RESEARCH ARTICLE

JEZ-B MOLECULAR AND DEVELOPMENTAL EVOLUTION WILEY

Teeth out of proportion: Smaller horse and cattle breeds have comparatively larger teeth

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Abstract

There are different descriptions of allometric relationships between important components of the mammalian skull. Craniofacial evolutionary allometry describes a pattern of increasing facial cranium in larger skulls. Another body of literature describes disproportionately larger teeth in smaller species or specimens, matching anecdotal observations with dental problems in dwarf breeds whose teeth appear "too large for their skulls." We test the scaling of tooth row length with body size and skull length in a data set comprising 114 domestic horses (representing 40 breeds) and in another data set of 316 domestic cattle (of >60 breeds). We demonstrate that smaller skulls have a relatively longer tooth row in both horses and cattle; larger specimens have relatively shorter tooth rows. Whereas in horses, larger skulls have a relatively longer diastema, the distance of the mesial maxillary premolar to the premaxilla was proportional to cranium length in cattle. While the reasons for these patterns remain to be detected, they support the hypothesis that tooth size might be less "evolvable," in terms of time required for changes, than body size. The pattern may affect (i) the selective breeding for dwarf breeds by setting minimum constraints for skull size, as described previously for domestic horses with the same data set; (ii) the susceptibility of small breeds for dental problems; and (iii) differences in chewing efficiency between breeds of different sizes. The findings support the existing concept that scaling of tooth to body size across taxa becomes more isometric the longer these taxa are separated in evolutionary time.

KEYWORDS
allometry, bovid, chewing, development, equid, molars, skull

1 | INTRODUCTION

It has been known for a long time that many dwarfed forms of mammals have, compared to their nondwarfed conspecifics or ancestors, comparatively larger teeth. This means that while they, of course, have absolutely smaller teeth, their teeth are not as small as expected from the reduction of body size. For nondomestic mammals, this has been suggested for dwarfed species in proboscids (Davies & Lister, 2001; Maglio, 1972), hippopotamids (Gould, 1975; Prothero & Sereno, 1982), and in human pygmies (Shea & Gomez, 1988), but not in rhinocerotids (Prothero & Sereno, 1982). The same has been suggested for smaller individuals within a species

for red deer (*Cervus elaphus*) (Lister, 1995; Lundholm, 1947, p. 30), white-tailed deer (*Odocoileus virginianus*) (Maffei et al., 1988), red foxes (*Vulpes vulpes*) and gray wolves (*Canis lupus*) (McKeown, 1975), and house mice (*Mus musculus*) (Lister & Hall, 2014). Additionally, several comparisons of the scaling of tooth size showed that in sexually dimorphic species, the larger sex had comparatively smaller molars (Carranza & Pérez-Barbería, 2007; Cochard, 1987; Fortelius, 1985; Gingerich, 1981; Kay, 1978). Finally, across mammals, tooth size scales to body mass in a way that larger species have relatively smaller teeth (Copes & Schwartz, 2010).

Explanations for the pattern have been sought in adaptations to higher food requirements in smaller species (Maglio, 1972), but the argument was devalued early on (Gould, 1975): if tooth size would reflect food intake, it should scale in a similar way as intake scales (i.e., to metabolic body weight, $kg^{0.75}$ [or some similar exponent]), which would not lead to distinctively larger teeth in smaller forms (Clauss et al., 2013). In the primates he investigated, Cochard (1987) showed that the proportionately larger teeth of females were not linked to an indicator of energetic requirements (neonate size), but just to sexual dimorphism—that is, how much the sexes represent deviations from the "average size" of the species. Therefore, explanations rather hinge on non-adaptive mechanisms, specifically different developmental trajectories in teeth as compared to overall body size (Shea & Gomez, 1988). As stated by Fortelius (1985, p. 45), "*teeth do not grow continuously but are formed at a given size long before the skull has reached its final dimensions.*" Hence, regulatory mechanisms that control skeletal growth may not directly affect the formation of the teeth.

For domestic species, the pattern has been known for even longer. For example, Antonius (1922) stated that it was a well-known fact that during a change in the size of a domestic animal body (meaning, in giant or dwarf breeds), the size of the teeth remains comparatively unchanged. For yak (*Bos grunniens*) and goats (*Capra hircus*), Leche (1904, cited in Fortelius, 1985) already reported the phenomenon. In dogs, "tooth crowding" in smaller breeds has been documented repeatedly (McKeown, 1975; Wagner, 1929;

Wayne, 1986; Weidenreich, 1941), meaning that there is comparatively less space in the skull and mandible for the teeth in smaller breeds; the same was documented in cats (Sieslack et al., 2021).

Wayne (1986) additionally showed that small domestic dog breeds have larger teeth than similar-sized nondomestic canids, which supports the concept that the pattern of disproportionately larger teeth in smaller forms depends on the (evolutionary) time of body size change, being more pronounced in cases of more recent, for example, intraspecific, body size changes. The same concept had been proposed by Marshall and Corruccini (1978) and Lister (1995), who suggested that in the early stages of body size change, still considered within the phenotypic flexibility of the species, smaller phenotypes would retain comparatively larger heads and teeth. After a period of genetic adaptation (aka canalization sensu Waddington, 1942) to the new body size, the new forms should, by contrast, represent a scaled version of the original *bauplan*. Lister (1996) provided evidence for this in two red deer populations that had spent different periods of time in a dwarfing process. Differences in whether dwarfed forms do or do not have disproportionately large teeth, as mentioned above for proboscids, hippopotamids, and rhinocerotids, may thus depend on the duration of the dwarfing process. More recent changes, as between the breeds of a species, should therefore be indicated by larger disparities in tooth versus overall body size.

Using data for dog breeds from Wagner (1929) as cited in Weidenreich (1941), exemplary scaling patterns are evident (Figure 1). While there is a linear scaling between femur length (a noncranial proxy for body size) and skull length (a cranial proxy for body size) (Figure 1a), the lower tooth row length does not scale isometrically (linearly) to either femur length (Figure 1b) or skull length (Figure 1c), but to a lower exponent, the confidence interval of which does not include 1.0. This means that larger breeds (with longer femora or longer skulls) have comparatively shorter tooth rows; in other words, smaller breeds have comparatively longer tooth rows.

