

ORIGINAL ARTICLE

Reading the carnivoran skeletal story: An acetabular viewpoint, with suggested implications across geological time

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Abstract

We compared acetabular traits among canid and non-canid museum specimens, using the same pre-established protocols. We hypothesized conserved, intersecting development-growth and insult-response biology, reflecting morphologically and being highly similar across carnivoran taxa. We evaluated acetabular traits from dry bone museum specimens of *Vulpes lagopus*, *Vulpes vulpes*, *Nyctereutes procyonoides*, *Urocyon cinereoargenteus*, *Canis lupus familiaris* and *Canis latrans*. The same was done from *Procyon lotor* (Procyonidae), *Taxidea taxus* (Mustelidae) and *Lynx rufus* (Felidae). We assessed intra-articular structures as: (a) acetabular fossa; (b) medial articular margin; (c) lateral articular margin; and (d) articular surface. Each scoring category included multiple subcategories. The primary observed traits across taxa included variably shaped mineralized foci, bony rimming of articular margins and rough-surfaced or worn articular bone. These traits occurred in a very similar fashion across taxa. We then evaluated only the most frequently occurring 80% of the data within the scoring category, observing only minor differences among taxa. The consistency of trait expression supports broad conservation and intersection of development and response capacities. The exact phylogenetic nature of the trait relationships requires further evaluation across development and growth; usually undetected early life damage; degrees of parallel responses across multiple diarthrodial joints within taxon; and the extent of morphological similarity across other carnivorans and non-carnivorans.

KEYWORDS

acetabulum, carnivoran, development, growth, phylogeny

1 | INTRODUCTION

Previously, we have reported studies of the canid coxofemoral joint. Those outcomes support the idea of a phylogenetically based morphological and physiological commonality between growth development and early incipient response capacity (Lawler et al., 2020; Lawler,

Tangredi, Owens, et al., 2021; Lawler, Tangredi, Becker, et al., 2021; Mustonen et al., 2017). In our context here, we use the short term ‘response capacity’ to refer to mechanical stress that is sensed by cells in the osteochondral unit (chondrogenic niche; osteogenic niche; synovial niche). The subsequent signalling leads to the expression of remodelling and/or repair physiology that will remain

within the obligate constraints imposed by clade history and homology across geological time (Tangredi & Lawler, 2019).

In clinical terms, altered biomechanical stress results in changes in articular cartilage and the release of pro-inflammatory cytokines. The thought that injury foreshadows inflammation thus is reflected by events that unfold in conditions such as canine coxofemoral osteoarthritis (OA) (Shively & Van Sickle, 1982). Nonetheless, it has been suggested that viewing joint deterioration as a 'very complex multifactorial disease' accepts multiple underlying influences that include injuries, genetics, nutrition, stress, ageing, and interacting biochemistry and biomechanics (De Bari et al., 2010; Felson, 2013; Gopalakrishnan et al., 2018; Musumeci et al., 2015). Felson (2013) pointed out that biomechanics largely govern progression, whether diarthrodial joint degeneration is covert or overt.

A logical question, then, might be whether similar stress responses across distantly related taxa might facilitate improved understanding of interacting population-based etiologies and influences. That is to say, should degenerative joint disorders among mammalian quadrupeds be considered more seriously as population-level problems?

Shively and Van Sickle (1982) studied hip joints of English Pointer pups over ages birth through 9 months. Postmortem evaluations revealed increasing prevalence of abnormal morphology over ages 5–9 months, with initial expression of pathological traits thus firmly documented to occur early in life. Similarly, D'Amico et al. (2011) reported that canine hip joint pathology (possibly of multifactorial origin) developed over ages 16 and 32 weeks. The latter two examples reveal 'the fact of the matter', although these are ages at which changes to diarthrodial joints are far less likely to be visible radiographically or clinically.

Moving from morphological to genomic and phylogenetic perspectives, Gopalakrishnan et al. (2018) described gene flow across *Canis*, illustrating the extensive nature of genetic interchange among canids over long geological time. If joint-relevant gene groups (networks) evolved to function as units, it is not surprising that genetic-associated disorders often seem to have their origins based in dysfunction that can be visible at population levels.

The present study was prompted by the foregoing population-related thoughts, framed as whether evaluation of non-canid carnivorans would yield outcomes that are similar to those that can be noted among canids. Neese et al. (2012) noted that 'Biological traits need both proximate and evolutionary explanations'. The idea refers to a 'near at hand' mechanistic understanding of a trait and its more distant evolutionary source. Ultimately, at younger

ages among carnivorans, a distillation of the point made by Neese et al. (2012) could be stated as: 'Do morphological traits of dry bone facilitate distinguishing what is pathology from what is unassociated or intercurrent growth-associated remodelling, in populations of younger mammals?'

2 | MATERIALS AND METHODS

2.1 | Taxa

In the first study phase, we evaluated museum dry bone specimens from (a) subfamily Caninae (tribe canini; $n=24$): Ancient and modern domestic dog (*Canis lupus familiaris*; $n=15$); ancient and modern coyote (*Canis latrans*; $n=9$); and (b) subfamily Caninae (tribe vulpini; $n=64$): Modern red fox (*Vulpes vulpes*; $n=30$); modern arctic fox (*Vulpes lagopus*; $n=9$); modern raccoon dog (*Nyctereutes procyonoides*; $n=16$); ancient and modern grey fox (*Urocyon cinereoargenteus*; $n=9$).

Urocyon is basilar among vulpini. Among extant canids, the grey fox's natural history is unique for its deeper history in geological time (Goddard et al., 2015). While not all of the dating and time-based progression of *Urocyon* from its origin are agreed upon universally, for this report, we analysed *U. cinereoargenteus* with the vulpini.

The specimens used for the first phase are curated at the Illinois State Museum Research and Collections Center, Springfield, IL (ISM); Illinois State Archaeological Survey, Champaign, IL (ISAS); East Tennessee State University Museum of Natural History, Johnson City, TN (ETMNH); Michael Etnier collection, Western Washington University, Bellingham, WA (MEWWU); University of Washington Burke Museum, Seattle, WA (UWBM); University of Wisconsin Zoology Museum, Madison, WI (UWZM).

