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Charles T. Robbins · Donald E. Spalinger
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Adaptation of ruminants to browse and grass diets: are anatomical-based browser-grazer interpretations valid?

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Abstract As a result of pioneering work of Hofmann (1973, 1989), nutritional ecologists classify ruminants into three feeding-type categories: browsers ("concentrate" feeders), grazers, and intermediate or mixed feeders. Hofmann proposed that these feeding types result from evolutionary adaptations in the anatomy of the digestive system and that one consequence is shorter retention of the digesta in the rumen of browsers, and thus a decreased efficiency of fiber digestion relative to that of grazers. We examined the hypotheses that (1) fiber digestion of browsers is lower than that of grazers, (2) salivary gland size is larger in all browsers than in grazers, (3) the browser's larger salivary glands produce larger volumes of thin serous saliva than those of grazers, and (4) thus, browsers have higher liquid passage rates than do grazers. We found that the extent of fiber digestion is not significantly different between browsers and grazers, although fiber digestion is positively related to herbivore size. In general, salivary gland size is approximately 4 times larger in browsers than grazers, but some browsers (e.g., greater kudu) have small, grazer-sized salivary glands. Resting (non-feeding or ruminating) saliva flow rates of mule deer (browser) and domestic sheep and cattle (grazers) were not significantly different from each other. Finally, ruminal liquid flow rates were not different between feeding types. We conclude that many of Hofmann's nutritional and physiological interpretations of anatomical differences amongst ruminants are not supportable.

Key words Ruminants · Browsers · Digestion · Foraging · Saliva

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Introduction

Ruminants occupy a diverse array of feeding niches throughout the world. Although they feed on plants of widely divergent physical and chemical compositions (e.g., lichens, grasses, and woody stems), ecologists classify ruminants into one of three general feeding categories, comprising grazers, browser/concentrate feeders, and intermediate feeders. These categories reflect the predilection of the animals for consuming grasses, browses/herbs/fruits, or a mixture of both, respectively (Hofmann 1973, 1989).

In a classic work, Hofmann (1973) examined the foraging preferences of these groups in relation to their digestive anatomy, and concluded that general digestive system adaptations correspond to the ecological role of the animal. He hypothesized that grazing ruminants are better adapted for consuming slowly digested plant fiber (typical of grasses and sedges) than are browsing ruminants because grazers have larger rumens, and the structure of the rumen and omasum retards the passage of food to the lower tract. Conversely, browsers have smaller and less complex rumens and omasums, and they have larger parotid salivary glands that produce a copious, serous saliva to help buffer the rapidly digestible ("concentrate") diet and aid in the passage of foods from the rumen. These differences have led Hofmann (1989, p. 453) to suggest that "all [browsers and intermediate] species cannot digest fibre as well as grazers".

Hofmann's nutritional and ecological interpretations have been a powerful abstraction of ruminant function, influencing the way that nutritionists and ecologists view ruminant evolution and behavior, and the organization and composition of herbivore communities (McNaughton and Georgiadis 1986; Owen-Smith 1991). However, until recently, Hofmann's hypotheses have not been rigorously tested. In the first major attempt to test Hofmann's ideas, Gordon and Illius (1994) concluded that there is no significant difference in digestive kinetics (fermentation rate, daily VFA (volatile fatty acid) (VFA) production, and mean total tract retention time of food)

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1989, p.449). We tested that statement by dissecting the salivary glands (parotid, mandibular and buccal) of five browsers [greater kudu (*Tragelaphus strepsiceros*), bushbuck (*T. scriptus*), nyala (*T. angasii*), giraffe, and common duiker (*Sylvicapra grimmia*)], five grazers [common reedbuck (*Redunca arundinum*), red hartbeest (*Alcelaphus buselaphus*), blesbok (*Damaliscus dorcas*), black wildebeest (*Connochaetes gnou*), gemsbok (*Oryx gazella*)], and two intermediate feeders [springbok (*Antidorcas marsupialis*) and impala (*Aepyceros melampus*)] killed during culling operations in South African game parks. Additionally, salivary gland and body weights were obtained for mule deer, black-tailed deer, white-tailed deer and moose (*Alces alces*) (browsers), domestic goats, fallow deer (*Cervus dama*), axis deer (*C. axis*), and mountain goats (*Oreamnos americanus*) (intermediate feeders), and domestic sheep and cattle (grazers) in the United States. The parotid lymph node was removed from all parotid

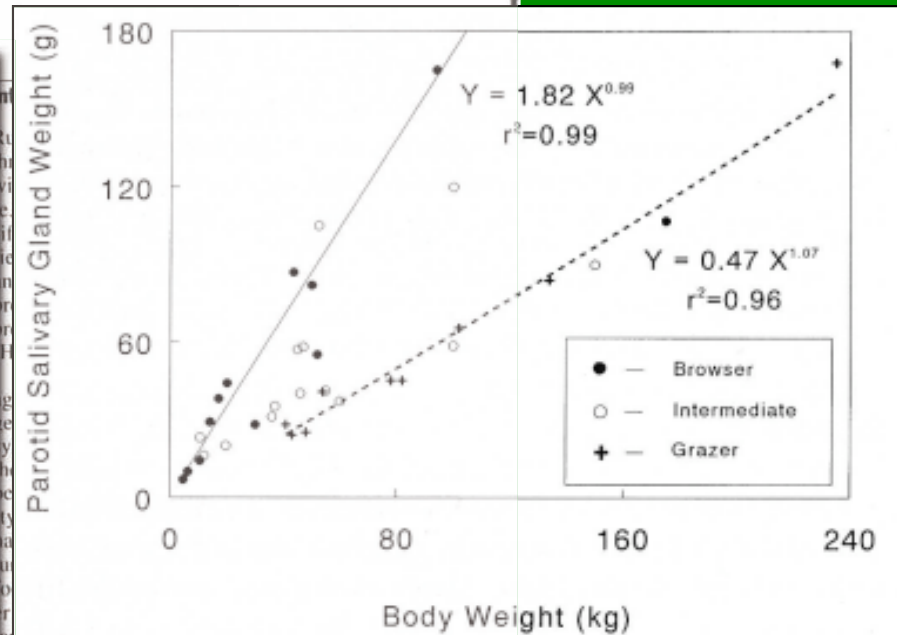
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Stephen S. Ditchkoff

A decade since “diversification of ruminants”: has our knowledge improved?

Received: 11 October 1999 / Accepted: 6 April 2000

Abstract In his landmark 1989 paper, R.R. Hofmann classified ruminants into three categories based upon digestive anatomy and preferred forages, and proposed that divergence of feeding strategies among ruminants is a result of morphological evolution of the digestive tract. Because of the hypothetical nature of these views and the ingrained beliefs that they challenged, several papers were published that reported tests of Hofmann’s predictions. The consensus among these papers was that Hofmann’s predictions were inadequate. I describe the experimental evidence that has been put forth in opposition to the ruminant diversification hypothesis and contend that we have failed to adequately test Hofmann’s predictions.

Key words Concentrate selectors · Intermediate feeders · Roughage eaters · Rumen bypass · Ruminant diversification

Early attempts to explain variation found in feeding strategies of free-ranging ruminants classified individual species as “browsers” or “grazers” based upon types of forage consumed. Though an important step in understanding the complexities of ruminant nutrition, Hofmann and Stewart (1972) recognized that feeding strategies of ruminants could not simply be classified into two categories, and proposed three categories (i.e., bulk and roughage eaters, selectors of concentrate forages, and intermediate feeders) based upon stomach structure and feeding ecology. Hofmann (1984) later documented variation in all portions of the digestive anatomy among the three categories of his system of ruminant classification. The dynamic interactions among body size, fermentation and passage rates, and energetic requirements, and their influence on dietary strategy formed the basis for these early classifications.

In a landmark paper, Hofmann (1989) expanded upon the concepts proposed by Hofmann and Stewart (1972) and Hofmann (1984) by providing a working hypothesis of the functional and morphological basis for diversity in ruminant feeding strategies. Hofmann (1989) proposed that feeding strategies ranged from nonselective intake of bulk roughage and efficient fermentation in the forestomach, to selectivity for concentrate forages (high in plant cell content) with increased post-ruminal digestion. This hypothesis challenged many beliefs regarding digestion in free-ranging ruminants and proposed that we reexamine the manner in which ruminant herbivores obtain nutrients from the environment.

Because of the magnitude of Hofmann’s hypothesis, several papers (Gordon and Illius 1994, 1996; Robbins et al. 1995) were published describing tests of his predictions. These researchers examined components of Hofmann’s hypothesis and concluded that they did not find support for morpho-physiological adaptations to diet type within classes of ruminants. They attributed differences in digestive function to body mass or food characteristics. As a result, the consensus has been that Hofmann’s hypothesis regarding gut morphology and function in classes of ruminants is inadequate (Robbins et al. 1995; Illius 1997). However, upon critical examination of both Hofmann’s hypotheses and subsequent critiques, I contend that we have not adequately tested Hofmann (1989). Although scientifically sound, the studies of Gordon and Illius (1994, 1996) and Robbins et al. (1995) did not completely examine components of the ruminant diversification hypothesis and therefore should not be considered to support or refute Hofmann (1989).

Hofmann (1989) proposed variations on the traditional theme of foregut fermentation in the ruminant. In addition to suggesting that hindgut fermentation may play an important role in some ruminant animals, he also commented on postruminal digestion of soluble components of the diet after rumen bypass via the reticular groove (Hofmann 1989, p. 448). While post-ruminal fermentation had previously received some attention (Van Soest 1982), selective bypass of the rumenoreticular

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Phylogenetic analysis of stomach adaptation in digestive strategies in African ruminants

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Abstract The stomach morphology of 28 species of artiodactyls that differ in feeding style (browser, mixed feeder, grazer) was analysed using a multivariate approach and phylogenetic correction in order to test whether stomach morphology was correlated with feeding style when body mass was controlled for. A total of 25 morphological traits of the stomach were used in the analysis. After the effects of body mass and phylogeny on stomach morphology were taken into account, there was no significant grouping of species according to feeding style. When information about the feeding style of each species was included in the analysis, the set of morphological traits separated the mixed feeders from the other two feeding styles, but grazers and browsers had similar morphological features. Most of the variance in stomach morphology was explained by body mass and a lesser proportion by phylogeny. The main morphological features that have previously been proposed as being adaptations in grazing species, namely, lengthening of the retention time of ingesta to achieve an increase in their fibre digestion capability by means of a larger relative stomach capacity, a greater subdivision of chambers and smaller openings, are not supported by the findings of this study. Thus, there is no consistent evidence to support a significant adaptive effect of stomach morphology to different diets in the Artiodactyla.

Keywords Allometry · Body mass · Comparative method · Feeding styles · Gut morphology

Introduction

The feeding habits of some ungulates in a natural habitat were, to our knowledge, first defined by Van Zyl (1965), but it was Hofmann who classified African ruminants into three feeding styles according to morphological adaptations of the digestive system (Hofmann 1973, 1989), as related to differences in diet composition (Hofmann 1968, 1984, 1988; Hofmann and Stewart 1972; Hofmann et al. 1995). Hofmann's categorisation of feeding styles has been extensively used in grazing ecology (Owen-Smith 1982; Gordon and Illius 1988, 1994, 1996; McNaughton 1991; Van Wieren 1996). Differences in stomach morphology between species that differ in diet triggered subsequent studies on other parts of the digestive system, for example, morphological adaptations of the organs involved in the selection (lips, muzzle: Janis and Ehrhardt 1988; Pérez-Barbería and Gordon 2001a) and the processing of food (teeth, jaws, jaw muscles: Fortelius 1985; Axmacher and Hofmann 1988; Janis 1988; Pérez-Barbería and Gordon 1999a, 2001a) and also in behavioural variables (activity time: Mysterud 1998; Pérez-Barbería and Gordon 1999b; home range: Mysterud et al. 2001; habitat use: Pérez-Barbería et al. 2001b). Based on Hofmann's (1973) classification, it has been assumed that grazing species achieve a greater extent of digestion of fibre in comparison with browsing species by means of food retention in the rumen, large stomach capacity, higher degree of stomach compartmentalisation and smaller openings between the rumen and omasum. However, a statistical relationship between the differences in stomach morphology, described by Hofmann (1973), and diet composition has not yet been demonstrated.

A recurrent problem which arises when studying the differences in the morphology or function of the digestive system, in relation to Hofmann's classification, is the possible confounding effect of body mass (Gordon and Illius 1994; Robbins et al. 1995; Iason and Van Wieren 1998). After controlling for body mass, Gordon and Illius (1994) found that there were no differences in wet

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Table 2 The data set used in this study comes from Hofmann (1973).

Variable no.	2	3	4	5	6	7	8	9	10
Species name									
<i>Giraffa camelopardalis</i>	750.0	105.0	16.0	144.1	2.0	104.5	24.5	24.0	19
<i>Syncerus caffer</i>	750.8	107.0	12.0	176.0	12.0	156.8	16.5	49.5	23
<i>Tragelaphus strepsiceros</i>	213.5	45.8	4.4	75.7	3.5	181.3	30.5	33.5	28
<i>Tragelaphus oryx</i>	420.0	53.0	6.5	171.0	2.3	80.0	40.0	42.5	44

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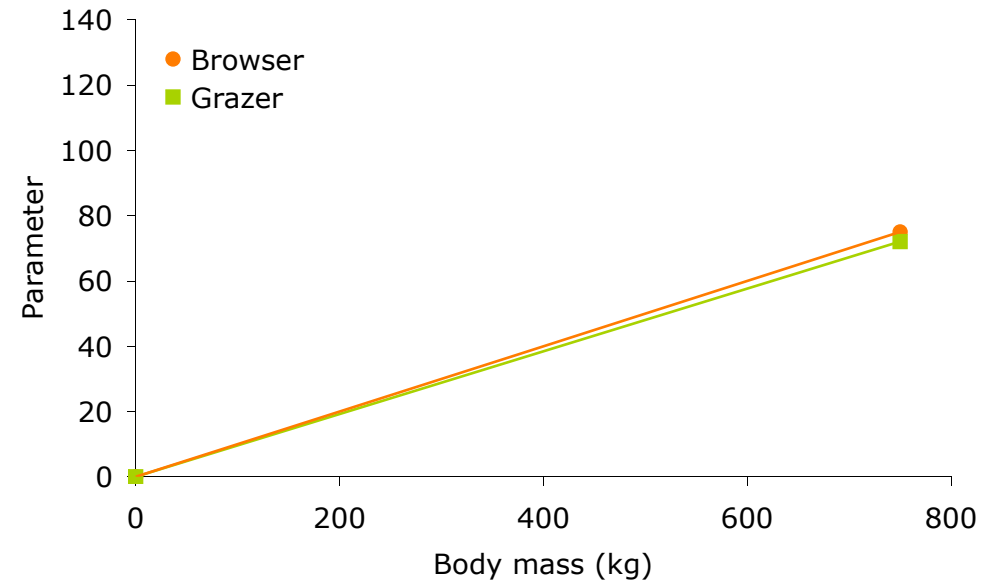


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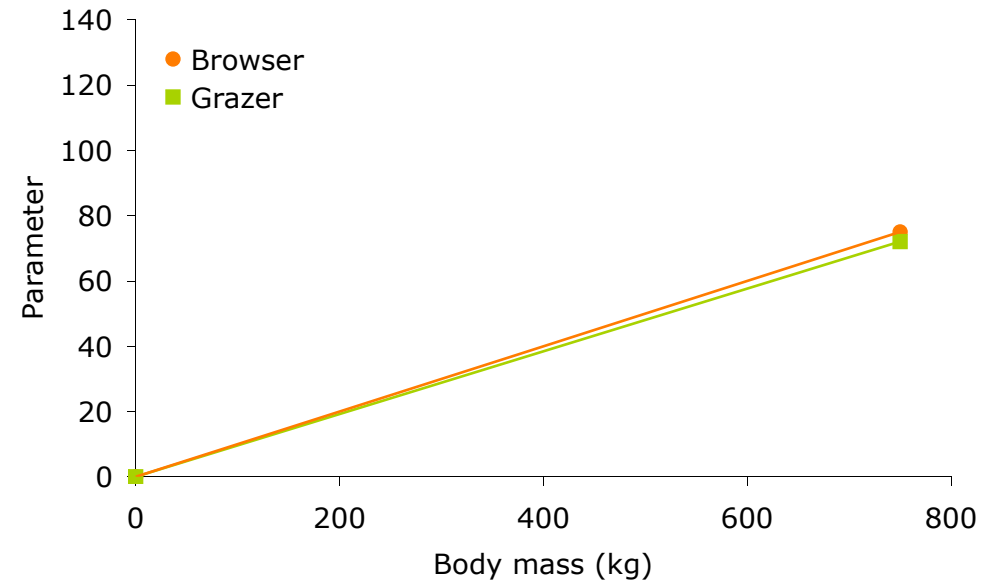


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A recurrent problem which arises when studying the differences in the morphology or function of the digestive system, in relation to Hofmann's classification, is the possible confounding effect of body mass (Gordon and Illius 1994; Robbins et al. 1995; Iason and Van Wieren 1998). After controlling for body mass, Gordon and Illius (1994) found that there were no differences in wet

The evolution of phylogenetic differences in the efficiency of digestion in ruminants

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This study investigates, for the first time (to our knowledge) for any animal group, the evolution of phylogenetic differences in fibre digestibility across a wide range of feeds that differ in potential fibre digestibility (fibre to lignin ratio) in ruminants. Data, collated from the literature, were analysed using a linear mixed model that allows for different sources of random variability, covariates and fixed effects, as well as controlling for phylogenetic relatedness. This approach overcomes the problem of defining boundaries to separate different ruminant feeding styles (browsers, mixed feeders and grazers) by using two covariates that describe the browser-grazer continuum (proportion of grass and proportion of browse in the natural diet of a species). The results indicate that closely related species are more likely to have similar values of fibre digestibility than species that are more distant in the phylogenetic tree. Body mass did not have any significant effect on fibre digestibility. Fibre digestibility is estimated to increase with the proportion of grass and to decrease with the proportion of browse in the natural diet that characterizes the species. We applied an evolutionary model to infer rates of evolution and ancestral states of fibre digestibility; the model indicates that the rate of evolution of fibre digestibility accelerated across time. We suggest that this could be caused by a combination of increasing competition among ruminant species and adaptation to diets rich in fibre, both related to climatically driven environmental changes in the past few million years.

Keywords: browser; grazer; phylogeny; evolution; digestibility; diet

1. INTRODUCTION

Despite considerable efforts in the analysis of the comparative anatomy of the digestive tract of ungulates, research has hitherto failed to demonstrate any relationship between differences in morphology and digestive efficiency between species, other than at a gross level (Robbins 1993). We offer a novel analysis that controls for confounding effects and highlights the flexibility of digestive adaptation in ruminants.

Previous research in this area demonstrates a number of weaknesses. The first weakness is the question of continuous versus discrete variables. Hofmann (1968, 1973) and Hofmann & Stewart (1972) described the stomach morphology of a number of species of African ruminants and using this information classified species into three groups (i.e. concentrate selectors, intermediate, and bulk and roughage eaters). Concentrate selectors (i.e. browsers) were the species whose diet mainly contained browse; bulk and roughage eaters (i.e. grazers) were species in which grass was the main component of the diet, and the third group, intermediate (i.e. mixed feeders), consumed a mixture of browse and grass, depending upon the habitat or season. Hofmann & Stewart (1972) and Hofmann (1973) pointed out that their stomach classification coincided with the main dietary habits of the

ruminant species. However, Hofmann's later papers (1985, 1988) established a composite criterion of species classification '...based on typical structures of the digestive tract ... and/or on feeding behaviour/forage selection' (Hofmann 1985, p. 398). This may be the cause of confusion in the literature as to the criteria used to classify species, almost entirely based on dietary habits but frequently linked with the stomach classification of Hofmann (1973) (see Iason & van Wieren 1999; Pérez-Barbería & Gordon 1999a, 2000, 2001; Brashares *et al.* 2000; Gagnon & Chew 2000; Pérez-Barbería *et al.* 2001a). As a result, the relationships that many studies find between the variables studied—dietary classification and stomach morphology—are confounded by circular argumentation (Pérez-Barbería *et al.* 2001a).

Hitherto, ruminant species have been classified into dietary groups using discrete boundaries based on information on stomach morphology or dietary habits (Axmacher & Hofmann 1988; Gordon & Illius 1988, 1994, 1996; Janis & Ehrhardt 1988; Spencer 1995; van Wieren 1996; Iason & van Wieren 1999; Pérez-Barbería & Gordon 1999a,b, 2000, 2001; Brashares *et al.* 2000; Gagnon & Chew 2000; Pérez-Barbería *et al.* 2001a). However, stomach morphology and dietary habits are continuous variables and they should be treated as such.

A second weakness of previous work has been an under-emphasis on phylogeny. Phylogeny has been demonstrated to be a significant factor in explaining the variability in a number of morphological traits (Pérez-Barbería & Gordon 1999a, 2001; Pérez-Barbería *et al.* 2001a) and behavioural variables (Pérez-Barbería &

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The evolution of phylogenetic differences in the efficiency of digestion in ruminants

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This study investigates, for the first time (to our knowledge) for any animal group, the evolution of phylogenetic differences in fibre digestibility across a wide range of feeds that differ in potential fibre digestibility (fibre to lignin ratio) in ruminants. Data, collated from the literature, were analysed using a linear mixed model that allows for different sources of random variability, covariates and fixed effects, as approach overcomes the problem of defining bound-
rowers, mixed feeders and grazers) by using two
proportion of grass and proportion of browse in
at closely related species are more likely to have
more distant in the phylogenetic tree. Body mass
y. Fibre digestibility is estimated to increase with
proportion of browse in the natural diet that characterizes
the species. We applied an evolutionary model to infer rates of evolution and ancestral states of fibre
digestibility; the model indicates that the rate of evolution of fibre digestibility accelerated across time.

We expect that:

(iii) species adapted to consuming different diets will differ in the efficiency with which they digest fibre when body mass has been taken into account;

ship between differences in morphology and digestive efficiency between species, other than at a gross level (Robbins 1993). We offer a novel analysis that controls for confounding effects and highlights the flexibility of digestive adaptation in ruminants.

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Evolutionary steps of ecophysiological adaptation and diversification of ruminants: a comparative view of their digestive system***

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Summary. A review is made of the ruminant digestive system in its morphophysiological variations and adaptations relating to foraging behaviour, digestive physiology, to interactions between plants and ruminants and to geographic and climatic diversity of ruminants' ecological niches. Evidence is provided for evolutionary trends from an extreme selectivity mainly for plant cell contents and dependence upon a fractionated fore- and hindgut fermentation, to an unselective intake of bulk roughage subjected to an efficient plant cell wall fermentation, mainly in the forestomachs. The review is based on detailed comparative morphological studies of all portions of the digestive system of 65 ruminant species from four continents. Their results are related to physiological evidence and to the classification of all extant ruminants into a flexible system of three overlapping morphophysiological feeding types: concentrate selectors (40%), grass and roughage eaters (25%) and intermediate, opportunistic, mixed feeders (35%). Several examples are discussed how ruminants of different feeding types are gaining ecological advantage and it is concluded that ruminants have achieved high levels of digestive efficiency at each evolutionary stage, (including well-documented seasonal adaptations of the digestive system) and that ruminant evolution is still going on. Deductions made from the few domesticated ruminant species may have, in the past, biased scientific evaluation of the free-ranging species' ecology. The main threat to a continuous ruminant evolution and diversity appears to be man's neglect for essential ecological interactions between wild ruminants and their specific habitats, which he alters or destroys.

Key words: Wild ruminants – Digestive system – Morphophysiological adaptation – Evolutionary trends – Plant-herbivore interactions

* Supported by German Research Community grant DFG Ho 273/6

** Dedicated to Professor Dr. Dr. h.c. Dietrich Starck on the occasion of his 80th birthday

Abbreviations: *bw* body weight; *CS* concentrate selector; *DFC* distal fermentation chamber (distended caecocolon); *GR* grass and roughage eater; *IM* intermediate (mixed) feeder; *PFC* proximal fermentation chamber (ruminoreticulum/forestomachs); *RR* Ruminoreticulum; *SCFA* Short-chain fatty acids (acetic, butyric, propionic acid set free by rumen bacteria); *SE* Surface enlargement (of absorptive mucosa)

Our growing scientific knowledge of the nutritional physiology of ruminants is documented in a vast number of publications annually, and every five years more than 600 researchers from all over the world meet in a different place to review and present new results. They discuss highly specialised aspects of physiology, metabolism, nutrition, biochemistry and digestive problems of these remarkable mammals – yet very few of them or of the thousands of others who deal scientifically with ruminants appear to be concerned that almost all of their results, their methods and models are based on merely two out of 150 species of extant ruminants. These two are sheep and cattle. Much fewer physiological and nutritional data available refer to the goat and far fewer still to the Asiatic water buffalo. Compared to all this, experimental data on wild African bovids, Eurasian cervids or American deer (let alone such oddities as the pronghorn "antelope", the giraffe or the musk ox – all of which are ruminants) cannot even be regarded as minimal. However, each new study on ruminants other than cattle, sheep and goats shakes the established ruminant image. It is different, though similar.

Ruminants are animals important to man. Some species are bioindicators of the first order in polluted human environments. More species are living barometers of man's inability to understand and handle ecological interactions and most, if not all ruminant species can benefit nutritionally from what man cannot digest.

Because they convert apparently indigestible carbohydrates and chemically trapped or protected proteins into nutritious and useful products, they deserve more than one approach. Ruminants are late-comers in evolution. Their stomach is a phylogenetic peak of complexity, not only compared with our own digestive tract.

But it is wrong to define ruminants simply as specialised fermentation machines which break down cellulose after chewing the cud.

Their digestive physiology is not based on an "all or nothing" principle and none of them is "primitive", although embryological evidence strongly suggests that roe deer or white-tailed deer, dik-diks or muntjac, kudu or moose are "older", earlier and still inefficient in breaking down cellulose. It will be shown, that ruminant evolution in the light of today's 150 living species is certainly "a bush, not a ladder" (Gould 1986). It has produced a fascinating array of animal forms ranging from 3 kg to over 1000



Explaining a putative contradiction

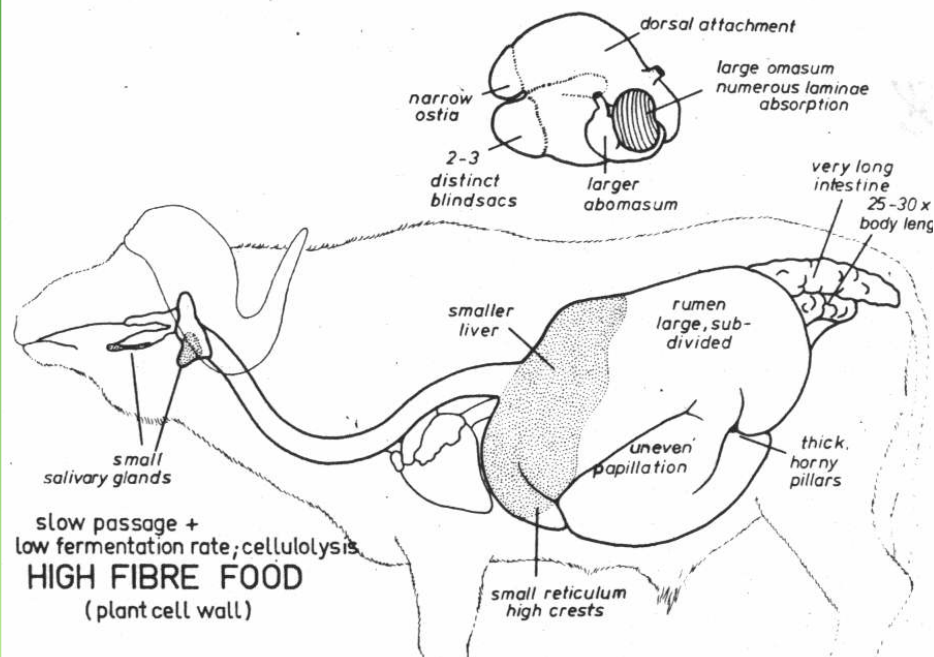


Fig. 1: The African buffalo, a non-selective roughage grazer.