A similar situation is suspected for domestic rabbits (Geiger & Sánchez-Villagra, 2022) and domestic horses, although literature evidence
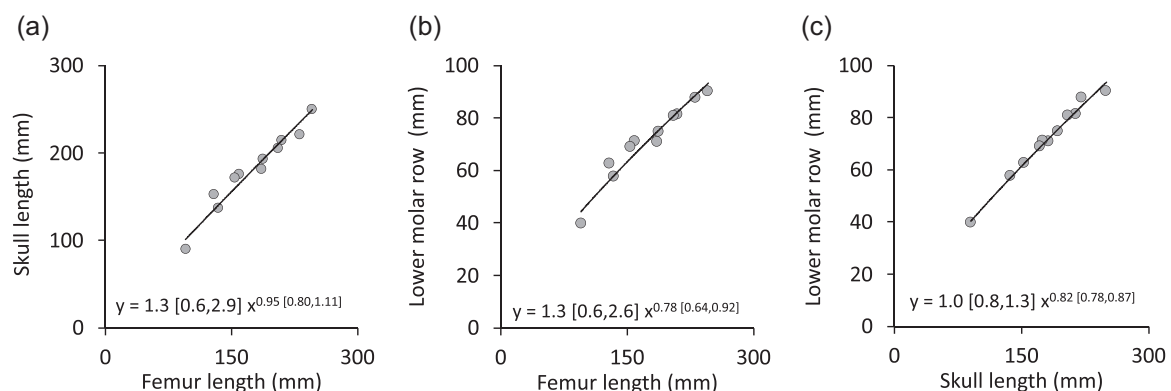

FIGURE 1 Examples of scaling relationships between length measures and their interpretation in domestic dog breeds (data from Wagner, 1929; as cited in Weidenreich, 1941). Allometric regression equations determined by linear regression of log-transformed data are given at the bottom of each graph. (a) Femur length (a noncranial proxy for body size) and skull length (a cranial proxy for body size) scale linearly with each other (note that the 95% confidence interval of the scaling exponent given in brackets includes 1.0). (b) Tooth row length scales to femur length and (c) skull length at lower exponents, indicating comparatively longer tooth rows in smaller breeds.

TABLE 1 Scaling relationships among skull variables in all studied horses

y	x	b	95% CI		Interpretation
Left mandible	Right mandible	1.00	0.99	1.02	Linear scaling between sides indicates symmetry
Left max. tooth row	Right max. tooth row	0.99	0.97	1.01	
Left mand. tooth row	Right mand. tooth row	1.01	1.00	1.02	
Left max. diastema	Right max. diastema	1.03	1.00	1.06	
Left mand. diastema	Right mand. diastema	0.99	0.97	1.02	
Foramen magnum area	Withers height	1.11	0.90	1.32	Skull and teeth measures scale with negative allometry, but teeth even more so than the skull, indicating that smaller forms have relatively larger skulls and even larger tooth rows
Cranium		0.83	0.74	0.93	
Mandible		0.88	0.77	0.98	
Max. tooth row		0.60	0.50	0.69	
Max. M1		0.54	0.39	0.70	
Mand. tooth row		0.81	0.70	0.92	
Max. diastema		1.06	0.91	1.22	Diastemata scale either isometrically or with positive allometry, indicating smaller forms have proportional or relatively shorter diastemata
Mand. diastema		1.22	1.07	1.37	
Cranium	Foramen magnum area	0.50	0.43	0.57	Skull scales isometrically to *Foramen magnum*
Mandible		0.50	0.43	0.56	
Max. tooth row		0.39	0.33	0.44	Teeth tend to scale with negative allometry, indicating that smaller forms have relatively larger teeth
Max. M1		0.34	0.24	0.43	
Mand. tooth row		0.46	0.39	0.53	
Max. diastema		0.64	0.54	0.75	Diastemata scale with positive allometry, indicating smaller forms have relatively shorter diastemata
Mand. diastema		0.64	0.53	0.74	
Max. tooth row	Cranium	0.73	0.66	0.79	Max. teeth scale with negative allometry, indicating that smaller forms have relatively larger teeth
Max. M1		0.65	0.50	0.79	
Max. diastema		1.29	1.19	1.39	Max. diastema scales with positive allometry, indicating smaller forms have relatively shorter diastemata
Max. diastema and tooth row		0.93	0.90	0.96	Diastema and tooth row together scale by trend with negative allometry but close to isometry, indicating that their separate, deviating scalings tend to equal each other out
Mand. tooth row	Mandible	0.89	0.82	0.96	Mand. teeth tend to scale with negative allometry, indicating that smaller forms have relatively larger teeth
Mand. diastema		1.34	1.24	1.43	Mand. diastema scales with positive allometry, indicating smaller forms have relatively shorter diastema
Mand. diastema and tooth row		1.02	0.98	1.07	Diastema and tooth row together scale isometrically, indicating that their separate, deviating scalings equal each other out
Max. M1	Max. tooth row	1.02	0.88	1.16	The first molar scales isometrically with its entire tooth row, indicating it is not different from the other cheek teeth
Mandible length	Cranium	1.00	0.98	1.03	Cranium and mandible scale isometrically with each other
Mand. tooth row	Max. tooth row	1.10	1.00	1.20	The mandibular tooth row tends towards a scaling with positive allometry with the maxillary tooth row
Mand. diastema	Max. diastema	0.95	0.89	1.01	The mandibular diastema increases isometrically or with slight negative allometry with the maxillary diastema

(Continues)

TABLE 1 (Continued)

y	x	b	95% CI		Interpretation
Max. diastema	Max. tooth row	**1.26**	1.04	1.48	Diastema length increases with positive allometry with a tooth row length
Mand. diastema	Mand. tooth row	**1.18**	1.02	1.34	

Note: Scaling exponents *b* (with 95% CI) according to $y = ax^b$, for three different datasets, as well as the resulting interpretation. The prediction based on proportionate (geometric or isometric) size changes is a linear scaling for two length measures (95% CI including 1.0), quadratic scaling of an area with length (95% CI including 2.0), and square-root scaling of a length with an area (95% CI including 0.5). Length measurements (in mm), except for Foramen magnum area (in mm²). Scaling exponents that do not meet geometric expectations are set in bold. If not otherwise indicated, all variables are lengths, and all measurements are from the right side (Table 4).

Abbreviation: CI, confidence interval.

is scarce. In the veterinary literature, dwarf rabbits appear to be particularly susceptible to dental problems (e.g., Reiter, 2008), and it is appreciated that the teeth of small horse breeds—ponies—appear large for the respective skull and mandible, based on the visual impression in radiographs (Dixon & Copeland, 1993). Lundholm (1947) collected data on the tooth row length in horses as compared to skull length from various literature sources, but he only compared the ratio of the two amongst horse species and breeds to test whether the tooth row:skull length ratio differed between domesticated and nondomestic equids, without relating it to size. Radinsky (1984) analyzed the difference in the scaling of the cheek tooth row and the facial skull length to braincase length in 18 specimens of small and large domestic horse breeds, finding that small domestic horses have relatively longer faces and cheek–tooth row lengths. In a previous evaluation of the data also used in the present study, Heck et al. (2019) demonstrated disproportionately large heads in the smaller horse breeds.

Here, we use a data set of landmarks from skulls of various horses from Heck et al. (2018) and additional measurements on the length of the upper first molar, to explore allometric relationships in the cranium and mandible, with a special focus on the length of the tooth row. Additionally, we perform a similar but reduced set of analyses for cattle skull data from Veitschegger et al. (2018). Based on general geometry, a linear or isometric scaling of one length measure with another one is the default expectation (Figure 1a). Deviations from this scaling are interpreted as an indication that a scaling exponent is below linearity or isometry (also referred to as "negative allometry") (Figure 1b,c), that is, smaller forms have a relatively larger characteristic. A scaling exponent above linearity or isometry (also referred to as "positive allometry") indicates that larger forms have a relatively larger characteristic.