In the second study phase, we evaluated museum dry bone specimens from three non-canid carnivoran taxa: raccoon (*Procyon lotor*; Procyonidae; $n=33$); badger (*Taxidea taxus*; Mustelidae; $n=10$); bobcat (*Lynx rufus*; Felidae; $n=20$). The specimens are curated at the Illinois State Museum Research and Collections Center (ISM), Springfield, IL (33 raccoons; 10 badgers; 4 bobcats) and at the University of Wisconsin Zoology Museum, Madison, WI (UWZM) (16 bobcats).

Additionally, we re-evaluated the data after we excluded the lowest 20% presence scores in each category and subcategory across canids and non-canids to assess whether the overall high frequencies of scores might be masking traits that have greater importance in a taxonomic sense.

For both studies, available specimens included one or both acetabula per individual. The specimens were

chosen based on numbers and availability, with a goal of including three non-canid taxa, each belonging to a different mammalian carnivoran family.

2.2 | Procedures

Specimen selection from a large database (DFL) was guided by the ability to describe and score features from digital photographs (Canon SX720 HS, Canon Inc., Melville NY 11747). Intra-acetabular structures of interest included the fossa, medial and lateral articular margins and articular surfaces.

The observations were recorded by intra-articular location, gross anatomy and spatial relationships (Tables 1–4). Each trait was scored as present (+); not present (–); or not available for evaluation (x). In some instances, magnification and/or backlighting supported evaluation and photographic documentation.

Sex and chronological age were not analysed, since there were no applicable records for numerous specimens. Additionally, age at death and status of trait progression are mutually confounding in the absence of historical data such as systemic anatomical and physiological evaluations, being thus far less interpretable. The subjects all were dry bone museum specimens. No animals were euthanized for these studies. Since we worked with cleared bone from museum skeletal remains, we did not require imaging beyond photography.

2.3 | Evaluation and data analyses

The database was heterogeneous with respect to: Numbers within taxa; approximate geological age; recent and ancient specimens; and single or bilateral available acetabula. The canid database included juvenile and adult specimens that were not segregated, having been so evaluated previously (Lawler et al., 2020; Lawler, Tangredi, Owens, et al., 2021; Lawler, Tangredi, Becker, et al., 2021). The non-canid database also included non-segregated juveniles and adults.

Overall statistical comparison of trait occurrence was limited by the descriptive nature of the database. The occurrence of each of the listed traits was analysed (Fisher's exact test, Preacher & Briggs, 2001) as a percentage of the total number of scoring categories and subcategories within each taxon (Tables 1–4; Tables S1 and S2).

As an illustrative example: The acetabular fossa of the domestic dog revealed 29 possible traits, summarily, over subcategories A–D (Table 1; Table S1). Dog specimens

TABLE 1 Scoring for acetabular fossa.

Left or right

- (A) Ligament attachment
 - (a) Boney surface only
 - (b) Remnant enthesophytes round ligament attachment
 - (c) Full fossa surface osteophytes, uniform
- (B) Accessory ligament groove
 - (a) Osteophytes present
 - (b) Osteophytes absent
- (C) Non-ligament fossa surface
 - (a) Boney surface only
 - (b) Light osteophyte cover
 - (i) Cranial
 - (ii) Dorsal
 - (iii) Caudal
 - (iv) Ventral
 - (v) Central
 - (c) Heavy osteophyte cover
 - (i) Cranial
 - (ii) Dorsal
 - (iii) Caudal
 - (iv) Ventral
 - (v) Central
- (D) Fossa shape
 - (a) Unremarkable
 - (b) Wide
 - (i) Full
 - (ii) Dorsal
 - (iii) Central
 - (iv) Ventral
 - (c) Narrow
 - (i) Full
 - (ii) Dorsal
 - (iii) Central
 - (iv) Ventral
 - (d) Skewed
 - (i) Cranial
 - (ii) Craniodorsal
 - (iii) Caudal
 - (iv) Caudodorsal

revealed features of interest in 15 of 29 categories overall (52%).

For subcategory A – trait(s) were observed in 2 of 3 possibilities (yielding a score of 67%).

For subcategory B – trait(s) were observed in 1 of 2 possibilities (yielding a score of 50%).

TABLE 2 Scoring for medial articular margin.

Left or right
(A) Extent of margin
(a) No pathology
(b) Full margin
(c) Intermittent focused pathology at:
(i) Cranial
(ii) Craniodorsal
(iii) Dorsal
(iv) Caudodorsal
(v) Caudal
(B) Character of margin
(a) Smooth
(b) Rough; irregular; variable
(c) Minimal
(d) Wide
(e) Impinging
(i) Cranial
(ii) Craniodorsal
(iii) Dorsal
(iv) Caudodorsal
(v) Caudal
(vi) Ventral
(f) Obliterated
(g) Porous

For subcategory C – trait(s) were observed in 8 of 11 possibilities (yielding a score of 73%).

For subcategory D – trait(s) were observed in 4 of 13 possibilities (yielding a score of 31%).

This pattern of evaluation was used for all four scoring protocols (Tables 1–4) over all taxa. Within these mathematical constraints, we considered how each taxon displayed the ranges of trait expression.

Finally, the data were evaluated for significant right vs. left lateralization, also using Fisher's exact test (Preacher & Briggs, 2001). For this evaluation, we included only specimens with both right and left acetabula present. Further analyses to assess relationships between and across taxa were not possible because of sample sizes and the general lack of variability in the database.

3 | RESULTS

Most observations were bilateral. Canid acetabular traits were not significantly right–left asymmetrical (see Lawler, Tangredi, Becker, et al., 2021). The non-canid acetabula were very similar to canids, revealing statistically

TABLE 3 Scoring for articular surface.

Left or right
(A) Surface character
(a) Smooth
(b) Rough
(c) Depression
(d) Wear
(e) Wide
(f) Osteophytes flat
(g) Osteophytes raised
(h) Bone loss
(i) Linear
(j) Porous
(k) Irregular
(l) Striated
(m) Eburnation
(B) Spatial medial-lateral
(a) Medial
(b) Central
(c) Lateral
(C) Spatial cranial-caudal
(a) Cranial
(b) Craniodorsal
(c) Dorsal
(d) Caudodorsal
(e) Caudal
(f) Ventral
(D) Distribution
(a) Focal
(b) Multifocal
(c) Focally disseminated
(d) Coalescing
(e) Disseminated

significant right–left asymmetry only at the *P. lotor* lateral articular margin (Table 5; Table S3).

