

# Avoiding the lockdown: Morphological facilitation of transversal chewing movements in mammals

Annika Avedik  | Maria J. Duque-Correa  | Marcus Clauss 

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

## Correspondence

Marcus Clauss, Clinic for Zoo Animals, Exotic Pets and Wildlife, Vetsuisse Faculty, University of Zurich, Winterthurerstr. 260, 8057 Zurich, Switzerland.

Email: [mclauss@vetclinics.uzh.ch](mailto:mclauss@vetclinics.uzh.ch)

## Abstract

The evolution of mammals is characterized, amongst other developments, by an increasing relevance of effective food processing in form of an increasingly durable dentition, complex occlusal surfaces, and transverse chewing movements. Some factors have received increasing attention for the facilitation of the latter, such as the configuration of the jaw joint, the chewing muscle arrangement and lever arms, or the reduction of interlocking cusps on the cheek teeth occlusal surface. By contrast, the constraining effect of the anterior dentition (incisors and canines) on transverse chewing motions, though known, has received less comprehensive attention. Here, we give examples of this constraint in extant mammals and outline a variety of morphological solutions to this constraint, including a reduction of the anterior dentition, special arrangements of canines and incisors, the nesting of the mandibular cheek teeth within the maxillary ones, and the use of different jaw positions for different dental functions (cropping vs. grinding). We suggest that hypselodont anterior canines or incisors in some taxa might represent a compensatory mechanism for self-induced wear during a grinding chewing motion. We propose that the diversity in anterior dentition among mammalian herbivores, and the evolutionary trend towards a reduction of the anterior dentition in many taxa, indicates that the constraining effect of the anterior dentition, which is rigidly linked to the cheek teeth by the osseous jaws, represents a relevant selective pressure in mammalian evolution.

## KEYWORDS

canines, chewing anatomy, chewing mechanics, dentition, herbivore, incisors, mastication

## 1 | INTRODUCTION

Herbivorous mammalian tooth evolution is characterized by at least two trends: First, an increase in species with higher-crowned or ever-growing cheek teeth (Jernvall & Fortelius, 2002; von Koenigswald, 2011; Tapaltskyan et al., 2015), generally interpreted

as an indication for selection for dental durability. Second, an increase in tribosphenic cheek tooth occlusal surface complexity (Jernvall et al., 1996; Yamanaka, 2022) is interpreted as selection for increased chewing efficacy. At the same time, several different mammalian chewing modes evolved from the ancestral orthal (up-and-down) movement that may or may have not included a rotation of the

This is an open access article under the terms of the Creative Commons Attribution-NonCommercial-NoDerivs License, which permits use and distribution in any medium, provided the original work is properly cited, the use is non-commercial and no modifications or adaptations are made.

© 2023 The Authors. *Journal of Morphology* published by Wiley Periodicals LLC.

mandible along its longitudinal axis (“hemimandibular roll”), with only a small transversal (typically, latero-medial for the working side) component (Bhullar et al., 2019, 2020; Crompton & Hiiemae, 1969; Grossnickle, 2017, 2020). Compared to earlier chewing mechanisms in mammaliform evolution, this ancestral chewing mode was suggested to already have represented a considerable increase in chewing efficacy (Bhullar et al., 2019; Grossnickle, 2017). Correspondingly, the subsequent evolution of transverse mandible movement is another hallmark of mammals (Bhullar et al., 2019; Grossnickle et al., 2022; Hiiemae, 1978; Turnbull, 1970; Weijs, 1994; Williams, 2019).

To yield the full potential of the complex occlusal cheek tooth surfaces, these surfaces need to be moved against each other, not only in a simple orthal movement or the short distance covered by a “hemimandibular roll,” but must grind transversely alongside each other in either a latero-medial (working side) movement (“yaw”), a propalinal (forward or backward) movement, or some combination of both (Fortelius, 1985; von Koenigswald, 2018). One prerequisite for such a transverse movement was the flattening of the tribosphenic cheek teeth's cusps so that no interlocking of the cheek teeth would occur (Bhullar et al., 2019). This transverse movement, however, represents not only a theoretical problem for the shape of the cheek teeth themselves, but for the whole oral processing apparatus that also comprises the anterior teeth, that is, the incisors and the canines. In the ancestral state, the mammalian dentition does not only comprise three molar and four premolar teeth, but also a canine and three incisors per jaw side (O'Leary et al., 2013). These anterior teeth are linked by bone—the upper and lower jaw—to the respective cheek teeth, and therefore, any movement made by the lower jaw to move the cheek teeth will move the incisors and canines as well, and vice versa. In an orthal jaw movement, this is not problematic, because—if properly aligned—all teeth (incisors, canines, cheek teeth) will reach their functional occlusal position at the same time (Figure 1). The only prerequisite for functionality of all teeth is that in the “closed” position, the incisors'

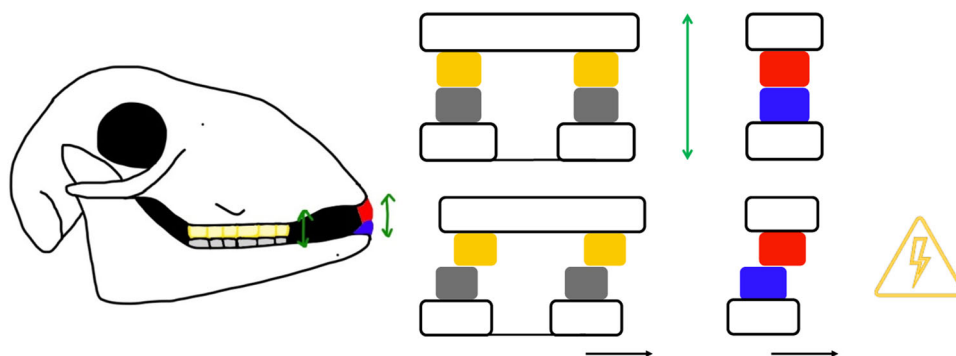
occlusion does not occur before the cheek teeth are occluded, or vice versa.

A purely orthal chewing movement, where the cheek teeth of both sides are in simultaneous occlusion, is a hypothetical construct that only applies, as a whole group, to early synapsids (Grossnickle et al., 2022). In mammals, the basal mode of chewing is considered to contain a certain degree of “hemimandibular roll” with some additional latero-medial movement (yaw; Bhullar et al., 2019; Crompton & Hiiemae, 1969). Some extant carnivores are potentially close to the hypothetical scenario, with only minimal transversal movement (yaw) of the lower jaw during a chewing stroke (Crompton & Hiiemae, 1969; Grossnickle, 2017).

