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Occlusion norms in mammals: an introductory study

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Abstract

Background and objectives: Human occlusion has evolved over time, influenced by environmental, dietary and ecological changes. Differences in occlusal characteristics between humans and other mammals are poorly understood. The aim of this study was to investigate the occlusion patterns in mammals of different dietary groups (herbivores, omnivores and carnivores).

Methods: Twenty-nine complete skulls (both cranium/ maxilla and mandible) of 14 mammals were categorised into three dietary groups: herbivores, omnivores and carnivores. Orthodontic parameters assessed in each skull included the arch form, curve of Spee, maxillary compensating curve, crowding, spacing, overbite, overjet, and crossbite. Specimens were also screened for dental pathology and abnormalities and those were quantified and described.

Results: There was great diversity of occlusal patterns across mammals both between and within dietary groups. Human occlusion norms were most frequently applied to primates (omnivores), being different to other species. Although not common, recorded dental pathology and abnormalities included caries, enamel hypoplasia/defects, shape abnormalities and supernumerary teeth, tooth wear, fractures, periodontitis, TMJ pathology, and periapical lesions/ bony fenestrations.

Conclusion: Occlusal patterns differed among dietary groups (herbivores, omnivores and carnivores), and often did not follow the “ideal” occlusion in humans. Future studies with larger sample sizes and more diverse species will help advance our understanding of the evolution and adaptation of mammalian occlusion.

Introduction

Occlusion describes the relationship between teeth of opposing arches as they come into contact with each other and the positioning of teeth in each arch (Davies & Gray, 2001; Hillson, 2005). Compared to humans, most mammals have modified occlusal relationships due to their dietary, environmental and ecological differences (Cuozzo et al., 2012). In general, mammals have a higher level of oral food processing compared to other vertebrates, because of their more efficient methods of extracting nutrients from food due to increased metabolism and energy demands (Schwenk, 2000).

In mammals, different tooth types and morphologies show specialisation for dietary habits. In addition to processing and gathering food, teeth are also used for display, agonistic behaviours (offense or defence),

and grooming. These functions might be carried out by specific teeth with specialised functions within the tooth arch (Crompton & Hiimae, 1969). In humans, teeth have an important role in mastication, speech and aesthetic purposes.

In humans, the “ideal” occlusal relationship takes into account molar relationships, crown angulation, crown inclination, absence of rotations, absence of spacing, and ideal occlusal plane (Andrews, 1972). The six criteria of normal occlusion in humans are as follows: 1) Molar relationship is Angle’s Class 1 molar relationship (mesiobuccal cusp of the maxillary first molar occludes with the mesiobuccal groove of the mandibular first molar); 2) All teeth have a mesial crown angulation; 3) Incisors have a labial crown inclination, whereas canines and posterior teeth have a lingual inclination; 4) Absence of rotations; 5) Absence of spacing; and 6) A flat or mildly concave curve of Spee (Andrews, 1972; Mitchell, 2013). An “ideal” incisal relationship, according to the British Standards of Incisor Class 1 Classification, is that the mandibular incisal edges occlude with or lie immediately below the cingulum plateau of the maxillary central incisors; the ideal overjet is around 2mm and ideal overbite is approximately 30% (Mitchell, 2013). The other components that are considered an “ideal” occlusion in the literature include parabolic arch forms (Read, 2016), a flat or mild curve of Spee and a convex maxillary compensating curve (Marshall et al., 2019), absence of crowding, spacing and crossbites (Mitchell, 2013; Proffit et al., 2006).

For a more holistic understanding of occlusion, the health of teeth and jaws must also be considered. Jaw bones and teeth can provide a wealth of information regarding the environmental, dietary, and evolutionary influences experienced by different species (Bergqvist, 2003). Trauma, diseases and physiological stresses can be reflected in the maturation patterns of dentine and enamel (Cuozzo et al., 2012; Goodman et al., 1980; von Arx, 1993), and evidence of pathologies such as carious lesions or periodontal disease remain recorded in post-mortem remains (Döring et al., 2018; Loch et al., 2011).

Previous studies of occlusion in mammals have focused on single species (Döring et al., 2018; Hoyer & Rawlinson, 2019; Johnson, 1940; Jung et al., 2016), on topics such as occlusion evolutionary trends (Butler, 1974; Reisz, 2006), evolutionary trends and prevalence of malocclusion in humans compared to other species (Butler, 1974), occlusion and functional movements of the jaw (Butler, 1974; Kaidonis et al., 2014), and malocclusion in domesticated animals

(Ackerman, 2011; Hoyer & Rawlinson, 2019; Johnson, 1940). There is a lack of comparative data on the differences in the occlusal anatomy and orthodontic parameters across different mammal species. Additionally, few studies have investigated the occlusion of domesticated and wild mammals, or animals with masticatory apparatuses suited to varied diets.

This pilot descriptive study aimed to investigate and compare patterns of dental occlusion in mammals in broad dietary groups (herbivores, omnivores and carnivores) with the so-called “ideal” occlusion norms in humans. Specimens were also screened for dental pathology and abnormalities and those were quantified and described. Elucidating occlusal relationships in other species would allow the inference of occlusal features associated with dietary habits and parafunctional activities in humans and other mammals.