The patterns of scored traits among canid and non-canid taxa are presented initially as an overall graphical summary (Figure 1). Across taxa, estimates of trait presence among the four major morphological categories generally approximate 50%–100% of the possible outcomes (Tables 1–4; Figures 1–5).

The outcomes within each of the four morphological groupings (fossa, medial articular margin, articular surface and lateral articular margin) reveal details (Figures 2–5). One caveat was that the scored traits across taxa, when accompanied by more extensive proliferative bony changes, can cause visual obstruction of one or more

TABLE 4 Scoring for lateral articular margin.

Left or right
(A) Extent of margin
(a) Full margin
(b) Intermittent focused pathology toward cranial-dorsal
(c) Intermittent focused pathology toward caudal-dorsal
(d) Variable margin
(B) Character of margin
(a) Smooth
(b) Rough; irregular; variable
(c) Minimal
(d) Wide, thick
(e) Impinging-obliteration:
(i) Cranial
(ii) Craniodorsal
(iii) Dorsal
(iv) Caudodorsal
(v) Caudal
(vi) Ventral
(f) Rim
(g) Sharp
(C) Periarticular osteophytes
(a) None
(b) Osteophytes present
(i) Cranial
(ii) Dorsal
(iii) Caudal
(iv) Ventral

of the other features. The latter can result in some ‘not present’ outcomes for obscured structures.

Among canids, subcategory trait scores for acetabular fossae indicated uniformly high presence for the individual traits ‘accessory fossa osteophytes’ (the ‘osteophytes’ term perhaps could be used advisedly here, absent direct histological confirmation, although the exact intraarticular locus does aid assessment) and ‘non-ligamentous fossa bone’ (not involving the site of *ligamentum teres* attachment) (Table 1; Figure 2). The domestic dog yielded lower trait scores for each of the foregoing traits, likely reflecting obstructed views. Among non-canid trait subcategories, scores for the acetabular fossa were varied (Table 1; Figure 2) but were uniformly high for ‘non-ligamentous fossa bone’. Trait scores for the raccoon generally were quite high.

Among canids, subcategory trait scores for the medial articular margin indicated uniformly high presence for the trait ‘extent’ and high but varied outcomes for the trait ‘character’ In particular, trait scores among canids

TABLE 5 Prevalence of bilateral acetabular traits across canid and non-canid taxa, tested by Fisher's exact test.

	Acetabular fossa			
	A	H	R ± L	P
Canid				
<i>U. cinereoargenteus</i>	0	0	14	1
<i>V. vulpes</i>	0	0	33	1
<i>V. lagopus</i>	0	0	8	1
<i>N. procyonoides</i>	0	0	16	1
<i>C. latrans</i>	0	0	29	1
<i>C. lupus familiaris</i> (modern)	0	0	15	1
<i>C. lupus familiaris</i> (prehistoric)	0	0	8	1
Non-canid				
<i>P. lotor</i>	0	0	28	1
<i>T. taxus</i>	0	0	9	1
<i>L. rufus</i>	0	0	18	1
	Medial margin			
	A	H	R ± L	P
Canid				
<i>U. cinereoargenteus</i>	1	1	12	0.14
<i>V. vulpes</i>	0	0	33	1
<i>V. lagopus</i>	0	0	8	1
<i>N. procyonoides</i>	0	0	16	1
<i>C. latrans</i>	0	0	31	1
<i>C. lupus familiaris</i> (modern)	0	0	15	1
<i>C. lupus familiaris</i> (prehistoric)	0	0	8	1
Non-canid				
<i>P. lotor</i>	0	0	28	1
<i>T. taxus</i>	0	0	9	1
<i>L. rufus</i>	0	0	18	1
	Articular surface			
	A	H	R ± L	P
Canid				
<i>V. vulpes</i>	0	0	33	1
<i>U. cinereoargenteus</i>	0	2	12	1
<i>V. lagopus</i>	0	0	8	1
<i>N. procyonoides</i>	0	0	16	1
<i>C. latrans</i>	4	5	17	0.02
<i>C. lupus familiaris</i> (modern)	0	0	13	1
<i>C. lupus familiaris</i> (prehistoric)	0	1	7	1
Non-canid				
<i>P. lotor</i>	0	0	28	1
<i>T. taxus</i>	0	0	9	1
<i>L. rufus</i>	0	0	18	1

(Continues)

TABLE 5 (Continued)

	Lateral margin			
	A	H	R ± L	P
Canid				
<i>U. cinereoargenteus</i>	1	2	11	0.21
<i>V. vulpes</i>	3	7	23	0.08
<i>V. lagopus</i>	0	4	4	1
<i>N. procyonoides</i>	0	0	16	1
<i>C. latrans</i>	6	9	14	0.09
<i>C. lupus familiaris</i> (modern)	0	0	15	1
<i>C. lupus familiaris</i> (prehistoric)	0	1	9	1
Non-canid				
<i>P. lotor</i>	7	4	17	<0.001
<i>T. taxus</i>	1	1	7	0.22
<i>L. rufus</i>	3	3	12	0.04

generally exceeded 75% presence (Table 2; Figure 3). Among non-canids, scores for both traits 'extent' and 'character' consistently were high but somewhat more variable than those of canids.

Among canids, subcategory trait scores for the acetabular articular surface varied across taxa for the trait 'surface' but did uniformly exceed 50% presence. Scores were less varied for 'cranial-caudal' but were uniformly high for 'medial-lateral' and for 'distribution'. Among non-canids, scores were uniformly high, and only slightly more variable for the 'articular surface' subcategory (Table 3; Figure 4). By contrast, 'articular surface' trait scores were lower for coyote and raccoon dog. Among non-canids, trait scores were uniformly high, and only slightly more variable for 'articular surface'.

Among canids, subcategory trait scores for the lateral articular margin generally were high for the traits 'extent' and 'osteophytes' (stated advisedly, as above), while those for 'character' were lower and more variable (Table 4; Figure 5). Since the raccoon dogs in the database had been farm-maintained and were older at harvesting (mid-life; mid-1980s), their appearance of generally higher trait scores would be expected among the canids, at least where traits of interest were not obscured. Among non-canids, the same trait scores were high in general (Table 4; Figure 5). Thus, the canid and non-canid groups yielded very similar outcomes.