2 | RESULTS

2.1 | Horses

2.1.1 | Symmetry

Measures from the left and right sides of the horse skull corresponded to each other, with a linear scaling between them, as expected due to symmetry (Table 1). From here on, only measures of the right side were investigated.
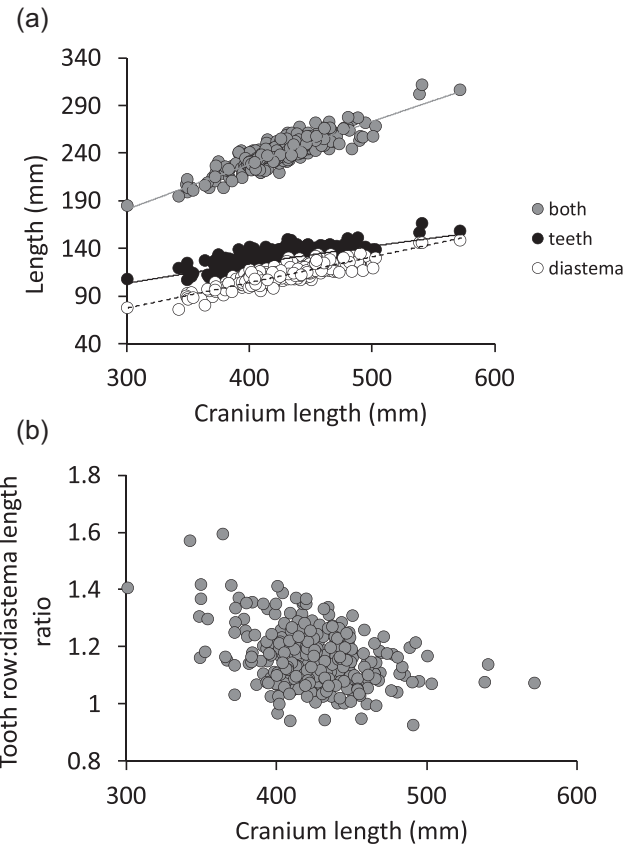

FIGURE 2 (a) Relationship between the (standard) withers height and the cranium length measurements in domestic horses; breeds with a withers height ≤113 cm are indicated as "dwarf" breeds. (b) The scaling relationships of maxillary diastema length, maxillary tooth row length, and the sum of both measures, with cranium length. (c) The length ratio of the maxillary tooth row: diastema against cranium length in all specimens of domestic horse breeds. For (b), the allometric equations with 95% confidence interval in brackets are as follows: diastema length = 0.03[0.02,0.06] cranium length$^{1.29[1.19,1.39]}$; tooth row length = 1.90[1.27,2.83] cranium length$^{0.73[0.66,0.79]}$; combined length = 0.87[0.71,1.06] cranium length$^{0.93[0.90,0.96]}$

2.1.2 | Scaling with body size proxies

Skull size proxies (cranial and mandibular lengths), tooth row lengths (maxillary and mandibular), or M1 length scaled with negative

TABLE 2 Scaling relationships among skull variables in all "nondwarf" horses

y	x	b	95% CI		Interpretation
Foramen magnum area	Withers height	**1.57**	**1.25**	**1.89**	*Foramen magnum* area scales with negative allometry
Cranium		1.15	1.00	1.29	Skull lengths tend to scale with positive allometry
Mandible		**1.17**	**1.03**	**1.32**	
Max. tooth row		0.87	0.73	1.02	Tooth rows tend to scale with negative allometry
Max. M1		**0.72**	**0.49**	**0.96**	
Mand. tooth row		0.95	0.81	1.09	
Max. diastema		**1.45**	**1.20**	**1.71**	Diastemata scale with positive allometry, indicating smaller forms
Mand. diastema		**1.56**	**1.33**	**1.78**	have relatively shorter diastemata
Cranium	Foramen magnum area	0.46	0.38	0.53	Skull scales isometrically to *Foramen magnum*
Mandible		0.46	0.39	0.54	
Max. tooth row		**0.36**	**0.30**	**0.43**	Teeth scale with negative allometry, indicating that smaller forms
Max. M1		**0.32**	**0.21**	**0.43**	have relatively larger teeth
Mand. tooth row		**0.39**	**0.32**	**0.45**	
Max. diastema		0.58	0.46	0.70	Diastemata scale isometrically
Mand. diastema		0.57	0.45	0.69	
Max. tooth row	Cranium	**0.74**	**0.66**	**0.81**	Max. teeth scale with negative allometry, indicating that smaller
Max. M1		**0.64**	**0.47**	**0.82**	forms have relatively larger teeth
Max. diastema		**1.30**	**1.18**	**1.41**	Max. diastema scales with positive allometry, indicating smaller forms have relatively shorter diastemata
Max. diastema and tooth row		**0.94**	**0.90**	**0.97**	Diastema and tooth row together scale by trend with negative allometry, but close to isometry, indicating that their separate, deviating scalings tend to equal each other out
Mand. tooth row	Mandible	**0.81**	**0.76**	**0.86**	Mand. teeth scale with negative allometry, indicating that smaller forms have relatively larger teeth
Mand. diastema		**1.29**	**1.19**	**1.40**	Mand. diastema scales with positive allometry, indicating smaller forms have relatively shorter diastema
Mand. diastema and tooth row		**0.96**	**0.93**	**0.98**	Diastema and tooth row together scale by trend with negative allometry, but close to isometry, indicating that their separate, deviating scalings tend to equal each other out
Max. M1	Max. tooth row	1.06	0.89	1.22	The first molar scales isometrically with its entire tooth row, indicating it is not different from the other cheek teeth
Mandible length	Cranium	1.00	0.97	1.04	Cranium and mandible scale isometrically to each other
Mand. tooth row	Max. tooth row	0.94	0.85	1.03	The mandibular tooth row increases isometrically or with slight negative allometry with the maxillary tooth row
Mand. diastema	Max. diastema	**0.91**	**0.84**	**0.98**	The mandibular diastema scales with negative allometry with the maxillary diastema
Max. diastema	Max. tooth row	1.13	0.89	1.38	Diastema length tends to increase with positive allometry with tooth row length, in particular, in the mandible
Mand. diastema	Mand. tooth row	**1.28**	**1.08**	**1.47**	

Note: The same analyses as in Table 4, but excluding the smallest breeds (Falabella, Shetland pony, Skyros horse, and Rhodes horse) from the data set. Scaling exponents that do not meet geometric expectations are set in bold. If not otherwise indicated, all variables are lengths (Table 4).
Abbreviation: CI, confidence interval.

allometry with all four, respectively applicable body size proxies (withers height, *foramen magnum* area, cranium length, and mandible length) when the small horse breeds were included, although there was some variation in the scaling pattern depending on the measurement and body size proxy (Table 1 and Figure 2b). Notably, the negatively allometric scaling for the teeth was distinctively lower than those of the skull size proxies (Table 1). In other words, smaller horses had proportionately larger skulls, and proportionately even

larger teeth. Only the diastemata scaled isometrically or at a slightly positive allometry with body size proxies, indicating that smaller horses had proportionally shorter diastemata (Table 1 and Figure 2). However, the negatively allometric scaling of skull size was due to the inclusion of the four very small varieties in the data set (Falabella, Shetland, Rhodes, and Skyros). Once these were excluded, cranium length scaling with withers height included isometry, whereas mandible length even scaled with positive allometry (Table 2 and Figure 2a).