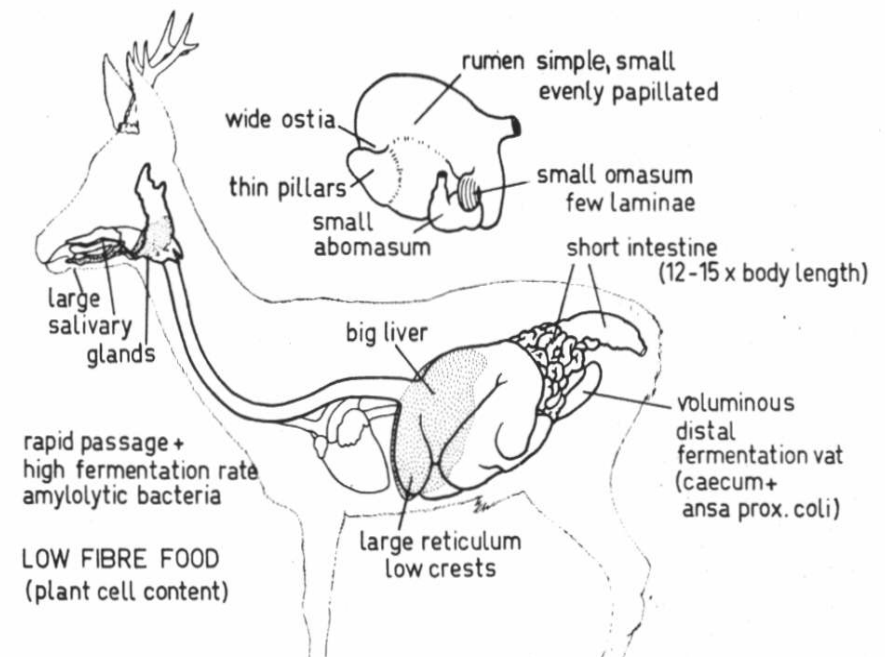


Fig. 2: The roe deer, a concentrate selector.

from Hofmann (1989)



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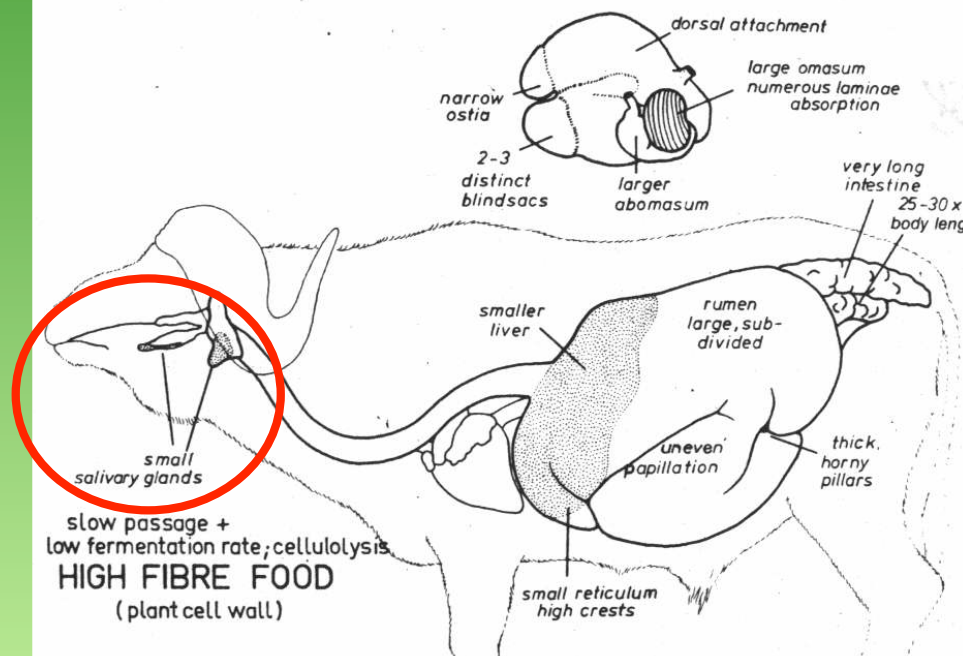


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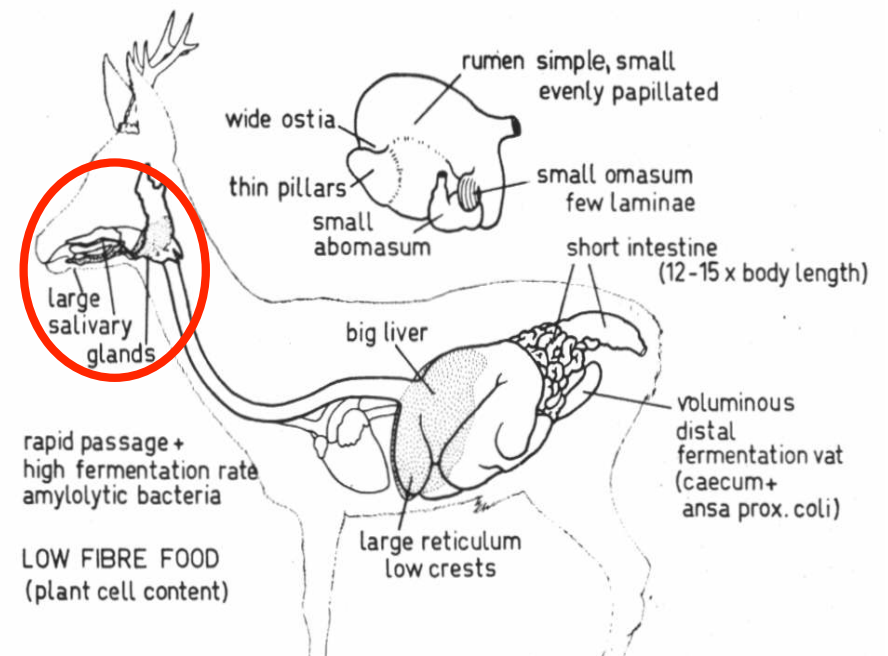


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Explaining a putative contradiction

a slow fluid turnover rate, while CS with high fermentation rates and a more rapid flow through a smaller RR (shorter retention) obviously required more buffer to protect them

liquid, which reduces retention time (as observed). Secondly, CS produce a much higher proportion of thin, proteinaceous *serous* saliva (all glands open into the mouth cavity)

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But there is another, third reason for much more (and more serous) saliva production in CS and IM: it is a

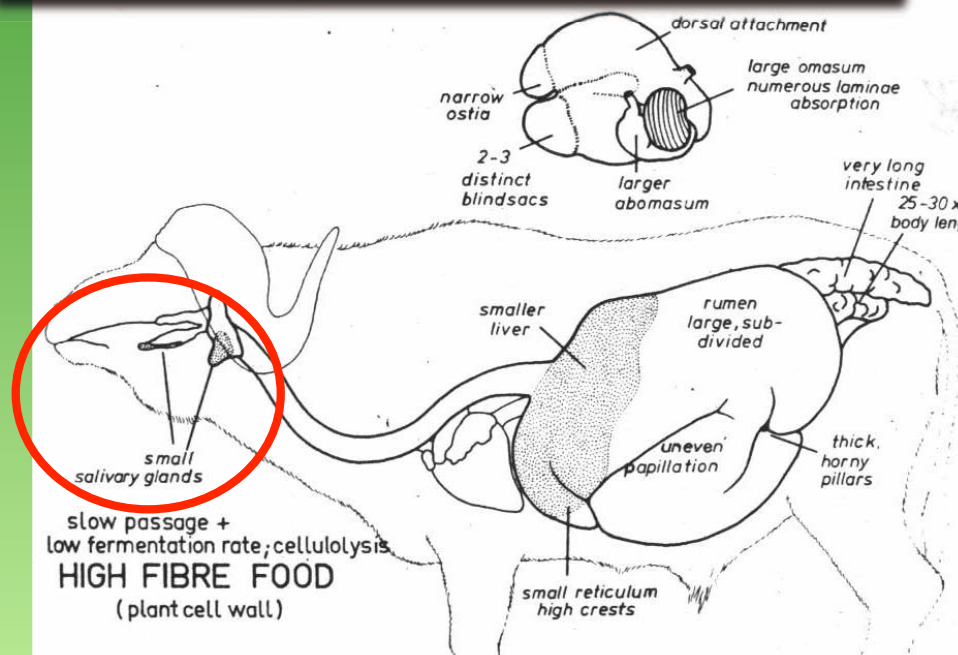


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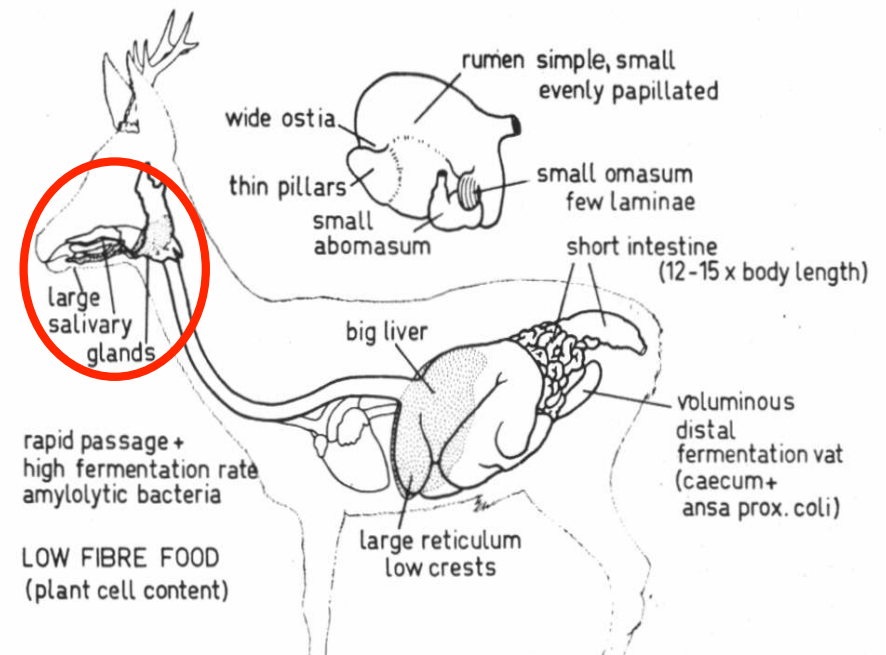


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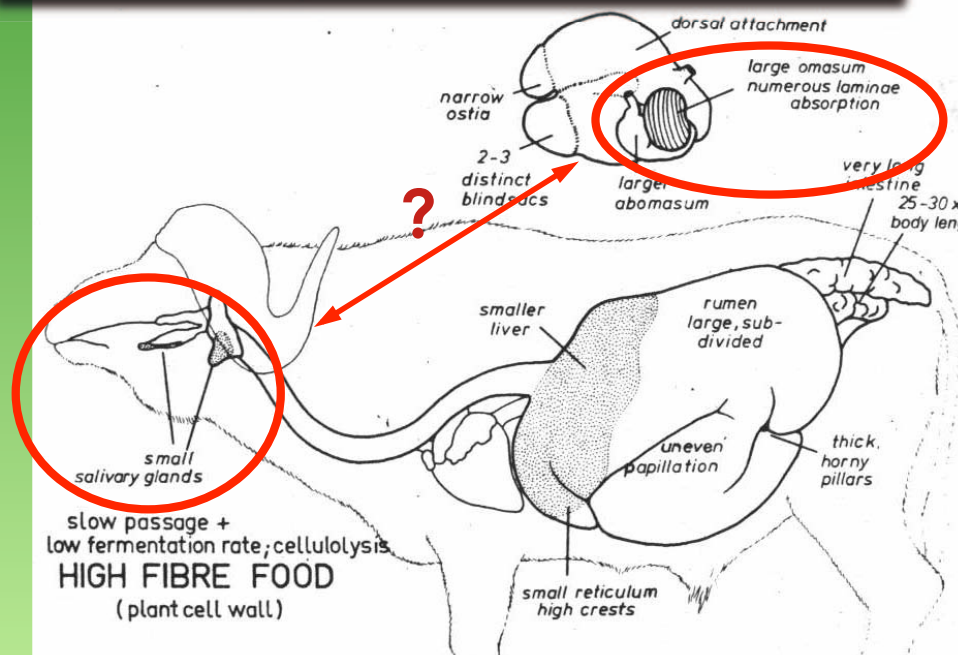


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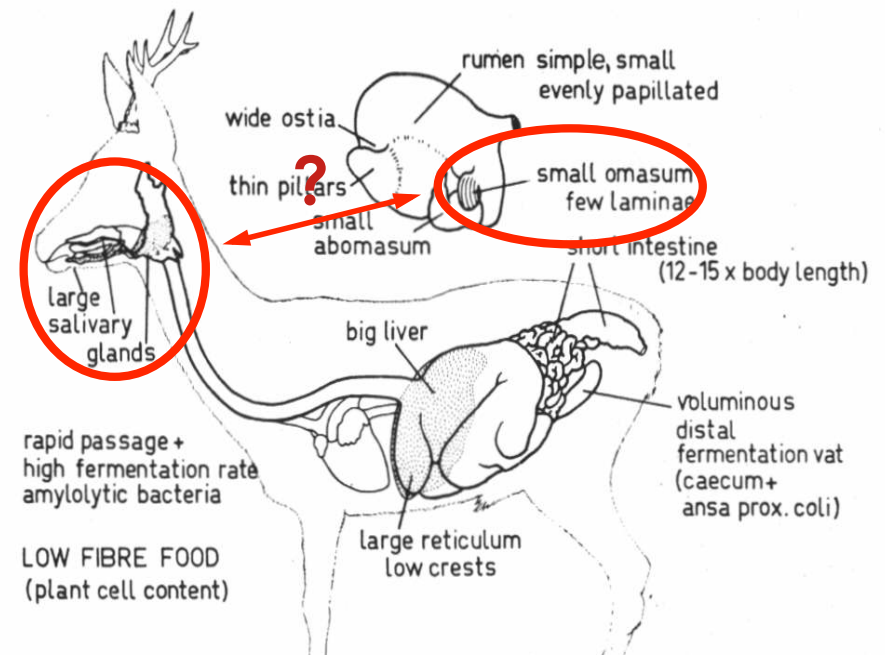


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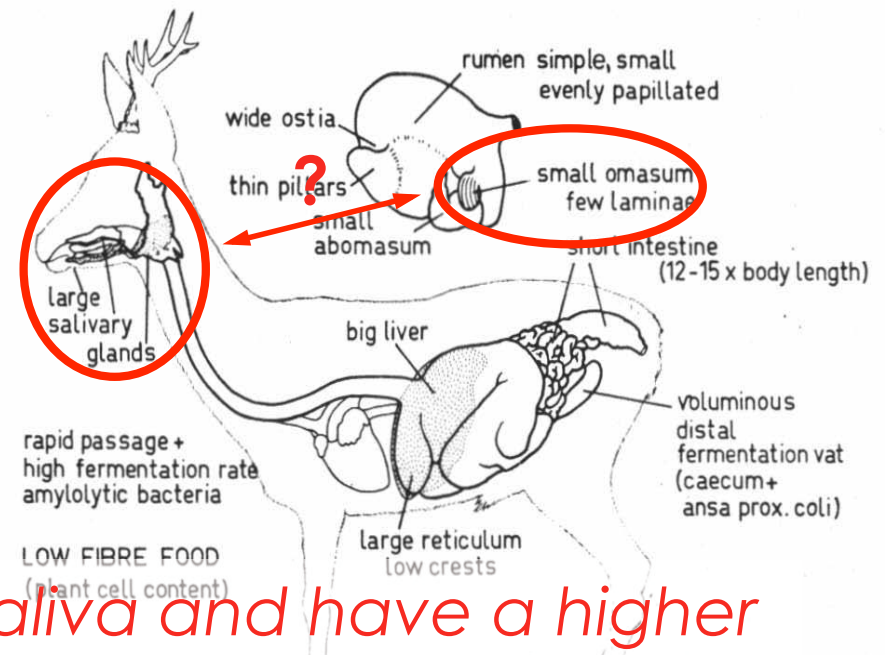
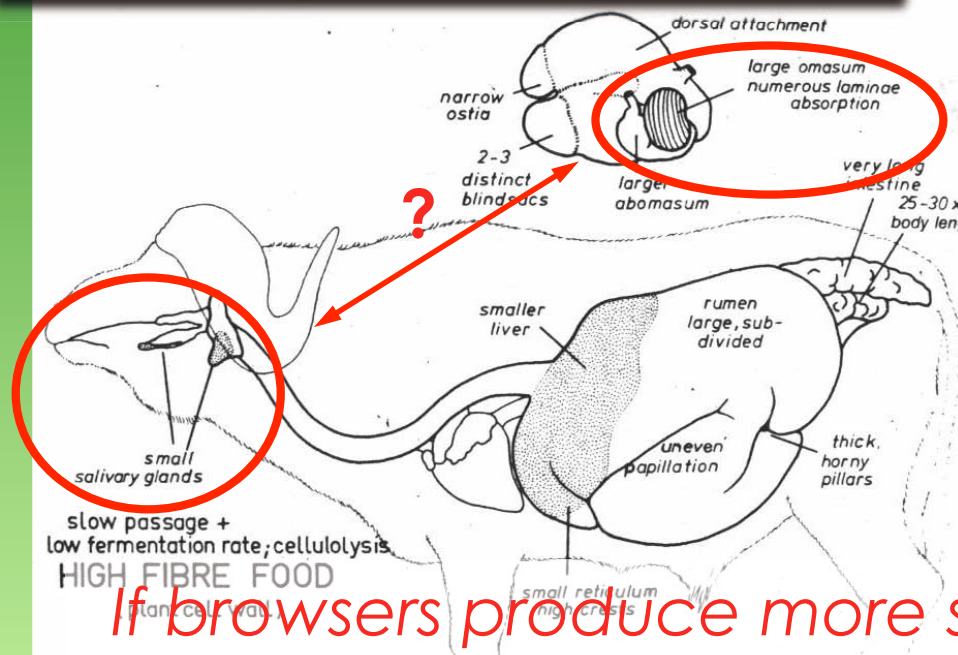
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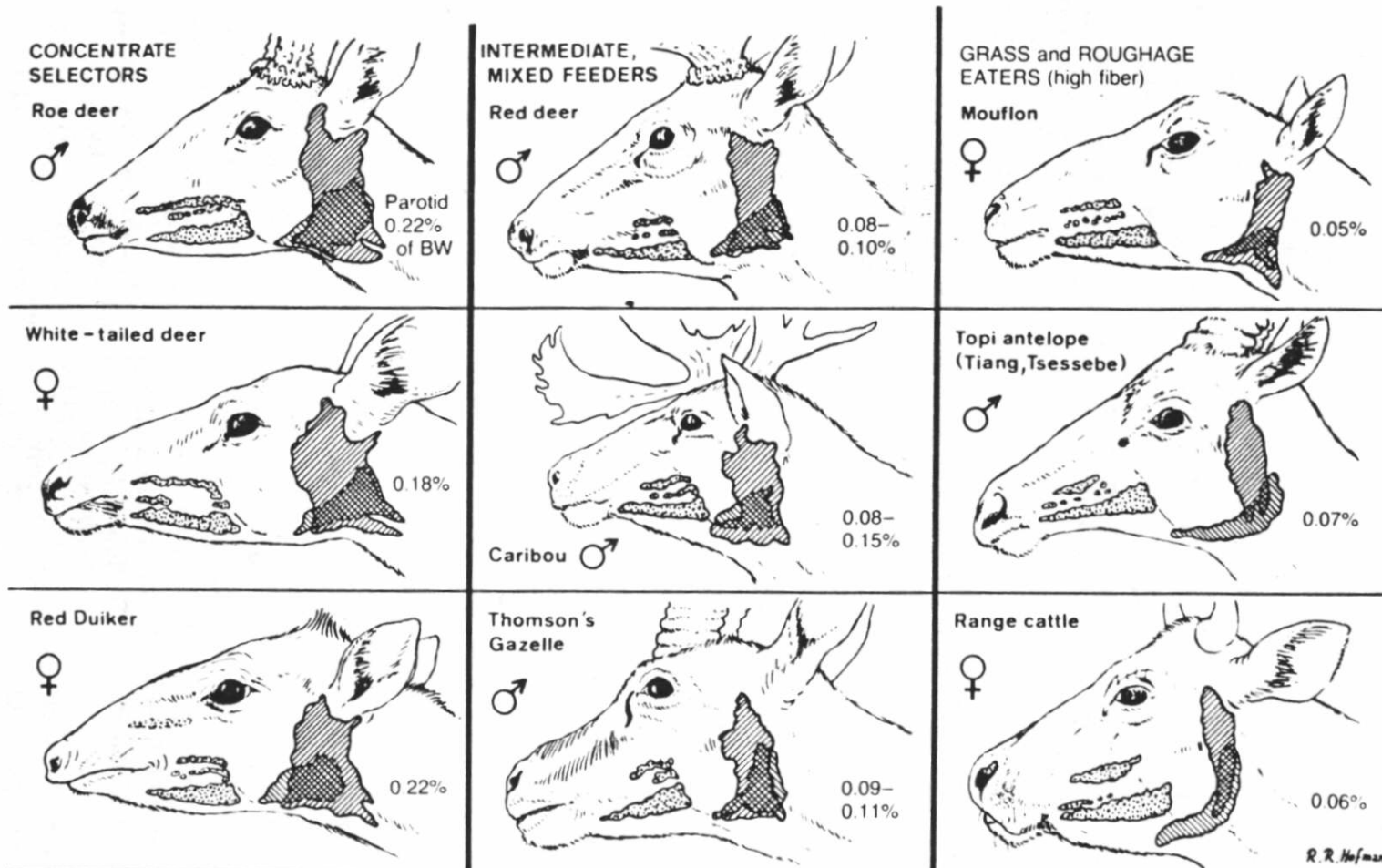


If browsers produce more saliva and have a higher fluid throughput through the rumen, why don't they have the larger omasa?

from Hofmann (1989)



Different salivary gland size



from Hofmann (1989)



Different salivary gland size

Browser

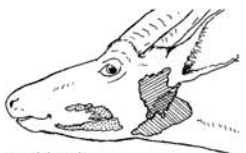
«Concentrate selector»



Günther's dikdik



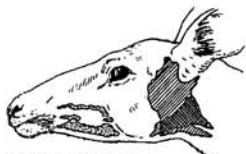
Red duiker



Bushbuck



Gerenuk



White-tailed deer



Moose

Intermediate feeder



Springbok



Thomson's gazelle



Chamois



Reindeer

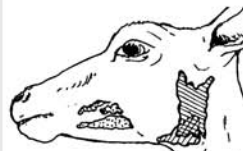


Takin



Red deer

Grazer



Mountain reedbuck



Himalaya tahr



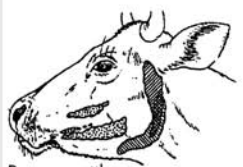
Mouflon



Topi/Tsessebe



Père David's deer



Range cattle



Different salivary gland size

Browser

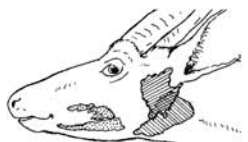
«Concentrate selector»



Günther's dikdik



Red duiker



Bushbuck



Gerenuk



White-tailed deer



Moose

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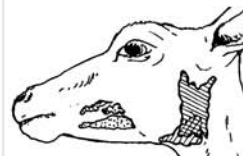


Takin



Red deer

Grazer



Mountain reedbuck



Himalaya tahr



Mouflon



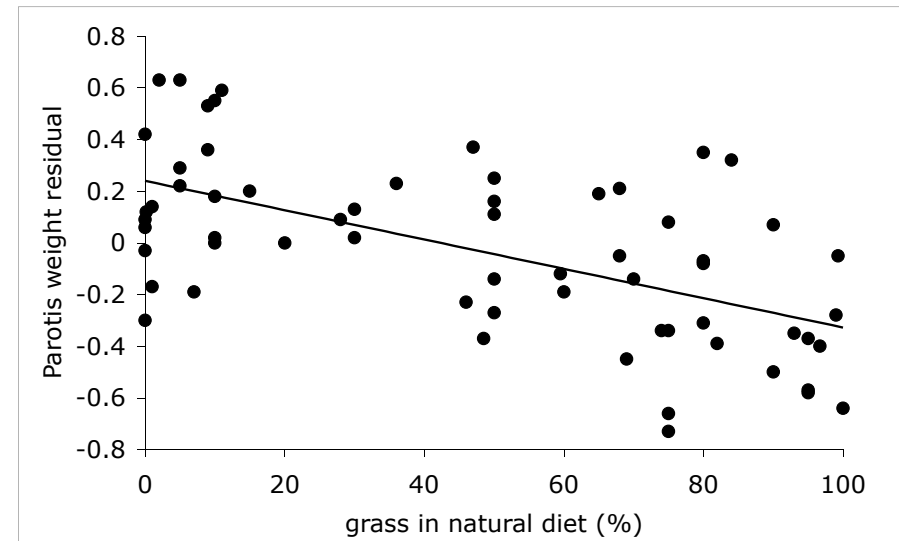
Topi/Tsessebe



Père David's deer



Range cattle



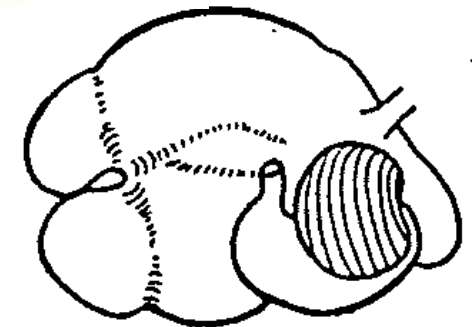
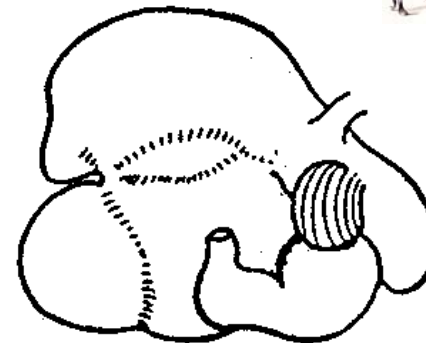
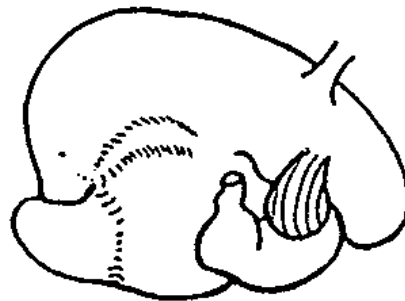
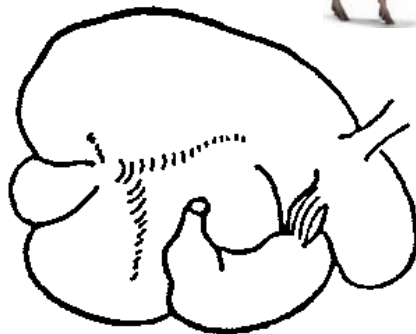
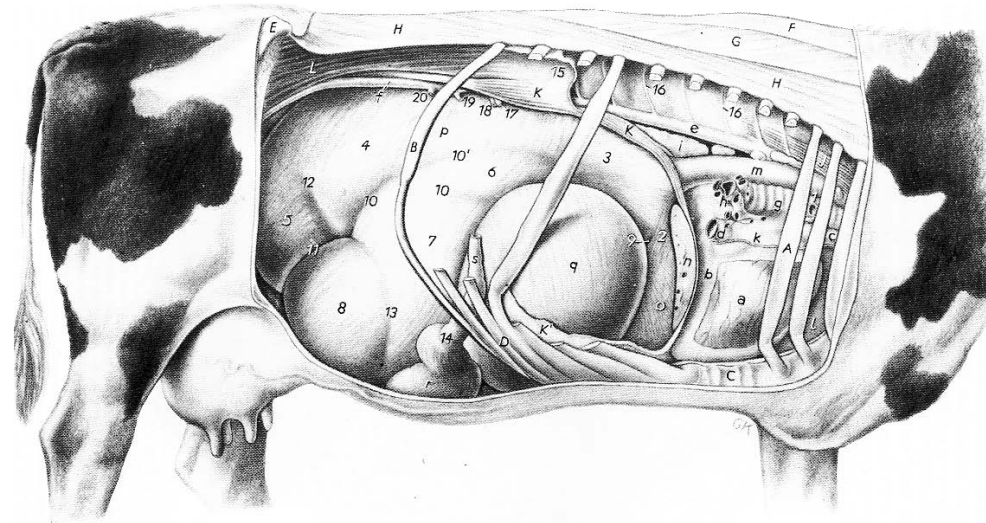
from Hofmann et al. (2008)



Different omasum size

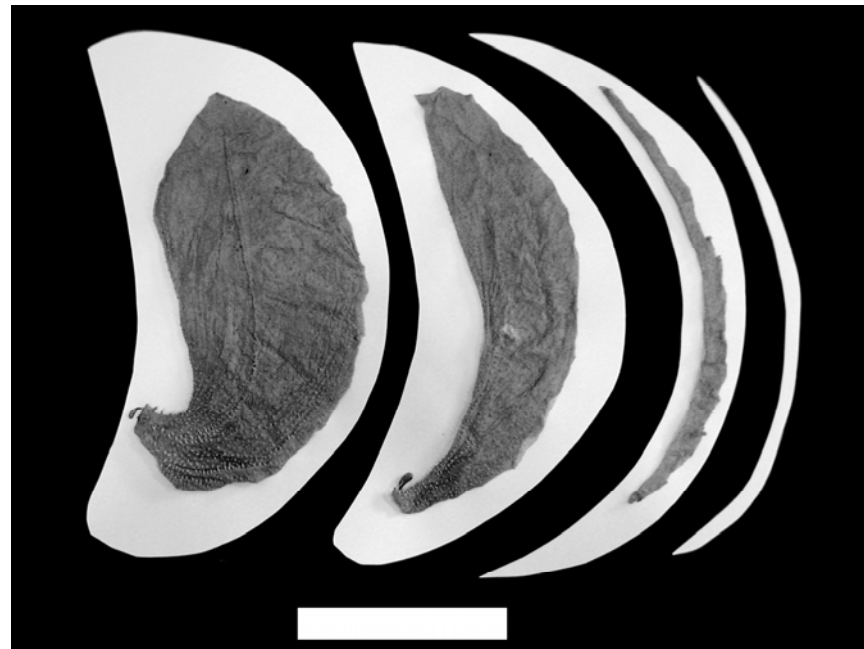
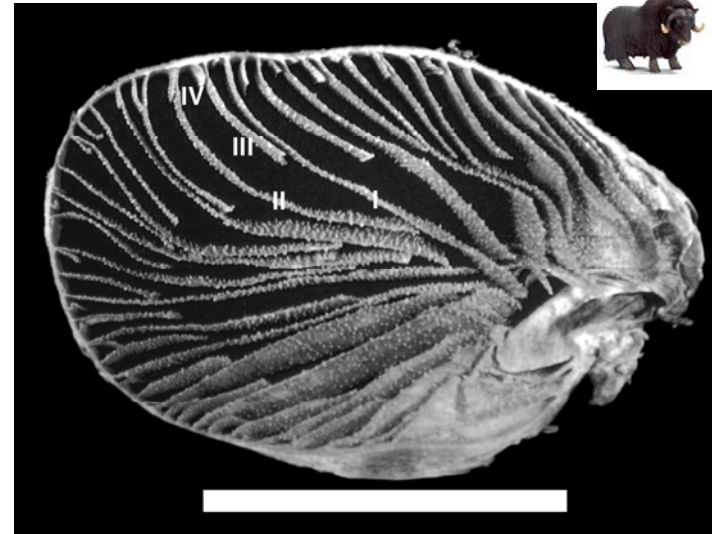
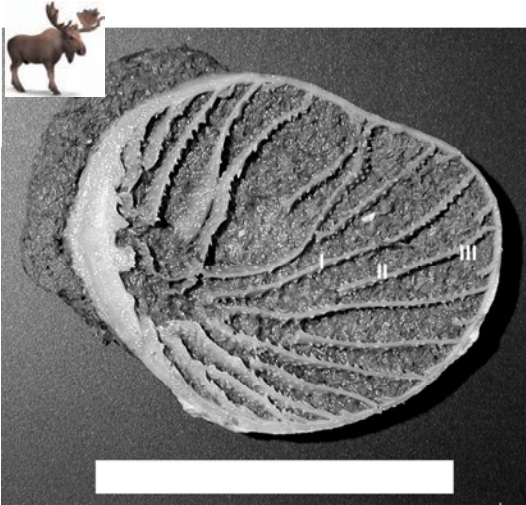


aus Hofmann (1973)
& Nickel et al. (1967)