Figures 6–11 present labelled photographs that illustrate some of the more commonly-expected traits, whether associated with development–growth or with response capacity. Spatial locations of described traits are notable for their similarity across taxa.

3.1 | Trait scores ≥20% of taxon data

Additional detail was revealed by examining traits that occurred more frequently within each intra-articular subcategory. Tables S1 and S2 were reviewed. Only traits that occurred at ≥20% presence were retained for Tables S4 and S5. Refer to Figures 6–11 for photographic illustrations.

3.1.1 | Acetabular fossa

Across all taxa, observations were held in common for *L. teres*-related assessments. However, light and heavy 'osteophyte-like' foci distributed differently. There were more 'light osteophyte-like' (used advisedly) precipitates at the caudal aspects of fossae, and more 'heavy osteophyte-like' precipitates at the cranial aspects of fossae, across taxa.

Fossa shape revealed fewer observations across taxa. 'Wide' acetabular fossae tended to occur ventrally among canids, whereas the same observation was not recorded at ≥20% presence among non-canids. Among canids and non-canids, a craniodorsal 'skewing' appearance was notable. Among taxa, the badger *L. teres* appeared to attach to the acetabular fossa at a more ventrocaudal locus.

3.1.2 | Medial articular margin

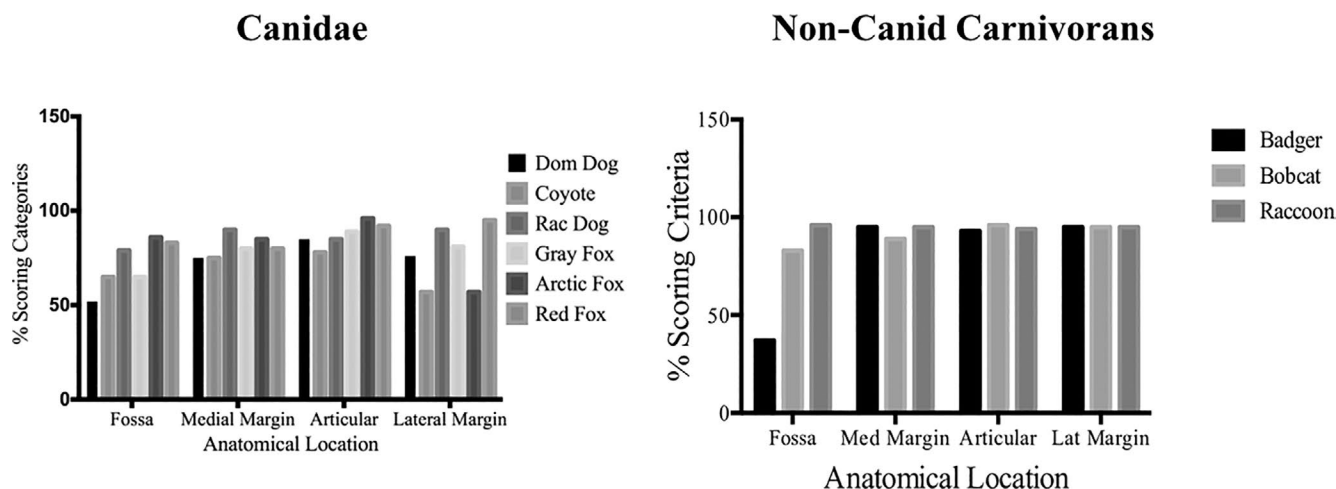
Most prominent across canid taxa was a rough, irregular, or variable articular margin. The arctic fox, coyote and juvenile bobcat revealed a higher presence of craniodorsal and dorsal intermittent articular margin traits.

3.1.3 | Articular surface

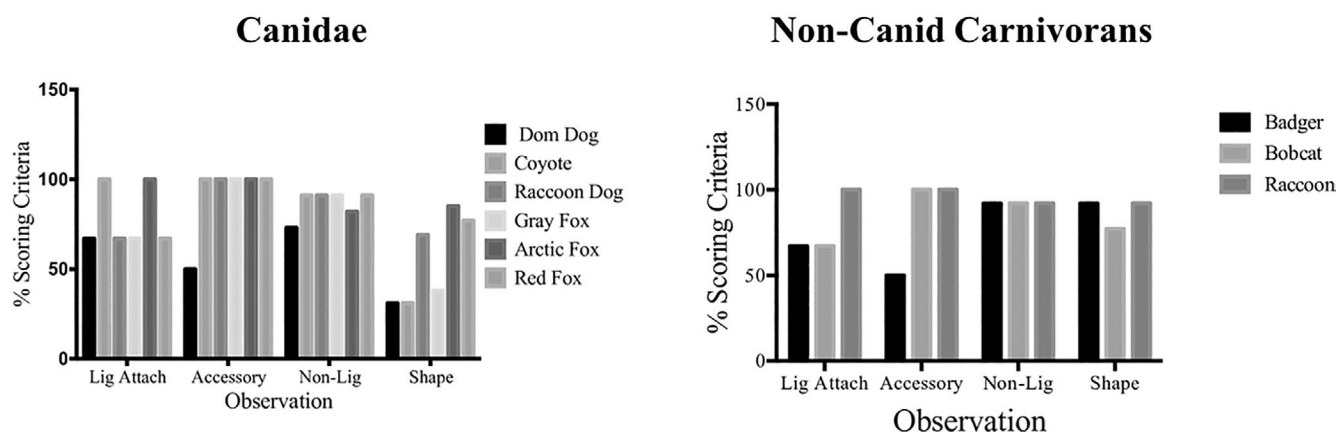
Few of the numerous possible observations for articular surface 'character' occurred at ≥20% presence. Only the arctic fox, grey fox and red fox yielded those greater frequencies. Spatial changes that occurred in a 'medial-to-lateral' pattern were prominent across taxa, while those that occurred in a 'cranial-to-caudal' pattern occurred only among canids at ≥20% presence.

Distribution of trait observations ranged from 'focal' (minimal) to 'disseminated'. All five grades of 'distribution' occurred commonly at ≥20% across taxa. However, among canids, scores of 'multifocal' and 'coalescing' predominated. Among non-canids, 'coalescing' and 'disseminated' scores predominated, while 'focal' and 'multifocal'

Comparison of Coverage: All Locations



Comparison of Coverage: Fossa



scores did not occur at $\geq 20\%$ presence. Thus, the non-canid group appeared to have greater expression of more spatially widespread intra-articular traits.