Material and Methods

Complete skulls (both cranium/maxilla and mandible) of 14 mammal species were analysed. Specimens belong to the University of Otago Faculty of Dentistry Comparative Anatomy Section collection (Table 1), consisting of both domesticated and wild species. Ethical approval was not required because this research used osteological material deposited in a museum. Incomplete, pathological or damaged skulls were excluded from analysis. Selected complete skulls were categorised into age classes (juvenile, sub-adult and adult) based on the following criteria: 1) the closing (maturity) of basal sutures—in particular the sphenoccipital suture (Cray et al., 2011; Geiger & Haussman, 2016), and 2) the presence of deciduous teeth (Mbizah et al., 2016) (Figure 1). Skulls with an open suture (juveniles) were excluded from the study; only sub-adult and adult individuals were analysed (Sone et al., 2004). The presence of deciduous teeth was determined by referring to the dental formula and eruption pattern for each species (Hillson, 2005); skulls with remaining deciduous teeth were considered juvenile and were excluded from the study. Skulls were categorised into three broad dietary groups (herbivores, omnivores

and carnivores). At least three different species were analysed in each dietary group (Table 1).

The following orthodontic parameters were analysed for each skull: arch form/shape, curve of Spee/maxillary compensating curve, crowding, diastemas, overbite, overjet and crossbite (Table 2). The maxillary compensating curve was defined as a curve in the occlusal plane of the maxillary buccal segment which corresponds to and aligns with the opposing mandibular curve of Spee (Marshall et al., 2019). Orthodontic parameters were based in previous studies (Döring et al., 2018; Du Toit et al., 2009; Nagao, 1919). The reference points for the curve of Spee/maxillary compensating curve was the height of the most posterior molar to the height of the first premolar. Curve of Spee/maxillary compensating curve were not assessed in the quadrant of interest if it involved partially erupted or missing teeth. Diastema is defined as spacing between adjacent teeth (Proffit et al., 2006). Each maxilla and mandible for each skull were articulated into maximum intercuspation (MIC), guided by the dental wear facets of the teeth, to record observations for overbite, overjet, and crossbites



Figure 1. Examples of juvenile (left) and mature (right) primate specimens. The arrow points the open (left) and closed (right) sphenoccipital suture.

Table 1. Sample characteristics. Dental formulae follow Hillson (2005) for all species except possum which follows Berkovitz and Shellis (2018).

Dietary category	Common name	Family and species name	Dental formula
Herbivore	Sheep (8)	Bovidae, <i>Ovis aries</i>	i0/3, c(0-1)/1, p(2-3)/(2-3), m3/3
	Rabbit (2)	Leporidae, <i>Oryctolagus cuniculus</i>	i2/1, c0/0, p3/2, m3/3
	Cow (1)	Bovidae, <i>Bos taurus</i>	i0/3, c(0-1)/1, p(2-3)/(2-3), m3/3
Omnivore	Primates (6)	Primates,	i2/2, c1/1, p2/2, m3/3
	Gibbon	<i>Hylobates sp.</i>	
	Macaque	<i>Macacus nemestrinus</i>	
	Possum (3)	Phalangeridae, <i>Trichosurus vulpecula</i>	i3/2, c1/0, p2/1, m4/4
	Pig (1)	Suidae, <i>Sus domesticus</i>	i(2-3)/3, c1/1, p(3-4)/(2-4), m3/3
Carnivore	Boar (1)	Suidae, <i>Sus scrofa</i>	i(2-3)/3, c1/1, p(3-4)/(2-4), m3/3
	Bear (1)	Ursidae, <i>Ursus arctos</i>	i3/3, c1/1, p(3-4)/(3-4), m2/3
	Dog (5)	Canidae, <i>Canis familiaris</i>	i3/3, c1/1, p4/4, m2/2
	Leopard (1)	Felidae, <i>Panthera pardus</i>	i3/3, c1/1, p(1-2)/2, m1/1

**Table 2.** Orthodontic parameters and categories/criteria assessed.

Parameters	Categories/Criteria
Arch form	Omega, V, Parabolic or U shape
Compensating Curve (Curve of Spee)	Straight (flat), convex, concave
Crowding	Presence or absence
Diastema (mm)	Presence or absence (including location) – if present, measured using calliper and values assessed relative to skull length
Diastema vs Arch Length Ratio	Average diastema length (for the right side) was divided by the right dental arch length
Overbite (mm)	Measured using calliper
Overjet (mm)	Measured using calliper
Crossbite	Anterior/Posterior – present or absent (including teeth involved)