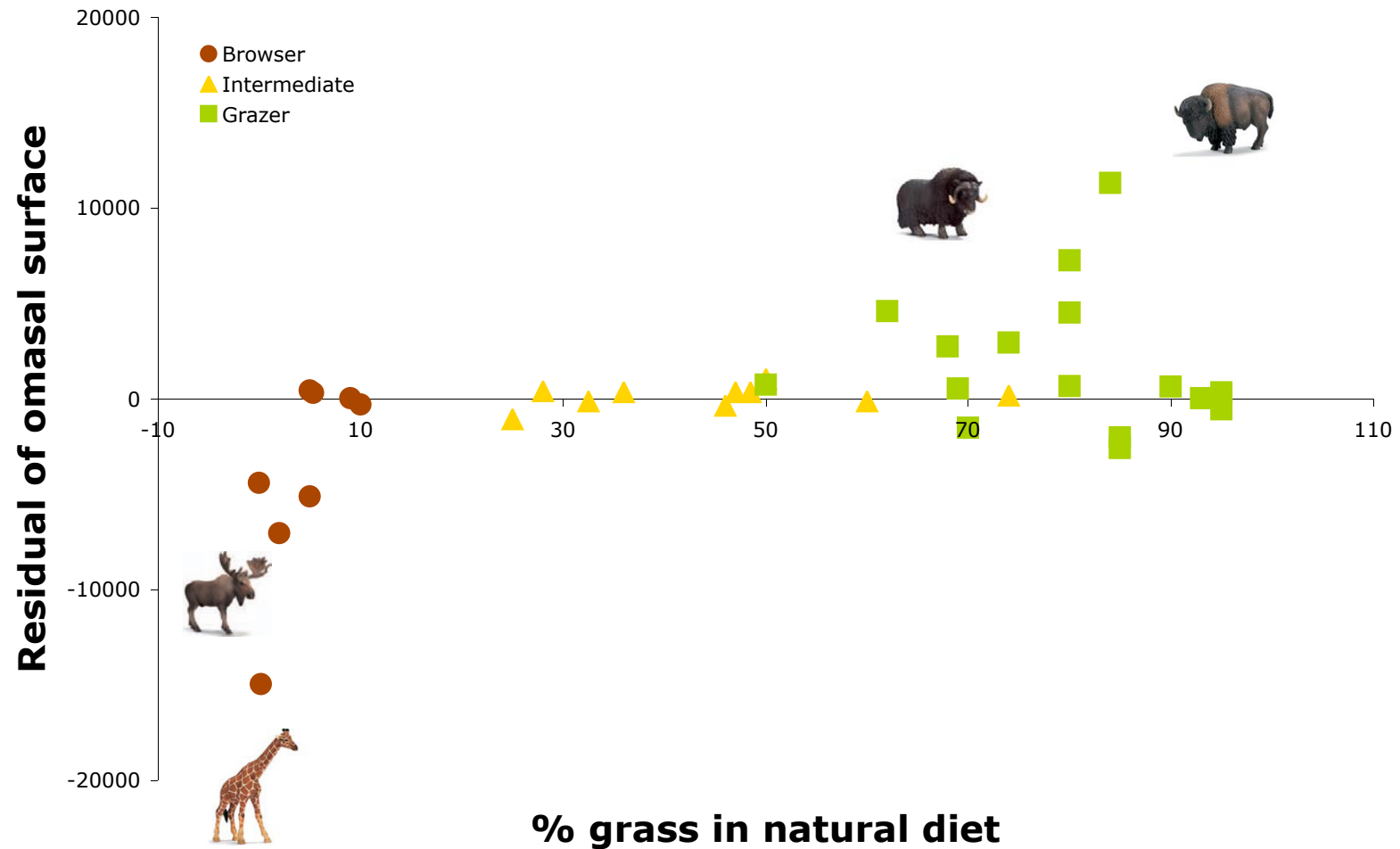
Different omasum size



from Clauss, Hofmann et
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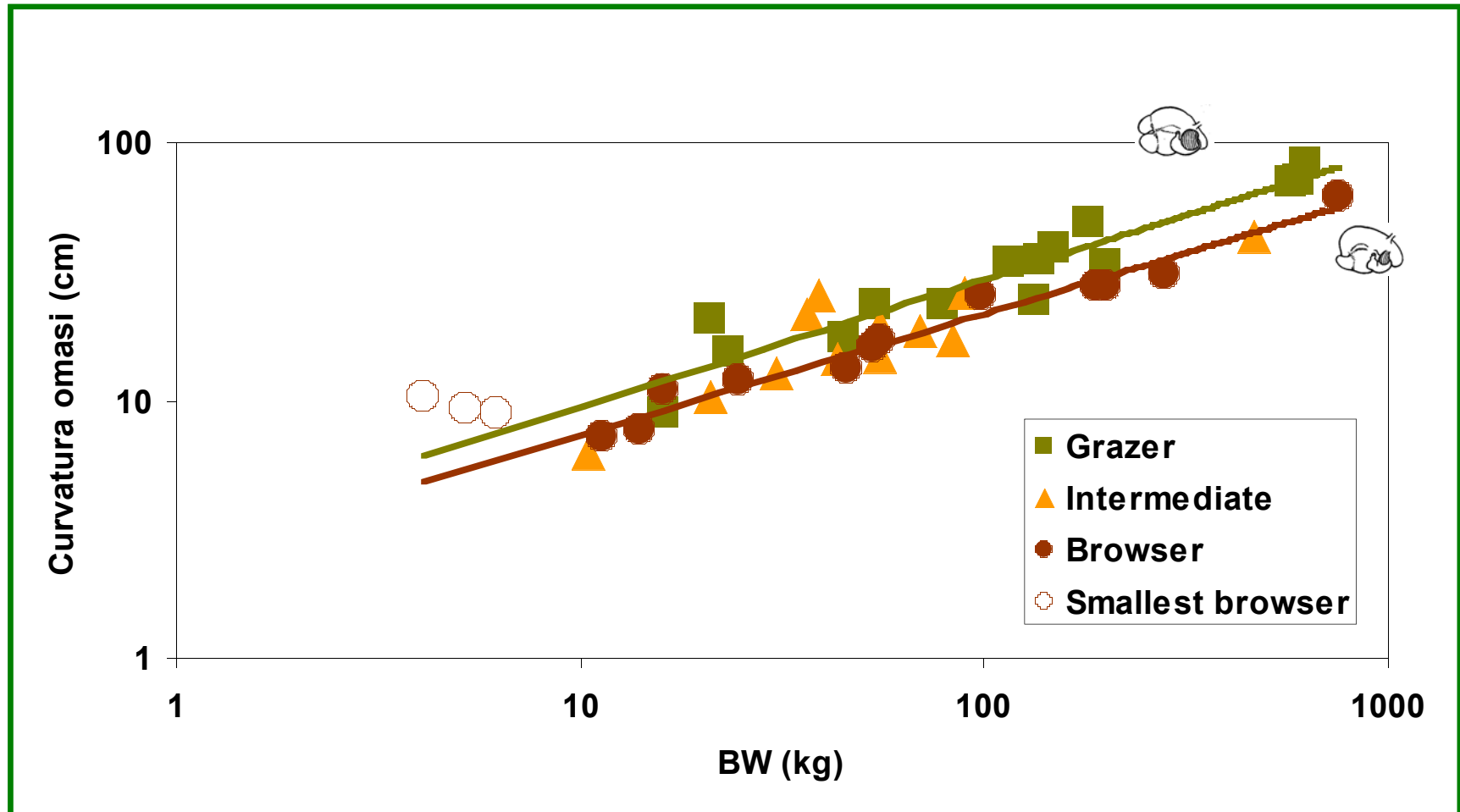
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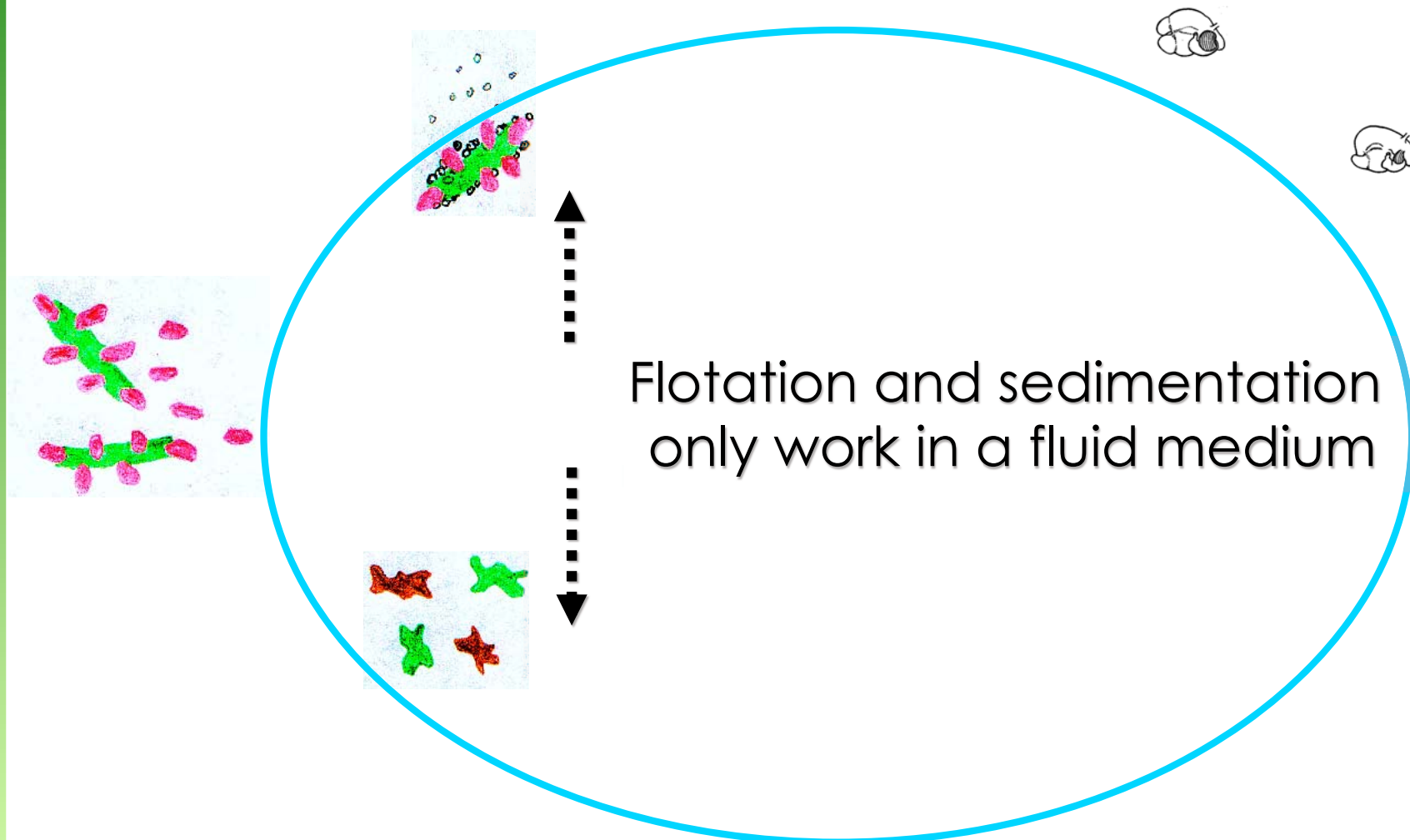
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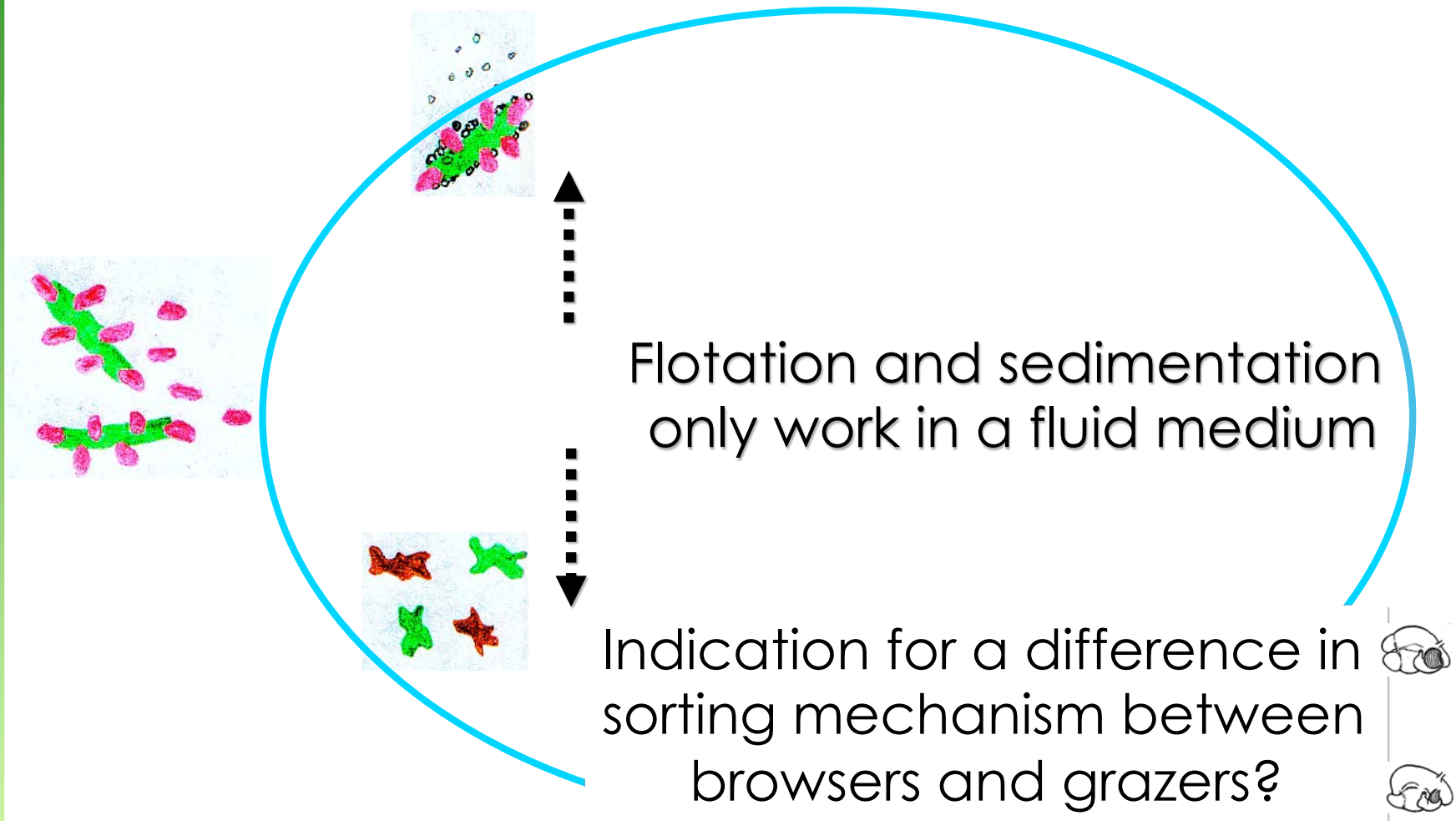


Sorting by density ...





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Our growing scientific knowledge of the nutritional physiology of ruminants is documented in a vast number of publications annually, and every five years more than 600 researchers from all over the world meet in a different place to review and present new results. They discuss highly specialised aspects of physiology, metabolism, nutrition, biochemistry and digestive problems of these remarkable mammals – yet very few of them or of the thousands of others who deal scientifically with ruminants appear to be concerned that almost all of their results, their methods and models are based on merely two out of 150 species of extant ruminants. These two are sheep and cattle. Much fewer physiological and nutritional data available refer to the goat and far fewer still to the Asiatic water buffalo. Compared to all this, experimental data on wild African bovids, Eurasian cervids or American deer (let alone such oddities as the pronghorn "antelope", the giraffe or the musk ox – all of which are ruminants) cannot even be regarded as minimal. However, each new study on ruminants other than cattle, sheep and goats shakes the established ruminant image. It is different, though similar.

Ruminants are animals important to man. Some species are bioindicators of the first order in polluted human environments. More species are living barometers of man's inability to understand and handle ecological interactions and most, if not all ruminant species can benefit nutritionally from what man cannot digest.

Because they convert apparently indigestible carbohydrates and chemically trapped or protected proteins into nutritious and useful products, they deserve more than one approach. Ruminants are late-comers in evolution. Their stomach is a phylogenetic peak of complexity, not only compared with our own digestive tract.

But it is wrong to define ruminants simply as specialised fermentation machines which break down cellulose after chewing the cud.

Their digestive physiology is not based on an "all or nothing" principle and none of them is "primitive", although embryological evidence strongly suggests that roe deer or white-tailed deer, dik-diks or muntjac, kudu or moose are "older", earlier and still inefficient in breaking down cellulose. It will be shown, that ruminant evolution in the light of today's 150 living species is certainly "a bush, not a ladder" (Gould 1986). It has produced a fascinating array of animal forms ranging from 3 kg to over 1000

2003

Evolutionary steps of ecophysiological adaptation and diversification of ruminants: a comparative view of their digestive system***

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Summary. A review is made of the ruminant digestive system in its morphophysiological variations and adaptations relating to foraging behaviour, digestive physiology, to interactions between plants and ruminants and to geographic and climatic diversity of ruminants' ecological niches. Evi-

Our growing scientific knowledge of the nutritional physiology of ruminants is documented in a vast number of publications annually, and every five years more than 600 researchers from all over the world meet in a different place to review and present new results. They discuss highly spe-

a shorter retention time of ingesta. At the end of long grazing periods the maximally filled GR ruminoreticulum shows a stratification of ingesta according to specific weight and particle size with lighter, longer parts floating above. CS normally do *not* fill their rumen above the "bottleneck" outlet to the omasum (reticulo-omasal orifice) and their better diluted mass of short-broken dicot material does *not stratify*. Their relatively larger reticulum is in wide connec-

teractions between wild ruminants and their specific habitats, which he alters or destroys.

Key words: Wild ruminants – Digestive system – Morphophysiological adaptation – Evolutionary trends – Plant-herbivore interactions

* Supported by German Research Community grant DFG Ho 273/6

** Dedicated to Professor Dr. Dr. h.c. Dietrich Starck on the occasion of his 80th birthday

Abbreviations: bw body weight; CS concentrate selector; DFC distal fermentation chamber (distended caecocolon); GR grass and roughage eater; IM intermediate (mixed) feeder; PFC proximal fermentation chamber (ruminoreticulum/forestomachs); RR Ruminoreticulum; SCFA Short-chain fatty acids (acetic, butyric, propionic acid set free by rumen bacteria); SE Surface enlargement (of absorptive mucosa)

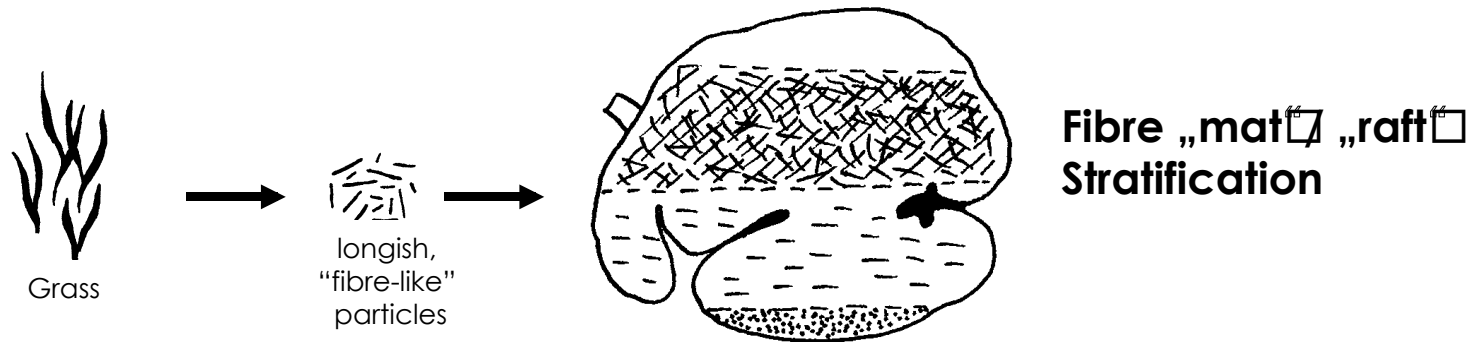
drates and chemically trapped or protected proteins into nutritious and useful products, they deserve more than one approach. Ruminants are late-comers in evolution. Their stomach is a phylogenetic peak of complexity, not only compared with our own digestive tract.

But it is wrong to define ruminants simply as specialised fermentation machines which break down cellulose after chewing the cud.

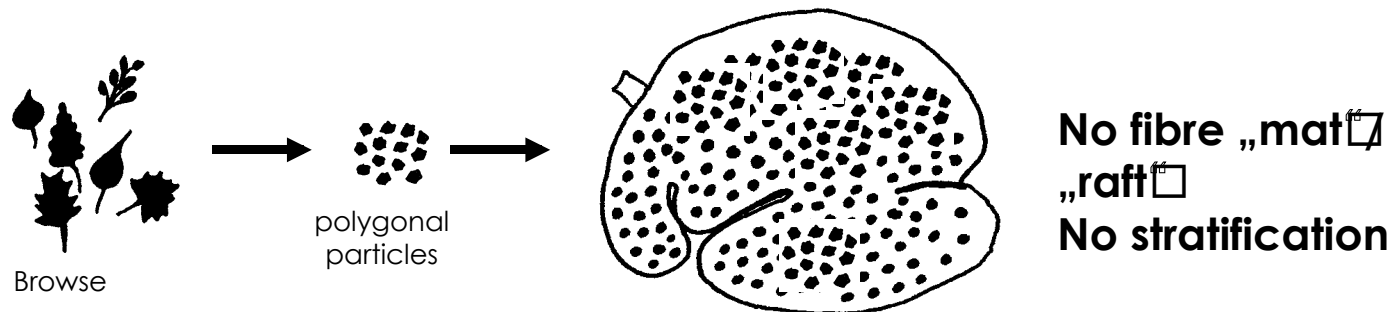
Their digestive physiology is not based on an "all or nothing" principle and none of them is "primitive", although embryological evidence strongly suggests that roe deer or white-tailed deer, dik-diks or muntjac, kudu or moose are "older", earlier and still inefficient in breaking down cellulose. It will be shown, that ruminant evolution in the light of today's 150 living species is certainly "a bush, not a ladder" (Gould 1986). It has produced a fascinating array of animal forms ranging from 3 kg to over 1000



Grazer



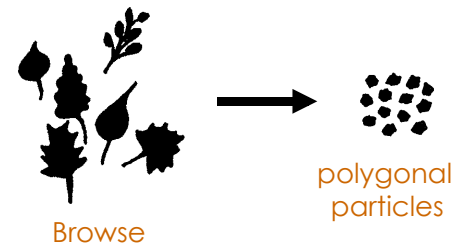
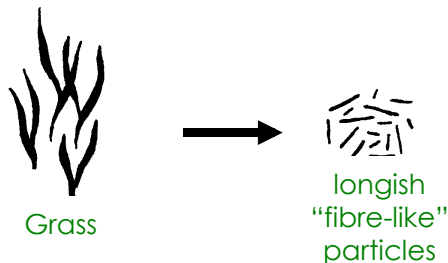
Browser





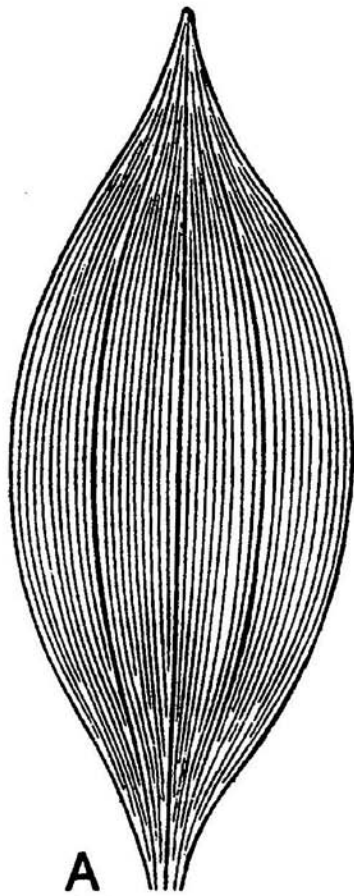
Differences in the physical structure between grass and browse

- Cell walls of grass are thicker than those of browse
- Grass and browse fractionate into particles of different shape

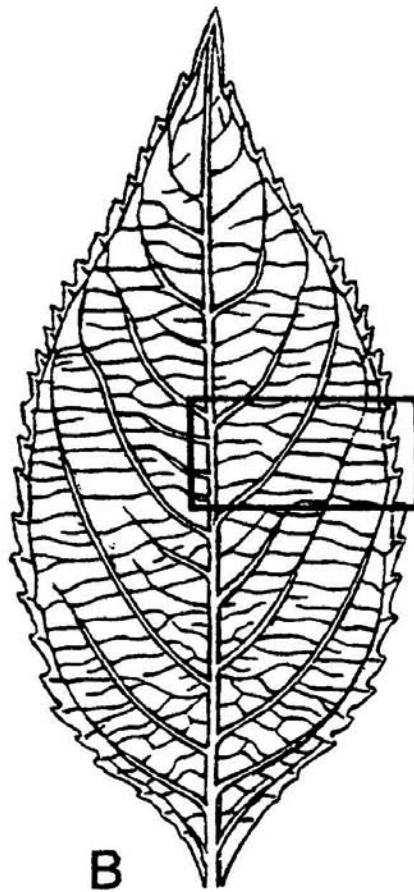




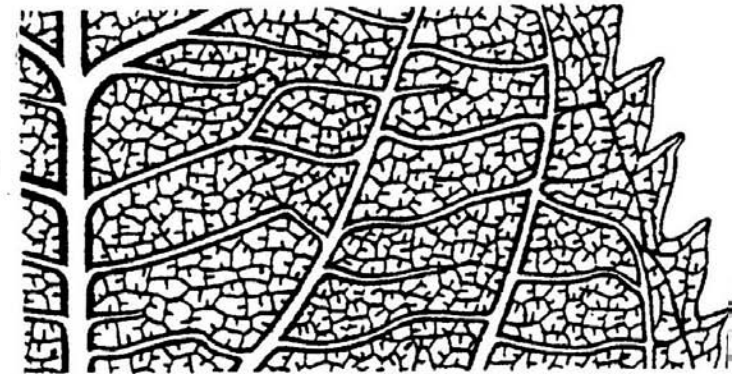
Differences in the physical structure between grass and browse



A
Monocotyledon



B
Dicotyledon

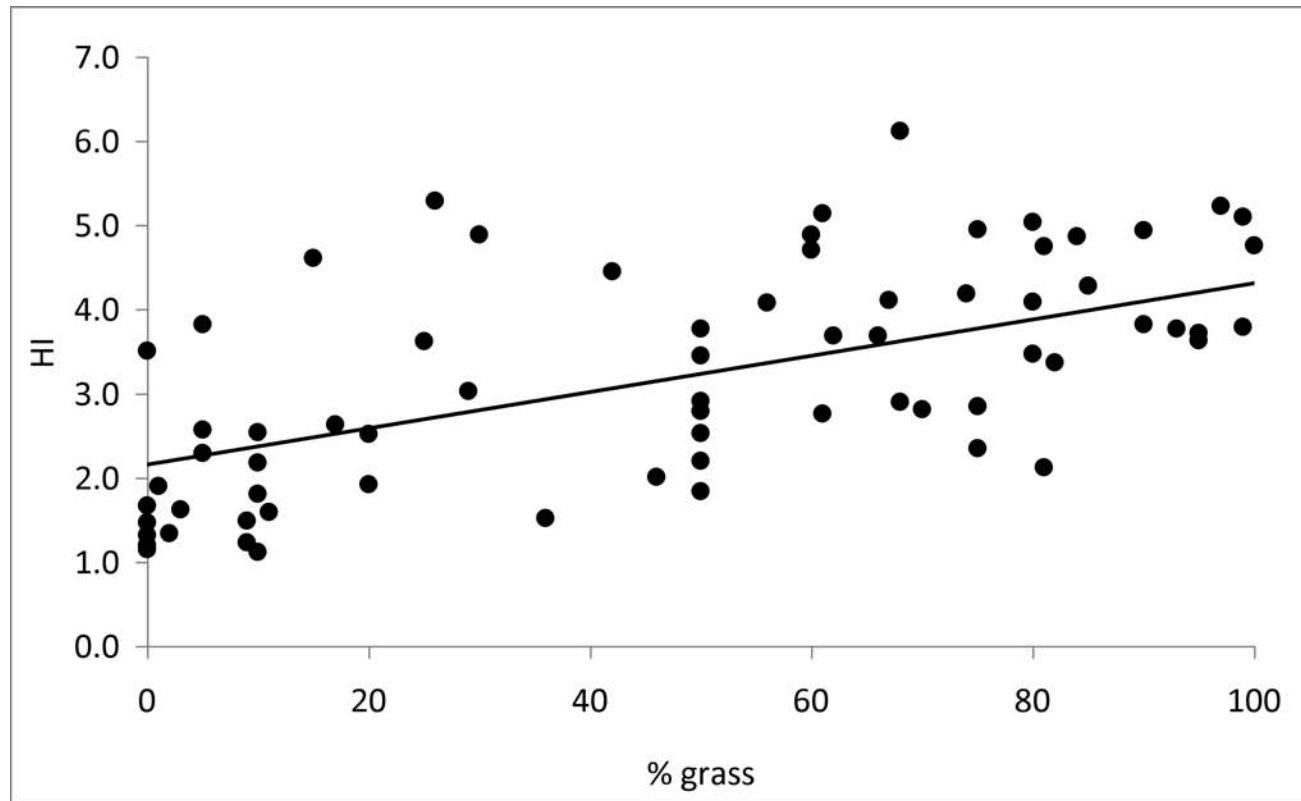


C



Dental adaptations

- An evident link: hypsodonty index and grass consumption



own evaluation, but similar findings published by Janis (1995), Perez-Barberia and Gordon (2001), Mendoza and Palmqvist (2008)



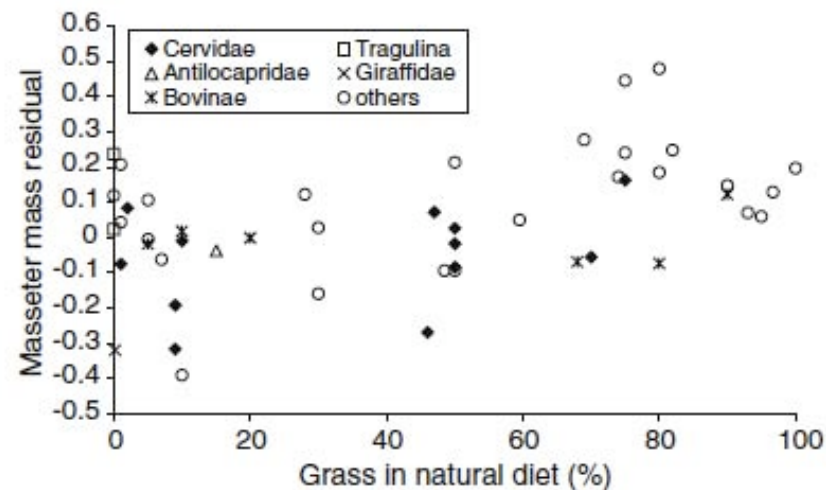
Masticatory adaptations

Oecologia (2008) 157:377–385
DOI 10.1007/s00442-008-1093-z

PHYSIOLOGICAL PHYSIOLOGY - ORIGINAL PAPER

Higher masseter muscle mass in grazing than in browsing ruminants

Marcus Clauss · Reinold R. Hofmann ·
W. Jürgen Streich · Jörns Fickel · Jürgen Hummel





Dental adaptations

Journal of Zoology

ZSL
LIVING CONSERVATION

Journal of Zoology. Print ISSN 0952-8369

Enamel ridge alignment in upper molars of ruminants in relation to their natural diet

T. M. Kaiser¹, J. Fickel², W. J. Streich², J. Hummel³ & M. Clauss⁴

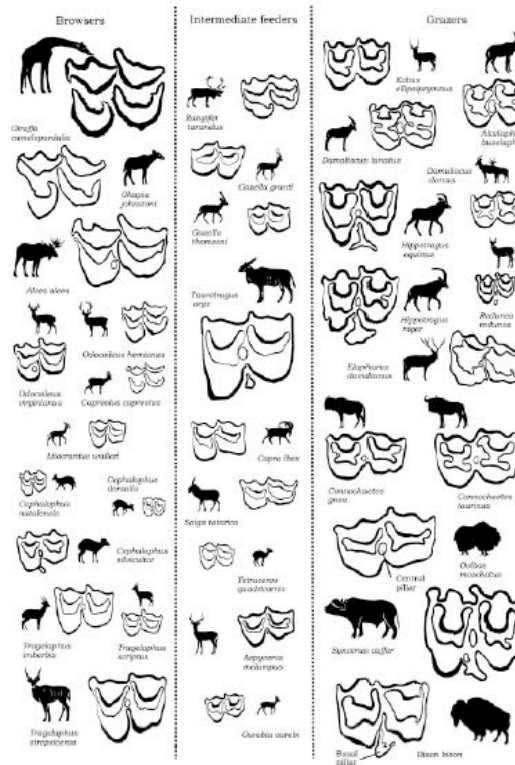
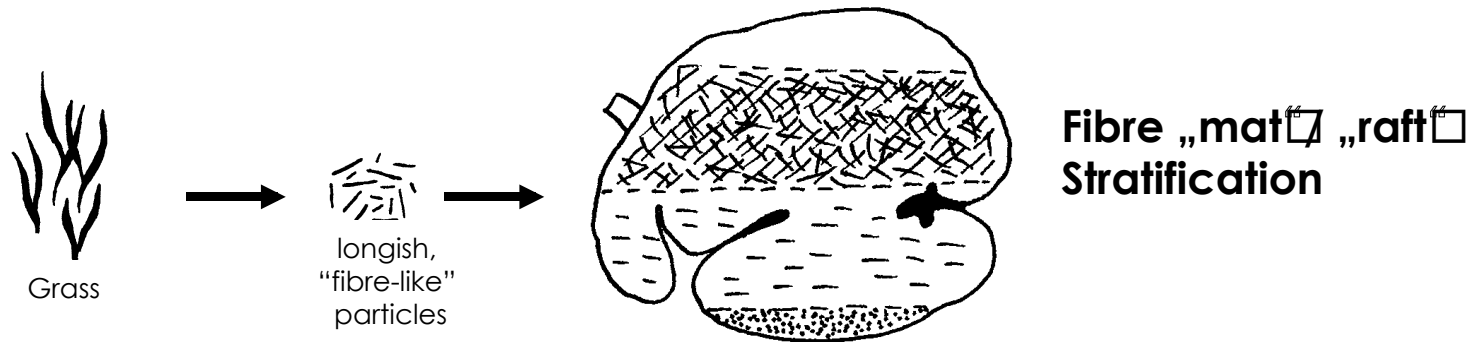


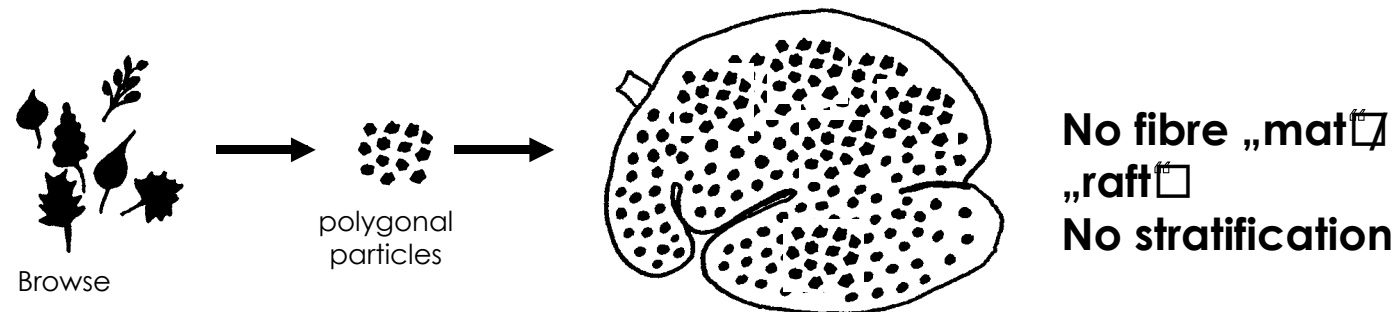
Figure 2 Upper second molar occlusal surfaces of some of the species included in this study. The occlusal enamel ridge pattern of a typical specimen is shown in original size. The buccal side of the molar is directed towards the top of the page, and the lingual side towards the bottom. Note the presence of central and basal pillars in some species. Animal pictograms are partly adapted from Mori & Carter (1971).



