# Aspects of food comminution in ungulates and their consequences for energy budget

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## Introduction

While green plant material represents the most commonly available food resource in terms of quantity, its nutritional quality poses considerable challenges. For chemical digestion, the lack of endogenous enzymes to digest the fibrous parts of plants (basically cell wall) is overcome in all major vertebrate herbivore lines by the development of large fermentation chambers within the digestive tract hosting symbiotic microbes (Stevens & Hume 1995). However, physical resistance of the material ingested as grass or browse represents another, equally relevant challenge herbivores are confronted with (Welch 1982). Reduction of particle size and disintegration of plant material in terrestrial herbivores is largely depending on the chewing process (Poppi et al. 1980, Murphy & Nicoletti 1984), which has been described to be responsible for about 80% of particle size reduction in forage like ryegrass or alfalfa in cattle (McLeod & Minson 1988). Comminution can be considered to be important because smaller ingesta particles will allow a denser packing of the digesta and therefore a higher intake. Even more important, it is of crucial significance for the speed of fermentation (Bjorndal et al. 1990); in contrast to cells without a cell wall, access to nutrients (cell solubles and cell wall itself) for microbes and consequently the host is depending on mechanical disruption of the fibrous cell wall as the major barrier (Fig. 6.1). Because smaller particles are fermented faster, animals that achieve a higher particle size reduction can afford shorter digesta retention times. This is evident in a comparison of reptiles and mammals (Fritz et al. 2010), but also within mammalian herbivores (Clauss et al. 2009b).

Degree of comminution can be regarded as an indicator for the elaborateness of the food processing system and also the level of metabolism of herbivores. Again, this is most obvious in herbivores with a low level of energy metabolism (brachymetabolic) like tortoises and herbivorous lizards, which show little to no particle size reduction beyond bite size (Fritz et al. 2010). At least some herbivorous dinosaurs, for which level of metabolism is a matter of discussion, were capable of some food comminution, e.g. ceratopsids and some ornithopods (Norman & Weishampel 1985, Weishampel & Jianu 2000). In birds, the gizzard is capable of comprehensive particle disintegration (Moore 1999, Fritz et al. 2011), while among extant mammals, a more or less comprehensive comminution by elaborated teeth is present in all lineages specialized on herbivory. Mammalian dentitions and chewing apparatus must surely be considered key innovations, contributing significantly to mammalian success in the large herbivore niche observed today (Ungar 2010, Berkovitz & Shellis 2018).

While in general all mammalian herbivores have developed an elaborate food comminution system, relevant differences become obvious when looking at it in more detail; important variables like the species-specific level of intake, retention time of food in the gut, digestion and metabolism of mammals influence each other, and food comminution is a crucial variable in this concert (Clauss et al. 2013). Differences between taxonomic groups are obvious and have triggered comparative research on their performance (Udén & Van Soest 1982, Fujikura et al. 1989, Fritz et al. 2009). Besides phylogenetic relationships, feeding preference (browse vs. grass) also takes considerable influence on the process of food comminution (Clauss et al. 2008, Codron et al. 2019).

In this contribution the focus will be on the process of food comminution in its effect on energy digestion and energy budget. While overall efficiency of the food comminution process of mammalian herbivores must be considered to be influenced by a concert of different factors, including, for example, the number of erupted teeth in juvenile animals (Grandl et al. 2018), effectiveness of

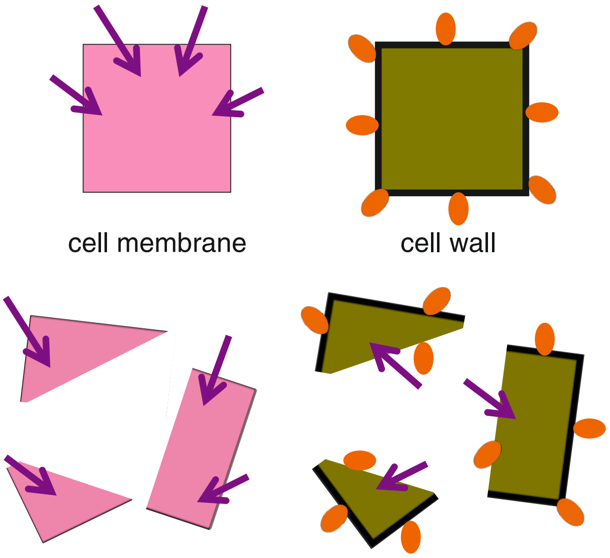

**Fig. 6.1.** Different digestibility of animal and plant cells. An animal cell without a cell wall can be directly digested by enzymes (upper left). In plant cells, the cell wall represents a barrier to digestive enzymes produced by vertebrates (upper right). Only cell-wall digesting microbes (orange ovals) can disrupt the cell wall so that enzymes can reach the inside of the cell (lower left). Disrupting cells mechanically will hence dramatically increase the rate of digestion (lower right.)

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dentition (e.g. occlusal area or enamel ridge length) and chewing behavior are considered to be major factors for chewing efficiency (Péréz-Barbería & Gordon 1998). After discussing relevant characteristics of food plants, a closer look on strategies of food comminution and on influencing factors on the process will be taken. Finally, major variables of the food comminution process will be summarized and compared for equids and ruminants as examples for two major and distinct herbivore lineages.

## Forage characteristics

When discussing adaptations and characteristics of herbivores, a look at the particularities of green plant material as food represents a logic starting point. Any adaptations seen in the feeding process of herbivores should have been triggered by characteristics of food. Among the factors to consider here are comminution resistance, particle fracture patterns in the comminution process and consequences of particle disruption for the digestion process. The dependence of particle disintegration on chewing is a consequence of lignification, since lignin represents the major material not degradable even by gut microbes. This can be easily visualized by investigating a *Ficus* leaf after the gut passage in *Iguana*, a well-fermenting but non-chewing herbivore: After gut passage, the lignified plant vascular system stays rather intact, while the rest of the tissue has been digested (Fig. 6.2). On the other hand, the less lignified a plant is, the more particle disintegration is possible simply due to gut microbial fermentation or peristalsis. Correspondingly, ingesta particle size in virtually non-lignified seagrasses (e.g. *Halophila ovalis*) has been shown to be continuously decreasing during gut passage in dugongs, most likely due to microbial activity on the available material (Lanyon & Sanson 2006).

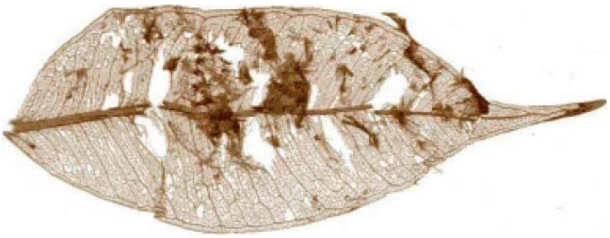

**Fig. 6.2.** *Ficus* leaf after gut passage in an iguana. Note that while much of the leaf parenchym was digested, the shape of the leaf stays intact. Photo: J. Fritz.