Table 3. Dental pathologies/abnormalities assessed and description

Dental pathology	Description
Caries (demineralised or cavitated)	<i>Demineralisation</i> – white opaque enamel surfaces or dark brown surfaces indicating tooth demineralisation. <i>Cavitation</i> – broken down enamel surface with dark brown underlying dentine.
Enamel hypoplasia/defects	Presence of pits, bands, or grooves indicating thin, defective or absent enamel.
<i>Antemortem</i> tooth loss	Tooth lost prior to death (either pathologically or congenitally), socket not visible.
Shape anomalies	Abnormally shaped crowns or tooth structure.
Supernumerary tooth	Presence of an extra tooth exceeding the number indicated in the dental formula.
Tooth wear	Presence of attrition, abrasion or erosion facets.
Tooth fractures	Broken crown with no evidence of caries. Edges worn, faceted and smooth.
Periodontal disease	Presence of calculus, furcation involvement, significant bone loss relative to adjacent teeth (horizontal/vertical/angular), osseous foramina (increased vascularity)
TMJ pathology	Presence of increased vascular foramina or osteophytes.
Periapical lesion/other bony fenestrations	Presence of bony fenestrations at the apex of the tooth or along the root surface.
Staining	Accumulation of exogenous stains on the tooth surface

(anterior/posterior). Measurements recorded for overbite and overjet were taken using a sliding calliper. Measurements were avoided in pathological areas or with artefactual damage. Each skull was also assessed for the presence of dental pathology/abnormalities (Table 3), following the definitions in the literature (Döring et al., 2018; Loch et al., 2011).

Results

Occlusal Characteristics

Arch Form

Herbivore and omnivore specimens analysed here displayed a parabolic maxillary arch form, while carnivores displayed an omega maxillary arch (Figure 2a and b). Both herbivores and carnivores had a V-shaped mandibular arch (Figure 2c), while most omnivores (four of five species) had a parabolic lower arch except for the bear which displayed a V-shaped lower arch form (Table 4).

Compensating Curve (Curve of Spee)

All species examined displayed a convex maxillary compensating curve. Carnivores showed a convex curve

of Spee, while herbivores (sheep and rabbit) had a flat curve of Spee. Omnivores displayed a concave curve of Spee with a few specimens (boar and bear) displaying convex curves (Figure 2 d and e; Table 4).

Crowding

No major maxillary or mandibular crowding was observed among the specimens studied. Mild cases of crowding included two possums (omnivores), which displayed mild distally rotated maxillary first premolars; three sheep (herbivores) with mandibular crowding and one dog (carnivore) with mild displacement of the canine and premolar (Table 4).

Presence of diastemas and diastemas vs. arch length ratio

Herbivores (except for rabbits) did not have maxillary diastemas while all omnivores and carnivores analysed presented maxillary diastemas (Fig. 2f). Mandibular diastemas were observed in all herbivores and carnivores. For omnivores, primates did not have mandibular diastemas, while pigs, boars, bears and possums had mandibular diastemas. Table 4 shows the ratio between maxillary and mandibular diastema

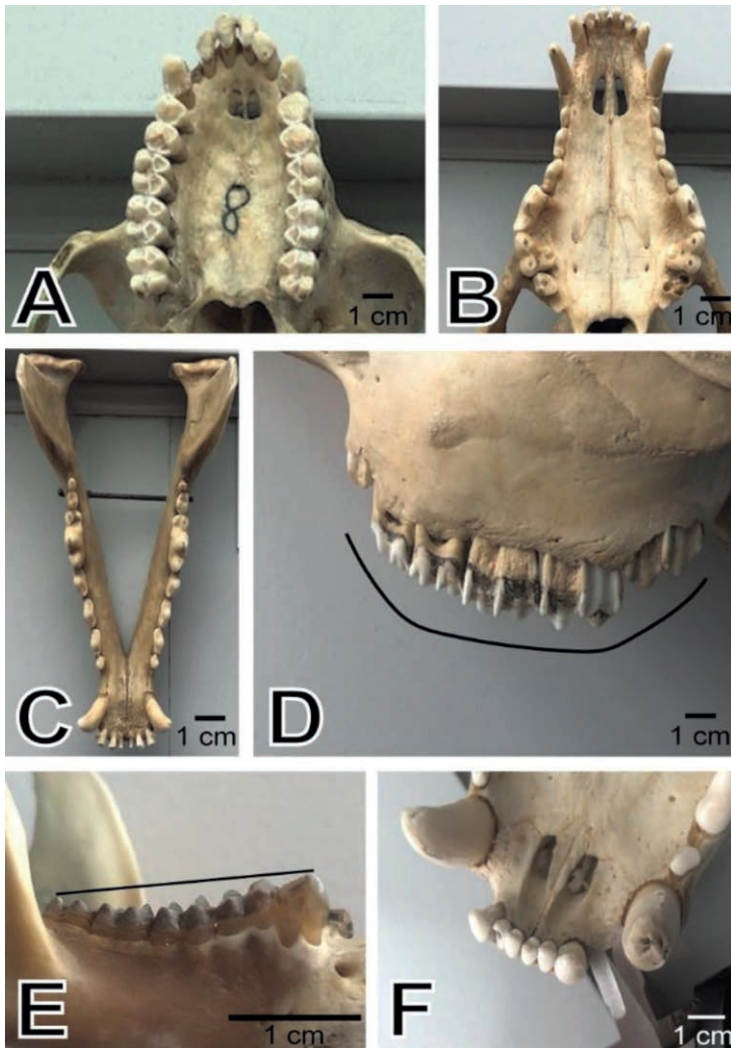


Figure 2. Orthodontic parameters and occlusal characteristics in mammals. A) Parabolic maxillary arch form in the gibbon. B) Omega-shaped maxillary arch form in the dog. C) V-shaped mandibular arch form in the dog. D) Convex maxillary compensating curve in the cow. E) Concave curve of Spee in the possum. F) Maxillary diastema between I3 and C in the leopard.