Here, we use the hypothetical construct of Figure 1 to outline some relevant elements of mammalian cranial anatomy that may have their origin in the structural problem of moving tightly joined elements of different functionality (incisors, canines, cheek teeth) in synchrony during a specific action—chewing.

Transversal chewing movements represent a double challenge. On the one hand, the incisors and canines must be positioned in such a way that they do not impede the transversal movement. On the other hand, there should be selective pressure to avoid a simultaneous occlusion of incisors and cheek teeth, because a transversal jaw movement for grinding chewing would then automatically move the occluding incisors against each other. This would not only represent a waste of chewing energy to overcome the friction between the incisors, but would also wear down the incisors (Figure 1).

In this qualitative review, we demonstrate different cases of reciprocal impairment of incisors/canines and cheek teeth, and outline different solutions in the jaw-tooth arrangement to avoid this impairment, across mammalian herbivores. General statements on dentitions and dental shapes derive, in addition to the more specific sources cited below, from Thenius (1989), Ungar (2010) and Berkovitz and Shellis (2018).



**FIGURE 1** Hypothetical scenario of a system where cheek teeth of both sides are in simultaneous resting occlusion at the same position that the incisors are in occlusion in. A transverse movement of the cheek teeth would automatically move the incisors along each other causing friction (increasing chewing costs) and wear. Upper cheek teeth are yellow, lower gray; upper incisors red and lower blue.

## 2 | CANINES

### 2.1 | Impairment of transversal chewing movements

The possibly most evident impairment of a transversal jaw movement is by interlocking canines (and neighboring incisors) that overlap the opposite jaw and thus prevent transverse (latero-medial or propalinal) jaw deflection (Figure 2). This arrangement is, for example, observed in peccaries and tapirs, which therefore have a primarily orthal chewing movement (Harris, 1975; Herring, 1972; Hohl et al., 2020; Kiltie, 1981). Kiltie (1981) considered this constraint an actual advantage for peccaries that prevented a dislocation of the jaw when biting on extremely hard seeds and nuts. As a result of the tooth attrition during the vertical chewing motion, the upper canines develop an attrition facet on their mesial surface and the lower canines on their caudal surface (Hillson, 2005). Herring (1972) states that the resulting striations on these wear facets suggest that the sharpening mastication movements are predominantly orthal. These interlocking canine teeth are mainly used as biting weapons (Schweinsburg & SOWLS, 1972; SOWLS, 1974).

Regardless of whether the canines will impair any particular chewing motion or not, if they are in contact during chewing, the friction during the chewing motion represents a certain additional chewing cost.

### 2.2 | Anatomical solutions

Different solutions to translational movement impairment by canines are displayed in Figure 3.

#### 2.2.1 | Canine arrangement

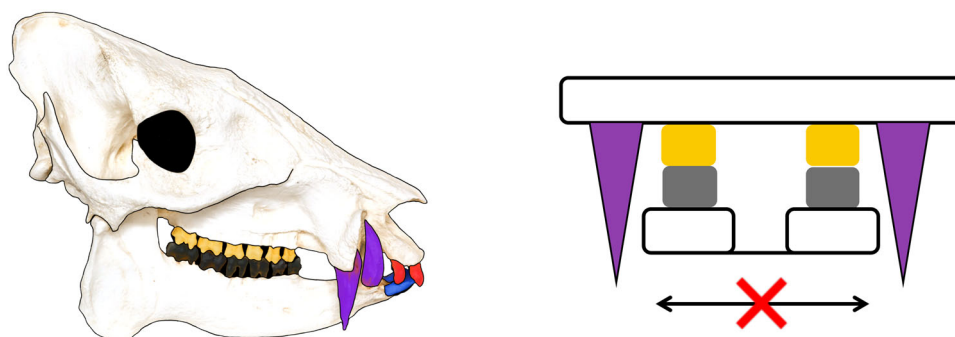
In the case of a protrusion of both upper and lower canines that makes them overlap when the jaws are at minimum gape, an

arrangement that does not constrain propalinal jaw movement appears impossible. Latero-medial movement, by contrast, can be facilitated given an appropriate arrangement and shape of the canines. In pigs (Suidae) and hippos (Hippopotamidae), the far-protruding canines are arranged in such a way that they can or could slide past each other during both, orthal and latero-medial jaw movement, and sharpen each other in doing so.

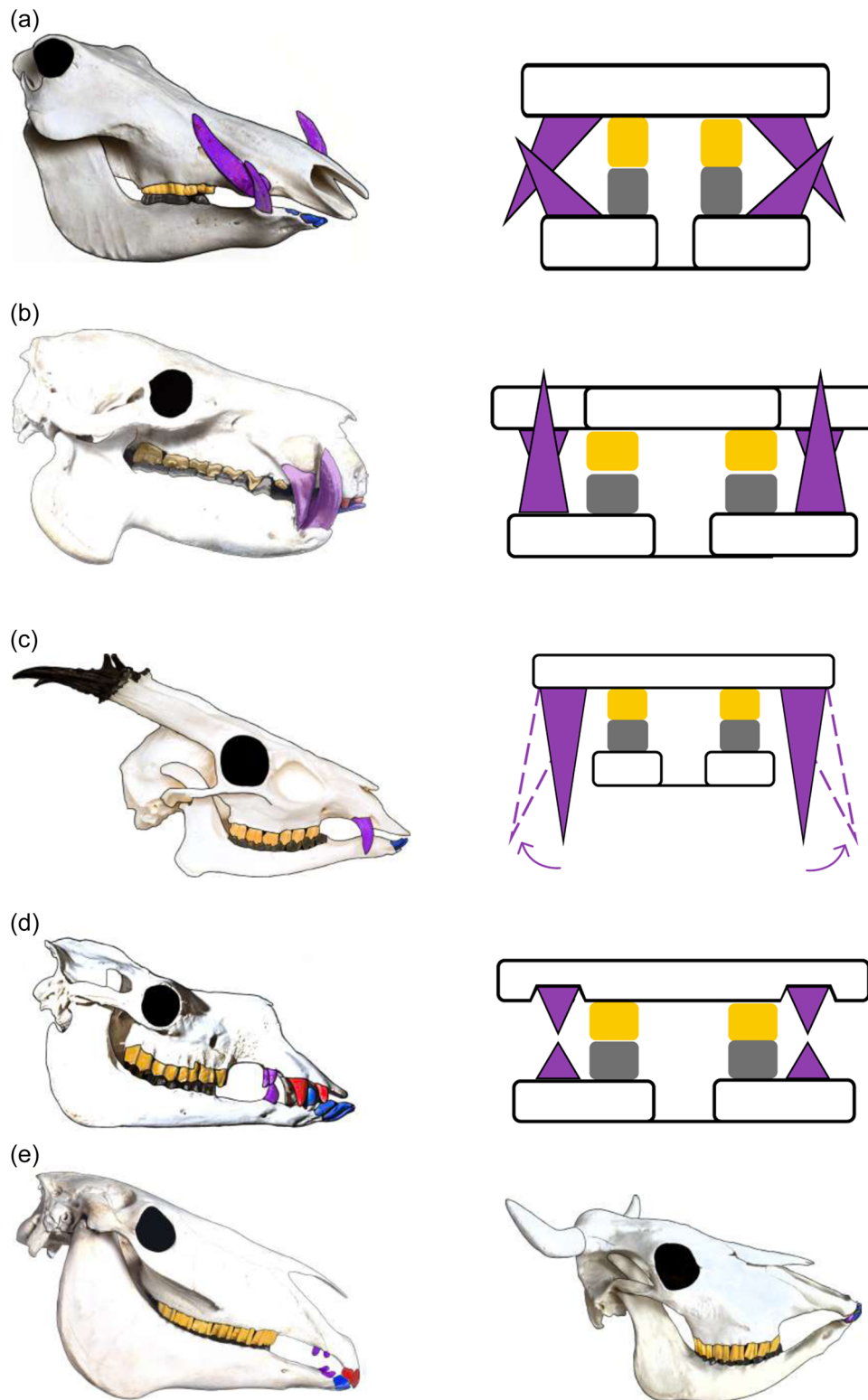
In pigs, there is no constraint on lateral jaw deflection due to the horizontal orientation of the ever-growing canines ("tusks"; Herring, 1971, 1972; Hillson, 2005; Popowicz & Herring, 2006). The upper canine exits the maxilla anterolaterally and then curves upward. During the chewing motion, the lower canine, which projects laterally, is moved against the upper canine, which sharpens both teeth, while the tip of the upper canine is not worn off by the contact and therefore not sharpened (Herring, 1972; Figure 3a).