Grazer



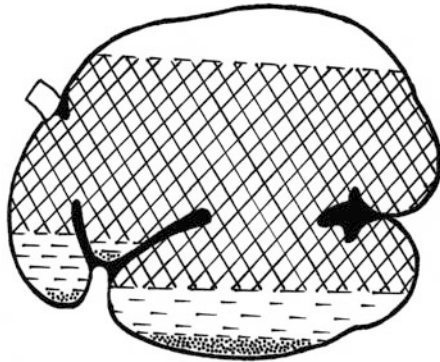
Browser



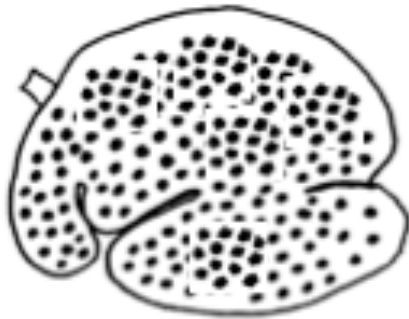


Differences in flotation behaviour between grass and browse?

Grazer



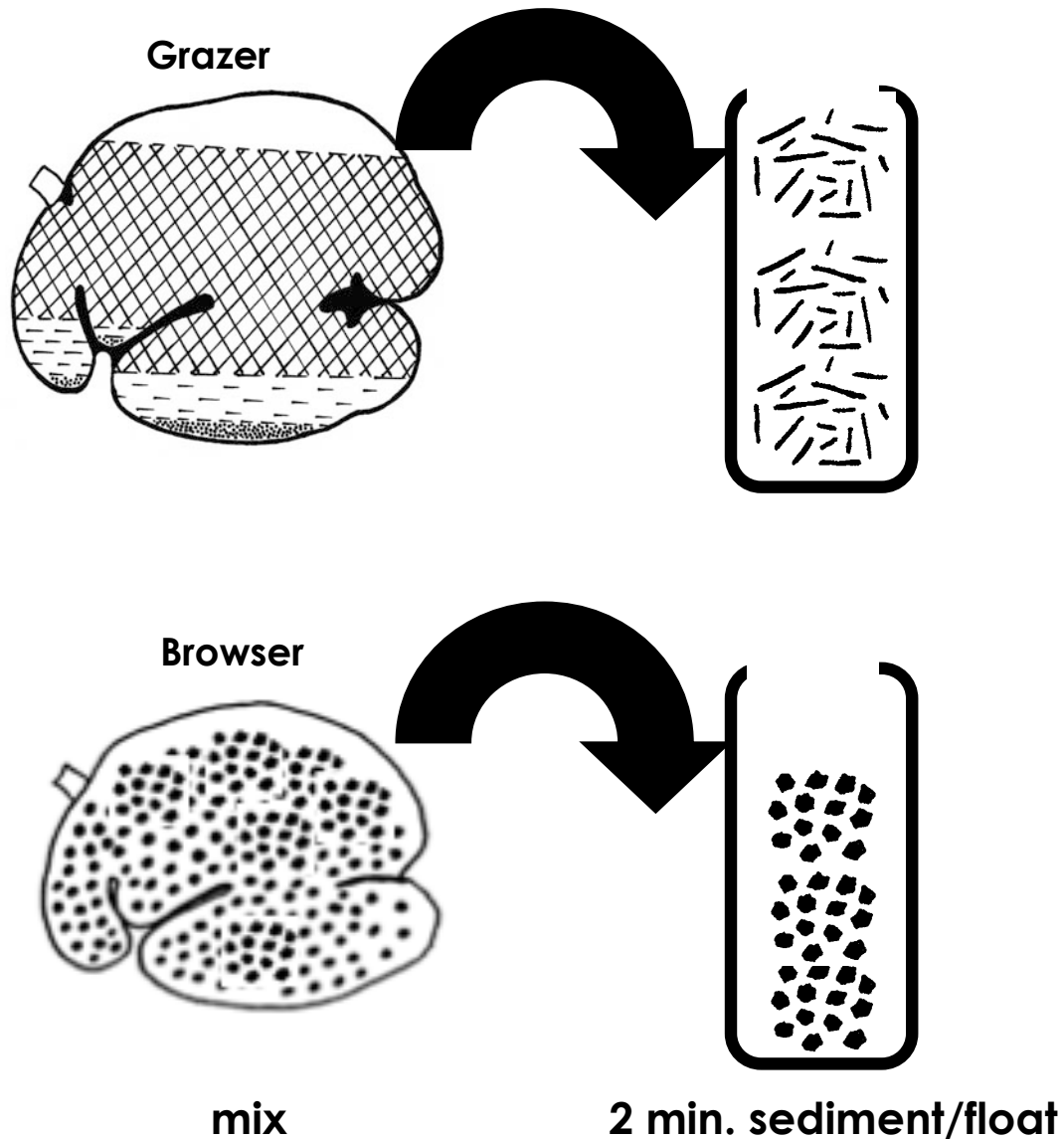
Browser



mix

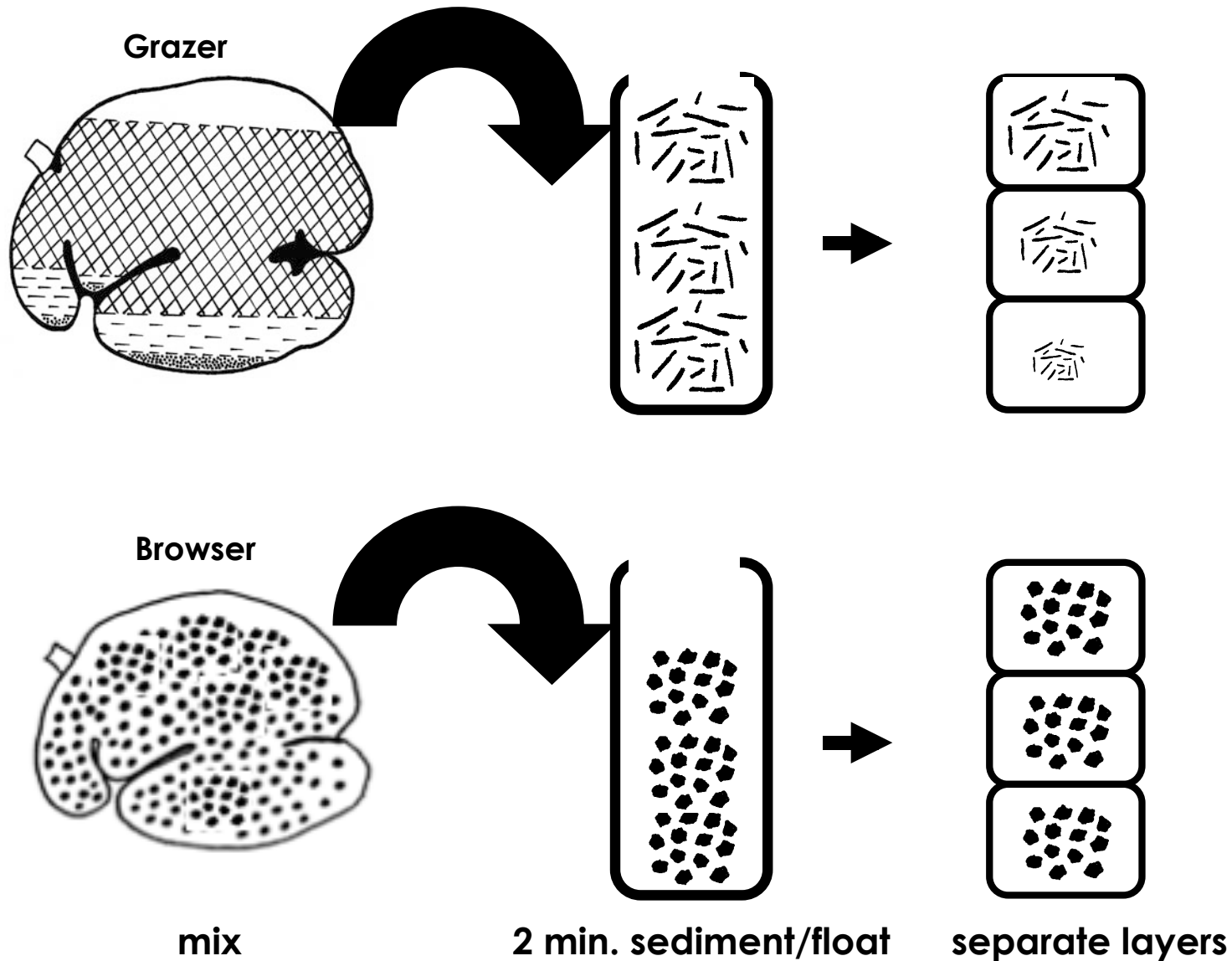


Differences in flotation behaviour between grass and browse?



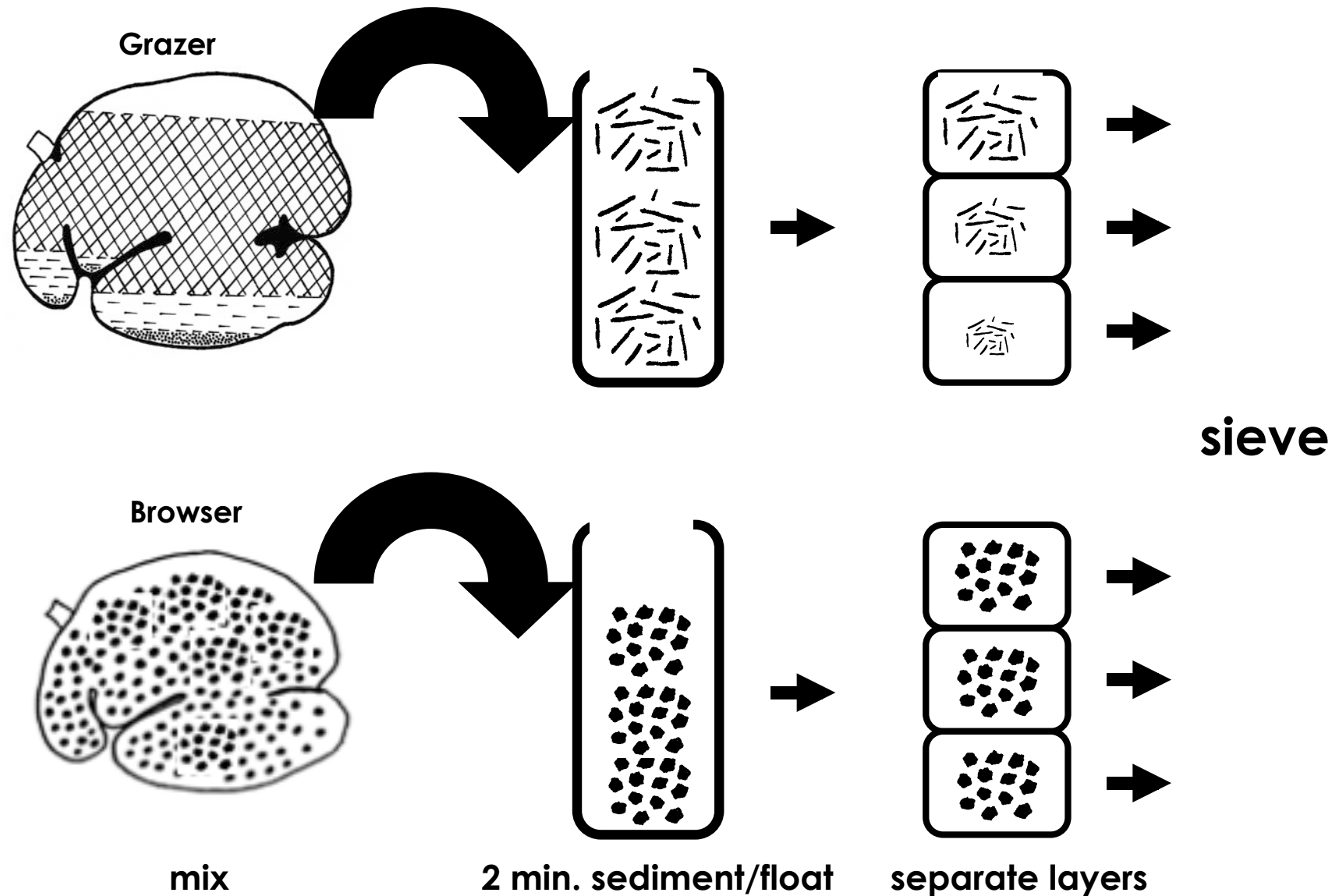


Differences in flotation behaviour between grass and browse?



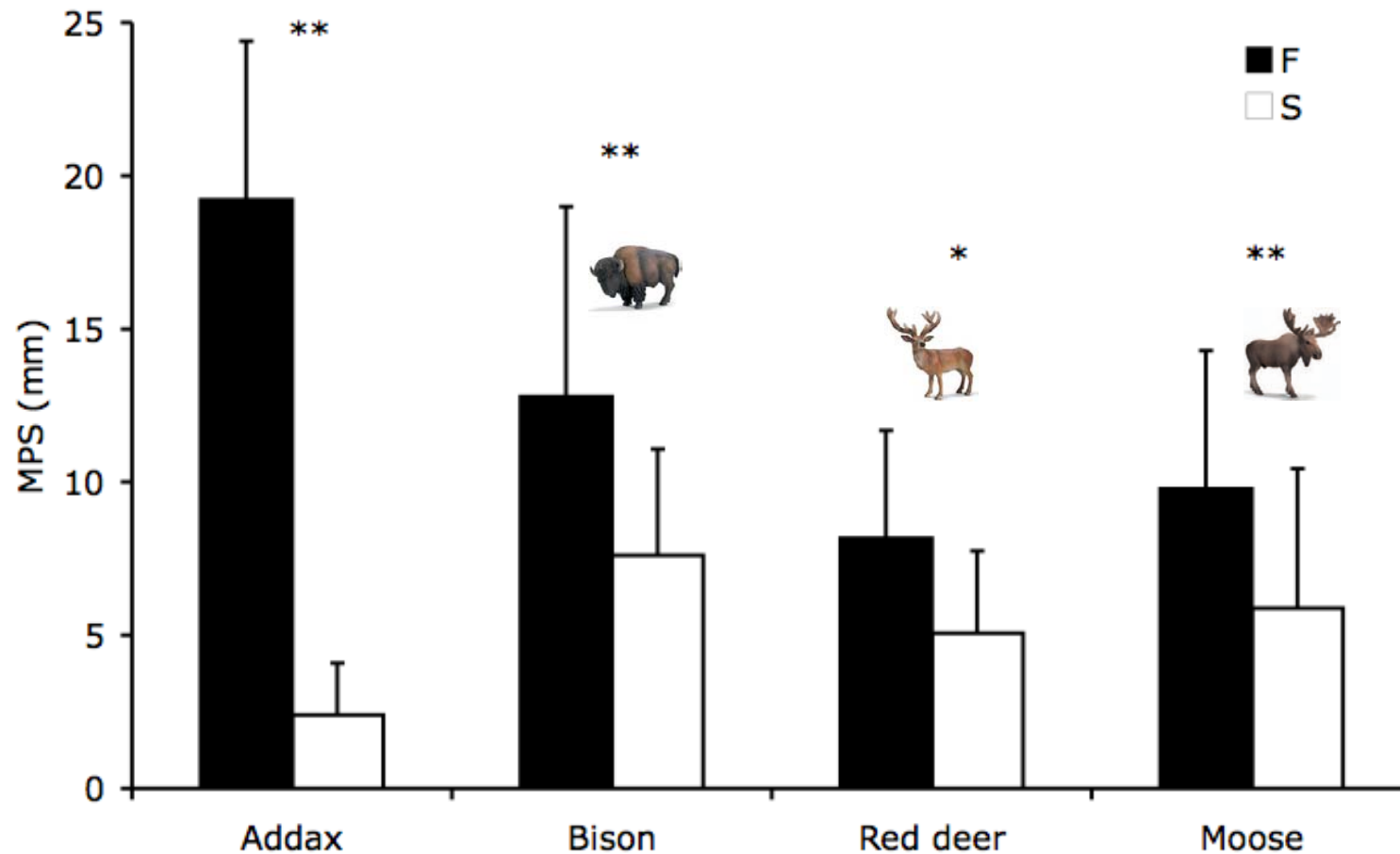


Differences in flotation behaviour between grass and browse?





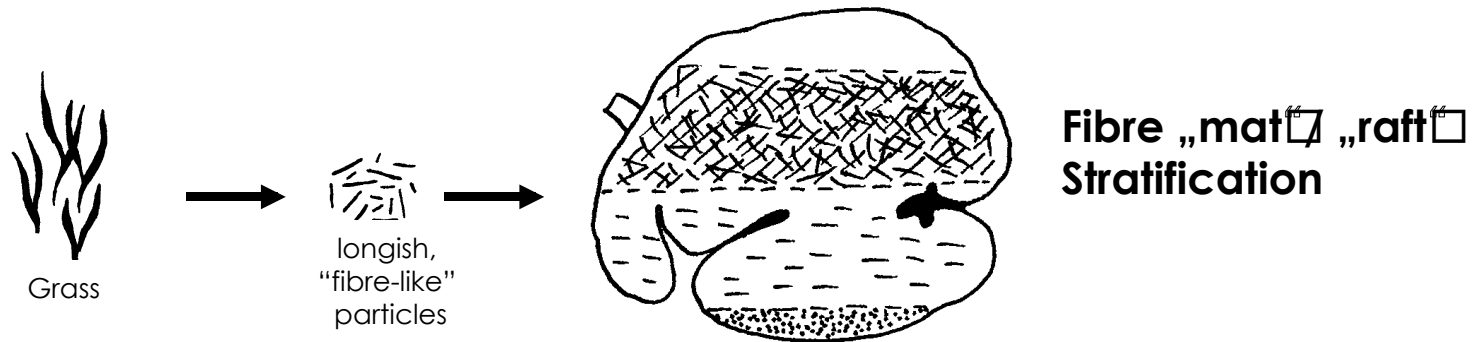
Differences in flotation behaviour between grass and browse? – **NO!**



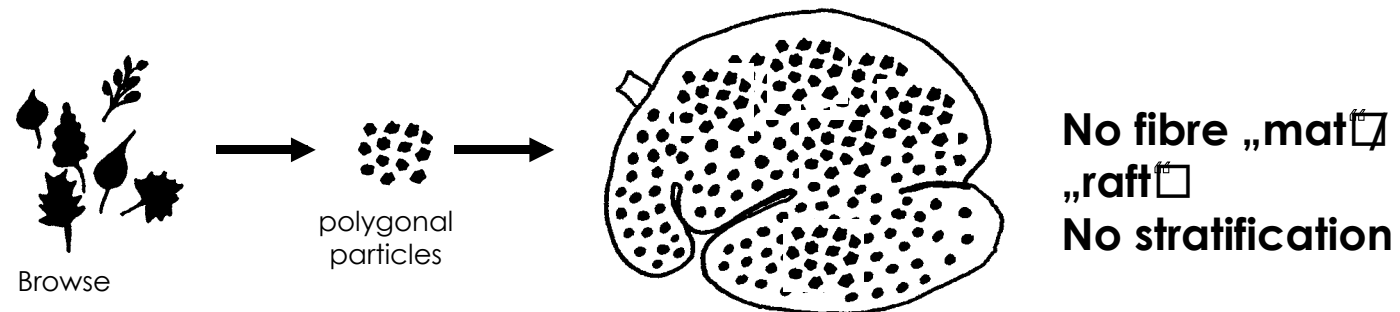
from Clauss et al. (2009)



Grazer

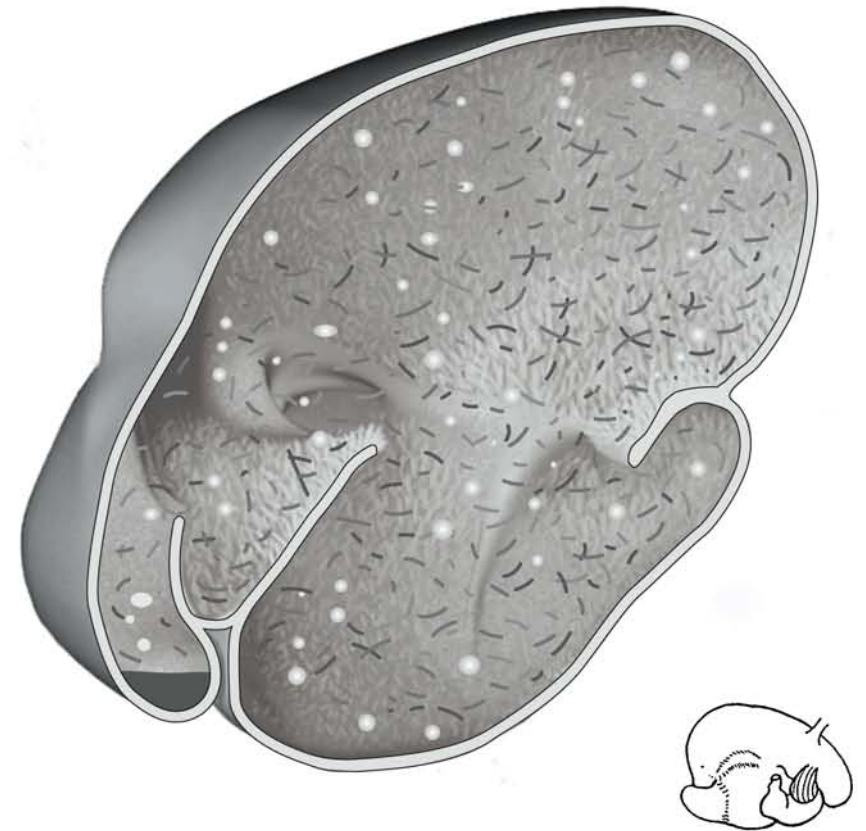
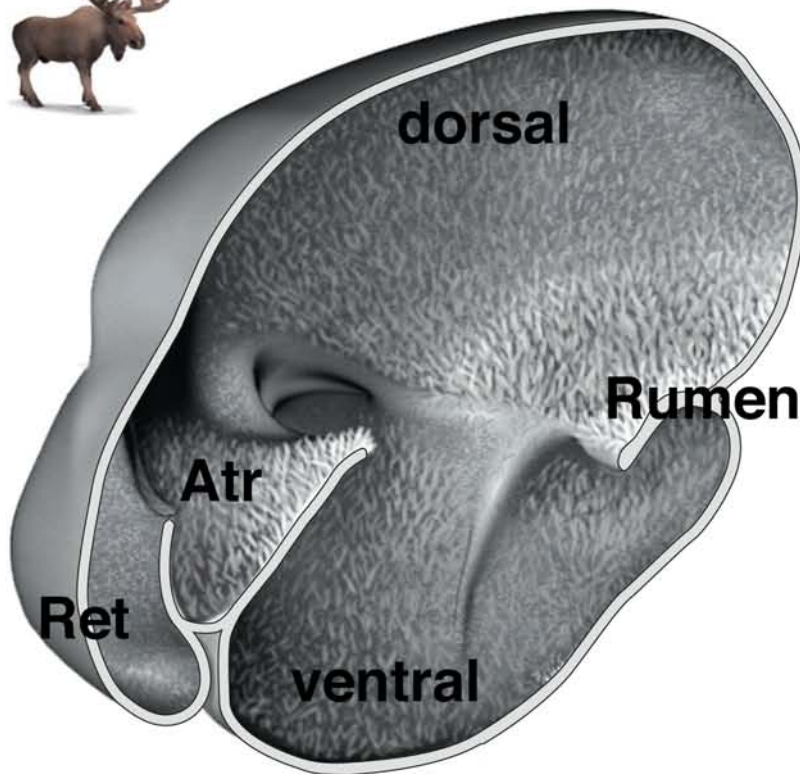


Browser



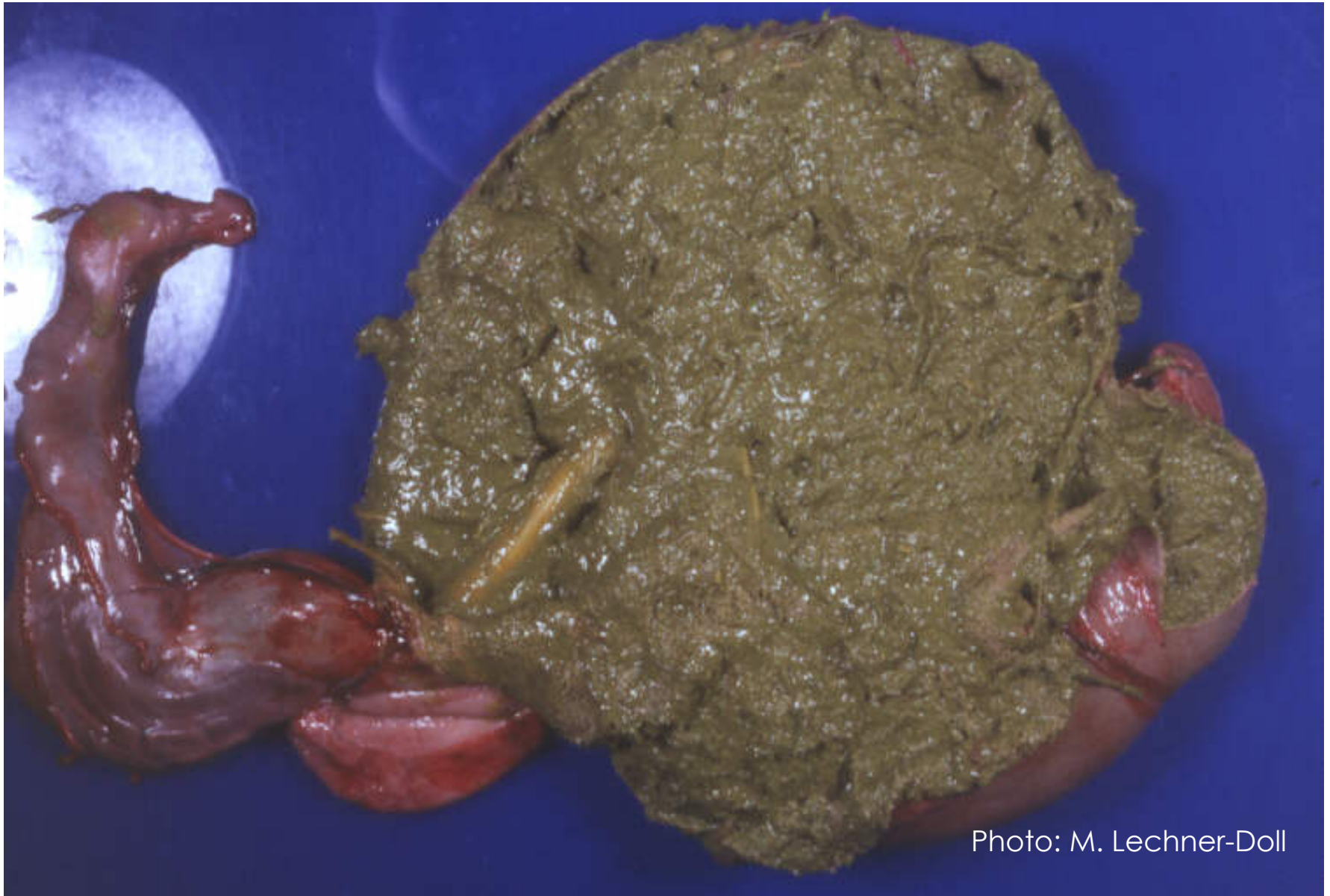


No stratification of rumen contents: 'moose-type'



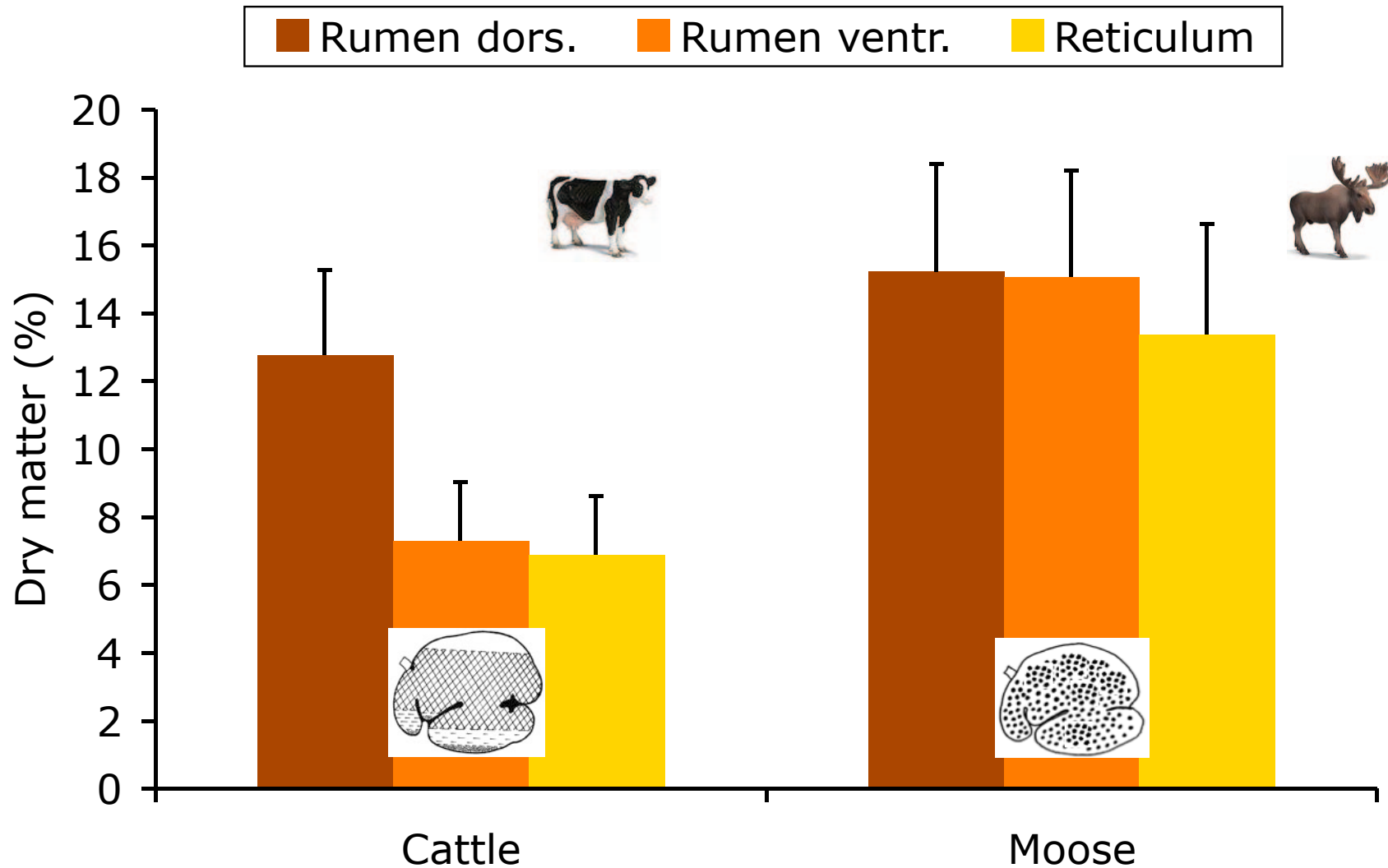


No stratification of rumen contents: 'moose-type'





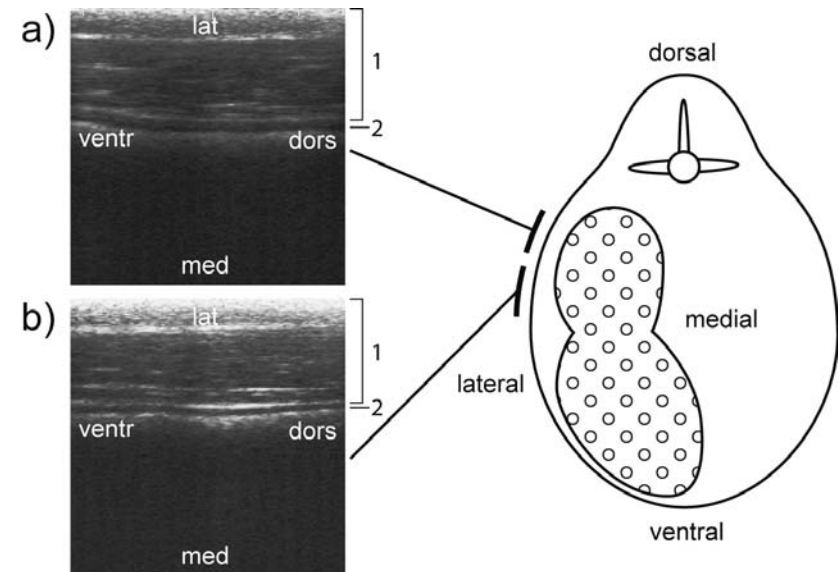
Stratification of rumen contents



from Clauss et al. (2010)