### Comminution resistance

Mechanical properties of green plant parts in the comminution process are among the first factors when characterizing the material as food. An evaluation of the fiber content (e.g. crude fiber, neutral-detergent fiber or acid-detergent fiber) is the typical approach of nutritionists. Neutral-detergent fiber (NDF) represents the sum of hemicelluloses + cellulose + lignin, acid-detergent fiber (ADF) that of cellulose + lignin, and crude fiber (CF) a less defined conglomerate of fractions of hemicellulose, cellulose, pectin and lignin. All these fiber fractions are closely associated with chewing efforts. For example, a relatively constant value of 3 h of chewing (rumination) has been assigned to 1 kg of CF (Piatkowski et al. 1990), and NDF content of the diet is regarded the most significant single predictor of feed intake and chewing duration in dairy cows (Mertens 1987, Nørgaard et al. 2010, Jensen et al. 2016).

However, for deeper insight, material science-orientated approaches may be preferable, using the energy necessary for comminution (comminution resistance) to rank and characterize materials (Sanson et al. 2001, Sanson 2006). Different approaches have been tried to arrive at such a quantification of the energy necessary to comminute a given amount of food. They range from technical approaches using material testing machines on individual plant parts (Sanson et al. 2001) or measuring the energy necessary to comminute a larger sample of the material in a mill (Laredo & Minson 1973, Paul & Mika 1981, Paul et al. 1981, Paul & Schild 1982, Paul 1984, Baron 1994, Blümmel et al. 1996) to even direct measurement of the metabolism of animals in relation to chewing activities (Susenbeth et al. 1998, 2004). For ruminants, energetic costs (measured as metabolizable energy ME) for chewing (eating + rumination) are estimated to be 10 % of maintenance energy requirements for high quality forage and up to 30 % (!) of maintenance energy requirements for low quality forage (straw); the cost for eating approaches values of 35 J/(min · kg BM) (BM = body mass) for species like cattle, sheep and horse, while costs for rumination are assumed to be only 27 % of those for eating (Susenbeth et al. 1998). This latter finding is best explained by the fact that material regurgitated for rumination has been washed, moistened, pre-fermented and softened by its previous stay in the rumen (Kennedy et al. 1993, Hatt et al. 2019, 2020).

Although less investigated, further characteristics of forages besides fibrousness may also influence the effort necessary for oral food comminution. Dry matter (DM) content is relevant in the nutrition of domestic ruminants, where grass based forages can be fed in ways differing considerably in DM. Fresh grass (DM: 230 g/kg) has been found to require considerably more energy effort for ingestive comminution (527 kJ/kg DM) than grass silage (DM: 310 g/kg; 355 kJ/kg DM) or grass hay (DM: 868 g/kg; 342 kJ/kg DM) (Susenbeth et al. 2004). These differences were not explained by fiber content (NDF contents: fresh grass 535 g/kg DM; grass silage 566 g/kg DM, grass hay 502 g/kg DM); instead, it can be speculated that variation in brittleness or in volume of identical amounts of DM are factors influencing the effort required for comminution.

### Fracture patterns

Somehow related to this topic, plant groups like grasses (monocot) and browse and forbs (dicot) appear to differ systematically in their fracture patterns: While grass is

**Fig. 6.3.** Fecal particles retained on 2 mm sieve after wet sieving. **A,** grass 1; **B,** grass 2; **C,** browse; **D,** alfalfa. Photos: G. Oleschinski.

comminuted into longish particles, particles developing from browse are of a more polyedric shape (Fig. 6.3) (Spalinger et al. 1986, Clauss et al. 2011). Such particle shapes potentially can have consequences e.g. for rumen stratification, which is far less present in browsing ruminants (Clauss et al. 2009a, Lechner et al. 2010), or for gut fill/ intake, as it has been suggested for alfalfa as an important dicot forage plant (Troelsen & Campbell 1968).

## Particle size and fermentation

Besides influencing physical behavior of food particles in the gut, comminution will also improve the energy budget of herbivores by accelerating the process of microbial fermentation substantially. The plant cuticle represents a largely impenetrable barrier to microbial access, which would only be possible e.g. via stomata without intensive comminution (see Fig. 6.1). In consequence, particle size is negatively correlated to degradation rate (Tab. 6.1). Only fungi, present to some degree in the gastro-intestinal tract of ruminants, have been described to have the capacity to penetrate this plant cuticle barrier and to facilitate bacterial access to fermentative material in this way (Van Soest 1994). Cellulose digestion is inherently a relatively slow process compared to polysaccharides like starch or pectin (Weimer 1996) and will always require relative long retention times to be effective. However, food comminution has the potential to speed up this process at least to some degree; this is reflected in the mean retention times of food in the gut of the respective herbivores, which are at the level of 90–250 h in herbivorous reptiles like tortoises, while those in ruminants are at the level of 48 h (Franz et al. 2011). The degree to which particle size influences

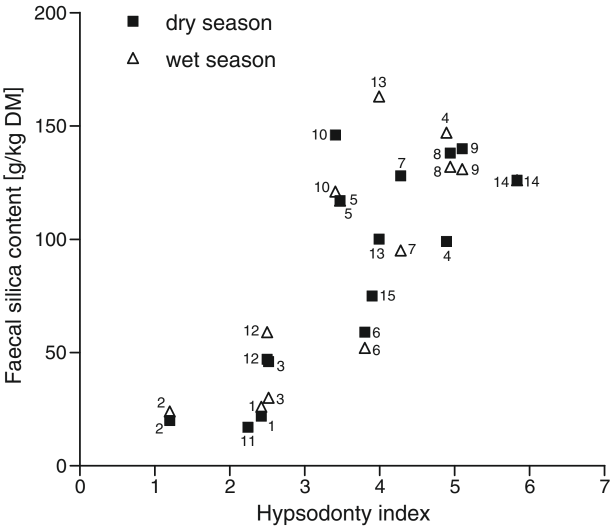

**Fig. 6.4.** Relation of fecal silica contents and hypsodonty index (degree of high-crownedness of teeth, estimated as ratio of tooth height/width of the 3rd molar). 1, greater kudu; 2, giraffe; 3, nyala; 4, impala; 5, waterbuck; 6, sable antelope; 7, roan antelope; 8, blue wildebeest; 9, tsessebe; 10, african buffalo; 11, black rhino; 12, african elephant; 13, warthog; 14, plains zebra; 15, white rhino. From Hummel et al. (2011).

fermentation rate may vary between plants, however. This was investigated in a sample of nine plants analyzed in an artificial fermentation system, the Hohenheim gas test. The samples were ranging from monocots (maize leaves; honey grass) to herbs (dandelion, ribwort) and browse (mulberry, hazel, elder, willow) and also included a leafy vegetable (endive). A significant influence of particle size (50, 20, 10, 6 and 2 mm, plus milled through a 1 mm sieve, standard size for chemical analyses) was obvious for most samples. The magnitude of the influence of particle size can be quantified as the relative increase of (fractional) fermentation rates with decreasing particle size, using a simple mono-exponential model. A high value indicates a high influence of particle size on fermentation rate, therefore. The effect was higher for the grass (14 %/mm) and maize (28 %/mm) samples (both monocots) compared to the 6 herb/browse samples with an average change of fractional fermentation rate of 7.3 ± 3.9 %/mm (dicots). The high standard deviation indicates that some dicots (e.g. mulberry) also reached a high level of ~15 %/mm. Differences in leaf morphology like structure of cuticle and lignification must be regarded as most likely reasons for such variation. No clear influence of particle size was seen for endive, as leafy vegetable the only sample bred for human consumption and therefore for low lignin content.