In contrast to laterally protruding canines in suids, the ever-growing canines of hippos (Hillson, 2005) protrude mainly vertically and thus will ultimately constrain lateral jaw deflection. This constraint is reduced in hippos by (i) upper canines that are short enough not to overlap with the lower jaw, and by (ii) sockets of the lower canines situated extremely laterally and projecting slightly laterally from the lower jaw, with the corresponding bony portion of the snout on the upper jaw being comparatively narrow, allowing the lower canines some lateral moving range (Figure 3b). The potential for latero-medial chewing movement is used in pygmy hippos (*Choeropsis liberiensis*), but not in common hippos (*Hippopotamus amphibius*). This is because in common hippos, there is an additional restriction of movement by the incisors (see below).

For several primates with large canines (*Mandrillus sphinx*, *Mandrillus leucophaeus*, *Papio papio*, *Papio cynocephalus*, *Papio anubis*, *Theropithecus gelada*), ZANOWIAK (1974) observed a lateromedial chewing component and showed that in sedated animals, a certain lateral positioning of the mandible was possible with "sufficient freedom of lateral excursion to allow a group functioning of the premolars and molars... the lateral movement became restricted by the maxillary canine only after the buccal cusps of the maxillary and mandibular teeth approached an edge-to-edge relationship." Similar



**FIGURE 2** Impairment of lateral (and propalinal) jaw deflection by interlocking canines that overlap the opposite facial bone (peccary *Pecari tajacu*). The same principle applies to interlocking incisors. Upper cheek teeth are yellow, lower gray; canines purple; upper incisors red and lower blue. Note that in the right column schemes, canines are placed laterally to the cheek teeth, whereas they are naturally in front of the cheek teeth.



**FIGURE 3** Solutions for canines: (a) laterally growing canines (warthog *Phacochoerus aethiopicus*), (b) canine position for lateral sliding (pygmy hippopotamus *Choeropsis liberiensis*, note the constraint of the protruding snout), (c) hinged canines (muntjac *Muntiacus reevesi*) (d) elevated diastema (camel), (e) reduced canine size (equids; horse *Equus caballus*)—up to “incisoriform canines” in ruminants (cattle, *Bos primigenius taurus*). Note that in the right column schemes, canines are placed laterally to the cheek teeth, whereas they are naturally in front of the cheek teeth. Upper cheek teeth are yellow, lower gray; canines purple; upper incisors red and lower blue.

observations were made for *Macaca fascicularis* by Kay et al. (1986). These authors briefly review other studies that demonstrated a certain restriction of lateral jaw deflection by primate canines. Therefore, the degree to which canines constrain lateral movements may depend on fine-scale anatomical positioning of canines in the upper and lower jaws, and the amount of lateral deflection aimed for.

### 2.2.2 | Hinged canines

In certain deer species like muntjac (*Muntjacus* spp.) and the Chinese water deer (*Hydropotes inermis*), the protruding upper canines are not fixed but loosely attached in their socket so they can “give” laterally (Aitchison, 1946; Figure 3c). Because of the morphology of the tooth and the socket, the tusks’ movement is confined to an upwards, backward, and outwards movement. The tooth is returned to its relaxed state by the elasticity of the fibers of the gum pad, which is closely attached to the annular ligament surrounding the tusk neck (Aitchison, 1946). The arrangement facilitates the use of canines for sexual display and weapons, while not impeding the latero-medial jaw movement during ingestion or rumination.

### 2.2.3 | Socket elevation

Camels have three caniniform teeth in the upper jaw—the single remaining incisor, the canine, and the first premolar. The upper caniniform incisor and the canine wear against the lower canine during latero-medial chewing (Figure 4), representing an example where the arrangement of the front teeth will increase the friction the chewing muscles have to overcome during transverse chewing.



**FIGURE 4** Cranial teeth of a Bactrian camel (*Camelus bactrianus*), with the three caniniform maxillary teeth (from left to right: first premolar, canine, incisor) and the caniniform premolar, canine and three incisors in the mandible. Note the wear facets of the lower canine, indicating attrition from both the upper canine and incisor. Photograph by Michelle Aimée Oesch.

The upper first (caniniform) premolar has its socket in a part of the maxillary bone that is “withdrawn” in the dorsal direction, giving the camelid skull one of its typical features of an “elevated maxillary diastema” (Figure 3d), thus allowing this tooth to be long without overlapping with the lower jaw and impeding a lateral movement.