length vs the total length of the tooth row. In herbivores, the maxillary diastema represented almost 60% of the arch length, while in omnivores it ranged between 6% and 12%, and 7% and 13% in carnivores. In herbivores, the mandibular diastema ranged between 36% and 50% of the length of the tooth row, while in omnivores it ranged between 7% and 15%, and between 8% and 19% for carnivores (Table 4).

Overbite

As sheep and cows do not have maxillary incisors, overbite could only be measured in rabbits (for the herbivores). In rabbits, overbite was 5%. Amongst omnivores, there was a wide variation in overbite scores within and across different species. Primate overbite scores ranged from 0% (edge-to-edge) to 15% overbite. For pigs, the maxillary central incisors were in anterior crossbite and displayed

a 90% overbite. All possums examined displayed 5% overbite. Carnivores displayed edge-to-edge bite except for the leopard which displayed 5% overbite (Table 4).

Overjet

For herbivores, overjet could only be measured in rabbits (1.46mm). Most omnivores and carnivores displayed overjet, with variation within and across different species. For omnivores, primate overjet scores ranged from 0.82mm to 8.67mm, 2.9mm for possums in average and 7.99mm reverse overjet for pigs due to anterior crossbite. Among carnivores, dog overjet scores ranged from 0.0mm to 2.77mm, and 4.46mm overjet for leopards (Table 4).

Crossbite

Anterior crossbite was not observed in most specimens sampled, except for three omnivores: the primates gibbon and macaque, and pigs. Half of the herbivores analysed had a bilateral buccal scissor bite and only one herbivore (cow) showed a posterior crossbite between the maxillary second molar and mandibular third molar. There were no posterior crossbites in omnivores with exception of the bear which showed bilateral buccal scissor bite; and the boar, which displayed a mild unilateral crossbite. All carnivores analysed had bilateral buccal scissor bite involving posterior teeth (Table 4).

Dental pathologies/abnormalities

Caries

Carious teeth were diagnosed in five individuals; four omnivores (two macaques, boar and bear) and one carnivore (dog). No herbivores had caries. The number of carious teeth per dietary group was low, with only 23/342 (6.7%) teeth of omnivores with caries, and 7/215 (3.3%) of carnivores (Figure 3a).

Enamel Hypoplasia/Defects

Enamel hypoplasia/defects were uncommon among the specimens analysed. One boar specimen had 2 teeth with enamel pitting and one dog had 4 teeth with horizontal grooves along the crowns (Figure 3b).

Antemortem tooth loss

Few *antemortem* tooth losses were observed (diagnosed by the absence of a socket); in three herbivores (sheep), two omnivores (one possum and one bear) and one carnivore (dog). The number of tooth losses ranged from one tooth (dog and bear) to five teeth (sheep).

Shape anomalies and supernumerary teeth

Only two herbivores (sheep) displayed shape anomalies in the form of “peg” shaped diminutive mandibular canines. Supernumerary teeth were observed in three carnivores (dogs), with bilateral mandibular supernumerary premolars.

Tooth Wear

Tooth wear was observed in all specimens analysed, commonly seen as generalised occlusal wear facets in



Table 4. Occlusion characteristics of mammals studied and human “norms” (following Marshall et al., (2019), Read (2016), Pieren & Bowen (2019), Proffit & Fields (1993))

Occlusal Characteristics	Human norms	Herbivore			Omnivore				Carnivore			
		Sheep	Cow	Rabbits	Primates		Pig	Boar	Possum	Bear	Dog	Leopard
					Gibbon	Macaques						
Maxillary Arch form	Parabolic	Parabolic			Parabolic				Omega			
Mandibular Arch form	Parabolic	V-shaped			Parabolic				V-Shaped	V-shaped		
Maxillary Compensating Curve	Convex	Convex			Convex				Convex			
Curve of Spee	Flat/Mild concavity	Flat			Concave		Convex	Concave	Convex	Convex		
Crowding	Ideally none	Mild			N/A				Mild	N/A		
Maxillary Diastema/Arch Length Ratio	N/A	N/A	0.58	0.11			0.10	0.12	0.06	0.07	0.13	
Mandibular Diastema/Arch Length Ratio	N/A	0.36	0.50	N/A			0.07	0.14	0.15	0.08	0.19	
Overbite (%)	20-30	N/A	5	5	8.5	1	90(crossbite)	N/A	5	N/A	0	5
Overjet (mm)	2-3	N/A	1.4	0.8	4.9	1.5	8	N/A	2.9	N/A	1.2	4.5
Anterior Crossbite	None	None			Yes		Yes	No	No	No	None	
Posterior Crossbite	None	Yes			No			Yes	No	Yes	Yes	

both posterior and anterior teeth with varying degrees of dentine exposure. However, six skulls presented wear patterns different from this; a leopard (carnivore) which displayed wear facets on the buccal and lingual surfaces of mandibular posterior teeth; a dog (carnivore) which displayed wear facets along the labial surfaces of mandibular central incisors; one macaque (omnivore) which had severe wear with significant dentine exposure and loss of tooth structure leading to pulp exposure; and three possums (omnivores) which displayed large buccal wear facets on maxillary premolar teeth.

