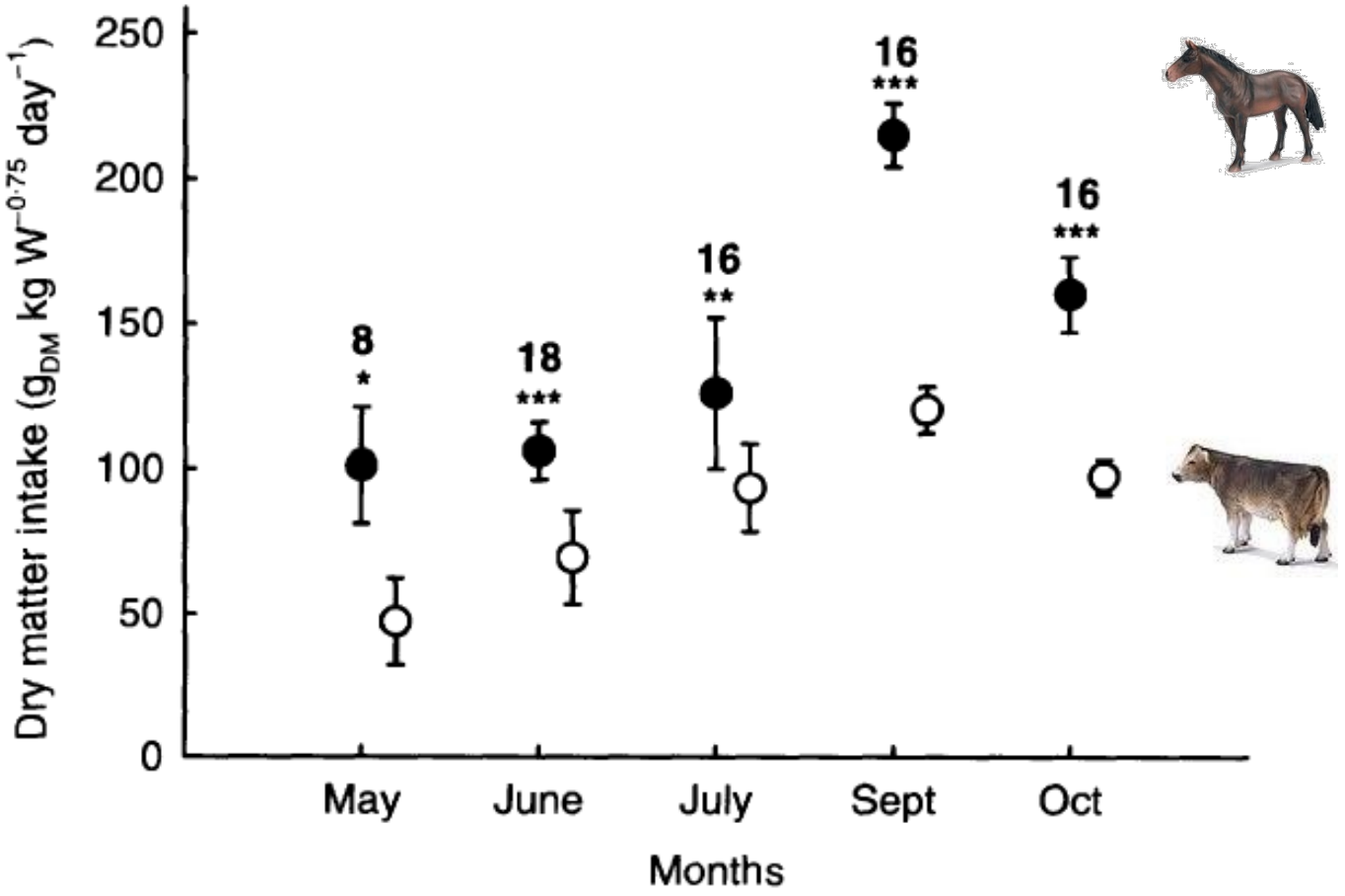


=> Equids have a strategy of lesser digestive efficiency compensated by higher intake

Comparative foraging and nutrition of horses and cattle in European wetlands

Journal of Applied Ecology 2002
39, 120–133

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

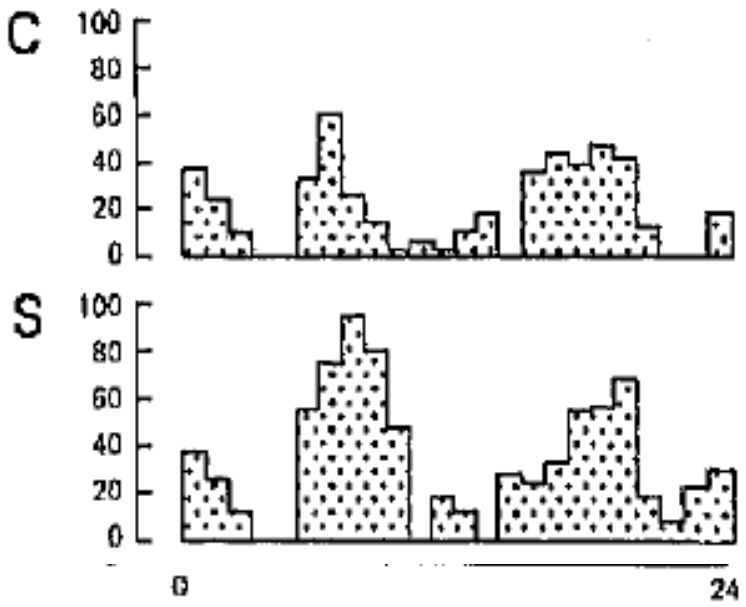


COMPARISON OF THE TIME BUDGETS AND CIRCADIAN PATTERNS OF MAINTENANCE ACTIVITIES IN SHEEP, CATTLE AND HORSES GROUPED TOGETHER

G.W. ARNOLD

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

Grazing

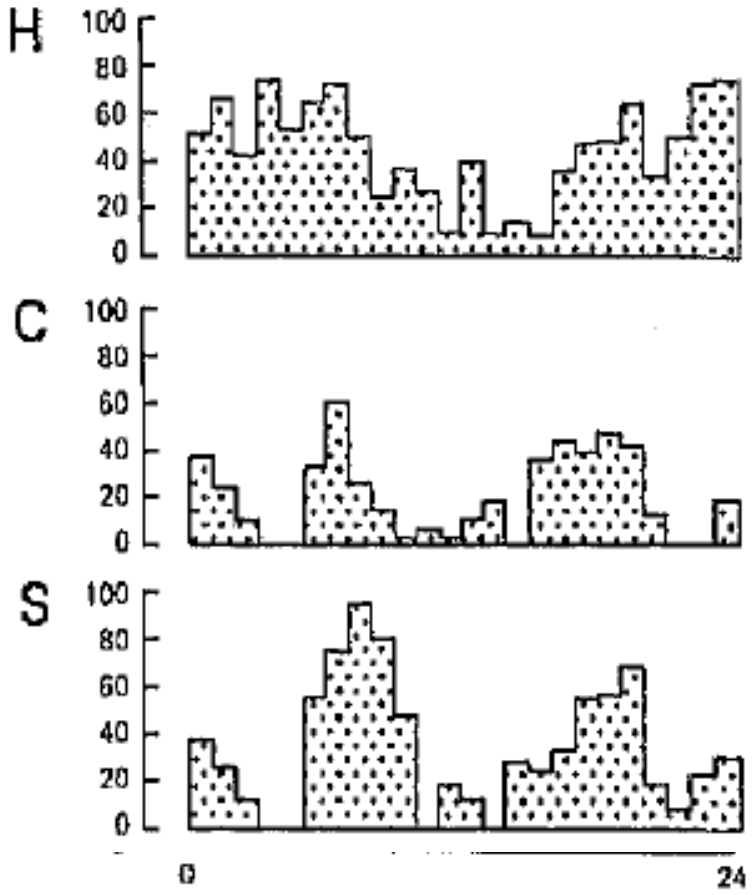


COMPARISON OF THE TIME BUDGETS AND CIRCADIAN PATTERNS OF MAINTENANCE ACTIVITIES IN SHEEP, CATTLE AND HORSES GROUPED TOGETHER

G.W. ARNOLD

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

Grazing



Differences in digestive physiology between equids and ruminants: a historical myth ?

A drawing dominates comparative concepts

A drawing dominates comparative concepts

THE EVOLUTIONARY STRATEGY OF THE EQUIDAE AND THE ORIGINS OF RUMEN AND CECAL DIGESTION

CHRISTINE JANIS

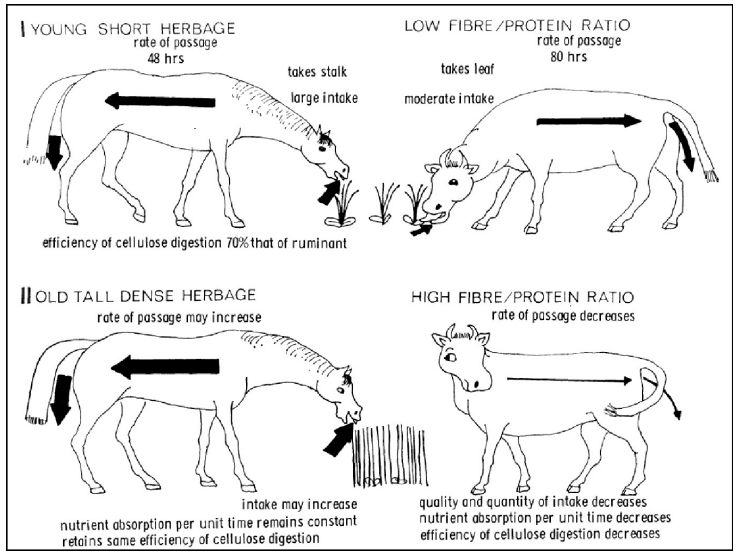
EVOLUTION 30:757–774. December 1976

A drawing dominates comparative concepts

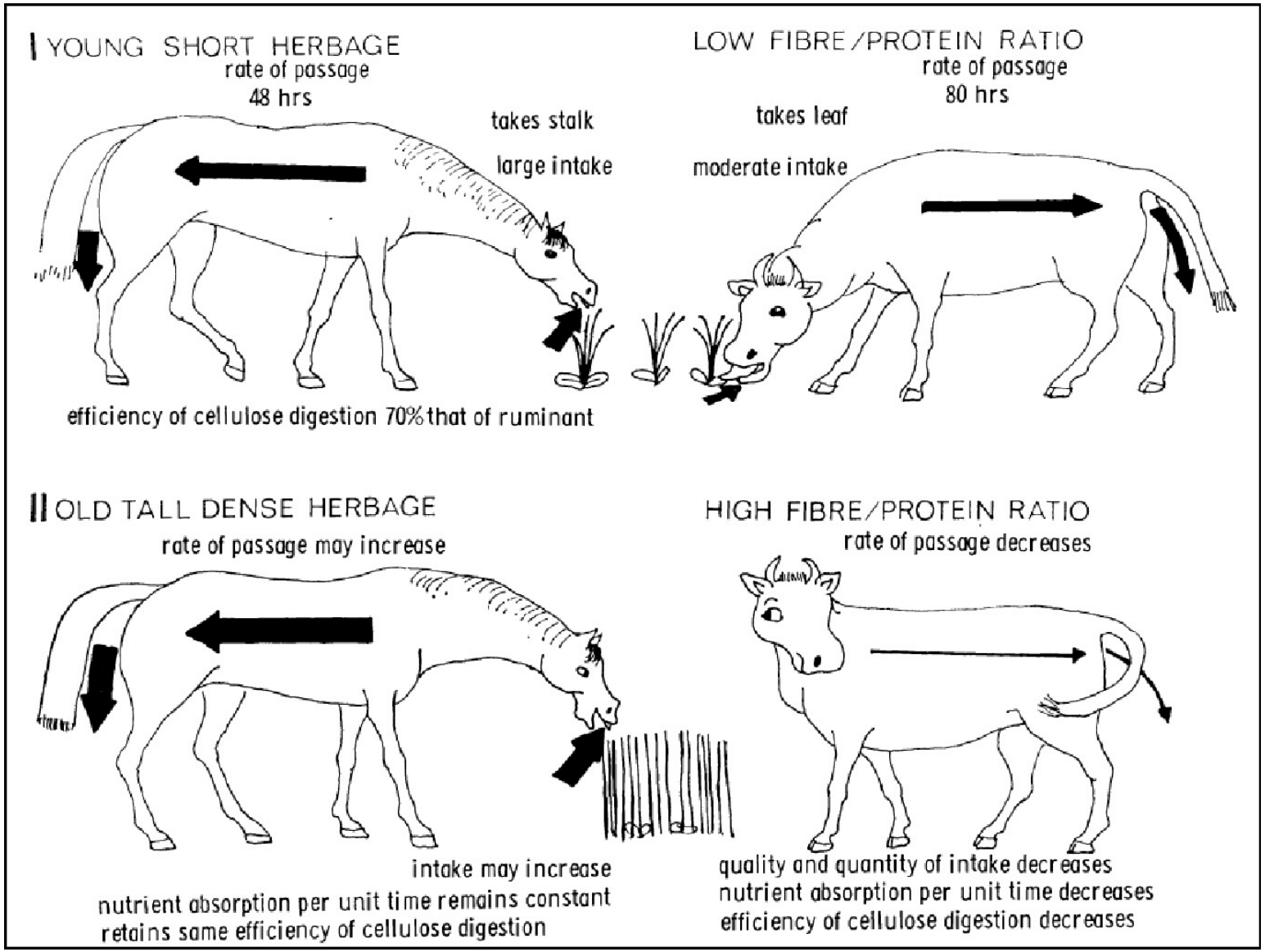
THE EVOLUTIONARY STRATEGY OF THE EQUIDAE AND THE ORIGINS OF RUMEN AND CECAL DIGESTION

CHRISTINE JANIS

EVOLUTION 30:757–774. December 1976



A drawing dominates comparative concepts



Janis (1976)

A drawing dominates comparative concepts

COMPARATIVE DIGESTIVE CAPACITIES OF HERBIVOROUS ANIMALS

P.J. Van Soest, T. Foose and J.B. Robertson

Proceedings of the Conrell Nutrition Conference 1983, 51-59

A. Young, short grass ; fibre / protein low

Intake	:	moderate	moderate
Passage rate	:	48 hrs.	80 hrs.
Cellulose digestion	:	70% that of ruminants	

B. Old, long grass ; fibre / protein high

Intake	:	increased	decreased
Passage rate	:	faster	slower
Nutrient absorption	:	similar	less
Cellulose digestion	:	decreased	similar-decreased

(adapted from Janis, 1976)

A drawing dominates comparative concepts

COMPARATIVE DIGESTIVE CAPACITIES OF HERBIVOROUS ANIMALS

P.J. Van Soest, T. Foose and J.B. Robertson

Proceedings of the Conrell Nutrition Conference 1983, 51-59

A. Young, short grass ; fibre / protein low

Intake	:	moderate	moderate
Passage rate	:	48 hrs.	80 hrs.
Cellulose digestion	:	70% that of ruminants	

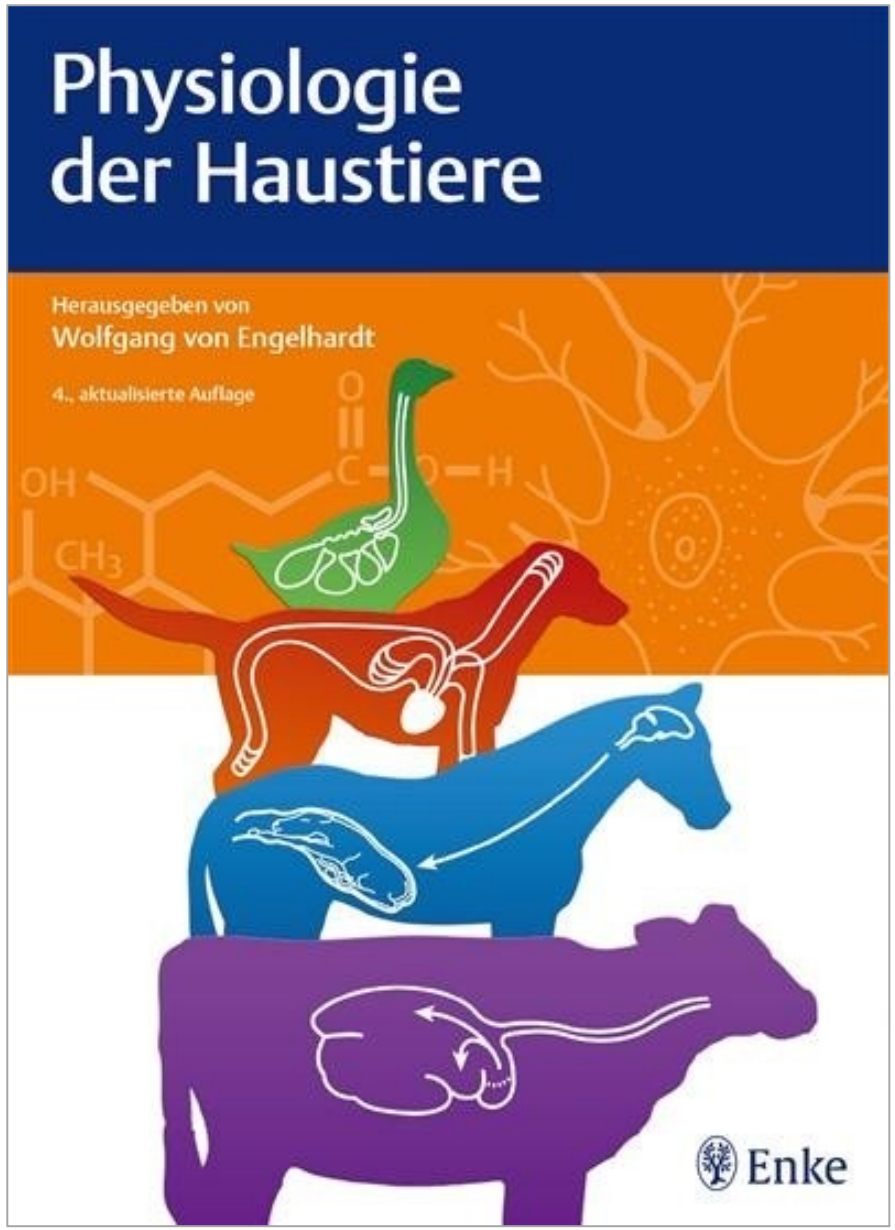
B. Old, long grass ; fibre / protein high

Intake	:	increased	decreased
Passage rate	:	faster	slower
Nutrient absorption	:	similar	less
Cellulose digestion	:	decreased	similar-decreased

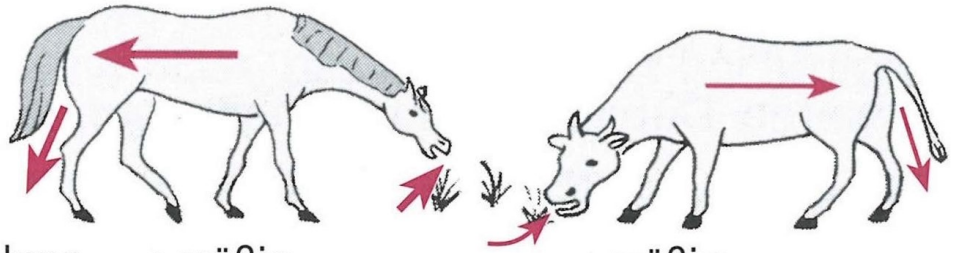
(adapted from Janis, 1976)

The principle may explain why bullshit has replaced horseshit over evolutionary time (Foose pers. comm.). Figure courtesy of W. von Engelhardt.

A drawing dominates comparative concepts

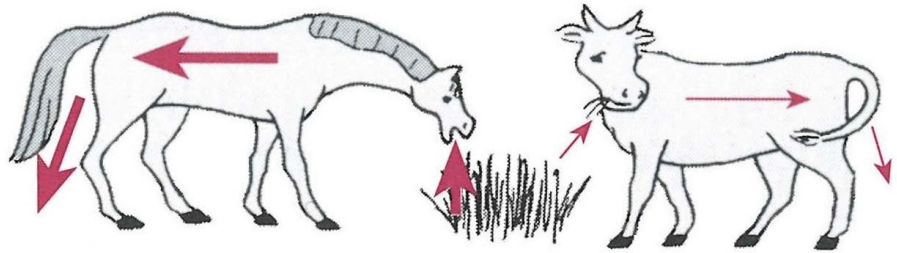


A Junges, kurzes Gras: Quotient Rohfaser zu Protein ist niedrig



Futteraufnahme	: mäßig	mäßig
Passage durch MDK	: 48 Std.	80 Std.
Celluloseverdauung	: 70% der Wiederkäuer	

B Altes, langes Gras: Quotient Rohfaser zu Protein ist hoch



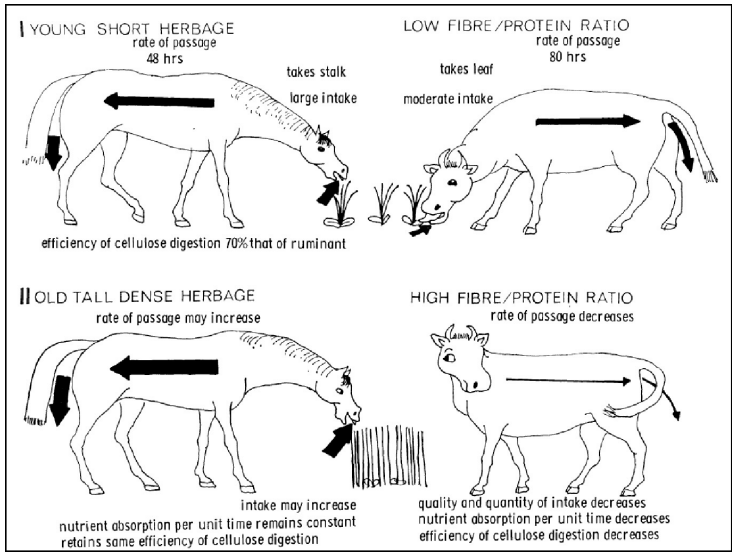
Futteraufnahme	: erhöht	vermindert
Passage durch MDK	: schneller	langsamer
Nährstoffresorption	: gleich	weniger
Celluloseverdauung	: vermindert	gleich - vermindert

A drawing dominates comparative concepts

THE EVOLUTIONARY STRATEGY OF THE EQUIDAE AND THE ORIGINS OF RUMEN AND CECAL DIGESTION

CHRISTINE JANIS

EVOLUTION 30:757–774. December 1976



Experiments on domestic ponies indicate that rate of intake may actually decrease with increasing fiber content of the food, although proportionally much less than in ruminants

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

Journal of Animal Science 1965 24: 834-843

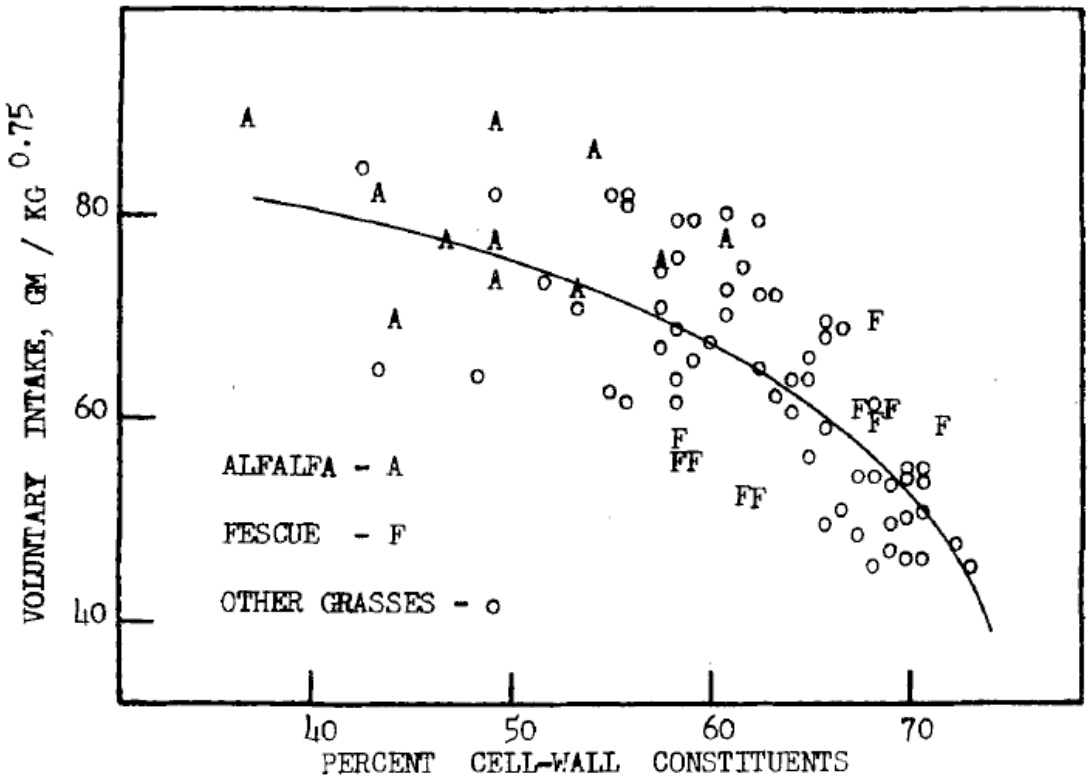
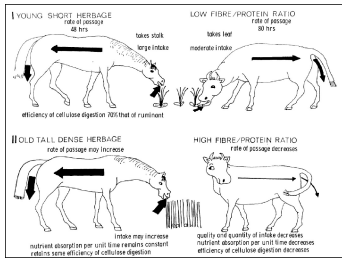


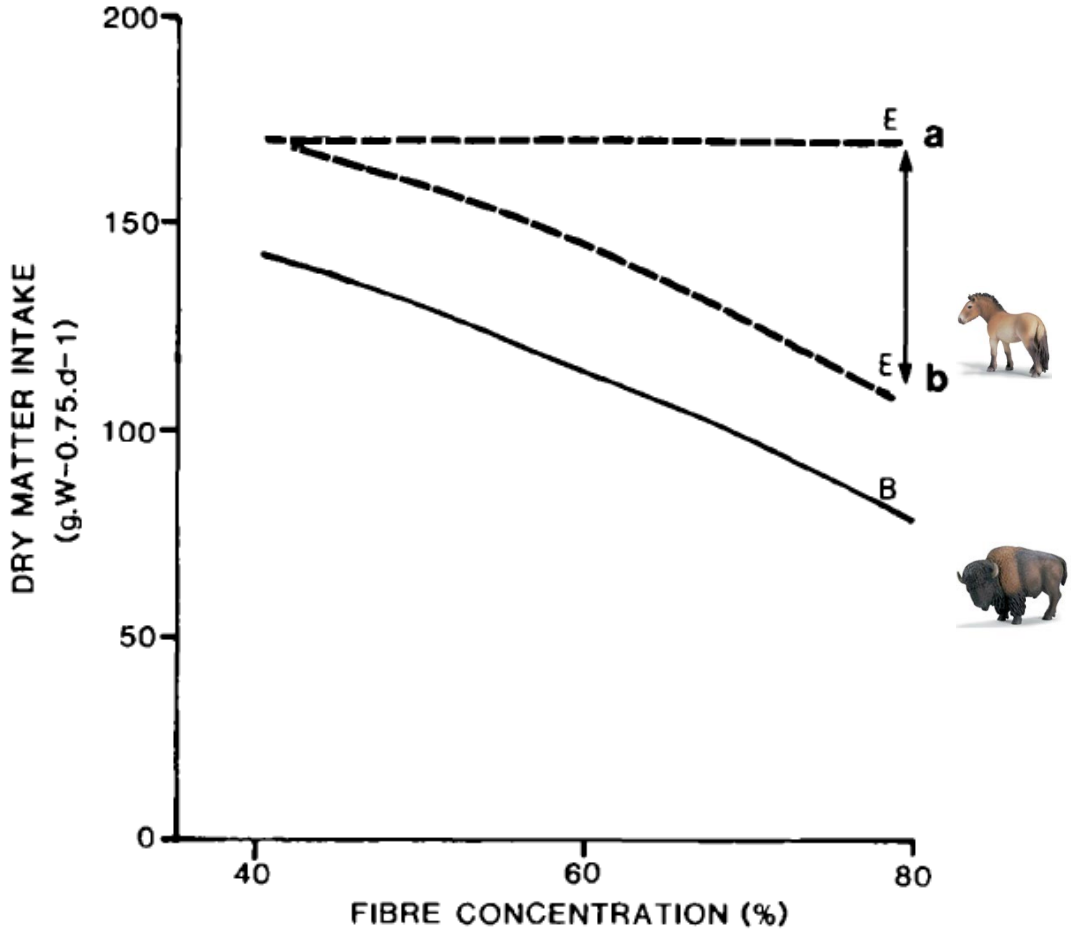
Figure 2. Relationship between voluntary intake and cell-wall constituents of 83 forages from West Virginia. Regression equation: $Y=110.4-1716/(100-X)$.

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]

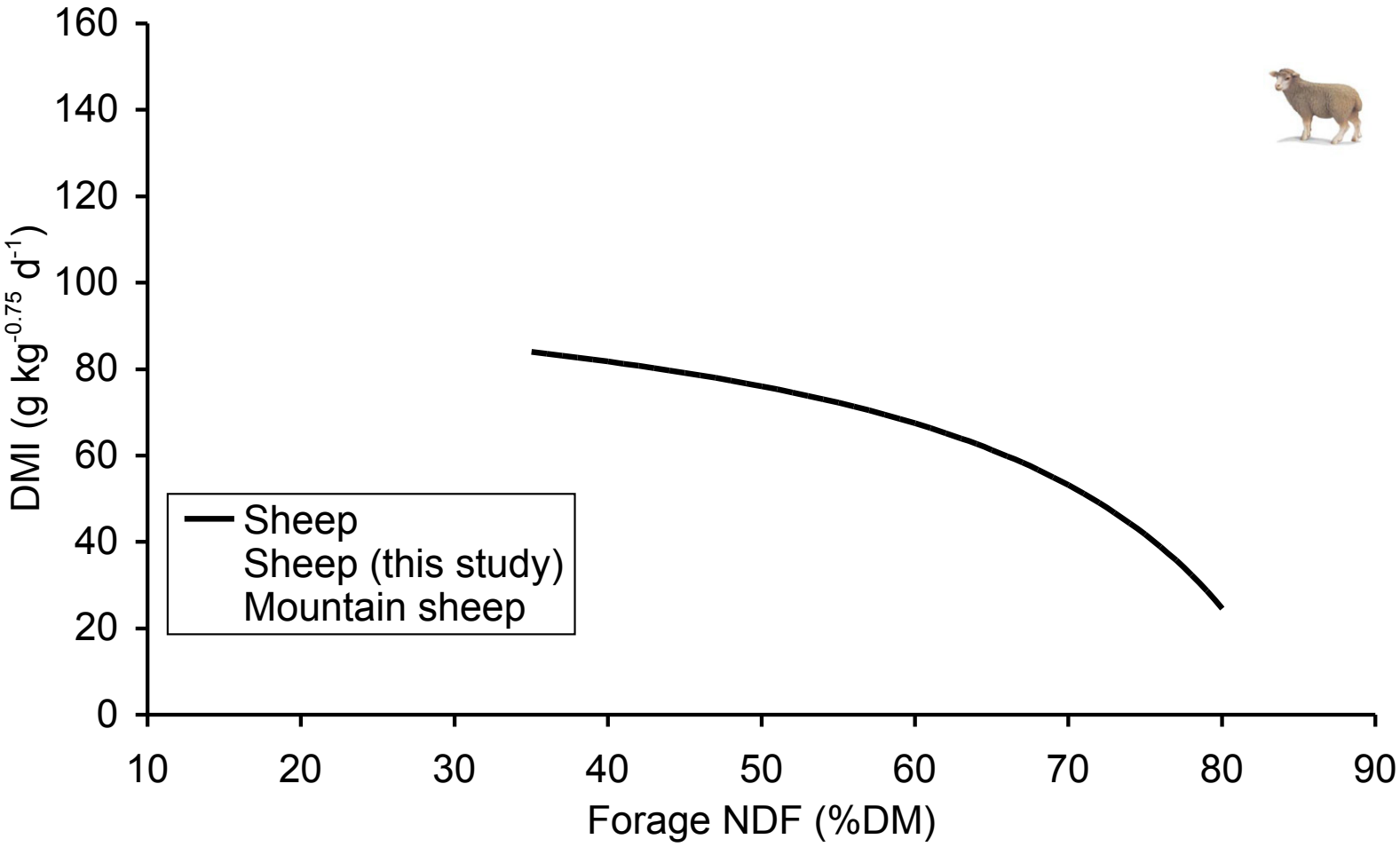




The relationship between forage cell wall content and voluntary food intake in mammalian herbivores

Kerstin MEYER Jürgen HUMMEL Marcus CLAUSS*

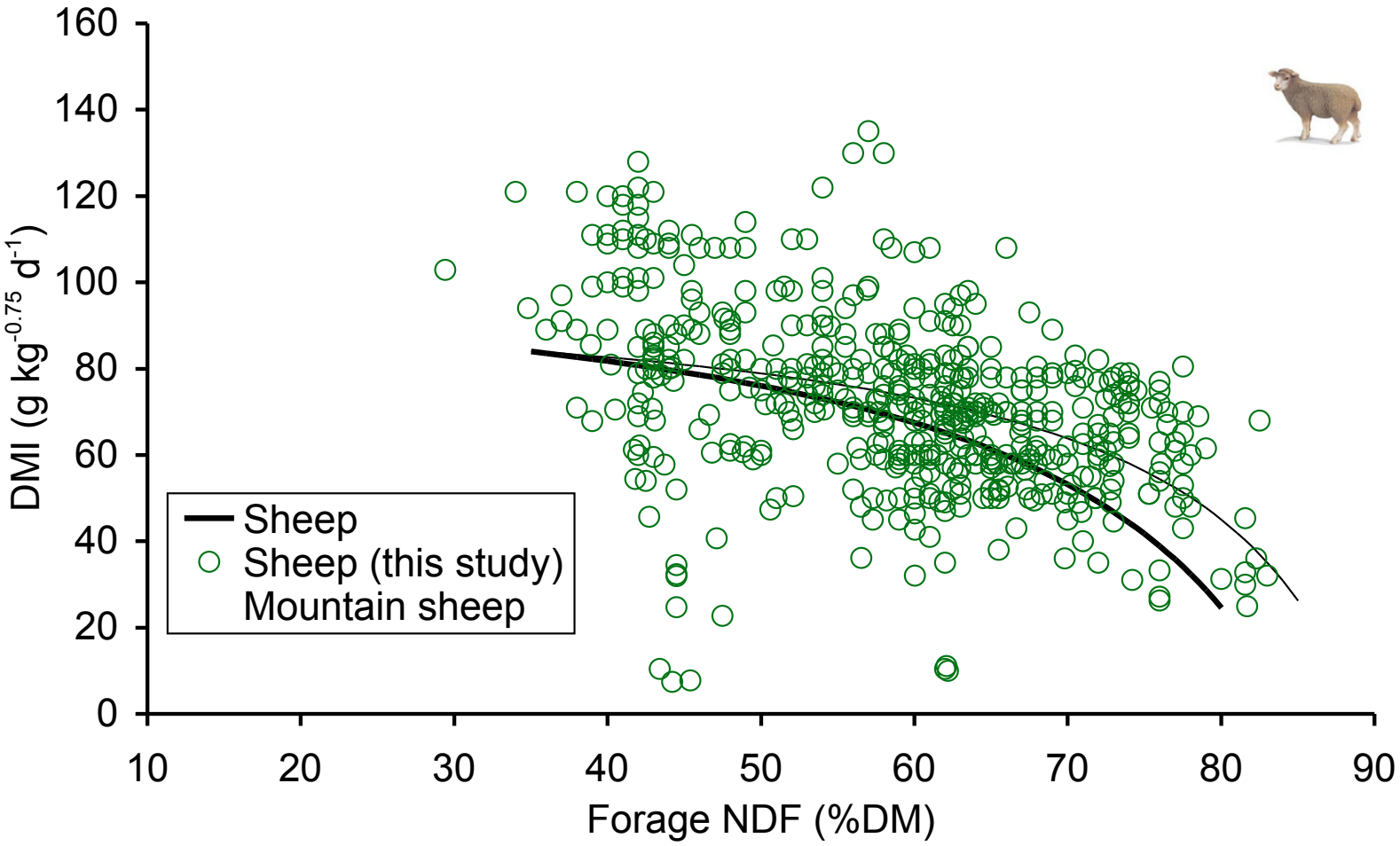
Mammal Rev. 2010, Volume 40, No. 3, 221–245



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



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

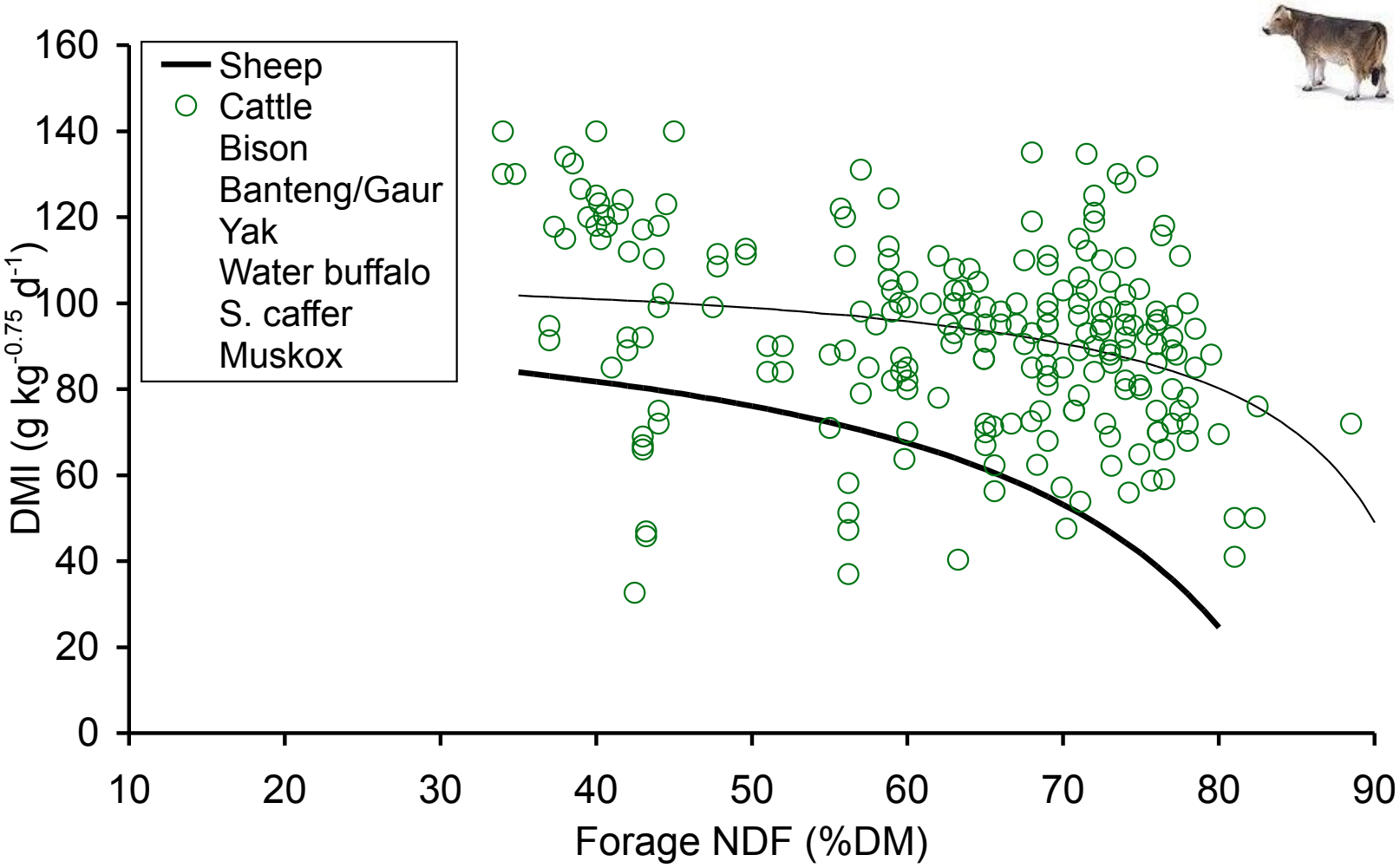
Kerstin MEYER Jürgen HUMMEL Marcus CLAUSS*

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

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

Kerstin MEYER Jürgen HUMMEL Marcus CLAUSS*

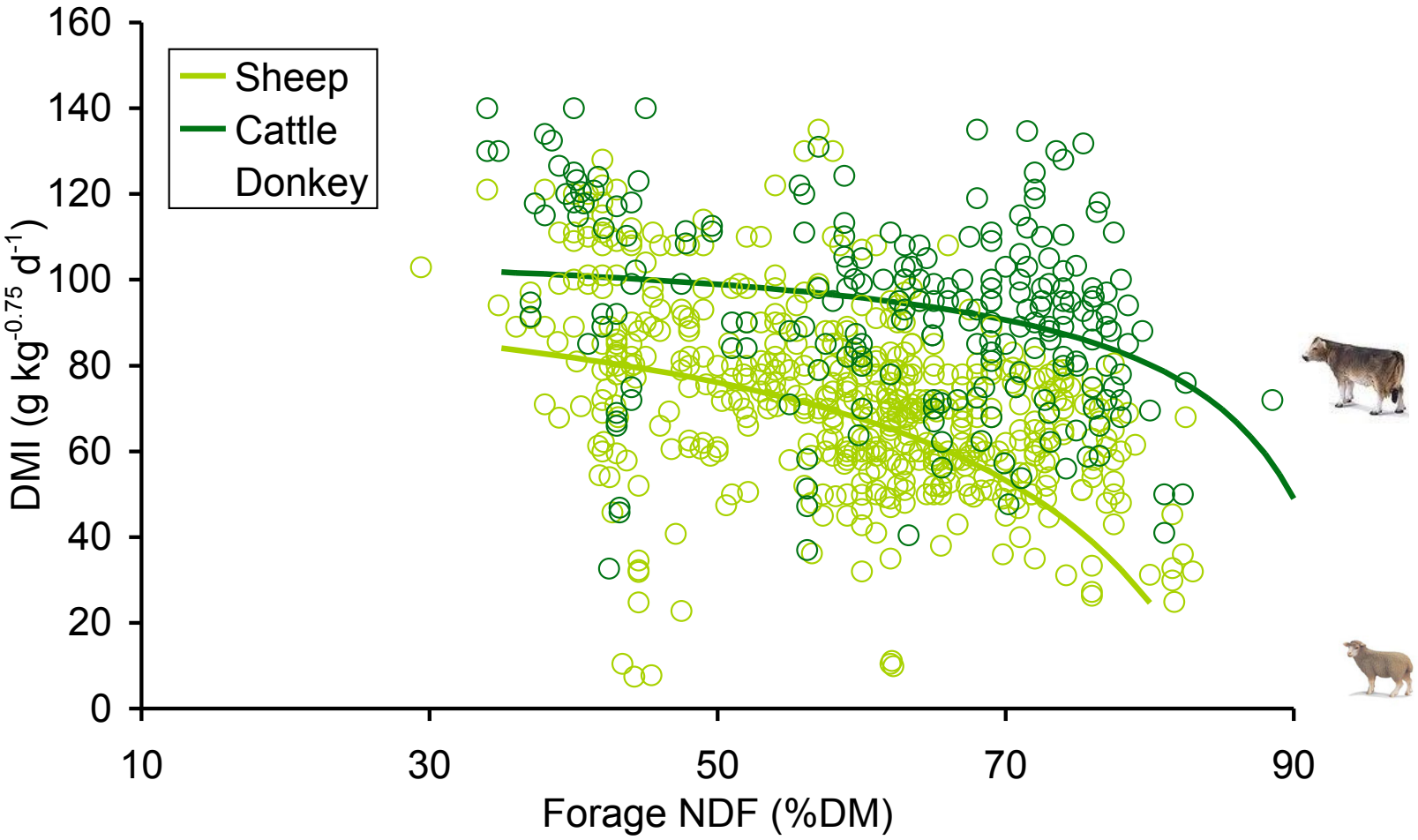
Mammal Rev. 2010, Volume 40, No. 3, 221–245



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

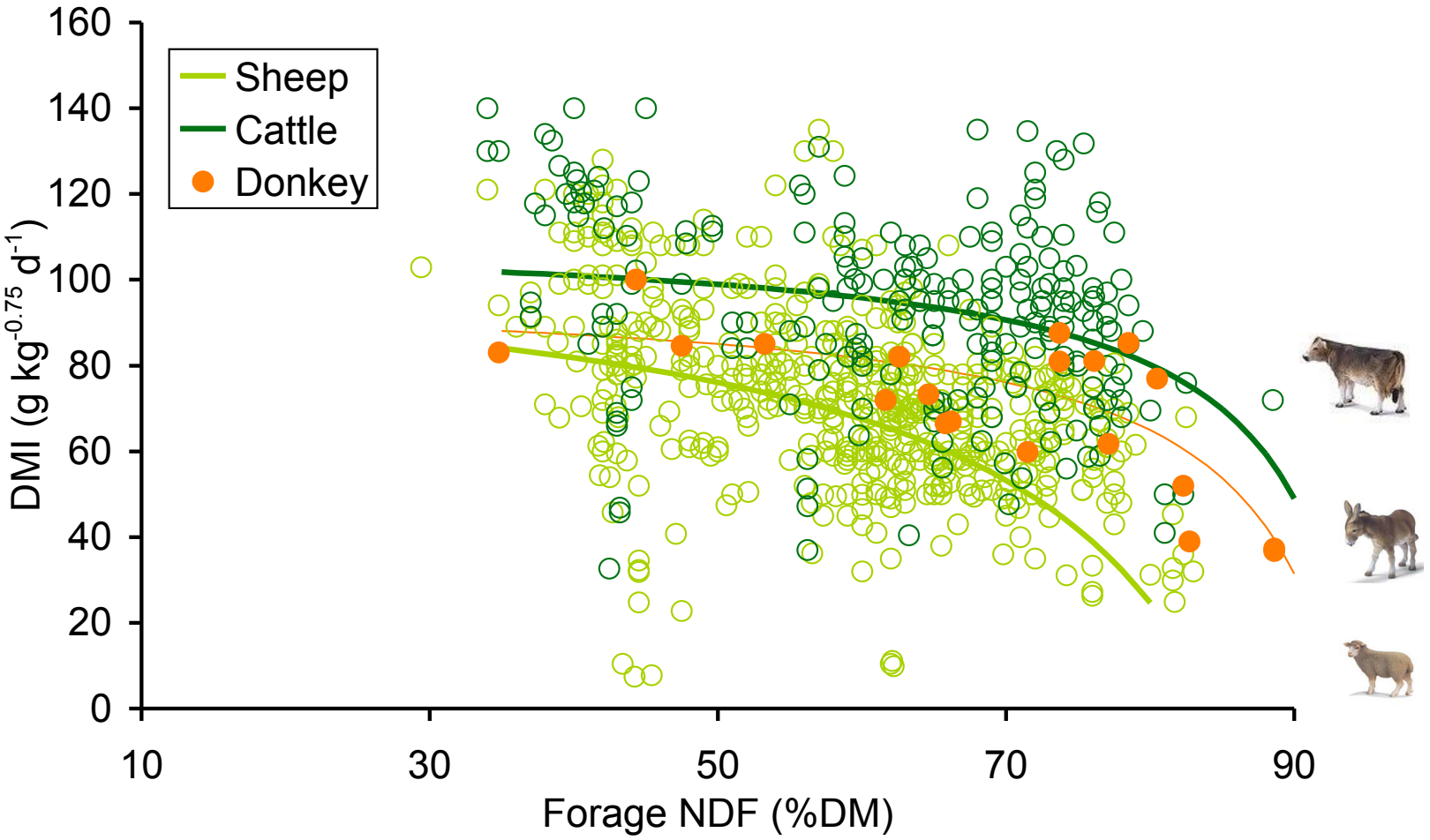


Meyer et al. (2010)

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

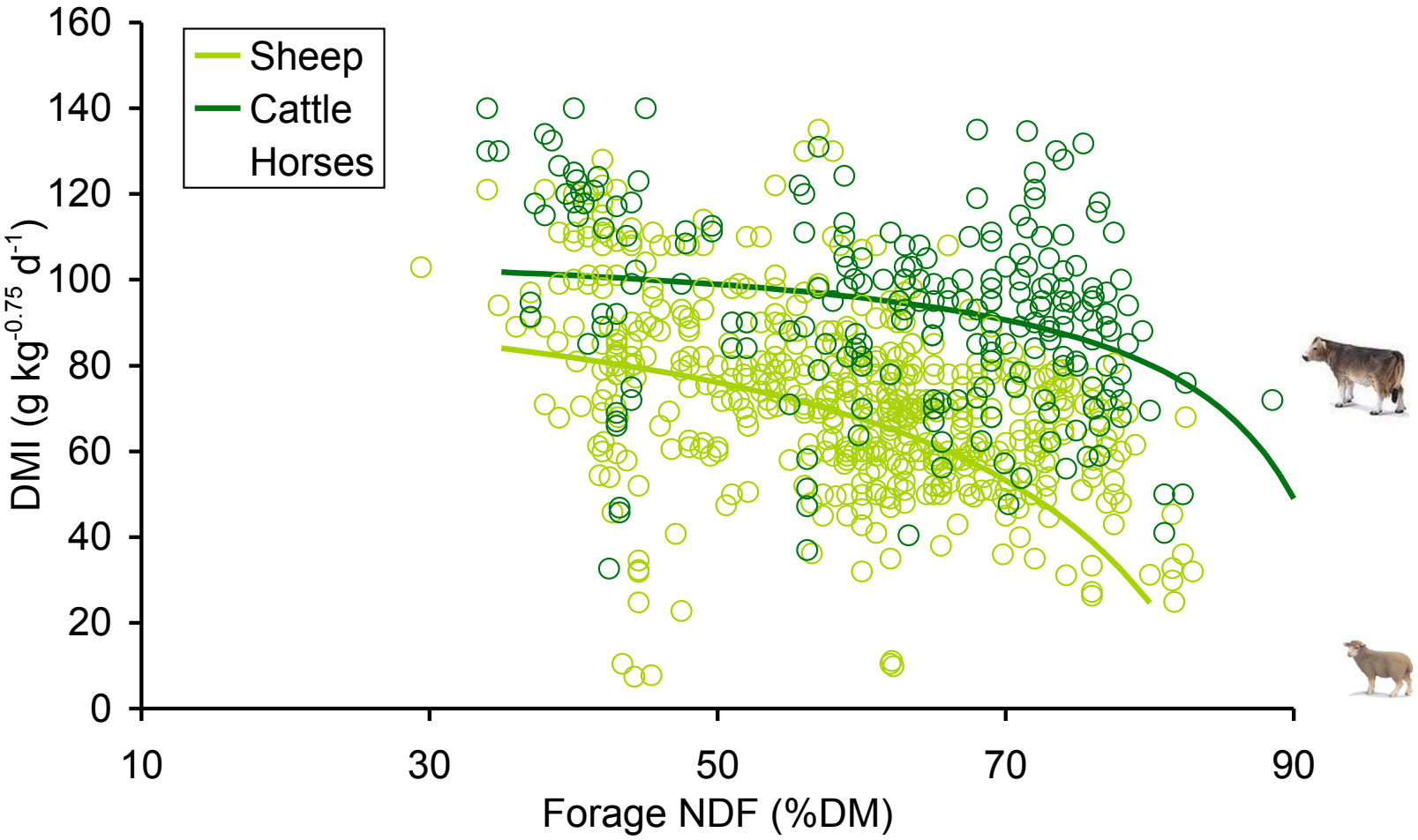


Meyer et al. (2010)