## Abrasiveness

The presence of abrasives in ingesta leads to increased tooth wear, up to the level of a serious loss of function in old animals. Abrasiveness associated with forage intake, either internally via phytoliths or externally via dust and sand, has been considered a major driver of the evolution of hypsodont teeth among herbivores. Since silica is the hardest material in ingested food, it has the highest potential to induce wear even on a material as tooth enamel (Williams & Kay 2001), generally considered to be the most abrasion-resistant animal tissue. While this relation appears straightforward and has been generally accepted, few attempts have been made to directly test this hypothesis. Besides its exceptional mechanical resistance, silica is also known to be chemically indigestible and is therefore used as a marker substance in digestion studies (Porter 1987). In consequence, fecal levels can be considered a reasonable proxy for the ingested amounts of silica, obviously slightly hampered by differences in overall digestibility of feeds. Since the residual ash of acid-detergent fiber (ADF) analysis recovers all silica in a sample (phytoliths + dust/sand) (Van Soest et al. 1991), it can be considered a valid and valuable methodological approach, allowing the quantification of larger sample sizes. In a study including 15 large herbivore species, a clear correlation between fecal silica levels (~ silica intake) and hypsodonty was found (Hummel et al. 2011) (Fig. 6.4). Browsing species had fecal silica contents of 17–46 g/kg DM, while grazing taxa had levels of 52–146 g/kg DM, with no difference found between wet and dry season. While the study demonstrates a clear

**Table 6.1.** Influence of food particle size on fermentation (DM, dry matter; NDF, Neutral-detergent fiber = hemicellulose + cellulose + lignin).

| Plant | Particle size | Fermentation rate | Degradation | Source |
|---|---|---|---|---|
| Grass | | NDF: | NDF (72 h) | 4) |
| (*Tripsacum dactyloides*, *Dactylis glomerata*), | <2 mm 1) | 0.066 h$^{-1}$ | 54.2 % | |
| Legume (*Trifolium pratense*) | <5 mm 1) | 0.048 h$^{-1}$ | 57.4 % | |
| Meadow hay | 0.1–0.4 2) | 6.43 ml gas/(g DM × h) | | 5) |
| | 0.4–1.0 2) | 5.10 ml gas/(g DM × h) | | |
| | 1.0–2.0 2) | 4.51 ml gas/(g DM × h) | | |
| Grass hay | | | DM (24 h) | 6) |
| | 5 mm 1) | | 21.6 % | |
| | 20 mm 1) | | 20.1 % | |
| | 40 mm 1) | | 17.2 % | |
| Grass (*Pennisetum purpureum*) | | DM: | DM (140 h) | 7) |
| | 3 mm 3) | 0.05 h$^{-1}$ | 83 % | |
| | 30 mm 3) | 0.03 h$^{-1}$ | 85 % | |

1) Particles passing the respective sieves
2) Particles passing the larger sieve size but retained on the following smaller sieve size
3) Exactly cut this size
4) Bowman & Firkins (1993)
5) Gerson et al. (1988)
6) Fadlalla et al. (1987)
7) Bjorndal et al. (1990)

relation of silica and development of high-crowned teeth, it could not answer the question which part of total silica (biogenic phytoliths or dust/sand) is responsible for most of the observed tooth wear. This question can be addressed with an experimental approach using diets varying the types of abrasives in a systematic way (Müller et al. 2014, Karme et al. 2016, Merceron et al. 2016, Ackermans et al. 2019, Martin et al. 2019). An alternative approach to the problem would be silica analysis methods that allow some differentiation; e.g., methods have been suggested to distinguish organic, soluble mineral and polymeric silica (Kolesnikov & Abaturov 1997, Kolesnikov & Gins 2001).

# Food comminution in herbivores

## Fecal particle sizes as a proxy for effectiveness of food comminution

The fact that digesta particle size is changed little after oral processing provides the opportunity to quantify chewing performance of different herbivores non-invasively via fecal particle size. It has been quantified using the wet sieving method mostly (Udén & Van Soest 1982, Kennedy 1984, Lechner-Doll 1986) (Fig. 6.5). While this is an established method, optical analysis is considered a valid alternative today (Luginbuhl et al. 1991, Péréz-Barbería & Gordon 1998, Nørgaard 2006, Kornfelt et al. 2013a, b). When applying wet sieving it should be kept in mind that the sizes given represent the sieve sizes and not the particles themselves. Especially the longish particles produced from grass may, by ‘toppling over’, be retained by sieves of a size much shorter than the actual particle length (Lechner-Doll 1986). While optical analysis is surely a valid practice, it obviously depends on an image of the sample without overlapping particles (which would not be recognized as separate entities). This requires protracted sample preparation, and thus puts some limitation on sample sizes, which influences representativeness. The quantification of very fine particles is another aspect where optical analysis should receive particular concern, since below certain particle sizes, resolution and particle clogging may become limiting.

Considering the fate of particles of different sizes in the digestive tract, various concepts have been put forward in the literature. For ruminants and camelids, it is well-established that larger particles are retained for a longer time than smaller particles, due to a sorting mechanism in the forestomach (Lechner et al. 2010, Clauss et al. 2011, Dittmann et al. 2015). This mechanism ensures that larger particles are re-submitted to rumination and hence ultimately reduced in size. Therefore, fecal particles reflect the effect of the sum of ingestive and rumination mastication. Since repeated rumination can compensate for a lower performance of the initial chewing process, reflections on the performance of tooth surfaces appear less direct in ruminants than in non-ruminating animals. A longer rumination time has the potential to compensate for less efficient teeth to a higher degree than the duration of ingestive mastication does in non-ruminating animals. Nevertheless, fecal particles still represent a valid estimate for the final result of total daily chewing efforts in ruminants.