2.1.3 | Scaling among skull proxies

Among each other, horse skull size proxies, cranium length and mandible length, as well as *Foramen magnum* area, showed the expected isometric scaling patterns (Tables 1 and 2).

2.1.4 | Scaling with skull size proxies

Tooth row length or first molar length scaled with negative allometry with skull size proxies in horses; in other words, horses with smaller skulls had proportionately larger teeth (Table 1). By contrast, diastema length scaled with positive allometry, indicating that horses with smaller skulls had proportionately smaller diastemata (Table 1 and Figure 2b). These patterns did not change qualitatively when the four small breeds were excluded (Table 2) and therefore represent a pattern valid even across breeds not considered particularly dwarfed.

When assessing the length of the combined diastema and tooth row against cranium or mandible length, respectively, the scaling was generally slightly negatively allometric (Tables 1 and 2 and Figure 2b). Taken together, this means that the relative reduction in tooth length and increase in diastema length in larger horses, or the relative increase in tooth length and decrease in diastema length in smaller horses, nearly but not completely equal each other out. In smaller forms, the diastema just does not decrease exactly to the same extent as the tooth row increases. However, the visualization of the length ratio of maxillary tooth row:diastema across skull sizes

(Figure 6c) indicates that there is a large amount of scattering in these data.

2.1.5 | Scaling within the tooth row/diastema

The scaling between the horse M1 length and the whole maxillary tooth row length was isometric (Tables 1 and 2), indicating that M1 is not different from the other cheek teeth. Horse diastema length scaled mostly with positive allometry with tooth row length (Tables 1 and 2), indicating that longer tooth rows were accompanied by disproportionately large diastemata.

2.2 | Cattle

In cattle, maxillary tooth row length scaled with negative allometry with cranium length; again, smaller cattle breeds had relatively longer tooth rows (Table 3 and Figure 3a). In contrast to horses, the 'diastema' length was proportional to cranium length with an isometric scaling. Thus, longer crania had relatively shorter combinations of tooth row and 'diastema.' In cattle, maxillary tooth row length and 'diastema' length clearly do not equal each other out, much less so than in horses. Nevertheless, in general, larger crania also have lower tooth row:'diastema' ratios, even though the range of this ratio is much smaller than in equids (Figure 2b). In cattle, longer tooth rows were accompanied by disproportionately small diastemata (Table 3).

3 | DISCUSSION

The scaling relationships in horses and cattle in the present study support the concept that teeth do not scale in proportion to body size within a species or among closely related species, but that larger individuals have relatively smaller, and smaller individuals with relatively larger teeth. These results support previous findings for dwarfed or sexually dimorphic forms of wild mammals (Carranza & Pérez-Barbería, 2007; Cochard, 1987; Davies & Lister, 2001; Fortelius, 1985; Gingerich, 1981; Gould, 1975; Kay, 1978; Lister, 1995; Lister &

TABLE 3 Analyses on the cattle data set

y	x	b	95% CI		Interpretation
Max. tooth row	Cranium	**0.62**	0.55	0.70	Max. teeth scale with negative allometry with the cranium, indicating smaller forms have comparatively larger teeth
Max. 'diastema'		1.03	0.96	1.10	Max. diastema scales isometrically with the cranium
Max. "diastema' and tooth row		**0.81**	0.76	0.85	Diastema and tooth row scale with negative allometry with the cranium, indicating smaller forms have comparatively longer tooth row/diastema length
Max. "diastema'	Max. tooth row	**0.63**	0.50	0.75	Longer tooth rows are accompanied by disproportionately smaller diastemata

Note: Scaling exponents that do not meet geometric expectations are set in bold. Since ruminants do not possess maxillary incisors and canines, the portion of the jaw anterior to the cheek teeth was approximated (maxillary "diastema" length). Data refer to the right side.
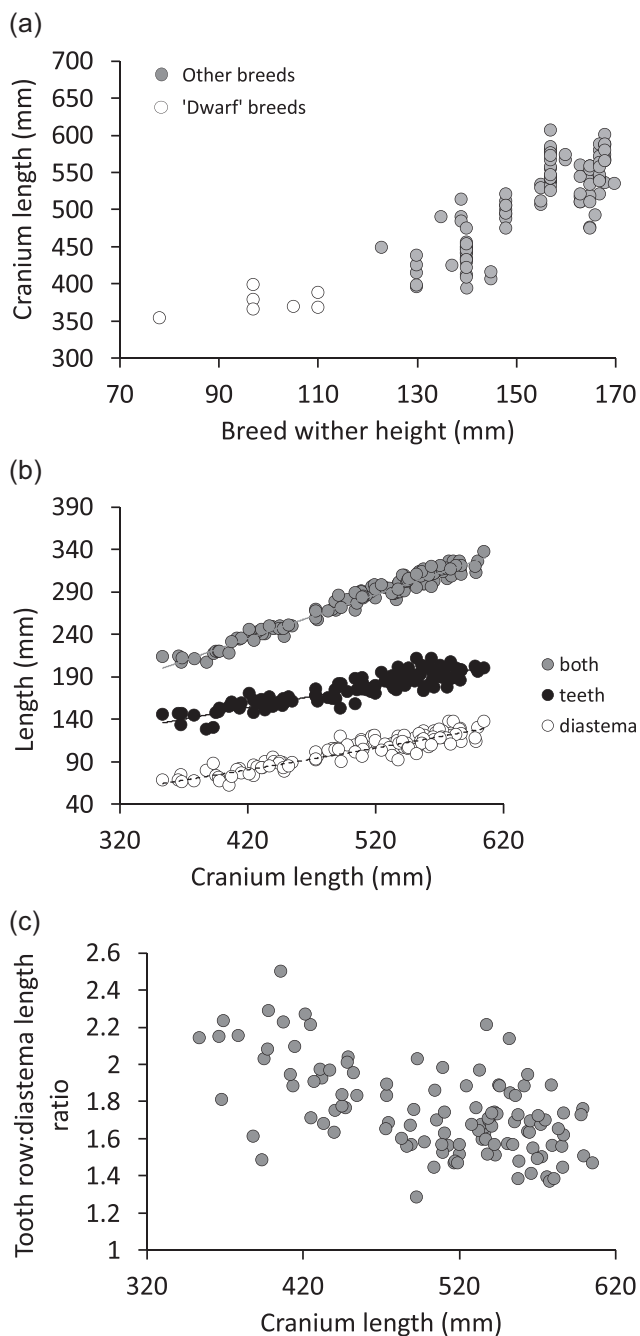
FIGURE 3 (a) Scaling relationships of maxillary 'diastema' length (the distance between the mesial premolar and the widest point of the premaxilla), maxillary tooth row length, and the sum of both measures, with cranium length in all specimens of domestic cattle breeds, and (b) the length ratio of the maxillary tooth row: 'diastema' against cranium length in all specimens of domestic cattle breeds. For (a), the allometric equations with 95% confidence interval in brackets are as follows: "diastema" length = $0.21[0.14, 0.32]$ cranium length$^{1.03[0.96,1.10]}$; tooth row length = $2.95[1.86, 4.67]$ cranium length$^{0.62[0.55,0.70]}$; combined length = $1.80[1.37, 2.37]$ cranium length$^{0.81[0.76,0.85]}$