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

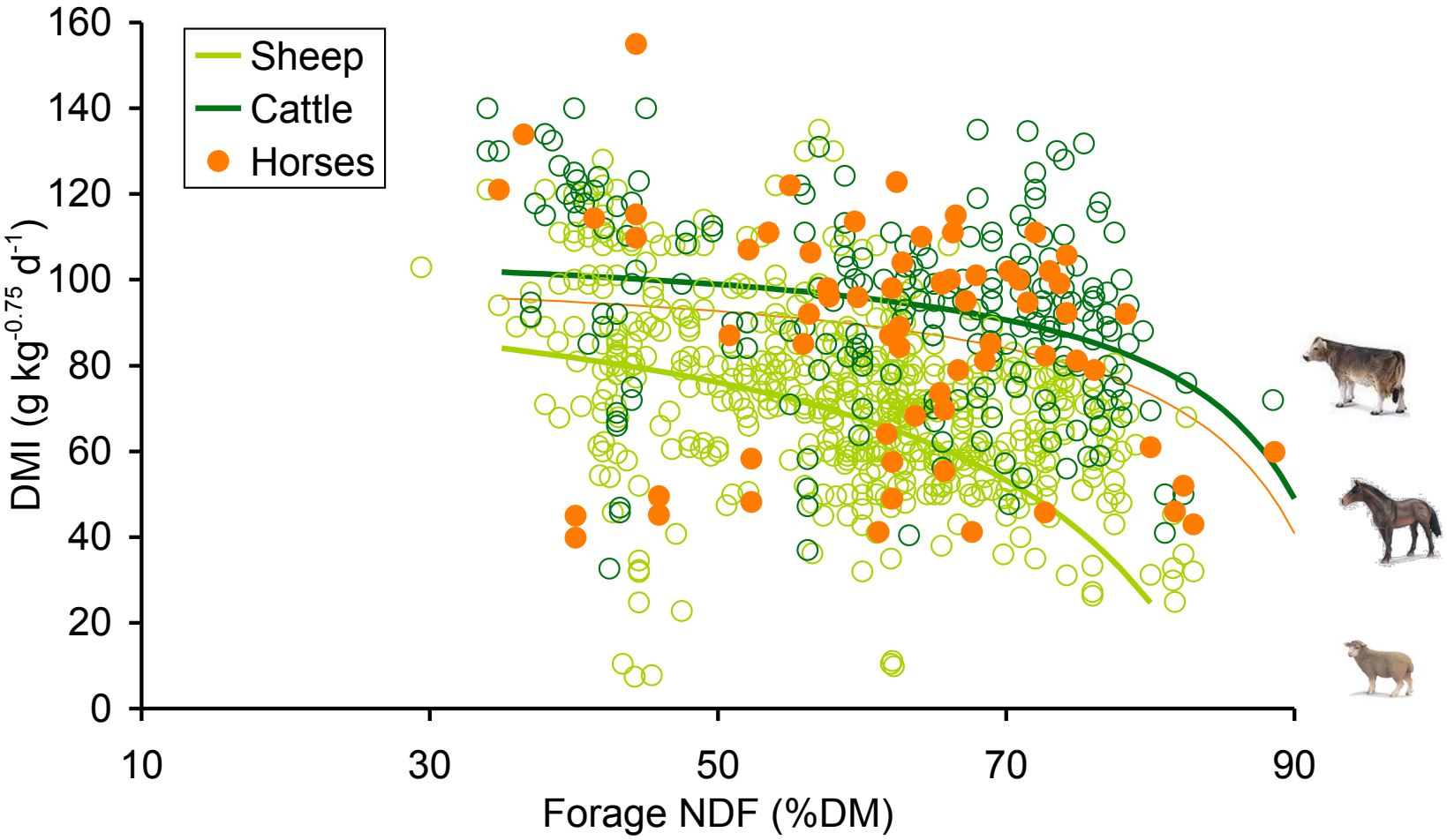


Meyer et al. (2010)

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

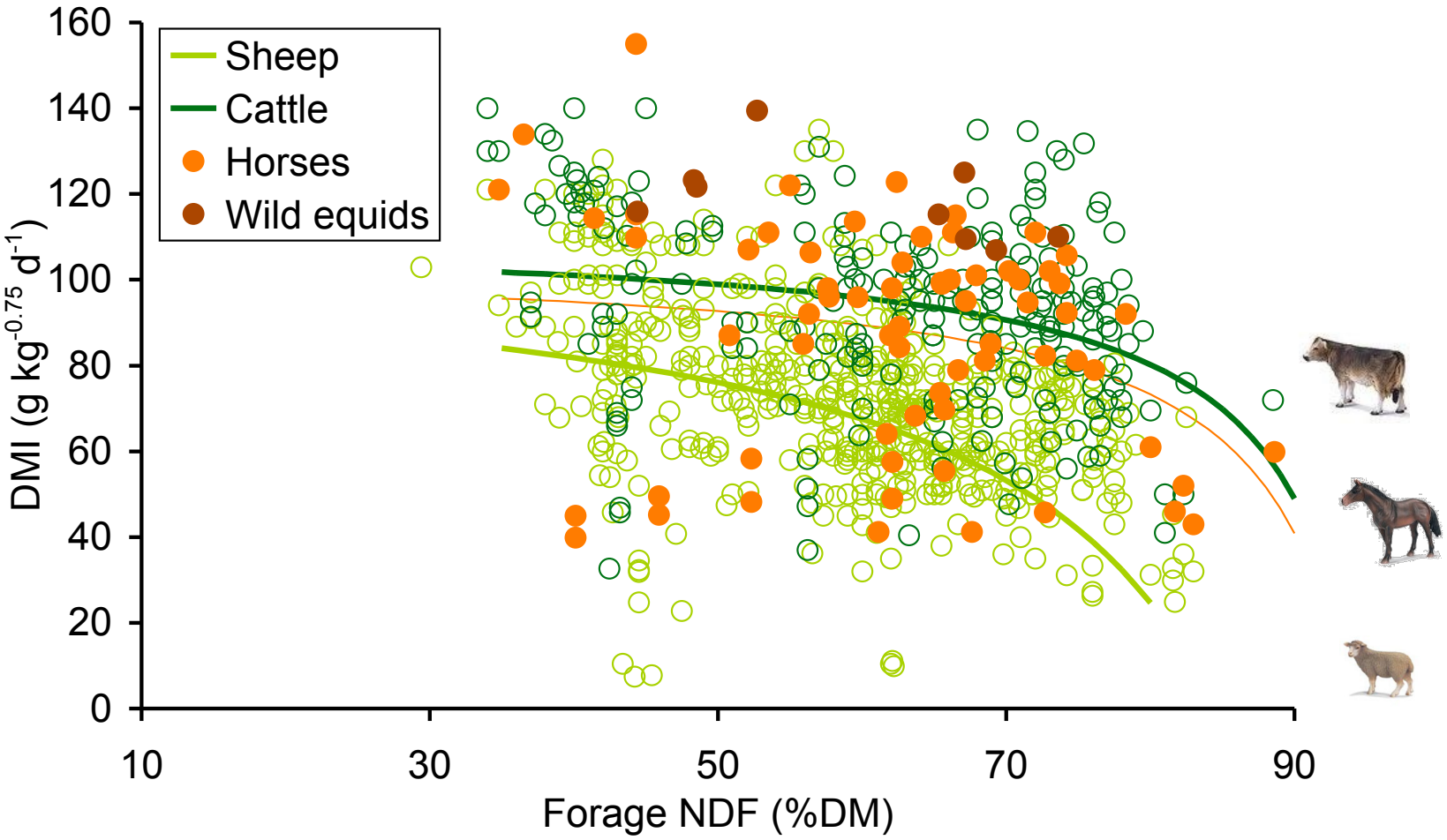


Meyer et al. (2010)

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

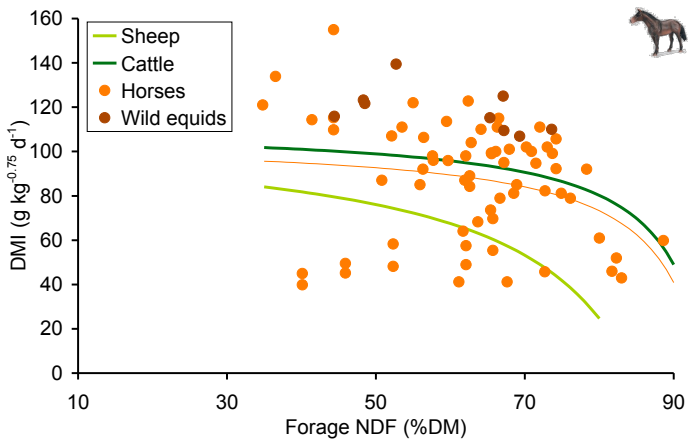


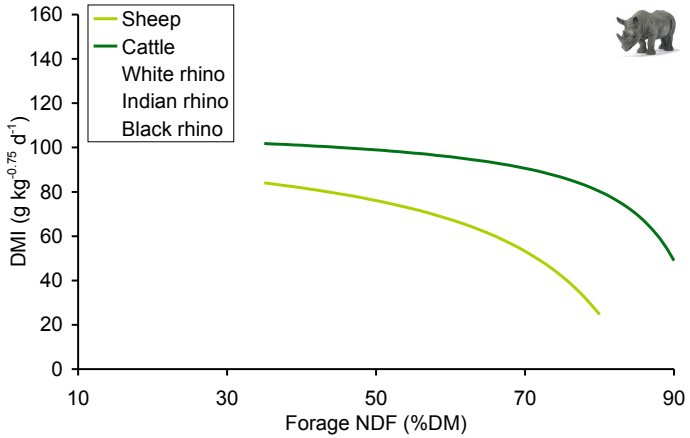
Meyer et al. (2010)

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

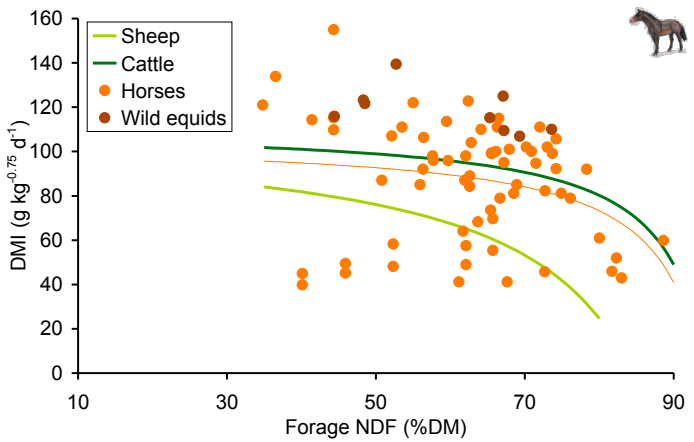


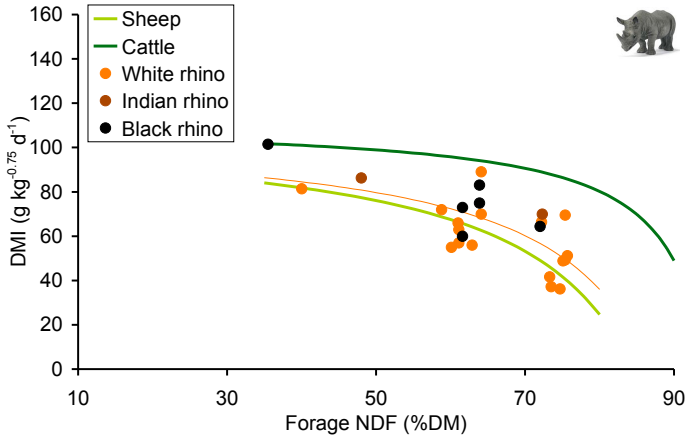


The relationship between forage cell wall content and voluntary food intake in mammalian herbivores

Kerstin MEYER Jürgen HUMMEL Marcus CLAUSS*

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



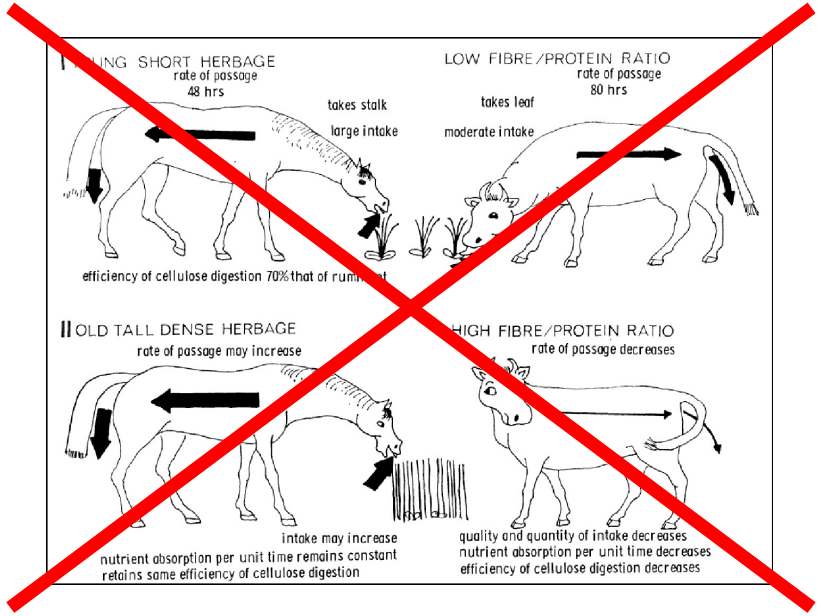


A drawing dominates comparative concepts

THE EVOLUTIONARY STRATEGY OF THE EQUIDAE AND THE ORIGINS OF RUMEN AND CECAL DIGESTION

CHRISTINE JANIS

EVOLUTION 30:757–774. December 1976

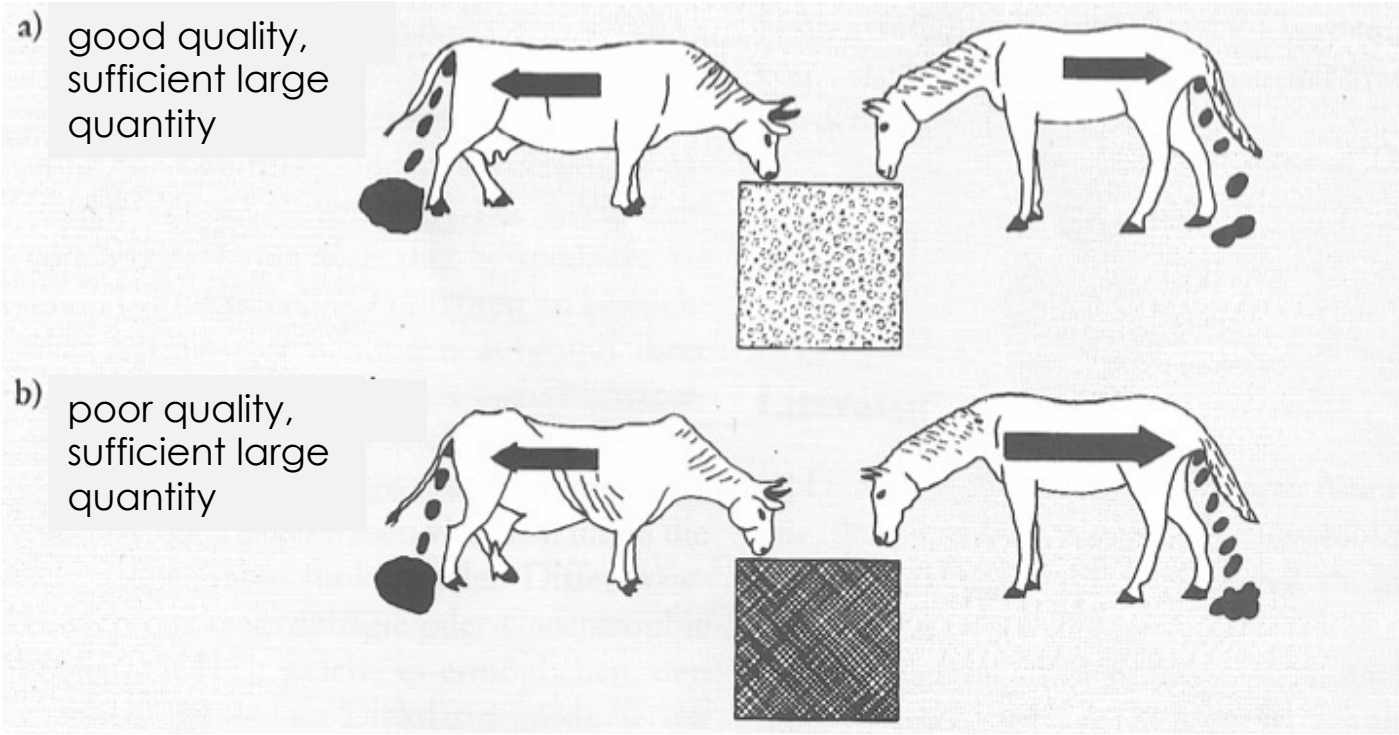


Experiments on domestic ponies indicate that rate of intake may actually decrease with increasing fiber content of the food, although proportionally much less than in ruminants

The digestive tract of herbivorous mammals

Peter Langer

Biologie in unserer Zeit
1987 17: 9-14



The digestive tract of herbivorous mammals

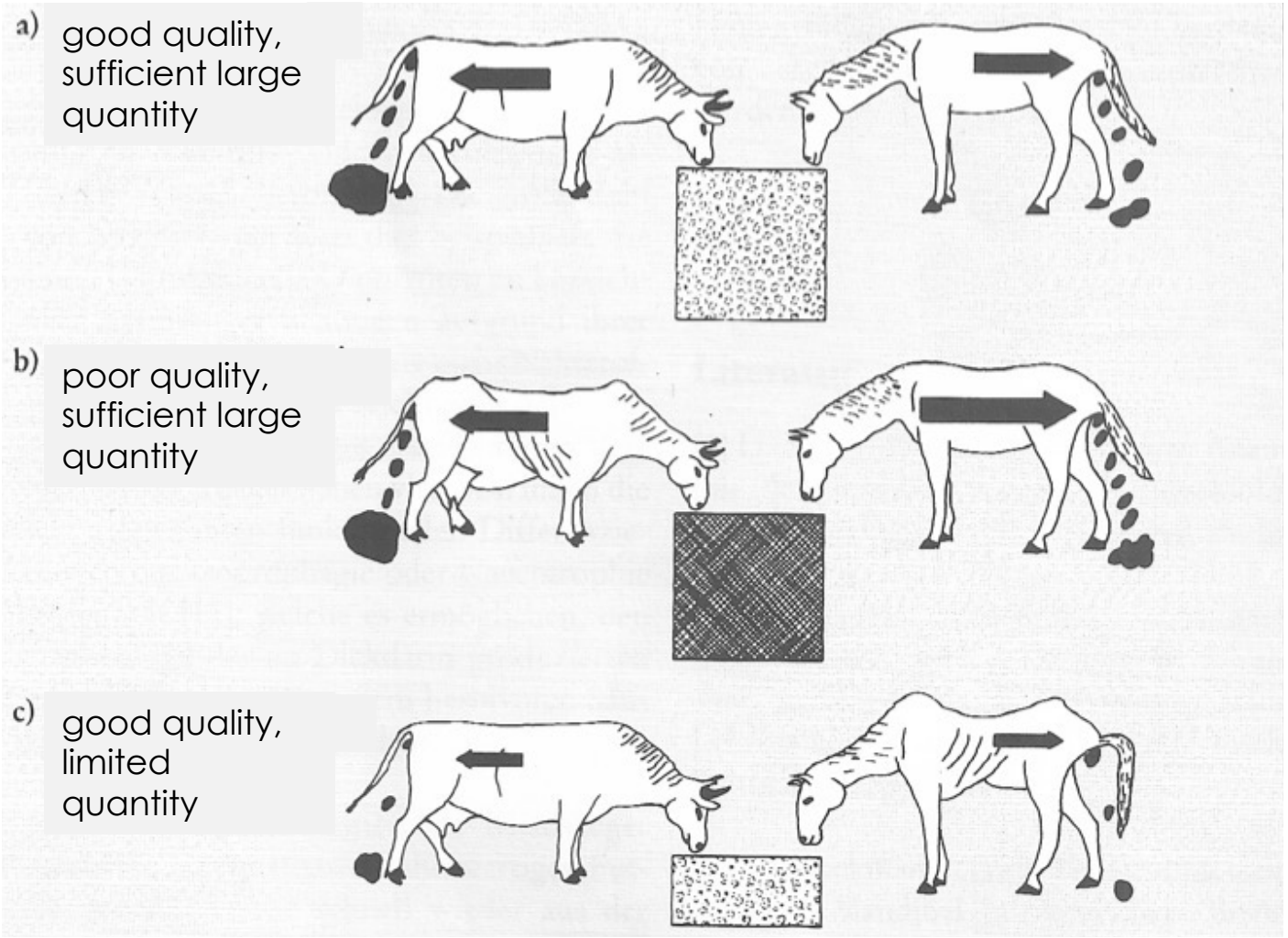
Peter Langer

Biologie in unserer Zeit
1987 17: 9-14

a) good quality, sufficient large quantity

b) poor quality, sufficient large quantity

c) good quality, limited quantity

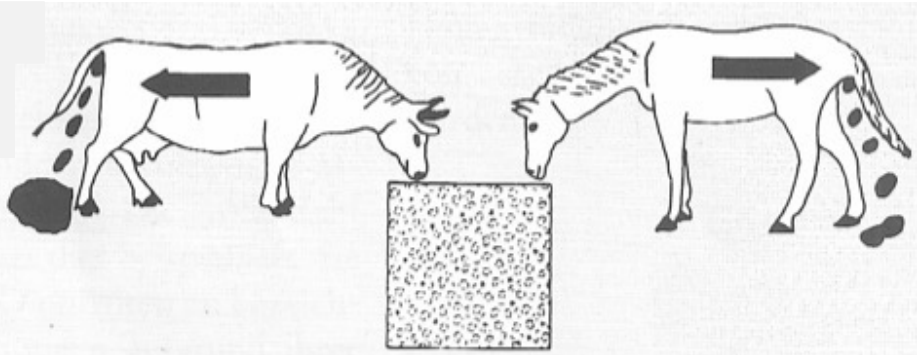


The digestive tract of herbivorous mammals

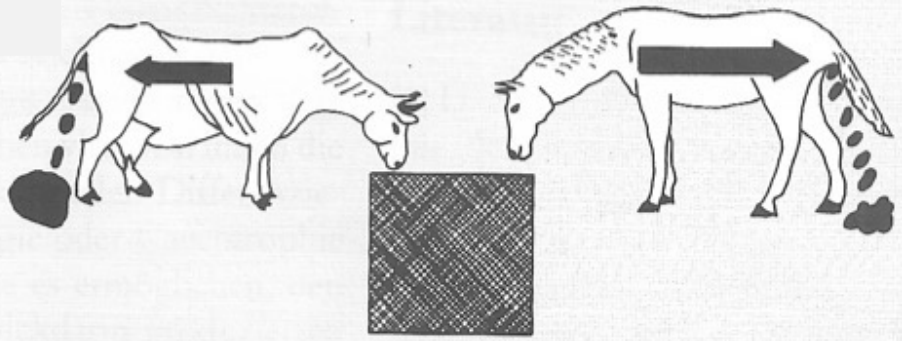
Peter Langer

Biologie in unserer Zeit
1987 17: 9-14

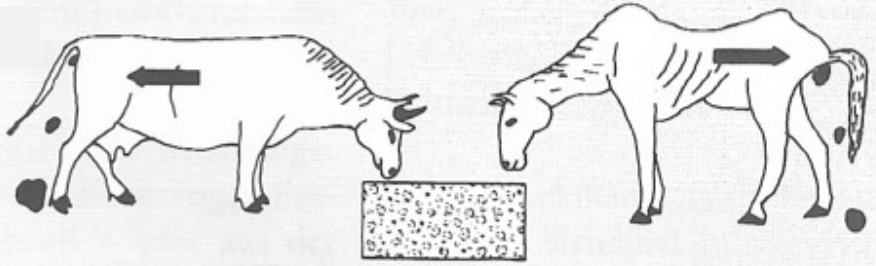
a) good quality, sufficient large quantity



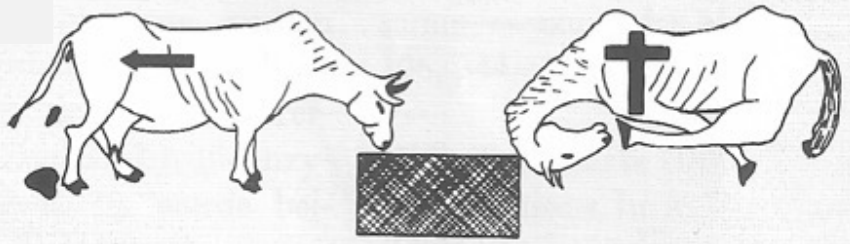
b) poor quality, sufficient large quantity



c) good quality, limited quantity



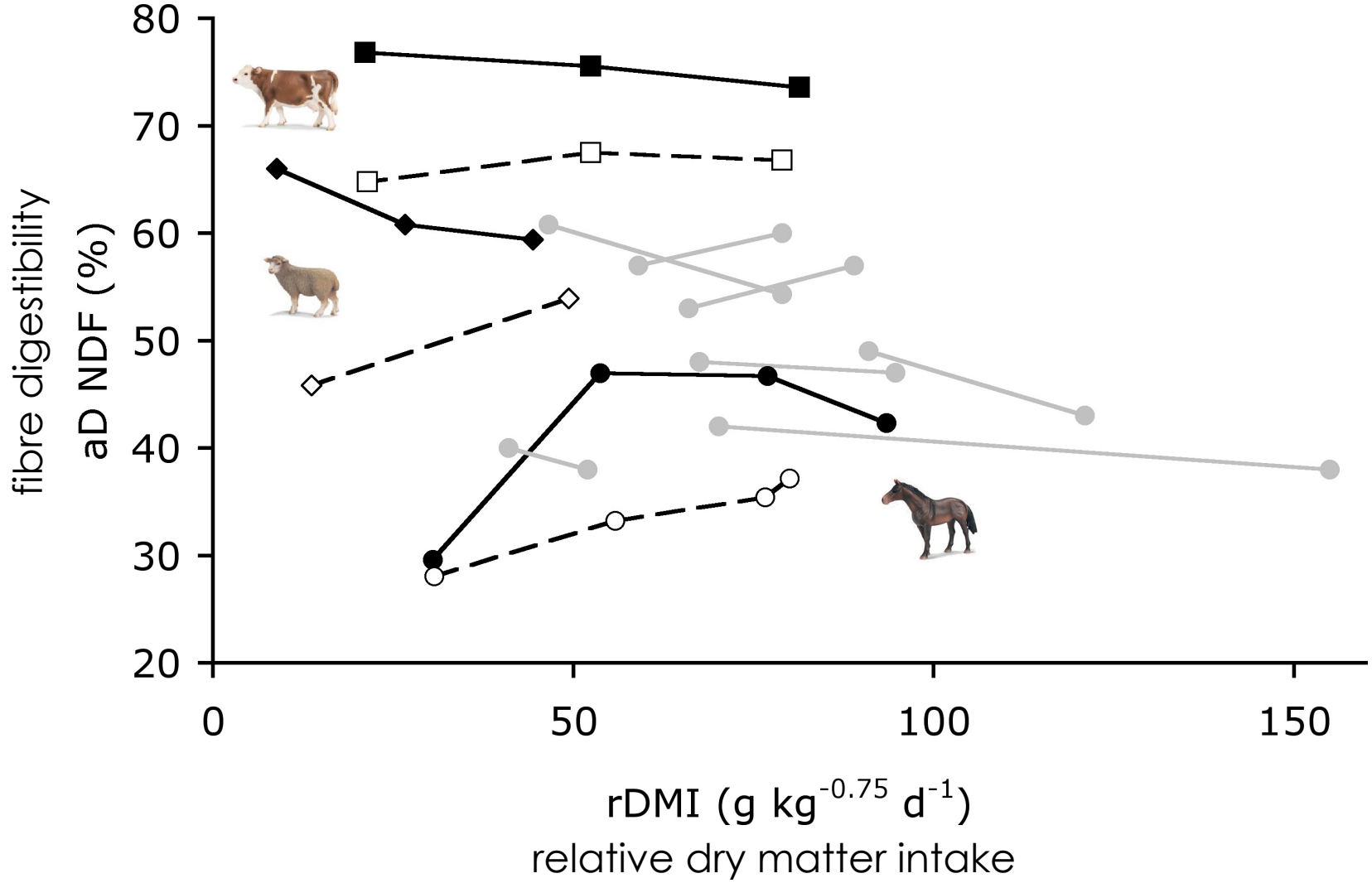
d) poor quality, limited quantity



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 **98** (2014) 107–118



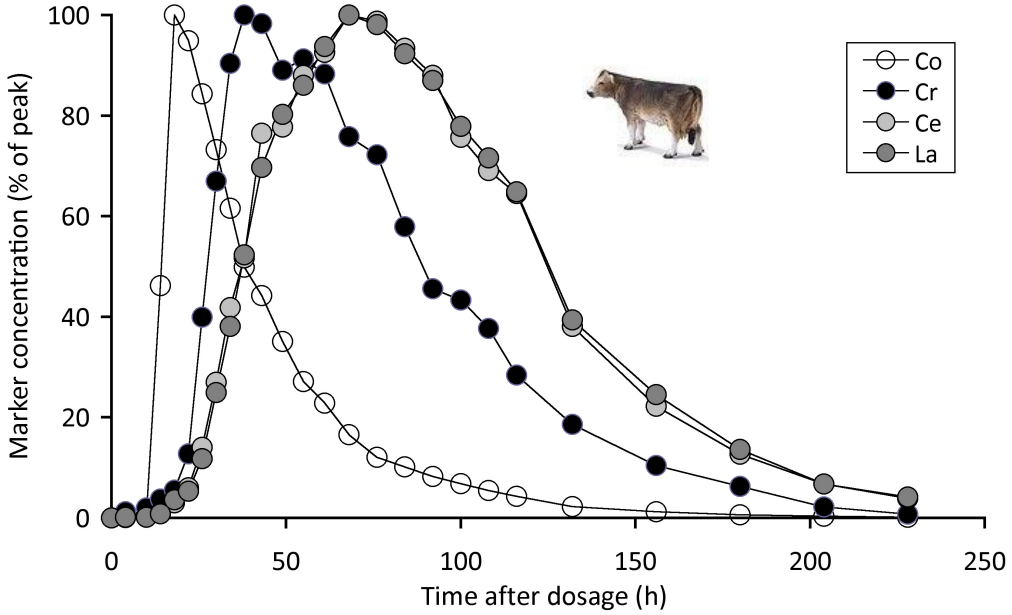
Differences in digestive physiology between equids and ruminants: selective particle retention

Selective particle retention

In ruminants, large particles are selectively retained in the rumen.

Selective particle retention

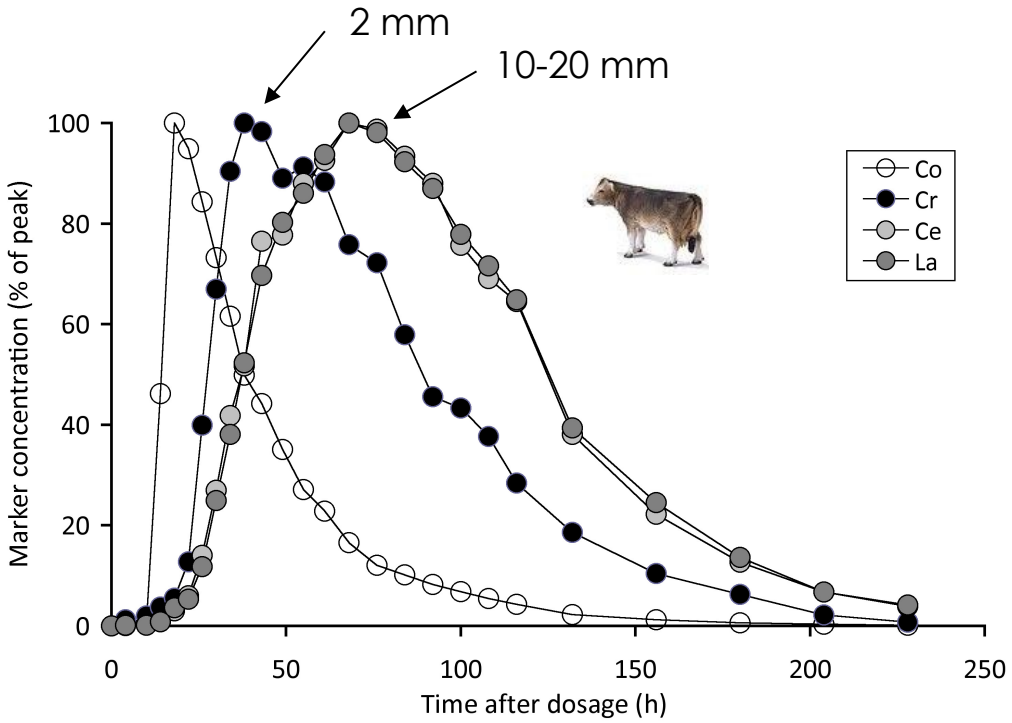
In ruminants, large particles are selectively retained in the rumen.



from Lechner et al. (2010)

Selective particle retention

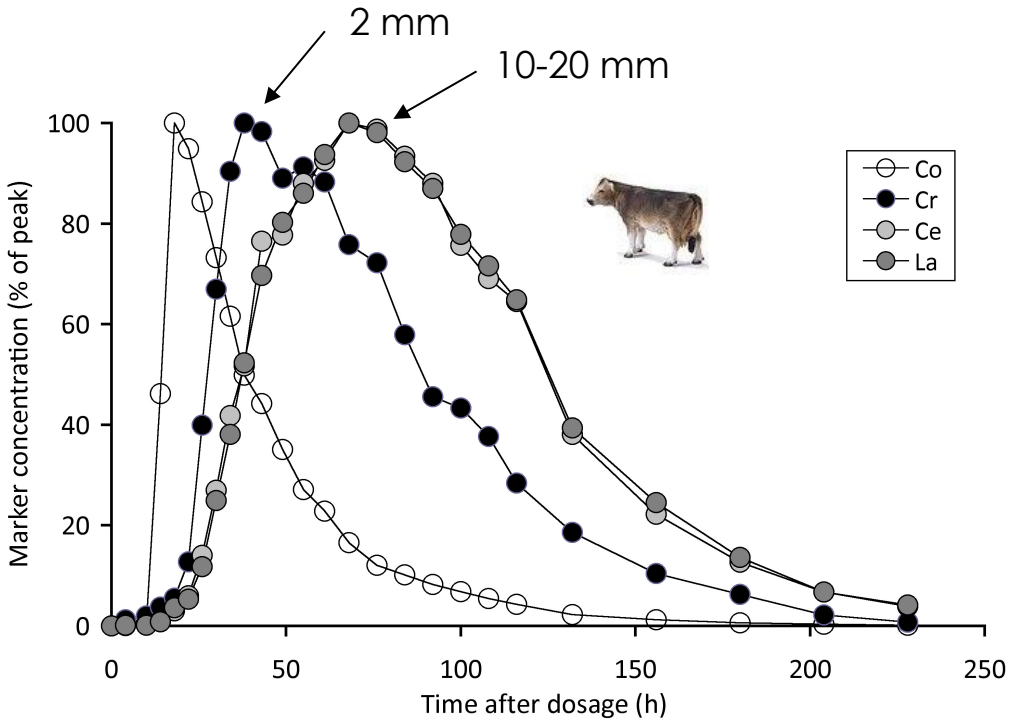
In ruminants, large particles are selectively retained in the rumen.



from Lechner et al. (2010)

Selective particle retention

In ruminants, large particles are selectively retained in the rumen.

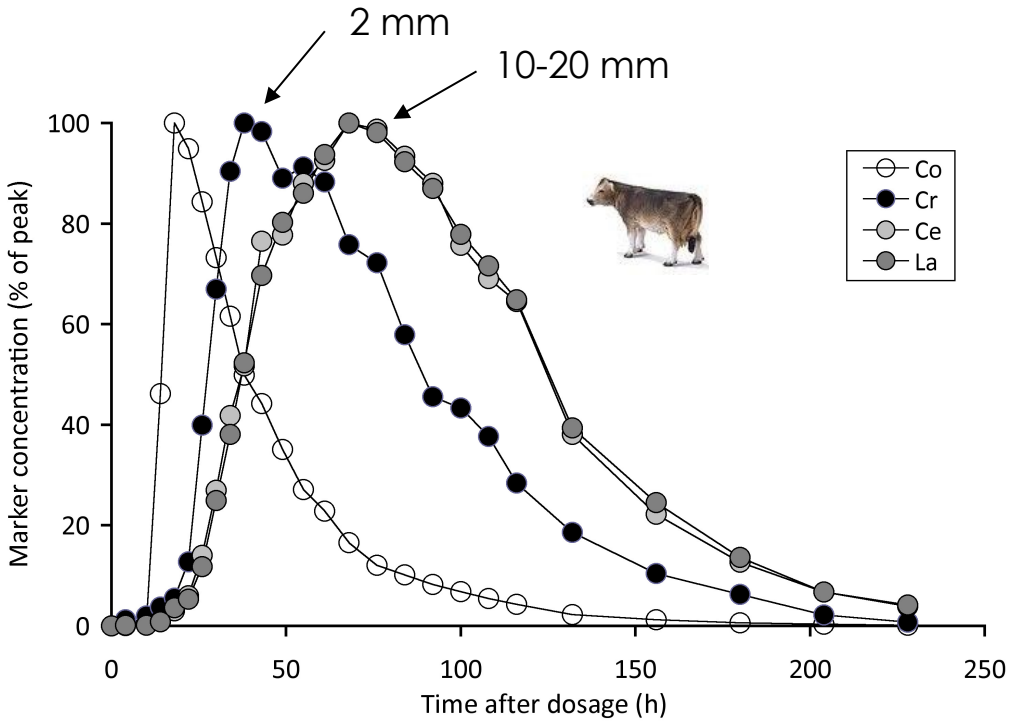


from Lechner et al. (2010)

In equids, the situation is not so clear.

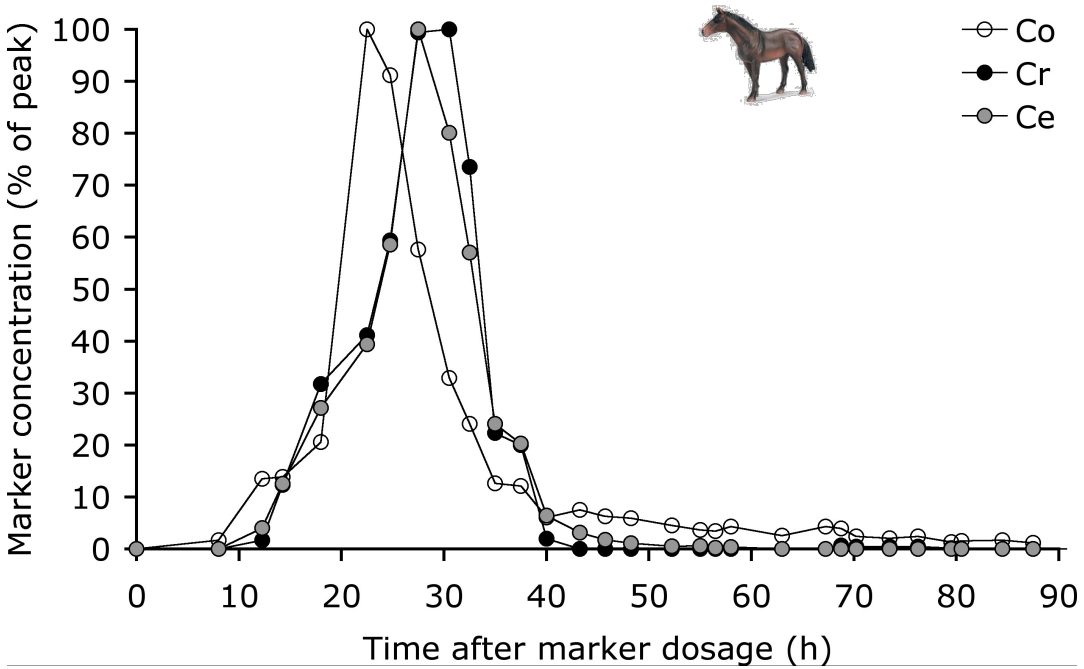
Selective particle retention

In ruminants, large particles are selectively retained in the rumen.



from Lechner et al. (2010)

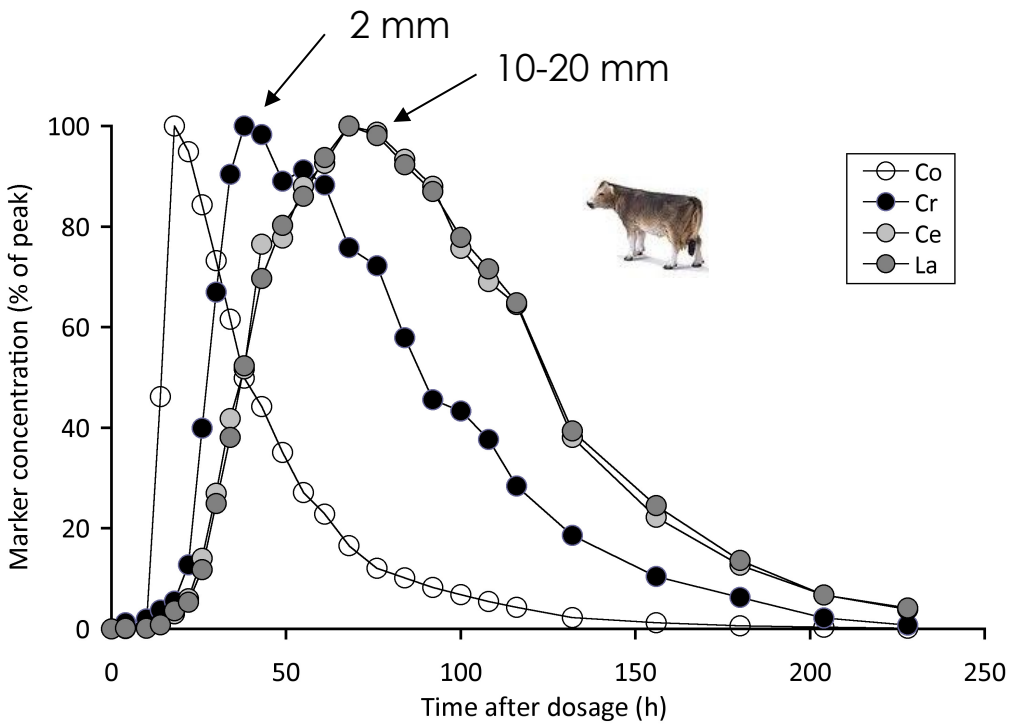
In equids, the situation is not so clear.



Clauss et al. (pers. obs.)

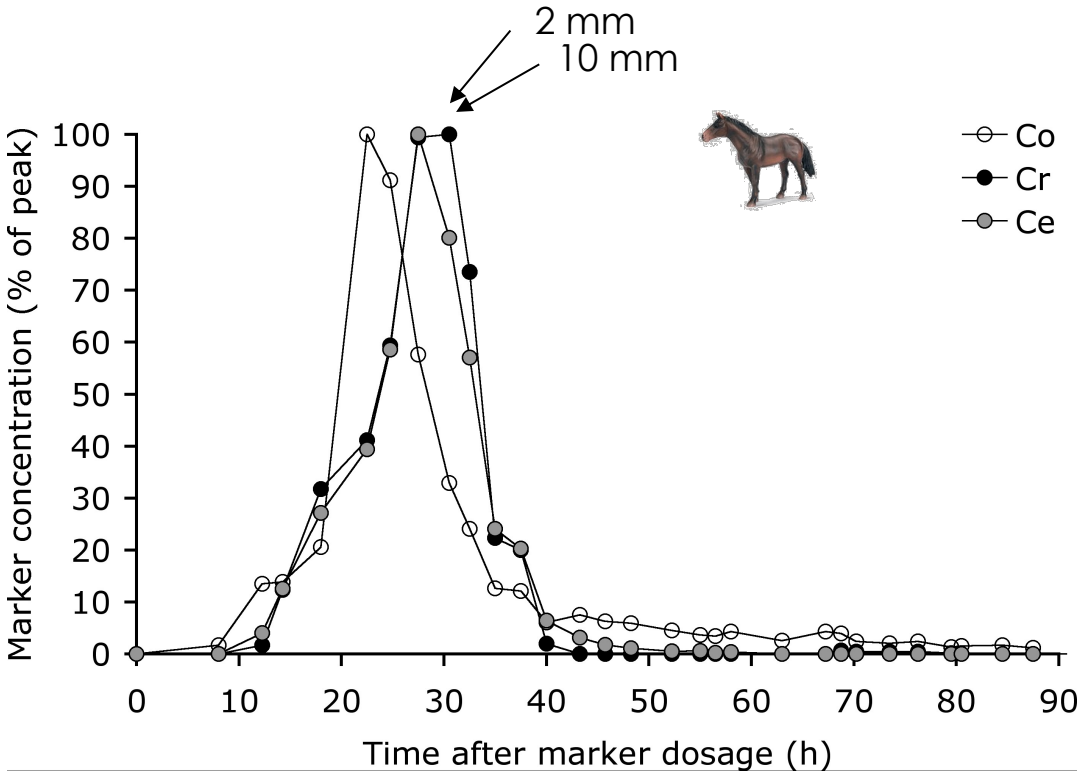
Selective particle retention

In ruminants, large particles are selectively retained in the rumen.



from Lechner et al. (2010)

In equids, the situation is not so clear.

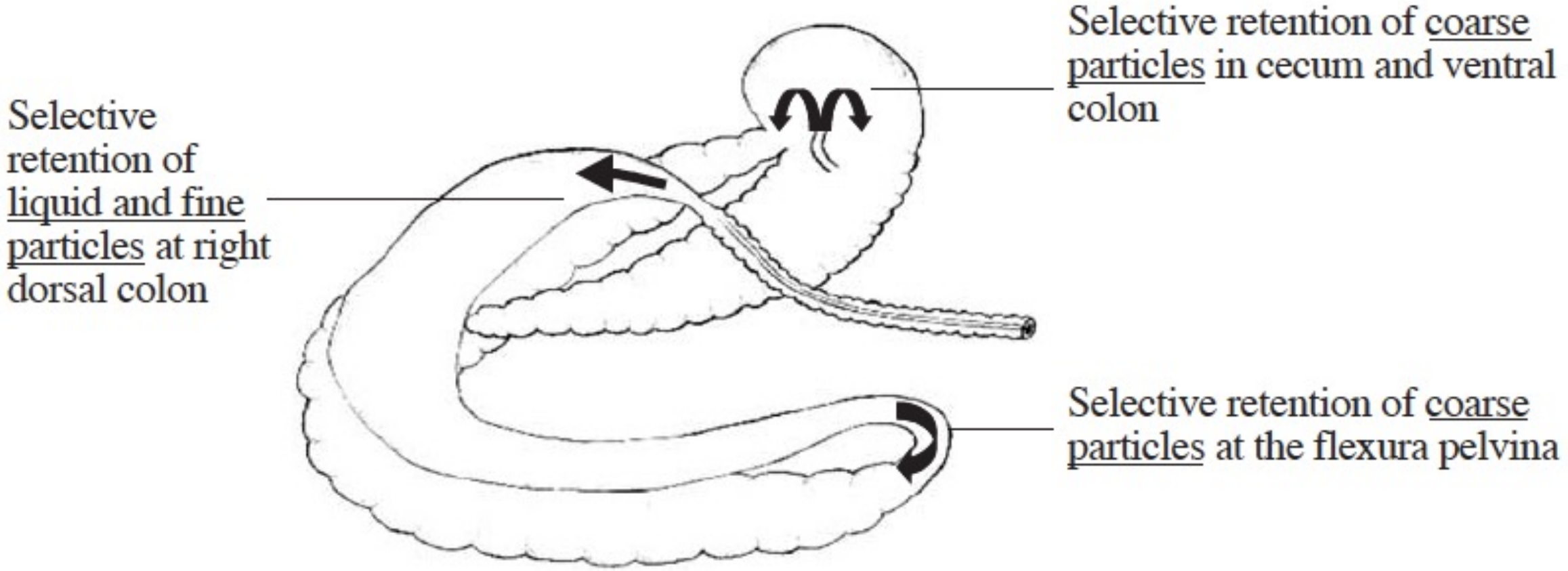


Clauss et al. (pers. obs.)

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

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

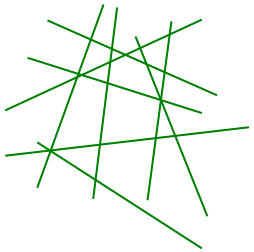
Livestock Science 99 (2006) 3–12



Comparative selective retention of particle size classes in the gastrointestinal tract of ponies and goats

J. Hummel[1] | F. Scheurich[1] | S. Ortmann[2] | L. A. Crompton[3] | M. Gerken[1] |
M. Clauss[4]

J Anim Physiol Anim Nutr. 2018;102:429–439.



Comparative selective retention of particle size classes in the gastrointestinal tract of ponies and goats

J. Hummel[1] | F. Scheurich[1] | S. Ortmann[2] | L. A. Crompton[3] | M. Gerken[1] |
M. Clauss[4]

J Anim Physiol Anim Nutr. 2018;102:429–439.

Comparative selective retention of particle size classes in the gastrointestinal tract of ponies and goats

J. Hummel[1] | F. Scheurich[1] | S. Ortmann[2] | L. A. Crompton[3] | M. Gerken[1] |
M. Clauss[4]

J Anim Physiol Anim Nutr. 2018;102:429–439.