In other large herbivores with a forestomach, but without the physiological adaptation of rumination, current evidence suggests that there is little differential passage of particles of different sizes (Clauss et al. 2004, Schwarm et al. 2009). For horses, in which such a differential passage had sometimes been postulated, it was recently demonstrated conclusively that large and small particles move through their digestive tract together (Hummel et al. 2018).

## Herbivore classes and influence of body mass

While comparative aspects of digestive physiology related to nutritional strategies like retention times have been in the focus of research for a longer time (Foose 1982, Duncan et al. 1990), comparative food comminution moved into the center of interest only more recently. Differences between large herbivores like elephants, rhinos, equids, tapirs, ruminants, camelids, pigs and hippos have been investigated in a comprehensive overview for animals on zoo diets (Fritz 2007, Fritz et al. 2009). In another data set, fecal particle size has been evaluated for 16 large herbivores (African

**Fig. 6.5.** Sieving machine as used for quantifying fecal particle sizes of herbivores. Photo: J. Hummel.

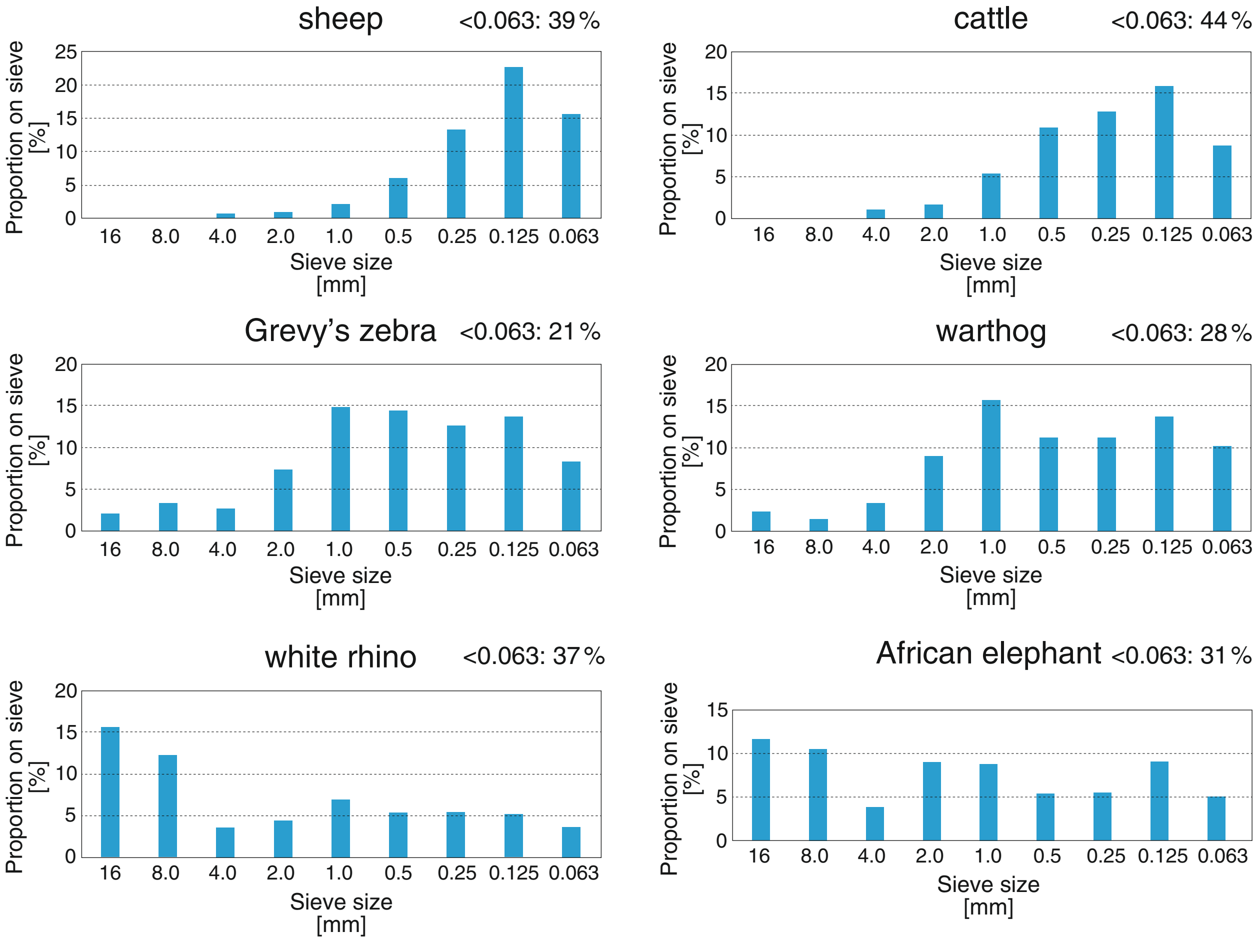

**Fig. 6.6.** Fecal particle size distributions of different herbivores. Based on data from Clauss et al. (2015); numbers in boxes represent the weight difference between initial sample and the sum of particles retained on the sieves.

elephant *Loxodonta africana*, white rhino *Ceratotherium simum*, Grevy's zebra *Equus grevyi*, Przewalski horse *Equus ferus przewalskii*, domestic horse and Shetland pony *Equus ferus caballus*, warthog *Phacochoerus africanus*, domestic cattle *Bos taurus primigenius*, forest buffalo *Synceros caffer nanus*, blue wildebeest *Connochaetes taurinus*, sable antelope *Hippotragus niger*, gemsbok *Oryx gazella*, waterbuck *Kobus ellipsiprymnus*, domestic sheep *Ovis orientalis aries*, domestic goat *Capra aegagrus hircus* and Bactrian camel *Camelus bactrianus*), all on a diet of ad libitum intake of meadow hay (Clauss et al. 2015) (Fig. 6.6). The hay had an NDFom (neutral-detergent fiber, ash-corrected) content of 720 g/kg OM and an ADL/NDFom ratio of 0.07. In both studies, animals of very large body mass (>1000 kg) like elephants, rhinos and hippos where characterized by particularly large fecal particle sizes, with averages of 5.1 and 5.0 mm for white rhinos and African elephants, respectively (reaching sizes of several centimeters for longest particles). It is an interesting aside that this is true although they differ considerably in their way of processing and chewing food, which becomes obvious e.g. when comparing fecal particles of browsing black rhinos and elephants in the same habitat. While ingested twigs will be present as clearly cut pieces in rhino feces, they will appear as rather "squeezed", but less sharply cut pieces in elephant dung (J. Hummel. pers. obs.).