Tooth Fractures

Molars (n=12) were the most fractured teeth, followed by premolars (n=4), canines (n=3) and incisors (n=2). In herbivores, fractured teeth involved five molars (sheep and rabbit) and one incisor (rabbit). In omnivores, three premolars (boar), one canine (macaque) and one molar (pig) had fractures. In carnivores, two canines and one premolar were fractured (leopard). The most common type of tooth fracture observed were uncomplicated enamel-dentine cuspal fractures (without pulp exposure) seen primarily on premolars (n=3; boar and leopard), canines (n=2; leopard) and molars (n=1; pig). Only one complicated root fracture (with pulp exposure) was observed on a macaque canine.

Periodontal disease

All specimens analysed showed evidence of previous periodontal disease (e.g. calculus deposits, horizontal/vertical bone loss, furcation involvement or increased vascular foramina). Two herbivores, six omnivores, and four carnivores had calculus deposits (Fig. 3c). Most skulls analysed displayed varying degrees of generalised horizontal and/or localised vertical bone loss. One carnivore, seven omnivores and two herbivores displayed areas of furcation. Increased vascular foramina were observed among all groups studied.

TMJ Pathology

Half of the specimens analysed displayed TMJ pathologies (e.g. bony pits, roughness, porosities, defects and vascular foramina). This was evident in six herbivores, five omnivores, and three carnivores.

Periapical Lesions and/or Bony Fenestrations

Bony fenestrations in root apices were uncommon. Five omnivore skulls displayed localised bony fenestrations on buccal bone; two macaques had bony fenestrations at the root apices (apex of the mesio-buccal root of the right maxillary first molar; and bilaterally at the apices of maxillary first and

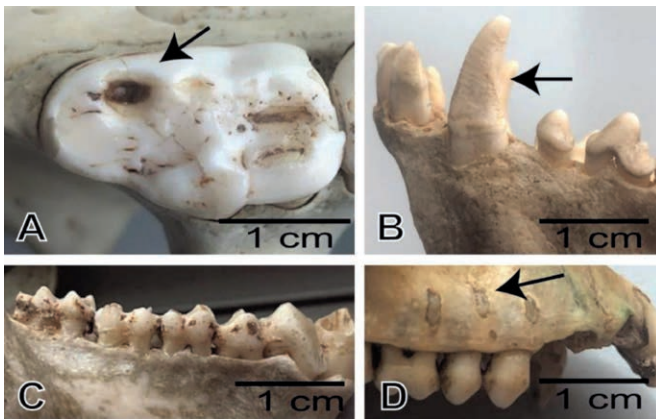


Figure 3 – Examples of dental pathologies and abnormalities in mammals. A) Occlusal caries in bear upper molar. B) Linear enamel hypoplasia in dog lower canine. C) Calculus deposits in macaque lower jaw. D) Apical bony fenestrations in macaque upper jaw.

second premolars and first molars; Fig. 3d). The gibbon displayed generalised bony fenestrations where the roots of the posterior maxillary teeth were protruding through the bone. In general, herbivores and carnivores did not display bony fenestrations. However, one sheep presented bilateral lingual large bony fenestrations in the posterior mandible.

Staining

Cows, sheep and possums displayed generalised black staining on smooth surfaces and occlusal tables of teeth. Generalised brown staining was noted on occlusal and smooth surfaces of the dentition of pigs, and generalised dark stained fissures were noted on the boar.

Discussion

This study investigated occlusion in mammals from different dietary groups (herbivores, omnivores and carnivores) and found varied occlusion patterns both within and across these dietary groups, diverging from the expected human norms of occlusion. Due to the shared ancestry (Read, 2016), primates were the mammals analysed which displayed most similarity to human occlusal norms.

In humans, the parabolic arch form was resulted from evolutionary changes such as decreased masticatory function/forces over time and morphological changes of the cranium and face (Read, 2016). In mammals, the upper arch is composed of the premaxilla and maxilla, with the premaxilla playing an integral structural role to support the nasal cavity and soft tissues such as the upper lip and nasal cartilages (Bels, 2006). However, in domesticated mammals (e.g. sheep, cow, rabbits, pigs, dogs) the maxillary arch is not necessarily only associated with dietary or masticatory habits (Bels, 2006). In this study, herbivores and omnivores displayed parabolic maxillary arch forms similar to humans; however, carnivores (domesticated dogs and wild leopard) displayed an omega maxillary arch form.