Comparative selective retention of particle size classes in the gastrointestinal tract of ponies and goats

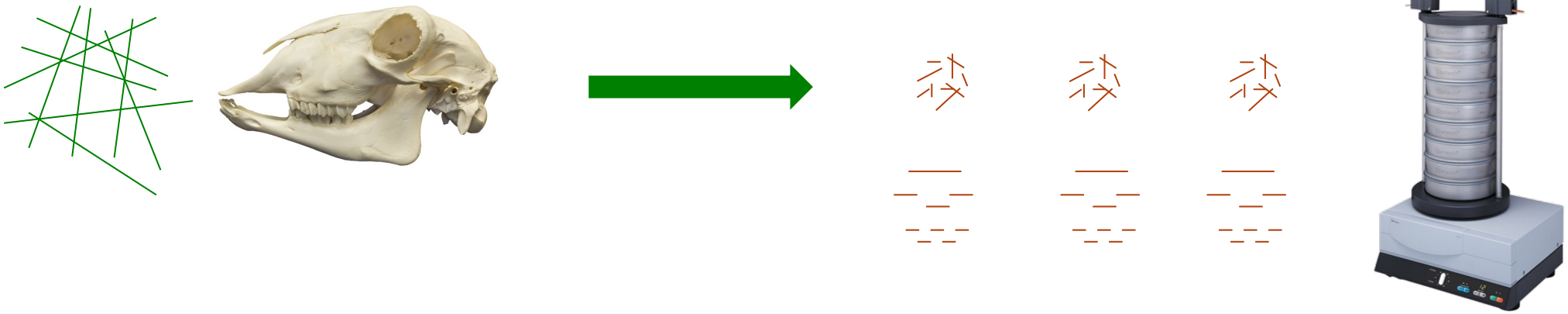
J. Hummel[1] | F. Scheurich[1] | S. Ortmann[2] | L. A. Crompton[3] | M. Gerken[1] |
M. Clauss[4]

J Anim Physiol Anim Nutr. 2018;102:429–439.

Comparative selective retention of particle size classes in the gastrointestinal tract of ponies and goats

J. Hummel[1] | F. Scheurich[1] | S. Ortmann[2] | L. A. Crompton[3] | M. Gerken[1] |
M. Clauss[4]

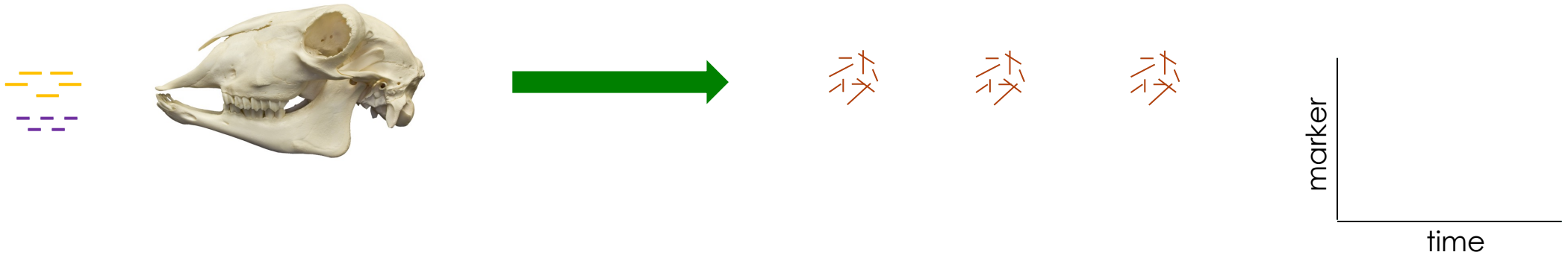
J Anim Physiol Anim Nutr. 2018;102:429–439.



Comparative selective retention of particle size classes in the gastrointestinal tract of ponies and goats

J. Hummel[1] | F. Scheurich[1] | S. Ortmann[2] | L. A. Crompton[3] | M. Gerken[1] |
M. Clauss[4]

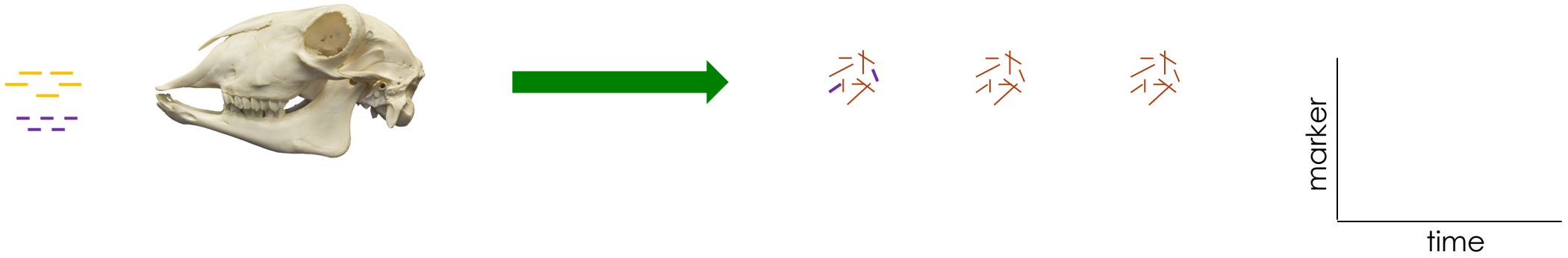
J Anim Physiol Anim Nutr. 2018;102:429–439.



Comparative selective retention of particle size classes in the gastrointestinal tract of ponies and goats

J. Hummel[1] | F. Scheurich[1] | S. Ortmann[2] | L. A. Crompton[3] | M. Gerken[1] |
M. Clauss[4]

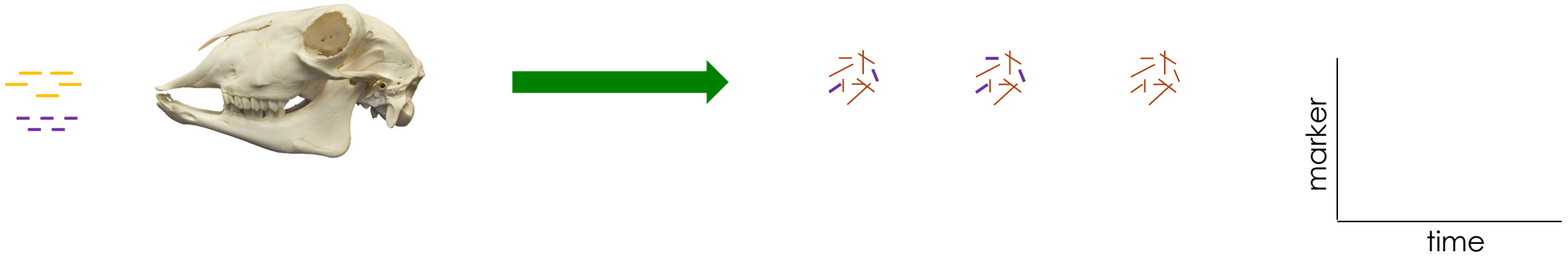
J Anim Physiol Anim Nutr. 2018;102:429–439.



Comparative selective retention of particle size classes in the gastrointestinal tract of ponies and goats

J. Hummel[1] | F. Scheurich[1] | S. Ortmann[2] | L. A. Crompton[3] | M. Gerken[1] |
M. Clauss[4]

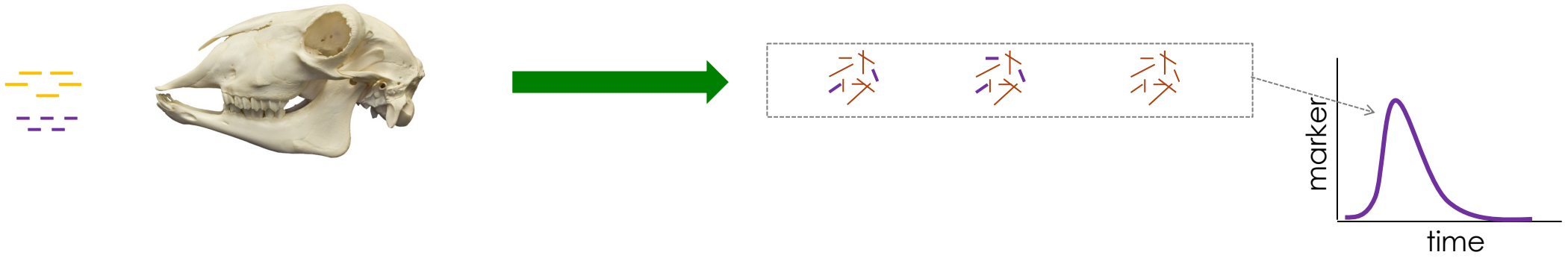
J Anim Physiol Anim Nutr. 2018;102:429–439.



Comparative selective retention of particle size classes in the gastrointestinal tract of ponies and goats

J. Hummel[1] | F. Scheurich[1] | S. Ortmann[2] | L. A. Crompton[3] | M. Gerken[1] |
M. Clauss[4]

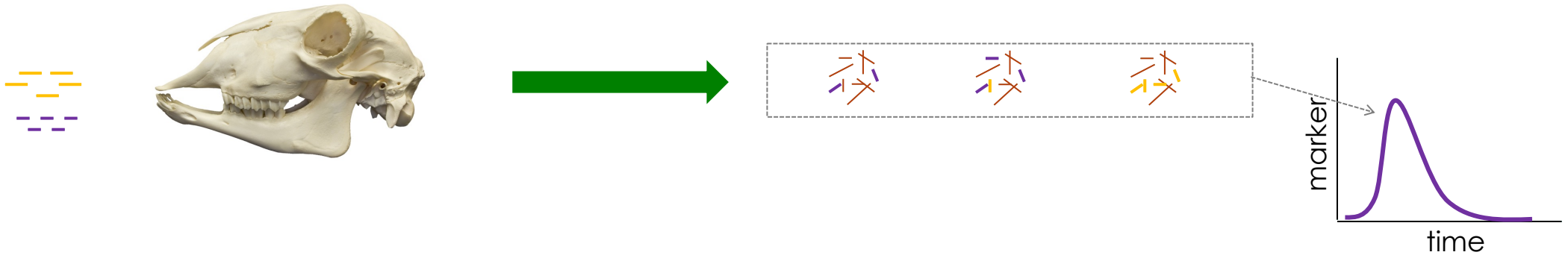
J Anim Physiol Anim Nutr. 2018;102:429–439.



Comparative selective retention of particle size classes in the gastrointestinal tract of ponies and goats

J. Hummel[1] | F. Scheurich[1] | S. Ortmann[2] | L. A. Crompton[3] | M. Gerken[1] |
M. Clauss[4]

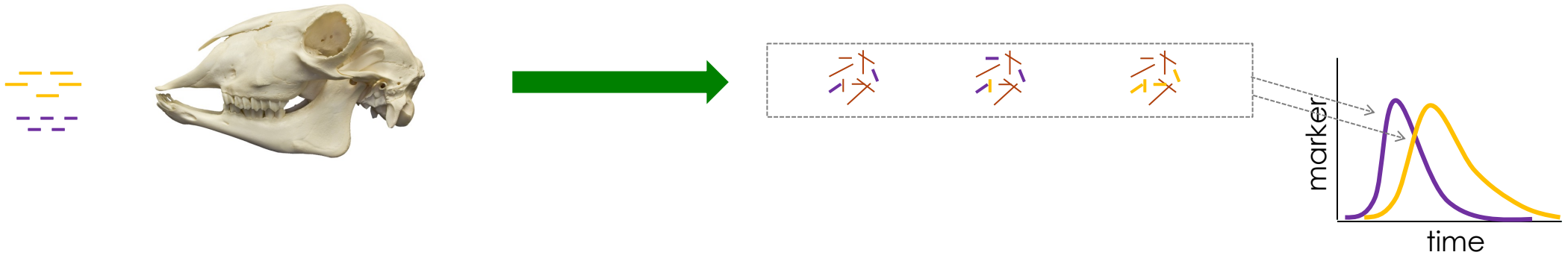
J Anim Physiol Anim Nutr. 2018;102:429–439.



Comparative selective retention of particle size classes in the gastrointestinal tract of ponies and goats

J. Hummel[1] | F. Scheurich[1] | S. Ortmann[2] | L. A. Crompton[3] | M. Gerken[1] |
M. Clauss[4]

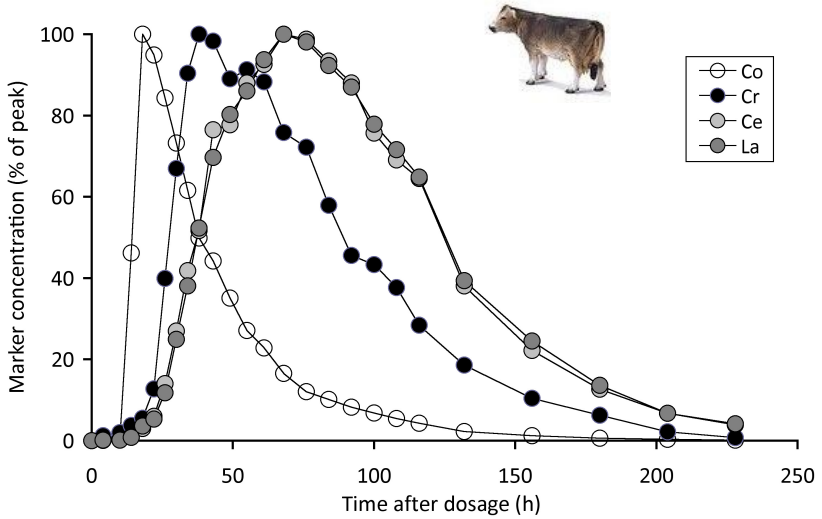
J Anim Physiol Anim Nutr. 2018;102:429–439.



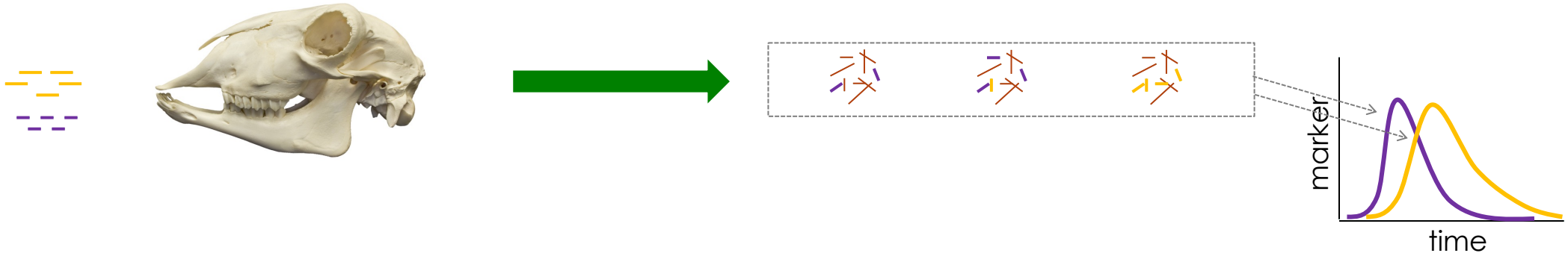
Comparative selective retention of particle size classes in the gastrointestinal tract of ponies and goats

J. Hummel[1] | F. Scheurich[1] | S. Ortmann[2] | L. A. Crompton[3] | M. Gerken[1] | M. Clauss[4]

J Anim Physiol Anim Nutr. 2018;102:429–439.



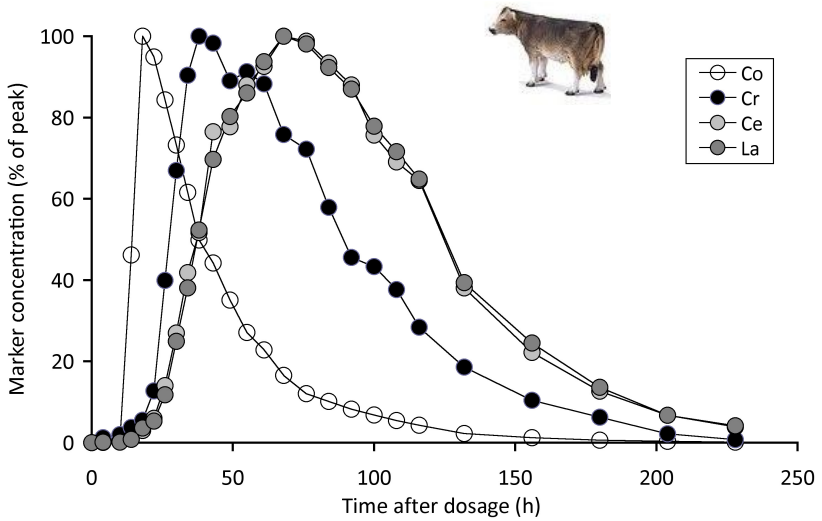
from Lechner et al. (2010)



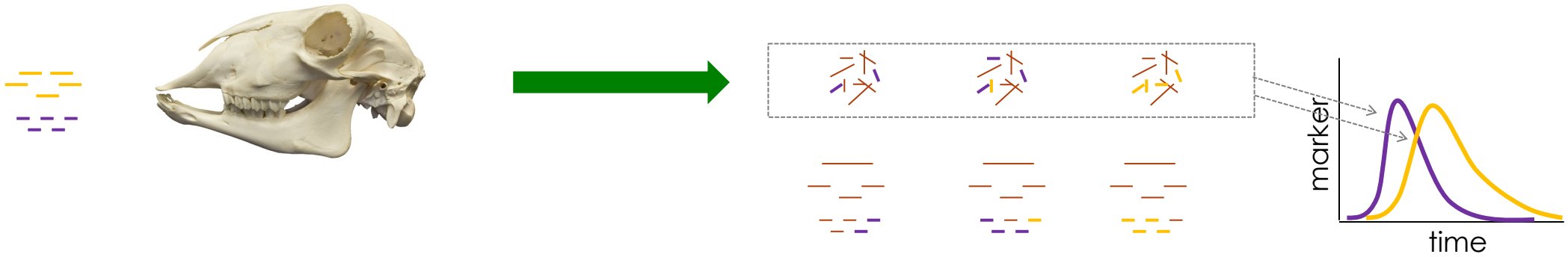
Comparative selective retention of particle size classes in the gastrointestinal tract of ponies and goats

J. Hummel[1] | F. Scheurich[1] | S. Ortmann[2] | L. A. Crompton[3] | M. Gerken[1] | M. Clauss[4]

J Anim Physiol Anim Nutr. 2018;102:429–439.



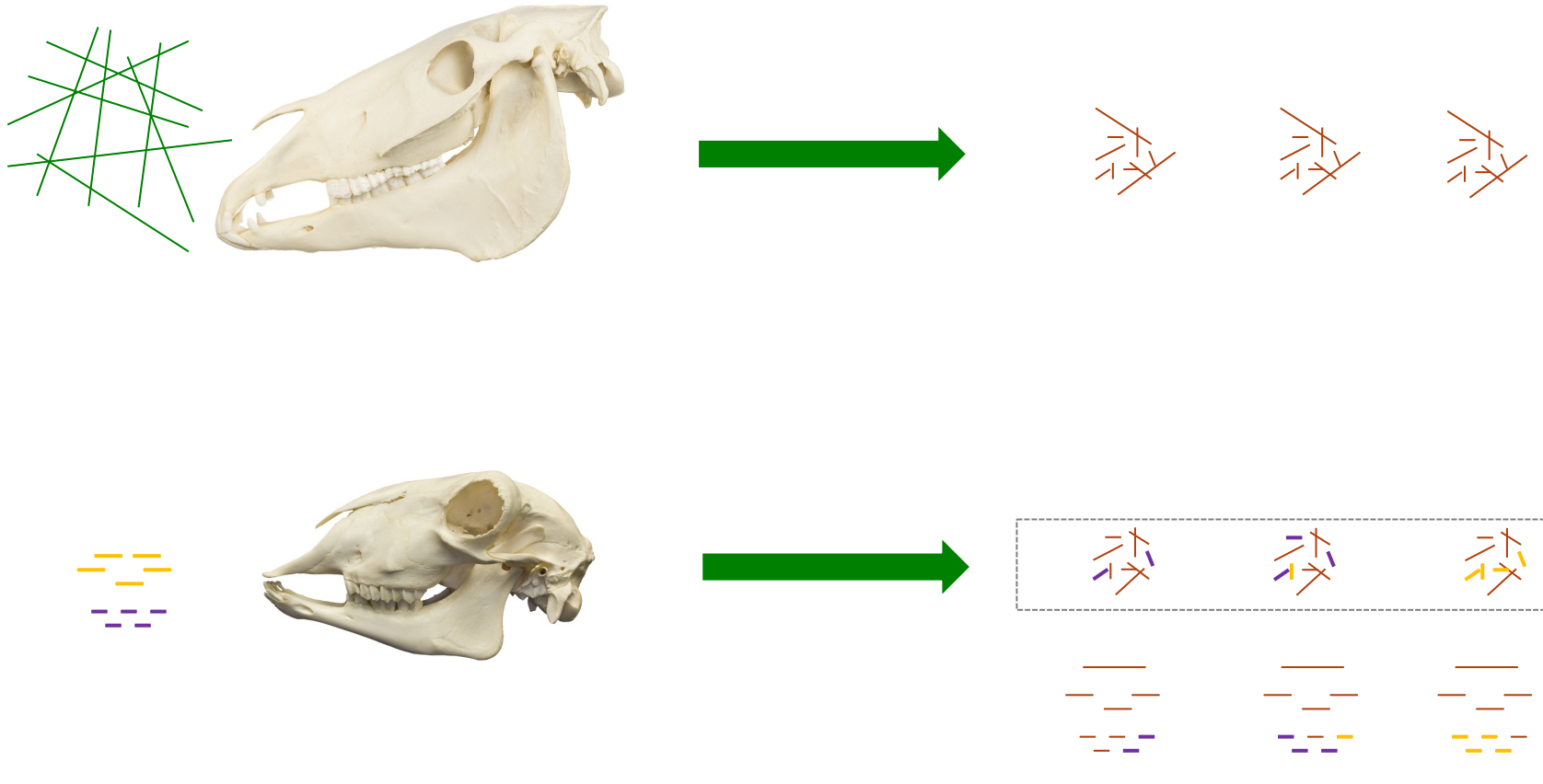
from Lechner et al. (2010)



Comparative selective retention of particle size classes in the gastrointestinal tract of ponies and goats

J. Hummel[1] | F. Scheurich[1] | S. Ortmann[2] | L. A. Crompton[3] | M. Gerken[1] |
M. Clauss[4]

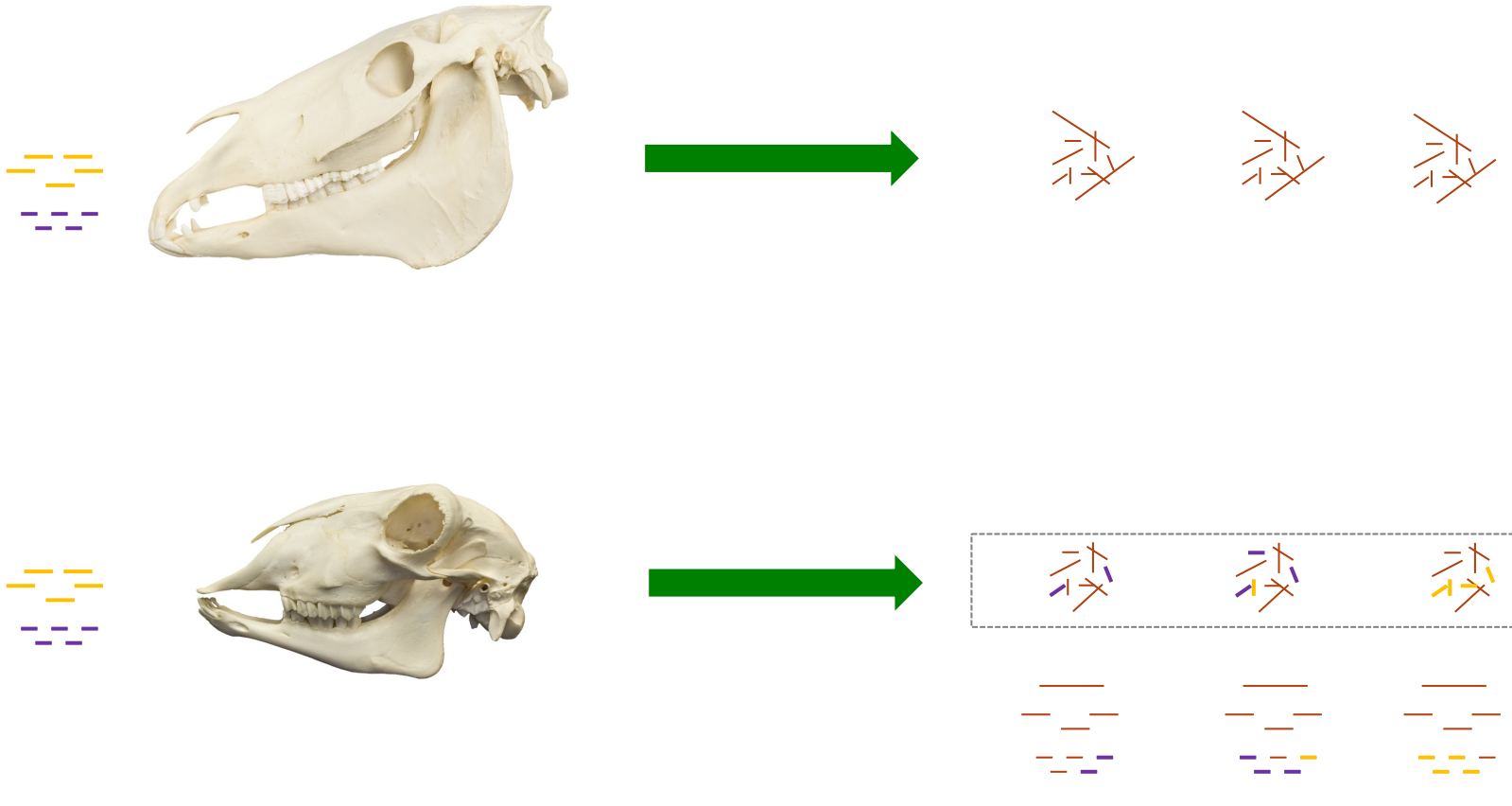
J Anim Physiol Anim Nutr. 2018;102:429–439.



Comparative selective retention of particle size classes in the gastrointestinal tract of ponies and goats

J. Hummel[1] | F. Scheurich[1] | S. Ortmann[2] | L. A. Crompton[3] | M. Gerken[1] |
M. Clauss[4]

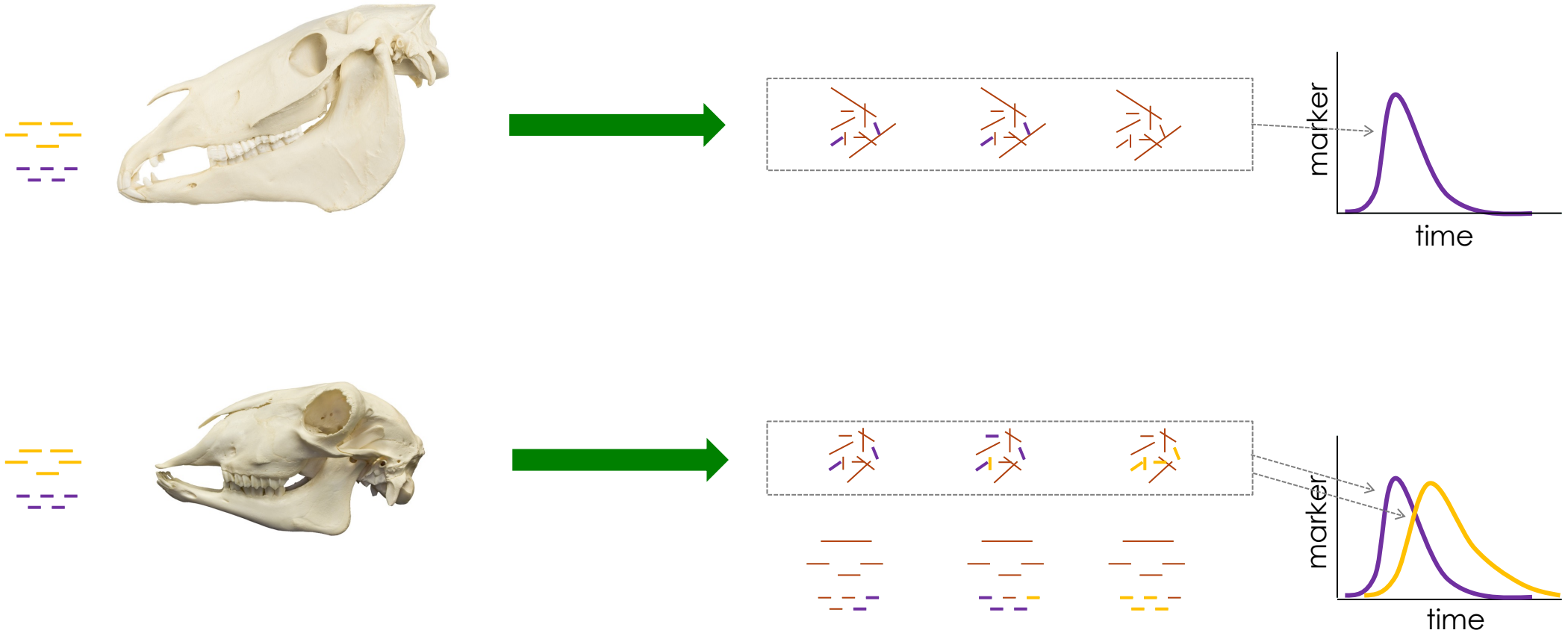
J Anim Physiol Anim Nutr. 2018;102:429–439.



Comparative selective retention of particle size classes in the gastrointestinal tract of ponies and goats

J. Hummel[1] | F. Scheurich[1] | S. Ortmann[2] | L. A. Crompton[3] | M. Gerken[1] |
M. Clauss[4]

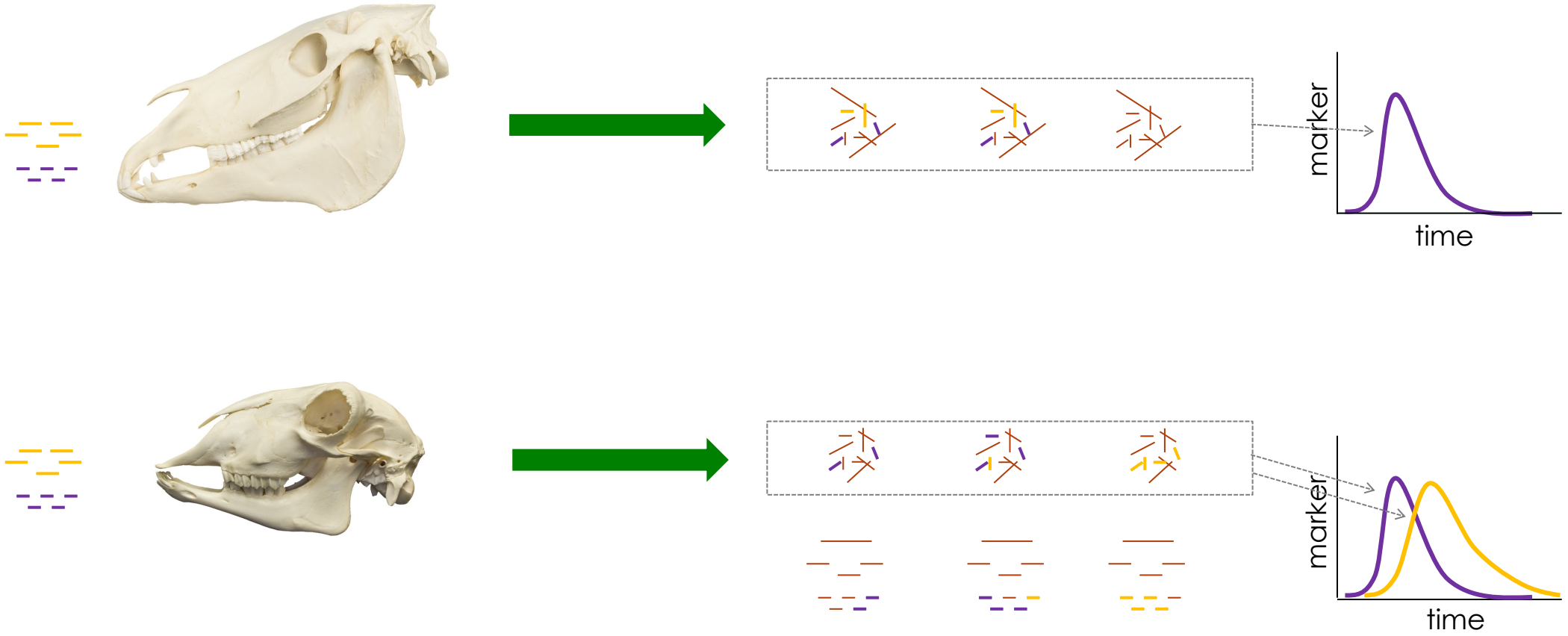
J Anim Physiol Anim Nutr. 2018;102:429–439.



Comparative selective retention of particle size classes in the gastrointestinal tract of ponies and goats

J. Hummel[1] | F. Scheurich[1] | S. Ortmann[2] | L. A. Crompton[3] | M. Gerken[1] | M. Clauss[4]

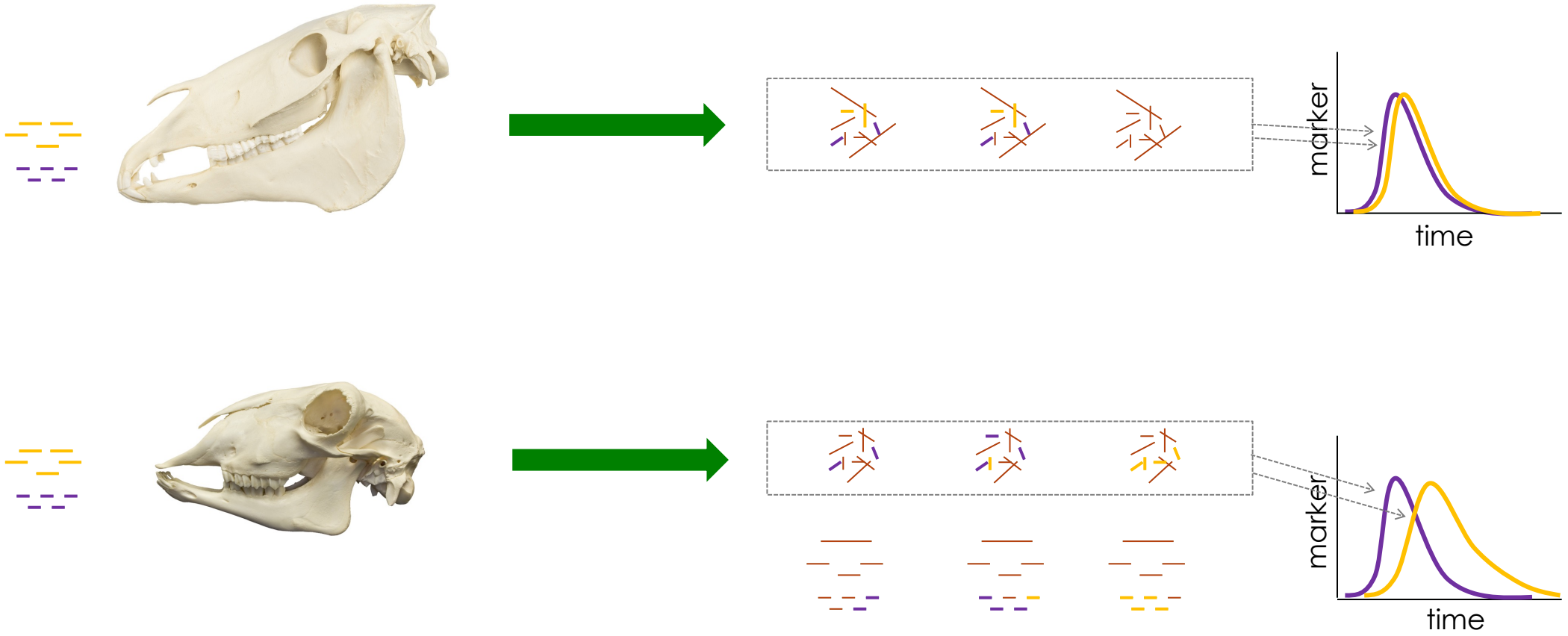
J Anim Physiol Anim Nutr. 2018;102:429–439.



Comparative selective retention of particle size classes in the gastrointestinal tract of ponies and goats

J. Hummel[1] | F. Scheurich[1] | S. Ortmann[2] | L. A. Crompton[3] | M. Gerken[1] |
M. Clauss[4]

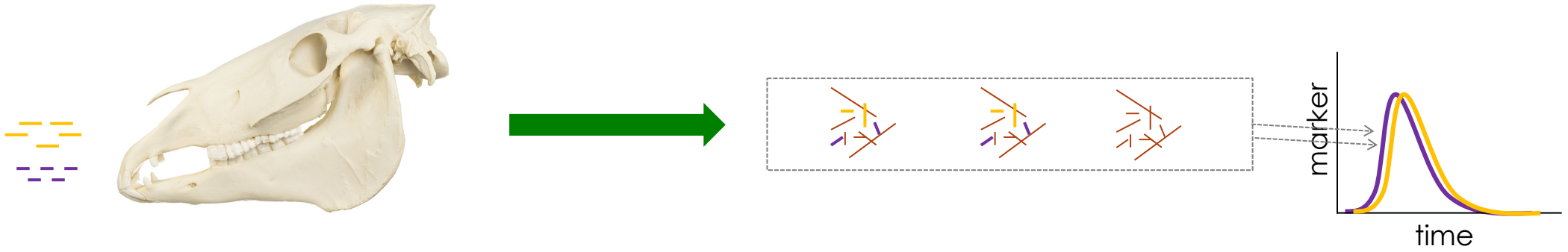
J Anim Physiol Anim Nutr. 2018;102:429–439.

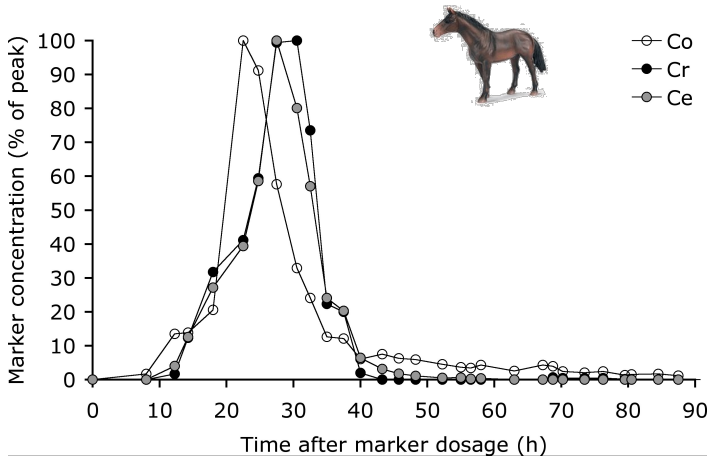


Comparative selective retention of particle size classes in the gastrointestinal tract of ponies and goats

J. Hummel[1] | F. Scheurich[1] | S. Ortmann[2] | L. A. Crompton[3] | M. Gerken[1] |
M. Clauss[4]

J Anim Physiol Anim Nutr. 2018;102:429–439.



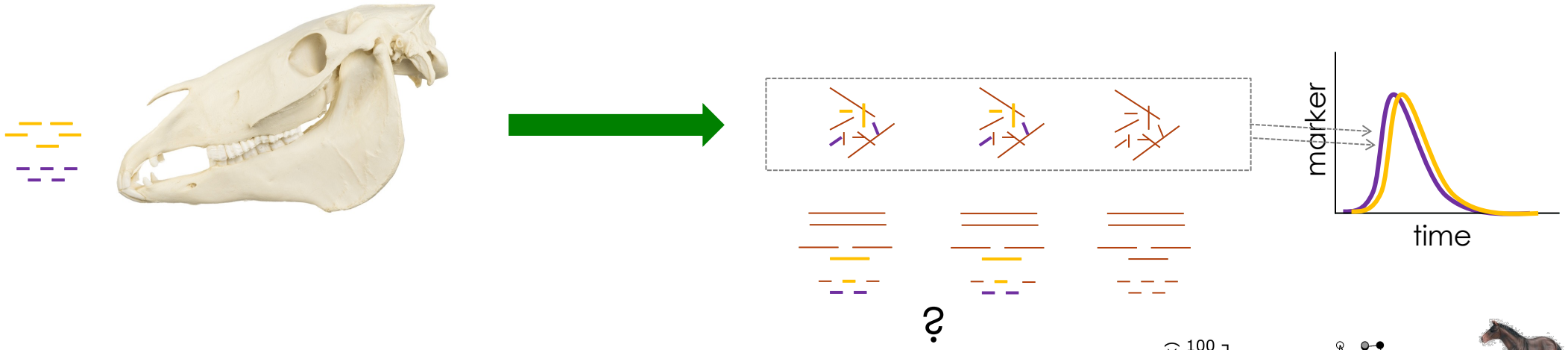


Clauss et al. (pers. obs.)

Comparative selective retention of particle size classes in the gastrointestinal tract of ponies and goats

J. Hummel[1] | F. Scheurich[1] | S. Ortmann[2] | L. A. Crompton[3] | M. Gerken[1] |
M. Clauss[4]

J Anim Physiol Anim Nutr. 2018;102:429–439.

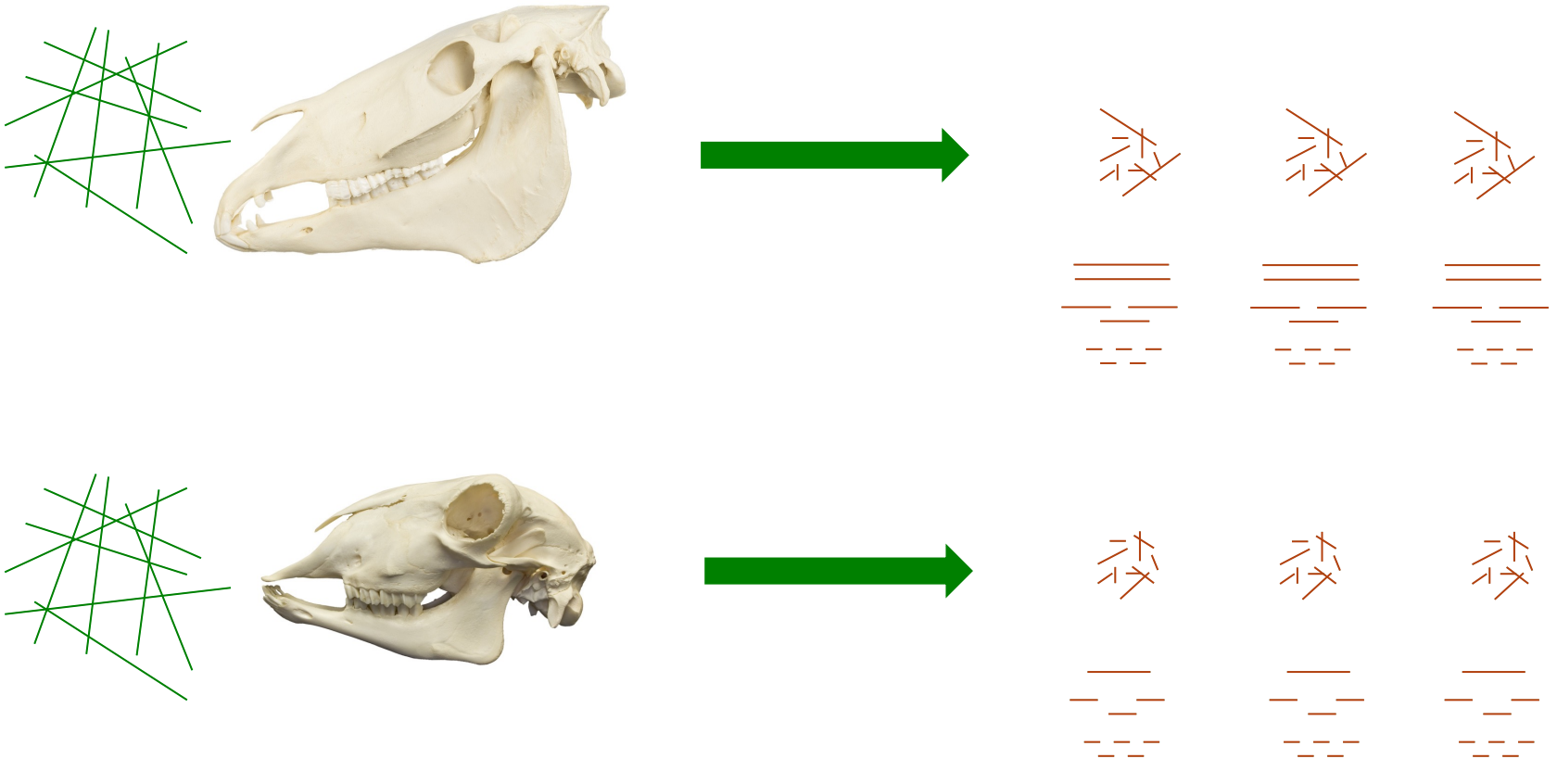


Clauss et al. (pers. obs.)

Comparative selective retention of particle size classes in the gastrointestinal tract of ponies and goats

J. Hummel[1] | F. Scheurich[1] | S. Ortmann[2] | L. A. Crompton[3] | M. Gerken[1] |
M. Clauss[4]

J Anim Physiol Anim Nutr. 2018;102:429–439.



Comparative selective retention of particle size classes in the gastrointestinal tract of ponies and goats

J. Hummel[1] | F. Scheurich[1] | S. Ortmann[2] | L. A. Crompton[3] | M. Gerken[1] |
M. Clauss[4]

J Anim Physiol Anim Nutr. 2018;102:429–439.

Comparative selective retention of particle size classes in the gastrointestinal tract of ponies and goats

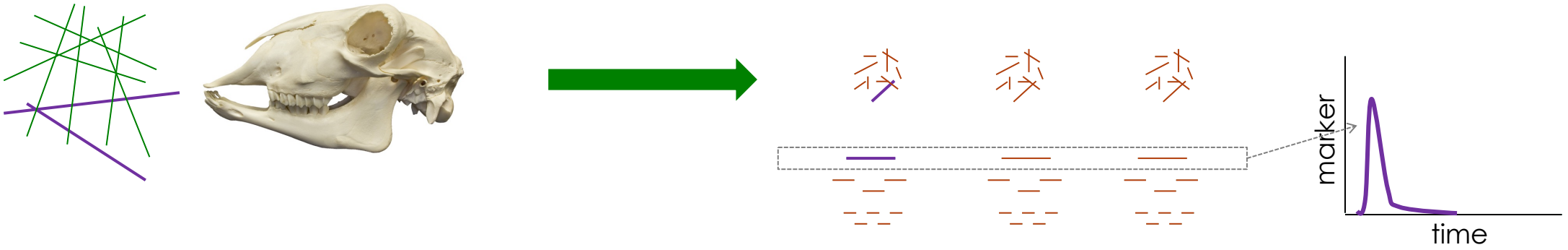
J. Hummel[1] | F. Scheurich[1] | S. Ortmann[2] | L. A. Crompton[3] | M. Gerken[1] |
M. Clauss[4]

J Anim Physiol Anim Nutr. 2018;102:429–439.

Comparative selective retention of particle size classes in the gastrointestinal tract of ponies and goats

J. Hummel[1] | F. Scheurich[1] | S. Ortmann[2] | L. A. Crompton[3] | M. Gerken[1] |
M. Clauss[4]

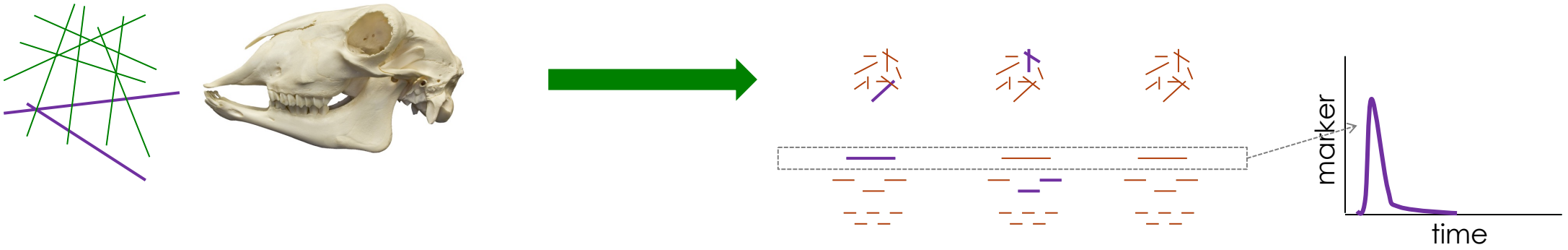
J Anim Physiol Anim Nutr. 2018;102:429–439.



Comparative selective retention of particle size classes in the gastrointestinal tract of ponies and goats

J. Hummel[1] | F. Scheurich[1] | S. Ortmann[2] | L. A. Crompton[3] | M. Gerken[1] |
M. Clauss[4]

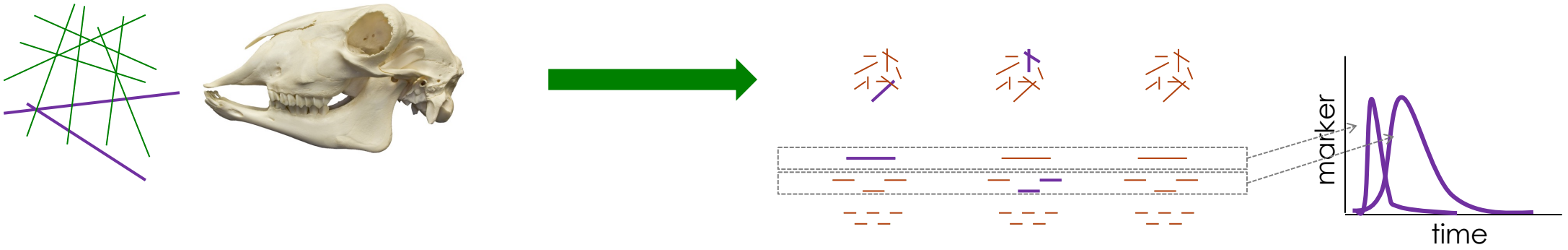
J Anim Physiol Anim Nutr. 2018;102:429–439.