Equids were intermediate (∅ 1.24 ± 0.22 mm), while ruminants and camels invariably had the by far smallest particle sizes (∅ 0.39 ± 0.10 mm) (Fig. 6.6). The warthog as artiodactyl hindgut fermenter had a fecal particle size similar to that seen in equids. In the ruminant data set, no major influence of body size was evident: Cattle were on a rather comparable level than e.g. sheep. Interestingly, the Bactrian camel as the only camelid in the sample plots with ruminants in principle, but has slightly larger fecal particles than any other ruminating animal (all Ruminantia). Functionally, camels are ruminants, achieving a comparable digestive efficiency, but are characterized by a slightly lower metabolism and food intake than true ruminants (Jalali et al. 2012, Dittmann et al. 2014). While sharing dental characteristics like selenodont teeth and missing upper incisors, camels differ in details of their chewing behavior, in particular in chewing each individual bolus on both sides alternating. This is in contrast to (true) Ruminantia which invariably chew a single bolus on one side of the jaw only, and change to the other side for the next bolus (Hendrichs 1965).

Given the large particle sizes found in many megaherbivores, the influence of body mass on fecal particle size became of interest. A scaling of fecal particle size with BM$^{0.14}$ has been proposed (Péréz-Barbería & Gordon 1998) for the data set of Udén (1978). It soon becomes obvious that, as outlined by Fortelius (1985), allometry among lines of considerable phylogenetic distance (e.g. elephants, rhinos, equids, hippos, ruminants) is different and generally much more pronounced from what is seen in closely related taxa or even breeds (e.g. equids reaching from a riding horse of 600 kg BM over a Przewalski horse of around 300–400 kg BM to Shetland ponies of a BM of 100 kg). If at all, only much smaller differences appear to be found in the latter case where animals of considerably different size, but uniform *bauplan* are compared. Among lineages of uniformly very large body size (elephants, rhinos, hippos), there appears to be a "megaherbivore" syndrome in the area of food comminution: Their very large fecal particle sizes render those groups distinctively different from e.g. equids or ruminants (the latter with the particularities in the food comminution outlined above). Potential explanations for the pattern could be the limited selectivity and in consequence diet quality in megaherbivores, or a higher gut fill in virtually predation-free taxa, compensating for less intense food processing.

Between breeds of a species or taxa of a distinct phylogenetic group, BM can largely vary, but virtually no effect of BM on fecal particle size is found; this is true within ruminants or equids. It has been described for horses that tooth size (and therefore also determinants of dentition performance like length of enamel cutting edges or occlusal surface) is decreasing disproportionately with BM, providing smaller breeds with a relatively larger tooth area (Radinsky 1984). In ruminants, in fact extensive breeds with a higher potential to use fiber-rich forage are often characterized by relatively small body mass (e.g. sheep: German grey heath, Skudde; cattle: Galloway, highland cattle), providing them – assuming this line of thought – with superior chewing capacity in relation to BM.

In this context, an example for differences in the food comminution process well-known from practical feeding of domestic ruminants becomes interesting. It is well established that digestibility of diets including kernels of maize and also other cereal grains benefits from a more thorough pre-feeding crushing when being fed to cattle, but not or far less when fed to sheep. In fact, whole maize kernels appear in feces of cattle (and in consequence lead to a reduced dry matter digestibility) if kernels/their hulls have not been cracked in some way prior to feeding (Wilson et al. 1973). While the practical evidence is convincing, it does not appear to be clear to which degree this is due to differences in rumen retention characteristics (leading to a faster outflow/preventing rumination of kernels) or due to closer enamel ridges in the smaller animal, avoiding escape of any undamaged kernels from the chewing process.

## Feeding types (browsers and grazers)

Many parts of the foraging process of herbivores can be influenced by the specialisation on certain forage plant types (Codron et al. 2019). While the dichotomy of grazer and browser may appear to be over-simplified, morphological patterns seen among herbivores largely follow their preference for the respective plant group (Figs. 6.7, 6.8). Among the obvious differences seen in tooth morphology are hypsodonty in grazing species and differences in presence of enamel cutting edges (Kaiser et al. 2010). For ruminants, a meta-analysis has described a shift of chewing from rumination to ingestion-chewing for goats compared to sheep (Dulphy et al. 1995). This observation is in line with the idea of rumination decreasing the burden of strong abrasiveness of a grass diet due to the intake of solid or grit (Hatt et al. 2019, 2020), since goats are characterized as intermediate feeding type with a strong preference for browse, and can be expected to ingest a far less abrasive diet when given the choice under free-ranging conditions. As mentioned, the difference between the feeding types in ingesta particle dimensions (longish in grass, polyedric in browse) is largely a characteristic of the respective forage (and not tooth morphology), but it is expected to have the potential to influence intake capacity of the respective herbivore (Troelsen & Campbell 1968) with a potentially higher intake capacity, at the same gut volume, in browsers.

Investigations on fecal particle sizes in feeding types have resulted in larger particles for browsing ruminant species on their respective zoo diets (Clauss et al. 2002), but not on the diets in their natural habitats (Hummel et al. 2008, Lechner et al. 2010), which suggests that either captive grazers are fed diets more similar to their natural ones, or that teeth of grazers are more universally efficient than those of browsers. In a study on feeding types in kangaroos, larger particles were found in the forestomach of three browsing compared to one grazing species (Lentle et al. 2003). In contrast to this, in rhinoceroses, larger particles were found in the grazer (white rhino) than in the browser (black rhino) when animals were fed a grass hay diet (Steuer et al. 2010). It should be added here that results of this study may have been influenced by the age of the animals, since at least two of the white rhinoceroses (*Ceratotherium simum*) were considerably older than the four browsing black rhinos (*Diceros bicornis*). It remains an open question to which degree differences in tooth morphology must be interpreted as adaptations resulting in improved comminution capacity for different forages, or if they just represent simplifications in browsers as herbivores with a diet less demanding in several aspects of comminution.

Less information is available for other herbivore lineages including taxa with a more browsing or grazing food selection, e.g. proboscideans. While both extant species are considered intermediate feeders, food choice of the African elephant could be demonstrated to be shifted towards browse compared to the Asian elephant (Cerling et al. 1999), which is also reflected in variables of digestive physiology like retention time (Hackenberger 1987). However, no systematic difference in fecal particle sizes was obvious in the study of Fritz (2007) and in a separate evaluation of four Asian and eight African zoo specimens (Tab. 6.2).

Practical feeding of specialized browsers in captivity has been receiving considerable attention for a long time (Clauss & Dierenfeld 2008); their capacity to comminute and ingest particular plant material is of relevance for their potential intake of different forages. Interestingly, considerably larger fecal particle sizes have been described for captive compared to free-ranging giraffe (Hummel et al. 2008), a result that was recently confirmed (Schüßler et al. 2017). The fact that in the latter study fecal particle size decreased from alfalfa hay to browse for identical individuals points to an interaction between tooth structure and forage type (and rather excludes an explanation assuming

**Fig. 6.7.** Grazing and browsing herbivores. Photos: Forages and giraffe J. Hummel, Grevy's zebra P. Steuer.

more strongly abraded teeth in a brachydont (low-crowned) browsing species like giraffe).