### 2.2.4 | Canine reduction

An evident adaptation to avoid any constraining effect of canines is to reduce their size so that they do not impair jaw movements. In equids, the canines are localized in the diastema and become so small that they cannot impair transverse movement anymore (Figure 3e). These rudimentary teeth are generally only present in male horses, although in some mares they might protrude as well (Hillson, 2005). In most extant ruminants the canines become so small that they become a functional fourth incisor (Popowics & Herring, 2006). They are localized directly adjacent to the incisors (Figure 3f). Alternatively, the canines can be lost completely, e.g. in rodents and lagomorphs, or in extant rhinoceroses (Tissier et al., 2020).

## 3 | INCISORS

### 3.1 | Impairment of chewing movements

#### 3.1.1 | Complete impairment of transversal chewing movements

In case the incisors are far-protruding (“tusk-like”) and interlocking, they can impair transversal movement in a similar way to interlocking canines. This is particularly evident in common hippos (Figure 5). Hippo incisors do not serve to crop food—this is done with their lips; they are rather used for fighting alongside the canines, and possibly for some digging (Laws, 1968). In the common hippo, the upper, vertical incisors overlap with the lower, horizontal incisors during cheek teeth occlusion in such a way that lateral jaw movement is nearly completely impaired. However, lateral wear facets on the lower incisors, matching medial wear facets on the upper incisors, indicate that transverse jaw movements do occur to the extent until the incisors meet, and leave these traces on each of them (Figure 5). In the hippo literature, these facets have been termed “oblique” (Stuenes, 1989). By contrast, in pygmy hippos, wear facets on the incisors are on the ventral tip of the vertically protruding upper incisor, and on the dorsal side of the horizontally protruding lower incisors, indicating transverse movement of the latter against the former (see below). Wear traces on hippo incisors have been used to infer chewing motions in both extant and fossil species (Coryndon, 1970), and this difference between common and pygmy hippos probably does not reflect a genus difference but



**FIGURE 5** Skulls of common hippopotamus (*Hippopotamus amphibius*). Note that the vertical upper incisors basically constrain lateral jaw movement (a) However, upper and lower incisors indicate that lateral jaw movements do occur to the degree possible, creating visible wear facets on the incisors (b, c). Photographs by Michelle Aimée Oesch.

can occur between more closely related (fossil) hippo species (Stuenes, 1989).

### 3.1.2 | Increasing friction in transversal chewing movements

If the functional occlusal position of the cheek teeth is the same at which the incisors occlude, then transversal jaw movements for grinding cheek teeth chewing will also grind the incisors against each other (Figure 1). This means friction has to be overcome by the chewing muscles and grinding chewing will wear down the incisors and create wear facets. Examples include the already mentioned pygmy hippo, where the lower incisors show wear traces created by the latero-medially gliding against the upper incisors. This can be seen for example, in Figure 629 of Thenius (1989). Sometimes, two distinct wear facets from the first and second incisor can be seen on the lower incisor (Figure 6). Another group of animals in which this can be observed are the Asian rhinoceroses that have retained one upper and one or two lower incisors (Figure 7). The first upper incisor of the greater one-horned rhino (*Rhinoceros unicornis*) shows an elongated oval form in the cross-section; there is visible abrasion on the upper incisor, causing a crescent-shape tooth form, caused by the tusk-like lower second incisor during the lateral mandible movement required for molar grinding (Rookmaaker & Visser, 1982).



**FIGURE 6** Skull of a pygmy hippopotamus (*Choeropsis liberiensis*) with maximal lateral deflection of the lower jaw, causing the animal's left lower canine to touch the snout part of the upper jaw (note that in live animals, there will be additional soft tissues, constraining this deflection somewhat more). Note two distinct wear facets on each lower incisor, with the mesial one tilted towards medially (created by attrition with the more mesial first upper incisor) and the caudal one tilted towards laterally (created by attrition with the more caudal second upper incisor). Photograph by Michelle Aimée Oesch.

## 3.2 | Anatomical solutions

Different solutions to translational movement impairment by incisors are displayed in Figure 8.



**FIGURE 7** Skull of a greater one-horned rhinoceros (*Rhinoceros unicornis*). Note the crescent-shaped wear facet on the upper incisor caused by lateral movement of the lower incisor. Photographs by Michelle Aimée Oesch.

### 3.2.1 | Mandible shifting

This approach is typical for lagomorphs, rodents and many primates, including humans. For this approach, the mandible must at least be able to move propalinally (forward-backward) in addition to an orthal movement, but can often also move laterally. Reiter (2008) summarizes the propalinal movement in rabbits as follows: “*Rostrorocaudal movement of the mandible shifts the mandibular condyle up or down a step in the mandibular fossa. In the caudal position, the cheek teeth are in alignment and the incisors are separated. When one temporomandibular joint is maintained in this position, the opposite mandible can slide down the temporal step into a more rostroventral position, separating the cheek teeth on that side and bringing the cheek teeth on the first side into occlusion for [transverse] chewing. Positioning both temporomandibular joints on the temporal step separates the cheek teeth slightly and brings the incisors into occlusion*” (Crossley, 1995, 2003) (Figure 8a). In other words, during grinding, the incisors slide past each other, while the molars of one side of the skull stay in contact. During incisor action, the whole mandible is shifted forwards, and at the height of the incisors meeting in action, the molars are apart, not impeding the gnawing movement.