Hall, 2014; Lundholm, 1947; Maffei et al., 1988; Maglio, 1972; McKeown, 1975; Shea & Gomez, 1988) and domestic mammals (Antonius, 1922; Leche, 1904; McKeown, 1975; Wagner, 1929; Wayne, 1986; Weidenreich, 1941). For domestic horses, cattle, and

rabbits, evidence for a similar pattern has mostly been anecdotal so far, was first described for horses as one of many analyses by Radinsky (1984), and is again corroborated in this issue (present study; for rabbits see Geiger & Sánchez-Villagra, 2022). The analyses of Radinsky (1984) show that across (fossil) equid species, maxillary tooth row length scales isometrically to braincase length, whereas for domestic horse breeds, it scaled with negative allometry at an exponent of 0.69. This exponent is included in the confidence interval of both maxillary tooth row and M1 length scaling, with cranium length in our data set (Tables 1 and 2).

We do not reiterate a critique of the narrative of 'larger animals have relatively lower energy requirements' here, but refer to Clauss et al. (2013) and Clauss (2019) for its pitfalls.[1] Rather, we follow previous work (Fortelius, 1985; Lister, 1995; Lister & Hall, 2014; Lister, 1996; Marshall & Corruccini, 1978) in concluding that the pattern of relatively smaller teeth in larger specimens is due to differences in evolvability, and nonadaptive in its nature. Specifically, body size may evolve (due to natural and/or artificial selection) at a faster rate than tooth size, facilitated by different ontogenetic mechanisms of tooth versus skeletal development, so that tooth size change may 'lag behind' body size changes in a given evolutionary lineage.

Other examples of comparatively 'conservative' characteristics that apparently do not change as easily, in terms of evolutionary time, as body size include some life history characteristics. For example, the length of the gestation period changes much less with body mass among closely related species as compared to across distantly related species (Clauss et al., 2014), and this pattern is particularly impressive in domestic breeds of a species, where gestation length is basically constant across sizes (Andersen & Plum, 1965; Bradford et al., 1972; Heck et al., 2017; Kirkwood, 1985). This constancy already led Geist (1966) to suggest in small species, a particularly long gestation period for their body size compared to larger sized relatives is an indication of recent dwarfing. Reasons for differences in the evolvability of characteristics, with 'drivers' (like overall body size) and 'laggers' (like tooth size or gestation length) remain to be described.

For teeth, this leads to the hypothesis that more recently diverged breeds of different body sizes might show tooth rows more 'out of proportion' than breeds that diverged long ago. In the case of domestic horse breeds, the relative recentness of the observed change in body size becomes apparent if it is viewed in an evolutionary context. *Merychippus*, a group of subhypsodont, Middle Miocene relatives of the hypsodont equids (Hulbert &

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[1]The fact that energy requirements (or intake) do not scale linearly with body mass across mammals, but (approximately) at body mass$^{0.75}$, can be translated into three sentences of identical mathematical correctness but of very different intuitive meaning: (i) larger animals have higher requirements (or intake) than smaller animals (in absolute terms); (ii) larger animals have lower requirements (or intake) than smaller animals (in relative terms where body mass is the basis, also called 'mass-specific'); (iii) larger and smaller animals have the same requirements (or intake) (in relative terms where metabolic body size kg$^{0.75}$ is the basis). The choice of the sentence appears to be often motivated by a rhetoric rather than a mathematical argument. Most importantly, none of these sentences has any argumentative power when standing alone. They only attain meaning when the stated mathematical relationship is put into the context of another mathematical relationship *of the same base of comparison.*

MacFadden, 1991), might serve as an example. These early horses had relative skull proportions similar to modern equids (Radinsky, 1984) and an estimated withers height similar to the smaller ones of the recent domestic horse varieties (Thomason, 1986). The timeframe in which similar magnitudes of body size change occurred in the equid lineage (interspecific) and in the domestic horse lineage (intraspecific; domestication approximately 8000 years ago, e.g., Larson & Fuller, 2014) vary by many orders of magnitude, even if the general trend of body size increase in equid evolution and decrease in some of the domestic horse lineages is interspersed by reversals. Additionally, such a pattern might be evident across mammalian species depending on their time of divergence (Lister, 1995; Lister, 1996; Lister & Hall, 2014). The observation of Janis (1990) across extant ungulates, and of Copes and Schwartz (2010) across mammals and within the majority of mammal clades, that tooth row size scales negatively allometrically with body size indicates that some degree of negative allometry may actually be the default across extant species—in contrast to the initial hypothesis of Gould (1975) who had suspected positive allometry. To further investigate this phenomenon, a taxon with a large variety of extant and extinct mainland and insular forms, where body mass estimates are possible that are independent of dental measurements, might be particularly suitable. Thus, variable periods of divergence could be compared. With their enormous body mass range as well as a variety of insular dwarfs (Forsten, 1989; Hulbert, 1993; Lister, 1995; MacFadden, 1992; Shoemaker & Clauset, 2014), and the variety of domestic breeds, equids might be particularly valuable for such a comprehensive approach. The findings of Forsten (1988), for example, who specifically mentions that various equids vary in their relative tooth size, might suggest that the search for an underlying mechanism might be fruitful. Ideally, such an endeavor should not limit itself to a single measure of the tooth size (like length in the present study), but include at least length, width, and area of individual teeth as well as of tooth rows.

Our observations have relevance for another aspect of mammalian morphology related to the cranium. A positive allometric scaling of the size of the facial cranium to the size of the basal cranium—with larger crania having relatively longer faces than smaller ones—has been found within various mammalian, avian, and reptilian clades and designated the 'cranial evolutionary allometry hypothesis' or 'CREA' (Cardini, 2019; Cardini & Polly, 2013; Radinsky, 1985). If facial and tooth size are assumed to be interlinked, CREA as a general trend cannot be matched in a straightforward way to the findings of the literature cited above for both nondomestic and domestic species, and with the results in Figures 1–3 and for rabbits in Geiger & Sánchez-Villagra (this issue). Notably, CREA has not been compared to, or reconciled with, studies investigating the scaling of teeth across mammals so far. However, it has been pointed out that teeth might be important in modifying the rule (Cardini, 2019; Tamagnini et al., 2017).