Comparative selective retention of particle size classes in the gastrointestinal tract of ponies and goats

J. Hummel[1] | F. Scheurich[1] | S. Ortmann[2] | L. A. Crompton[3] | M. Gerken[1] |
M. Clauss[4]

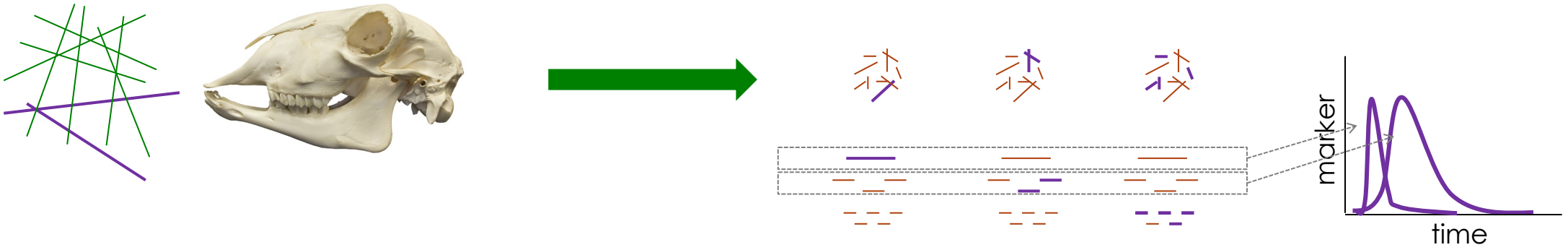
J Anim Physiol Anim Nutr. 2018;102:429–439.



Comparative selective retention of particle size classes in the gastrointestinal tract of ponies and goats

J. Hummel[1] | F. Scheurich[1] | S. Ortmann[2] | L. A. Crompton[3] | M. Gerken[1] |
M. Clauss[4]

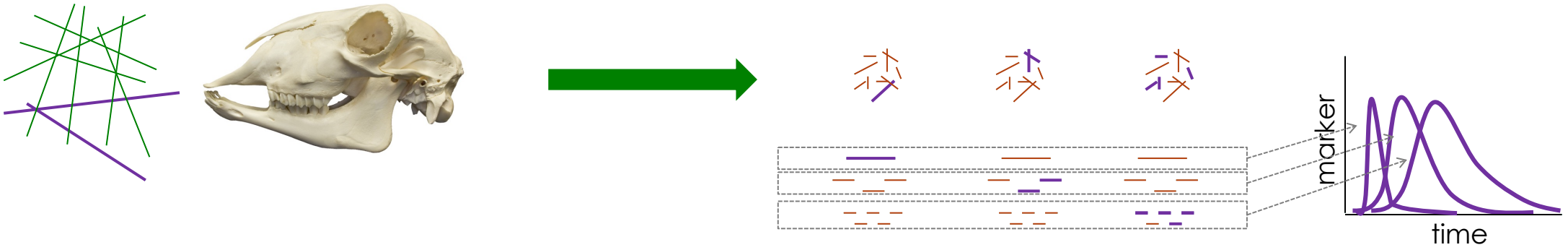
J Anim Physiol Anim Nutr. 2018;102:429–439.



Comparative selective retention of particle size classes in the gastrointestinal tract of ponies and goats

J. Hummel[1] | F. Scheurich[1] | S. Ortmann[2] | L. A. Crompton[3] | M. Gerken[1] |
M. Clauss[4]

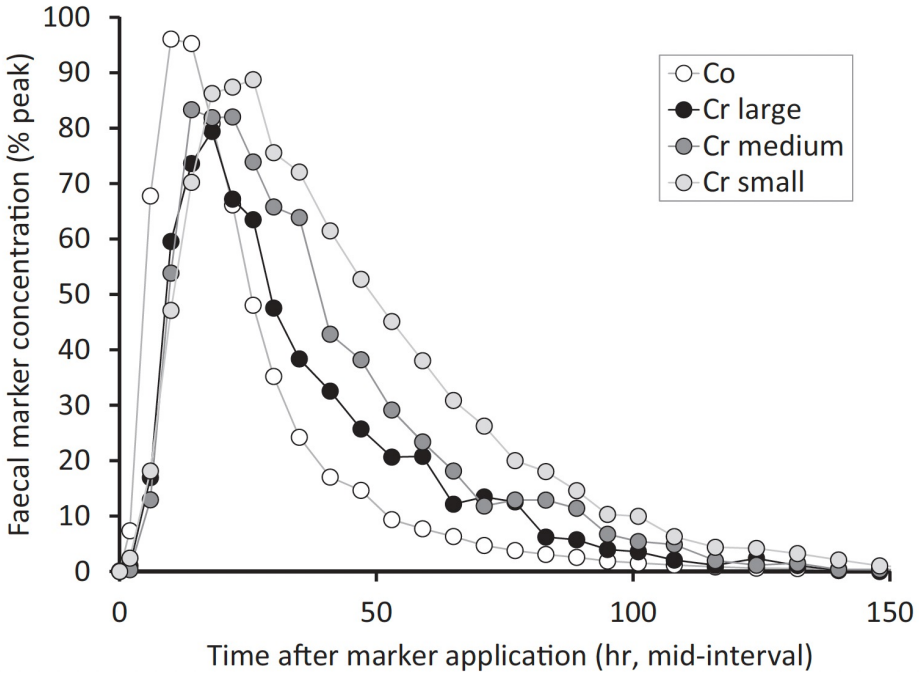
J Anim Physiol Anim Nutr. 2018;102:429–439.

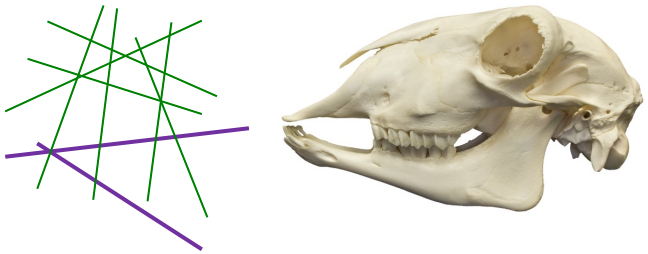


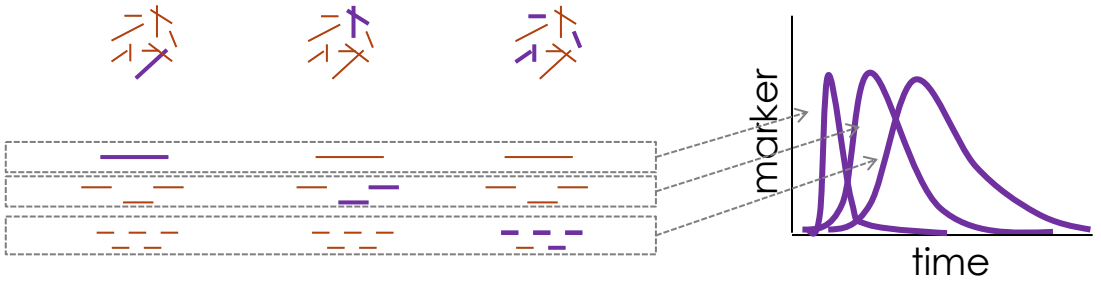
Comparative selective retention of particle size classes in the gastrointestinal tract of ponies and goats

J. Hummel[1] | F. Scheurich[1] | S. Ortmann[2] | L. A. Crompton[3] | M. Gerken[1] |
M. Clauss[4]

J Anim Physiol Anim Nutr. 2018;102:429–439.



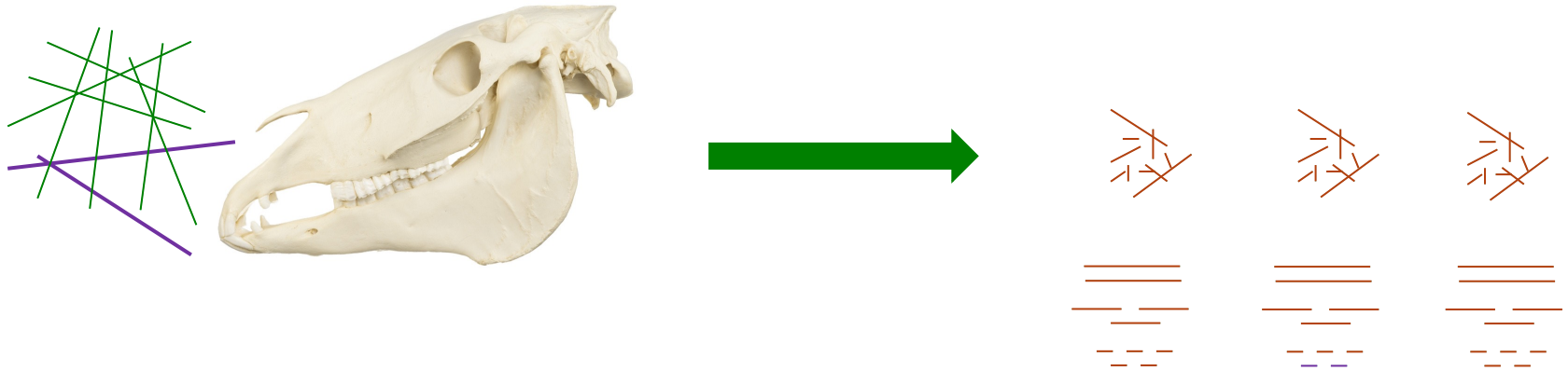




Comparative selective retention of particle size classes in the gastrointestinal tract of ponies and goats

J. Hummel[1] | F. Scheurich[1] | S. Ortmann[2] | L. A. Crompton[3] | M. Gerken[1] |
M. Clauss[4]

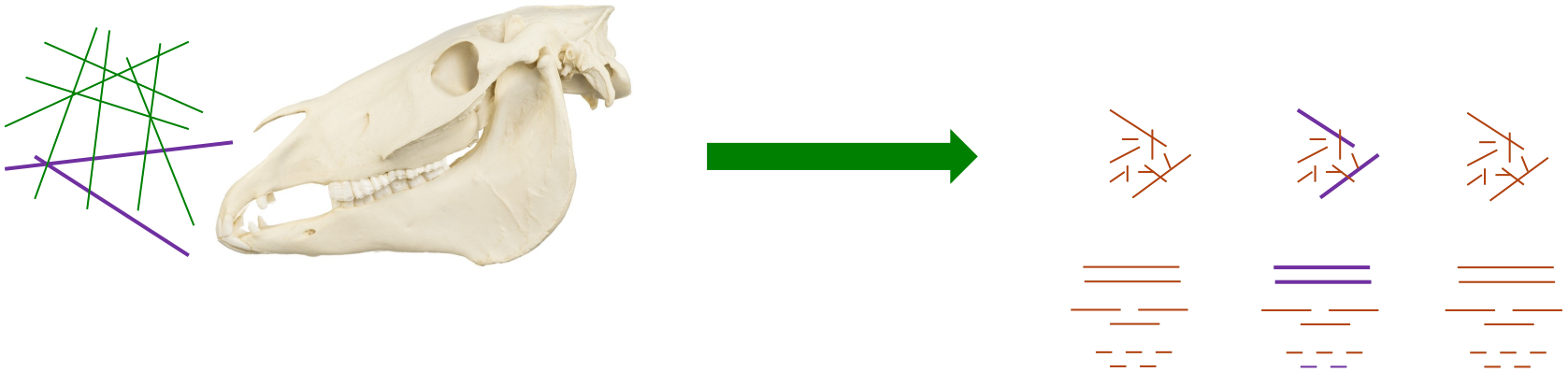
J Anim Physiol Anim Nutr. 2018;102:429–439.



Comparative selective retention of particle size classes in the gastrointestinal tract of ponies and goats

J. Hummel[1] | F. Scheurich[1] | S. Ortmann[2] | L. A. Crompton[3] | M. Gerken[1] |
M. Clauss[4]

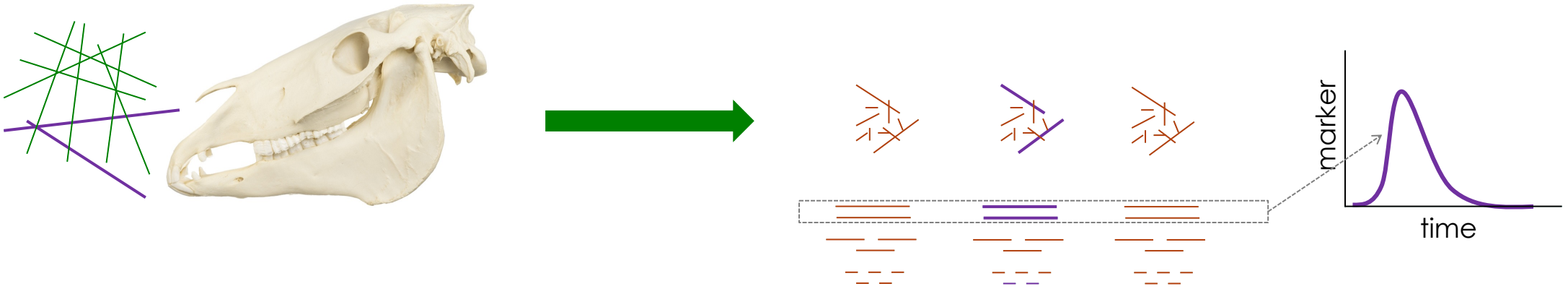
J Anim Physiol Anim Nutr. 2018;102:429–439.



Comparative selective retention of particle size classes in the gastrointestinal tract of ponies and goats

J. Hummel[1] | F. Scheurich[1] | S. Ortmann[2] | L. A. Crompton[3] | M. Gerken[1] |
M. Clauss[4]

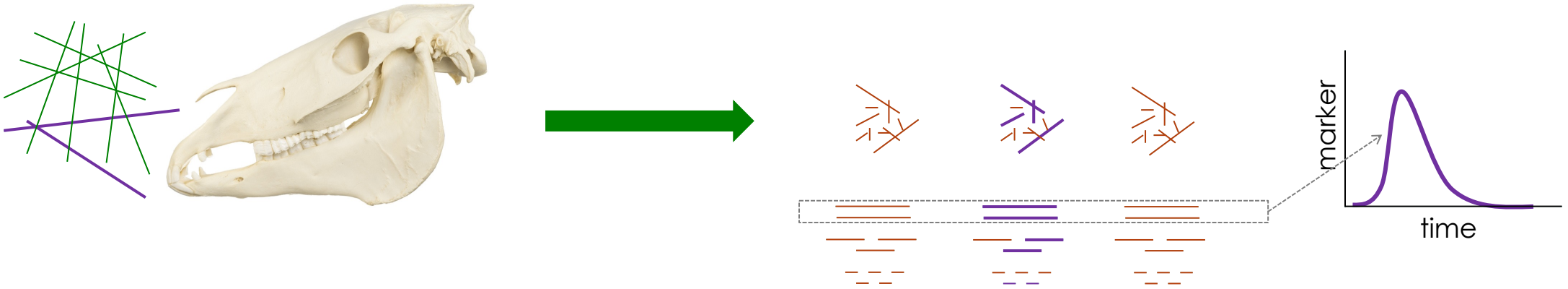
J Anim Physiol Anim Nutr. 2018;102:429–439.



Comparative selective retention of particle size classes in the gastrointestinal tract of ponies and goats

J. Hummel[1] | F. Scheurich[1] | S. Ortmann[2] | L. A. Crompton[3] | M. Gerken[1] |
M. Clauss[4]

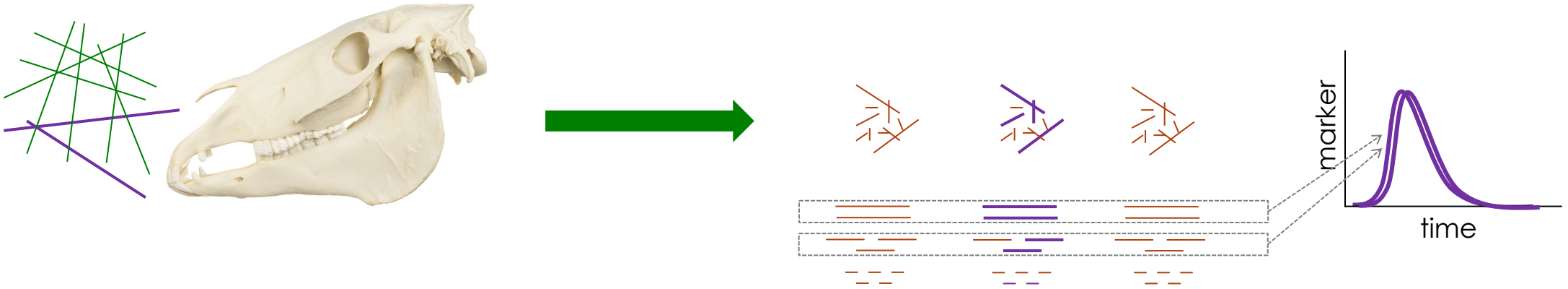
J Anim Physiol Anim Nutr. 2018;102:429–439.



Comparative selective retention of particle size classes in the gastrointestinal tract of ponies and goats

J. Hummel[1] | F. Scheurich[1] | S. Ortmann[2] | L. A. Crompton[3] | M. Gerken[1] |
M. Clauss[4]

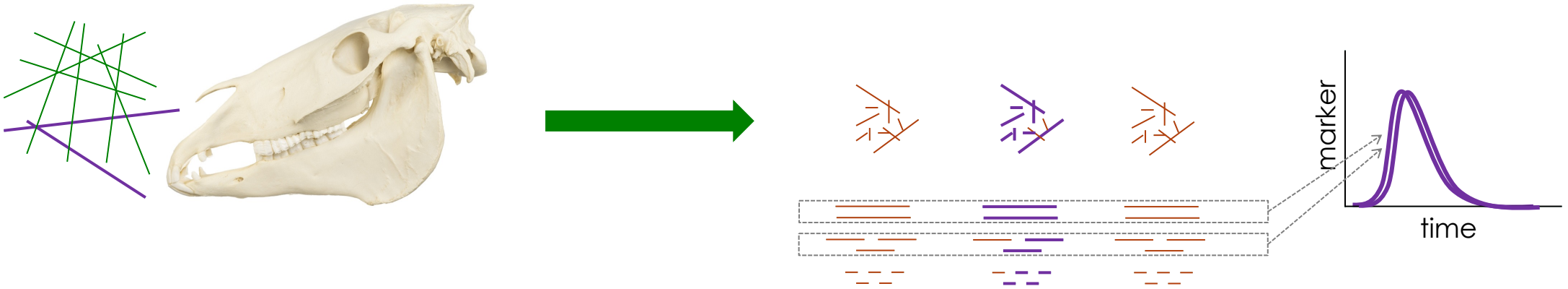
J Anim Physiol Anim Nutr. 2018;102:429–439.



Comparative selective retention of particle size classes in the gastrointestinal tract of ponies and goats

J. Hummel[1] | F. Scheurich[1] | S. Ortmann[2] | L. A. Crompton[3] | M. Gerken[1] |
M. Clauss[4]

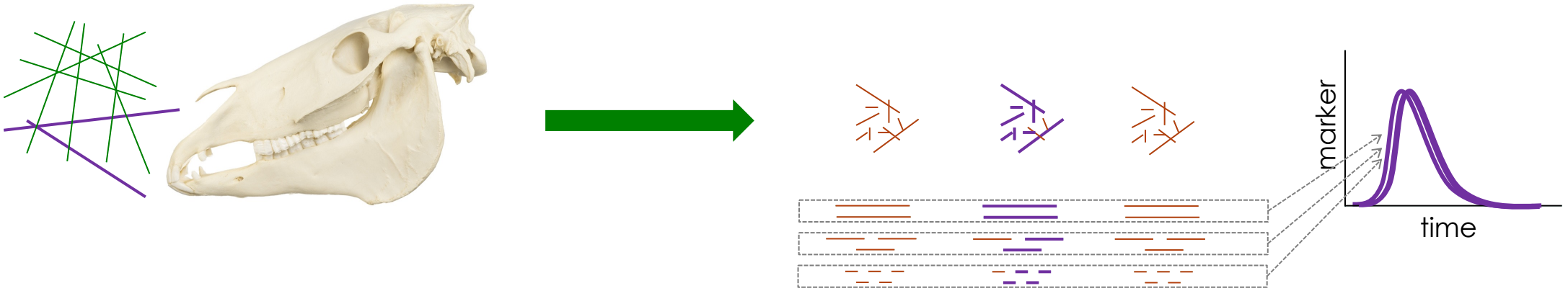
J Anim Physiol Anim Nutr. 2018;102:429–439.



Comparative selective retention of particle size classes in the gastrointestinal tract of ponies and goats

J. Hummel[1] | F. Scheurich[1] | S. Ortmann[2] | L. A. Crompton[3] | M. Gerken[1] |
M. Clauss[4]

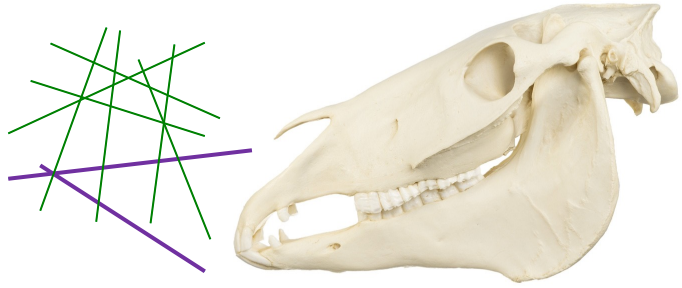
J Anim Physiol Anim Nutr. 2018;102:429–439.

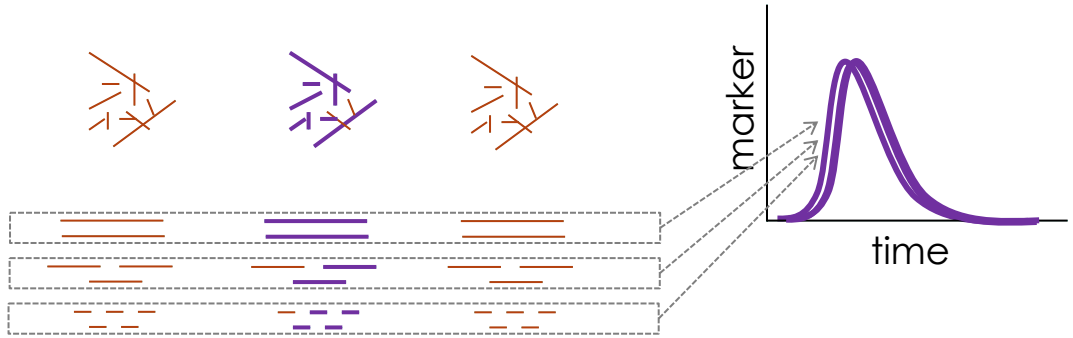


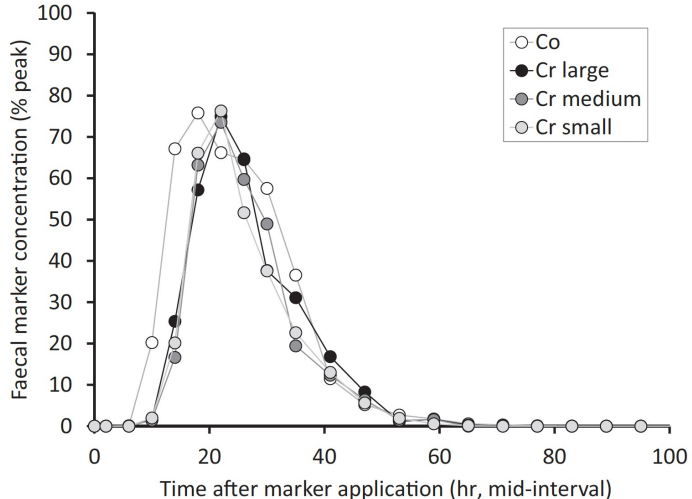
Comparative selective retention of particle size classes in the gastrointestinal tract of ponies and goats

J. Hummel[1] | F. Scheurich[1] | S. Ortmann[2] | L. A. Crompton[3] | M. Gerken[1] |
M. Clauss[4]

J Anim Physiol Anim Nutr. 2018;102:429–439.

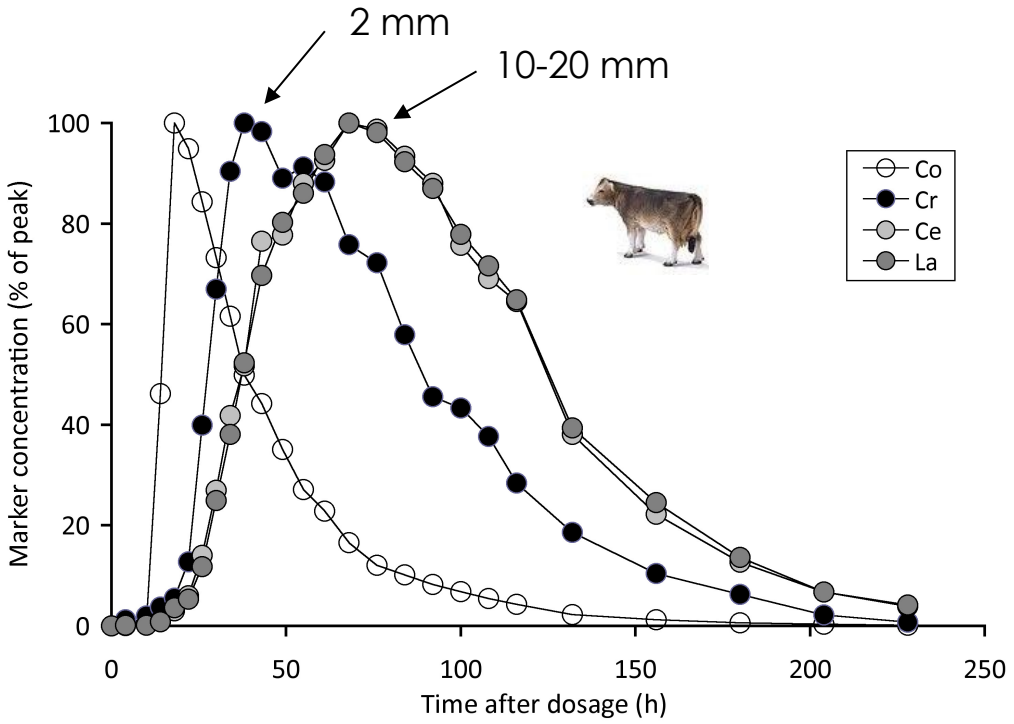






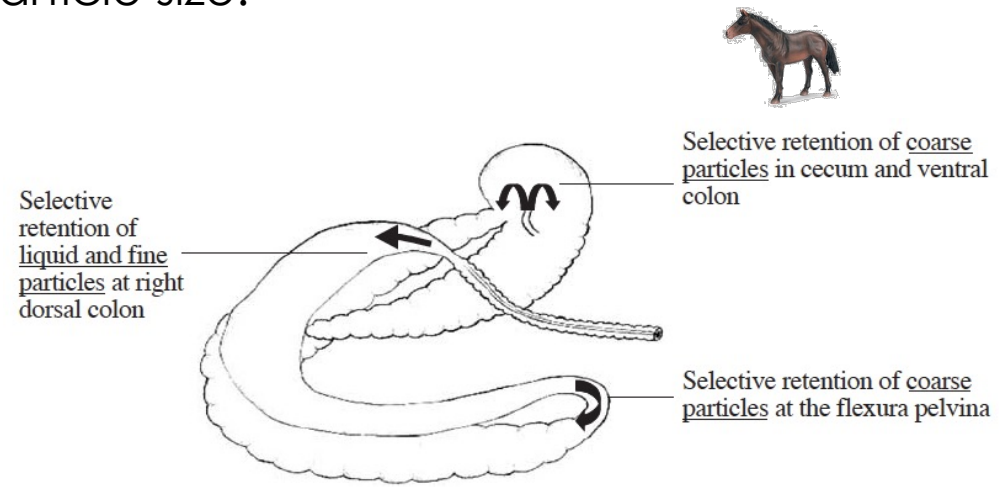
Selective particle retention

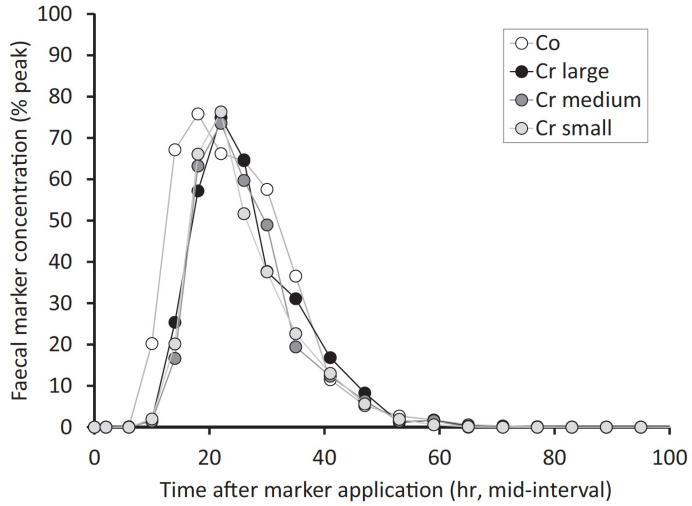
In ruminants, large particles are selectively retained in the rumen.



from Lechner et al. (2010)

In equids, there is no *net* selective retention by particle size.



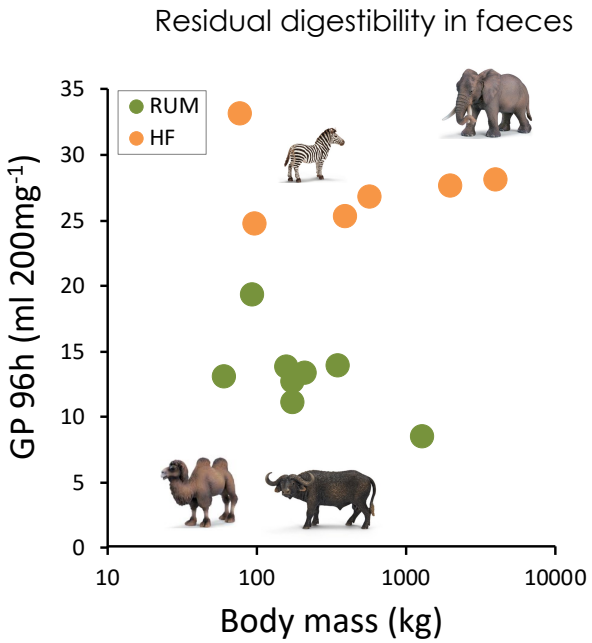


Differences in digestive physiology between equids and ruminants: chewing efficiency

Digestive physiology meets herbivore diversity

Marcus Clauss [a], Patrick Steuer [b], Kerstin Erlinghagen-Lückerath [b], Jacques Kaandorp [c], Julia Fritz [a], Karl-Heinz Südekum [b,*], Jürgen Hummel [b,d]

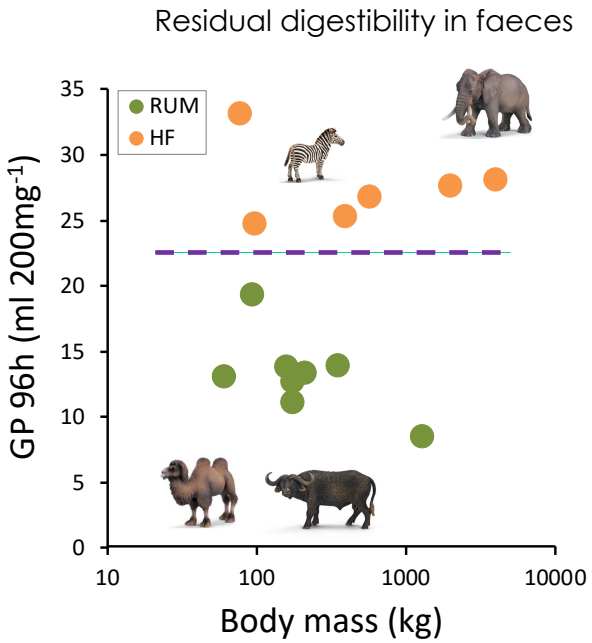
Comparative Biochemistry and Physiology, Part A 179 (2015) 182–191



Digestive physiology meets herbivore diversity

Marcus Clauss [a], Patrick Steuer [b], Kerstin Erlinghagen-Lückerath [b], Jacques Kaandorp [c], Julia Fritz [a], Karl-Heinz Südekum [b,*], Jürgen Hummel [b,d]

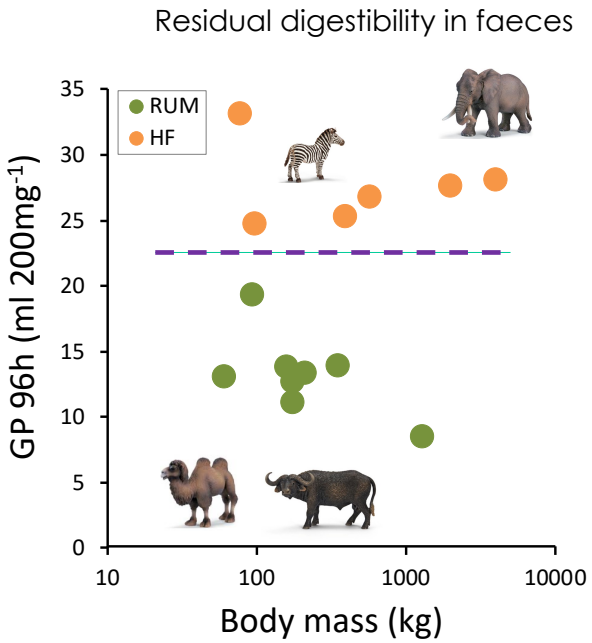
Comparative Biochemistry and Physiology, Part A 179 (2015) 182–191

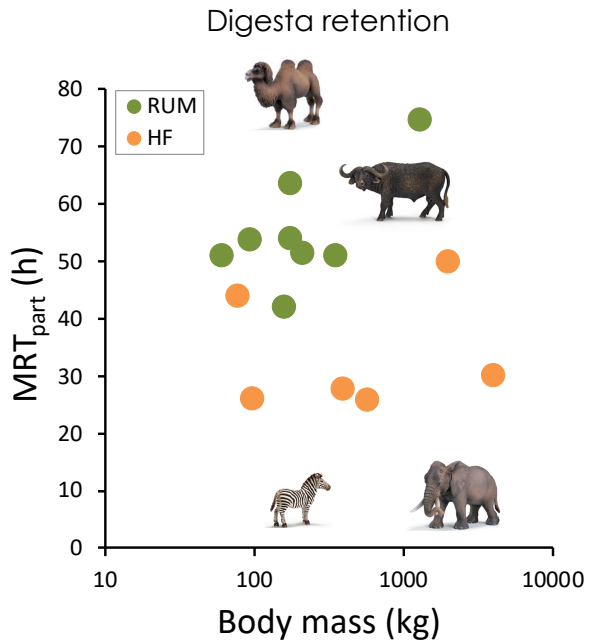


Digestive physiology meets herbivore diversity

Marcus Clauss [a], Patrick Steuer [b], Kerstin Erlinghagen-Lückerath [b], Jacques Kaandorp [c], Julia Fritz [a], Karl-Heinz Südekum [b,*], Jürgen Hummel [b,d]

Comparative Biochemistry and Physiology, Part A 179 (2015) 182–191

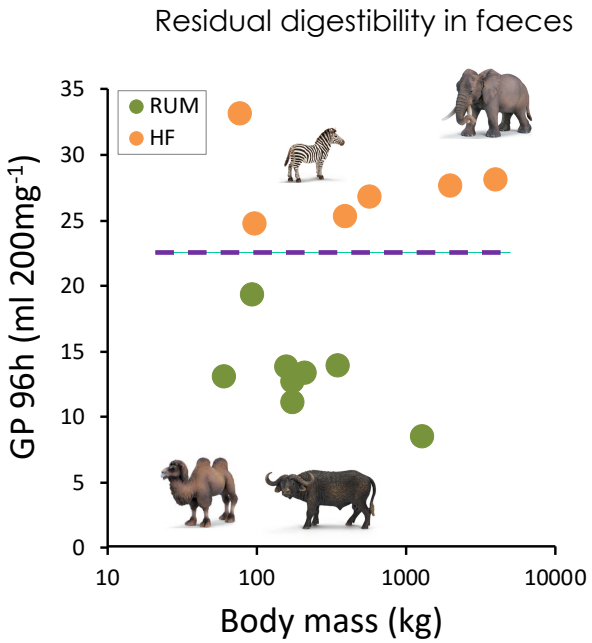


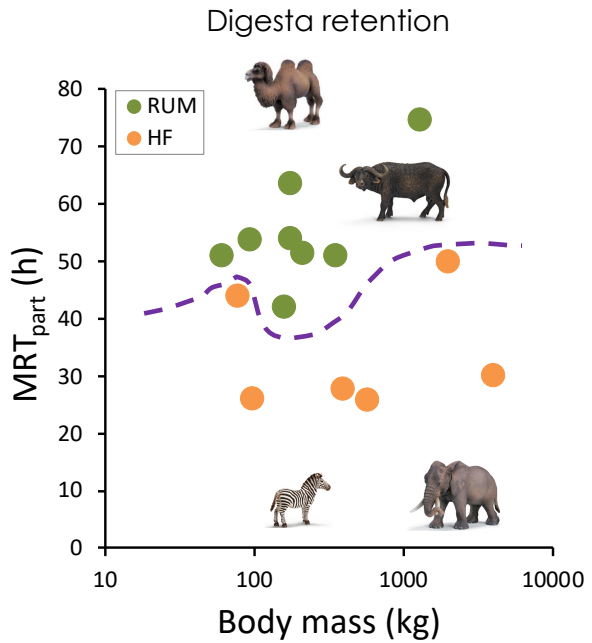


Digestive physiology meets herbivore diversity

Marcus Clauss [a], Patrick Steuer [b], Kerstin Erlinghagen-Lückerath [b], Jacques Kaandorp [c], Julia Fritz [a], Karl-Heinz Südekum [b,*], Jürgen Hummel [b,d]

Comparative Biochemistry and Physiology, Part A 179 (2015) 182–191



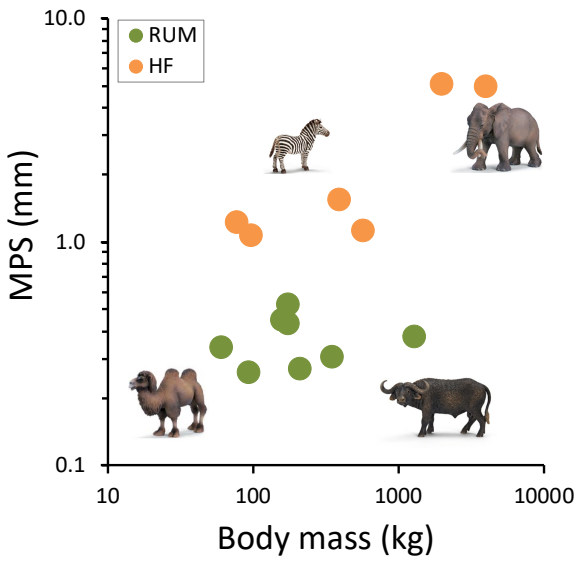


Digestive physiology meets herbivore diversity

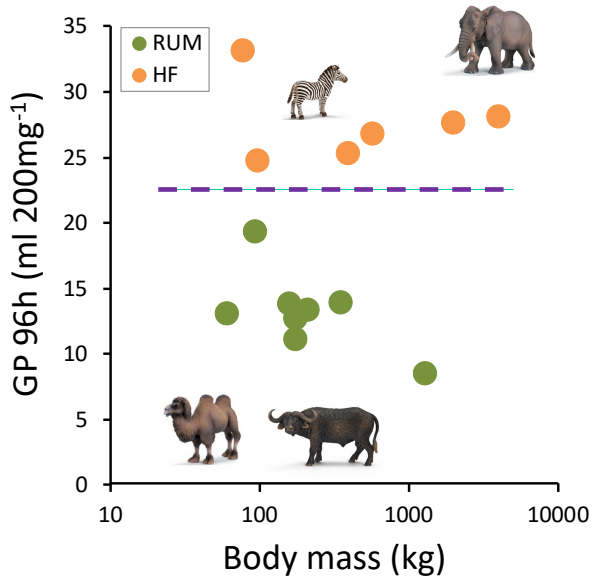
Marcus Clauss [a], Patrick Steuer [b], Kerstin Erlinghagen-Lückerath [b], Jacques Kaandorp [c], Julia Fritz [a], Karl-Heinz Südekum [b,*], Jürgen Hummel [b,d]

Comparative Biochemistry and Physiology, Part A 179 (2015) 182–191

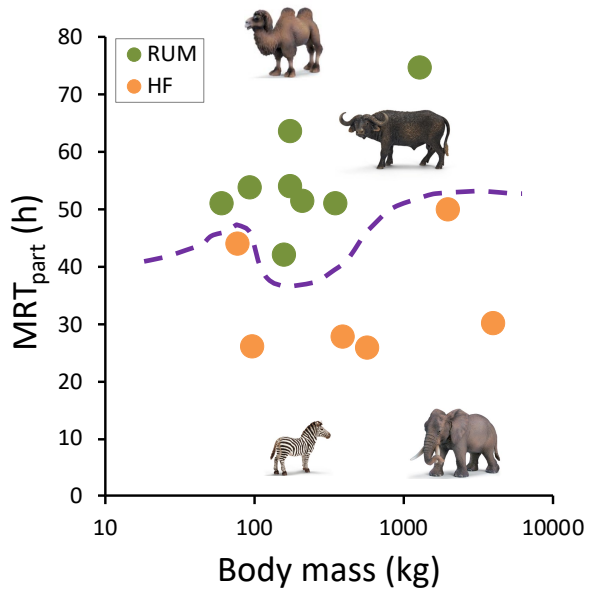
Faecal particle size



Residual digestibility in faeces



Digesta retention

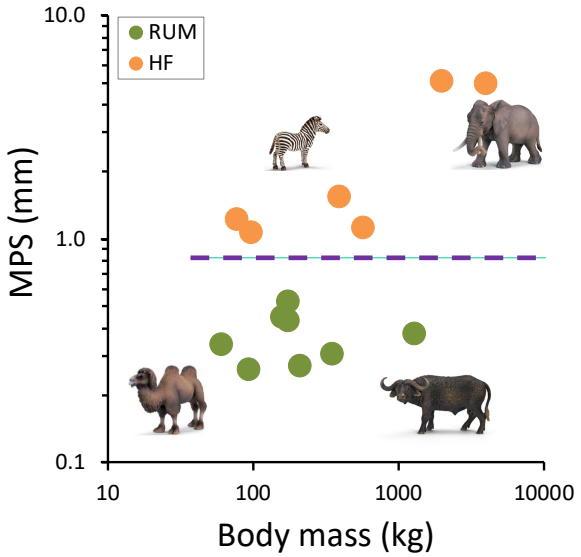


Digestive physiology meets herbivore diversity

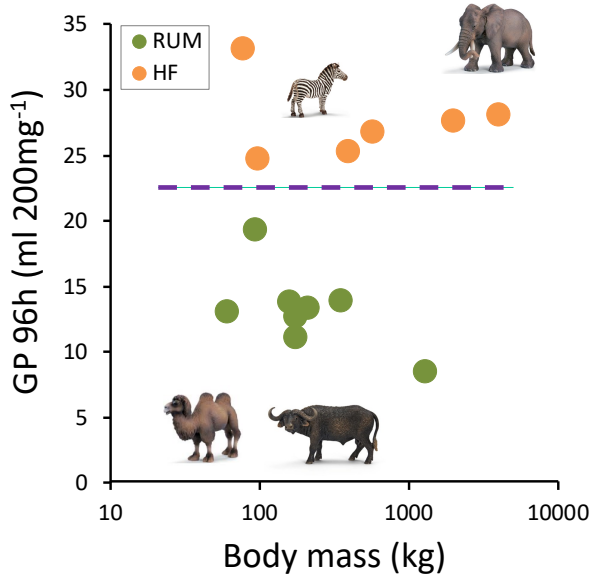
Marcus Clauss [a], Patrick Steuer [b], Kerstin Erlinghagen-Lückerath [b], Jacques Kaandorp [c], Julia Fritz [a], Karl-Heinz Südekum [b,*], Jürgen Hummel [b,d]

Comparative Biochemistry and Physiology, Part A 179 (2015) 182–191

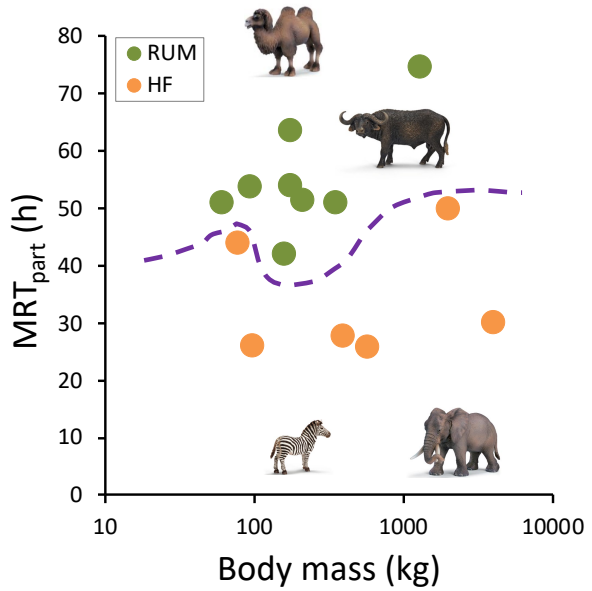
Faecal particle size



Residual digestibility in faeces



Digesta retention

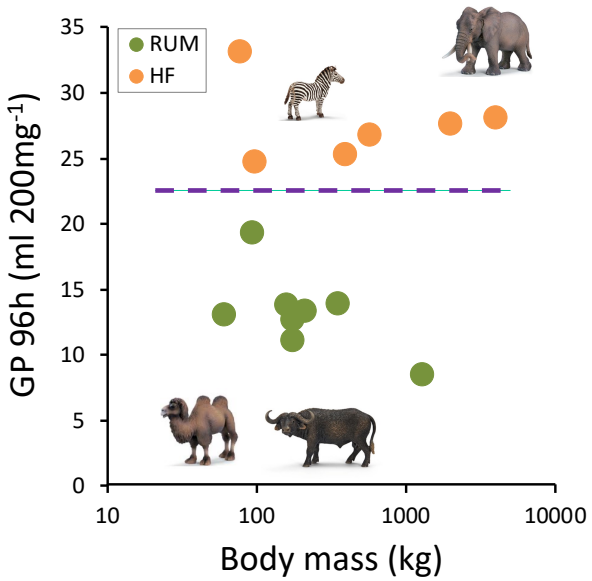


Digestive physiology meets herbivore diversity

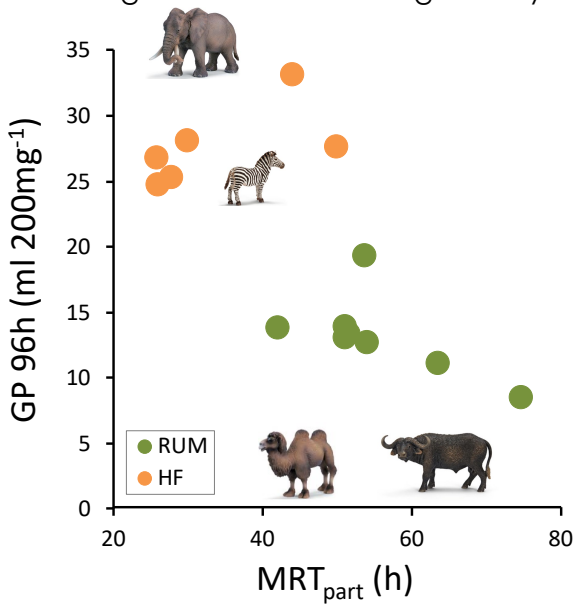
Marcus Clauss [a], Patrick Steuer [b], Kerstin Erlinghagen-Lückerath [b], Jacques Kaandorp [c], Julia Fritz [a], Karl-Heinz Südekum [b,*], Jürgen Hummel [b,d]

Comparative Biochemistry and Physiology, Part A 179 (2015) 182–191

Residual digestibility in faeces



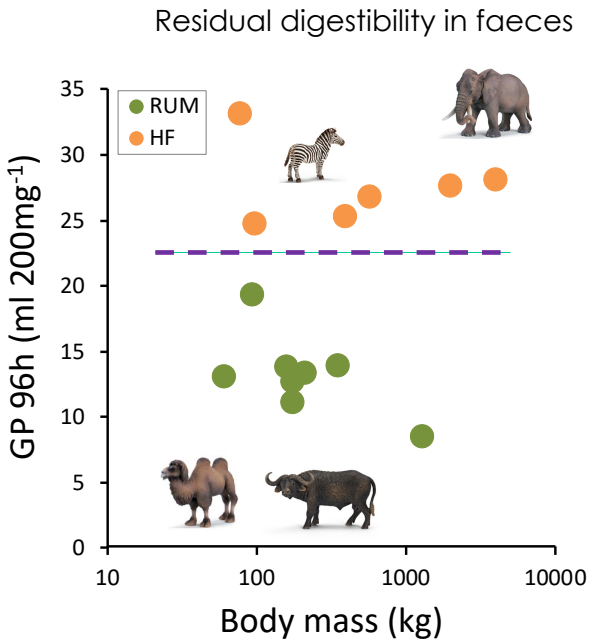
Digesta retention vs. digestibility

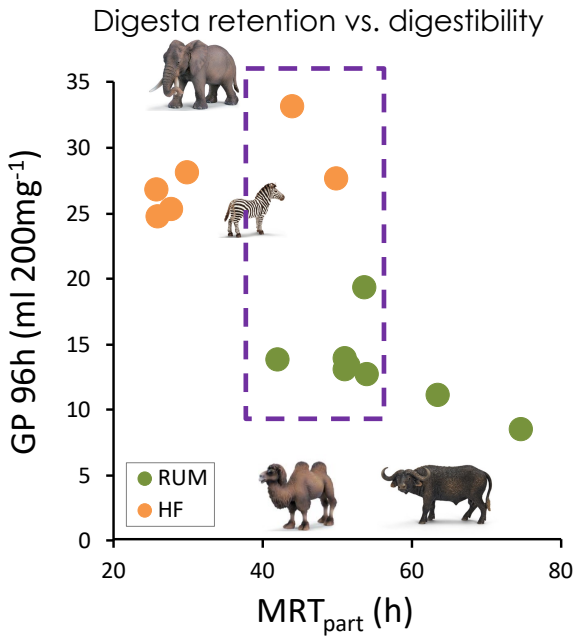


Digestive physiology meets herbivore diversity

Marcus Clauss [a], Patrick Steuer [b], Kerstin Erlinghagen-Lückerath [b], Jacques Kaandorp [c], Julia Fritz [a], Karl-Heinz Südekum [b,*], Jürgen Hummel [b,d]