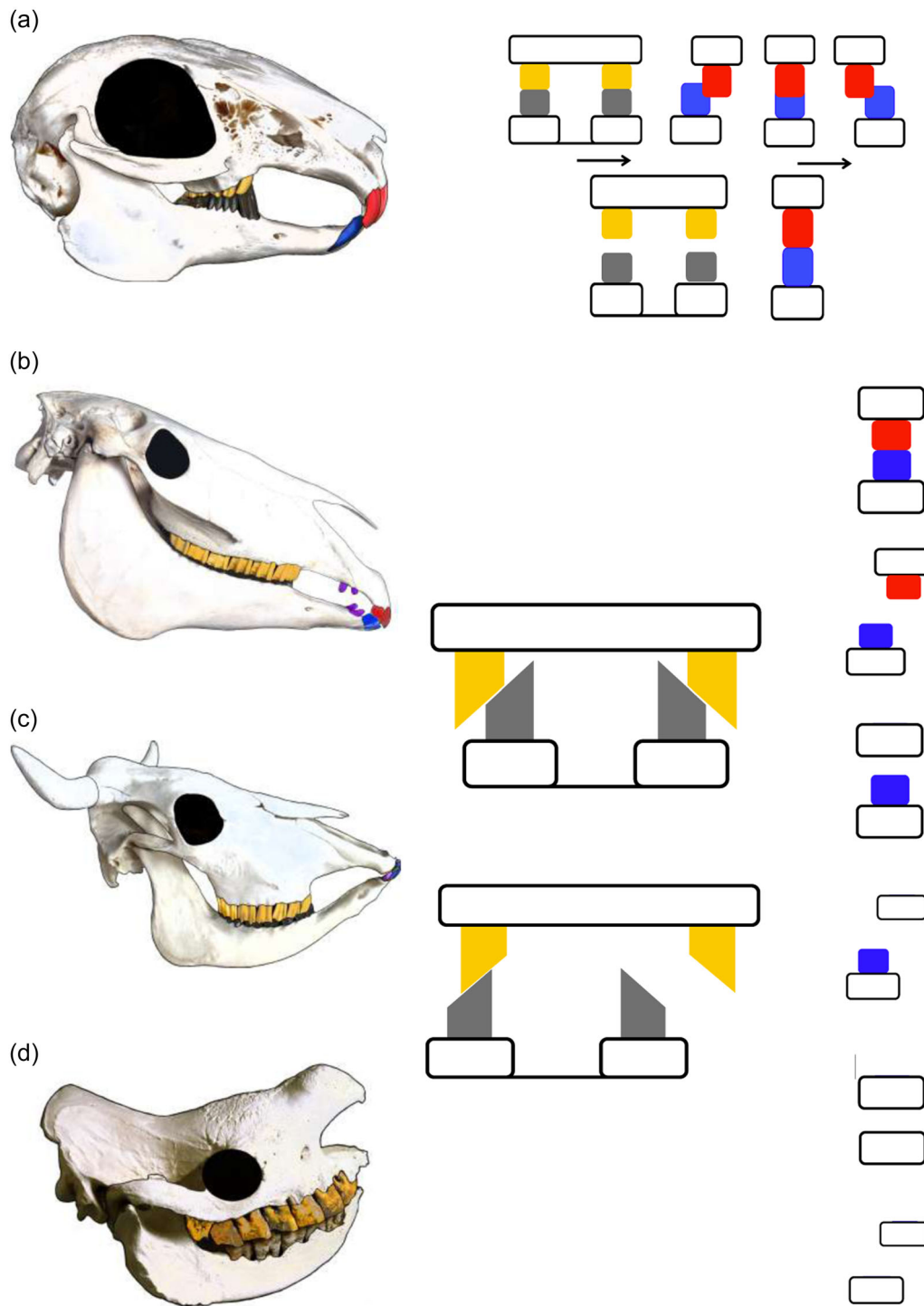
In many rodents, the same principle applies, even though the chewing stroke is in a propalinal movement: during propalinal movement of the cheek teeth, the lower incisors do not reach occlusion with the upper ones; only when the mandible is brought further forward for gnawing, incisal occlusion is attained (Hiimäe & Ardran, 1968; Stefen et al., 2011). Human mandibles can move in a similar manner (Hylander, 2006), and this likely applies to other primates as well that are not constrained by their canine arrangement.

### 3.2.2 | Nested cheek teeth positioning

Another solution to overcome the impairment of the incisors is to develop either a narrower mandible in comparison to the maxilla (anisognathism; Crompton & Hiimäe, 1969; Fortelius, 1985) or an oblique occlusal surface (Figure 8b–d), or a combination of both, as for example, in equids (Bonin et al., 2007; Listmann et al., 2016). Note that anisognathism is a general feature of most mammals; components of this solution are widespread and occur in combination with other solutions mentioned in this contribution. When the incisors are occluded, the mandibular cheek teeth are positioned inside the maxillary ones (Hendrichs, 1965); the latter therefore appear to overlap the former in lateral views of skulls of such species. This approach is in line with the well-known fact that herbivores, during transverse chewing, only use the cheek teeth on one side of the jaw—also because of the anisognathism, the cheek teeth of either side cannot be in simultaneous occlusion (Crompton & Hiimäe, 1969; Fortelius, 1985). If the lower cheek teeth are nested “inside” of the upper ones, due to a narrow mandible and/or oblique chewing surface, the incisors can meet when the mandible is in its centric relation, which also corresponds to the jaw’s resting position; and they will be separated during a grinding power stroke when the postcanine teeth occlude.

### 3.2.3 | Incisor loss

The incisors can be lost in only one jaw (typically, the maxilla), as in ruminating herbivores. Camelids have lost some, and taxonomic ruminants have lost all of the maxillary incisors (Janis & Ehrhardt, 1988). As a result, during grinding chewing, the front teeth are not restricted in their movement (Figure 8c).



**FIGURE 8** Solutions for incisors: (a) jaw shifting (lagomorphs, rodents, primates; rabbit *Oryctolagus cuniculus*), combinations of (b) resting lower cheek teeth “inside” the upper ones (anisognathy) (equids; horse *Equus caballus*) with (c) partial incisor loss (ruminants, camelids; cattle, *Bos primigenius taurus*) or (d) complete incisor loss (African rhinoceroses, black rhinoceros *Diceros bicornis*). Upper cheek teeth are yellow, lower gray; canines purple; upper incisors red and lower blue.

A reduction of the anterior dentition is a hallmark of rhinoceros evolution (Tissier et al., 2020). African rhinoceros (*Diceros bicornis* and *Ceratotherium simum*) species have lost all upper and lower anterior teeth (Hullot et al., 2019; Figure 8d). Evidently, the complete loss of canines and

incisors means that no movement constraints are exerted on the mandible. These species crop their food with their pointed or broad lips.

That the loss of parts of the anterior dentition is observed frequently in herbivores supports the argument that it is not only the



prevention of the inadvertent wear of the anterior dentition that lies behind the various anatomical solutions (in which case, only solutions would occur that retain functional anterior teeth), but also the avoidance of friction during chewing movements (so that it is more advantageous to have no rather than worn anterior teeth).

## 4 | DISCUSSION

Our review provides a coherent, plausible (but not testable) narrative that explains various observations made in mammalian dentitions. In particular, we emphasize that the solid osseous link between the anterior dentition—incisors and canines—and the cheek teeth requires anatomical adaptations if grinding chewing of the cheek teeth is important for an organism. In a hypothetical “original” or “complete” state (O’Leary et al., 2013), the anterior dentition can represent a constraint or an impediment to transverse grinding chewing motions, either due to interlocking with the opposite teeth or jaw, or due to relevant friction between opposing teeth. Although we screened a large volume of literature, we cannot be sure that the interplay of anterior and posterior dentition has only been discussed earlier as a phenomenon in specific taxa (see above), but not as a fundamental principle. We did not locate descriptions of this phenomenon in several textbooks covering teeth or biomechanical principles (Berkovitz & Shellis, 2018; Preuschoft, 2022; Thenius, 1989; Ungar, 2010), yet we do not consider it likely that we are the first to comment on it.