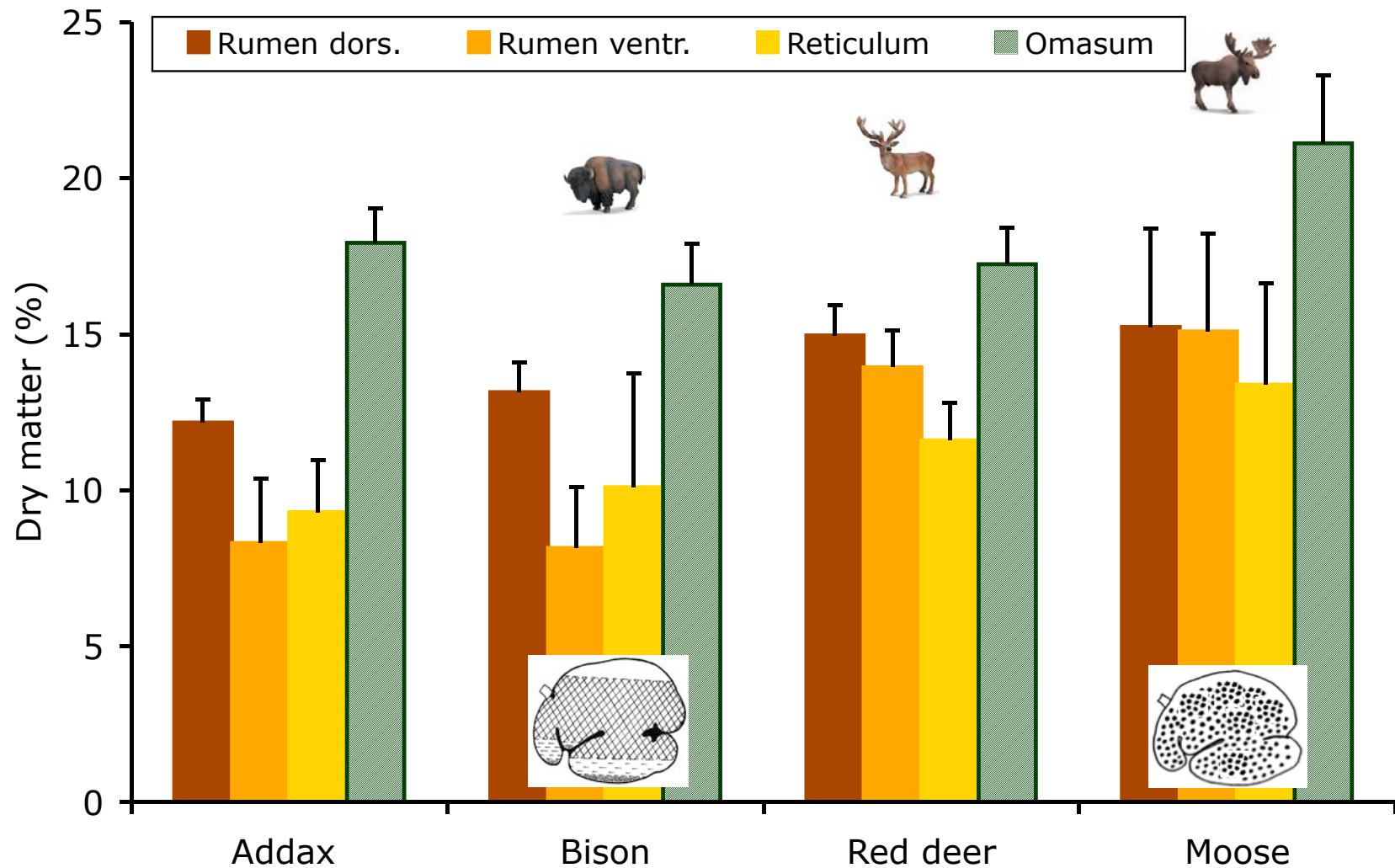
Testing stratification by ultrasound - moose



from Tschuor & Clauss (2008)

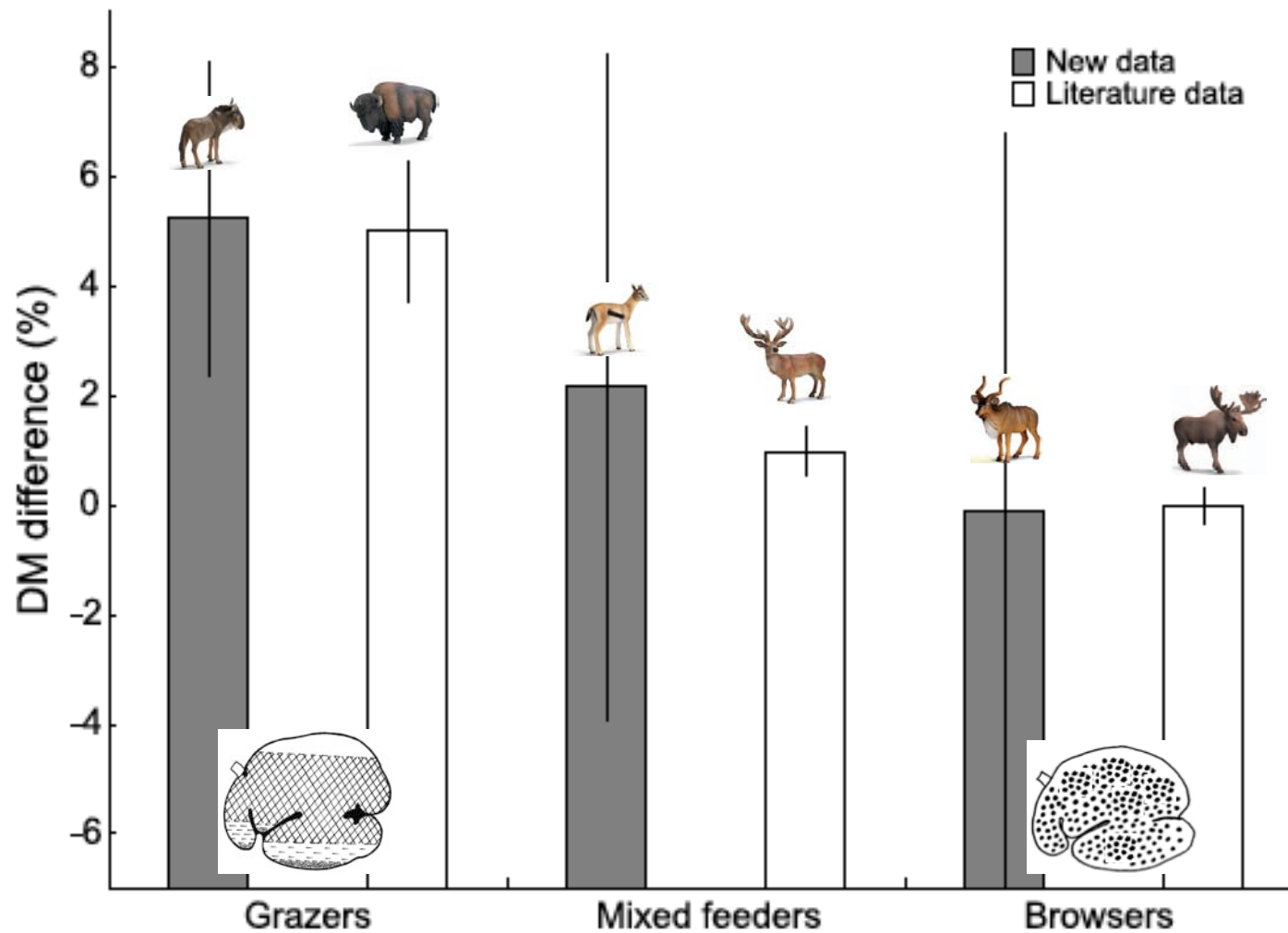


Testing stratification by dry matter content





Testing stratification by dry matter content



from Codron & Clauss (2010)



Testing stratification by rumen morphology

- Rumen papilla growth is stimulated by volatile fatty acids
- Differences in ruminal papillation should indicate differences in rumen contents stratification (e.g., a gas accumulation (CO_2 , methane) will displace volatile fatty acids)



Testing stratification by rumen morphology



from Clauss, Hofmann et al. (2009)



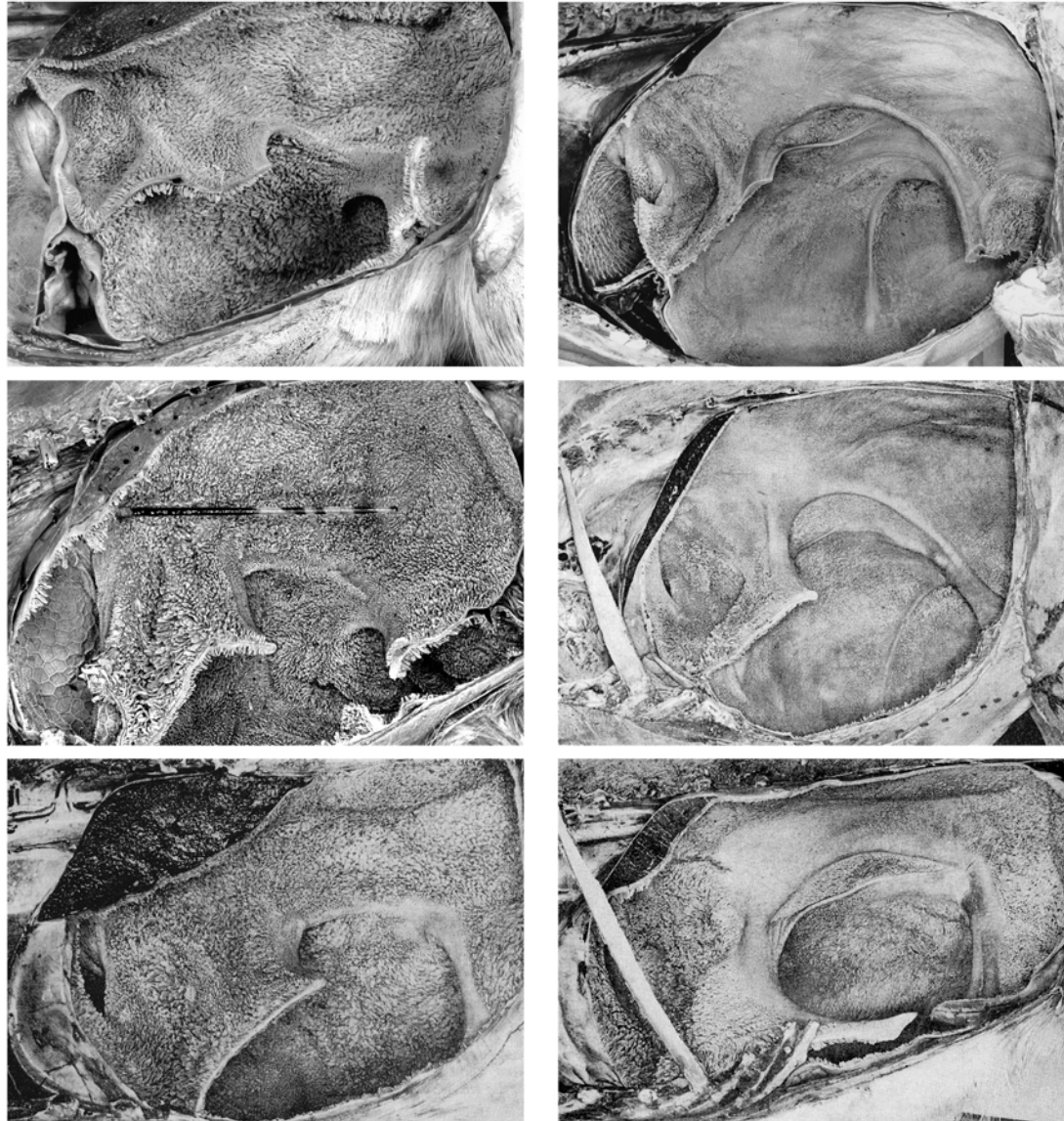
Testing stratification by rumen morphology



from Clauss, Hofmann et al. (2009)



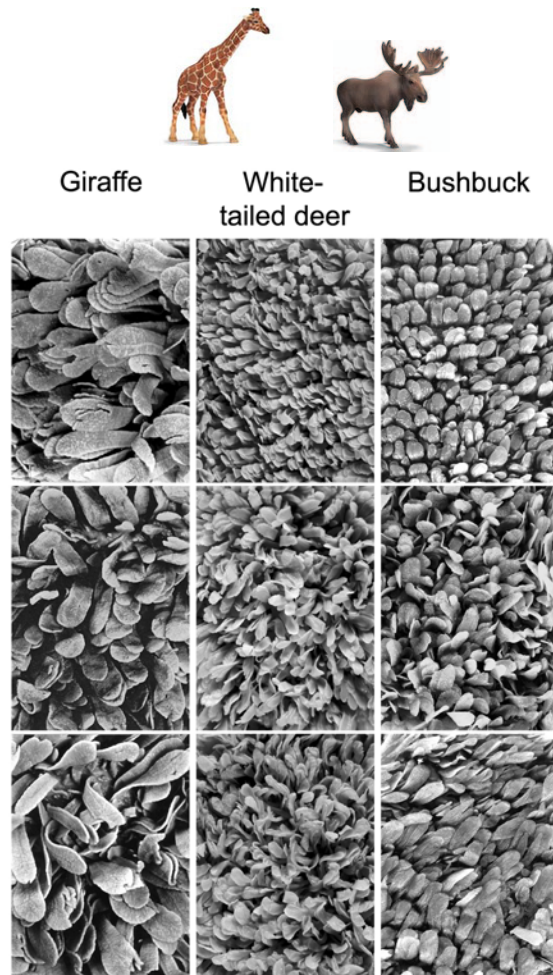
Testing stratification by rumen morphology



from Clauss, Hofmann et al. (2009)