The mandible is the primary attachment site for the muscles of mastication; its shape is associated with dietary and masticatory habits (Bels, 2006). In this study, herbivores and carnivores displayed a V-shaped mandible, while omnivores had a parabolic mandibular arch. In primates, the change in shape of both maxillary and mandibular arch forms among species is attributed to differences in masticatory habits and in the distribution of mechanical stresses (Read, 2016). In this study, we observed similar arch forms across primates, with all displaying parabolic maxillary and mandibular arch forms. Primates in general seem to have greater variation in arch form among arches, and within species; unlike humans with a parabolic shape in both arches (Read, 2016). This was likely influenced by a softer diet in humans compared to wild primates (Read, 2016).

A flat to mild curve of Spee (slight concavity) in the mandibular arch is considered ideal in terms of human occlusion, whereas an “exaggerated” curve of Spee (deep concavity) results in compromised occlusion with inefficient mastication due to imbalance of the masticatory muscles (Kumar & Tamizharasi, 2012). A flat curve of Spee provides optimal “static intercuspation”, which is considered a treatment aim in orthodontics (Kumar & Tamizharasi, 2012). However, a concave curve of Spee would confer biomechanical advantages by increasing the crush/shear ratio and forces in the posterior teeth, thus improving chewing forces during mastication (Kumar & Tamizharasi, 2012). A concave curve of Spee is common in most mammals; a greater concavity generates higher crush/shear ratio in molars (Osborn, 1993). This allows mammals to optimise the crush and shear forces required to process and break down hard nuts/grains (crush) and raw flesh (shear force) as needed (Osborn, 1993). It would be expected that carnivores and omnivores would have concave curves of Spee to provide efficiency in crushing and shearing forces during mastication. In this study, almost all carnivores displayed a convex curve of Spee, the only exception being the leopard with a flat curve of Spee. Domesticated animals such as dogs consume pre-processed diets which are softer and less mechanically demanding than the diets of their wild counterparts (Wu, 2018). Dogs would have less need for increased crushing and shear forces in their mastication, thus a convex (reverse) curve of Spee might have developed over time. Decreased masticatory efficiency from a shorter masseter muscle (meaning a shorter distance between the zygomatic arch and the border of the mandible attachments, and between the height of the TMJ condyle and the occlusal plane) can be compensated by an increased crush/shear ratio, resulting in a greater concavity in the curve of Spee (Osborn, 1993). It is expected that carnivores, with the shortest distance between the height of the TMJ condyle and occlusal plane, may have the most concave curve of Spee. However, this was not observed here; likely because most carnivores analysed were domesticated dogs, without the crush/shear forces so vital for the diet and hunting habits of wild carnivores (Osborn, 1993).



Most omnivores displayed a concave curve of Spee whereas the boar and bear displayed bilateral convex curves. Pigs and boars, although closely related, had different curves of Spee; differences may be due to our small sample size but also related to differences in diet. Wild boars have more diverse diets ranging from nuts and small reptiles, to some livestock (Team, 2018; Thomson & Challies, 1988). Domesticated pigs consume softer diets such as pre-processed pellets with nuts and grains and soft vegetables (SPCA). Bears are omnivores, with diets ranging as broadly as berries, livestock, bamboo and salmon (Gende et al., 2001; Peyton, 1980). It is possible that dietary differences will generate different occlusal features. For example, bears who consume more fish and livestock may show more concave curves of Spee due to shear force requirements, whereas bears with softer diets based on berries and honey may display more flat or convex curves of Spee. In this study, most herbivores displayed a convex curve of Spee.

In humans, the maxillary compensating curve should align with the curve of Spee, *i.e.* a concave curve of Spee is expected to have a convex maxillary compensating curve and vice-versa (Marshall et al., 2019). All species analysed here displayed a convex maxillary compensating curve; this contradicts human norms as the maxillary compensating curves did not always correlate to the opposing curves of Spee. In humans, the maxillary compensating curve aligns with and *compensates* for the opposing mandibular curve of Spee (Marshall et al., 2019). In this study, all dogs and most sheep displayed a convex curve of Spee opposing a convex maxillary compensating curve. This pattern was also seen in the bear, boar and in one possum (omnivores). A study of occlusal movements in the possum described two movements; a vertical sectorial movement in the premolar region and an anteromedial shearing and grinding stroke in the molar area (Young et al., 1990). Wear striations in the teeth suggest that the mandible rotates around the contralateral condyle from the working side. There was no evidence of balancing contact facets in the contralateral side, suggesting an anisognathous jaw movement (Young et al., 1990).

The biomechanics of having both a convex curve of Spee and convex maxillary compensating curve may be better appreciated in ruminants (sheep and cows). Ruminants primarily chew their food into a bolus to swallow, before regurgitating the bolus for rumination (Bels, 2006). Chewing and rumination decreases the amount of shear force needed to masticate plant-based diets (Bels, 2006). This could explain the convex curves of Spee observed in the herbivore species studied here, as a greater concavity of the curve of Spee allows for increased crush/shear forces (Kumar & Tamizharasi, 2012). Ruminants primarily rely on chopping and grinding rather than shearing movements (Bels, 2006); it is possible that having both a convex curve of Spee and maxillary compensating curve allows for more efficient chopping and grinding

movements of the jaw. Human “norms” in terms of the curve of Spee could only be observed in primates, pigs and most possums; with a concave curve of Spee opposing a convex maxillary compensating curve.