**Table 6.2.** Mean particles sizes in feces of zoo elephants (all diets were based on grass hay, in zoos B and C supplemented with some straw, tree branches and limited concentrates).[1]

| | Mean particle size [mm] | Diet | Age [years] |
|---|---|---|---|
| African elephant | 4.2 | Zoo A | 23 |
| | 5.5 | Zoo A | 23 |
| | 7.6 | Zoo A | 23 |
| | 5.8 | Zoo A | 23 |
| | 5.5 | Zoo A | 23 |
| | 5.6 | Zoo A | 29 |
| | 8.0 | Zoo B | 21 |
| | 5.6 | Zoo B | 26 |
| Asian elephant | 6.1 | Zoo B | 55 |
| | 7.9 | Zoo B | 40 |
| | 7.1 | Zoo C | 42 |
| | 12.9 | Zoo C | 28 |

## Feed intake during lactation

While food comminution must be sufficient to meet metabolic requirements, its highest performance is necessary in times of significant additional nutrient requirements like during lactation. The latter can be considered to be the period of highest energy requirements and of highest food intake in mammals. Changes like increased rumination investment, increased digesta particle sizes, increased gut fill and increased passage rate are potential consequences of increased food intake (Welch & Smith 1969). In sheep, increasing intake from 0.5 to 1.0 kg DM decreased time spent ruminating per kg DM for approximately 20 %, while chewing during feeding was influenced very little (Grimaud 1999, as cited in Baumont et al. 2006).

Changes can be expected to be most extreme in the case of domestic animals bred for milk production like high yielding dairy cows, well known for a particularly high increase in energy requirements during lactation. In fact, increasing fecal particle sizes are reported by some authors for ruminants with increased feed intake (Luginbuhl et al. 1990, Okine & Matthison 1991), while other studies did not see an increase (Kovács et al. 1997a, b, 1998). In dairy goats, a triplication of feed intake (from 0.9 to 2.8 kg DM; maintaining a constant ratio of 50 % concentrate/50 % grass hay) during lactation led to considerable changes in mean retention time of particles ($\mathrm{MRT}_{\mathrm{particle}}$) (from 71 ± 8.9 h to 31 ± 2.3 h) and in organic matter digestibility (from 68 ± 2.1 % to 59 ± 2.1 %), but only to minor differences in

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[1] Two other results of the latter data set deserve attention: (1) The oldest individual in this sample (55 years) was not characterized by a deviating fecal particle size, demonstrating the effectiveness of the lifelong tooth replacement mechanism in elephants. (2) The elephant characterized by conspicuously large fecal particles (12.9 mm) was an individual with a known history of tooth problems, potentially resulting in less effective chewing.

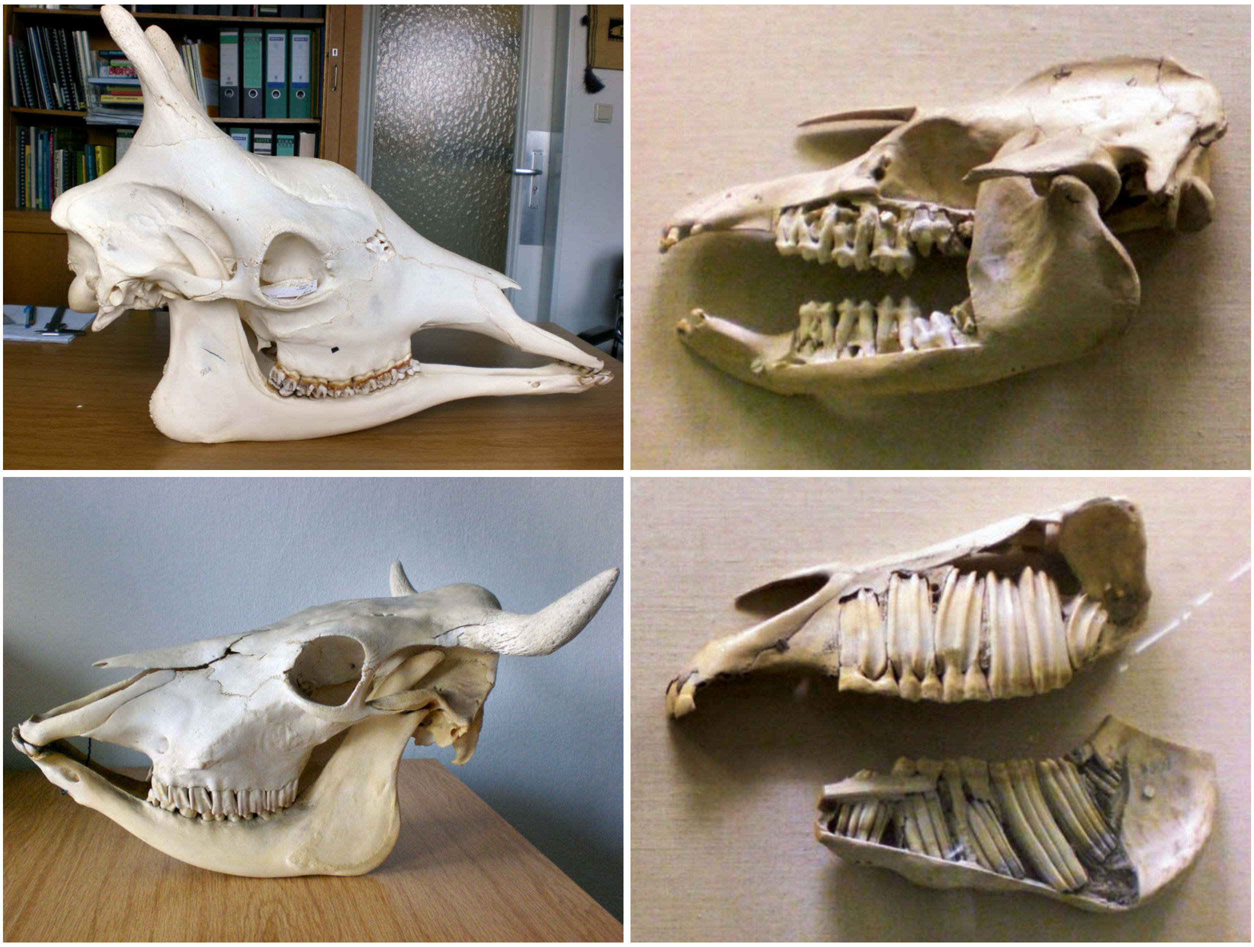

**Fig. 6.8.** Comparative head morphology of browsers and grazers. Artiodactyls/ruminants: brachydont (low-crowned) giraffe (*Giraffa camelopardalis*, upper left) and hypsodont (high-crowned) cattle (*Bos taurus taurinus*, lower left); perissodactyls: brachydont tapir (*Tapirus* sp., upper right) and hypsodont domestic horse (*Equus caballus*, lower right). Note that hypsodont species must shift the eye socket to the rear due to the space taken by maxillary molars. Photos: J. Hummel.

fecal particle sizes (from 0.53 ± 0.02 mm to 0.59 ± 0.02 mm for mean particle size) (Findeisen 2012).