3.1.4 | Lateral articular margin

Scores involving the lateral articular margin at presence $\geq 20\%$ presence were common across canid and non-canid taxa, for 'extent of margin involvement' and for 'periarticular osteophytes' (used advisedly). For 'character' of features, observations at $\geq 20\%$ presence was dominated by canids.

4 | DISCUSSION

4.1 | Overview

From earlier studies, Mustonen et al. (2017), Lawler et al. (2020), Lawler, Tangredi, Owens, et al. (2021) and Lawler, Tangredi, Becker, et al. (2021) applied the descriptor 'pathology' to many observations. Here, we have termed the observations 'traits' to align with the overarching population thinking in this report.

The observations were substantially similar across taxa and across intra-articular structures, with some taxon-related variation in the proportionality of expression. From

Comparison of Coverage: Medial Margin

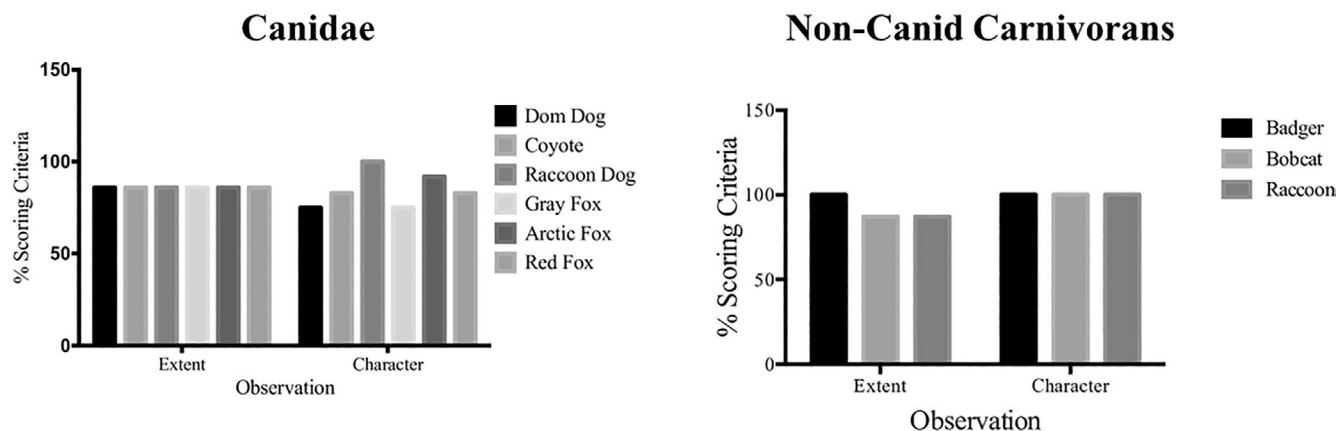


FIGURE 3 Comparison chart showing feature percent scores identified for canids and non-canids: Medial articular margin: extent of features, character of features (See Table 2).

Comparison of Coverage: Articular

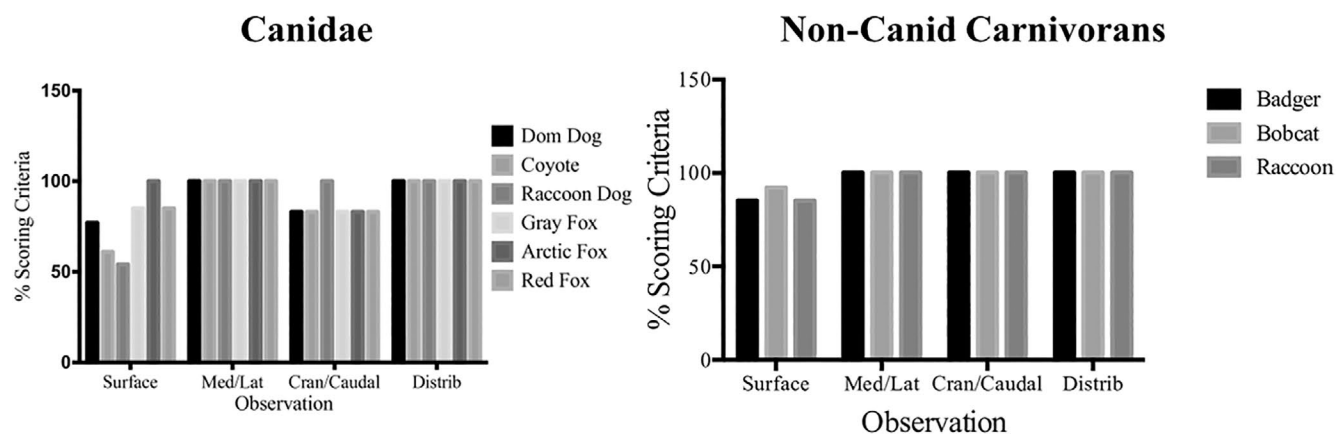


FIGURE 4 Comparison chart showing feature percent scores identified for canids and non-canids: Articular surface: surface character, spatial pattern medial-lateral, spatial pattern cranial-caudal, extent of distribution (See Table 3).

a clinical perspective, such trait responses may or may not be reflected in degrees of physical debilitation. Thus, in various biomedical circumstances, the observer must exercise caution to avoid overstating biological implications, particularly when evaluating museum specimens.

For traits that vary in their expression among taxa, considering natural history and ecology, as well as population genomic effects requires new types of study designs.

4.2 | Trait frequency

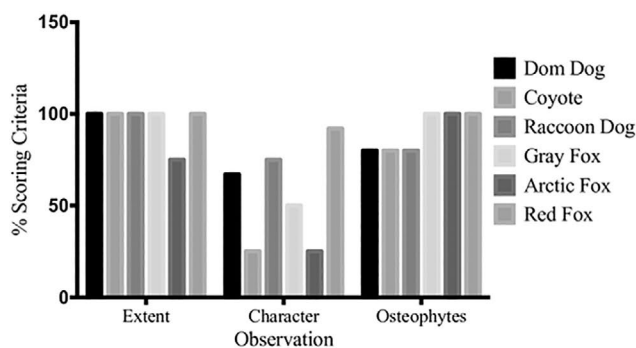
The effect of 'screening out' numerous low-frequency observations likely clarified the data set somewhat. This screening analytical step (retaining traits with $\geq 20\%$

presence) could have removed observations that were related to more incidental natural history effects or to chronological age at death (recalling the confounding with state of abnormal trait progression). However, further studies are required to explore these possibilities. The observed broad taxon-based expression of traits also could reflect genomic and physiological processes that are held in common between development-growth and response capacity across taxa (Lawler et al., 2016; Lawler, Tangredi, Becker, et al., 2021; Lawler, Tangredi, Owens, et al., 2021; Mustonen et al., 2017; Tangredi & Lawler, 2019).