The theory that the rolling of the non-fused mandible represents an early mammalian adaptation to cheek tooth grinding appears plausible (Bhullar et al., 2019), as this movement potentially avoids the anterior dentition’s constraining effect. Varying degrees of constraint and impediment of transverse jaw motions exist among extant mammals—from compulsory orthal chewing in peccaries and tapirs, to largely constrained transversal chewing motions in common and less impeded chewing motions in pygmy hippos, to again less impeded lateromedial chewing in the greater one-horned rhino or in camelids, to the unimpeded transversal chewing motions in lagomorphs, rodents, equids, African rhinos, or ruminants. The variation in morphological solutions bespeaks the selective pressure to avoid this impediment. The integration of the anterior dentition in the morphological complex of food processing, so far mostly characterized by the jaw joint, chewing muscles, their insertion sites and lever arms, and cheek teeth cusps (Bhullar et al., 2019; Grossnickle, 2020), thus represents a further step in understanding the evolution of mammalian chewing.

Based on our qualitative review, we cannot make quantitative statements with respect to the evolutionary success of different morphological solutions, measured for example by the diversity of species that share a particular morphology. We also emphasize that one needs to refrain from linking evolutionary success to a single morphological or physiological measure, possibly with the exception of the overall rate of reproduction within a given niche (Clausen et al., 2019). The fact that solutions such as the loss or reduction of

canines and incisors are widespread among extant mammals, whereas examples of visible impairments such as in hippos, Asian rhinos or camelids appear in fewer species today than may have been in the fossil record, can only hint towards a potential contributing effect of anterior dentition morphology on extant diversity. To evaluate whether the mechanical aspects of craniodental morphology outlined in this contribution played a decisive role in mammalian herbivore evolution, studies of the fossil record that include this aspect would be required.

For example, Tissier et al. (2020) outline how the reduction of the anterior dentition is an overarching theme in rhinoceros evolution. These authors call this reduction “one of the major adaptive traits of the *Rhinocerotidae*” (without speculating on the actual, adaptive value) and demonstrate that a loss of certain anterior teeth occurred several times in the history of this taxon. For the extinct taxon of *Chalicotheriidae*, Coombs (1978) postulated an evolutionary history of progressive loss of the anterior dentition. For the extinct taxon of *Bronthoteriidae*, Mhlbachler (2008) describes a similar development. Examples of other taxa that might be interesting in the respect of the evolutionary history of anterior tooth loss and the nesting of the mandibular dentition inside of the maxillary one include the *Artiodactyla* (with camelids, and ancestors of ruminants), the *Equidae*, or the *notoungulates* for which substantial reduction of the anterior dentition has also been documented (Billet, 2011). Possibly, comparing this aspect between multituberculates and rodents might shed additional light on the respective functional merit of their dentition (Adams et al., 2019). As a random example, Joeckel (1990), in the interpretation of the masticatory system of the *Entelodontidae*, bases the suggestion that lateromedial jaw movements were feasible on the anatomy of the mandibular condyle, which is in contrast to the observation in the same study that when “fully occluded, entelodont incisors and canines form an alternating, interlocking array.” The author concludes that there was an ontogenetic change in the capacity for lateromedial chewing: “At least in earlier stages, apical wear [of the incisors] did not result completely from tooth-to-tooth wear during transverse jaw movements: when the molars were positioned for an effective transverse power stroke, the anterior dentition was already partially interdigitated.”

As a narrative argument, the chewing of hippos can serve as an example to illustrate the effect of a constrained chewing motion: Among extant mammalian herbivores, hippos have the lowest chewing efficacy (Fritz et al., 2009), which is intuitively explained by their restricted transversal chewing motion. The incisors of the common hippo indicate, by their wear facets (Figure 5), that animals apparently attempt a lateromedial chewing stroke—an observation supported by the corresponding traces on pygmy hippo incisors (Figure 6). In common hippos, the lateromedial movement is basically prevented to occur during occlusion by the incisors. To compensate for their low chewing efficacy, hippos have particularly long digesta retention times, which may in turn prevent them from having the high food intake rates observed in many other herbivores (Clausen et al., 2007, 2009).

While an interlocking arrangement of anterior teeth can prevent transverse chewing motions completely, different arrangements may facilitate these motions but make them more costly due to friction along the anterior teeth, which should theoretically not impede chewing efficacy but reduce chewing efficiency. The energetic costs of chewing are notoriously difficult to quantify (Hummel et al., 2020), so this hypothesis remains speculative, but serves as an argument for strong selective pressure towards anterior tooth reduction and loss. One aspect of this kind of self-induced, constant incisor and canine wear might be that affected teeth are often hypselodont in compensation, such as hippopotamus canines and incisors. Possibly, the hypselodontology of vicugna (*Vicugna vicugna*) incisors (Miller, 1924) might represent a vestigial character in this respect that was lost in other camelids due to reduced incisor wear after the reduction of maxillary incisors. Whether this and other reported occurrences of incisor hypselodontology might derive from a compensation for self-induced wear during transverse chewing, for example in some hyraxes or some notoungulates, remains to be investigated.

To conclude, we draw attention to the mechanical challenge that the anterior dentition might constrain, or might impede and hence be worn down during, transverse chewing motions. We suggest that both the diversity in, and the evolutionary trend towards a reduction of, the anterior dentition is indication that this challenge represented a relevant selective pressure in mammalian evolution.

#### AUTHOR CONTRIBUTIONS

Marcus Clauss initiated the review. Annika Avedik, Maria J. Duque-Correa, and Marcus Clauss performed the literature research. Annika Avedik and Maria J. Duque-Correa produced the illustrations. Annika Avedik and Marcus Clauss wrote the first draft of the manuscript which later received input from Maria J. Duque-Correa.

#### ACKNOWLEDGMENTS

We thank Christine Janis and Gertrud Rössner for constructive comments on a first draft of this manuscript, Nicole Ackermans for a preliminary version of some schematic drawings, and Michelle Aimée Oesch for the photographs. Maria J. Duque-Correa was supported by a grant of the Swiss National Science Foundation (CRSII5\_189970/1 to Marcus Clauss).

#### CONFLICT OF INTEREST

The authors declare no conflict of interest.