While it can be expected that results on fecal particle sizes are influenced by the selective retention mechanism in ruminants, an effect of increased intake should be more direct in non-ruminating animals. Only limited data are available in this respect. However, in a study on rabbits, no difference in fecal particle size was present if feed intake was increased twofold during lactation from 110 g DM/day to 220 g DM/day (again with a constant ratio of 50 % grass hay/50 % pelleted concentrate) (Findeisen 2012). While retention time was influenced again from 31 ± 2.5 h to 19 ± 3.1 h for $\text{MRT}_{\text{particle}}$, no change in mean fecal particle size was present (0.56 ± 0.02 mm and 0.59 ± 0.02 mm), suggesting that the animals maintained chewing intensity (per unit food), and thus most likely increased their daily chewing time with increasing intake.

## Tentative calculations on the energy budget of food comminution in herbivores

Several interactions of food comminution and energy budget have been outlined in the sections above and are summarized in Figure 6.9. A comparison of performance of herbivorous reptiles and mammals clearly demonstrates the advantageous consequences of food comminution.

Particle size reduction by chewing requires energy investment by the animal. This becomes evident from studies in which the energy required for eating forages of different particle size is quantified – typically, the same forage offered in a size-reduced form (chopped, or ground) facilitates intake at lower energetic costs (Osuji et al. 1975, Susenbeth et al. 1997).

When comparing the comminution and forage energy processing capacity of herbivores, a set of variables becomes interesting for a complete description of food processing strategy. These include:

(1) Intake and particle size of ingested food;
(2) fecal particle sizes, food digestibility and retention time;

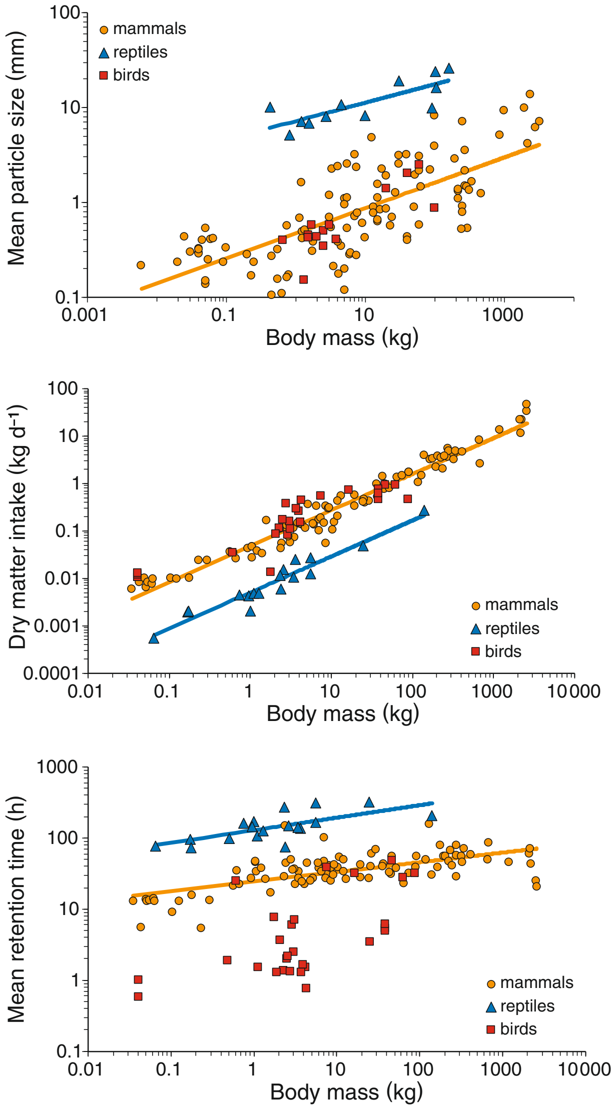

**Fig. 6.9.** Aspects of digestive physiology in herbivores. Data from Clauss et al. (2007), Fritz et al. (2009, 2010, 2012), Franz et al. (2011).

(3) characteristics of dentition influencing particle comminution per chew (total length of cutting edges) (in the short term invariable part of the chewing process);
(4) duration and frequency of chewing during feeding and rumination (how many chews per day and per unit of feed, amplitude of chewing strokes (= number of cutting edge contacts of a single stroke), plus possibly chewing force);
(5) energy requirement for chewing (energy effort per chew or per unit of feed intake).

Available variables have been summarized in Table 6.3 for two extant herbivores, equids represented by the horse and ruminants by cattle. The differences in fecal particle sizes are obvious and have been quantified as mean particle sizes of 1.24 and 0.38 mm for horse and cattle, respectively. The energy needed for a single feeding chewing stroke can be considered to be higher in horses, which have been described to have three times the chewing muscle mass of a comparably or even larger ruminant (bison) (Becht 1953, as cited in Fortelius 1985). Data from Osuji et al. (1975) and Vernet et al. (1995) support this assumption in showing that ingestive activity represents a higher proportion of overall maintenance energy intake in horses compared to ruminants. In addition, ruminants shift much of their chewing efforts to pre-digested material, which appears to lower the burden of comminution energy. Considerably less energy necessary for grinding has been found in pre-fermented compared to untreated feed (Kennedy et al. 1993). This is reflected in the values published by Susenbeth et al. (1998), indicating a threefold higher energy requirement for chewing during feeding compared to rumination, and supported in other studies on sheep and cattle (Suzuki et al. 2008, 2014).

Using the different published data to make more detailed, quantitative comparisons includes a large number of uncertainties and potential sources for mistakes. Experiments in which all measures – body mass, food intake, chewing behavior, particle size reduction, and energy required for chewing – have been recorded on the same animals, on the same diets, do not exist. But we consider such calculations an informative exercise nevertheless, and present two different sets of calculations.

For the first, we assume that chewing energy in ingestive chewing is the same for horses and cattle, and simply use data measured in cattle by Susenbeth et al. (1998) for horses and cattle. For the second, we use data from Vernet et al. (1995) to calculate the energy required for ingestion of a given amount of dry matter for cattle and horses, and assume that the proportion of energy required for rumination in cattle is the same as that in the data of Susenbeth et al. (1998). One of the many differences in the approaches between the two studies is the use of animals with empty rumens by Susenbeth et al. (1998), which ensures that only costs due to chewing but not energy due to initiated digestion is recorded. Correspondingly, values using the Vernet et al. (1995) data are generally of a higher magnitude. This is also the reason why data from the two studies cannot be compared directly.