The bilaterally uniform outcomes suggest that the response capacities of the right and left acetabula can adjust equally to movement and strain (Gersch et al., 2005;

Comparison of Coverage: Lateral Margin

Canidae



Non-Canid Carnivorans

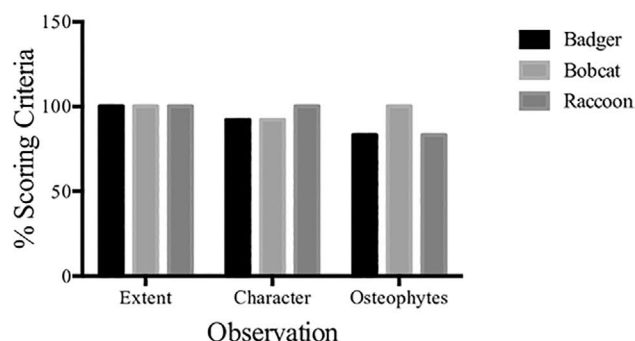


FIGURE 5 Comparison chart showing feature percent scores identified for canids and non-canids: Lateral articular margin: extent of margin, surface character, periarticular osteophytes (See Table 4).



FIGURE 6 Raccoon, adult. Right acetabulum, lateral view. Buried specimen. (a) Long arrow: Heavily mineralized, rough dorsal fossa surface, cranial-to-caudal. Ventral fossa more lightly mineralized. (b) Medium arrow: Lateral articular margin smooth, significantly thickened. (c) Short arrow: Smooth raised feature, linear, flattened, central articular surface, raised from remaining surface.

Pelttari et al., 2015; Song et al., 2020; Stevens et al., 2013), at least at the morphological level of this study.

4.3 | Importance of natural history, ecology, and population-based variability

In light of the foregoing thoughts, it appears that simultaneously considered development, function, and abnormality, done by visual assessment of museum skeletal specimens, usually will require additional context. Carrano (1999) and Martín-Serra et al. (2015) described cursorial (running down prey) versus non-cursorial (pounce and grappling prey with the forelegs) locomotor hunting habits. While such categorizations are useful conceptually, we suggest that they are better thought of as representing poles of a continuum among taxa. The latter idea would be more consistent with the data set from our observations.

Finarelli and Goswami (2013) noted that evolutionary influences on specific traits may or may not reflect the deeper-time history of a given clade. That is, prior to their own disappearance, now-extinct subclades may have accumulated trait admixtures that influenced subsequent genomic makeup. Such evolutionary trends may be invisible, absent of data from successive (lost) intervening taxa (Finarelli & Goswami, 2013).

Despite the complexity of many natural history and ecological studies, and the complexity associated with epigenomic and genomic interactions with the foregoing, there remains a bedrock of deeply conserved gene networks that govern skeletal development and response capacity.

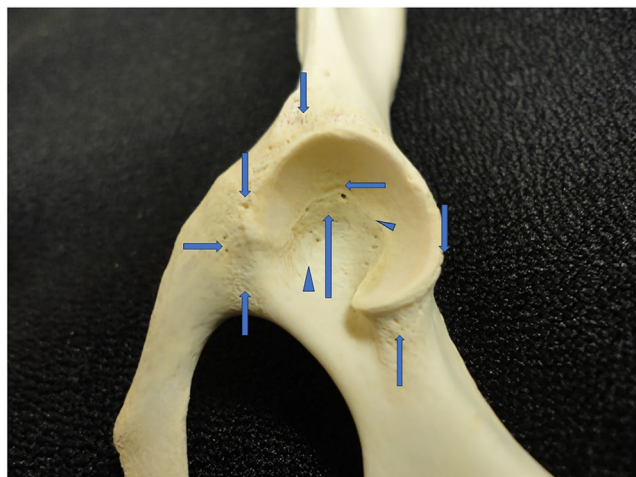


FIGURE 7 Raccoon, juvenile. Left acetabulum, lateral view. (a) Long arrow: Heavily mineralized dorsal fossa surface, relatively smooth cranial-to-caudal. Arrowhead in fossa: Ventral fossa more lightly mineralized. (b) Medium arrows (7): Loci of remodelling-growth. (c) Small arrowhead along dorsal track of medial articular margin: The margin is visible over its cranioventral-to-caudoventral course; it is not thickened, excessively irregular, or rough-surfaced.

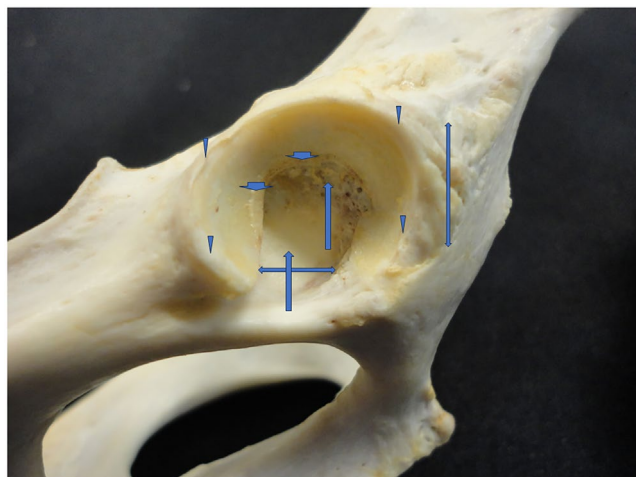


FIGURE 8 Bobcat, adult. Right acetabulum, lateral view. (a) Vertical double-head arrow: Broad locus of bone proliferation. (b) Horizontal double-head arrow: Curvature of cranioventral medial articular margin and surface narrows the ventral fossa aspect. (c) Longer arrows (2): Heavily mineralized dorsal fossa surface. Ventral fossa more lightly mineralized. (d) Arrowheads (4): Thickened, irregular lateral articular margin. (e) Flat arrowheads (2): Broad, flattened medial articular margin, impinging on the medial articular surface.