Directly comparing the scaling patterns described in the dental literature and also in the present study to that of CREA is complicated, due to the absence of a noncranial body size proxy in the CREA literature. Without such a proxy, it is unclear whether CREA means that larger species have relatively longer faces (and braincases increasing isometrically with body size), relatively shorter braincases (and faces increasing isometrically with body size), or a combination of both. The original investigation by Radinsky (1985) indicated that rather than becoming 'long-faced', larger mammals become 'short-braincased'. Actually, the relationship between the facial cranium and body mass was isometric in the data set of that author. This matches ample evidence for an increase of relative brain size in smaller mammals ('Rule of Haller'; e.g., Burger et al., 2019). An isometric scaling of the facial cranium, on the other hand, is mirrored by our finding that diastema and tooth row length combined scaled close-to-isometrically with skull length in horses. Coupled with the findings of Copes and Schwartz (2010), this would lead to the hypothesis that larger mammals have proportionate faces (craniofacial isometry), with relatively shorter
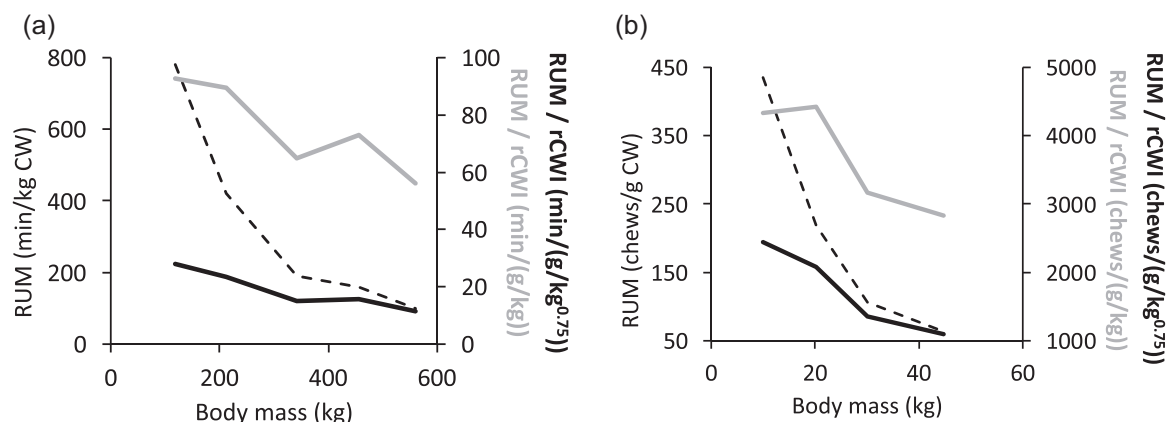

FIGURE 4 Ontogenetic change of chewing intensity (measured as time spent ruminating RUM or number of rumination chews per ingested cell wall CW) in (a) cattle (calves, heifers, cows) (data from Welch, 1982) and (b) goats (from kits to adults) (data from Hooper & Welch, 1983). Intake expressed in absolute terms (primary y-axis, stipled line) or in two different relative terms (relative cell wall intake rCWI, as g/kg body mass, gray line, or g/kg$^{0.75}$ metabolic body weight, black line). Note that chewing intensity decreases over ontogeny regardless of how intake is expressed.

tooth rows and relatively longer diastemata (dental and diastema allometry), and relatively shorter braincases (basocranial allometry). Comparisons of brain, facial, and tooth size relative to each other as well as to body size, across different ecological niches (including toothless forms), would be worthwhile avenues for future research.

Whether a disproportionate increase in diastema length in larger horses (or larger mammals in general), or a proportionately scaling

diastema in cattle, fulfill adaptive functions, or are simply a side effect of other scaling relationships, remains to be investigated. In horses, the diastema helps to create a gap between the upper and lower incisors during cheek tooth action, preventing incisal wear during grinding chewing. Due to the loss of the upper incisors in ruminants, this latter group may have one reason less for long diastemata. Yet, bovids may benefit from long faces for other reasons (Spencer, 1995). Large data sets that combine information on basicranium and facial cranium length, as well as tooth row and diastema length (or some respective size measures), will help resolve these questions.

In terms of a breeding goal of dwarf forms, tooth size might well represent a constraint for both the facial cranium and hence the total cranium. For veterinary science, these results correspond to the impression that in smaller horses, the teeth are more 'crowded' in the oral cavity (Dixon & Copeland, 1993). Whether this leads to size-dependent differences in chewing efficiency remains to be determined. The mean particle size in the feces of horses, including different horse breeds, albeit on undefined diets, do not suggest a systematic change with body size (Clauss et al., 2015). In cattle, similar comparisons would be even less informative, because, in ruminants, the size of particles in the feces is determined by a size threshold for outflow from the reticulorumen, so that chewing efficiency will not measurably increase beyond that threshold (Poppi et al., 1980, 1985), but would—if anything—translate into a faster outflow from the reticulorumen and hence ahigher intake capacity.

In studies that quantified both chewing activity and food intake, a common finding is that larger animals use a lesser number of chews, or less chewing time, in relation to food intake; this is often interpreted as a higher chewing efficiency in larger animals (Bae et al., 1983; Gross et al., 1995; Hooper & Welch, 1983; Shipley et al., 1994; Welch, 1982). When using data from such studies to plot a measure of chewing behavior (number of chews or chewing time for total chewing or only rumination chewing, depending on the studies) against absolute and relative food intake, a pattern emerges. Those studies that assess an ontogenetic trajectory find that with increasing size (and hence, also age), animals chew less, both per absolute food intake and also per relative food intake (Figure 4). This is generally explained by the increase in the chewing surface that becomes available during ontogeny due to molar eruption (Grandl et al., 2018). In studies that compare mature specimens that differ in
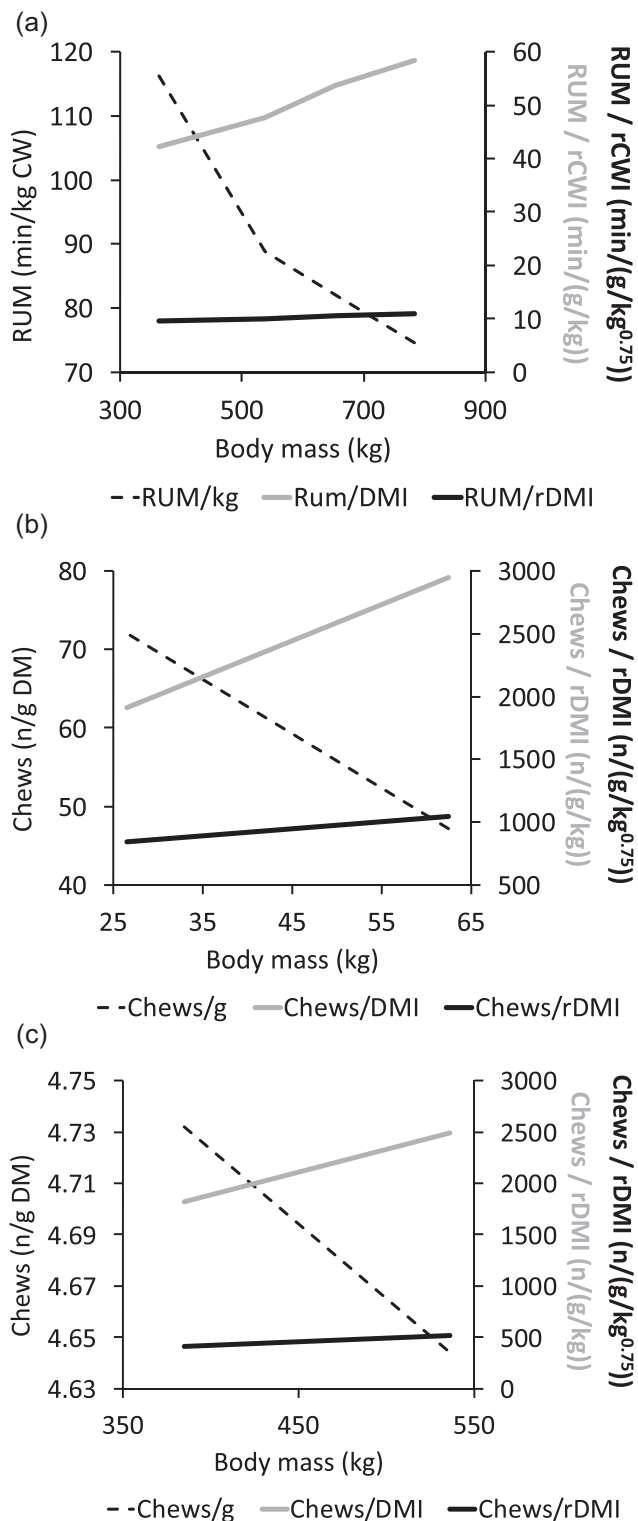
FIGURE 5 Scaling of chewing intensity (measured as time spent ruminating RUM or number of rumination chews per ingested cell wall CW or per ingested dry matter DM) in (a) mature cattle of different breeds (data from Bae et al., 1983); (b) mature female (smaller) and male (larger) Nubian ibex (*Capra ibex nubiana*) (data from Gross et al., 1995); and (c) mature horses of two different breeds (data from Shingu et al., 2001). Intake expressed in absolute terms (primary *y*-axis, stipled line) or in two different relative terms (relative cell wall or dry matter intake—rCWI or rDMI, as g/kg body mass, gray line, or g/kg$^{0.75}$ metabolic body weight, black line, both secondary *y*-axis). Note that chewing intensity decreases with body mass on an absolute basis but increases on a relative basis in all three cases.