Comparative Biochemistry and Physiology, Part A 179 (2015) 182–191



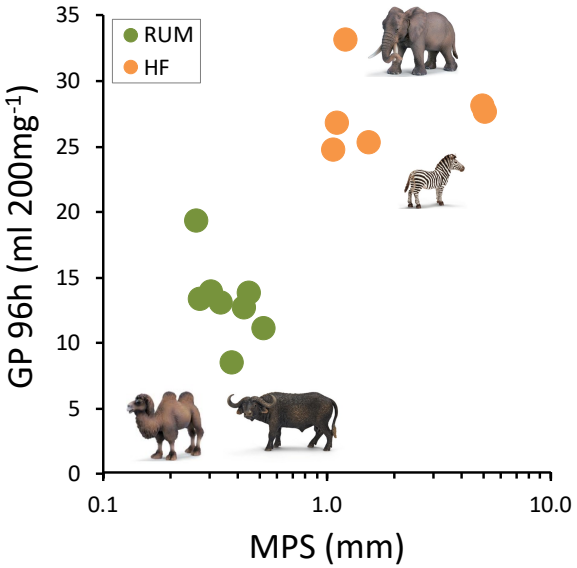


Digestive physiology meets herbivore diversity

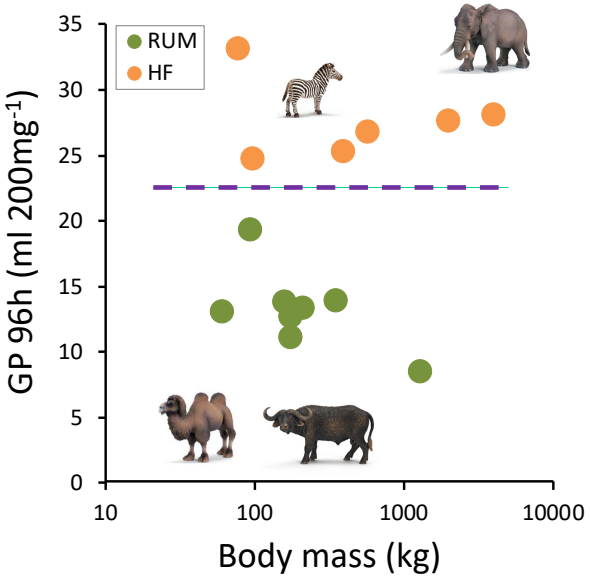
Marcus Clauss [a], Patrick Steuer [b], Kerstin Erlinghagen-Lückerath [b], Jacques Kaandorp [c], Julia Fritz [a], Karl-Heinz Südekum [b,*], Jürgen Hummel [b,d]

Comparative Biochemistry and Physiology, Part A 179 (2015) 182–191

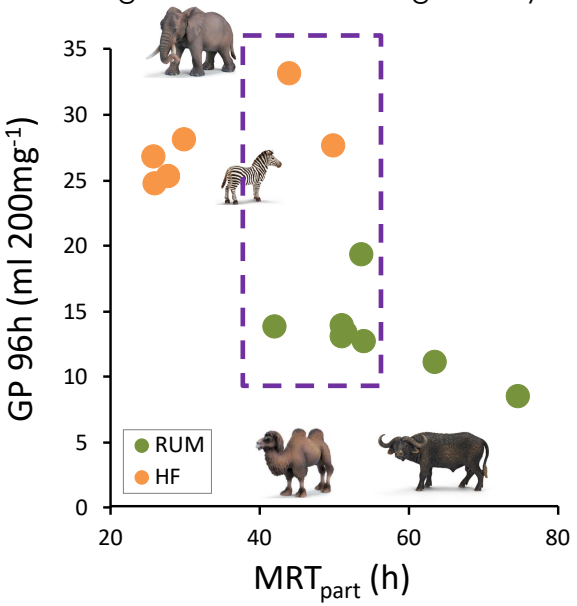
Faecal particle size vs digestibility



Residual digestibility in faeces



Digesta retention vs. digestibility

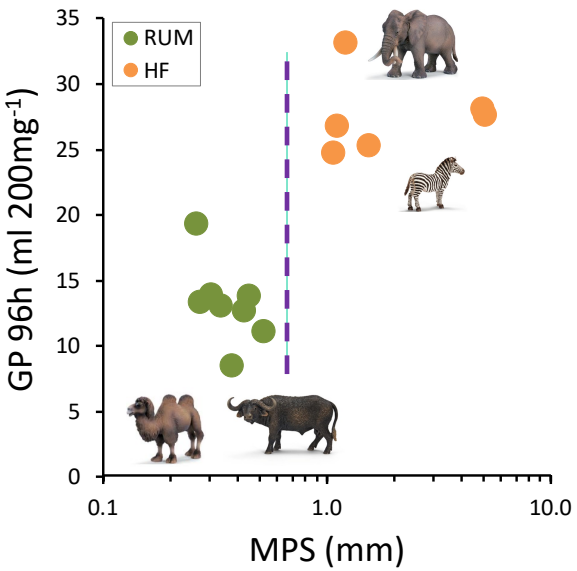


Digestive physiology meets herbivore diversity

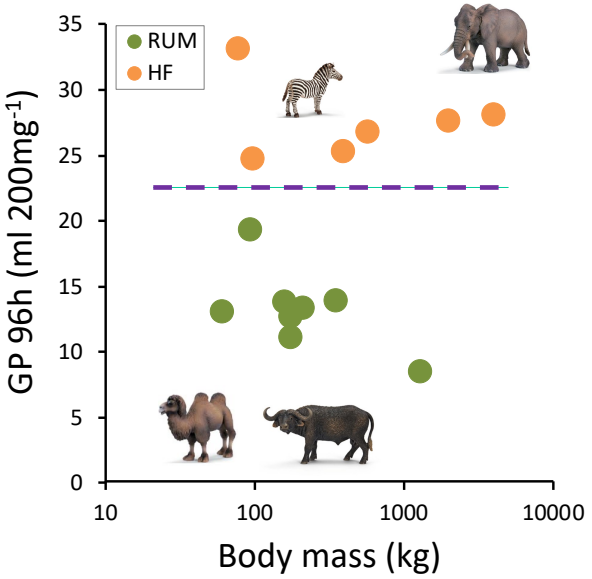
Marcus Clauss [a], Patrick Steuer [b], Kerstin Erlinghagen-Lückerath [b], Jacques Kaandorp [c], Julia Fritz [a], Karl-Heinz Südekum [b,*], Jürgen Hummel [b,d]

Comparative Biochemistry and Physiology, Part A 179 (2015) 182–191

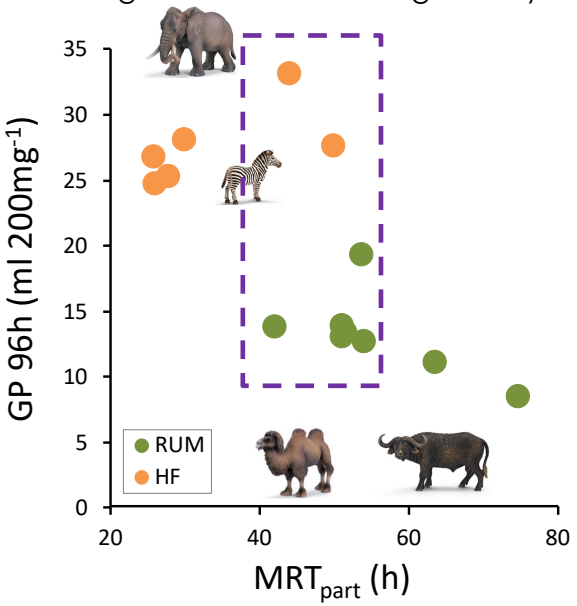
Faecal particle size vs digestibility



Residual digestibility in faeces



Digesta retention vs. digestibility

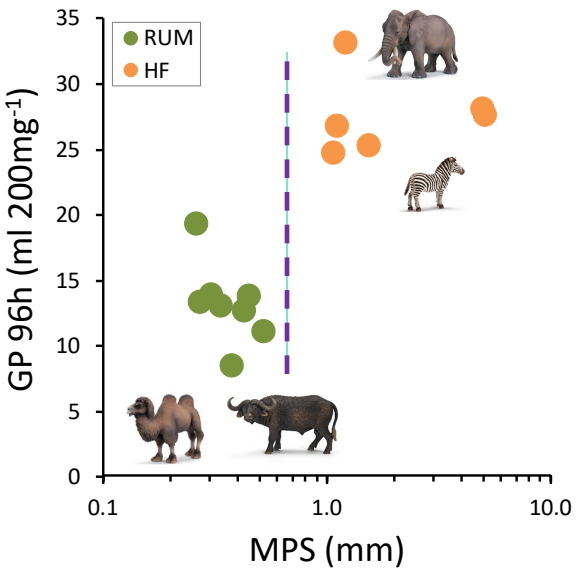


Faecal particle size: Digestive physiology meets herbivore diversity

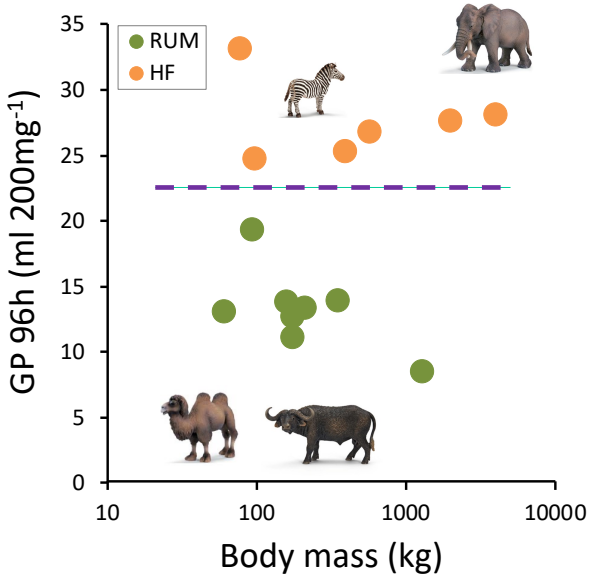
Marcus Clauss [a], Patrick Steuer [b], Kerstin Erlinghagen-Lückerath [b], Jacques Kaandorp [c], Julia Fritz [a], Karl-Heinz Südekum [b,*], Jürgen Hummel [b,d]

Comparative Biochemistry and Physiology, Part A 179 (2015) 182–191

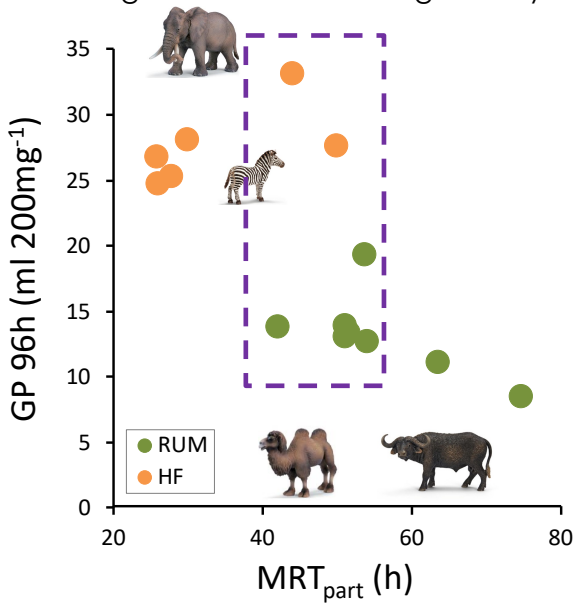
Faecal particle size vs digestibility



Residual digestibility in faeces



Digesta retention vs. digestibility



Parallel evolution

among

Perissodactyls

Artiodactyls

Parallel evolution

among

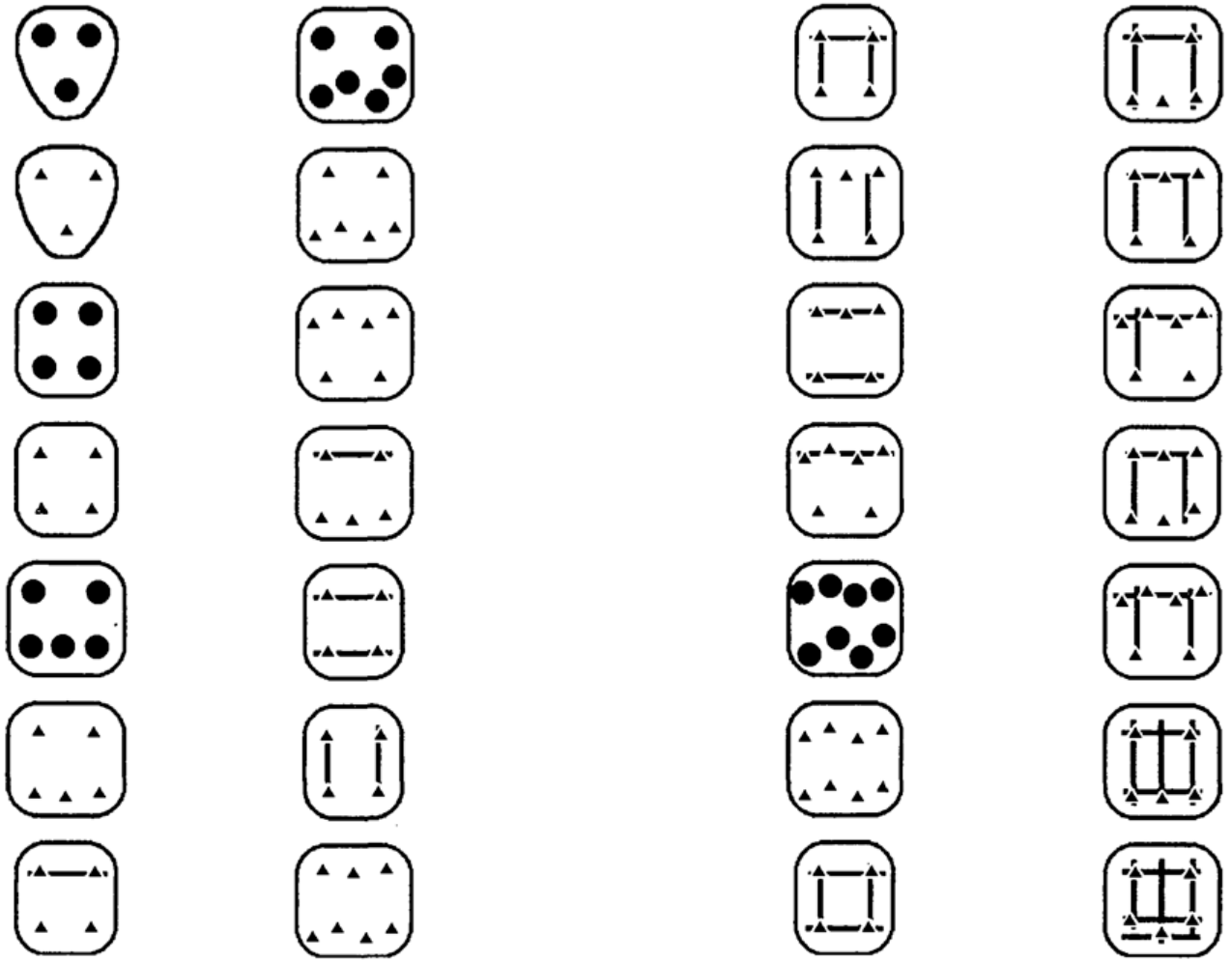
Perissodactyls

Artiodactyls

Equids

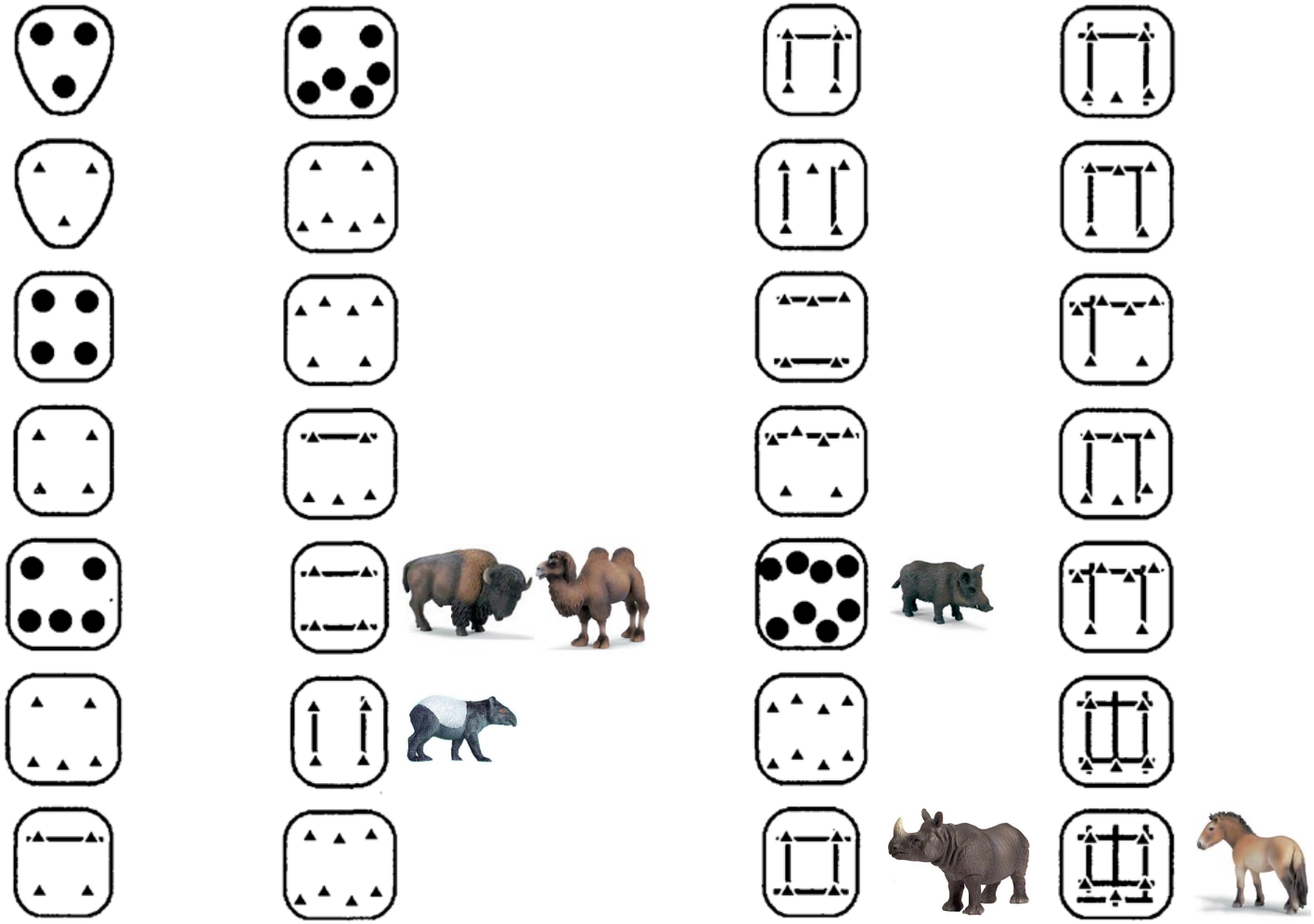
achieve
comparatively high
chewing efficiencies
and food intakes

Large mammal molar surfaces



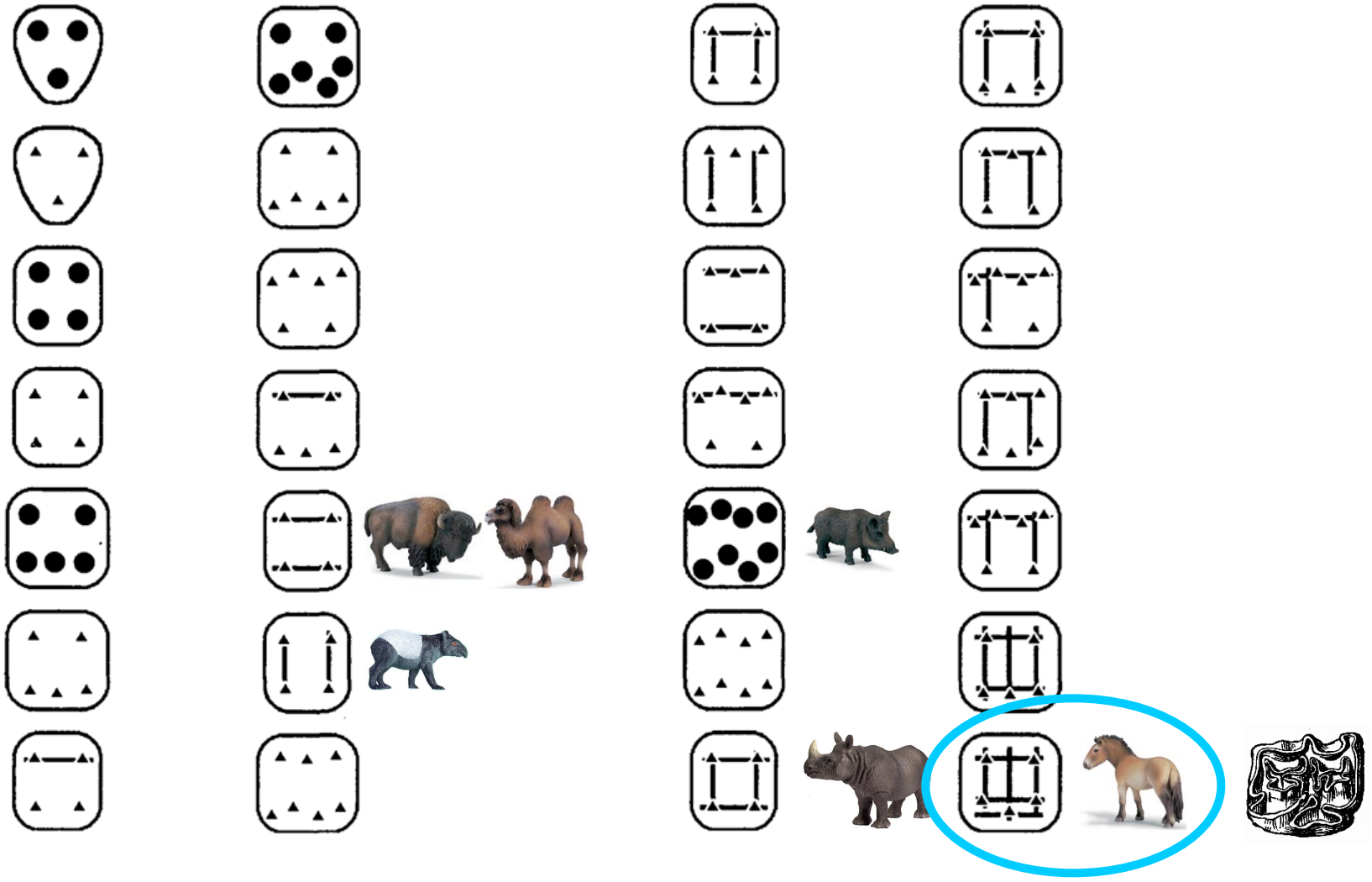
from Jernvall et al. (1996)

Large mammal molar surfaces



from Jernvall et al. (1996)

Large mammal molar surfaces

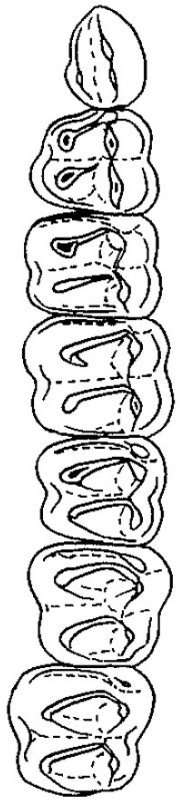


from Jernvall et al. (1996)

Equids: masters of complex enamel folding

https://www.sciencedaily.com/releases/2011/04/110404151341.htm

Parallel evolution



Perissodactyls

among

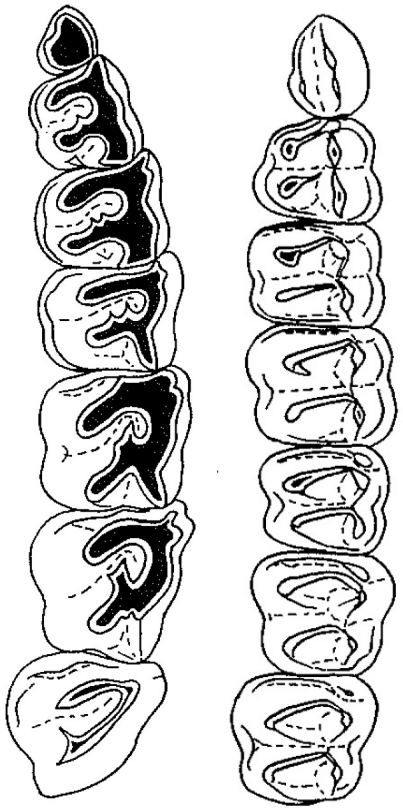
Artiodactyls

Equids

achieve
comparatively high
chewing efficiencies
and food intakes

from Thenius (1989)

Parallel evolution



Perissodactyls

among

Artiodactyls

Equids

achieve
comparatively high
chewing efficiencies
and food intakes

from Thenius (1989)

Parallel evolution

Perissodactyls

among

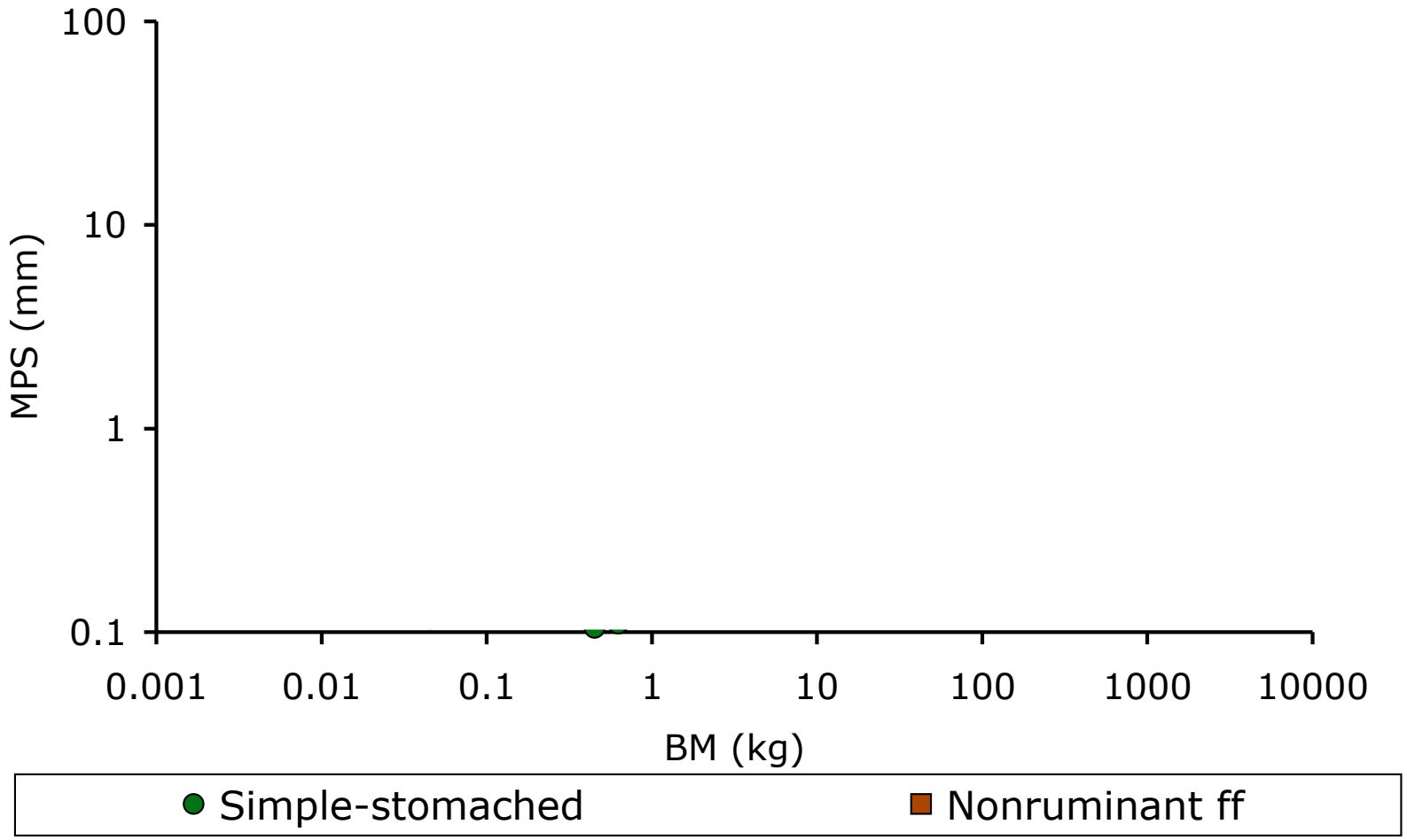
Artiodactyls

Equids

achieve
comparatively high
chewing efficiencies
and food intakes

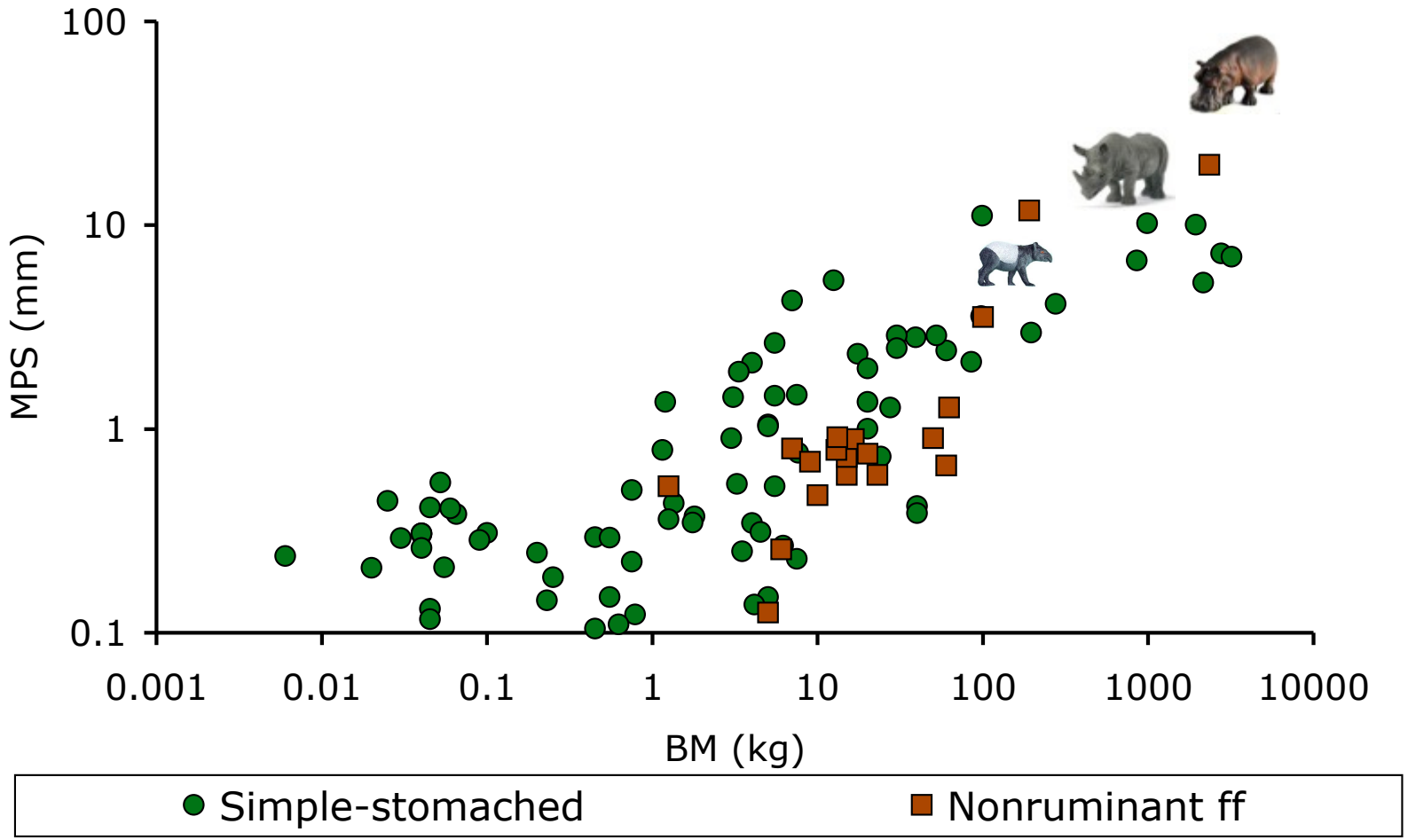
from Thenius (1989)

Mammalian chewing efficiency: faecal particle size



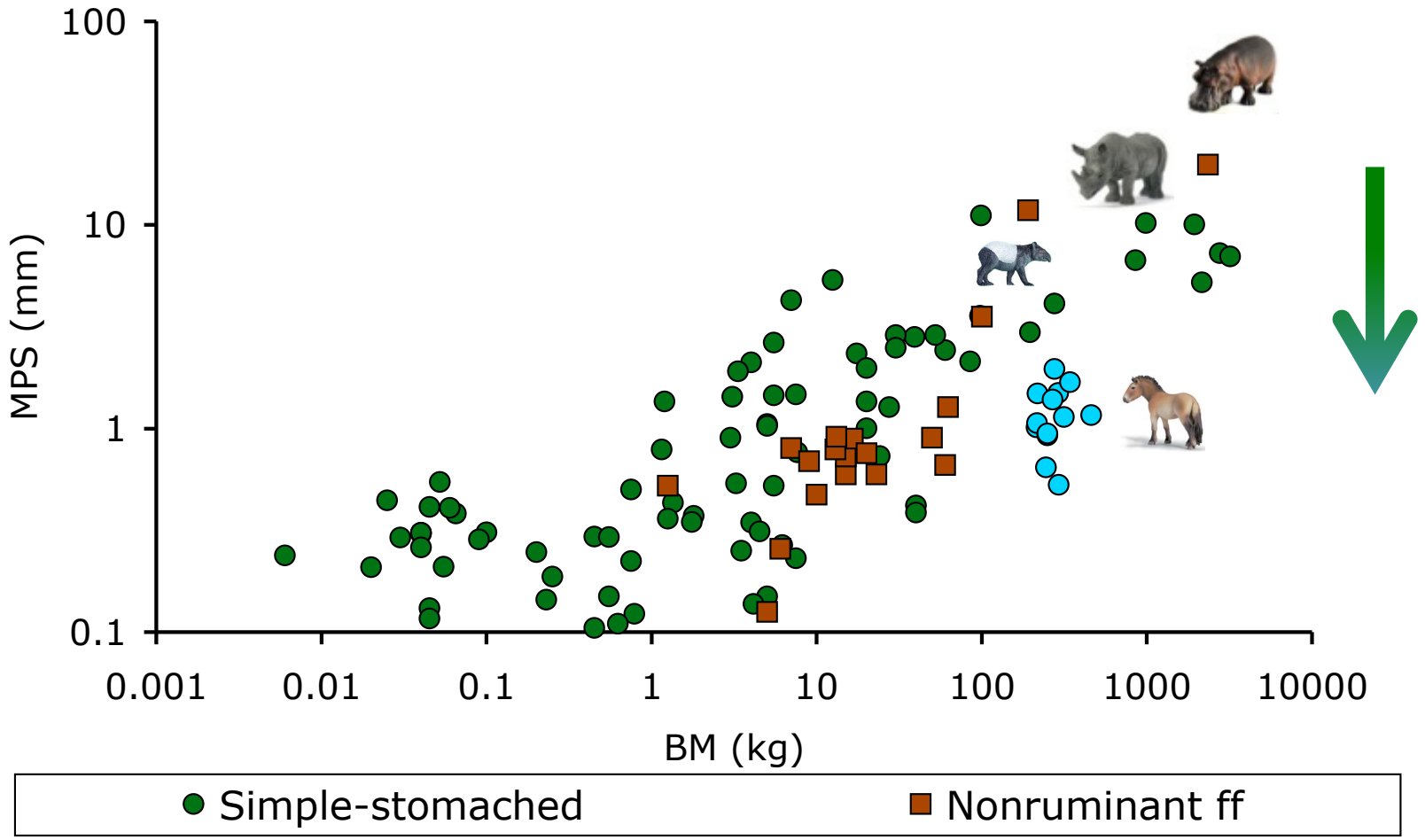
from Fritz et al. (2009)

Mammalian chewing efficiency: faecal particle size



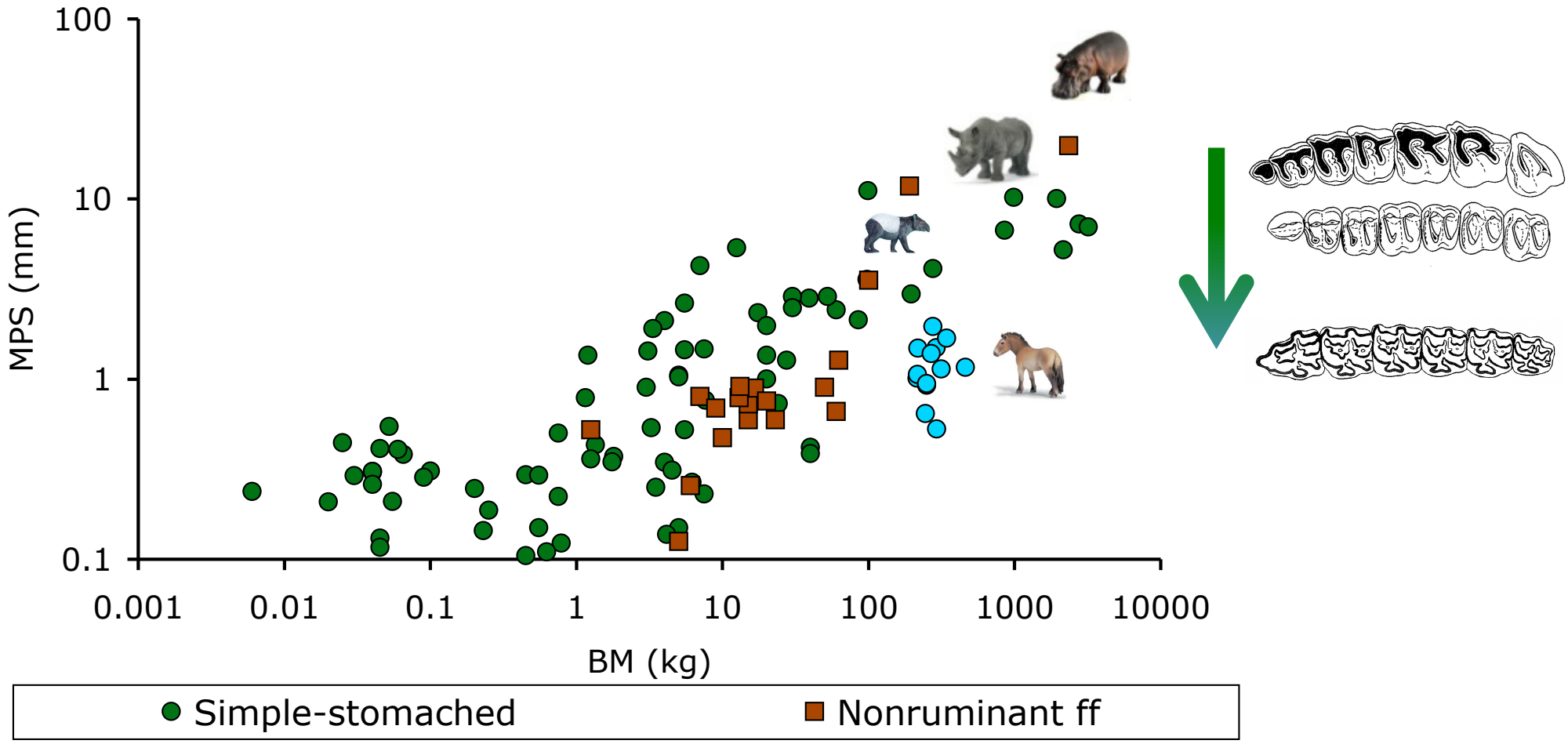
from Fritz et al. (2009)

Mammalian chewing efficiency: faecal particle size



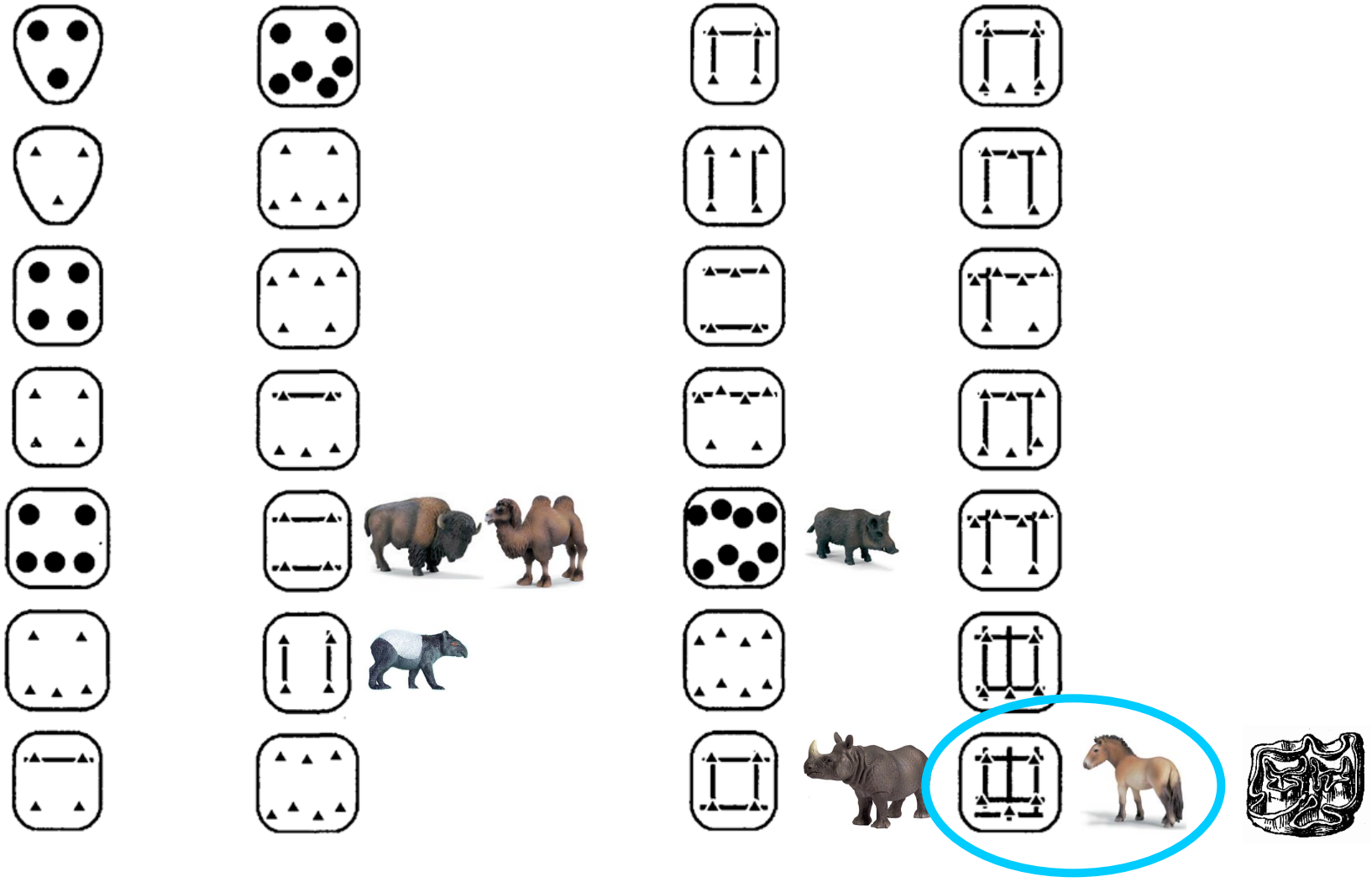
from Fritz et al. (2009)

Mammalian chewing efficiency: faecal particle size



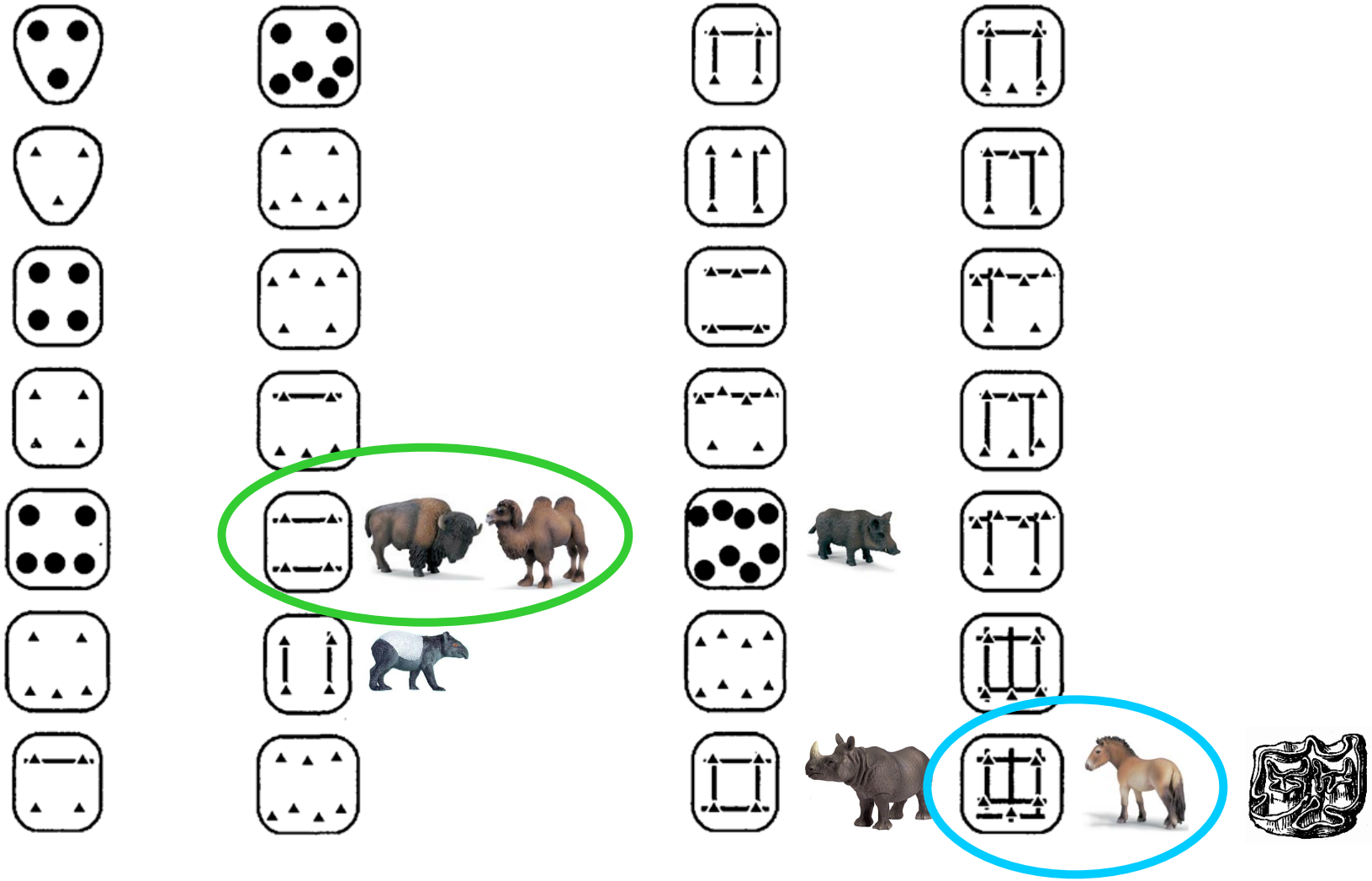
from Fritz et al. (2009)

Large mammal molar surfaces



from Jernvall et al. (1996)

Large mammal molar surfaces



from Jernvall et al. (1996)

Parallel evolution

Perissodactyls

among

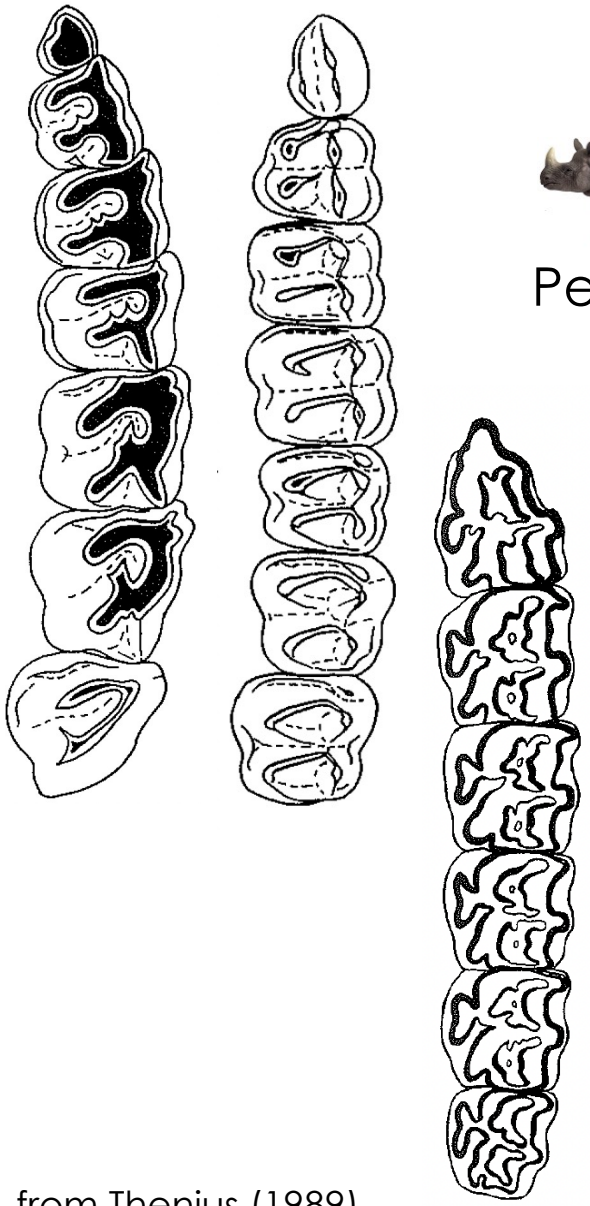
Artiodactyls

Equids

achieve
comparatively high
chewing efficiencies
and food intakes

from Thenius (1989)

Parallel evolution



from Thenius (1989)