Crowding of teeth is a common orthodontic problem in humans and a major contributing factor in malocclusions. The prevalence of malocclusions, including crowding, is higher in modern humans and is attributed to a shift towards processed diets that require less masticatory forces (Evensen & Øgaard, 2007). A similar observation can be made in domesticated species which have higher prevalence of malocclusion and dental disease compared to wild animals (Okuda et al., 2007). Among the specimens studied here, dental crowding was uncommon, except for two possums and three sheep that displayed mild crowding.

Herbivores such as sheep and cows do not have maxillary anterior teeth, instead having a fibrous pad that occludes against the lower dentition which allows increased grazing efficiency (Fubini & Ducharme, 2016). The mandibular incisors and canines are loosely implanted to allow for some degree of mobility, which reduces the risk of trauma on the fibrous pad (Fubini & Ducharme, 2016). In humans, on the other hand, tooth mobility is often considered pathological and indicative of periodontal disease (Glargia & Lindhe, 1997). In sheep and cows, the main function of the anterior dentition is not to incise but to efficiently grasp food, also relying on the tongue and mobile lips to grasp pasture closer to the ground (Fubini & Ducharme, 2016).

Maxillary and mandibular diastemas were observed in all dietary groups. The diastema/arch length ratios for both the maxillary and mandibular dentitions were greater in herbivores compared to omnivores and carnivores. In humans, diastemas are more common in the maxillary arch, anteriorly to the premolars (Lavelle, 1970). However, the adult human occlusion “norm” does not involve diastemas (Sanjeev et al. 2012). In line with this, the mandibular arch of studied primates did not present diastemas.

As sheep and cows do not have a maxillary anterior dentition, overbite and overjet scores could not be measured for these animals. Among the omnivores, carnivores and rabbits (herbivores), there was great variation in overjet and overbite measurements within and across sampled specimens. In this study, rabbits, gibbon, macaques, possums, dogs and the leopard displayed a range of overbite scores indicating a proportion of vertical overlap of the maxillary anterior dentition over the labial aspect of the mandibular anterior dentition. Overbite scores ranged from 0% (edge-to-edge occlusion) to 15%. The average overbite scores was 3.5%, which is relatively low compared to the suggested human occlusion norms of about 20-30% (Pieren & Bowen, 2019). Among carnivores, with exception of the leopard, all specimens had edge-to-edge bites. Few studies have investigated overbite in mammals; further research with a more diverse sample and larger sample sizes will allow for the prevalence and extent of overbite to be elucidated.

Most specimens in this study displayed a range of positive overjet measurements, except for one pig which had negative overjet because of its associated anterior crossbite. In this study, overjet scores ranged from 0mm (edge-to-edge) to 8.67mm. These findings aligned with the human occlusion norms which involve the maxillary anterior dentition occluding anteriorly to the mandibular anterior dentition, generating a positive overjet score. The 'ideal' human occlusion often involves a 2-3mm overjet (Proffit & Fields, 1993). Within our sample, the average overjet score was 3.10mm; slightly higher than in humans.

In this study, some herbivores displayed posterior crossbite. More than half of the sheep specimens had buccal posterior scissor bites, while the others could not be assessed because of unpredictable maximum intercuspation. A high prevalence of posterior crossbite might be normal for sheep, as the masticatory and TMJ functional patterns involves significant lateral movements to allow for occlusal table contacts required to grind their fibrous diet. Herbivores have flattened articular surfaces in the TMJ for increased translational and lateral movements (Bels, 2006). In humans, scissor bite is considered a type of malocclusion, often associated with either a maxillary arch that is larger than the mandibular arch or with a functional shift (Baik et al., 2019; Krishnaswamy et al., 2016). In omnivores and carnivores, posterior crossbites were relatively uncommon, similar to humans.

This study also assessed the occurrence of pathologies and dental abnormalities in the specimens studied. Caries was relatively uncommon (3.3% of teeth studied) compared to humans; this is related with the high consumption of processed and carbohydrate-rich foods in modern human populations (Davies, 2013). In this study, five omnivores and one carnivore specimen had carious lesions, which were absent in herbivores. Enamel hypoplasia/defects were uncommon in our sample (0.6% of teeth studied); identified in one boar and one dog specimen as enamel pitting and horizontal grooves along the crown. The clinical presentation of these enamel defects can be related to physiological stresses during enamel development. In humans, enamel pitting and grooves have been linked to early childhood disease, physiological stress and nutritional deficiencies (El-Najjar et al., 1978).

Few *antemortem* tooth losses were identified, involving three herbivores (sheep), two omnivores (possum and bear) and one carnivore (dog). Three out of five dogs had supernumerary teeth (five premolars instead of four); the high prevalence could suggest of supernumerary teeth are common in dogs. Shape anomalies were observed in two sheep which displayed "peg" shaped mandibular canines. These were shape anomalies rather than retained deciduous teeth as they differed from sheep deciduous mandibular canines described in the literature (Geiger et al., 2020).