#### DATA AVAILABILITY STATEMENT

No data is linked to this article.

#### ORCID

Annika Avedik  <http://orcid.org/0000-0003-3038-4458>

Maria J. Duque-Correa  <http://orcid.org/0000-0001-8431-2228>

Marcus Clauss  <http://orcid.org/0000-0003-3841-6207>

#### REFERENCES

- Adams, N. F., Rayfield, E. J., Cox, P. G., Cobb, S. N., & Corfe, I. J. (2019). Functional tests of the competitive exclusion hypothesis for multituberculate extinction. *Royal Society Open Science*, 6, 181536.
- Aitchison, J. (1946). Hinged teeth in mammals: a study of the tusks of muntjacs (*Muntiacus*) and Chinese water deer (*Hydropotes inermis*). *Proceedings of the Zoological Society of London*, 116, 329–338.
- Berkovitz, B. K., & Shellis, R. P. (2018). *The teeth of mammalian vertebrates*. Academic Press.
- Bhullar, B.-A. S., Manafzadeh, A. R., Miyamae, J. A., Hoffman, E. A., Brainerd, E. L., Musinsky, C., & Crompton, A. W. (2019). Rolling of the jaw is essential for mammalian chewing and tribosphenic molar function. *Nature*, 566, 528–532.
- Bhullar, B.-A. S., Manafzadeh, A. R., Miyamae, J. A., Hoffman, E. A., Brainerd, E. L., Musinsky, C., & Crompton, A. W. (2020). Reply to: Jaw roll and jaw yaw in early mammals. *Nature*, 582, E9–E12.
- Billet, G. (2011). Phylogeny of the Notoungulata (Mammalia) based on cranial and dental characters. *Journal of Systematic Palaeontology*, 9, 481–497.
- Bonin, S. J., Clayton, H. M., Lanovaz, J. L., & Johnston, T. (2007). Comparison of mandibular motion in horses chewing hay and pellets. *Equine Veterinary Journal*, 39(3), 258–262.
- Clauss, M., Jürgen Streich, W., Schwarm, A., Ortman, S., & Hummel, J. (2007). The relationship of food intake and ingesta passage predicts feeding ecology in two different megaherbivore groups. *Oikos*, 116, 209–216.
- Clauss, M., Müller, D. W. H., & Codron, D. (2019). Within-niche pace of life acceleration as a fundamental evolutionary principle: A mammal pilot test case. *Evolutionary Ecology Research*, 20, 385–401.
- Clauss, M., Nunn, C., Fritz, J., & Hummel, J. (2009). Evidence for a tradeoff between retention time and chewing efficiency in large mammalian herbivores. *Comparative Biochemistry and Physiology Part A: Molecular & Integrative Physiology*, 154, 376–382.
- Coombs, M. C. (1978). A premaxilla of *Moropus elatus*, and evolution of Chalicotheriid anterior dentition. *Journal of Paleontology*, 52, 118–121.
- Coryndon, S. C. (1970). The extent of variation in fossil hippopotamus from Africa. *Symposium of the Zoological Society of London*, 26, 135–147.
- Crompton, A. W., & Hiemae, K. (1969). How mammalian molar teeth work. *Discovery*, 5, 23–34.
- Crossley, D. A. (1995). Clinical aspects of lagomorph dental anatomy: The rabbit (*Oryctolagus cuniculus*). *Journal of Veterinary Dentistry*, 12, 137–140.
- Crossley, D. A. (2003). Oral biology and disorders of lagomorphs. *Veterinary Clinics of North America: Exotic Animal Practice*, 6, 629–659.
- Fortelius, M. (1985). Ungulate cheek teeth: developmental, functional, and evolutionary interrelations. *Acta Zoologica Fennica*, 180, 1–76.
- Fritz, J., Hummel, J., Kienzle, E., Arnold, C., Nunn, C., & Clauss, M. (2009). Comparative chewing efficiency in mammalian herbivores. *Oikos*, 118, 1623–1632.
- Grossnickle, D. M. (2017). The evolutionary origin of jaw yaw in mammals. *Scientific Reports*, 7, 45094.
- Grossnickle, D. M. (2020). Jaw roll and jaw yaw in early mammals. *Nature*, 582, E6–E8.
- Grossnickle, D. M., Weaver, L. N., Jäger, K. R. K., & Schultz, J. A. (2022). The evolution of anteriorly directed molar occlusion in mammals. *Zoological Journal of the Linnean Society*, 194, 349–365.
- Harris, J. M. (1975). Evolution of feeding mechanisms in the family Deinotheriidae (Mammalia: Proboscidea). *Zoological Journal of the Linnean Society*, 56, 331–362.
- Hendrichs, H. (1965). Vergleichende untersuchung des wiederkauverhaltens. *Biol Zentrbl*, 84, 681–751.