Perissodactyls

among

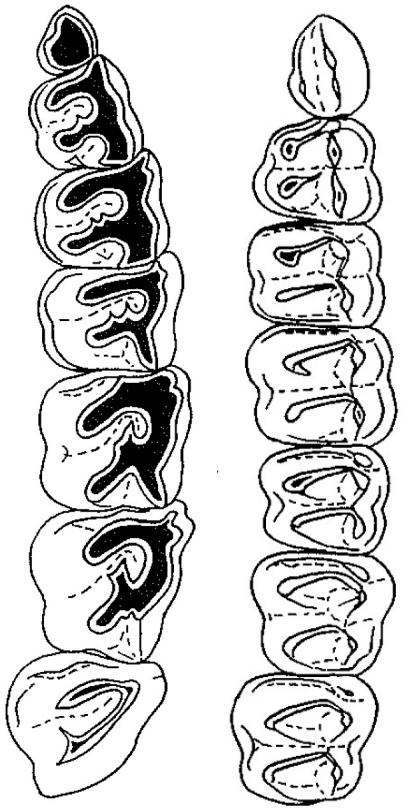
Artiodactyls

Equids

Ruminants

achieve
comparatively high
chewing efficiencies
and food intakes

Parallel evolution



Perissodactyls

among

Artiodactyls

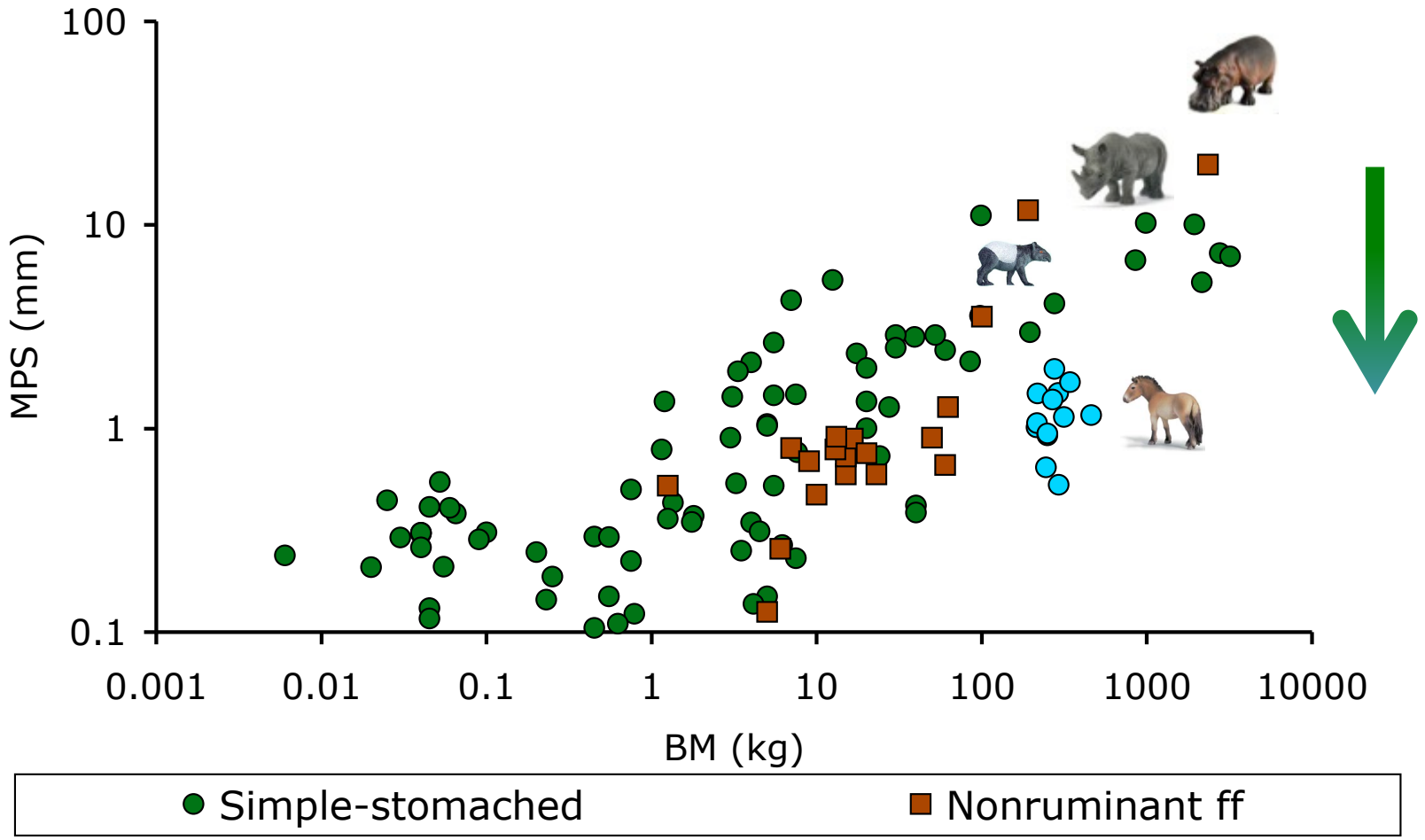
Equids

Ruminants

achieve
comparatively high
chewing efficiencies
and food intakes

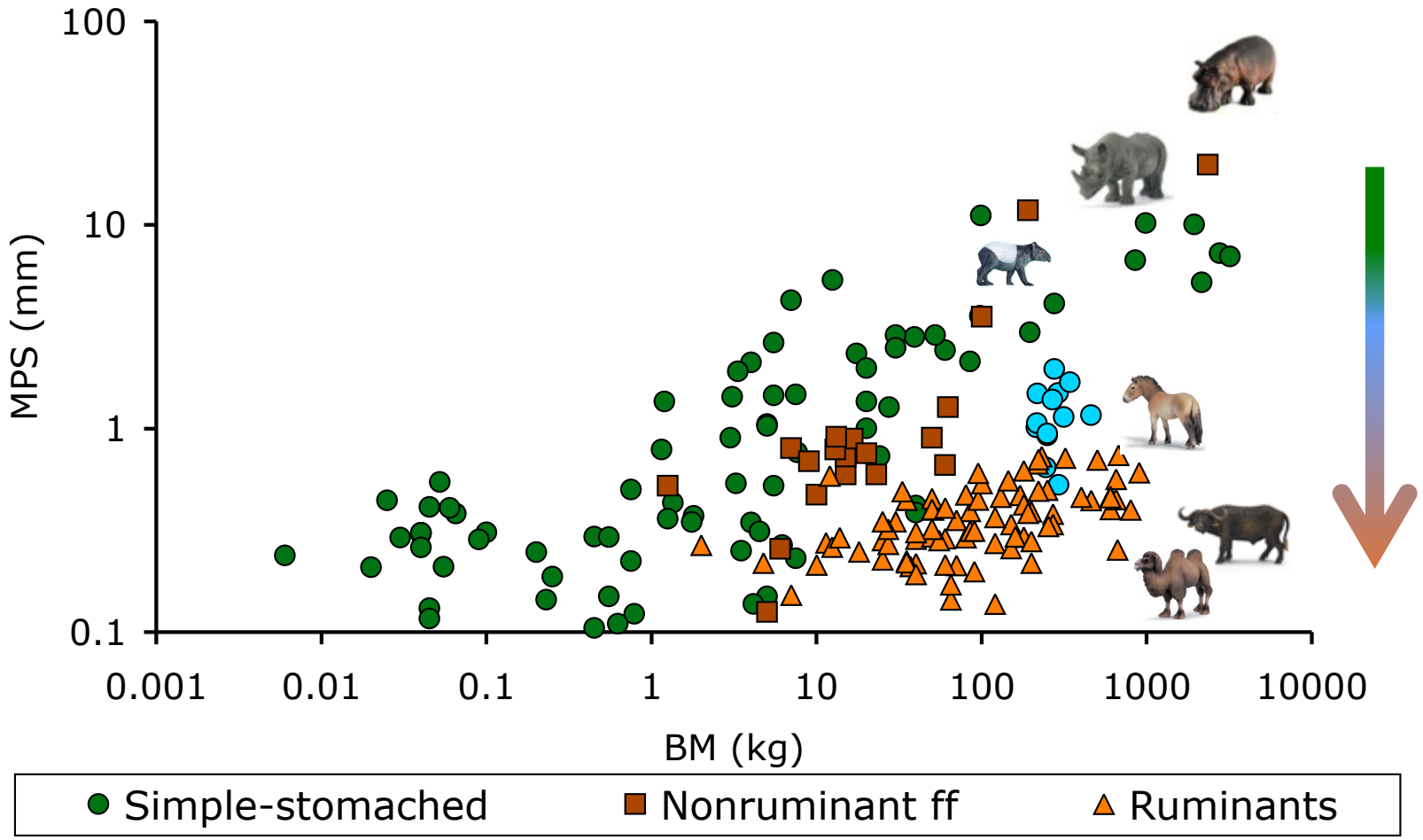
from Thenius (1989)

Mammalian chewing efficiency: faecal particle size



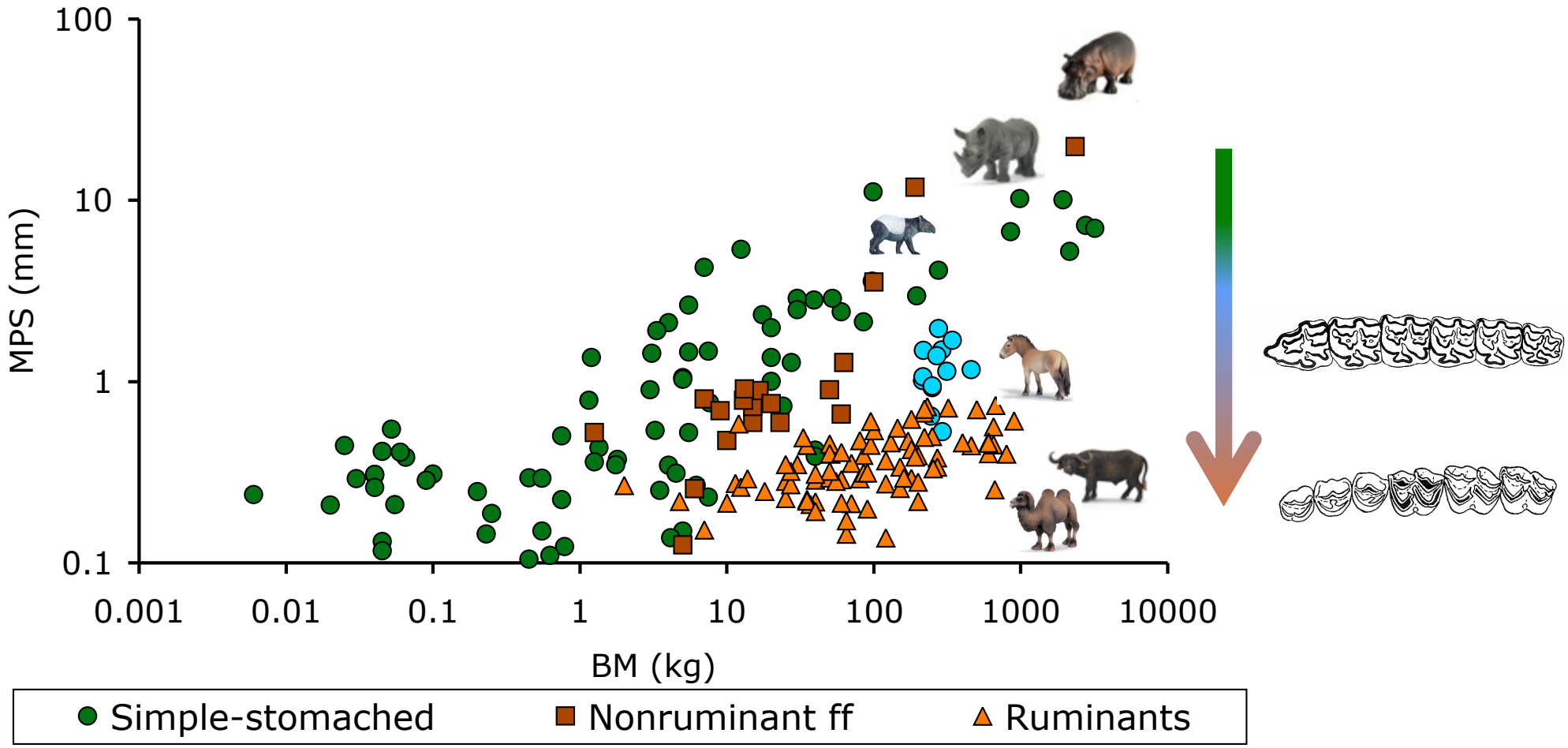
from Fritz et al. (2009)

Mammalian chewing efficiency: faecal particle size



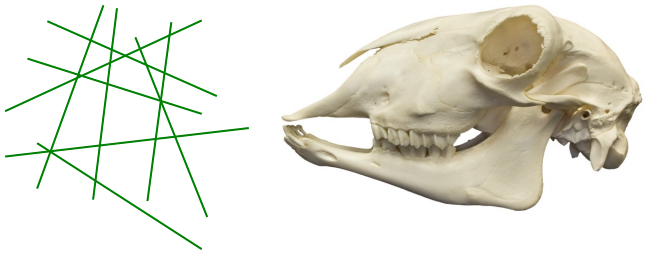
from Fritz et al. (2009)

Mammalian chewing efficiency: faecal particle size

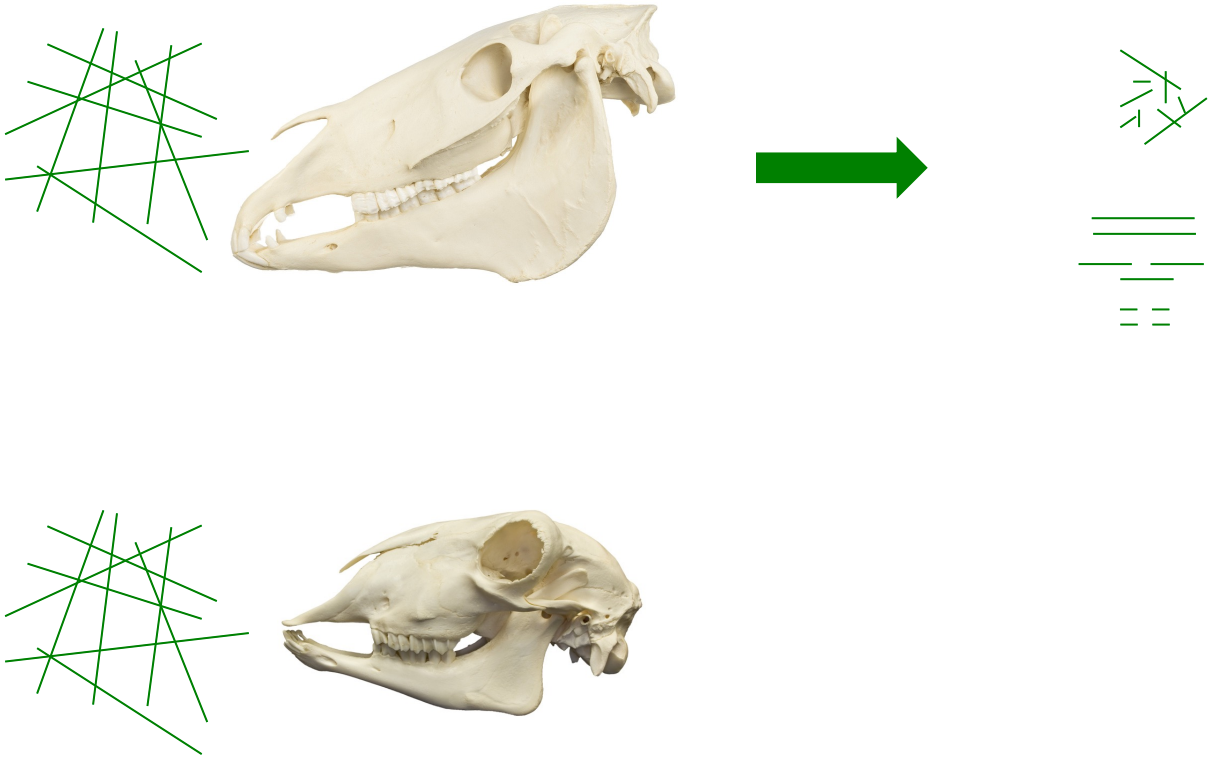


from Fritz et al. (2009)

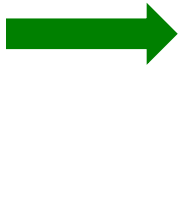
Sorting beats complicated teeth

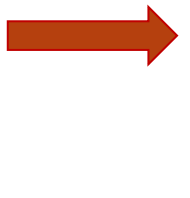


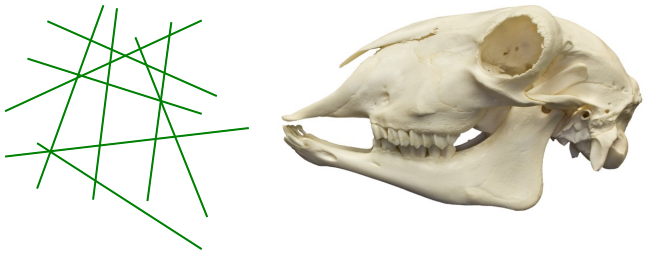
Sorting beats complicated teeth



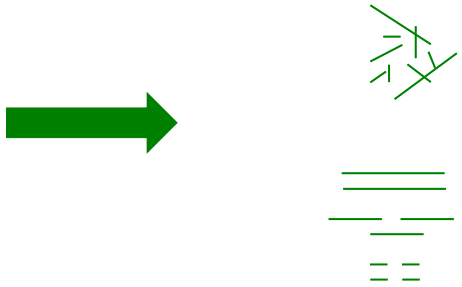
Sorting beats complicated teeth

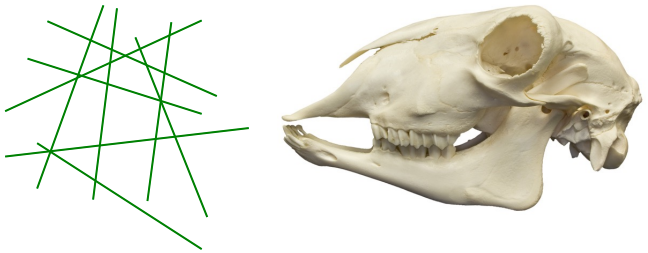




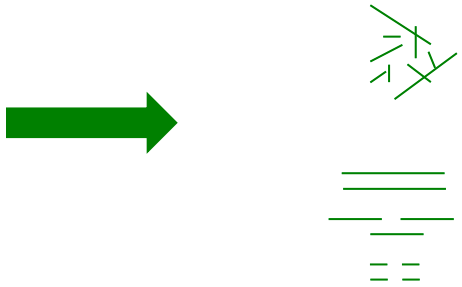


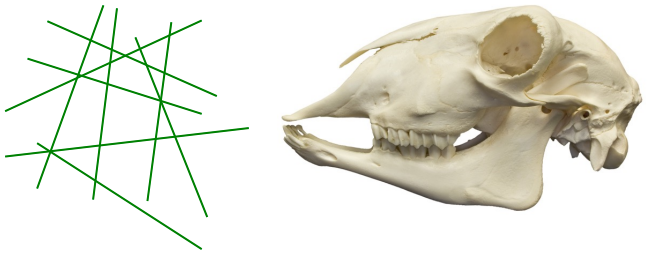
Sorting beats complicated teeth

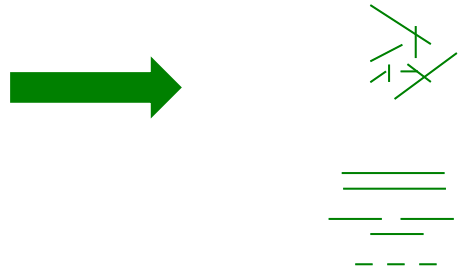




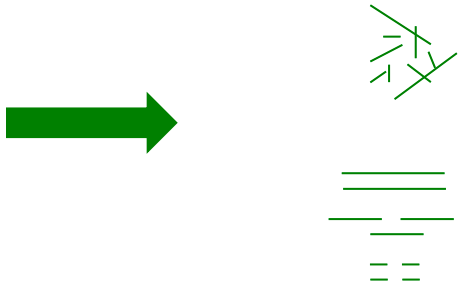
Sorting beats complicated teeth

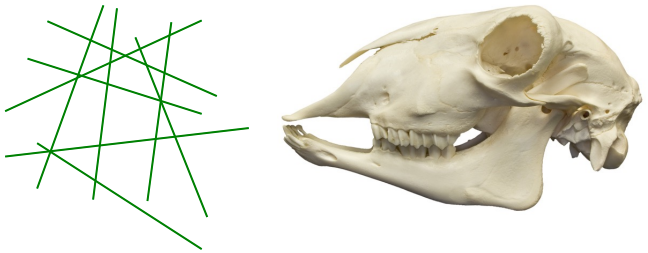


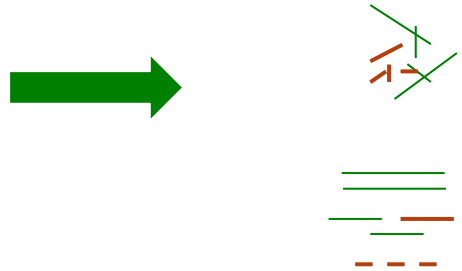




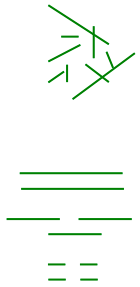
Sorting beats complicated teeth

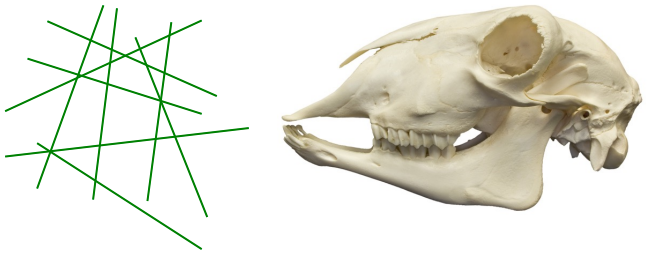


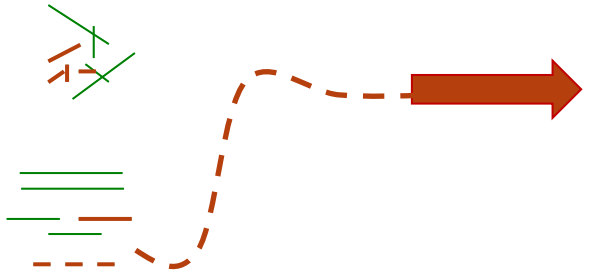




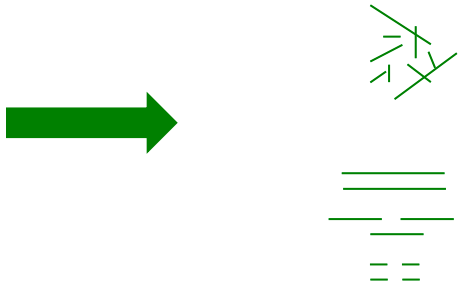
Sorting beats complicated teeth

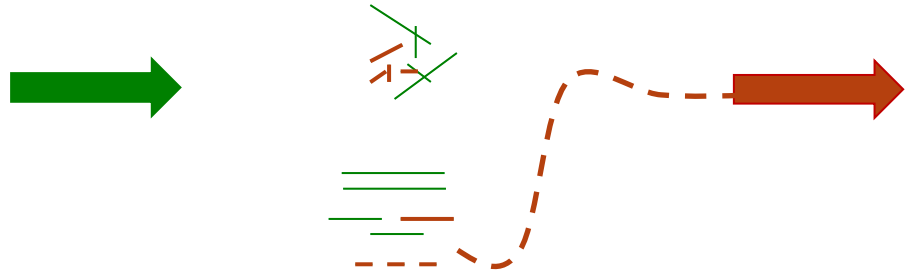




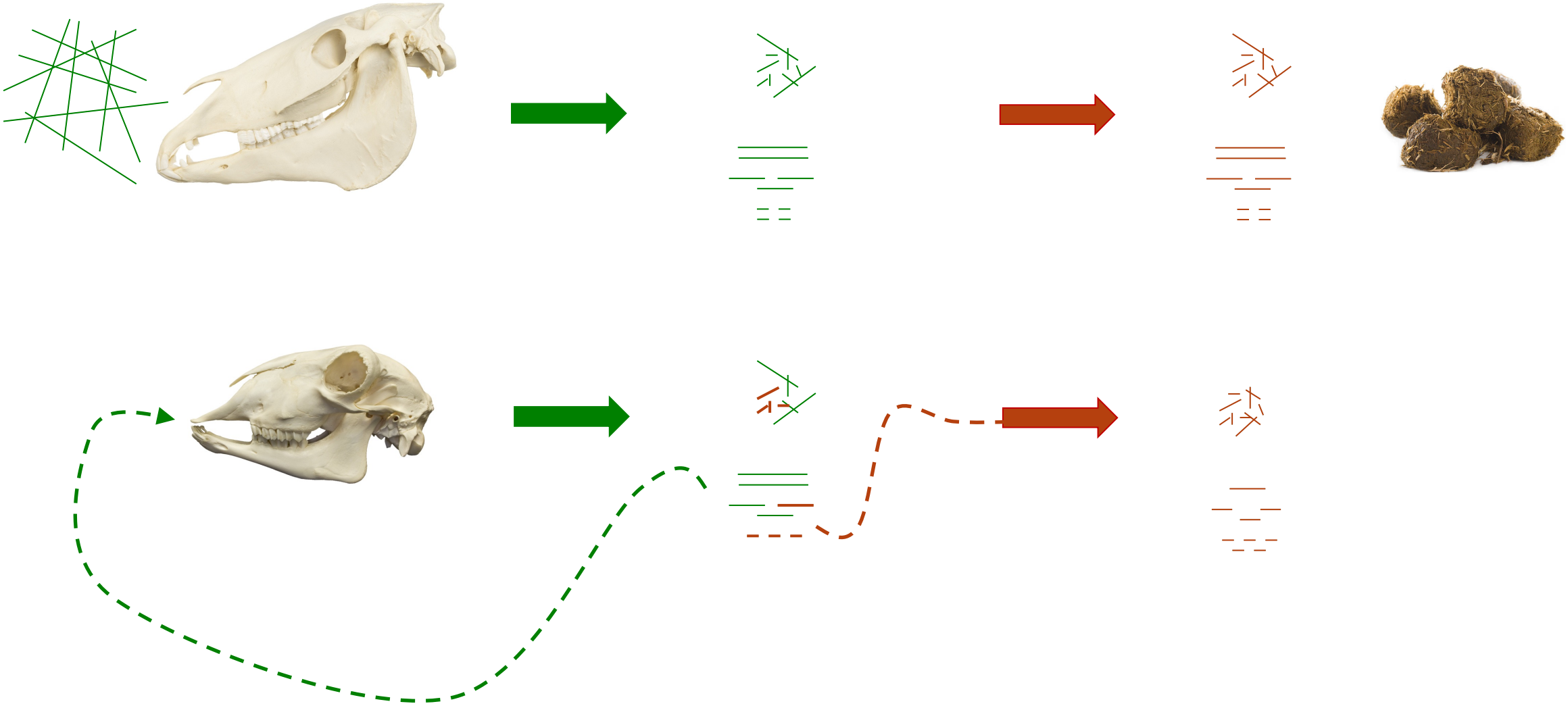


Sorting beats complicated teeth

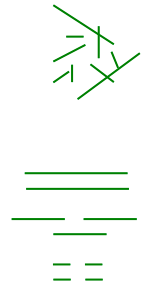


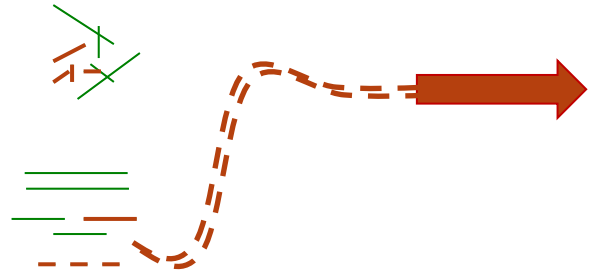


Sorting beats complicated teeth

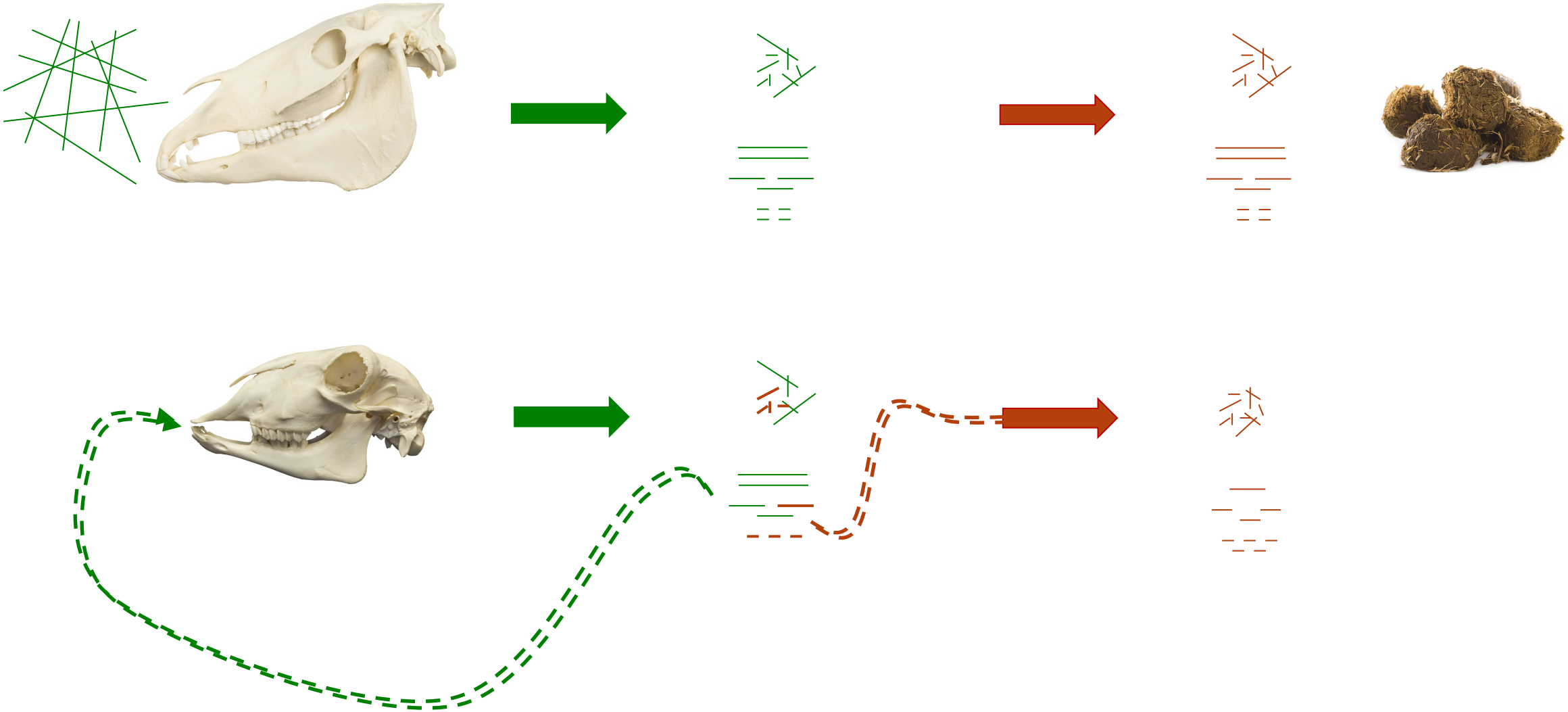


Sorting beats complicated teeth

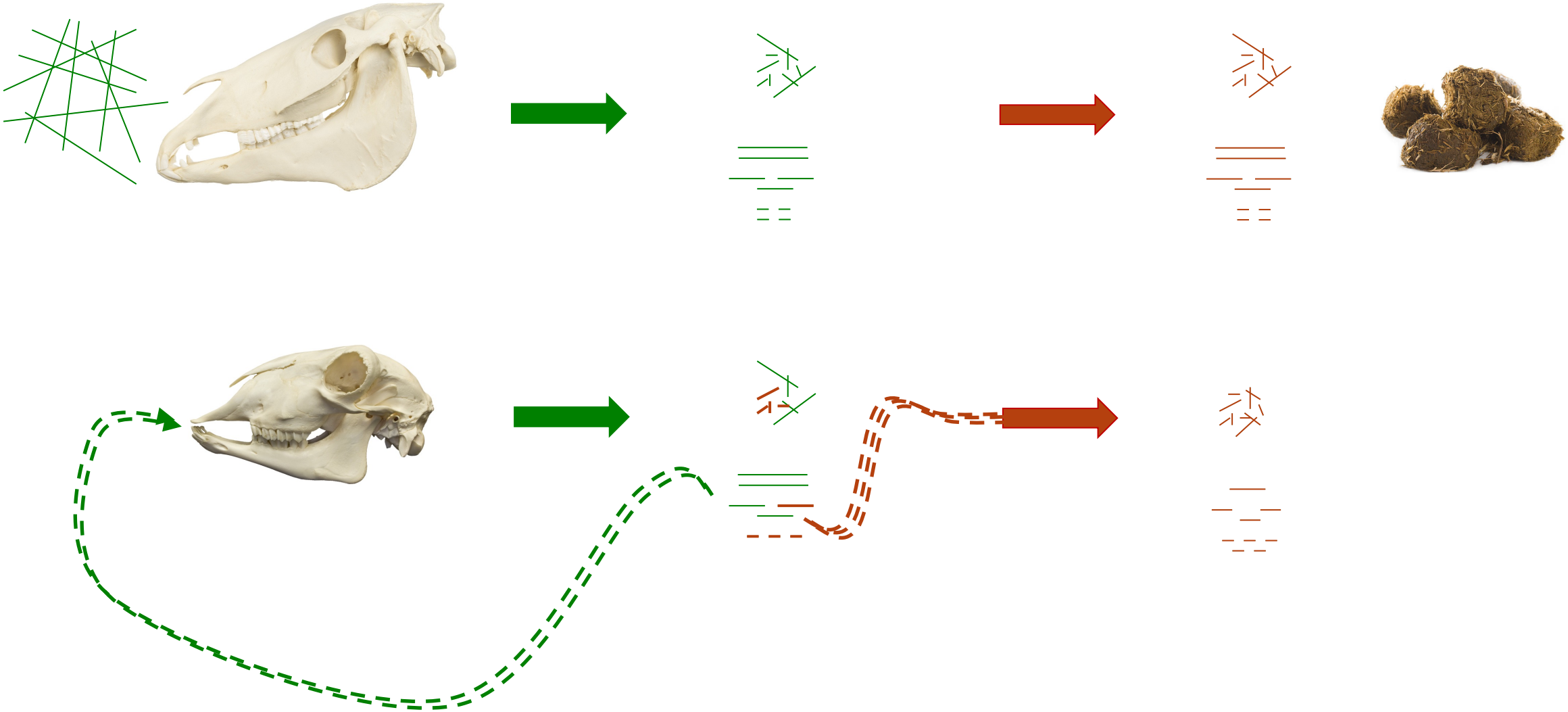




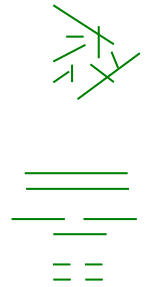
Sorting beats complicated teeth

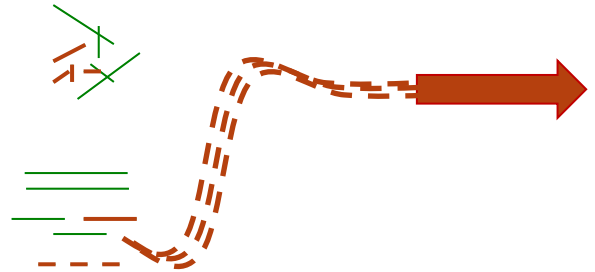


Sorting beats complicated teeth

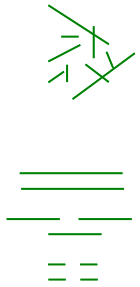


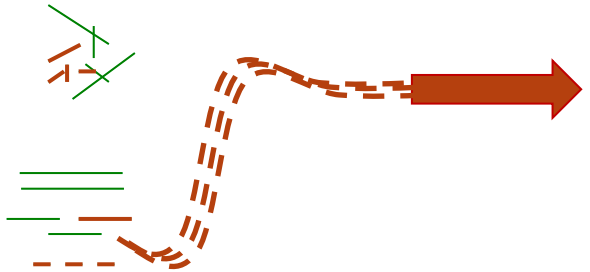
Sorting beats complicated teeth





Sorting beats complicated teeth

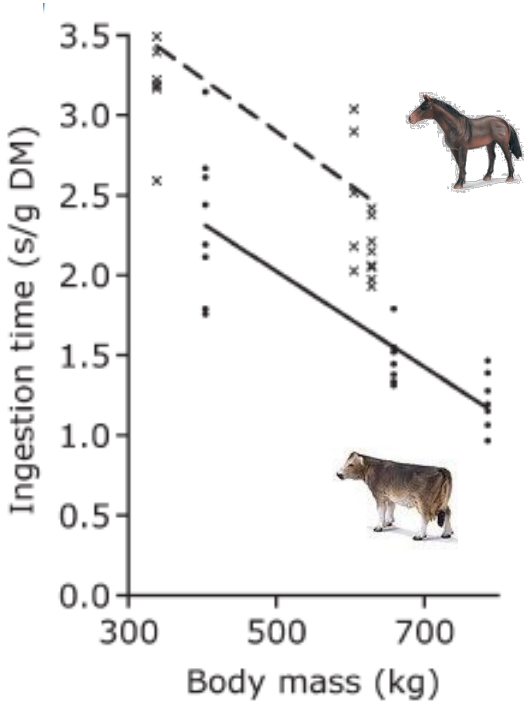


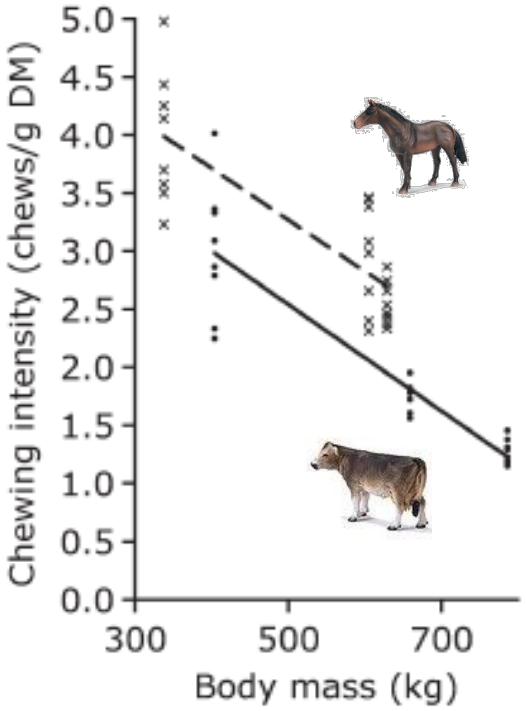


Comparative ingestive mastication in domestic horses and cattle: a pilot investigation

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

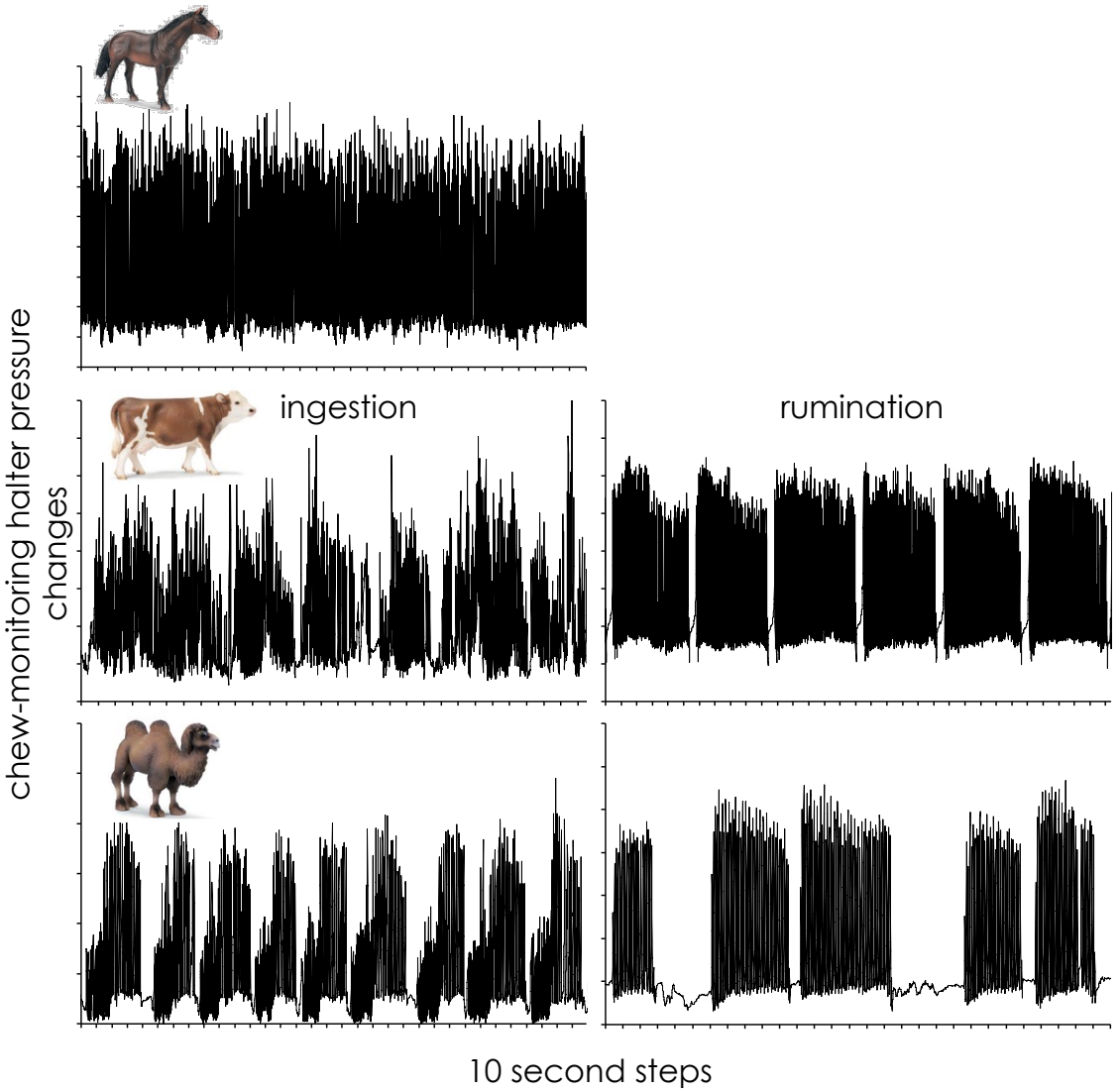




Ingestive mastication in horses resembles rumination but not ingestive mastication in cattle and camels

J. Exp. Zool. 2017;**327**:98–109.

Marie T. Dittmann[1,2,3] | Michael Kreuzer[2] | Ullrich Runge[4] | Marcus Clauss[3]



Parallel evolution

among

Perissodactyls

Artiodactyls

Equids

Ruminants

achieve
comparatively high
chewing efficiencies
and food intakes

Parallel evolution

among

Perissodactyls

Artiodactyls

Equids

Ruminants

achieve
comparatively high
chewing efficiencies
and food intakes

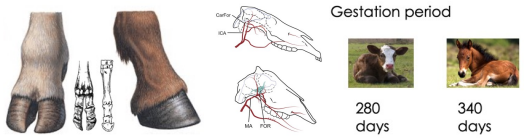
… but ruminants have evolved the more efficient system

Summary

Summary

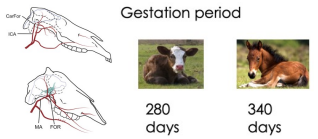
Summary

1. The evolutionary decline in equid diversity has been linked to ‘disadvantages’ compared to bovid/cervid ruminants

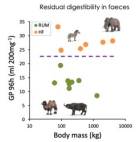


Summary

1. The evolutionary decline in equid diversity has been linked to ‘disadvantages’ compared to bovid/cervid ruminants

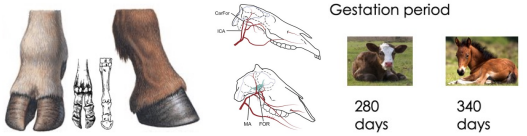


2. Digestive efficiency is prominent among these disadvantages

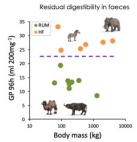


Summary

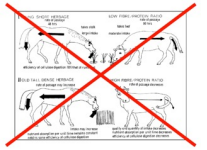
1. The evolutionary decline in equid diversity has been linked to ‘disadvantages’ compared to bovid/cervid ruminants

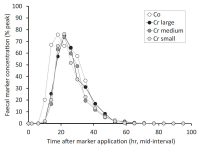


2. Digestive efficiency is prominent among these disadvantages



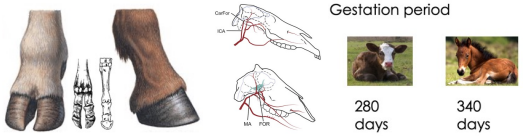
3. Equids do not have a proven tolerance for lower-quality forage and no size-discriminating retention mechanism



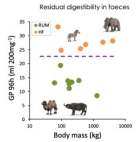


Summary

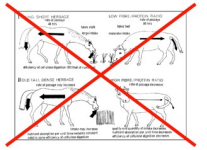
1. The evolutionary decline in equid diversity has been linked to ‘disadvantages’ compared to bovid/cervid ruminants

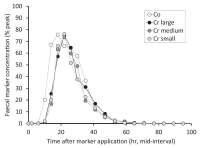


2. Digestive efficiency is prominent among these disadvantages

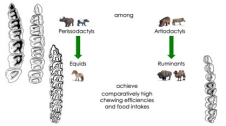


3. Equids do not have a proven tolerance for lower-quality forage and no size-discriminating retention mechanism



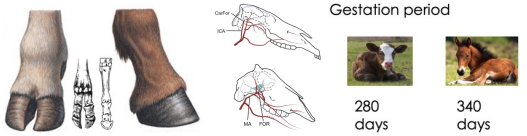


4. The most distinct feature of both equids and ruminants is the relatively high chewing efficiency within their respective orders

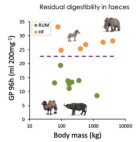


Summary

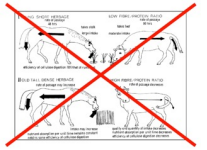
1. The evolutionary decline in equid diversity has been linked to ‘disadvantages’ compared to bovid/cervid ruminants

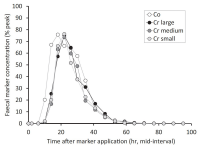


2. Digestive efficiency is prominent among these disadvantages

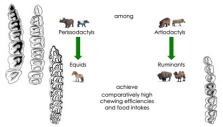


3. Equids do not have a proven tolerance for lower-quality forage and no size-discriminating retention mechanism

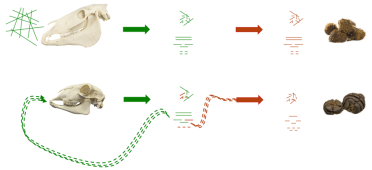


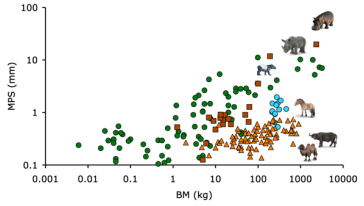


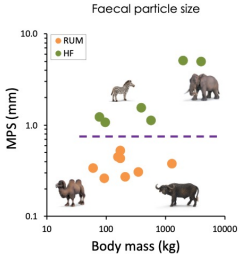
4. The most distinct feature of both equids and ruminants is the relatively high chewing efficiency within their respective orders

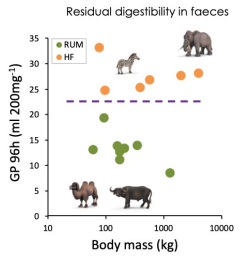


5. The ruminant approach to achieving a high chewing efficiency is more efficient (and conveys additional advantages)

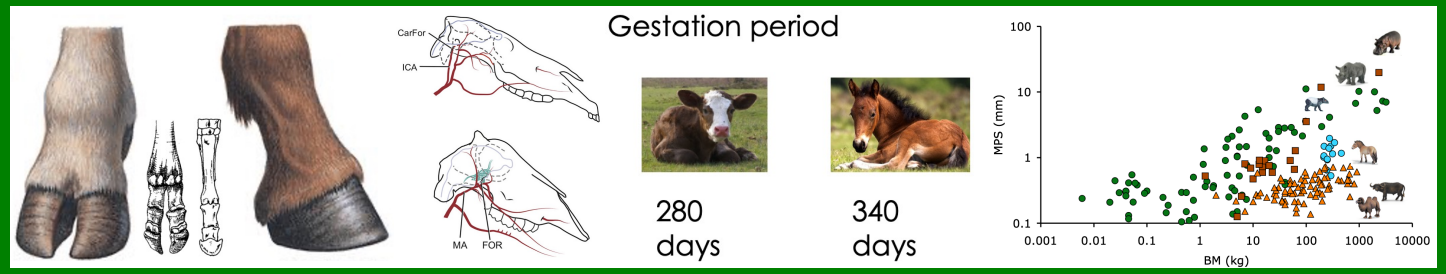


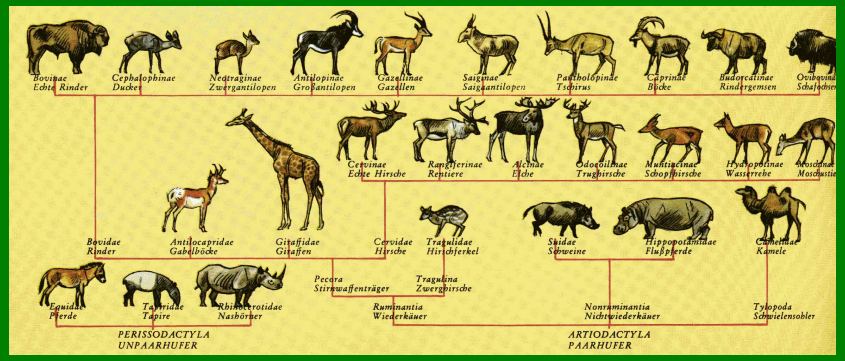




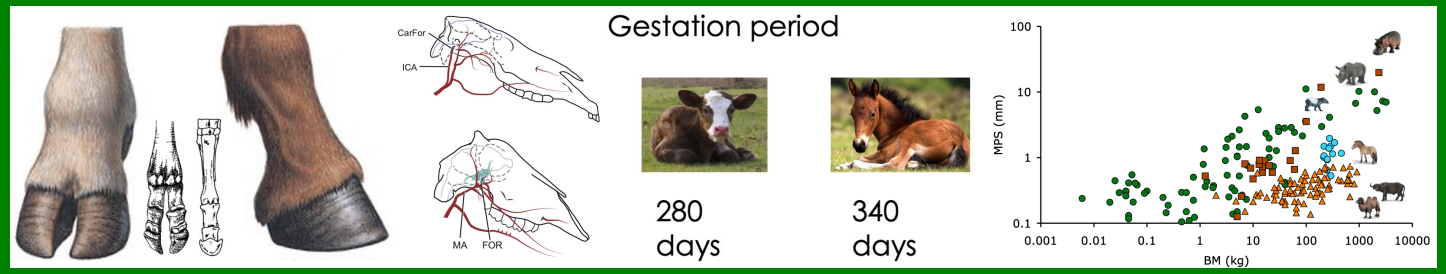


… so maybe the most intriguing question is not "why have equids largely disappeared?"