All specimens displayed tooth wear, commonly seen as generalised occlusal wear facets in both posterior and anterior teeth with varying degrees of dentine

exposure. In humans, tooth wear can be physiological (natural wear of teeth and loss of occlusal vertical dimension due to aging) (Bartlett & Dugmore, 2008; Kaidonis, 2008) or pathological (due to bruxism, severe erosive wear or abrasion from aggressive tooth brushing techniques) (Bartlett & Dugmore, 2008; Kaidonis, 2008). Many animals are known to perform thegosis, the sharpening of anterior teeth through attrition to antagonise an enemy (Murray & Sanson, 1998). This may be a contributor to some of the tooth wear observed here, along with increased abrasion due to tougher diets compared to the soft processed diets consumed by humans. In this study, posterior teeth were fractured most commonly, possibly due to higher occlusal forces experienced by molars and premolars compared to anterior teeth (Banerji et al., 2010). Tooth fractures can be a result of high masticatory loading forces or due to antagonistic/fighting displays (Van Valkenburgh, 1988).

Periodontal disease, inferred through the presence of calculus deposits, bone loss, furcation and increased vascular foramina, was common in all groups studied. Periodontal disease is prevalent in 20-50% of the human population (Nazir, 2017). Due to the small sample size in this study, we cannot infer if the apparent high prevalence of periodontal disease reflects the disease prevalence within each species. Unlike humans who typically brush their teeth, other mammals might not have active ways to disrupt dental biofilm formation, increasing the chance of calculus formation and inflammatory processes that lead to periodontal disease.

TMJ pathology was relatively frequent in the sample studied, presenting in half of the skulls analysed and almost half the skulls within each dietary group. TMJ pathologies are not common in humans and are often associated with conditions such as osteoarthritis or degeneration of the TMJ (Tanaka et al., 2008; Wang et al., 2015). Future studies analysing condylar movements of the TMJ during function within each species may offer insight as to why TMJ pathologies (bony pits, roughness, porosities, defects and vascular foramina) were common in the mammals studied here.

In this study, only six skulls (four primates, one possum and one sheep) displayed signs of bony fenestrations at the apex or along the roots on the buccal bony plate. In humans, bony fenestrations are associated with infections (e.g. periapical pathologies or periodontal infections), or less commonly due to traumatic occlusions, abnormal contours of root apices or as a result of orthodontic tooth movement (Implantologists, 2019). The bony fenestrations in the specimens studied here may be due to localised infections, or in cases of generalised fenestrations, due to excessive masticatory, occlusal or parafunctional forces that have displaced the posterior teeth buccally.

There are some limitations in this study. A small sample size meant that we could not draw conclusions about occlusal norms for each species nor could we accurately evaluate the prevalence of dental pathologies/abnormalities within each species. While the small sample size available limits statistical analysis, in this pilot investigation the dentition of each animal was



thoroughly investigated both in terms of occlusion characteristics and pathologies/abnormalities. The results of the current study are thus indicative and should be interpreted with caution. Another limitation is the lack of soft tissues, which would have more reliably accounted for how dental arches articulate and how the mandibular condyles sits in the glenoid fossa. To mitigate this, we used the occlusal wear facets to guide skulls into maximum intercuspation (MIC) so a repeatable and reliable occlusion could be achieved despite the lack of soft tissues. In order to eliminate inter-observer bias, we ensured that only one calibrated researcher carried out all the measurements/assessments undertaken here.

Future studies with a comparative assessment of mammal occlusion in a larger sample would provide more information on species-specific norms of occlusion and the prevalence of malocclusion, including a comparison of occlusal characteristics between domestic and wild animals. Future species-specific studies could investigate these patterns in a large number of specimens to complement the approach undertaken in this pilot study (*i.e.* fewer specimens of several species with herbivore, omnivore and carnivore diets). Domestic animals are often exposed to pre-processed softer diets compared to their wild counterparts, which might influence the prevalence of malocclusions (Kaifu et al., 2003). Since occlusion is a heritable trait (Ackerman, 2011; Hoyer & Rawlinson, 2019), such results could contribute towards more extensive occlusion evaluation in breeding programs, improving outcomes for the animals. Future studies may also consider examining fresh deceased specimens so soft tissues can also be examined, including assessing condylar TMJ movements during function. This descriptive pilot study may stimulate further

research on occlusion in mammals and how this relates to the “ideal” occlusion in humans, advancing our understanding of the evolution and adaptation of mammalian occlusion.

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Authors contributions

AT: conception or design of the work, data collection, data analysis and interpretation, drafting the article, critical revision of the article, and final approval of the version to be published.

NC: conception or design of the work, data collection, data analysis and interpretation, drafting the article, critical revision of the article, and final approval of the version to be published.

LM: conception or design of the work, critical revision of the article, and final approval of the version to be published.

CL: conception or design of the work, data analysis and interpretation, critical revision of the article, and final approval of the version to be published.

Conflicts of interest

None reported.

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