body size, either because they belong to different breeds, or to different sexes, the pattern does not apply. In these comparisons, chewing per absolute food intake still decreases with body size, but the chewing investment per relative food intake increases for the larger specimens (Figure 5). This finding is in accord with the observation that among mature specimens, smaller ones have relatively more chewing surface. The fact that the difference between the size groups is less when expressing the relative food intake on the basis of metabolic body weight suggests that possibly, any putative advantage for smaller specimens is small, and that the observed differences in tooth row length might level each other out on a metabolic basis. On the other hand, whether the higher relative chewing investment of larger specimens can be a constraint remains to be investigated as an alternative hypothesis.

4 | MATERIALS AND METHODS

We used the sample of mature domestic horse skulls investigated by Heck et al. (2018), which comprises a variety of domestic horse varieties, ranging from very small forms (a Falabella pony) to very large ones (Shire horses). For cattle, we used the sample of mature individuals investigated in Veitschegger et al. (2018), featuring various domestic varieties, including indicine cattle, the extinct brachycephalic Niata cattle, as well as the extinct wild relative of domestic cattle, the aurochs (*Bos primigenius*). From the three-dimensional landmark data by Heck et al. (2018) (Table S1) and Veitschegger et al. (2018) (Table S1), we extracted linear cranial and mandibular dimensions (Table 4 and Figure 6) using the Pythagorean Theorem. Hitherto unreported length measurements of the maxillary first molar, taken calipers by L. H. in many of the same specimens, were added to the data set (Table 4 and Figure 6). In addition, three specimens of the enigmatic and small-bodied Skyros and Rhodes horses (Dimitriadis, 1937) were newly measured for the current study. These measurements were adapted from the landmark descriptions in Heck et al. (2018) (Table 4 and Figure 6) and taken with calipers by M. G. The Skyros and Rhodes specimens are housed at the Palaeontological Institute and Museum at the University of Zurich, Switzerland (PIMUZ; soon to be transferred to the Naturhistorisches Museum Bern, Switzerland). For a full list of specimens and measurements, see Table S1. Not all measurements were available for all specimens; for example, no mandible was available for the smallest breed (the

TABLE 4 Linear cranial and mandibular dimensions used in this study

Skull dimension (this study)	Landmarks	Landmark description
Horses		
Cranium length	37–60	Point between first incisors from ventral side to the ventral tip of the *Foramen magnum*
Mandible length	U2–U13 (right) U3–U14 (left)	Posterior tip of the third lower incisor to the lateral tip of the condylar process
Maxillary tooth row length	40–41 (right) 42 – 43 (left)	Anterior tip of the second premolar to the posterior tip of the third molar
Mandibular tooth row length	U7–U9 (right) U8–U10 (left)	Anterior tip of the second premolar to the posterior tip of the third molar
Maxillary diastema length	1–40 (right) 2–42 (left)	Posterior tip of the upper third incisor to the anterior tip of the upper second premolar
Mandibular diastema length	U2–U7 (right) U3–U8 (left)	Posterior tip of the lower third incisor to the anterior tip of the lower second premolar
Foramen magnum width	61–62	Posteriormost tips of the occipital condyle (on the left and the right side of the *Foramen magnum*)
Foramen magnum height	36–60	Dorsalmost point on the margin of the foramen magnum to the ventral tip of the *Foramen magnum*
M1 length	NA (M1)	Maximum anteroposterior length of the upper (maxillary) first molar
Cattle		
Cranium length	1–49	Medialmost point of the alveolar process (premaxilla) on the left side to the inferior–medial border of the foramen magnum
Maxillary tooth row length	43–45 (right)	Anterior border of the second premolar to the posterior border of the third molar
Maxillary 'diastema' length	4–43 (right)	Lateralmost point of the anterior part of the premaxilla to the anterior border of the second premolar