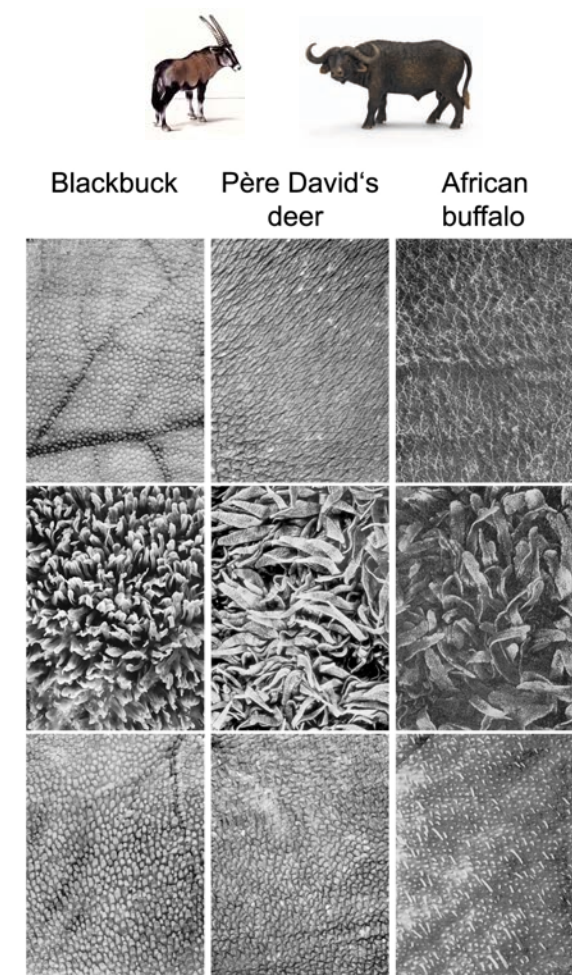
Stratification and rumen papillation



dorsal

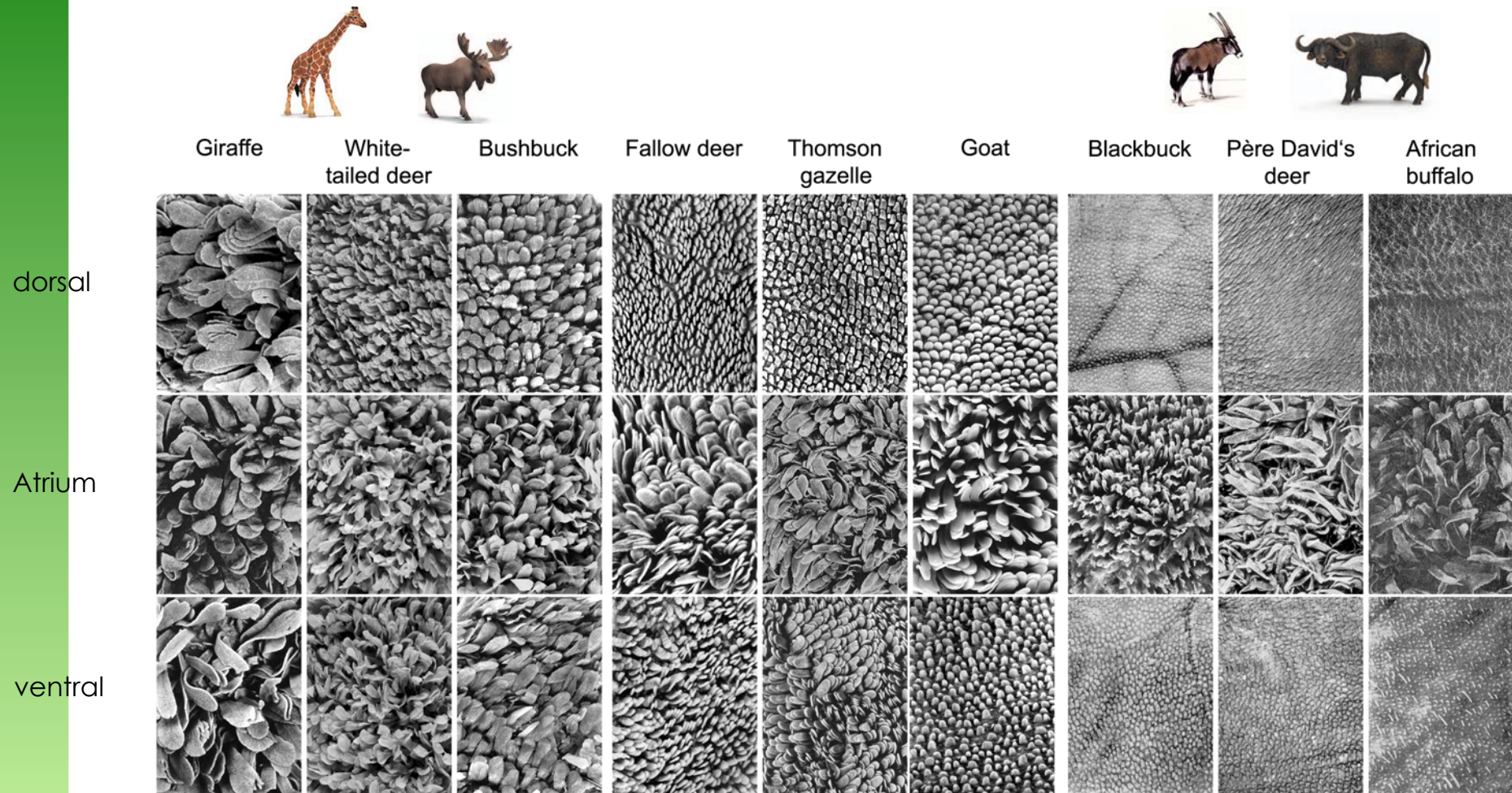
Atrium

ventral



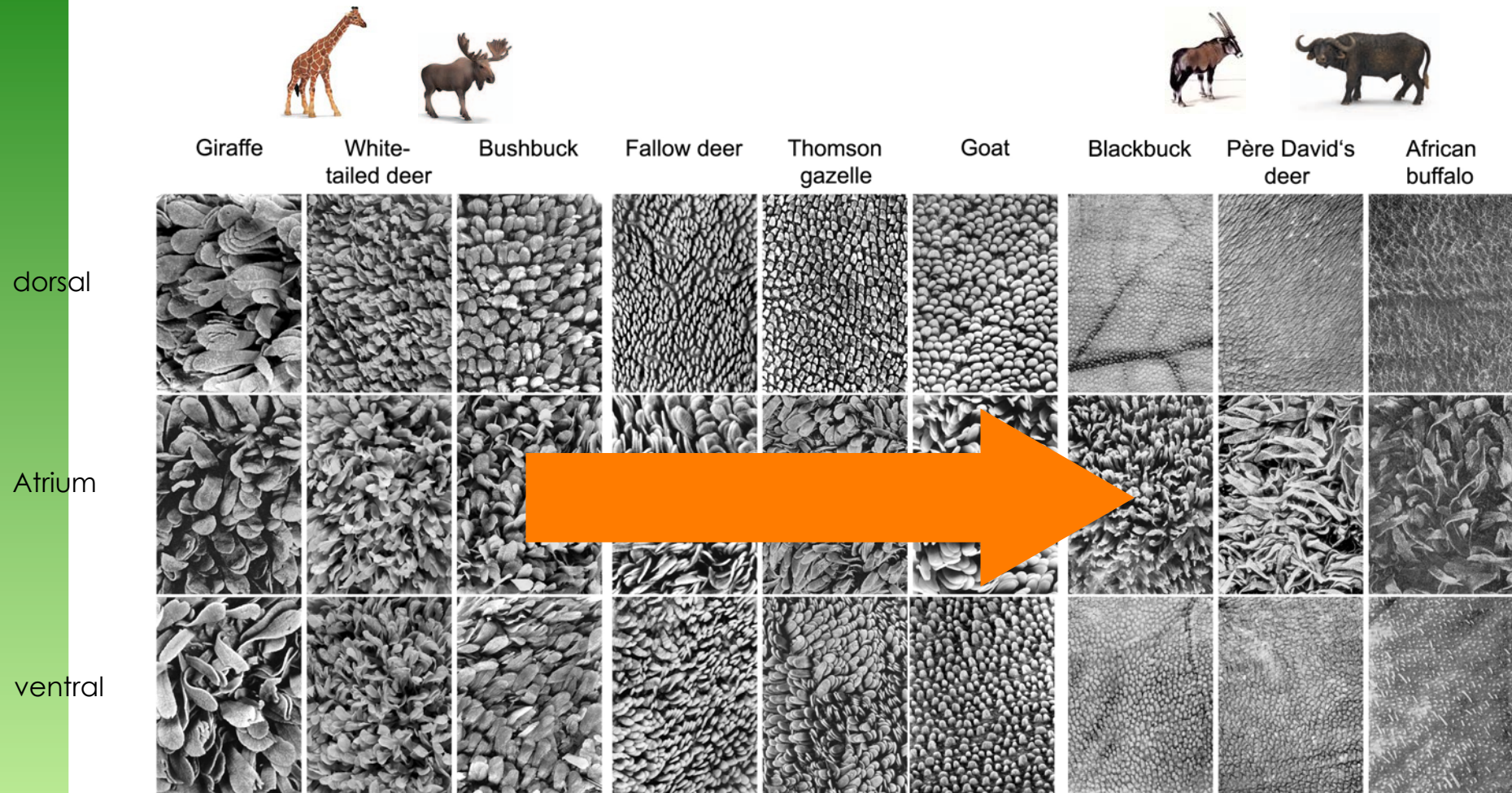


Stratification and rumen papillation



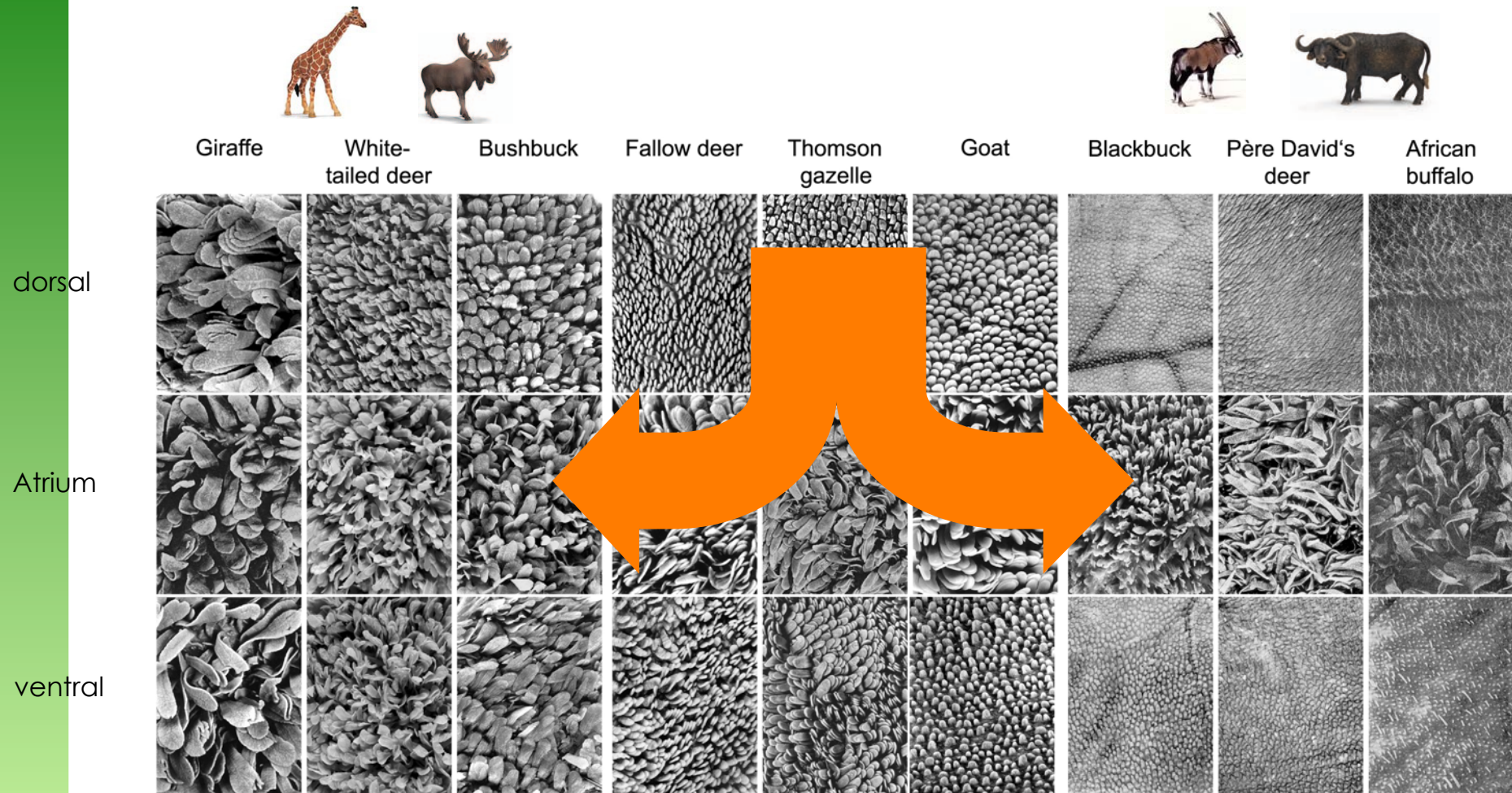


Stratification and rumen papillation



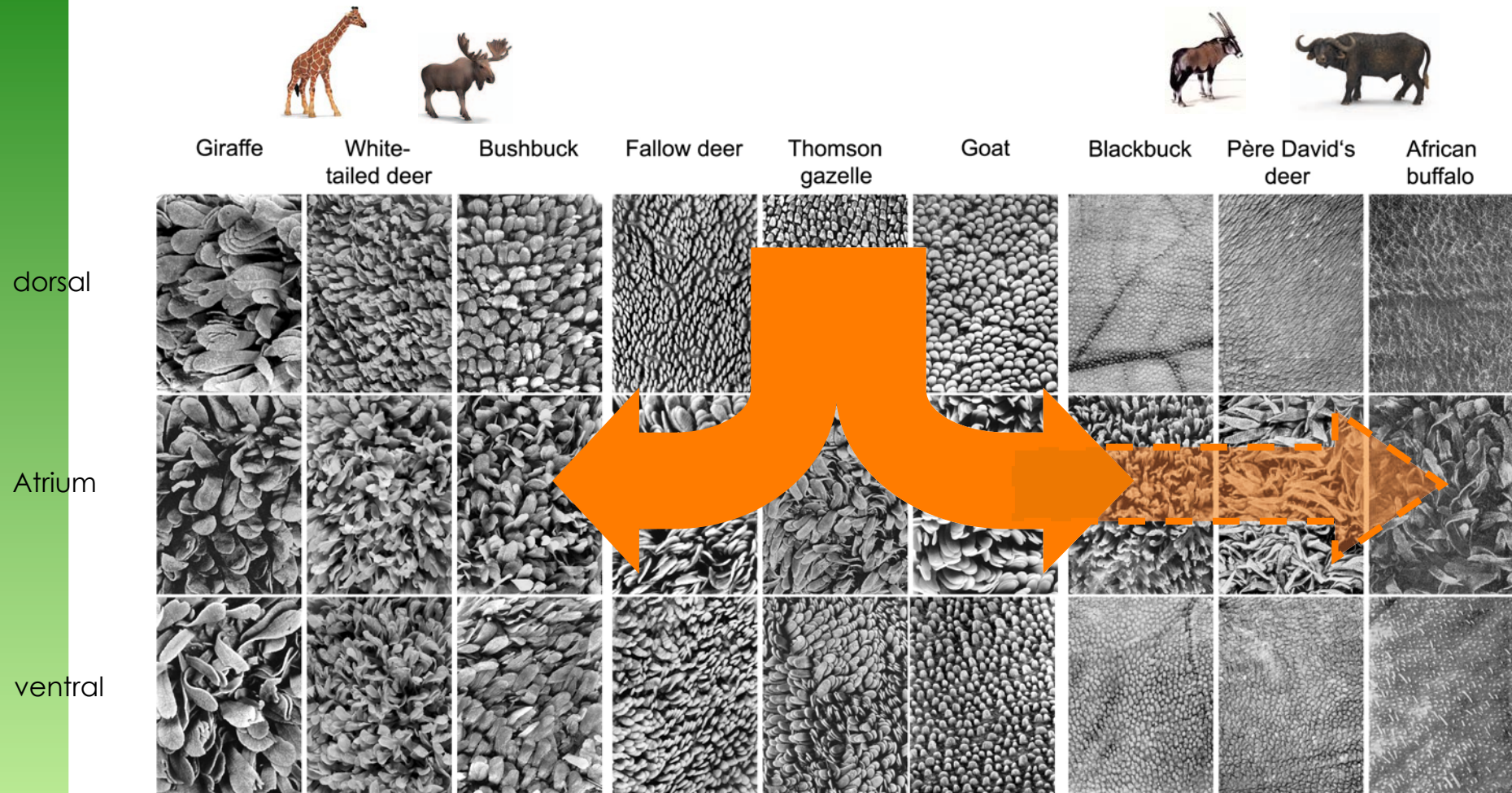


Stratification and rumen papillation



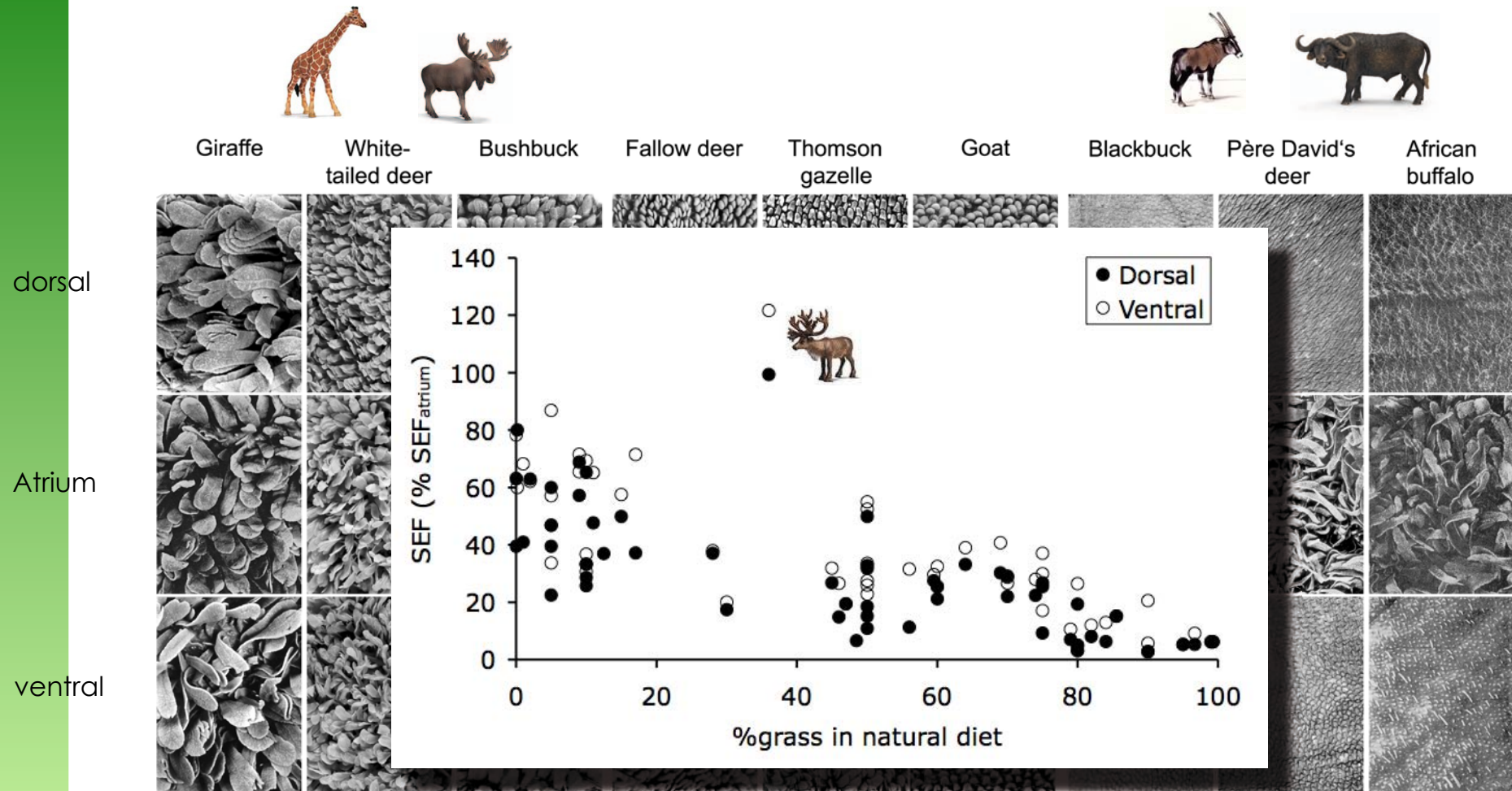


Stratification and rumen papillation





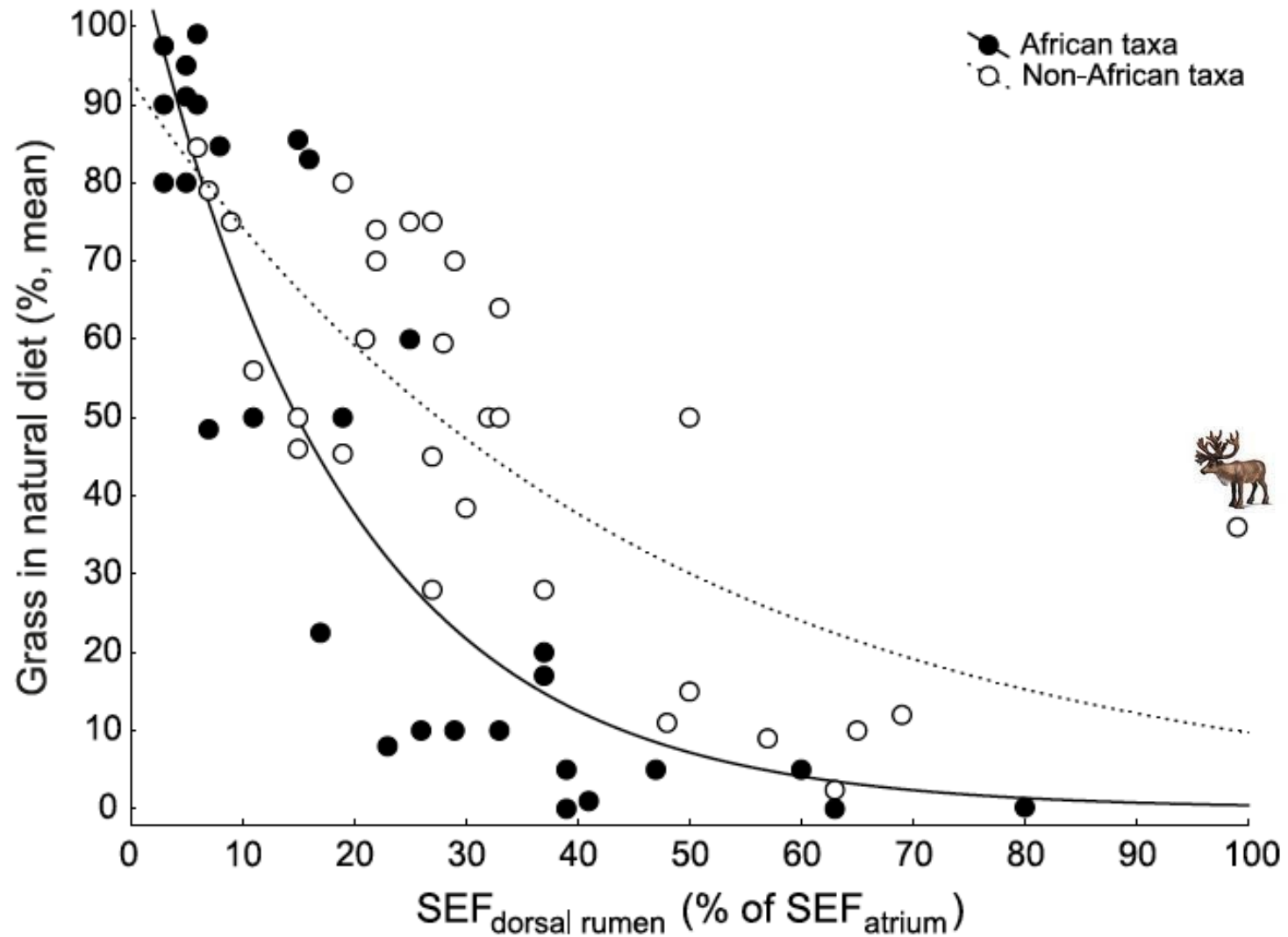
Stratification and rumen papillation



from Clauss, Hofmann et al. (2009)



Stratification and rumen papillation



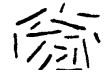
from Codron & Clauss (2010)



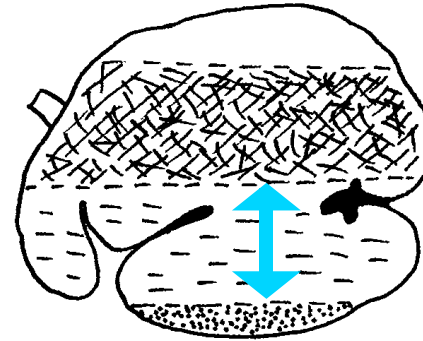
Grazer



Grass



longish,
"fibre-like"
particles



**Low viscosity fluid:
Separation due to
flotations/sedimentation;
clear separation of gas
dome**

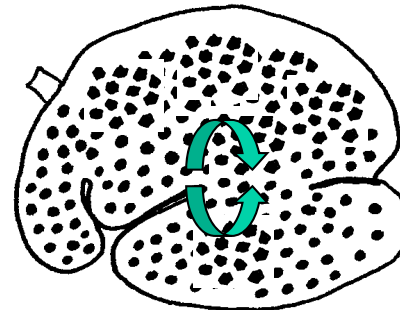
Browser



Browse



polygonal
particles

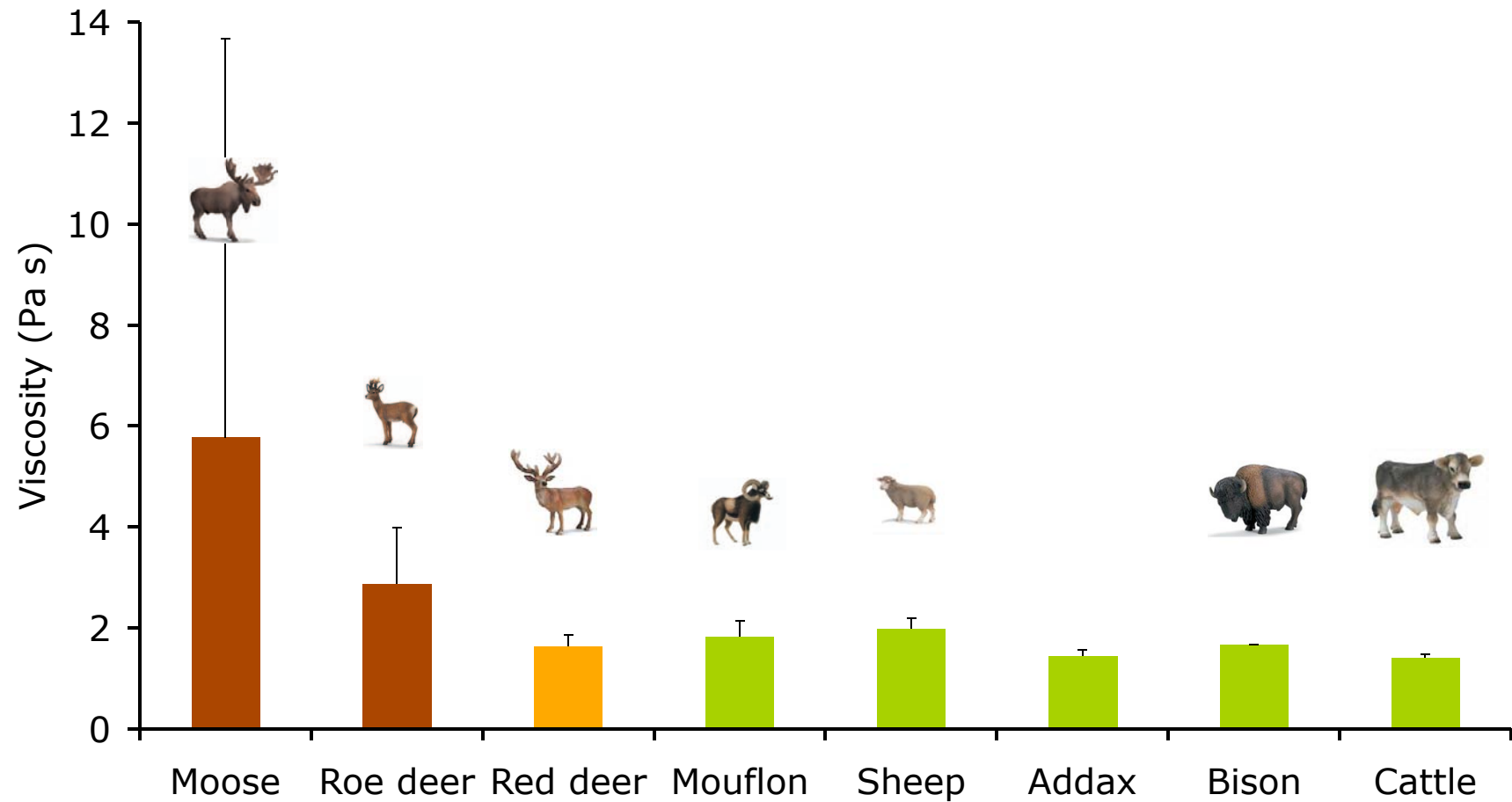


**High viscosity fluid:
Separation due to
flotation/sedimentation
less possible; gas
bubbles distributed
evenly in the contents**

from Clauss et al. (2003)



Rumen fluid viscosity



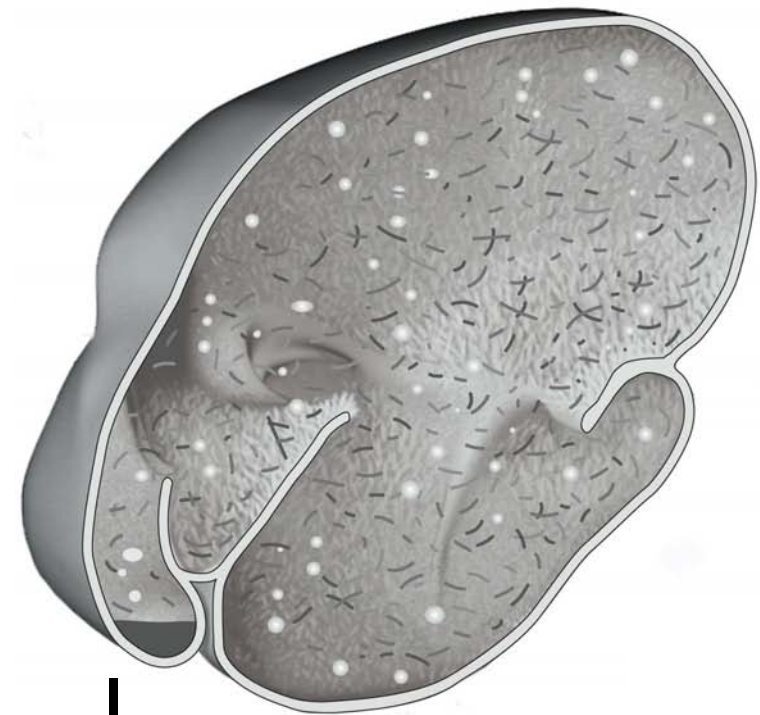
from Hummel et al. (2009) and Clauss et al. (2009ab)



Difference in fluid retention



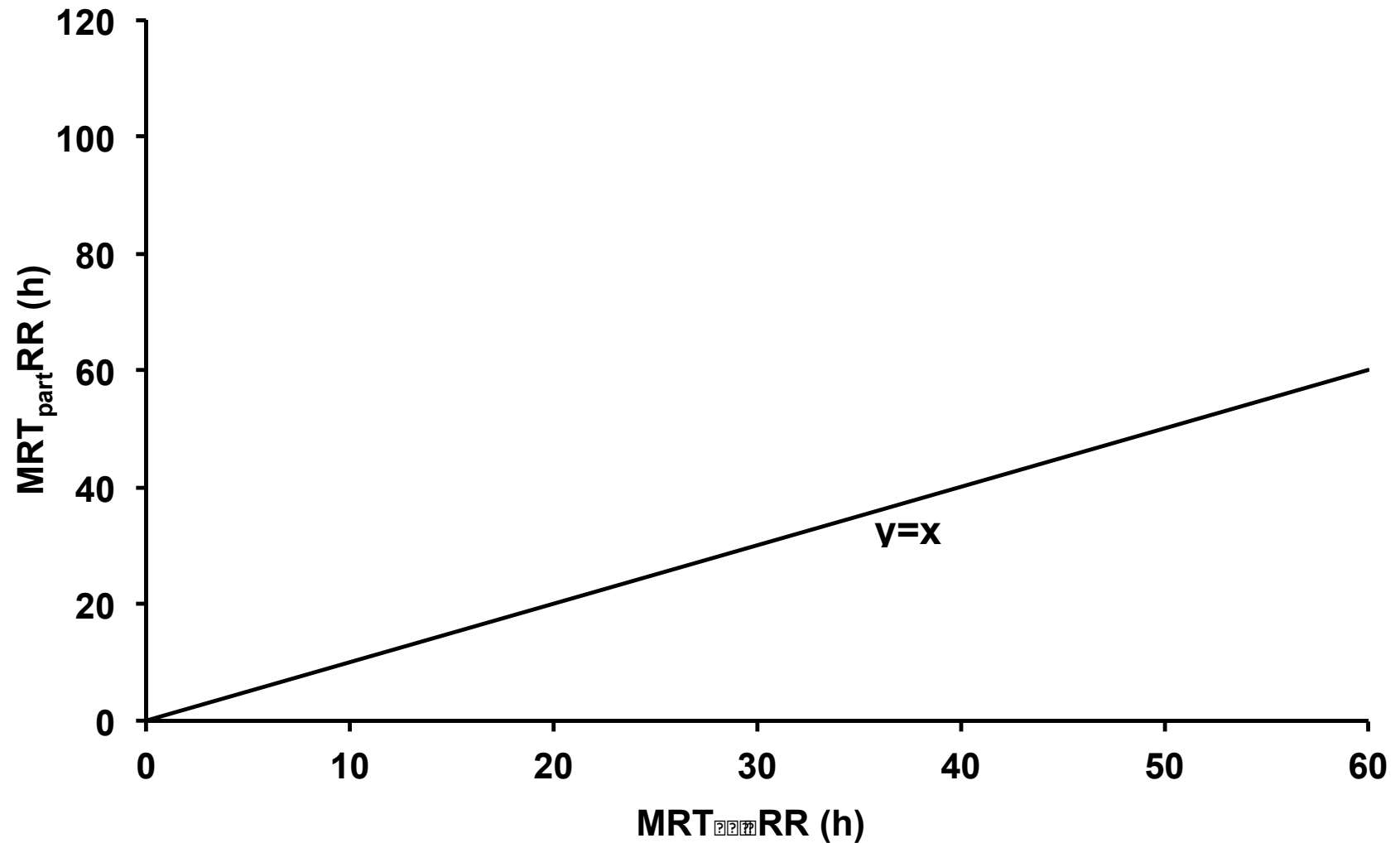
**large difference between
fluid and particle passage**



**small difference
between fluid and
particle passage**



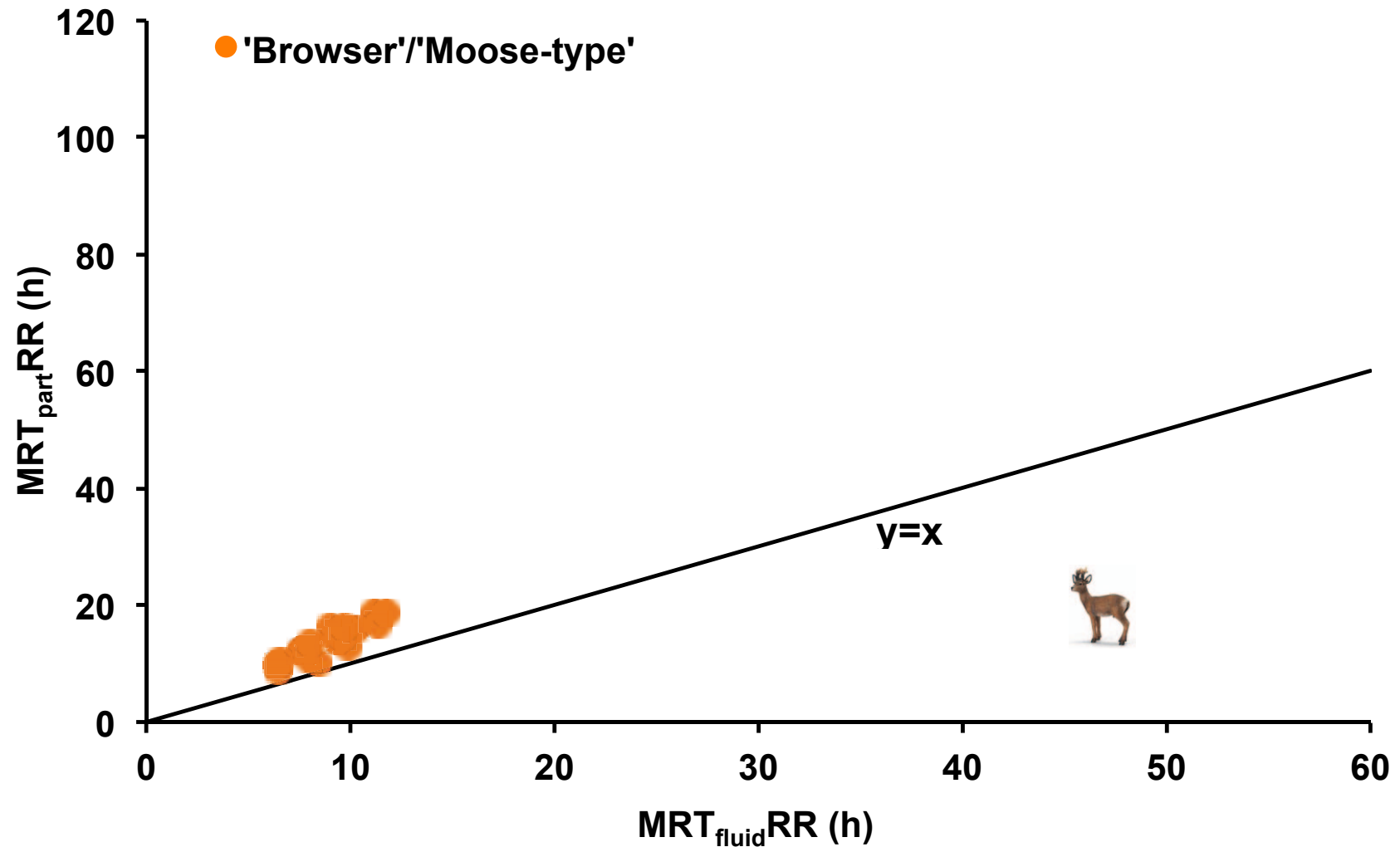
Fluid and particle retention



from Clauss et al. (2010)



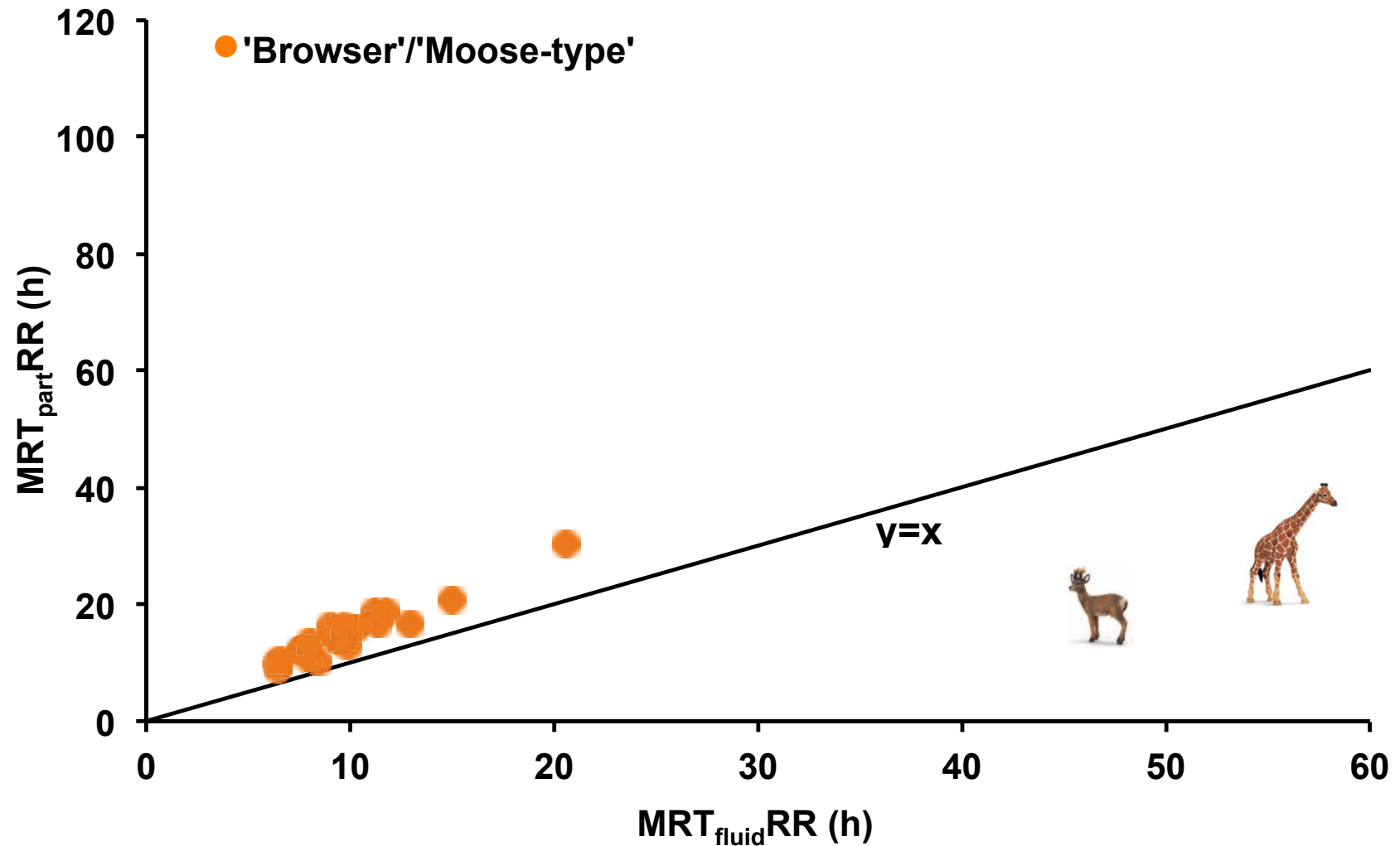
Fluid and particle retention



from Clauss et al. (2010)



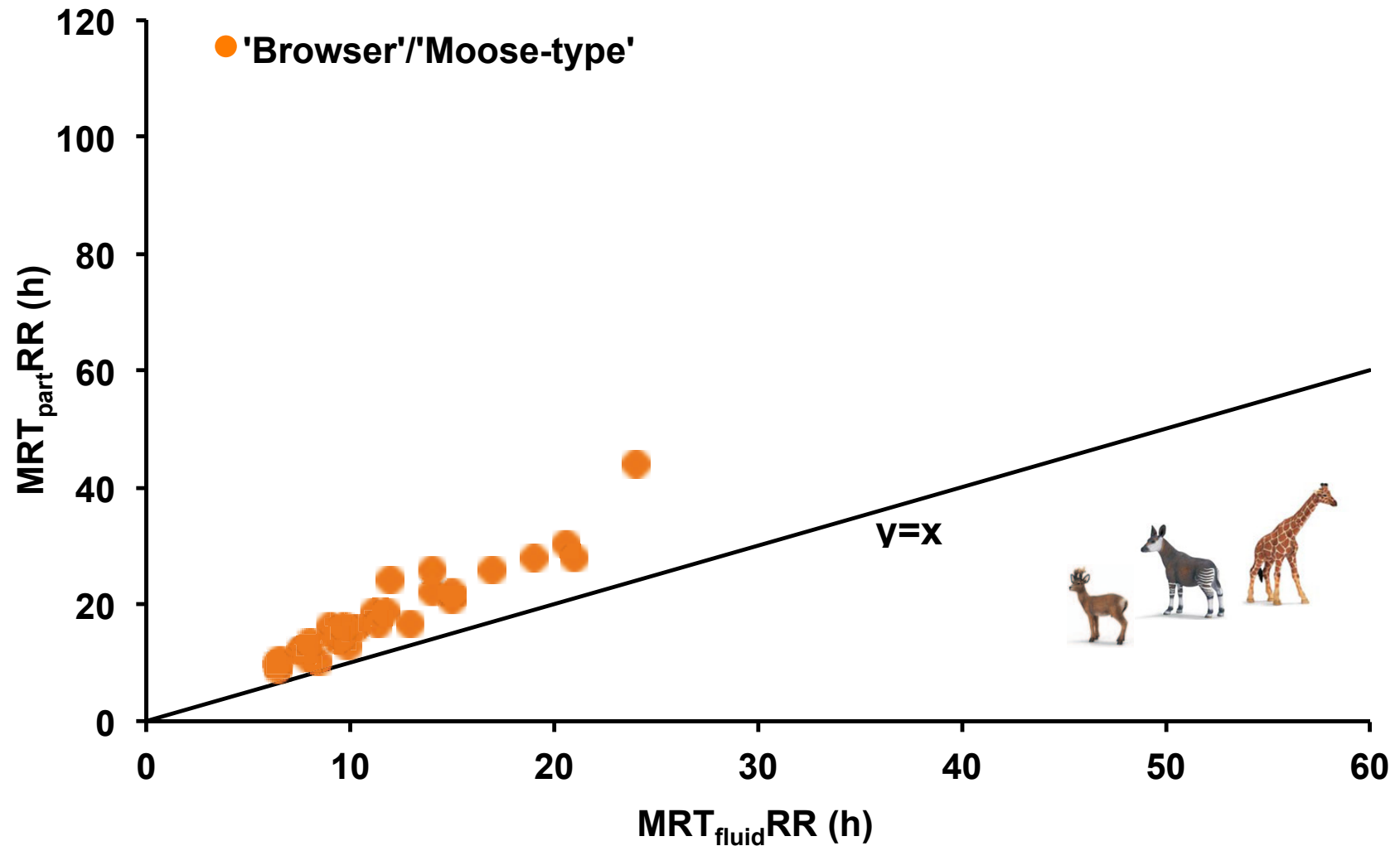
Fluid and particle retention



from Clauss et al. (2010)



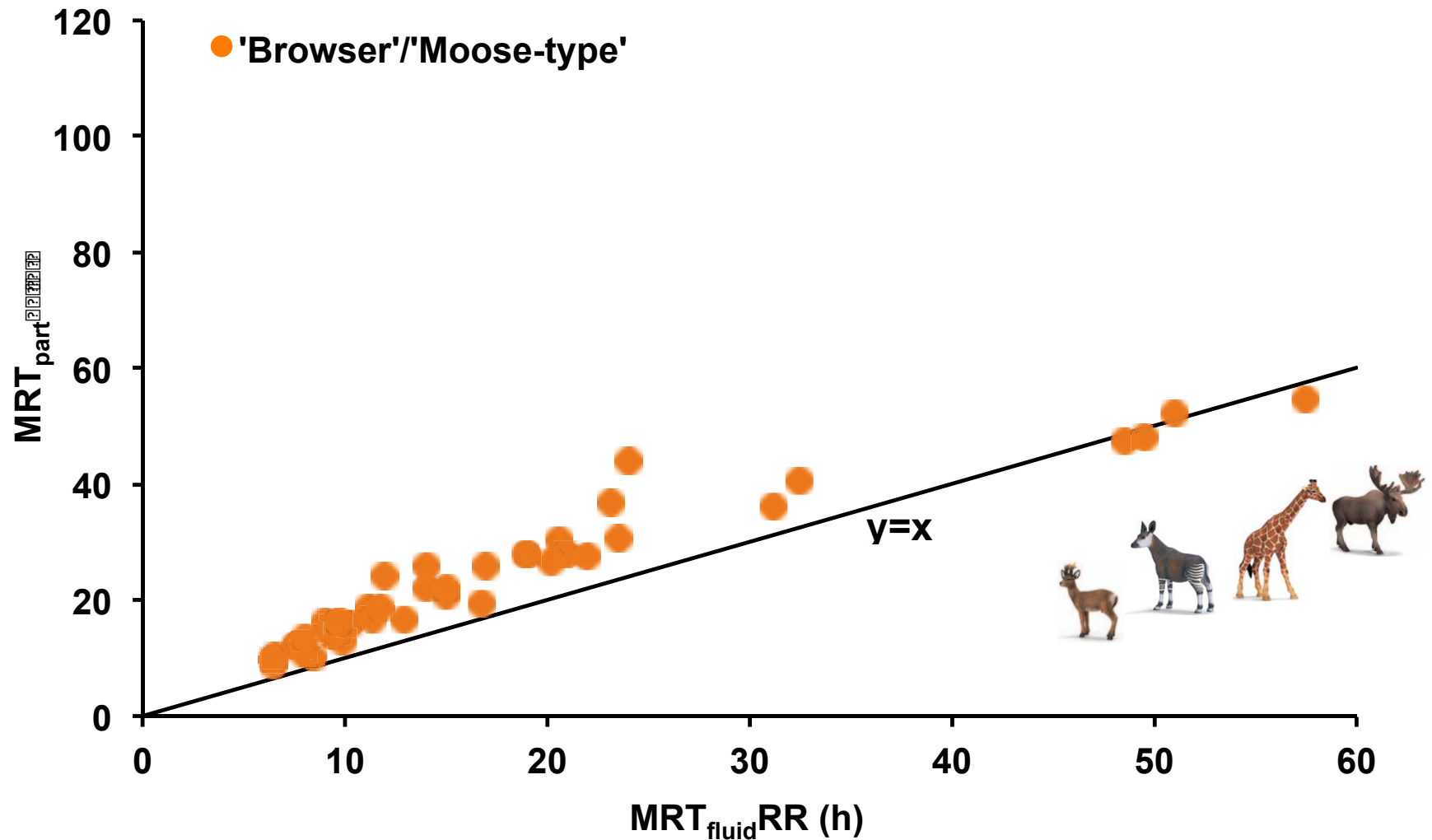
Fluid and particle retention



from Clauss et al. (2010)