- Herring, S. (1971). Functional aspects of suoid cranial anatomy. [PhD thesis, University of Chicago].
- Herring, S. W. (1972). The role of canine morphology in the evolutionary divergence of pigs and peccaries. *Journal of Mammalogy*, 53, 500–512.
- Hiimäe, K. M. (1978). Mammalian mastication: A review of the activity of the jaw muscles and the movements they produce in chewing. In P. M. Butler & K. A. Joysey (Eds.), *Development, function and evolution of teeth* (pp. 359–398). Academic Press.
- Hiimäe, K. M., & Ardran, G. M. (1968). A cinefluorographic study of mandibular movement during feeding in the rat (*Rattus norvegicus*). *Journal of Zoology*, 154, 139–154.
- Hillson, S. (2005). *Teeth*. Cambridge University Press.
- Hohl, C. J. M., Codron, D., Kaiser, T. M., Martin, L. F., Müller, D. W. H., Hatt, J.-M., & Clauss, M. (2020). Chewing, dental morphology and wear in tapirs (*Tapirus* spp.) and a comparison of free-ranging and captive specimens. *PLoS One*, 15, e0234826.
- Hullot, M., Antoine, P.-O., Ballatore, M., & Merceron, G. (2019). Dental microwear textures and dietary preferences of extant rhinoceroses (Perissodactyla, Mammalia). *Mammal Research*, 64, 397–409.
- Hummel, J., Clauss, M., & Südekum, K.-H. (2020). Aspects of food comminution in ungulates and their consequences for energy budget. In T. Martin & W. Koenigswald (Eds.), *Mammalian Teeth—Form and Function* (pp. 87–101). Dr. Friedrich Pfeil.
- Hylander, W. L. (2006). Functional anatomy and biomechanics of the masticatory apparatus. In D. M. Laskins, C. S. Greene, & W. L. Hylander (Eds.), *The temporomandibular joint: a biological basis for the clinical practice* (pp. 3–34). W.B. Saunders.
- Janis, C. M., & Ehrhardt, D. (1988). Correlation of relative muzzle width and relative incisor width with dietary preference in ungulates. *Zoological Journal of the Linnean Society*, 92, 267–284.
- Jernvall, J., & Fortelius, M. (2002). Common mammals drive the evolutionary increase of hypsodonty in the Neogene. *Nature*, 417, 538–540.
- Jernvall, J., Hunter, J. P., & Fortelius, M. (1996). Molar tooth diversity, disparity, and ecology in Cenozoic ungulate radiations. *Science*, 274, 1489–1492.
- Joeckel, R. M. (1990). A functional interpretation of the masticatory system and paleoecology of entelodonts. *Paleobiology*, 16, 459–482.
- Kay, C. N., Scaring, R. P., & Kay, E. D. (1986). A cineradiographic study of the role of the canine in limiting lateral jaw movement in *Macaca fascicularis*. *Journal of Dental Research*, 65, 1300–1302.
- Kiltie, R. A. (1981). The function of interlocking canines in rain forest peccaries (Tayassuidae). *Journal of Mammalogy*, 62, 459–469.
- von Koenigswald, W. (2011). Diversity of hypsodont teeth in mammalian dentitions - construction and classification. *Palaeontographica Abteilung A*, 294, 63–94.
- von Koenigswald, W. (2018). Specialized wear facets and late ontogeny in mammalian dentitions. *Historical Biology*, 30, 7–29.
- Laws, R. M. (1968). Dentition and ageing of the hippopotamus. *African Journal of Ecology*, 6, 19–52.
- Listmann, L., Schrock, P., Failing, K., & Staszuk, C. (2016). Occlusal angles of equine cheek teeth. *Livestock Science*, 186, 78–84.
- Mihlbachler, M. C. (2008). Species taxonomy, phylogeny, and biogeography of the Brontotheriidae (Mammalia: Perissodactyla). *Bulletin of the American Museum of Natural History*, 311, 1–475.
- Miller, G. S. (1924). A second instance of the development of rodent-like incisors in an artiodactyl. *Proceedings of the United States National Museum*, 66, 1–3.
- O'Leary, M. A., Bloch, J. I., Flynn, J. J., Gaudin, T. J., Giallombardo, A., Giannini, N. P., Goldberg, S. L., Kraatz, B. P., Luo, Z.-X., Meng, J., Ni, X., Novacek, M. J., Perini, F. A., Randall, Z. S., Rougier, G. W., Sargis, E. J., Silcox, M. T., Simmons, N. B., Spaulding, M., ... Cirranello, A. L. (2013). The placental mammal ancestor and the post-K-Pg radiation of placentals. *Science*, 339, 662–667.
- Popowics, T. E., & Herring, S. W. (2006). Teeth, jaws and muscles in mammalian mastication. In V. Bels (Ed.), *Feeding in domestic vertebrates: From structure to behaviour* (pp. 61–83). CAB International.
- Preuschoft, H. (2022). *Understanding body shapes of animals. Shapes as mechanical constructions and systems moving on minimal energy level*. Springer Nature.
- Reiter, A. M. (2008). Pathophysiology of dental disease in the rabbit, guinea pig, and chinchilla. *Journal of Exotic Pet Medicine*, 17, 70–77.
- Rookmaaker, L. C., & Visser, R. P. W. (1982). Petrus Camper's study of the Javan rhinoceros (*Rhinoceros sondaicus*) and its influence on Georges Cuvier. *Bijdragen tot de Dierkunde*, 52, 121–136.
- Schweinsburg, R. E., & Sowls, L. K. (1972). Aggressive behavior and related phenomena in the collared peccary. *Zeitschrift für Tierpsychologie*, 30, 132–145.
- Sowls, L. K. (1974). Social behavior of the collared peccary *Dicotyles tajacu*. In V. Geist & F. Walther (Eds.), *The behavior of ungulates and its relation to management* (pp. 144–165). IUCN.
- Stefen, C., Ibe, P., & Fischer, M. S. (2011). Biplanar X-ray motion analysis of the lower jaw movement during incisor interaction and mastication in the beaver (*Castor fiber* L. 1758). *Mammalian Biology*, 76, 534–539.
- Stuenkel, S. (1989). Taxonomy, habits, and relationships of the subfossil Madagascan hippopotami *Hippopotamus lemerlei* and *H. madagascariensis*. *Journal of Vertebrate Paleontology*, 9, 241–268.
- Tapaltsyan, V., Eronen, J. T., Lawing, A. M., Sharir, A., Janis, C., Jernvall, J., & Klein, O. D. (2015). Continuously growing rodent molars result from a predictable quantitative evolutionary change over 50 million years. *Cell Reports*, 11, 673–680.
- Thenius, E. (1989). *Zähne und Gebiss der Säugetiere*. De Gruyter.
- Tissier, J., Antoine, P.-O., & Becker, D. (2020). New material of Epiacceratherium and a new species of Mesacceratherium clear up the phylogeny of early Rhinocerotidae (Perissodactyla). *Royal Society Open Science*, 7, 200633.
- Turnbull, W. D. (1970). Mammalian masticatory apparatus. *Fieldiana, Geology*, 18, 147–356.
- Ungar, P. S. (2010). *Mammal teeth: origin, evolution and diversity*. John Hopkins University Press.
- Weijjs, W. A. (1994). Evolutionary approach of masticatory motor patterns in mammals. In V. Bels, M. Chardon, & P. Vandewalle (Eds.), *Advances in comparative and environmental physiology: Biomechanics of feeding in vertebrates* (pp. 281–320). Springer.
- Williams, S. H. (2019). Feeding in mammals: comparative, experimental, and evolutionary insights on form and function. In V. Bels & I. Q. Whishaw (Eds.), *Feeding in vertebrates: evolution, morphology, behavior, biomechanics* (pp. 695–742). Springer Nature.
- Yamanaka, A. (2022). Evolution and development of the mammalian multicuspid teeth. *Journal of Oral Biosciences*, 64, 165–175.
- Zanowiak, P. P. (1974). Dynamics of dental occlusion in baboons. *Journal of Dental Research*, 53, 1208–1214.

**How to cite this article:** Avedik, A., Duque-Correa, M. J., & Clauss, M. (2023). Avoiding the lockdown: Morphological facilitation of transversal chewing movements in mammals. *Journal of Morphology*, 284, e21554. <https://doi.org/10.1002/jmor.21554>