Note: Measurements were extracted from landmark data for horses by Heck et al. (2018; tab. 5 and fig. 4) and for cattle by Veitschegger et al. (2018; tab. S5 and fig. S4). Landmark numbers correspond to the ones provided in these studies, as well as in Figure 1. Since ruminants do not possess maxillary incisors and canines, the portion of the jaw anterior to the cheek teeth was approximated (maxillary 'diastema' length).
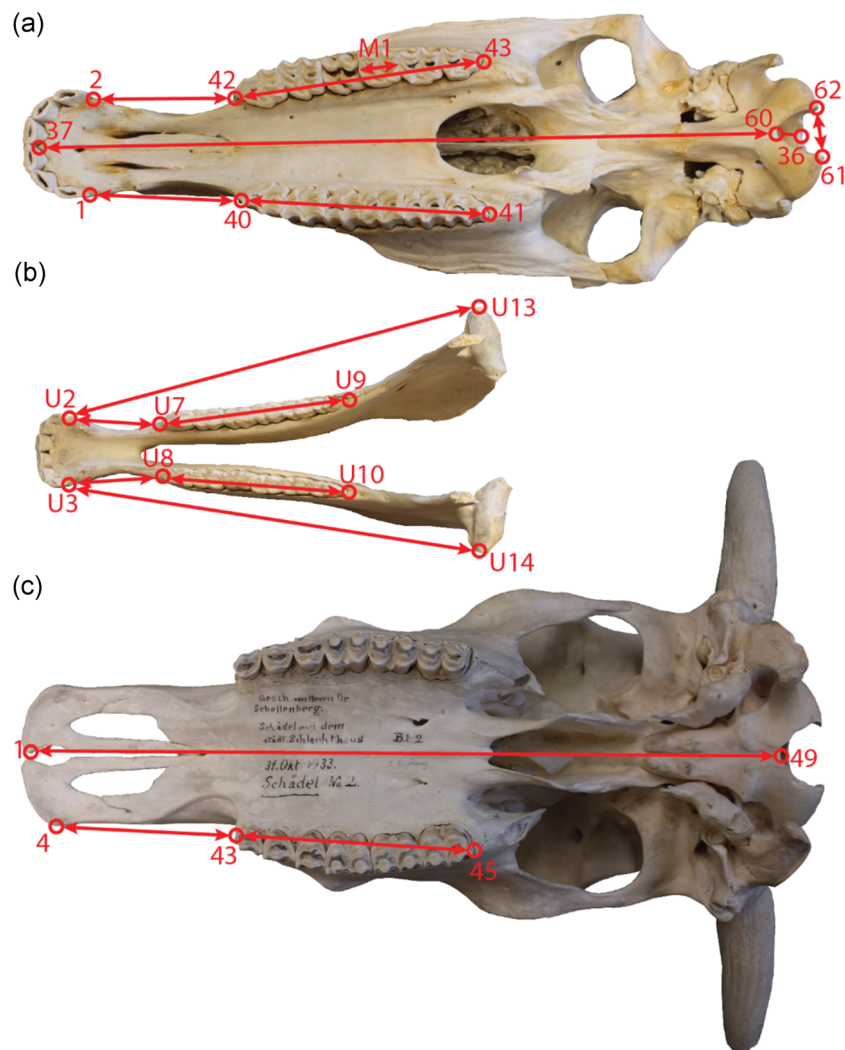
Abbreviation: NA, not applicable.

FIGURE 6 Landmarks and linear measurements were used in this study. Landmark numbers in the horse cranium in ventral view (a) and the horse mandible in dorsal view (b) correspond to the ones defined by Heck et al. (2018; tab. 5 and fig. 4). Landmark numbers in the cattle cranium in ventral view (c) correspond to the ones defined by Veitschegger et al. (2018; tab. S5 and fig. S4). Linear measurements are described in Table 4 in this study. Depictions of horses are modified from Heck et al. (2018). Crania are scaled to the same total length; the mandible is not to scale.

Falabella). Unfortunately, other, possibly important measures of the teeth (e.g., width) were not available.

Four different proxies for body size were used in the horses: (i) as a noncranial measure, the average withers height of the breed was taken from Heck et al. (2019) for the data by Heck et al. (2018), as well as from Dimitriadis (1937) and Sánchez-Villagra (personal communication, September 9, 2021) for the Skyros and Rhodes horses, respectively. Because this measure is not directly linked to the specimens whose crania were measured (often, skulls in museum collections are not associated with individual body size data), it contains an unknown potential error, for example, due to potential variation in withers height within a breed across geographical regions. As cranium-derived body size proxies, we used (ii) the foramen magnum area calculated as an oval as FOR = (1/4)($\pi \times w \times h$), where w is the width and h the height of the foramen magnum (Radinsky, 1967). (iii) cranium length, and (iv) mandible length were also used as body size

proxies. At the same time, both cranium length and mandible length served as proxies for skull size. In the cattle, only one size proxy was available (cranium length). The length of the maxillary and mandibular tooth rows, the length of the upper first molar, and the length of the maxillary and mandibular diastema were the target-dependent variables in the horses; maxillary tooth row length and maxillary 'diastema' length were the target-dependent variables in the cattle (since ruminants do not possess maxillary incisors and canines, the portion of the jaw anterior to the cheek teeth was used).

We analyzed data by allometric equations according to

$$y = ax^b,$$

where a indicates the y-intercept and b the scaling factor (slope, allometric coefficient), with clear expectations about the 95% confidence interval (95% CI) for the scaling factor b based on geometry: A 'proportional', 'geometric', or 'isometric' scaling of a length measure

with a length measure implies a scaling exponent of 1.0 (linearity) in the 95% CI. A 'proportional', 'geometric', or 'isometric' scaling of an area measure with a length measure implies a scaling exponent of 2.0 (quadratic scaling) in the 95% CI. A 'proportional', 'geometric', or 'isometric' scaling of a length measure with an area measure implies a scaling exponent of 0.5 (square root scaling) in the 95% CI. Note that in this strict definition, the term 'allometric scaling' must not be used for any geometric (=isometric) scaling. We refer to lower exponents as either 'less-than-linear' (negative allometry) or 'more-than-linear' (positive allometry) if linearity is the geometric expectation for proportional changes, and as 'less-than-geometrically' (negative allometry) and 'more-than-geometrically' (positive allometry) in scaling relationships in which the *Foramen magnum* area was involved. Analyses were performed using ordinary least squares linear regressions of log-transformed data. The 'dwarf' horse breeds Falabella and Shetland pony have already been described as constituting an exception from the ordinarily observed cranial length to withers height ratio among horses because they were found to exhibit particularly large crania relative to withers height (Heck et al., 2019). A similar peculiarity was also evident in the present study for these breeds and the Skyros and Rhodes horses, that is, all breeds with a withers height of 78–110 cm, with a 13 cm gap to the next breed. To account for the unusual proportions of these breeds, all analyses were repeated after excluding these specimens from the data sets. Analyses were performed in R (R Core Team, 2017). Scaling was considered significant if the 95% CI of *b* excluded zero, which was always the case; therefore, no *p* values are given. For ease of reading, only results for *b* are displayed in the main text, but the Supporting Information Material contains the full set of *a* estimates.

5 | CONCLUSION

In conclusion, horse data clearly show that in smaller skulls of domestic breeds, the tooth row is relatively larger and the diastema relatively smaller. In domestic cattle, the same pattern applies for the tooth row but not the diastema. This trend may well limit the degree of dwarfism that can be reached by selective breeding, and may be responsible for the trend in very small horse breeds to have disproportionately large skulls. However, even in those horse breeds where skull size scales in proportion with withers height, the tooth row is out of proportion in the described manner. As this pattern mirrors other reports within and across species, we follow previous propositions that this is an indication of different evolvability, where tooth size is more refractory to evolutionary changes than body size. With respect to the cranial evolutionary allometry hypothesis, the results suggest that the dental and nondental portions of the facial cranium should be further investigated in their scaling with body size across species.

CONFLICTS OF INTEREST

The authors declare no conflicts of interest.

ETHICS STATEMENT

Not applicable—only work with museum specimens.

AUTHOR CONTRIBUTIONS

Marcus Clauss, Laura Heck, and Madeleine Geiger designed the study. Laura Heck, Kristof Veitschegger, and Madeleine Geiger took the measurements. Marcus Clauss analyzed the data. Marcus Clauss wrote the first draft of the manuscript, and then received input from all coauthors

DATA AVAILABILITY STATEMENT

The data that supports the findings of this study are available in the Supporting Information Material of this article.

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PEER REVIEW

The peer review history for this article is available at https://publons.com/publon/10.1002/jez.b.23128.

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