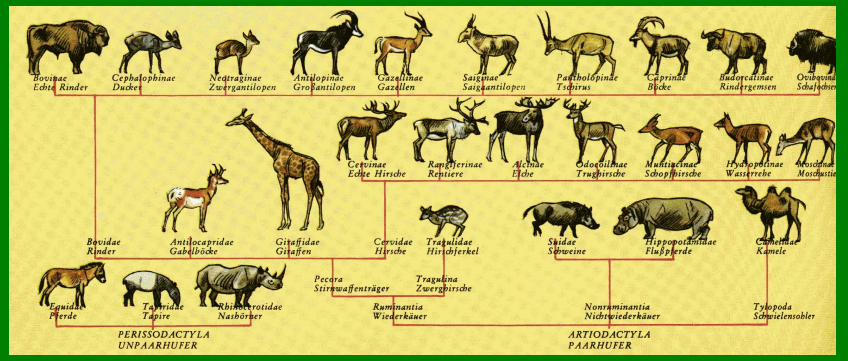




… so maybe the most intriguing question is not "why have equids largely disappeared?"



… but "why have some equid species survived?"

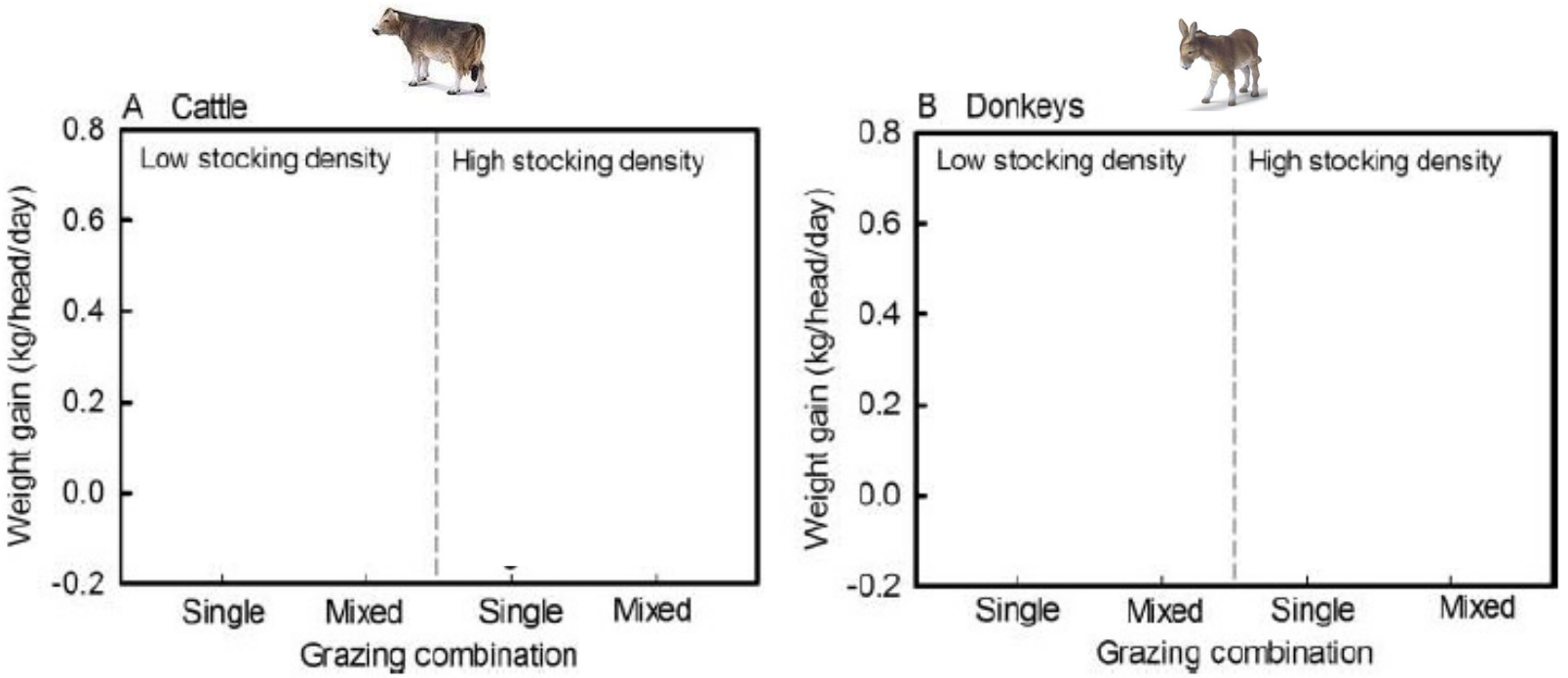


Ruminant – Equid – Facilitation?

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

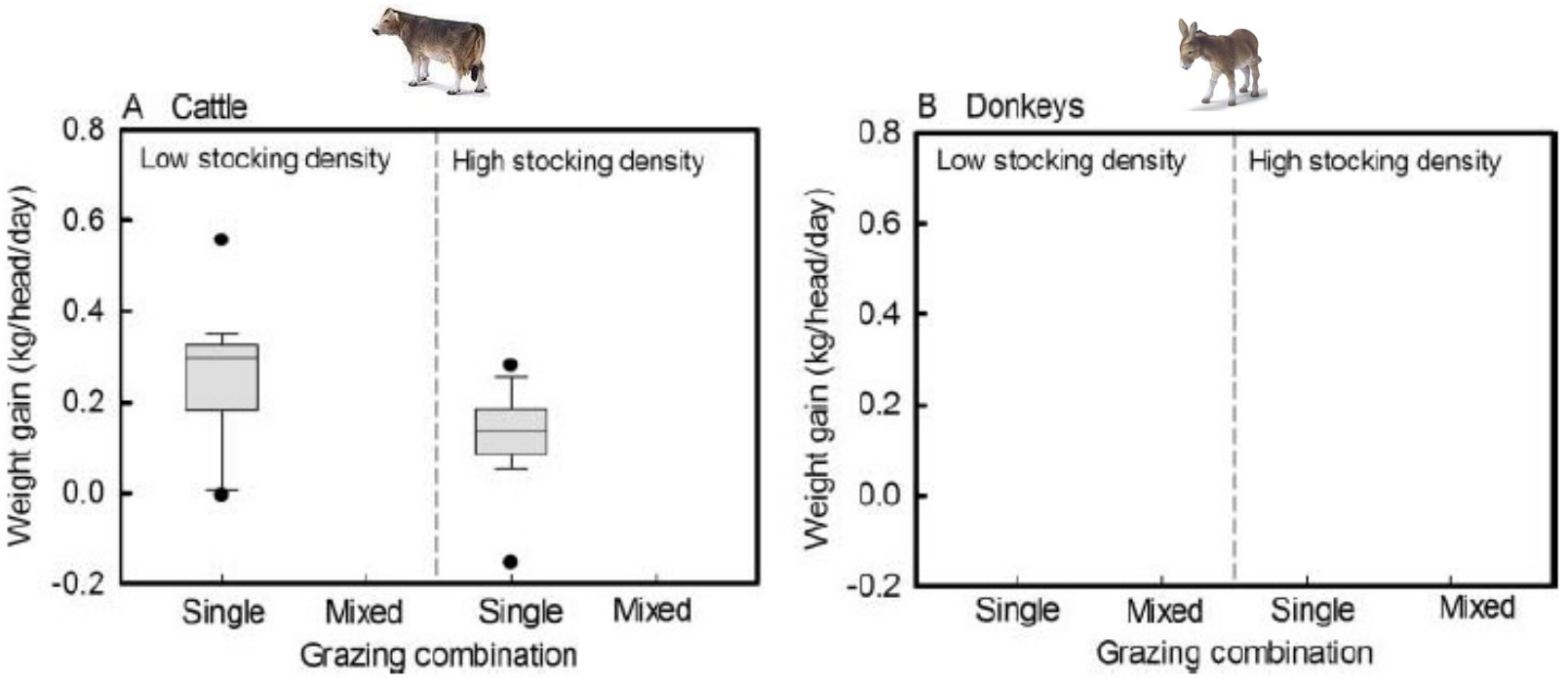


Ruminant – Equid – Facilitation?

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

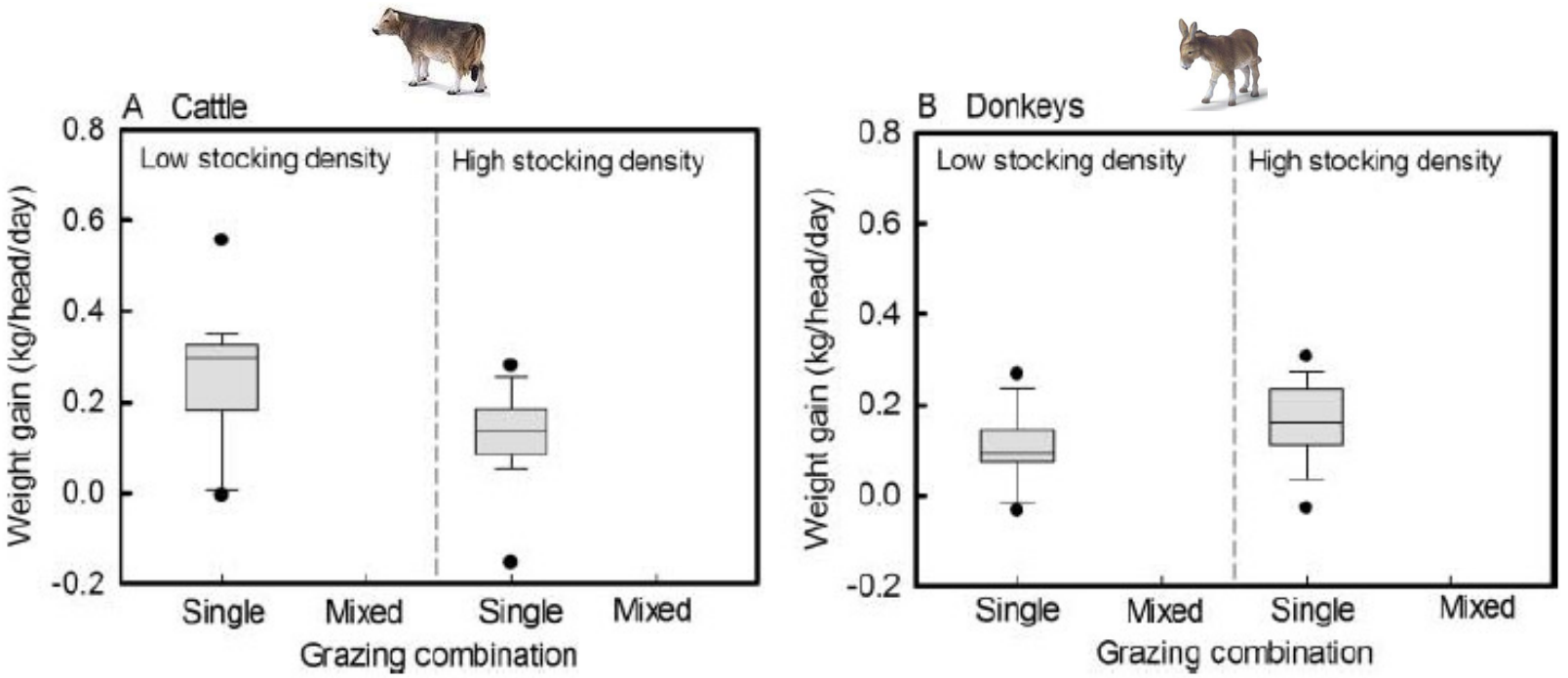


Ruminant – Equid – Facilitation?

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

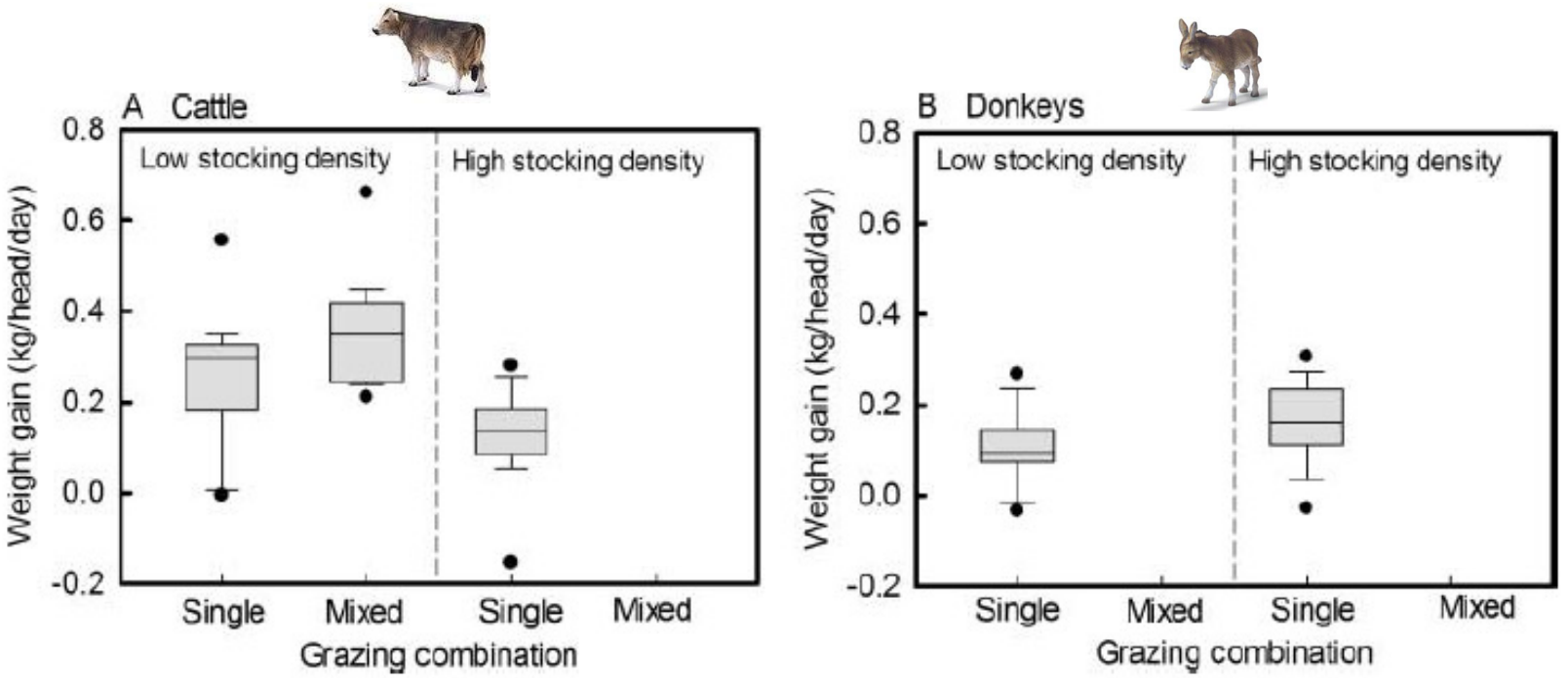


Ruminant – Equid – Facilitation?

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

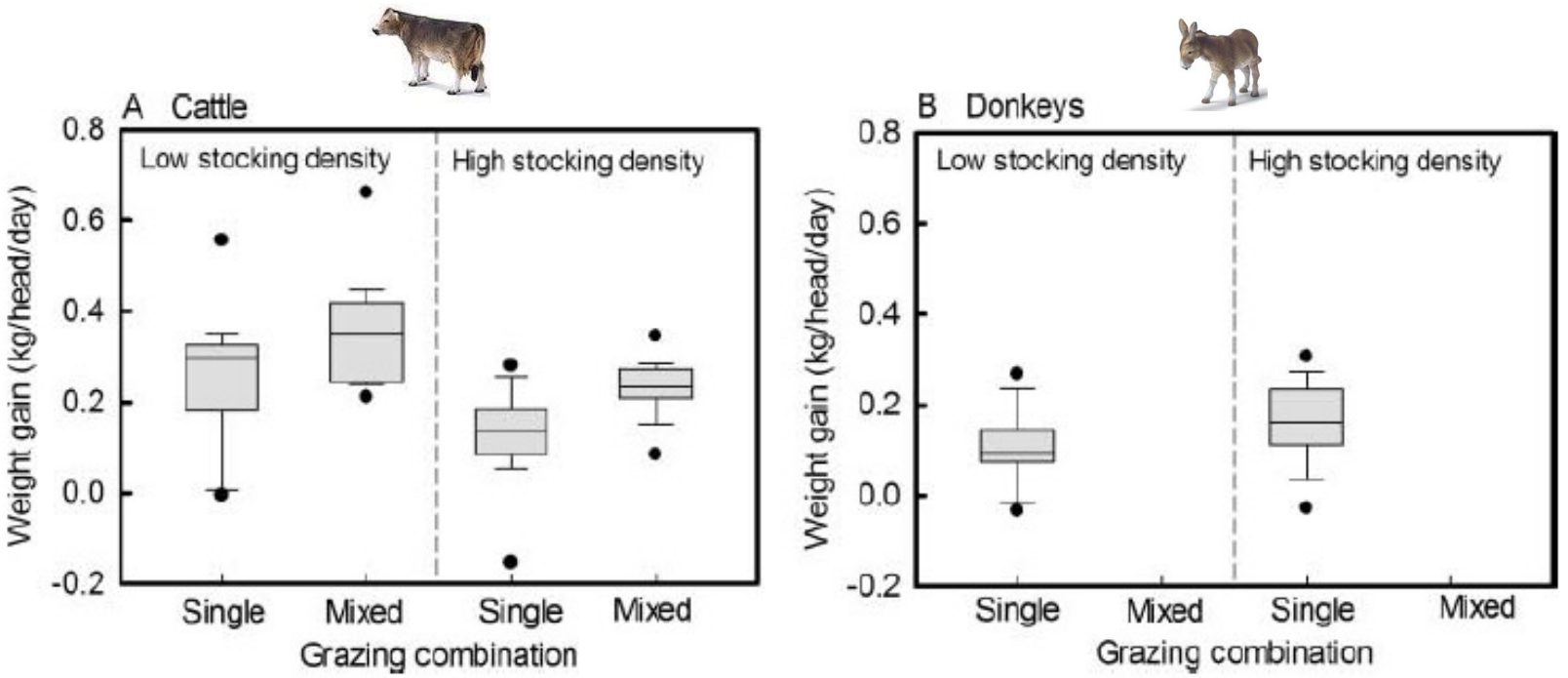


Ruminant – Equid – Facilitation?

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

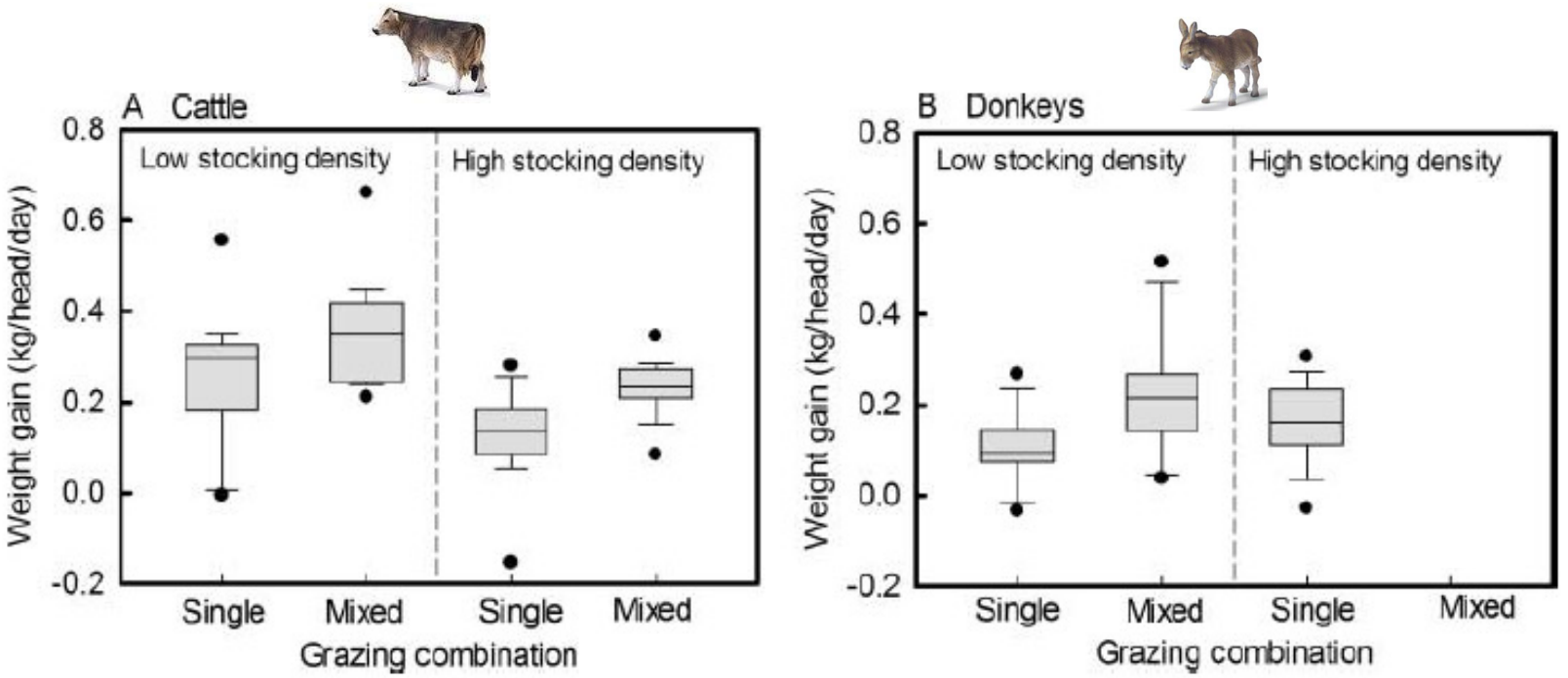


Ruminant – Equid – Facilitation?

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

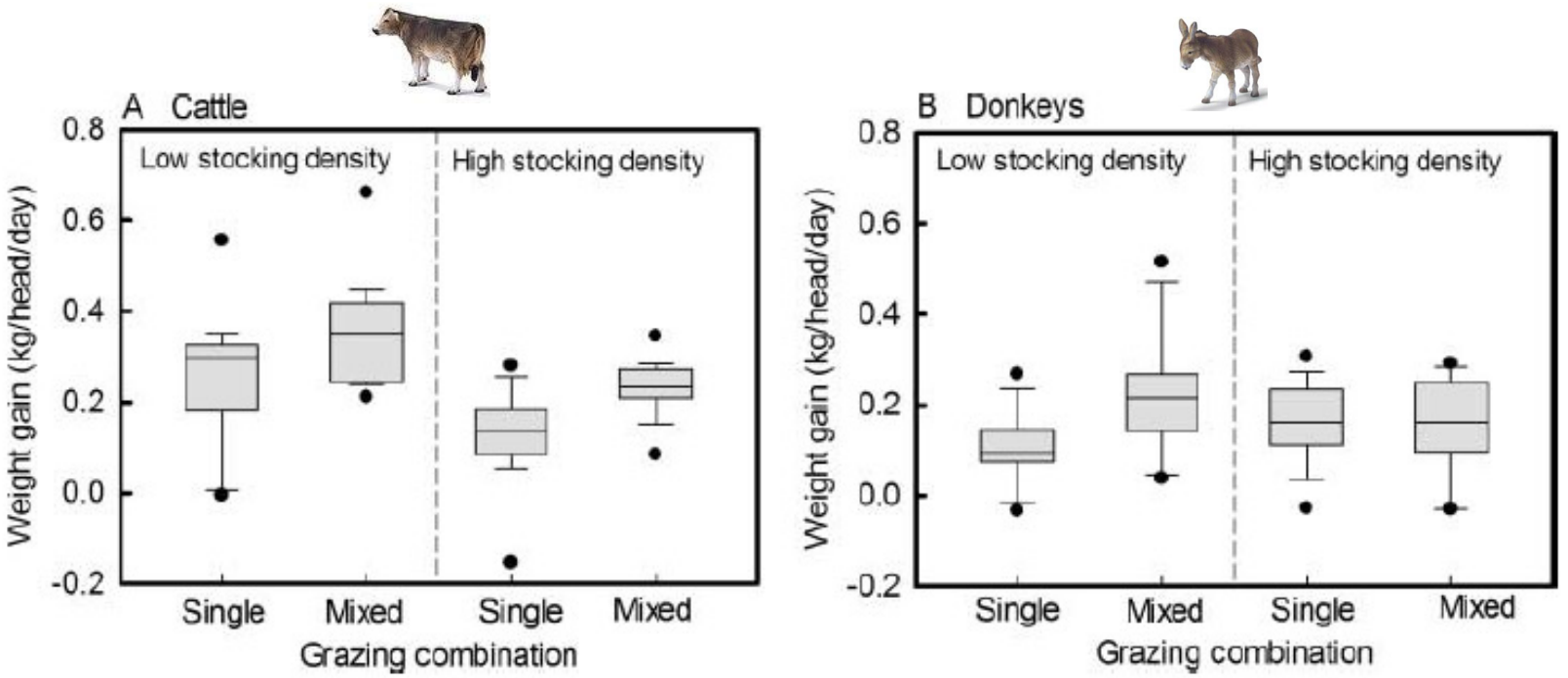


Ruminant – Equid – Facilitation?

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

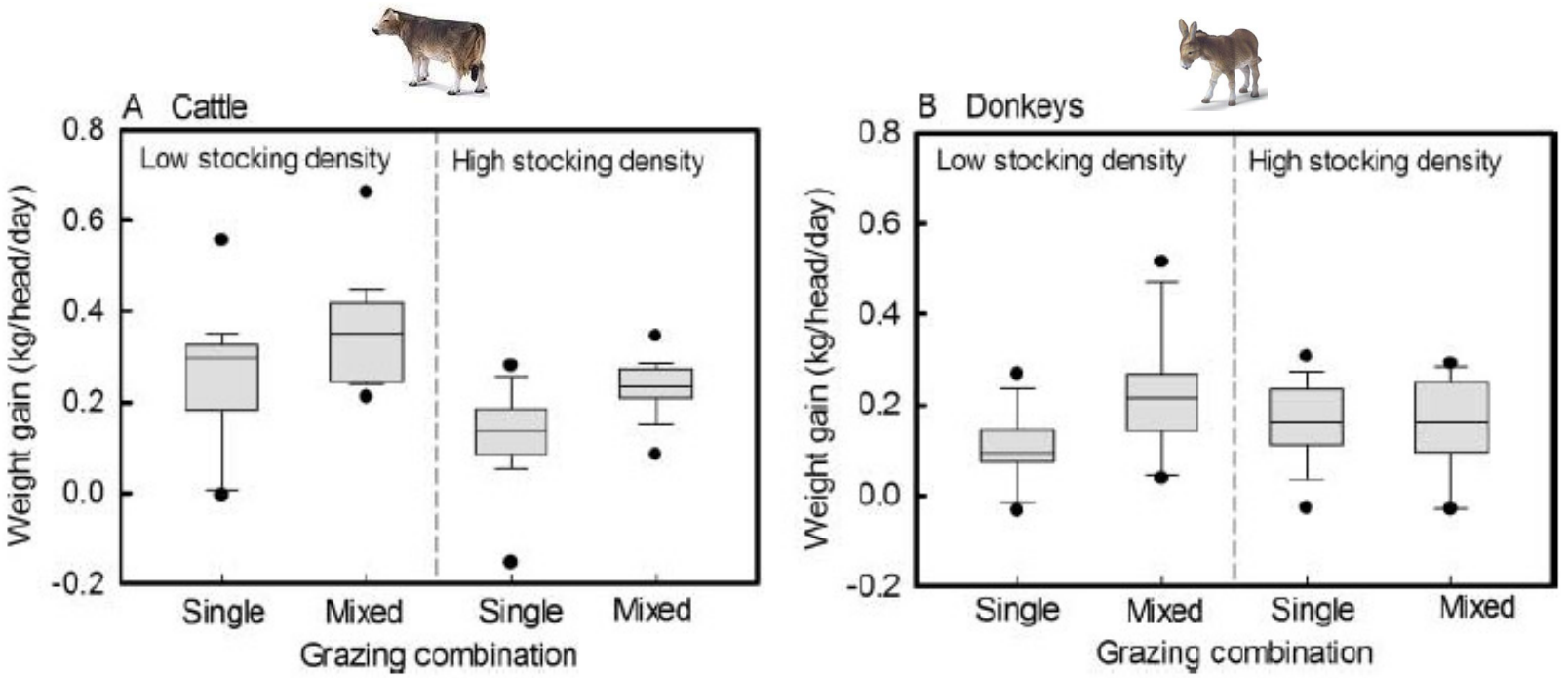


Ruminant – Equid – Facilitation?

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

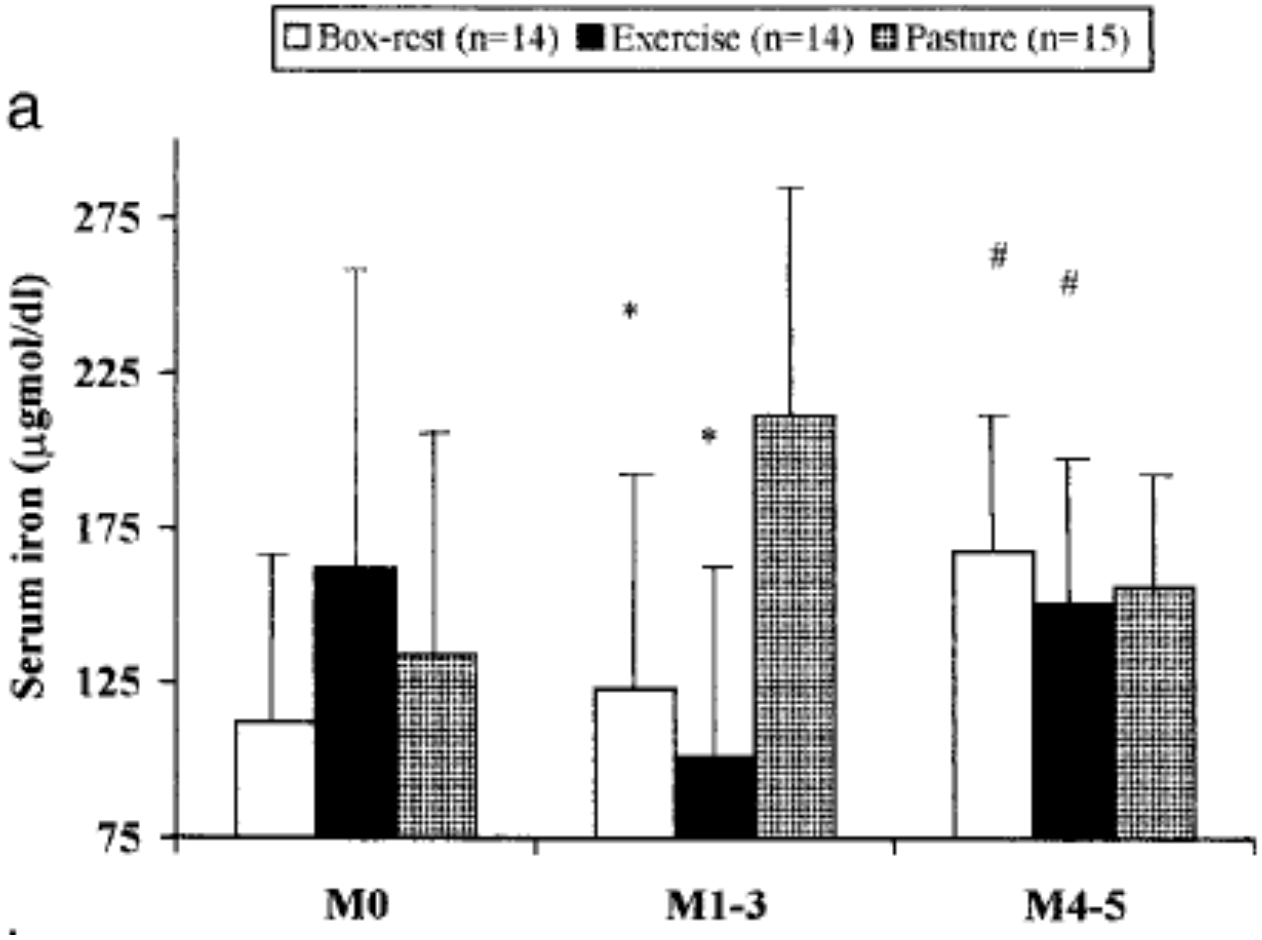


thank you
for your attention

Iron Deficiency in Stabled Dutch Warmblood Foals

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

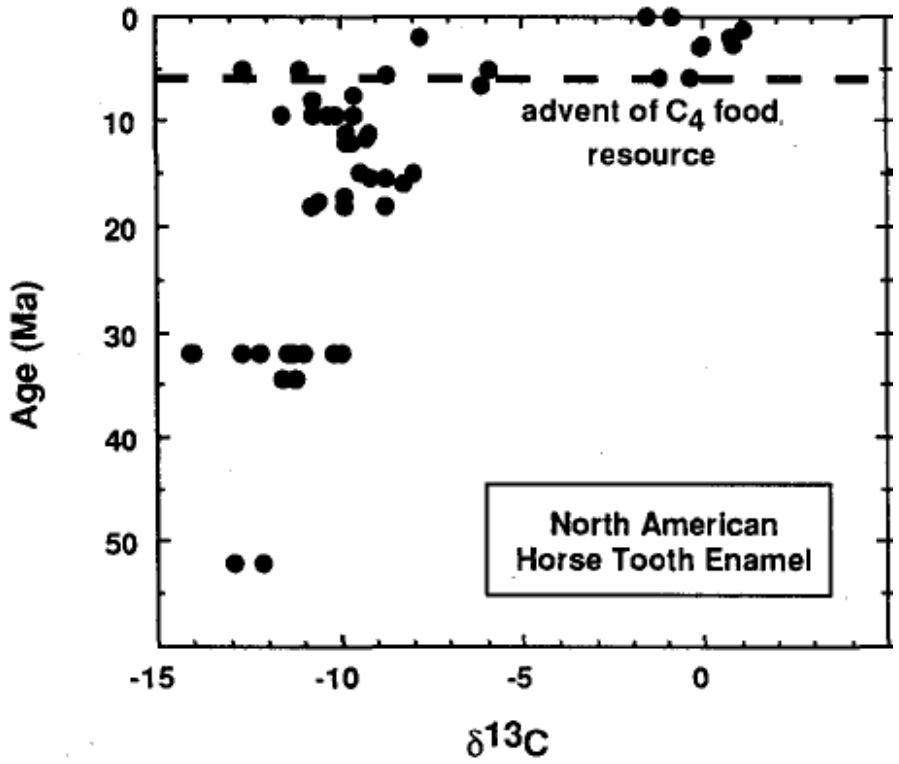
J Vet Intern Med 2001;15:482–485



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

Yang Wang[a], Thure E. Cerling[a] and Bruce J. MacFadden[b]

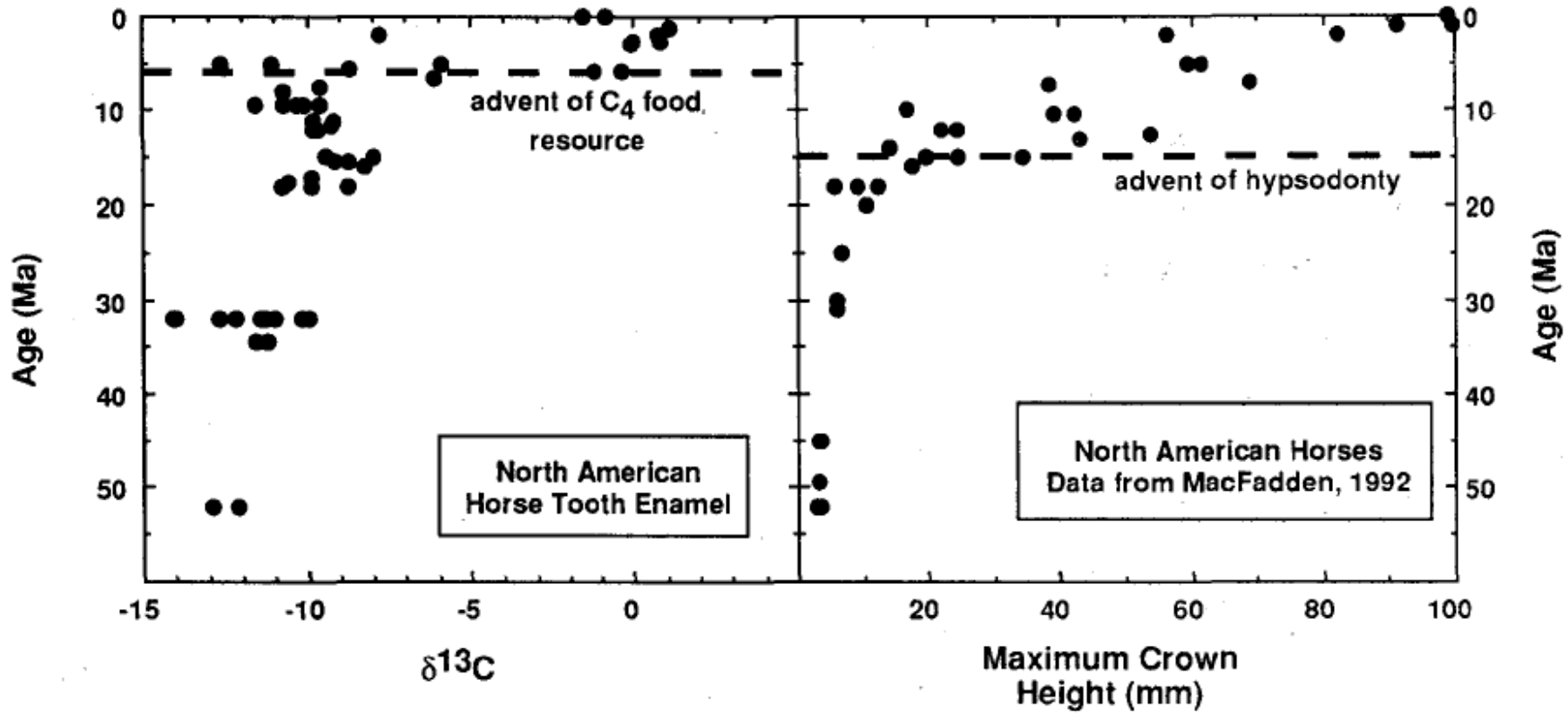
Palaeogeography, Palaeoclimatology, Palaeoecology, 107 (1994): 269–279



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

Yang Wang[a], Thure E. Cerling[a] and Bruce J. MacFadden[b]

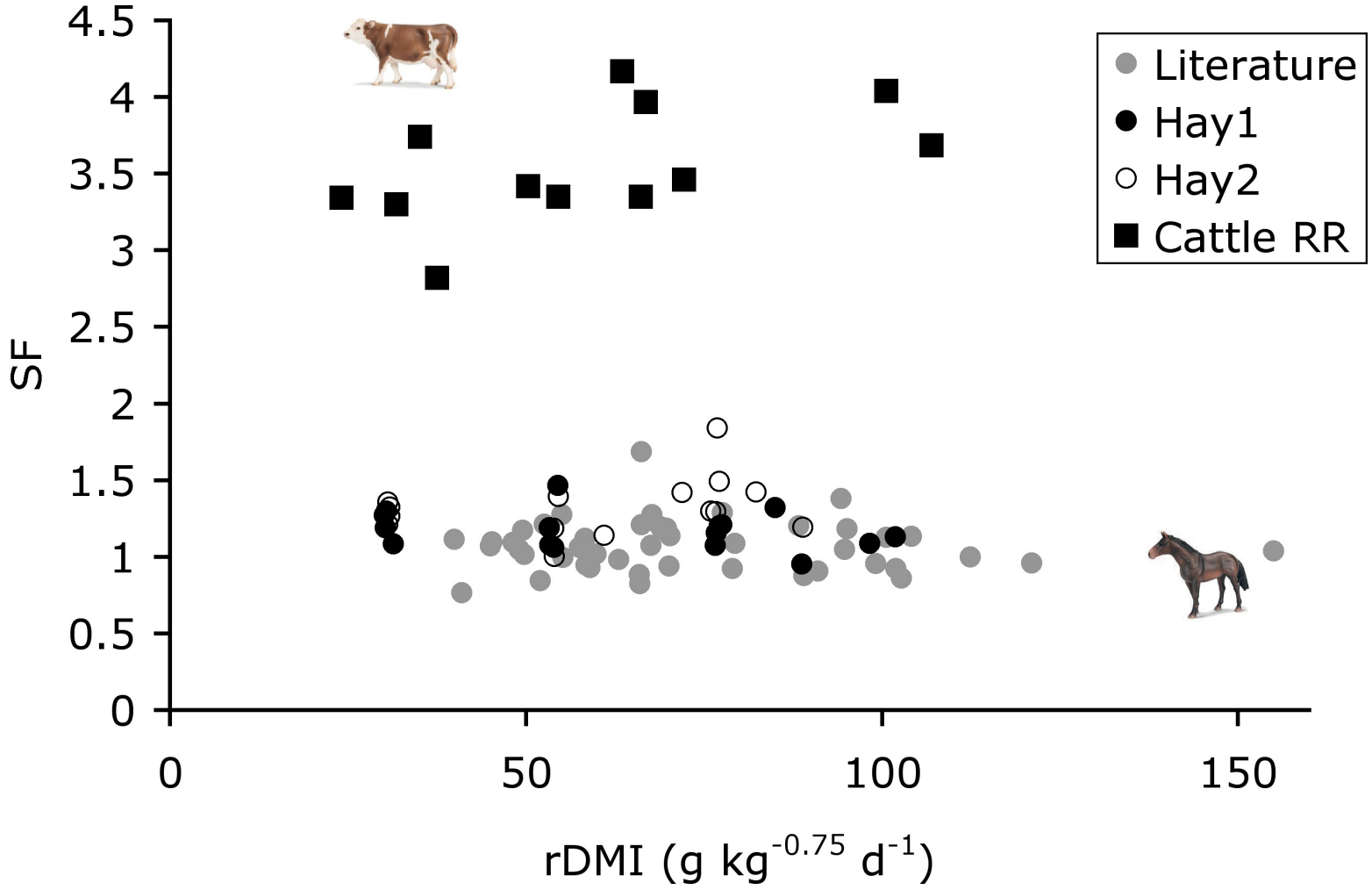
Palaeogeography, Palaeoclimatology, Palaeoecology, 107 (1994): 269–279

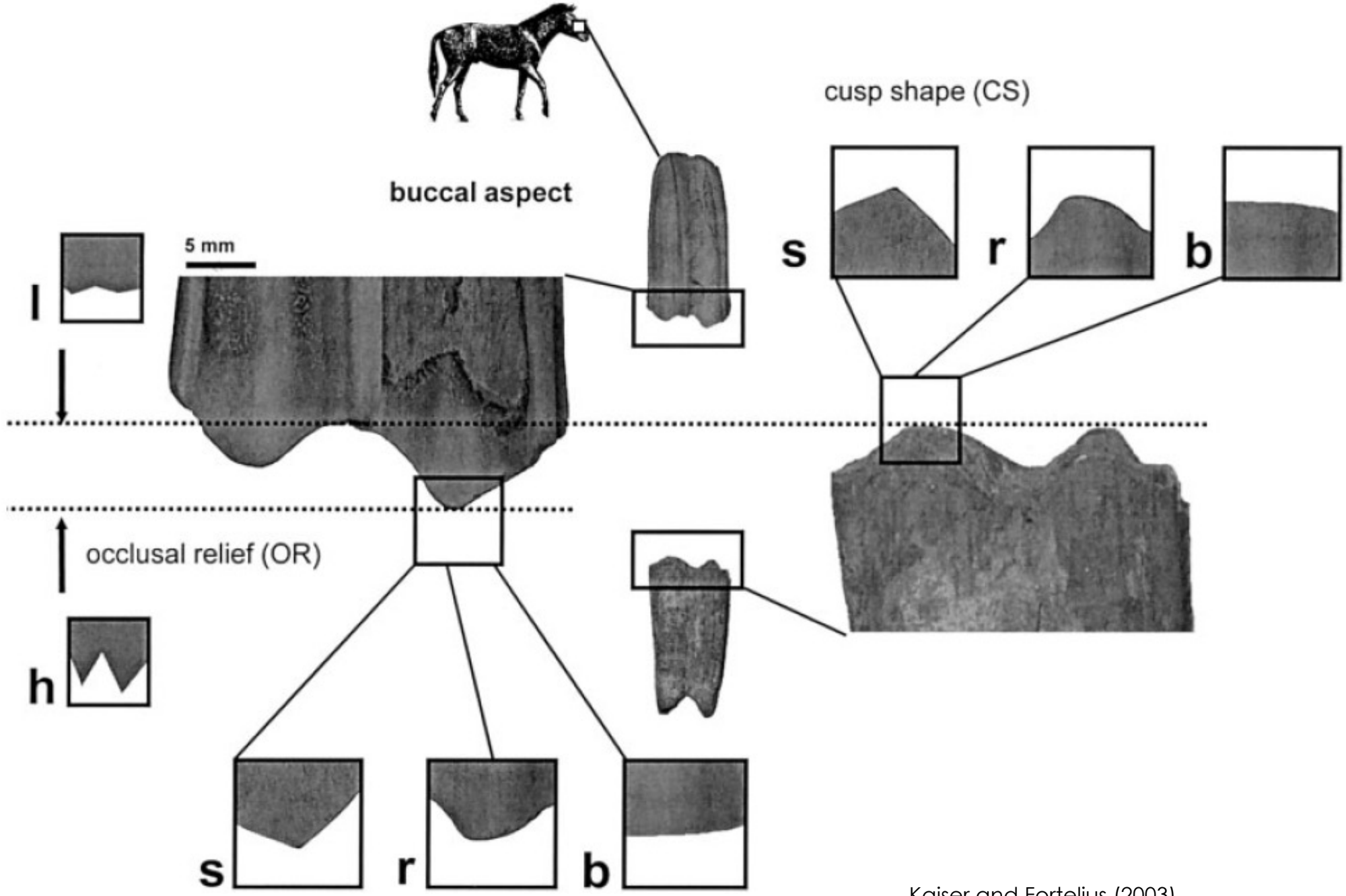


The effect of very low food intake on digestive physiology and forage digestibility in horses

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 **98** (2014) 107–118



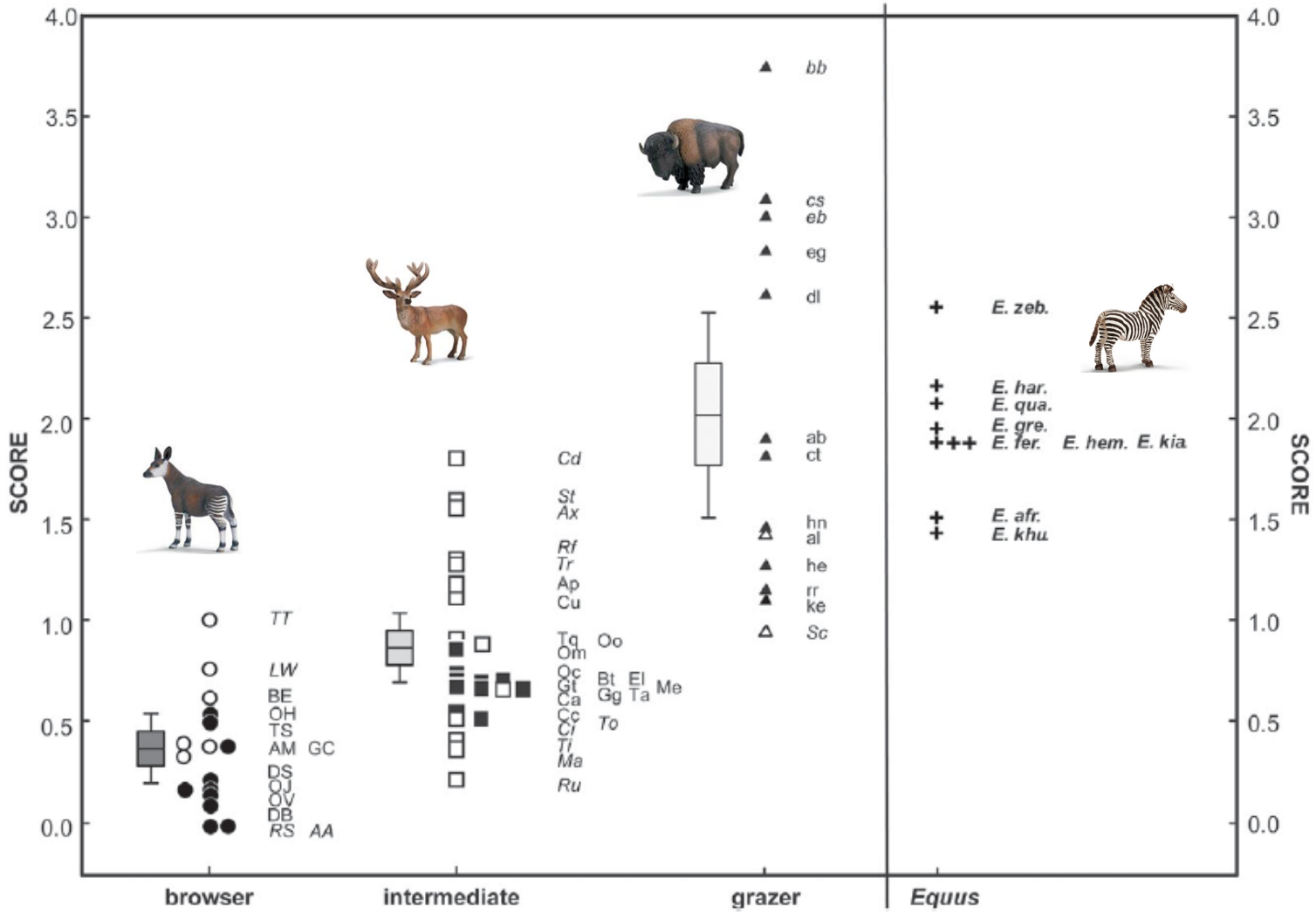


Kaiser and Fortelius (2003)