Gene flow is the movement of genes among genetically distinguishable populations, resulting in viable offspring (Mallet, 2014; Petit & Excoffier, 2009). However, gene flow can also lead to allele incompatibility and non-viable offspring, or a surviving F_1 generation can be sterile (Darwin, 1876; Mallet, 2014). Intraspecific gene flow helps

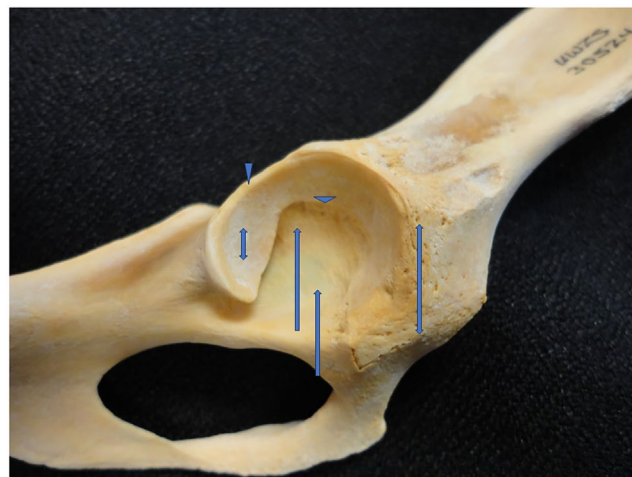


FIGURE 9 Bobcat, juvenile. Right acetabulum, lateral view. (a) Vertical double-head arrow: Broad dorsoventral locus of bone remodelling-growth. (b) Longer arrows (2): Moderately mineralized dorsal fossa surface. Ventral fossa more lightly mineralized. (c) Short double-head arrow: Locus of dried adhered fat, following post-mortem exuding from bone. (d) Arrowhead at lateral articular margin: Minimally thickened margin. (e) Flat arrowhead: Indistinct dorsal (and cranial) medial articular margin, as remodelling-growth proceeds.

to define a species and promote its cohesion, whereas interspecific gene flow can result in the genetic invasion of a species' genome (introgression) and affect species integrity (Petit & Excoffier, 2009). Essentially, variable outcomes are to be expected from gene flow processes.

High gene flow and successful hybridizing necessarily imply: Compatible reproductive biology; biogeography (often a larger range); compatible reproductive timing; ancestral admixtures; larger effective population size; long-distance movement; and minimal population structure (Carmichael et al., 2007; Gopalakrishnan et al., 2018). It is instructive to note that the 'original' blueprint for the observed phenotypes among extant mammalian carnivoran taxa has extended over long geological time.

There are complex interactions among plasticity, selection and gene flow. High gene flow may tend to maximize fitness at an 'average' environmental condition. Also, high genomic plasticity can promote gene flow (Crispo, 2008). Thus, hybridization has the potential to enrich variation, increase adaptive phenotype production and stimulate evolution (Anderson & Stebbins Jr., 1954). Under certain conditions, a 'hybrid swarm' also can result in the adaptive radiation of new species (Fontdevila, 2019; Seehausen, 2013). Influential conditions include physical barriers (topography); historical factors (previous colonization, range expansion, glacial isolation); and/or ecological factors (climate, habitat type, prey selection) (Pilot et al., 2006).

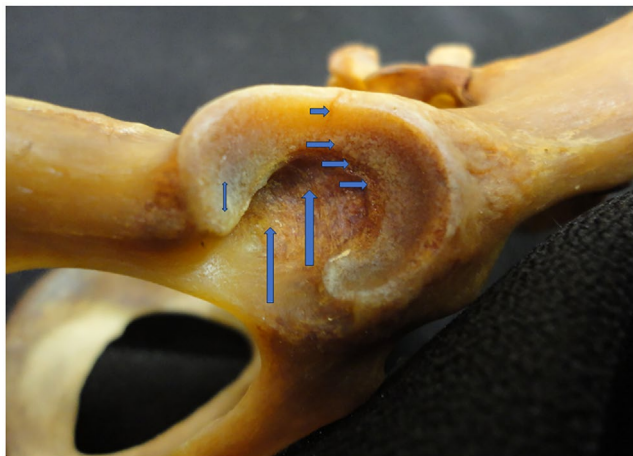


FIGURE 10 Badger, adult. Right acetabulum, lateral view. (a) Long arrows (2): Heavily mineralized dorsal fossa surface, relatively smooth cranial-to-caudal. Ventral fossa only slightly less mineralized. (b) Short double-head arrow: Locus of dried adhered fat, following post-mortem exuding from bone. (c) Small horizontal arrow, dorsal, near lateral articular margin: Post-mortem crack. (d) Staggered horizontal arrows (3) near dorsomedial articular margin: (A) top arrow indicates raised boney proliferation, part of a generally linear pattern on the dorsomedial articular surface. (B) Middle arrow indicates bone erosion of medial articular surface in a roughly curvilinear pattern from mid-dorsal to cranioventral. (C) Ventral arrow indicates irregular, rough, thickening of the medial articular margin.

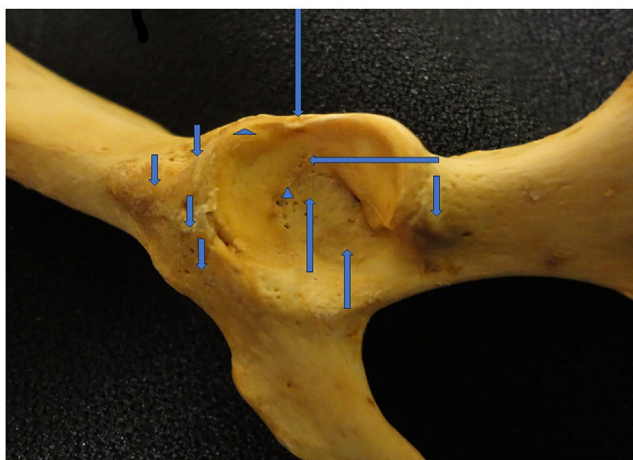


FIGURE 11 Badger, juvenile. Left acetabulum, lateral view. (a) Long horizontal arrow: Incomplete mineralizing of normal remodelling-growth pattern. (b) Long vertical arrow: Remodelling-growth of dorsolateral articular margin. (c) Medium arrows (2) in fossa: Moderately mineralized dorsal fossa surface. Ventral fossa more lightly mineralized. (d) Shorter arrows point ventrally (5): Loci of remodelling-growth. (e) Flat arrow at craniodorsal lateral articular margin: Prominence as remodelling-growth proceeds. (f) Triangle at craniodorsal medial articular margin: Indistinct medial articular margin, cranioventral to mid-dorsal, as remodelling-growth proceeds.