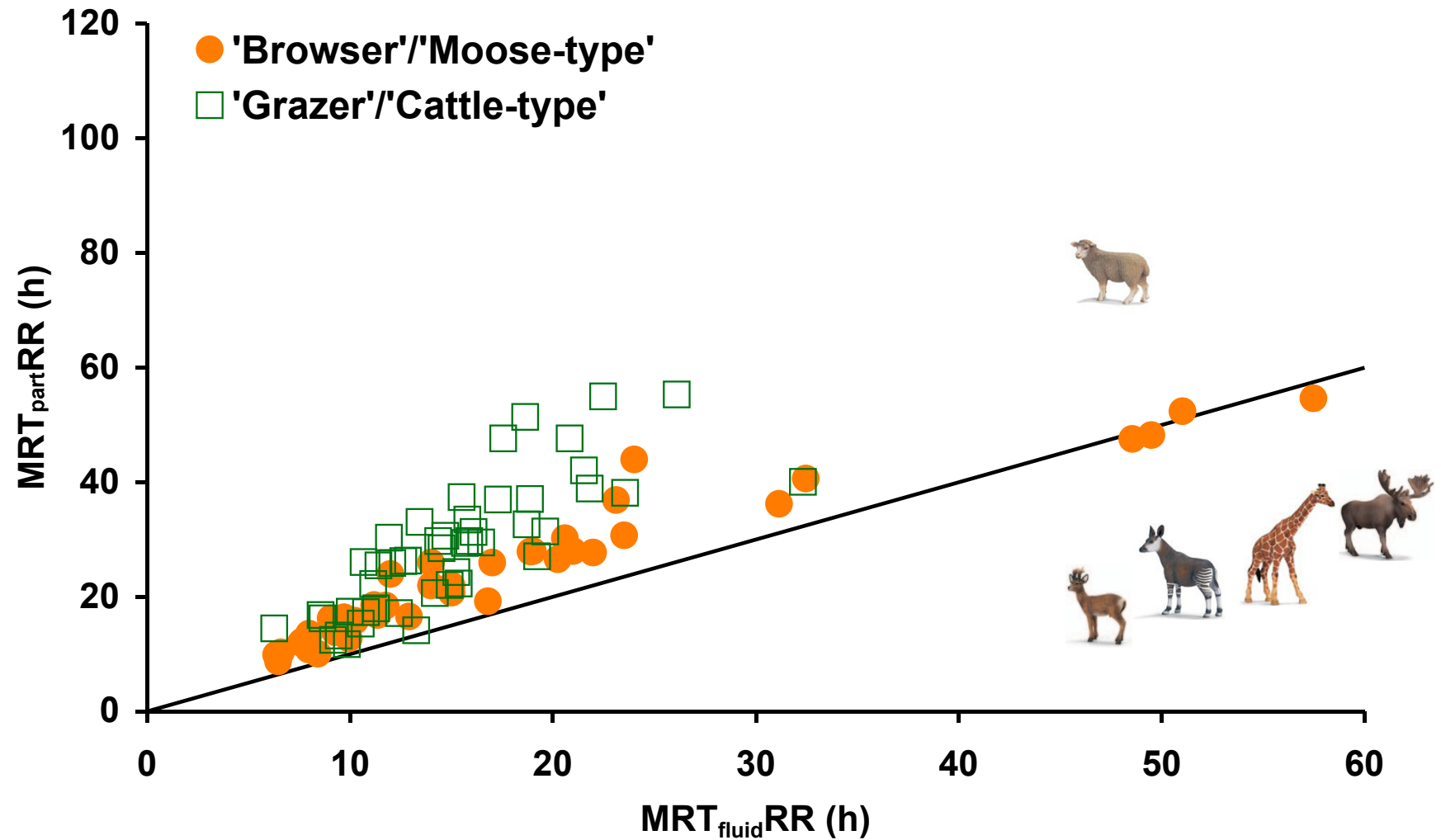
Fluid and particle retention



from Clauss et al. (2010)



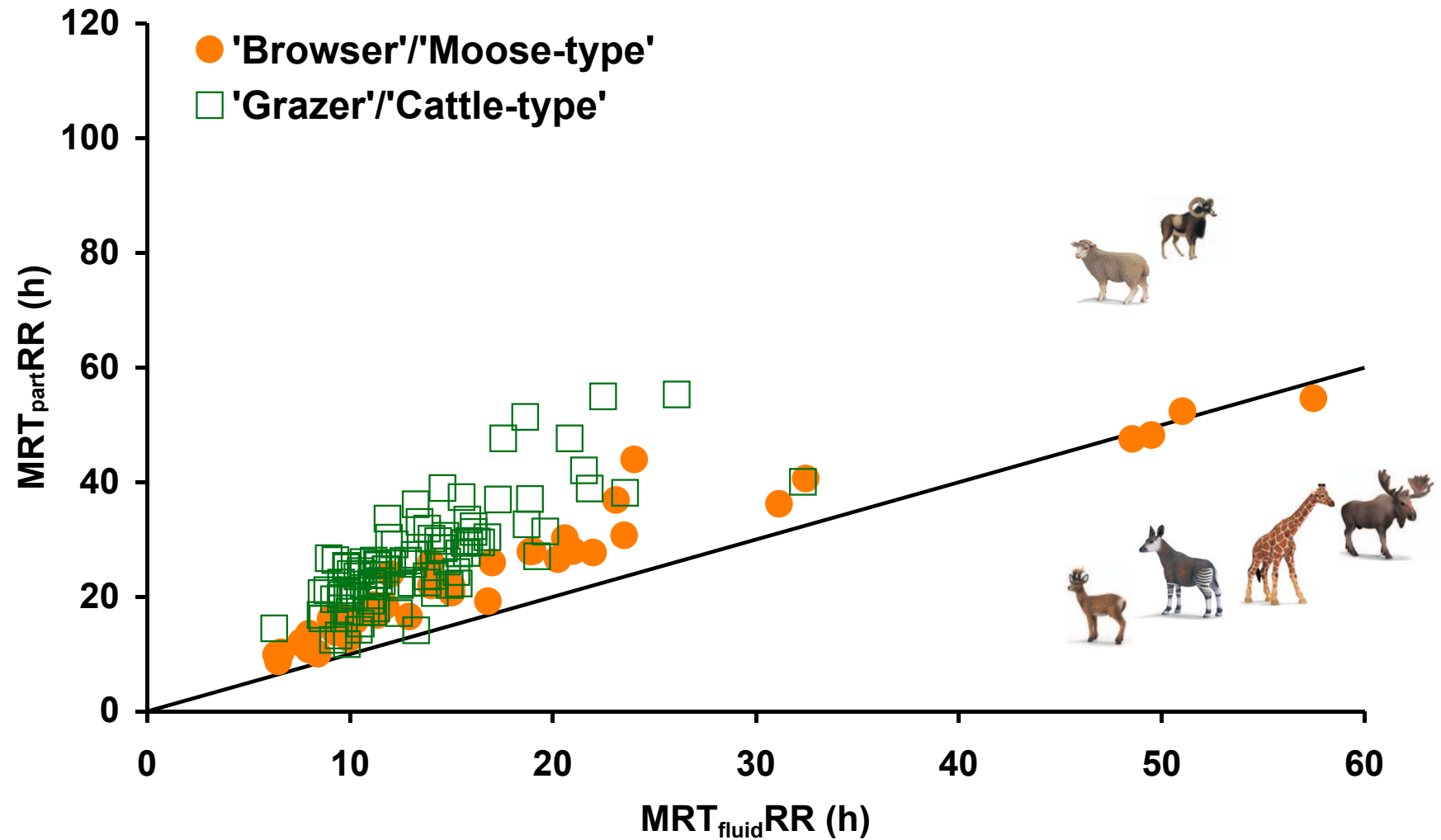
Fluid and particle retention



from Clauss et al. (2010)



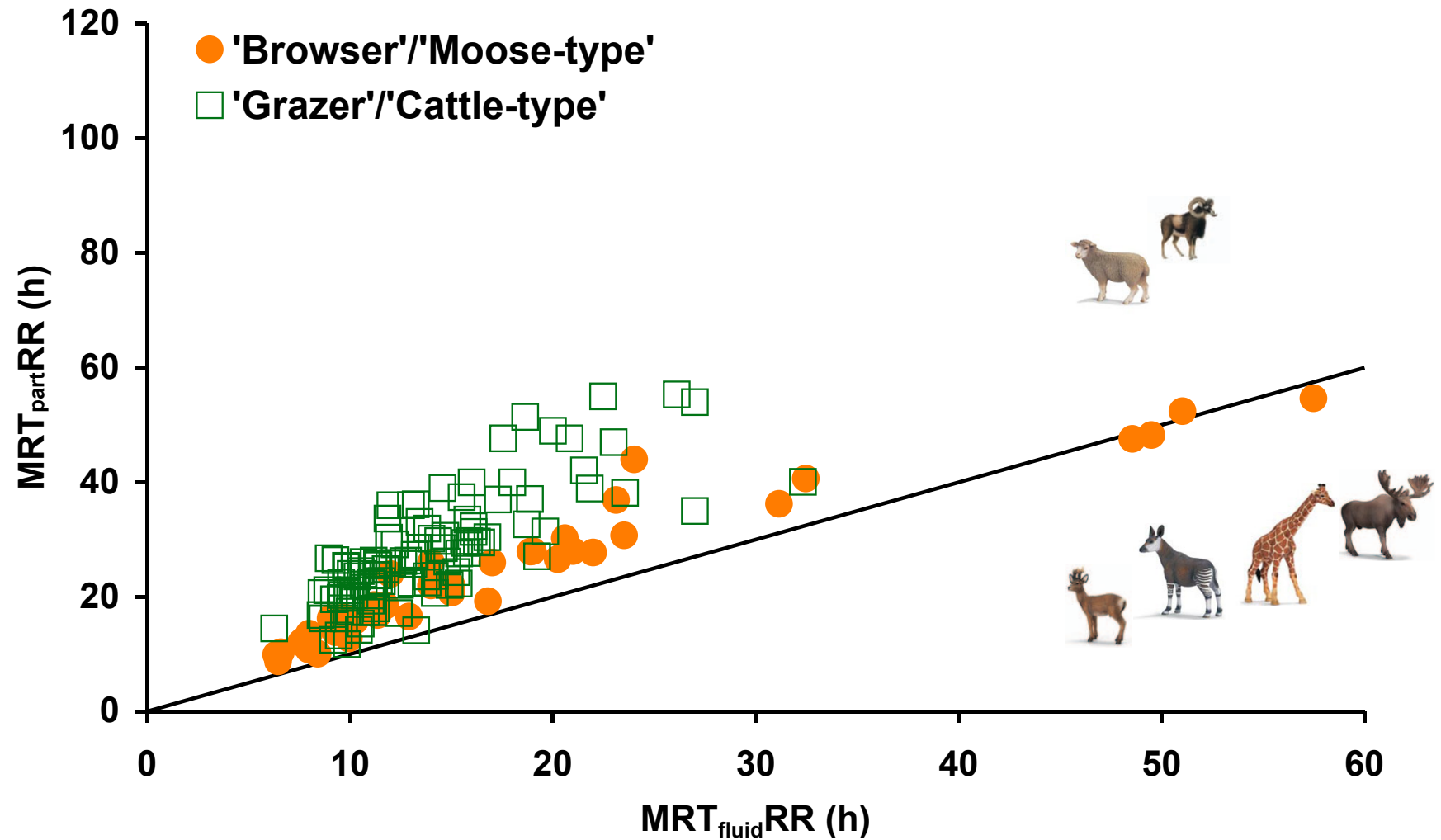
Fluid and particle retention



from Clauss et al. (2010)



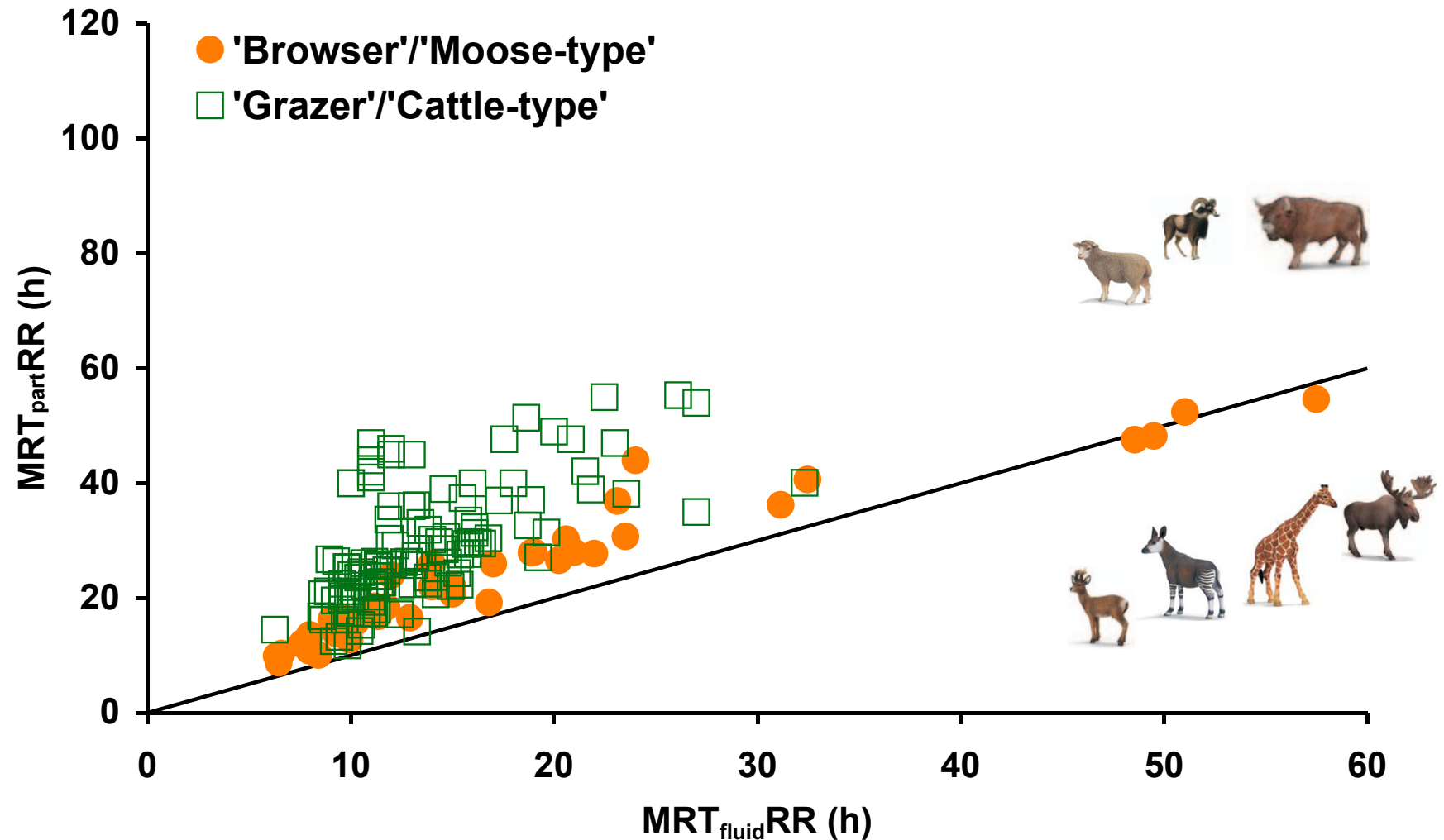
Fluid and particle retention



from Clauss et al. (2010)



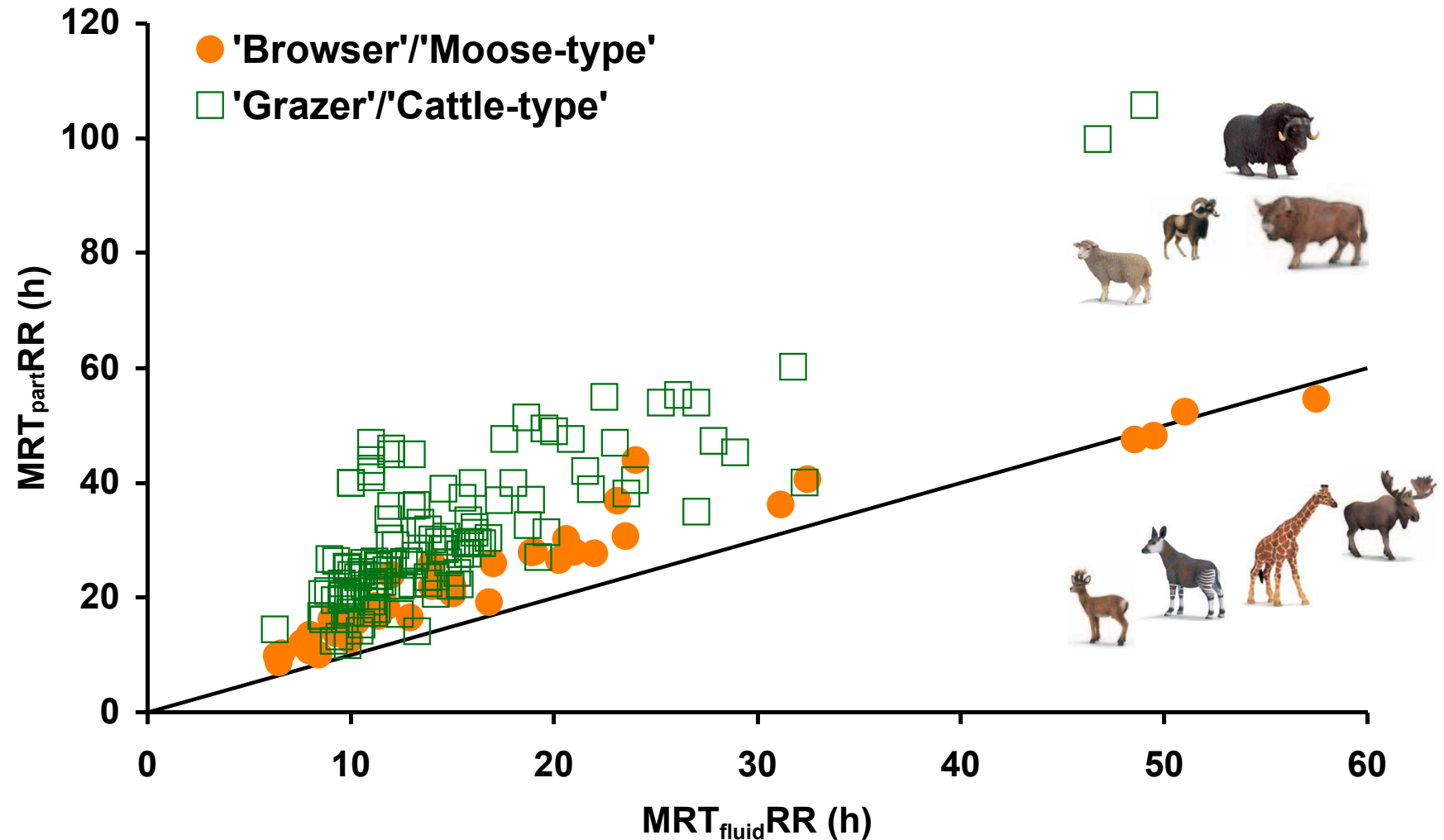
Fluid and particle retention



from Clauss et al. (2010)



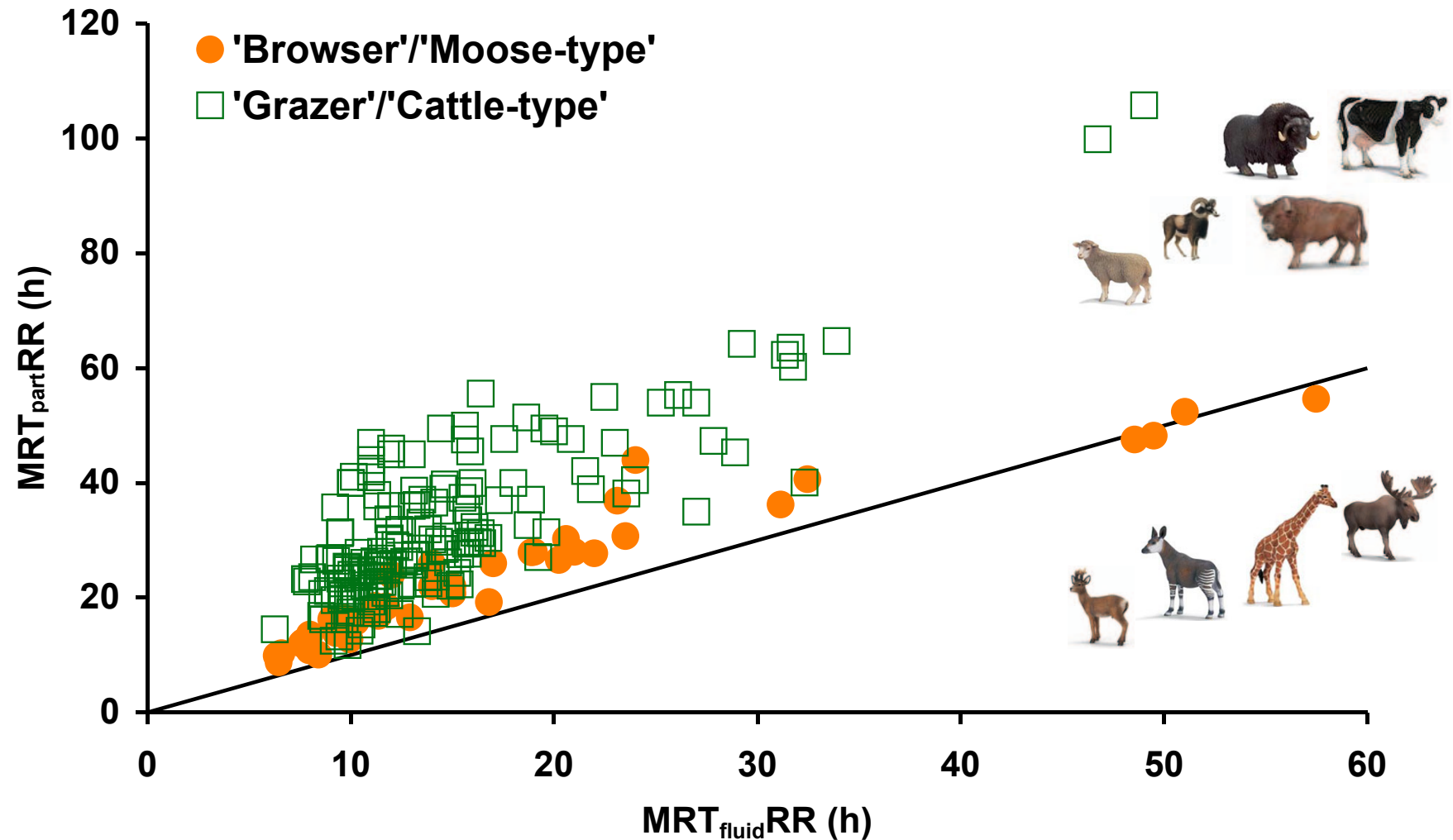
Fluid and particle retention



from Clauss et al. (2010)



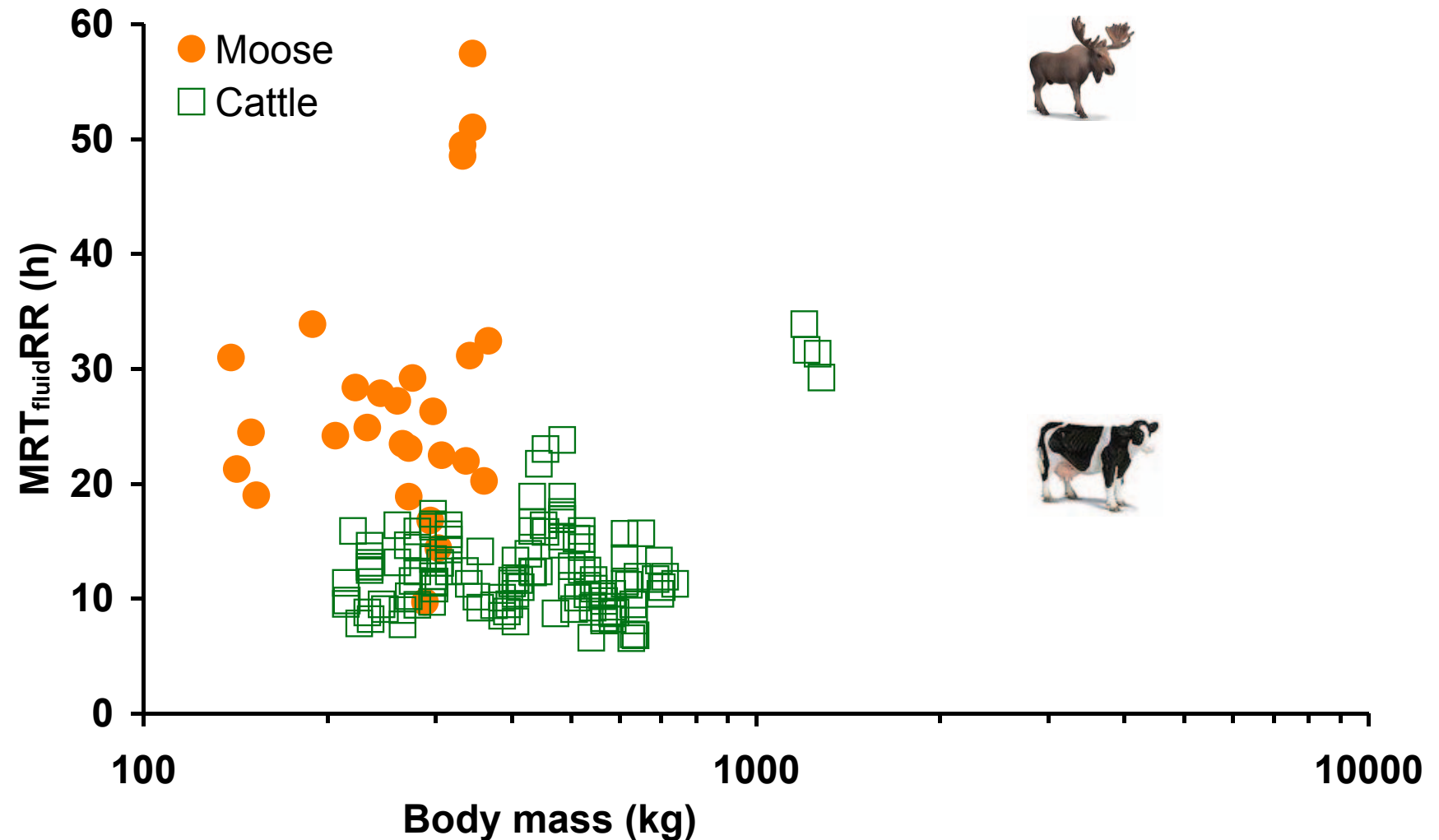
Fluid and particle retention



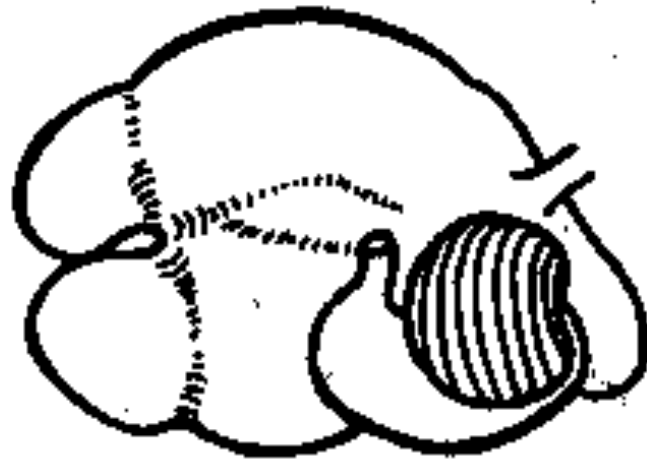
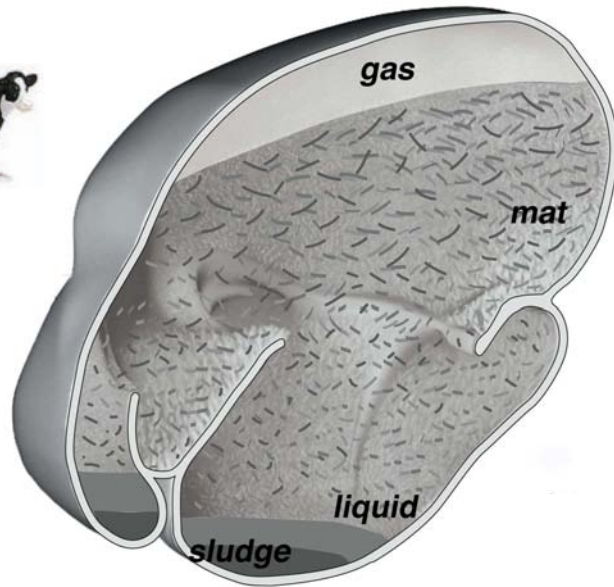
from Clauss et al. (2010)



Absolute fluid retention - moose vs. cattle



from Clauss et al. (2010)



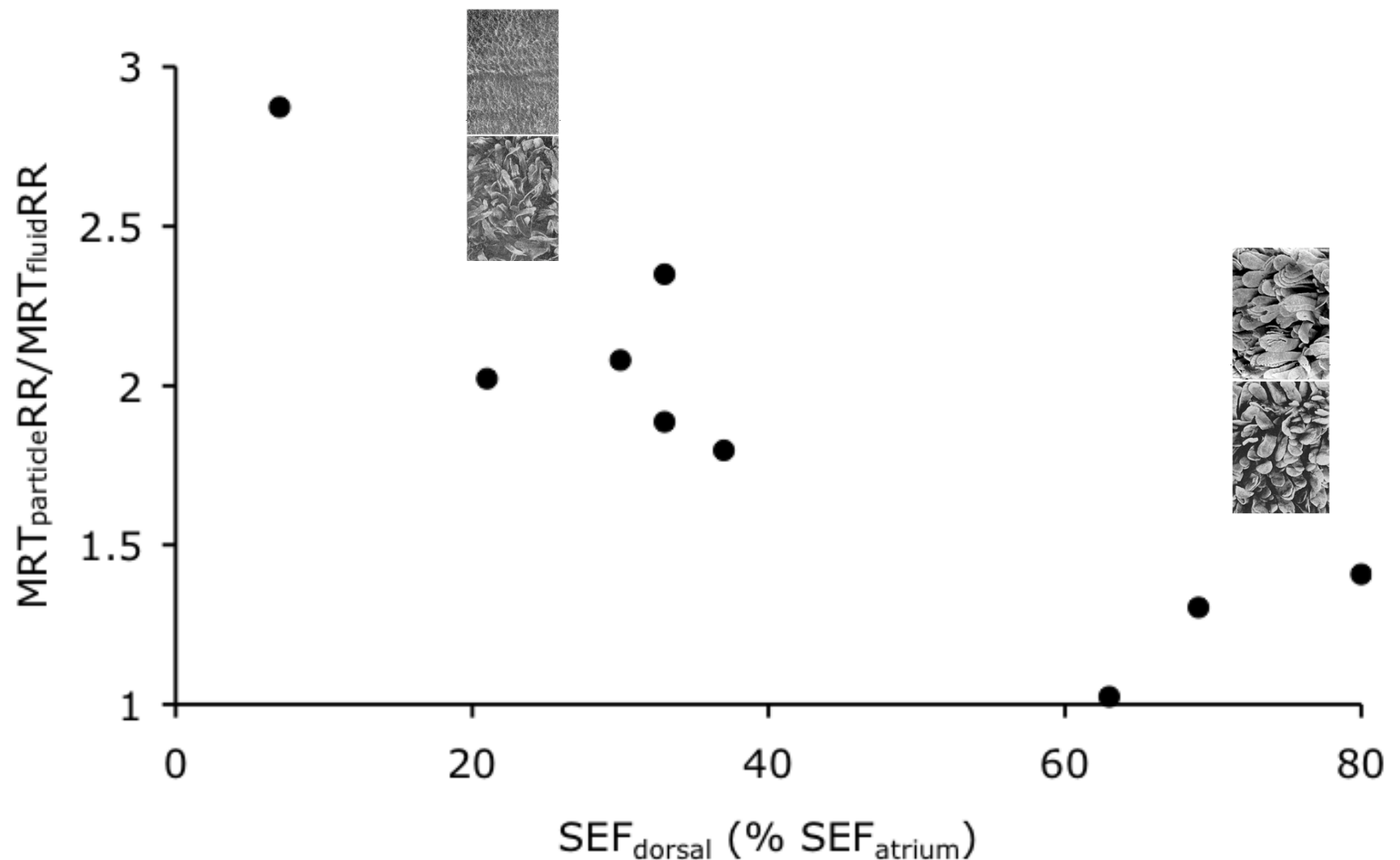
**large omasum – high
water absorption
capacity**