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

Ellen SCHULZ* Thomas M. KAISER

Mammal Review **43** (2013) 111–123

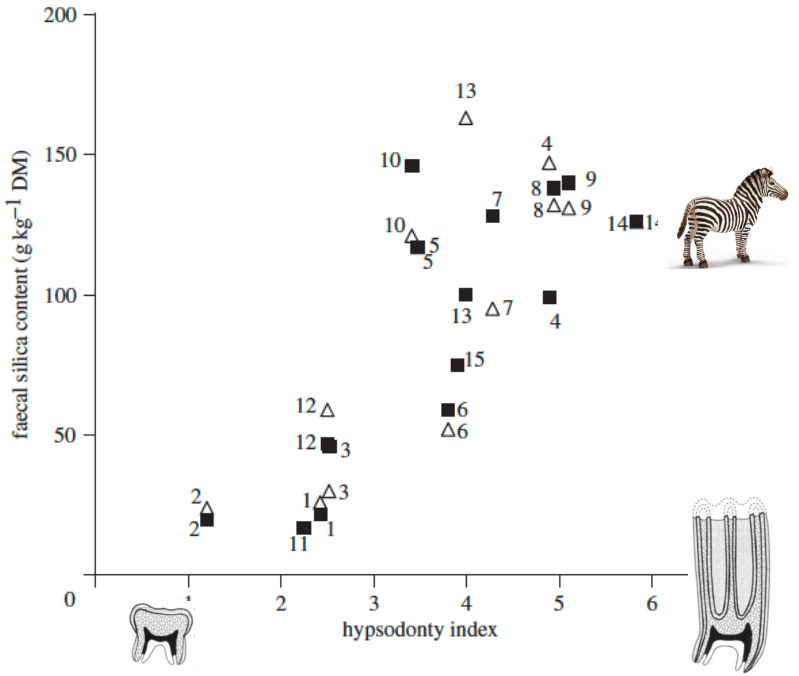


Adapted to abrasive diets

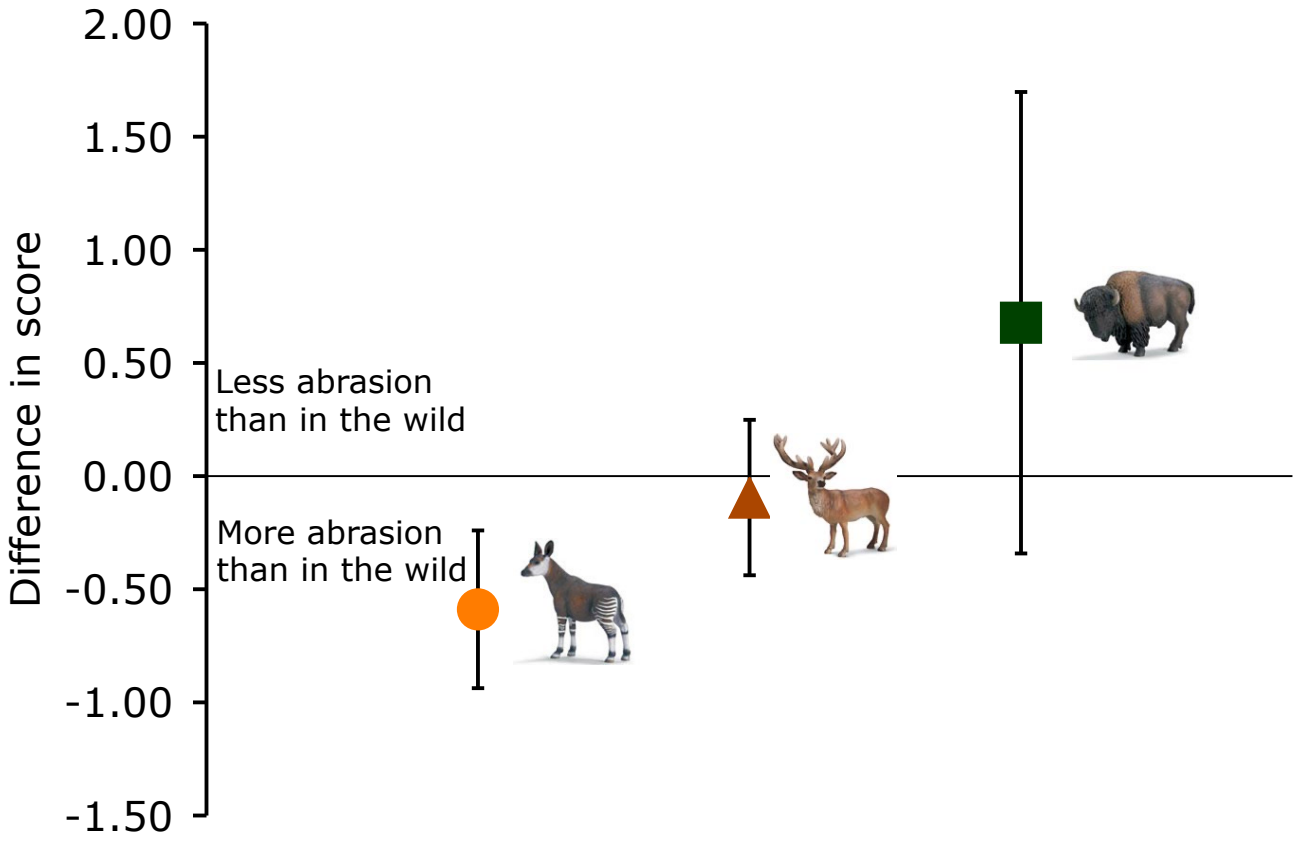
Another one bites the dust: faecal silica levels in large herbivores correlate with high-crowned teeth

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

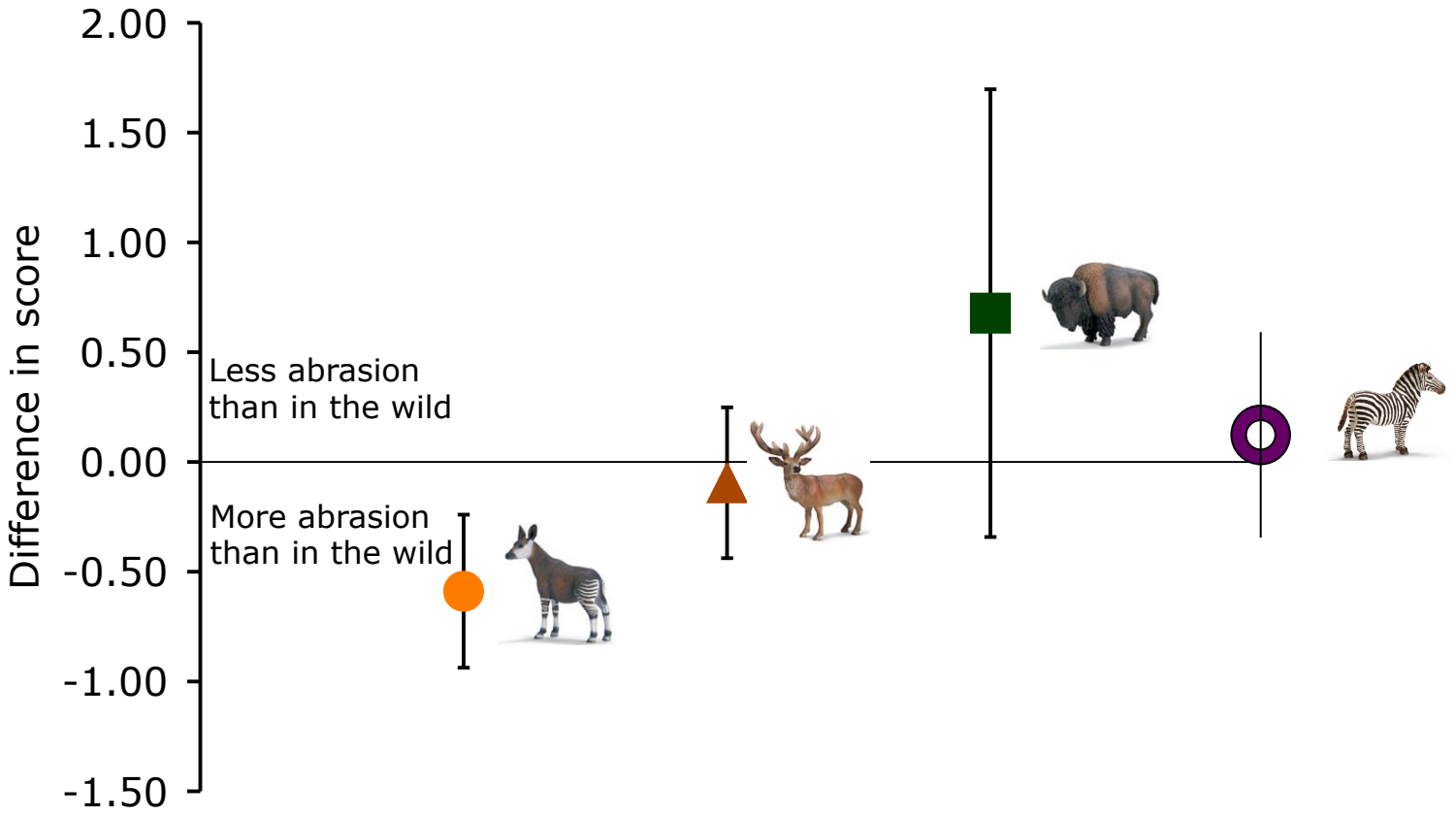


Diet and mesowear: zoo vs. wild



from Kaiser et al. (2009)

Diet and mesowear: zoo vs. wild



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

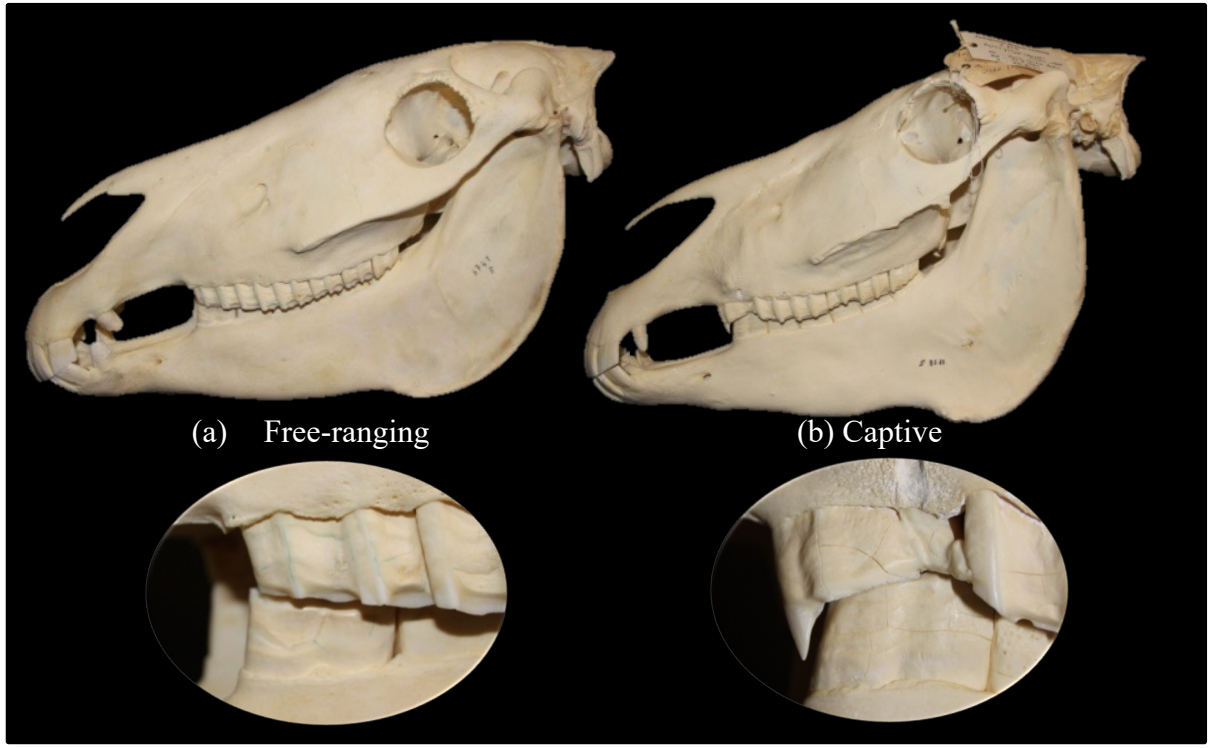
Wild equids in captivity

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

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?)

- *Incidents of dental abnormalities*

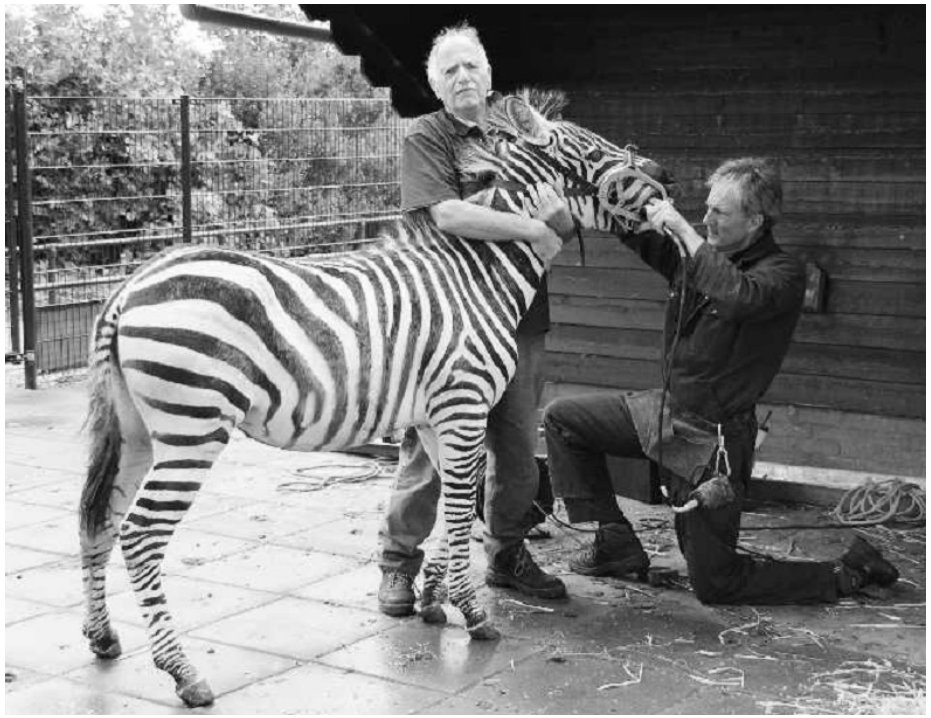


from Taylor et al. (in prep.)

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?)

- *Incidents of dental abnormalities*



Hoyer et al. (2012)

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?)

- *Incidents of dental abnormalities*

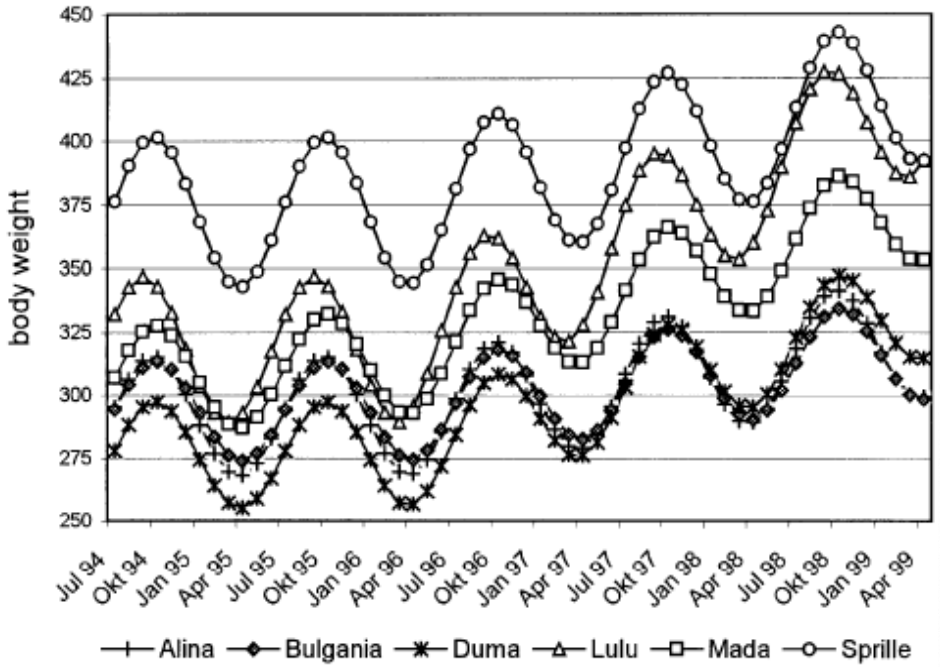
- *Hoof overgrowth/laminitis*

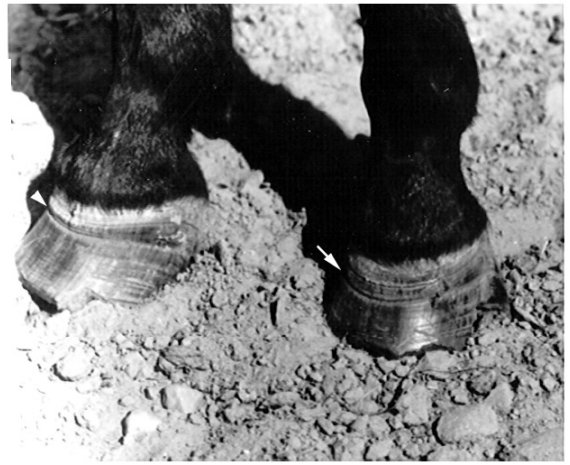
Equid seasonality

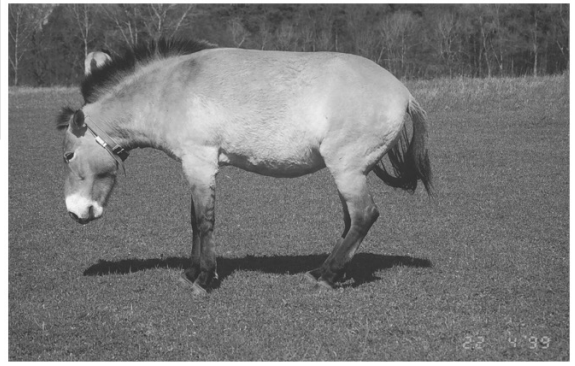
Laminitis in Przewalski horses kept in a semireserve

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

J. Vet. Sci. (2001), **2**(1), 1–7







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?)

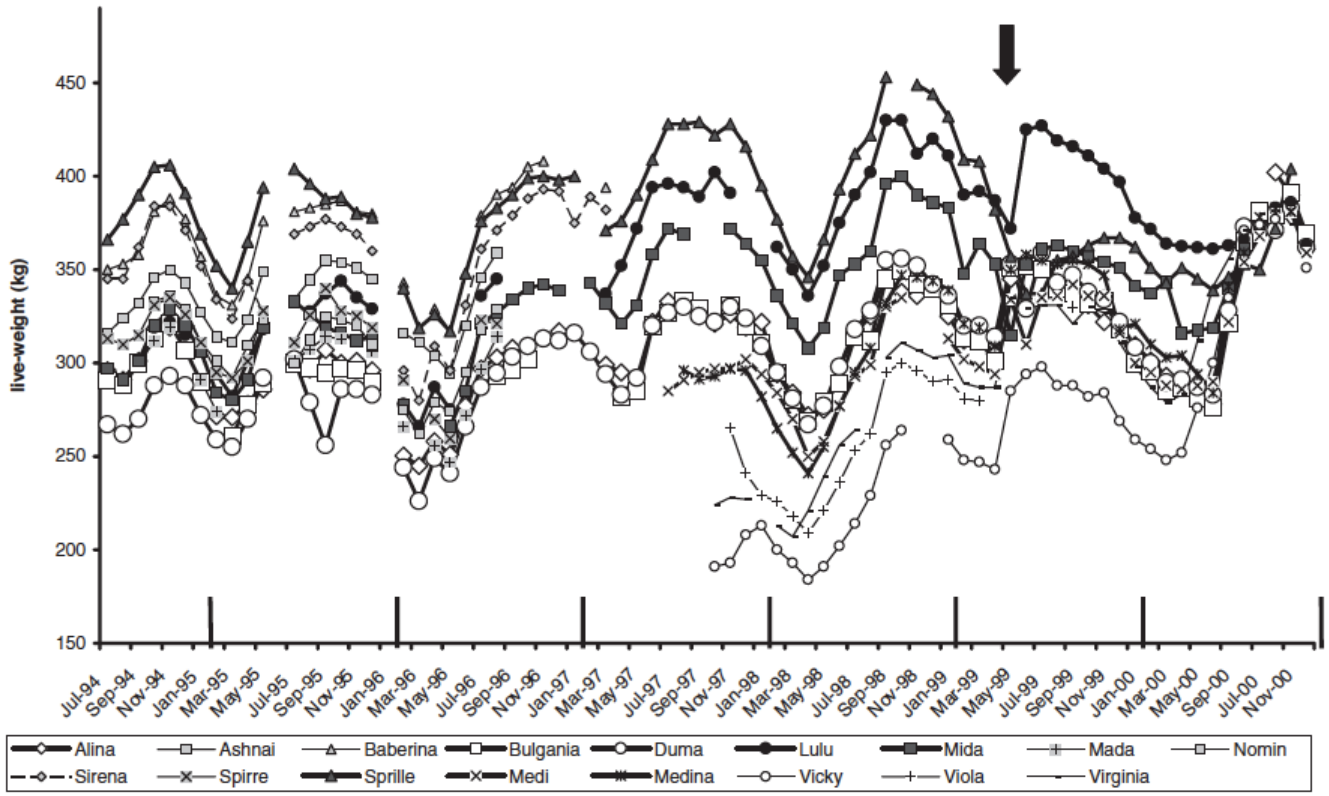
- *Incidents of dental abnormalities*
- *Hoof overgrowth/laminitis*
- *Obesity*

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



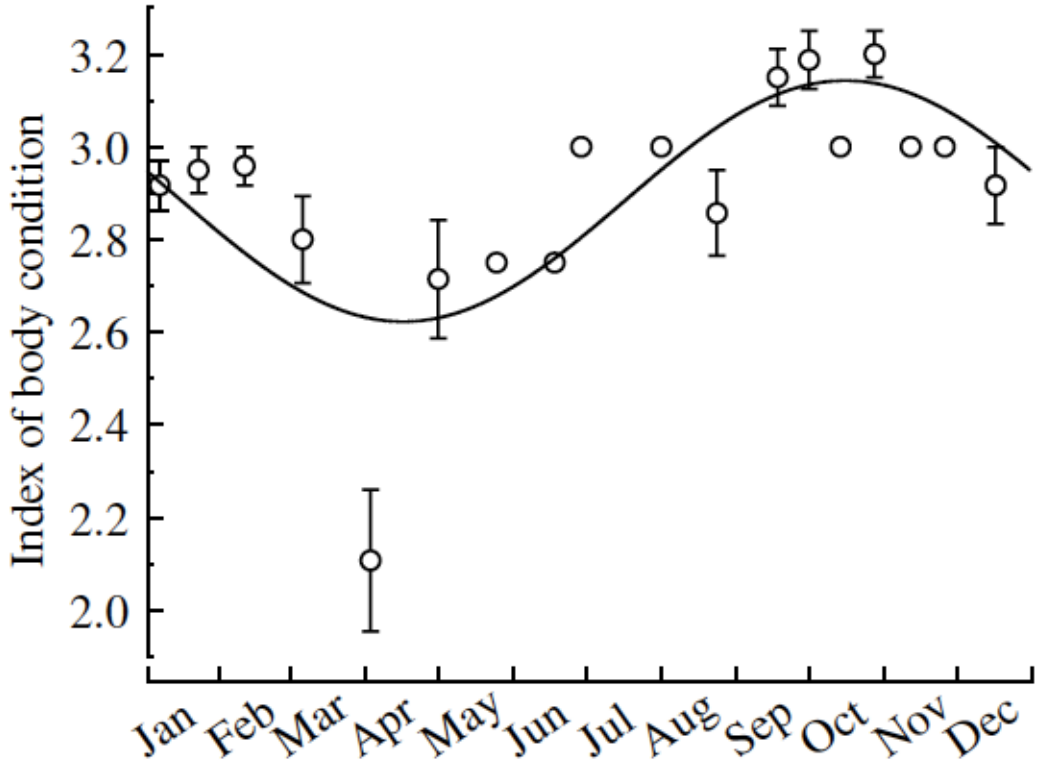
Equid seasonality

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

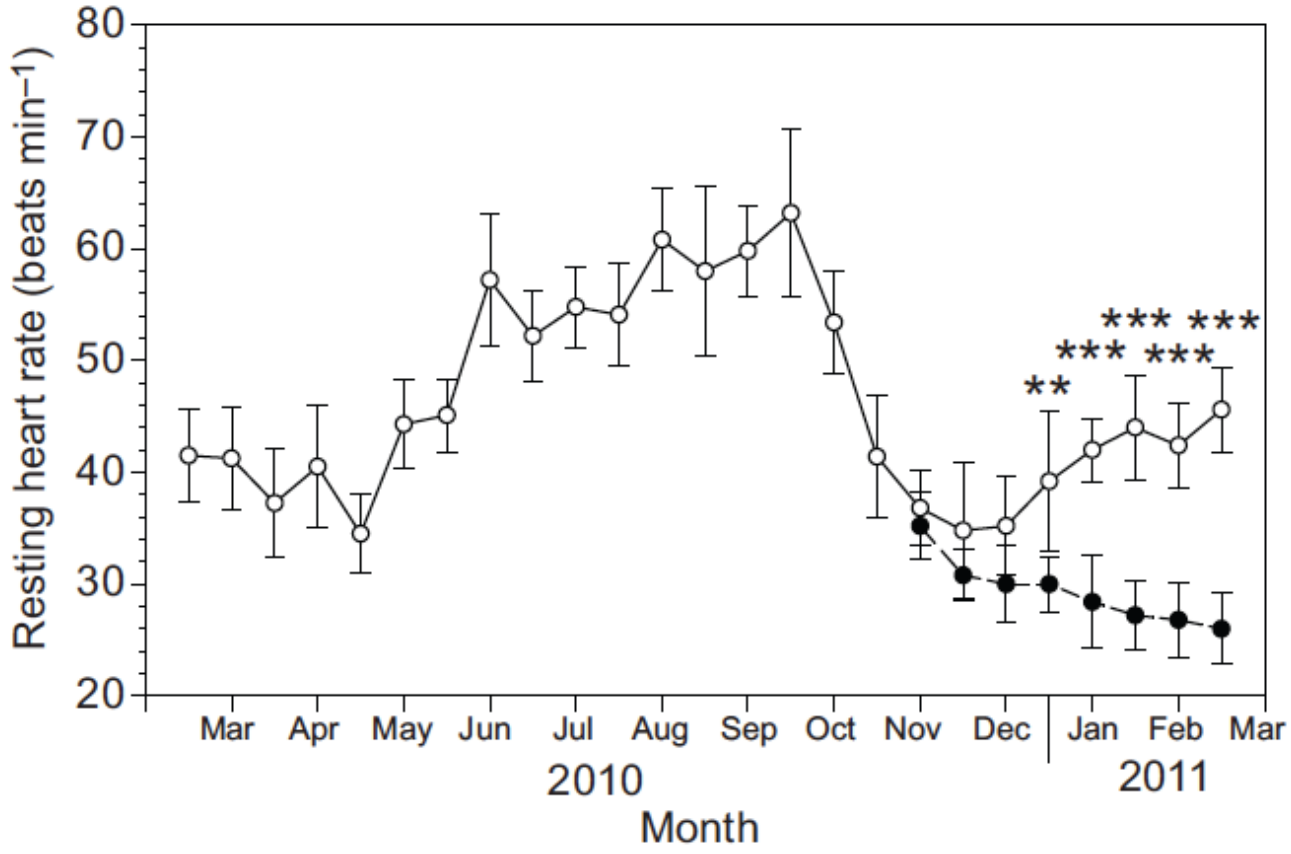


Equid seasonality

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

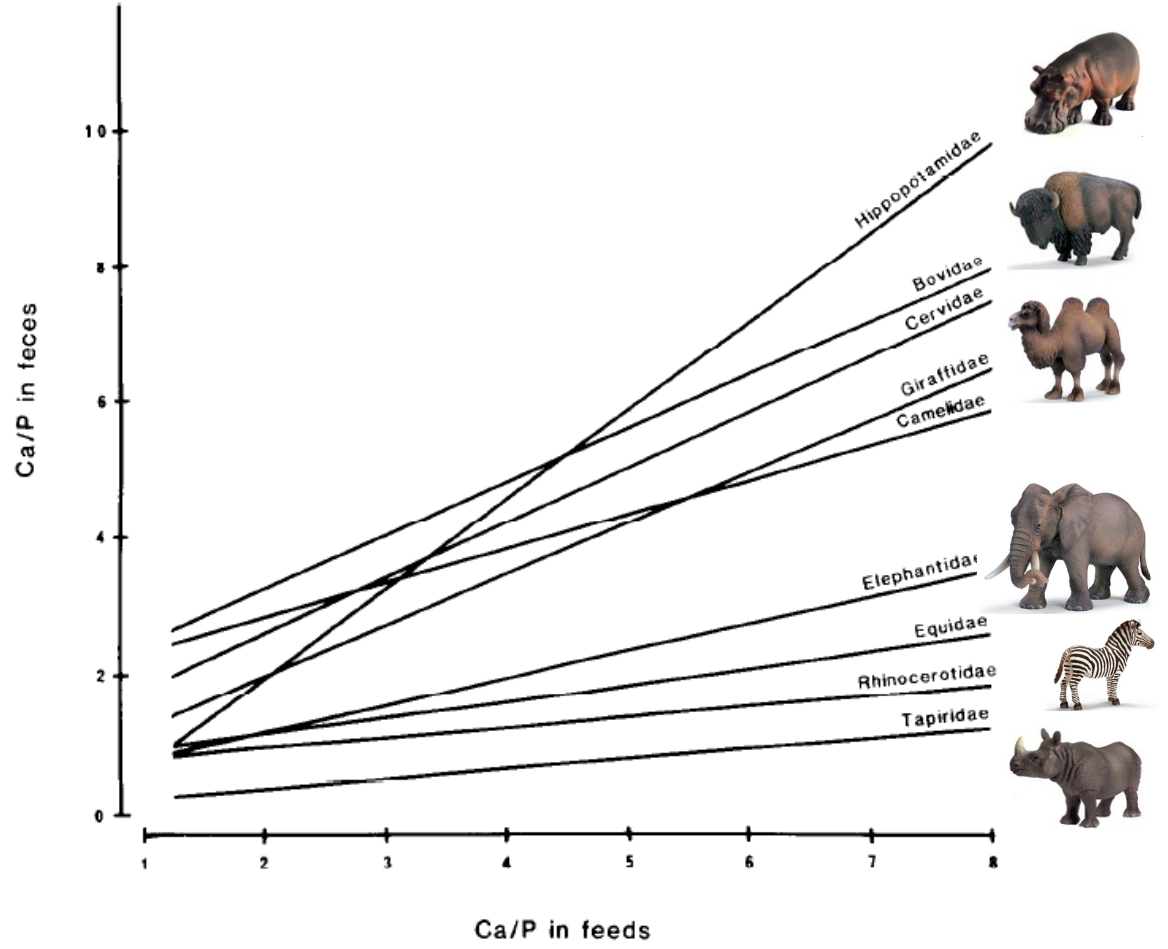


Other differences: Calcium digestibility

CALCIUM EXCRETION IN FECES OF UNGULATES

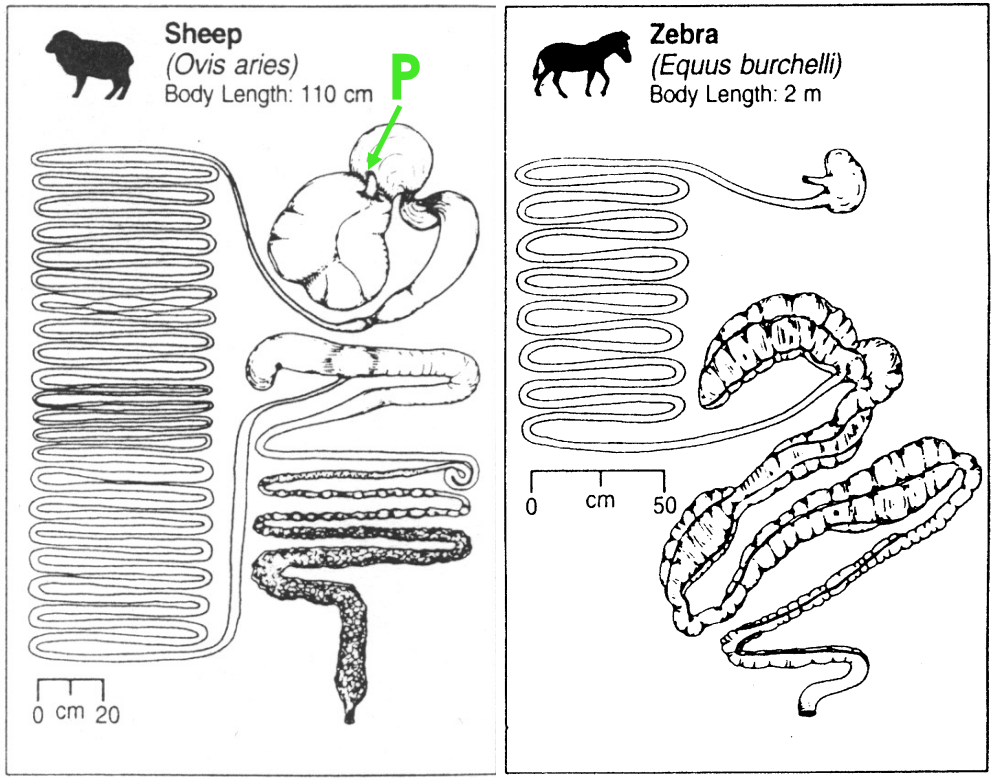
H. F. SCHRYVER, T. J. FOOSE*, J. WILLIAMS and H. F. HINTZ

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



Other differences: Calcium digestibility

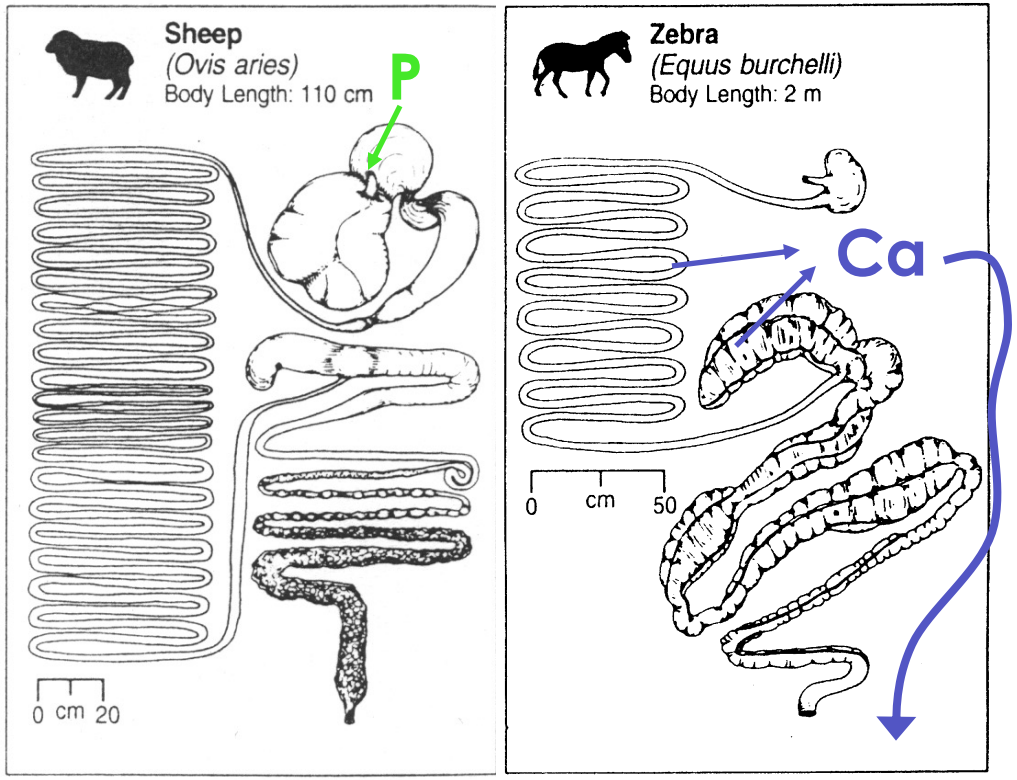
Phosphorus is supplied directly to microbes via saliva



from Stevens & Hume (1995)

Other differences: Calcium digestibility

Phosphorus is supplied directly to microbes via saliva



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

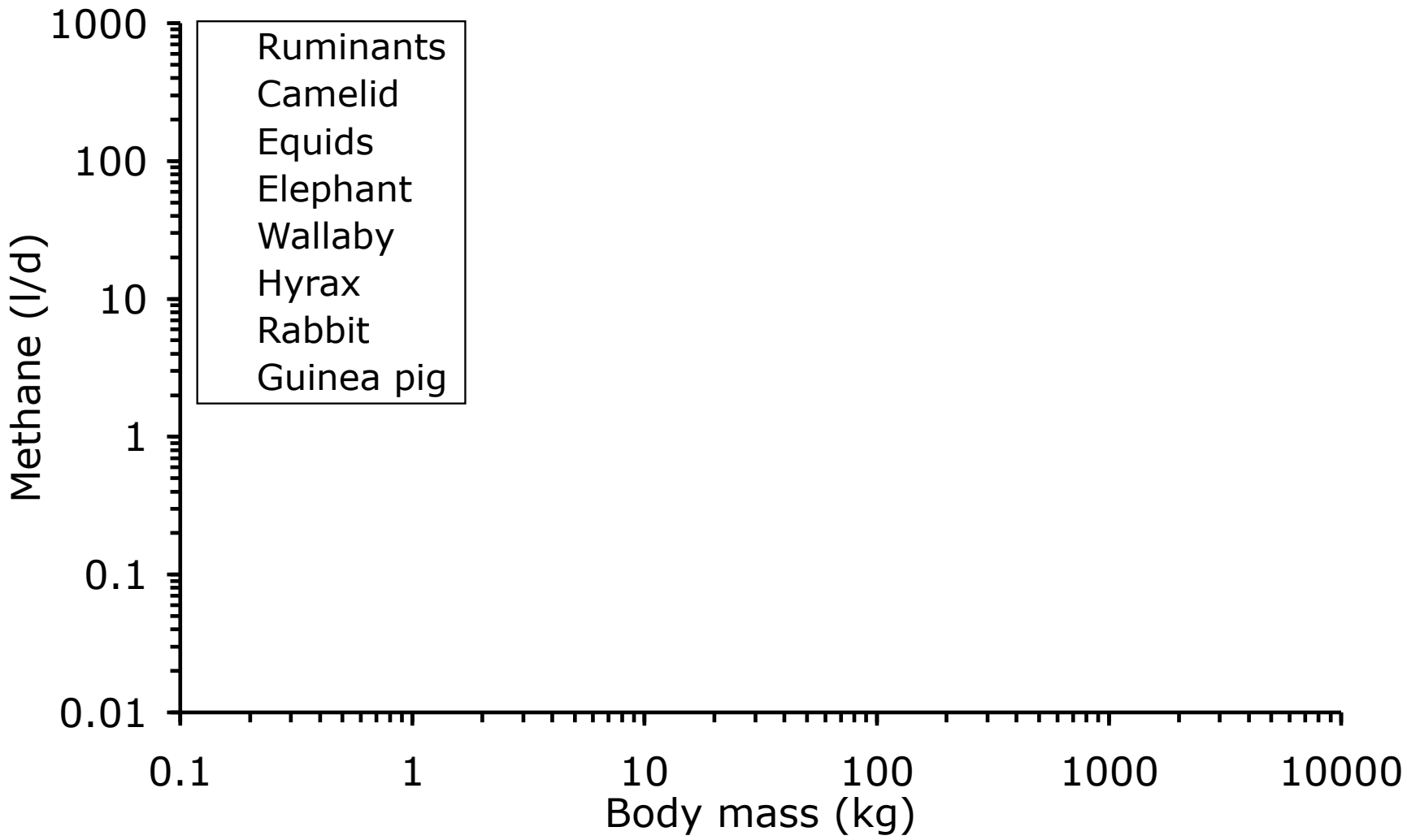
from Stevens & Hume (1995)
hypothesis by Clauss & Hummel (2008)

Why equids?

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

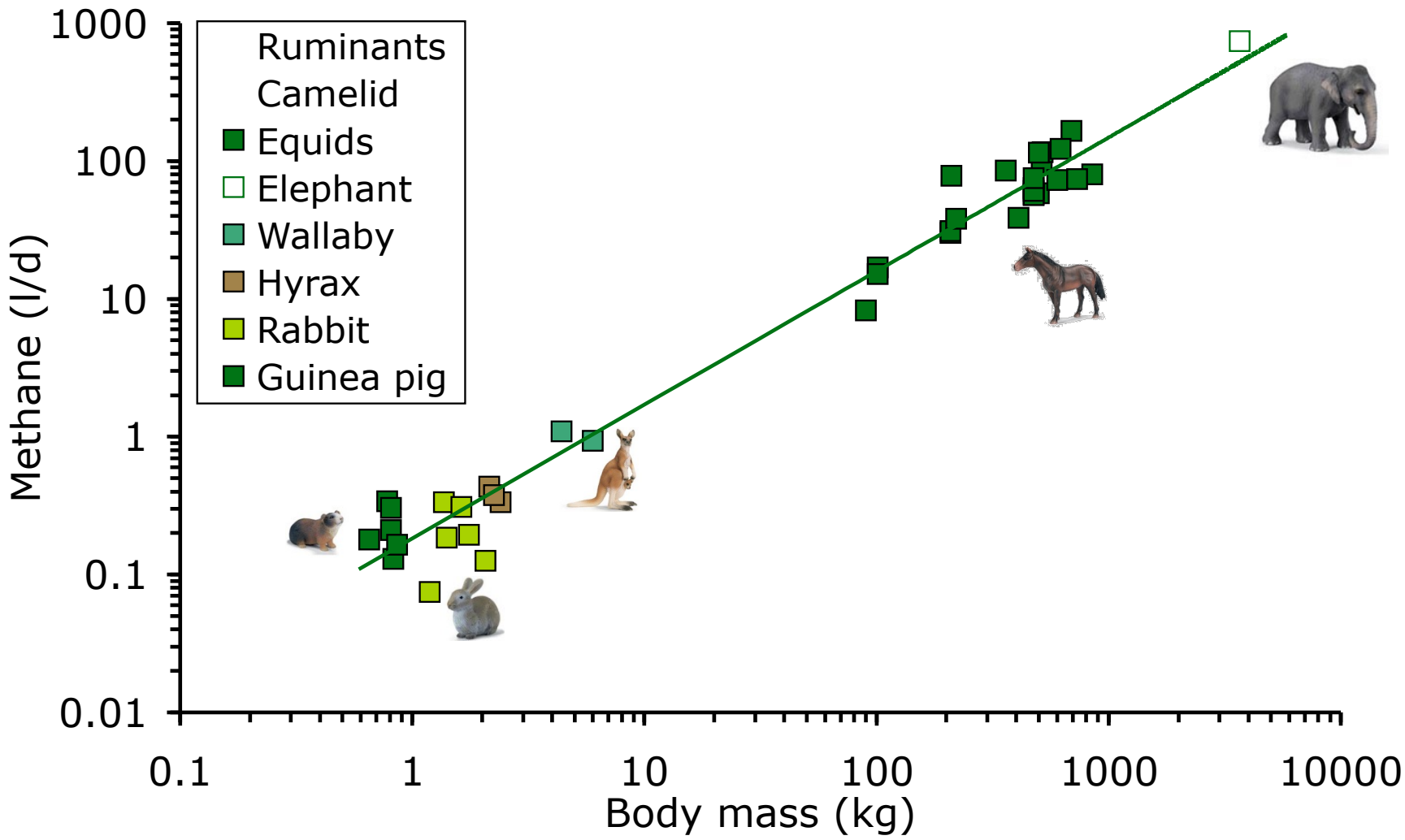
Why / how do equids survive (only in the upper ruminant body size range, and only in the grazing niche)?

Other differences: Methane production?



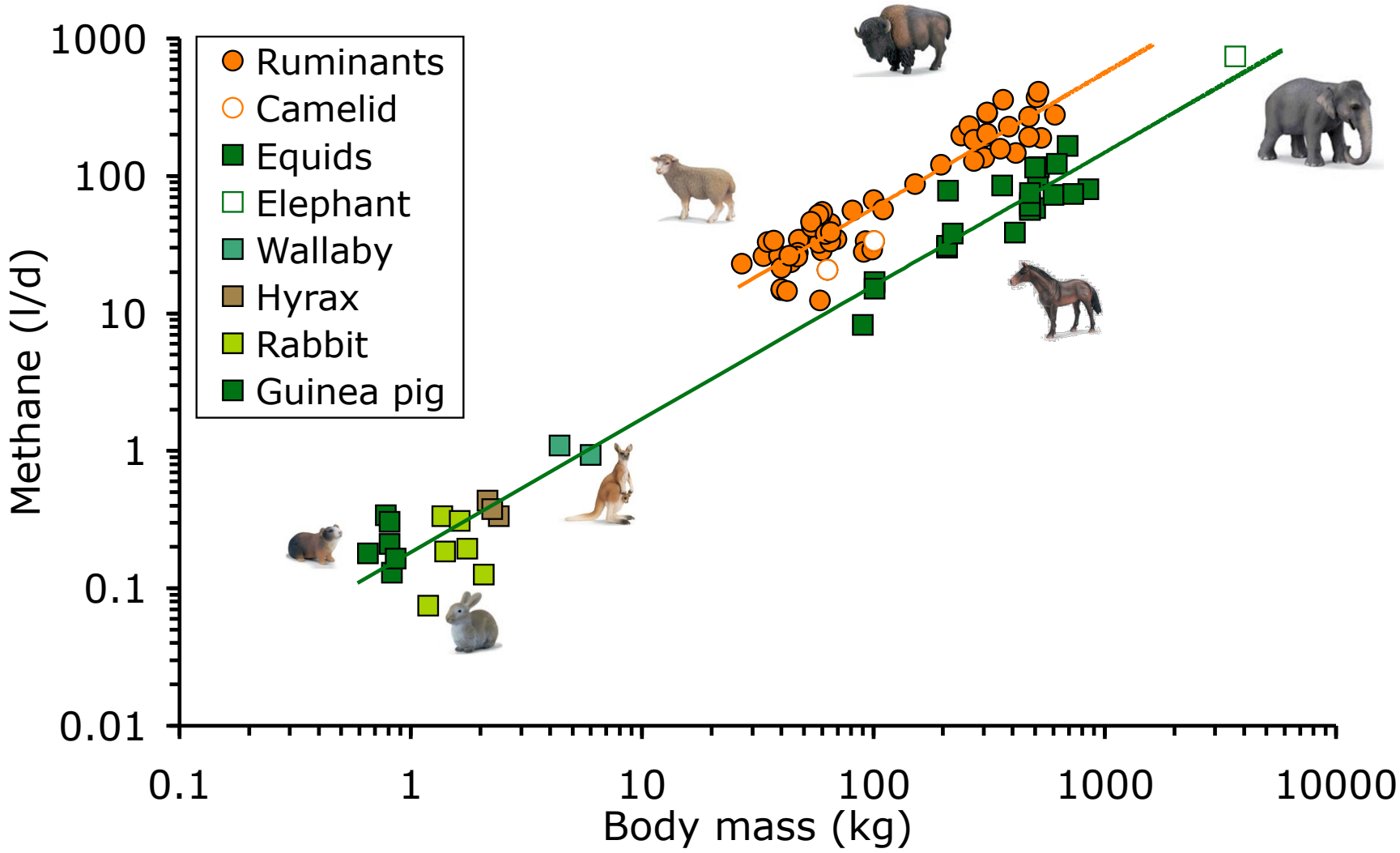
from Franz et al. (2010)

Other differences: Methane production?



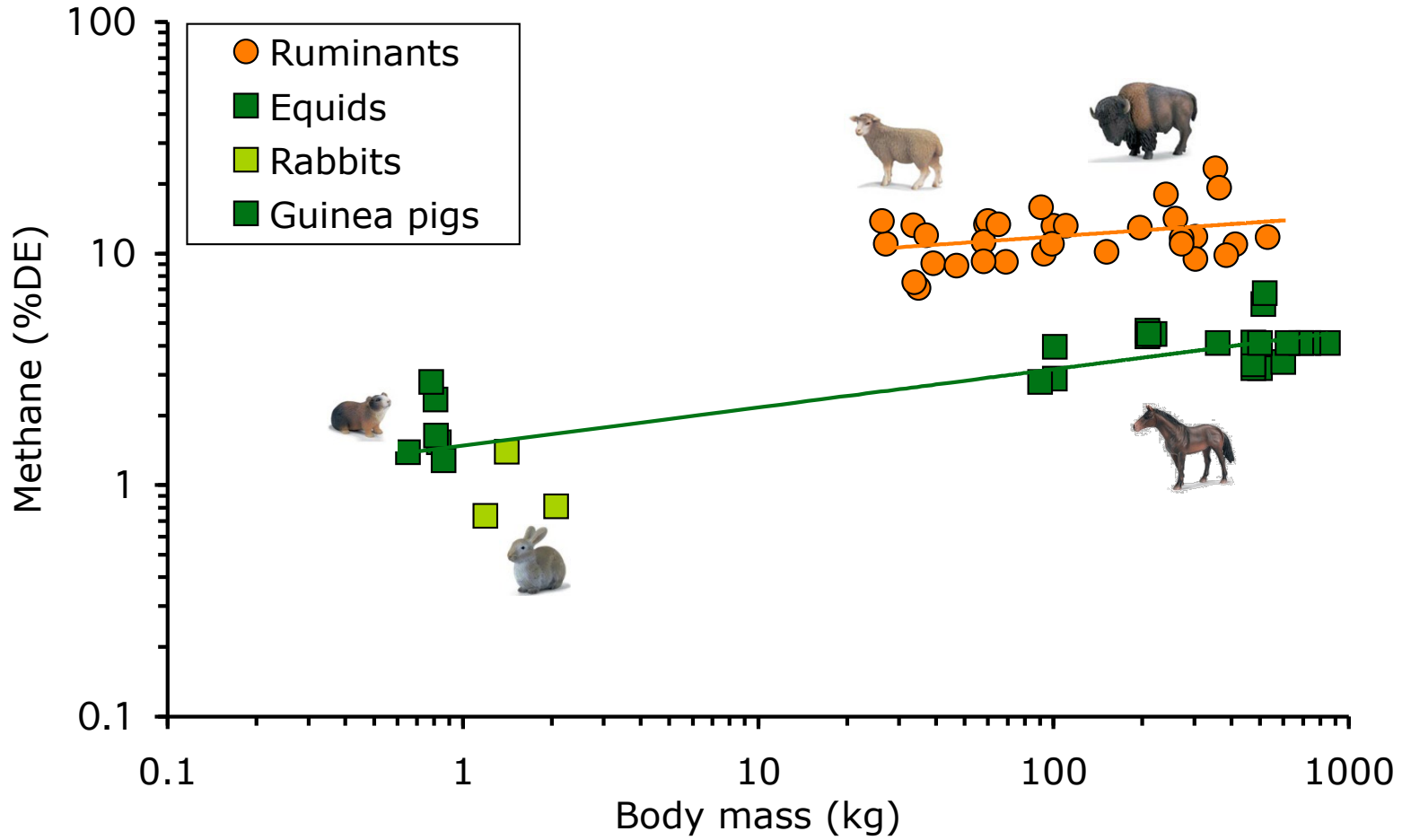
from Franz et al. (2010)

Other differences: Methane production?



from Franz et al. (2010)

Other differences: Methane production?



from Franz et al. (2010)