4.4 | Potential directions for further studies

Gene networks are defined by Romano et al. (2015) as ‘multiple genes that have evolved to work together through evolutionary time.’ The relationships among the component genes include (Romano et al., 2015): (1) Proteins encoded by genes that interact directly (high connectivity); (2) Proteins that perform similar functions in metabolic pathways; (3) Proteins that target specific cell types or tissues. In this genetic context, studies that are focused on individual genes seem less likely to yield expanding knowledge about these integrated functions (Romano et al., 2015).

Stevens et al. (2013) stated that gene clusters associated with human developmental pathways are conserved, although the evolutionary relationships within a complex network remain a neglected area of research (Romano et al., 2015). Nonetheless, there are some promising research areas that appear to have application for further studies of the population-based traits that we have evaluated. For example, one prominent study area could include the Homeobox (*Hox*) regulatory gene family that is among the best-studied of highly conserved gene networks (Pelttari et al., 2015). It consists of 39 genes, controlling many aspects of development that include regulating the formation of body organs and tissues, especially limb morphology (Fang et al., 2023). There are four identified clusters of *Hox* genes among Mammalia (Garcia-Fernandez, 2005), located on different chromosomes (Lappin et al., 2006). They are expressed in sequence during skeletal development (Garcia-Fernandez, 2005).

The *Hox* network remains functional in the adult by directing the differentiation of mesenchymal stem cells into osteoblasts (Rux & Wellik, 2017; Song et al., 2020), and by *Hox* reactivation to support post-fracture bone callus formation (Gersch et al., 2005). Gersch et al. (2005) observed that ‘bone regeneration recapitulates skeletal development’. In the adult, *Hox* genes maintain regional specificity (Rux & Wellik, 2017). Pelttari et al. (2015) suggested a role of *Hox* genes in the early development of osteoarthritis. Recently, Butterfield et al. (2021) reported 14 genes that are involved with severe joint osteoarthritis in mutant mice, including the *Hox* transcription factor gene *Pitx1*, in heterozygous *Pitx1*^{+/-} mice.

Not surprisingly, therefore, strong conservation of *Hox* genes is evident (Pelttari et al., 2015) among Carnivora (Fang et al., 2023). In fact, unclustered *Hox* genes occur in the genomes of plants and fungi, and in unicellular animals, thus revealing the stunningly ancient nature of the *Hox* gene family (Lappin et al., 2006).

Lastly, groups of genes that influence mammalian osteoarthritis have an epigenomic regulatory component

(Simon & Jeffries, 2017). Target genes that have been identified include a SOX9 promoter gene that is involved in chondrogenesis. Both DNA methylation and histone modification are reported (Simon & Jeffries, 2017). Thus, while interactions at the genomic level add a great deal of complexity to studies of joint traits in pathobiology, this 'gene family' idea for new studies of animal joint disorders appears to hold great potential to advance knowledge.

5 | CONCLUSIONS

Among the taxa that were evaluated, the carnivorous 'life-style' is rigorous, with the clear exception of the domestic dog. Nonetheless, the dog yielded observations that were very similar to the nondomestic taxa that we evaluated, even well outside of Canidae. Considering the varied natural histories and phylogenetic distances, it is noteworthy that: (a) coxofemoral joint trait parallelism occurred at the same intra-articular acetabular loci; (b) the trait observations occurred in juveniles and adults; (c) the trait observations occurred across taxa with only minor proportional differences in trait expression. Based on our assessment of the database, we suggest that across-taxa similarity over geological time could lead to new population-based research. In particular, an interesting topic for further consideration is the possibility that osteoarthritis should be regarded as a population-based problem.

One critically important practical implication is that any intrinsic or extrinsic joint insult(s) that may occur subsequent to growth–development and expression of response capacity unavoidably will superimpose on prior trait-associated changes (Lawler, Tangredi, Becker, et al., 2021; Lawler, Tangredi, Owens, et al., 2021). Furthermore, our data suggest that trait-associated physiological processes that are held in common across development–growth and response capacity can overlap and interact to produce a continuum of responses (Tangredi & Lawler, 2019).

At least in part, the foregoing observations also could account for the increasing severity of degenerative joint disease among taxa possessing human-selected traits and their consequences. The same may be true among wild taxa that inherit the strongly conserved genomic biology. Our observations and the circumstances further suggest that new markers for early degenerative joint disease should be sought, quite possibly to include grouped genes and physiological pathways that are reflected in early and usually subclinical events during life.

Again, by way of interpretive caution, we note an earlier study (Kieser & Groeneveld, 1992), wherein the research approach involved mandibular and dental landmarks and measures. That study included and compared domestic dogs (*C. l. familiaris*); black-backed jackals

(*C. mesomelas*); side-striped jackals (*C. adustus*); and cape foxes (*Vulpes chama*). The authors found that landmark-associated metrics of larger subjects were 'scaled-up versions of smaller canids'. The authors observed also that the morphologies 'appear to have evolved in concert with one another and relatively independently of differences in dimorphism, size, or functional demands'. The point is well-taken, and it underscores the importance of avoiding overgeneralizing of outcomes of individual studies (Lorenzen et al., 2012).

AUTHOR CONTRIBUTIONS

Dennis Lawler: Conceptualization (equal); investigation (equal); methodology (equal); resources (equal). **Basil Tangredi:** Conceptualization (equal); investigation (equal); methodology (equal). **Christopher Widga:** Conceptualization (equal); investigation (equal); methodology (equal); resources (equal). **Michael Etnier:** Data curation (equal); investigation (equal); methodology (equal); resources (equal). **Terrance Martin:** Conceptualization (equal); data curation (equal); investigation (equal); methodology (equal); resources (equal). **Kurt Schulz:** Formal analysis (equal); investigation (equal); methodology (equal); resources (equal); software (equal); validation (equal). **Luci Kohn:** Conceptualization (equal); data curation (equal); formal analysis (equal); investigation (equal); methodology (equal); resources (equal); software (equal); validation (equal).

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