**small omasum – lower
water absorption
capacity**



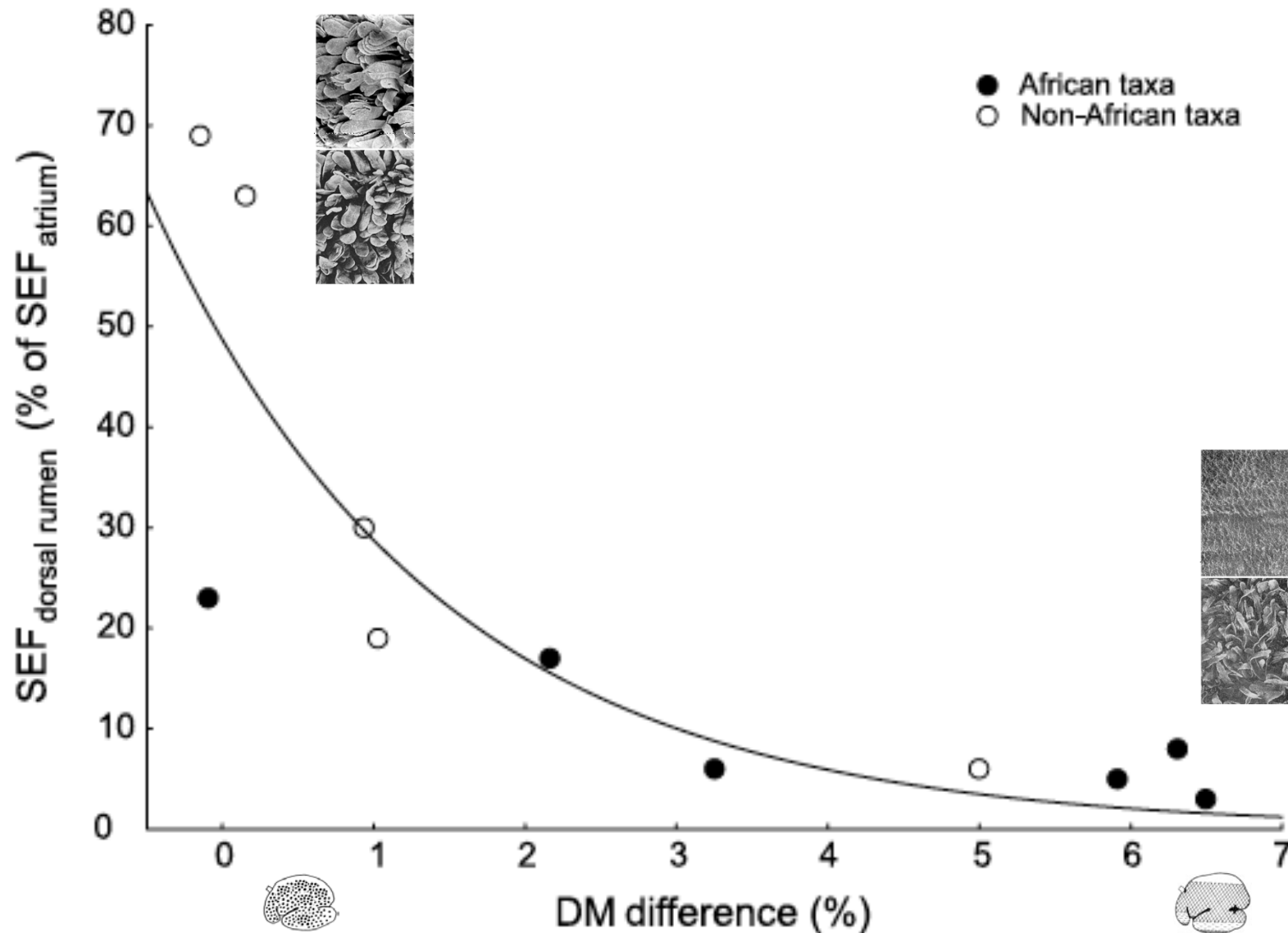
Rumen morphology (papillation) and physiology (passage pattern) match



from Clauss, Hofmann et al. (2009)

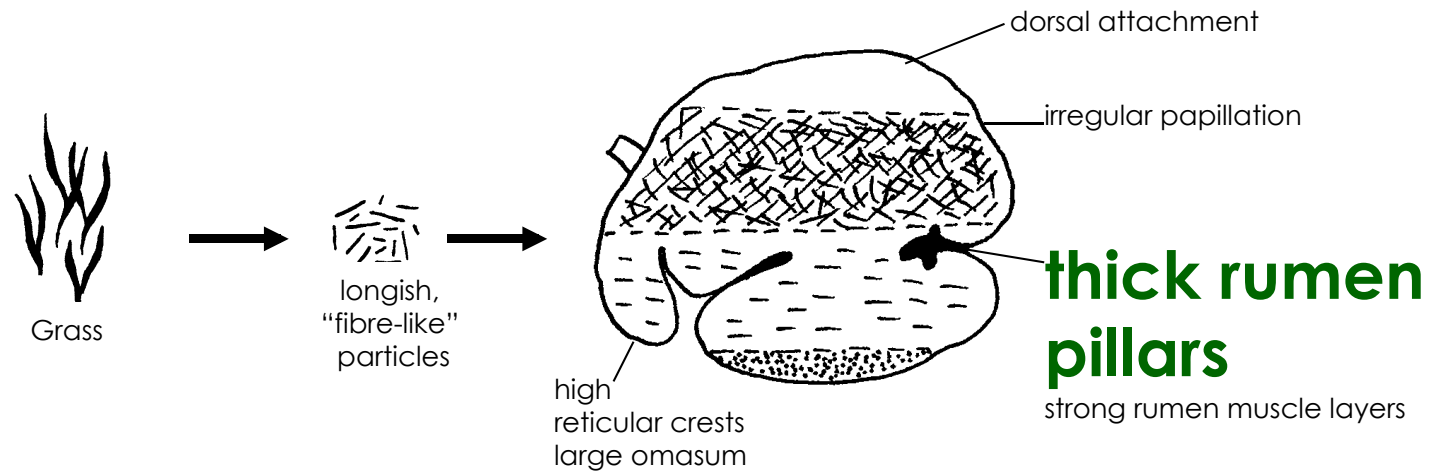


Rumen morphology (papillation) and physiology (passage pattern) match

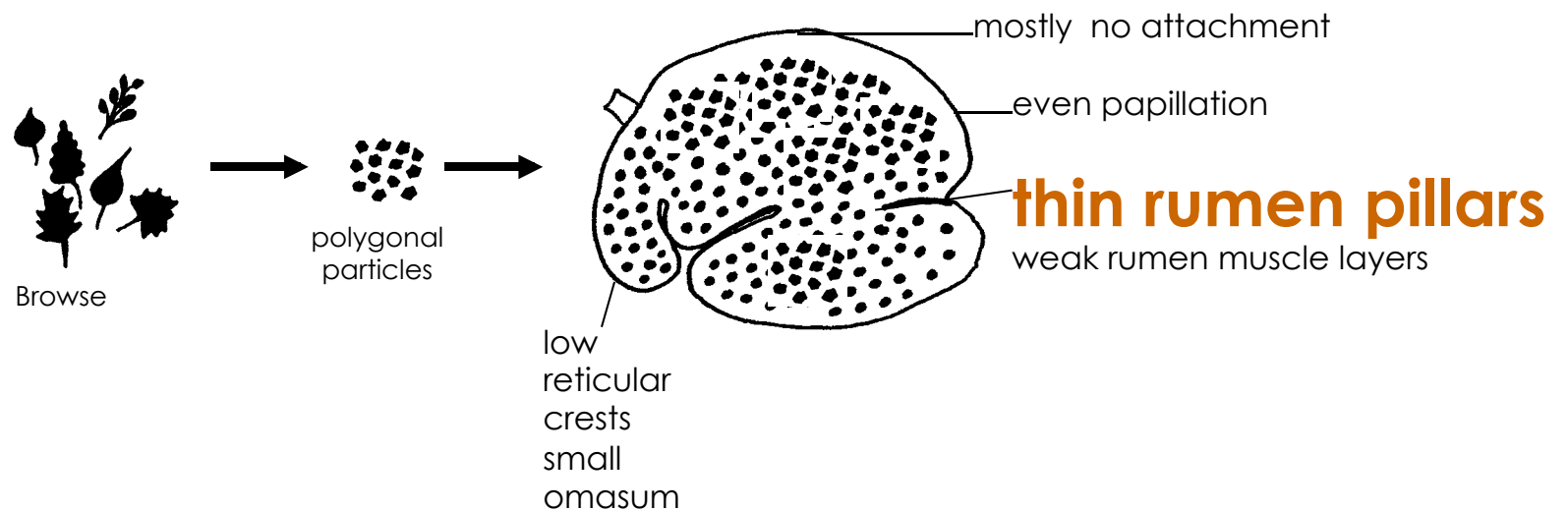




Grazer

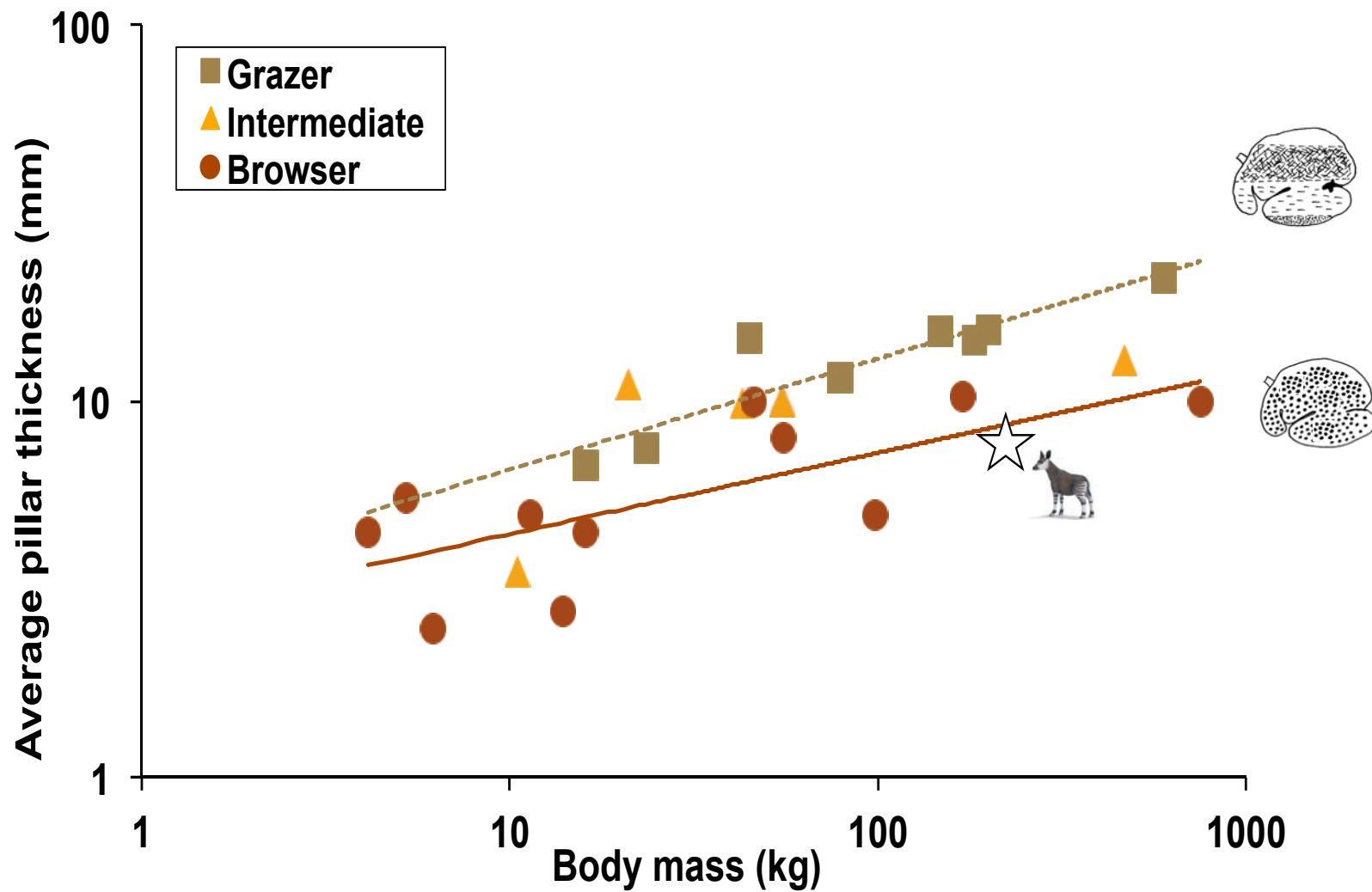


Browser

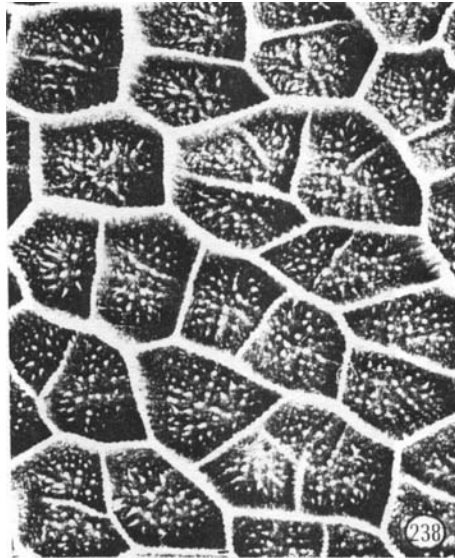
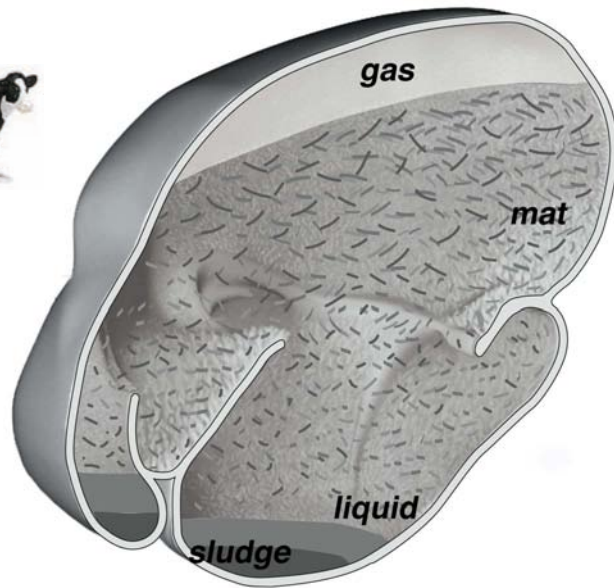




Rumen pillar thickness



from Clauss et al. (2003, 2006)



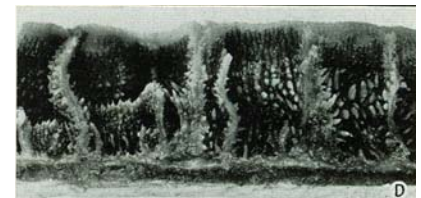
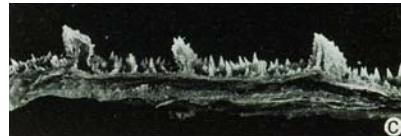
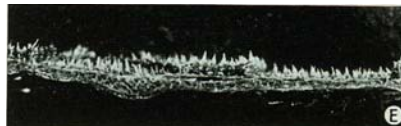
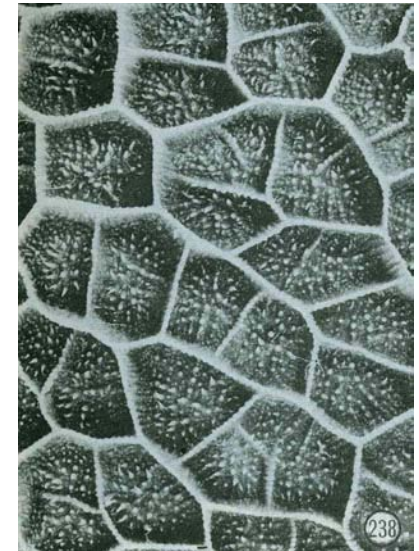
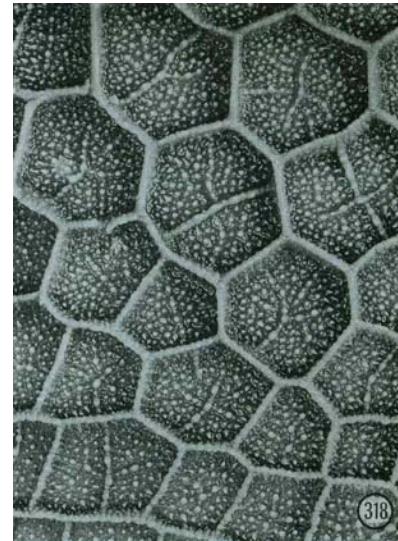
**prominent reticular crest
deep honeycomb cells**



**low reticular crest
shallow honeycomb cells**



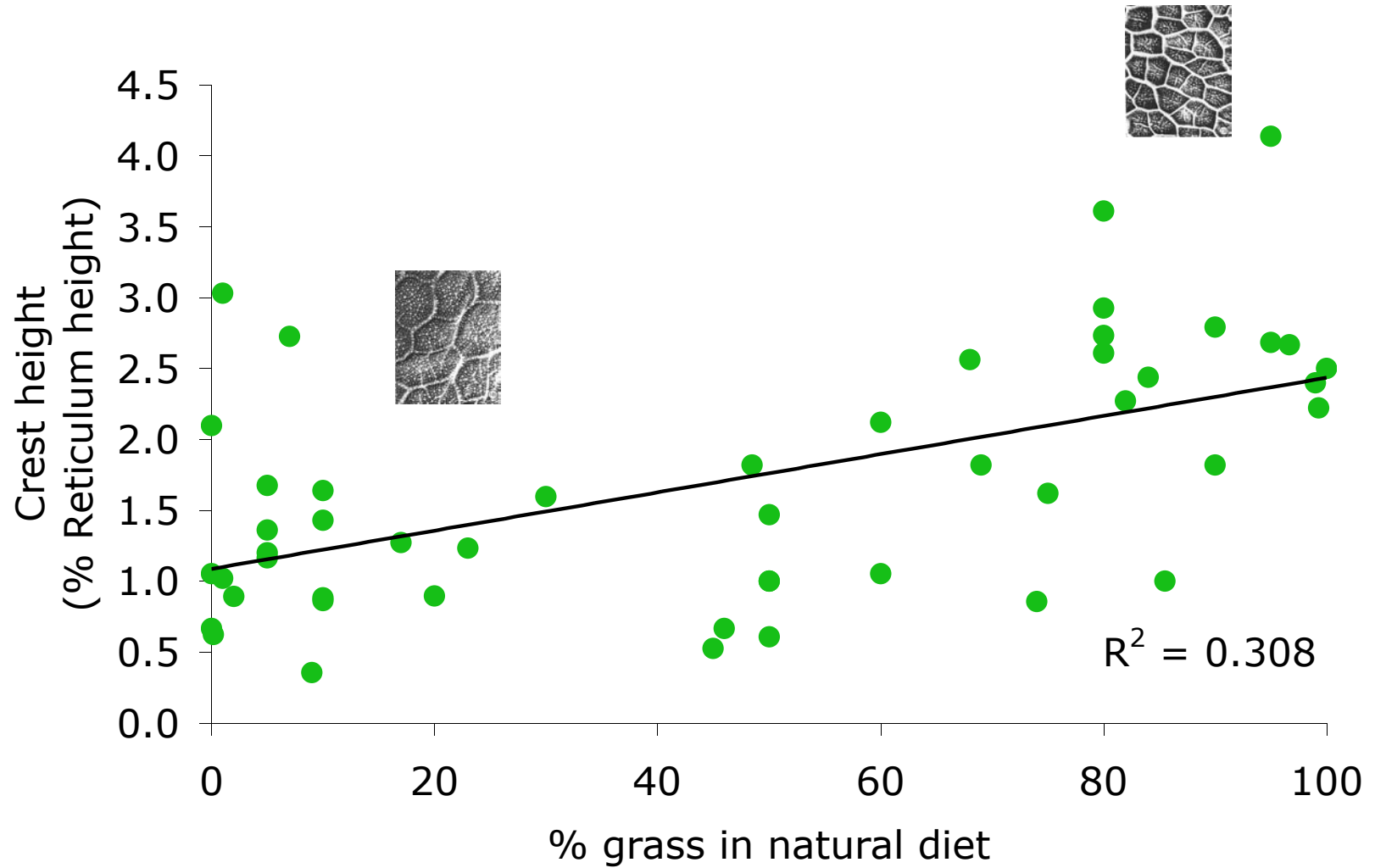
Reticular crests



from Hofmann (1969 & 1973)



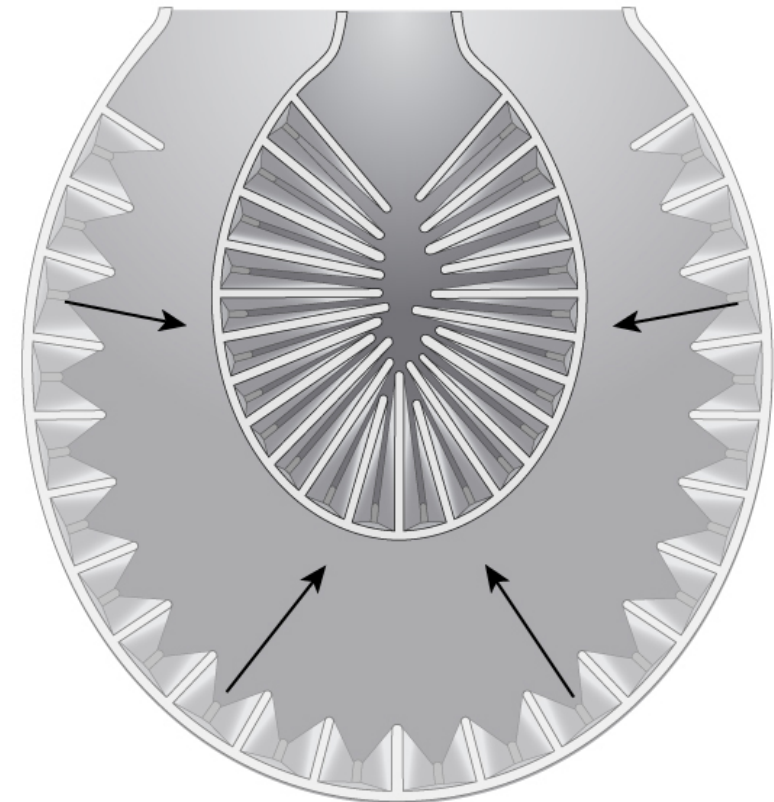
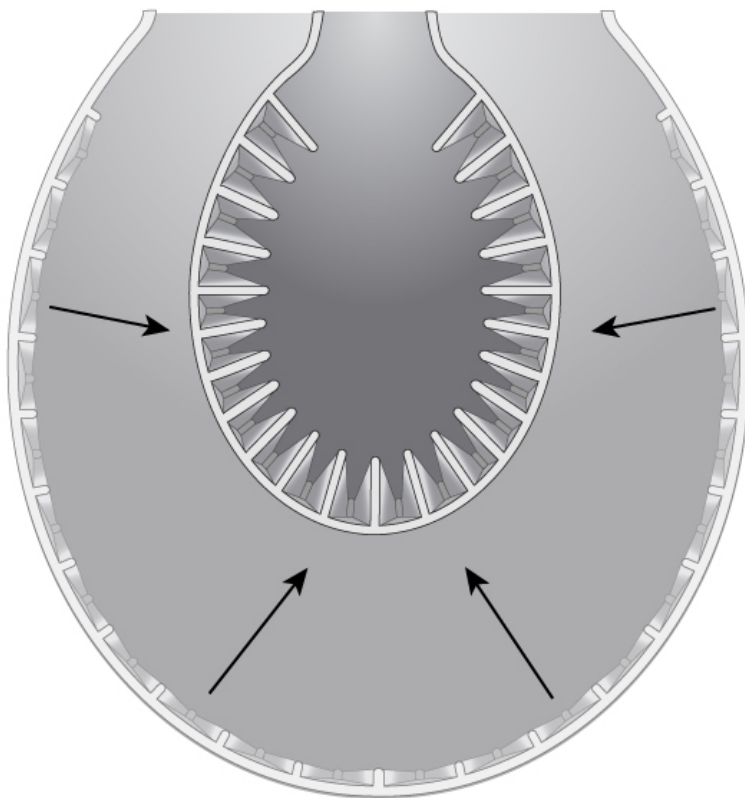
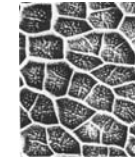
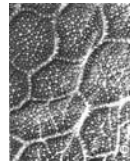
Reticular crests



from Clauss, Hofmann et al. (2010)



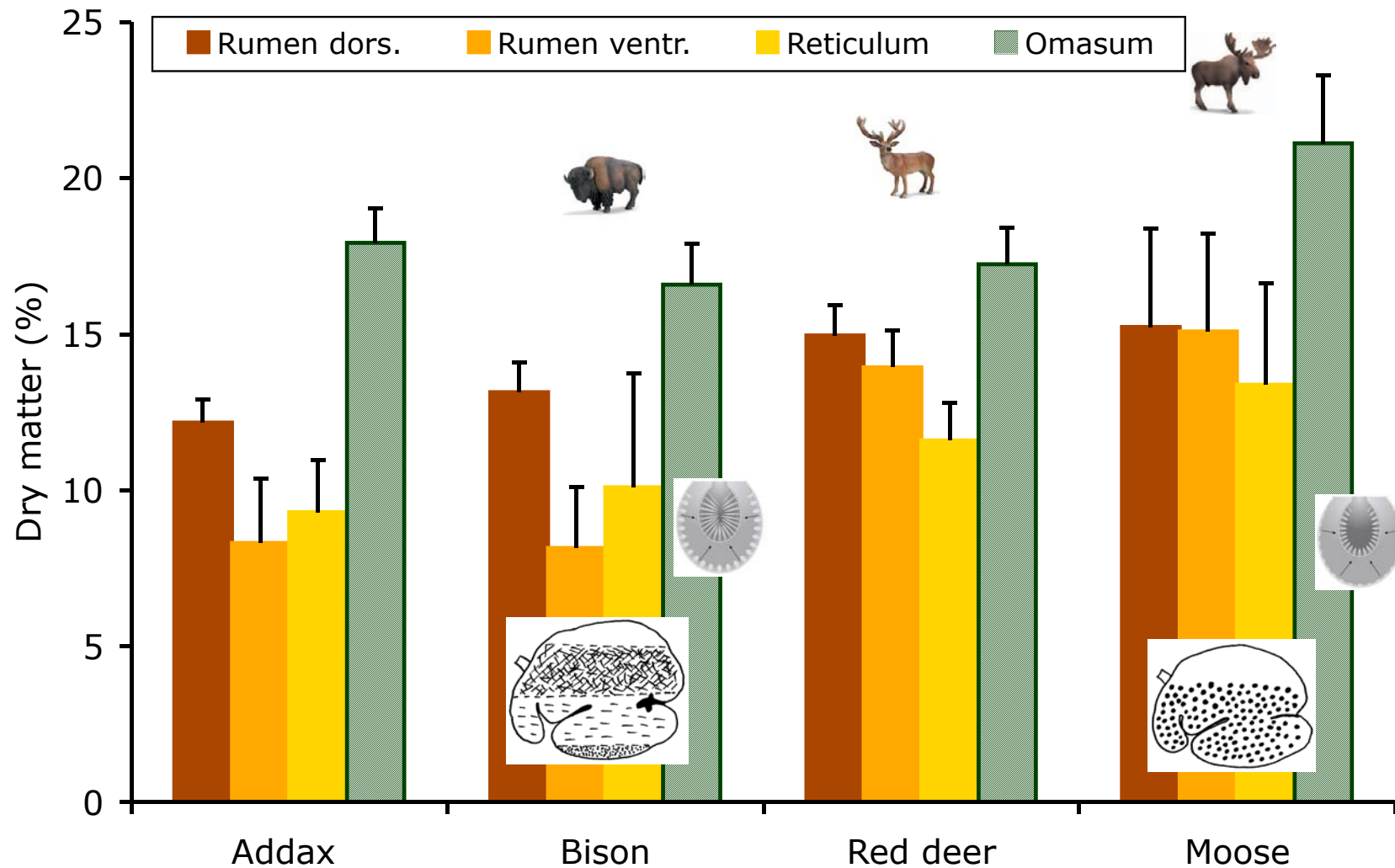
Reticular crests



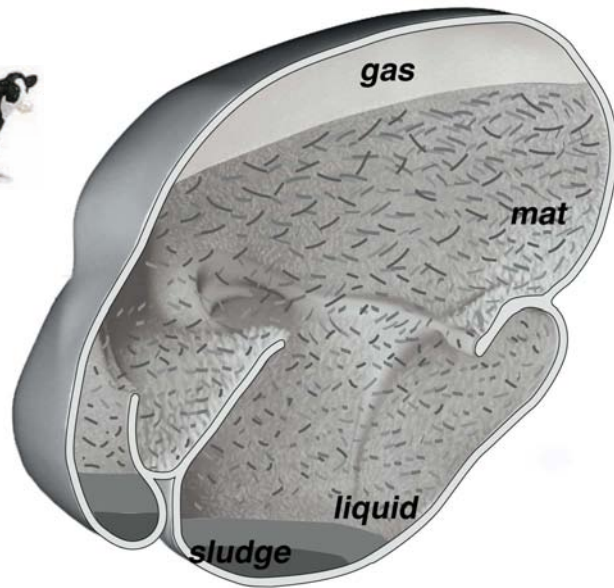
from Clauss, Hofmann et al. (2010)



Testing stratification by dry matter content



from Clauss et al. (2009)



**no escape of
unsaturated fatty acids
or
un-fermented sugars**



**escape of
unsaturated fatty
acids and
un-fermented sugars
possible**

Metabolic evidence of a ‘rumen bypass’ or a ‘ruminal escape’ of nutrients in roe deer (*Capreolus capreolus*)

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Abstract

As short chain fatty acids produced in the forestomach are insufficient to satisfy the energy requirements of the concentrate selecting roe deer (*Capreolus capreolus*), it is proposed that these animals may have other mechanisms to avoid energy losses due to microbial fermentation. Nutrients bypassing down the ventricular groove (rumen bypass) or ruminal escape of unfermented or partially fermented nutrients may be two alternatives. As metabolic evidence for incomplete fermentation in the forestomach we investigated: (1) the abundance of the sodium-dependent glucose co-transporter (SGLT1) in the duodenum; (2) enzyme activities of maltase, saccharase and α -amylase in duodenal and pancreatic tissue; and (3) the proportion of essential, polyunsaturated fatty acids in depot fat samples from ruminants of different feeding type and — for comparison — from animals with a simple stomach. The high abundance of SGLT1, high enzyme activity and the high proportion of polyunsaturated fatty acids in the concentrate selecting ruminants support the hypothesis of rumen bypass or ruminal escape of nutrients in roe deer and reflect differences in nutrient utilization by ruminants that belong to different feeding types. © 2001 Elsevier Science Inc. All rights reserved.

Keywords: Concentrate selectors; Enzyme activities; Feeding type; Roe deer; Rumen bypass; Ruminal escape; Ruminants; Polyunsaturated fatty acids; Sodium-dependent glucose co-transporter

1. Introduction

Roe deer (*Capreolus capreolus*) are the most abundant cervids in Europe and with a body weight of 20–30 kg the smallest indigenous rumi-

nant species. As energy requirements increase proportional to metabolic weight (Kleiber, 1961) roe deer require relatively more energy per unit of body mass for maintenance compared with that required by larger animals. To optimize the intake of energy they select easily digestible forage, especially dicotyledons, with a high proportion of soluble plant cell contents (Tixier et al., 1997). Due to this selective feeding behaviour and a number of morphological and physiological par-

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higher content of
unsaturated fatty
acids in browsers

glucose transporter
(absent in the small
intestine of grazers)
are present in
browsers



Vitamin E status

Dierenfeld (1989):

***On comparable supplementation,
grazers seem to have a lesser
vitamin E-status than browsers.***