We assume two similar-sized animals of 600 kg with typical values for intake (Table 6.3). Total ME requirements for maintenance would be around 60 MJ/day for a 600 kg animal, assuming an energy requirement of 0.5 MJ/kg BM$^{0.75}$ (GfE 1995, 2014). The first approach using the Susenbeth et al. (1998) data suggests a daily energy expenditure for chewing of 1.38 MJ ME for the horse compared to 1.08 MJ ME for cattle. The value for cattle is composed of 0.70 MJ due to ingestion and only 0.38 MJ due to rumination. The cost of rumination chewing would therefore be only about half the value of that for chewing during feeding, irrespective of the higher amount of chews spent during rumination. The second approach using the Vernet et al. (1995) data yields a daily energy expenditure for food processing of 10.05 MJ ME for the horse and 4.21 MJ ME for cattle, suggesting a more distinct difference.

Assuming a uniform particle size of 50 mm in the diet of horse and cattle, the difference to the mean fecal particle size can be calculated (representing the reduction of particle size; 49.62 mm for cattle and 48.76 mm for the horse), weighted by the daily intake (7.5 kg DM for a 600 kg cow and 12.6 kg DM for a 600 kg horse) and divided by the daily amount of chews to arrive at a number quantifying the "particle comminution capacity" of a single chewing stroke. Thus, the particle comminution capacity of cattle is 49.62 mm · 7.5 kg DM/34 074 chews = 0.011 mm · kg/chew; whereas that of horses is 48.76 mm · 12.6 kg DM/27 625 chews = 0.022 mm · kg/chew. In other words, a single chewing stroke in the horse is about twice as efficient as that of cattle. Most likely, this is achieved by a combination of an extended chewing surface due to the molarisation of horse premolars (whereas the premolars of cattle are, on the opposite, reduced), and the most intricate set of enamel folds found in large mammal molars to date (plus possibly the more elaborate chewing muscles in horses). The calculation thus is evidence for the putative power of morphological adaptations to achieve a high chewing efficiency.

When putting this particle comminution capacity in perspective with the required daily energy expenditure for chewing, our two different approaches lead to diverging results. In the first approach, horses achieve 0.022 mm · kg/chew using 1.38 MJ ME, or 0.016 mm · kg/chew per MJ ME. Cattle achieve 0.011 mm · kg/chew using 1.08 MJ ME, or 0.010 mm · kg/chew per MJ ME. Based on this approach, the ruminant system partially, but not completely compensates for the difference in chewing efficiency based on the effect per chew. In the second approach, with a much larger difference in energy used for chewing, horses achieve an energetic efficiency of chewing of 0.0022 mm · kg/chew per MJ, and cattle are even superior at 0.0026 mm · kg/chew per MJ. Based on the many assumptions necessary to derive the figures, these results should not be used to construe an energetic advantage of ruminants based on chewing only, but rather underline that very different organismal solutions – the equid and the ruminant system – arrive at similar efficiencies, where differences may or may not await detailed investigation. While it may appear surprising that the ruminant system is not distinctively superior in these calculations, one needs to consider in addition the higher digestive efficiency achieved by ruminants, which is also due to their higher digesta particle comminution. In evolutionary terms, animals should not be conceptualized at excelling at individual feats, such as chewing efficiency, but in overall traits such as energetic efficiency that, ultimately, results in an efficiency of turning environmental resources into offspring (Clauss et al. 2019).

## Conclusion and final remarks

- Efficient food comminution is a key requirement for evolutionary successful herbivores.
- Physical processing and processing characteristics of animal food represent interesting fields of research, where we still have much to learn.
- In most plants, an increasing effect of particle comminution on fermentation rate is present; on average, it appears to be higher in grass than in browse.
- In the comparison of grazer vs. browser, all available data on differences on the level of physical characteristics of forage and its interaction with morphology/physiology of the animal (particle shapes, rumen

**Table 6.3.** Variables relevant for the energy budget of food comminution of ruminants and horses.

| | | Cattle | Horse | |
|---|---|---|---|---|
| Body mass (kg) | | 600 | 600 | |
| Intake (g DM/kg BM$^{0.75}$) | | 62 | 104 | Foose (1982) |
| (kg DM/day) | | 7.5 | 12.6 | |
| Chewing frequency (chews/min) | Ingestion: | 75 (65–85)[1], 73[2] | 77[2] | [1] Jarrige et al. (1995), |
| | Rumination: | 60 (55–65)[1] | | [2] Dittmann et al. (2017) |
| Total number of chews per day | Ingestion: | 13 942[3] | 27 625[4] | [3] Piatkowski et al. (1977) |
| | Rumination: | 20 132[3] | | [4] Porzig & Sambraus (1991) |
| | Total: | 34 074 | 27 625 | |
| Total duration (min/d) | Ingestion: | 185 | 359 | |
| | Rumination: | 336 | | |
| | Total: | 521 | 359 | |
| Energy requirement chewing (J/(min · BM$^{0.75}$) | Ingestion: | 30 | 30 | Susenbeth et al. (1998) |
| | Rumination | 8.9 | | |
| Daily energy for chewing (MJ) | Ingestion: | 0.70 | 1.38 | Susenbeth et al. (1998) |
| | Rumination: | 0.38 | | |
| | Total: | 1.08 | 1.38 | |
| | Ingestion: | 2.73 | 10.05 | using data from Vernet et al. (1995) for ingestion, and assuming the proportions of energy for ingestion and rumination as Susenbeth et al. (1998) |
| | Rumination: | 1.48 | | |
| | Total: | 4.21 | 10.05 | |
| Fecal particle size (mean size, mm) | | 0.38 | 1.24 | Clauss et al. (2015) |
| Chewing efficiency (mm · kg/chew) | | 0.011 | 0.022 | |
| Energy efficiency for comminution (mm · kg/chew · MJ) | | 0.010 | 0.016 | using energy from Susenbeth et al. (1998) |
| | | 0.0026 | 0.0022 | using energy from Vernet et al. (1995) |
| Change of fermentation rate with particle size | | 15 %/mm particle size (grass) | | |

stratification, abrasiveness) point to differences at least as large as those on the chemical level.

- Body size appears to be a relevant factor for food comminution when observing it on the level of larger phylogenetic groups like ruminants, elephants, rhinos or equids, while within these groups, the influence of body size is far less pronounced. This opens the possibility that larger forms are not optimized in the particular trait under consideration (here: chewing efficiency), but that they have survived for other reasons that prevent the superiority of smaller forms to take effect on niche occupation.
- On a comparative level, data that facilitate a comparison of species in terms of chewing efficiency (accounting for the energy required to achieve a specific degree of particle size reduction by chewing, and weighting by the effects on intake capacity and rate of digestion) are still largely missing. Tentative comparisons between horses and ruminants illustrate that different morphophysiological solutions for a biological challenge exist. The degree by which such differences in a single system (here: digestive physiology) can account for perceived differences on the scale of 'evolutionary success' remains speculative.

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