


# A morphological analysis of carnivoran ossicles from Rancho La Brea

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## Abstract

The morphology of the mammalian middle ear—including the size, shape, and stiffness of individual ossicles—controls their vibrational response to sound and, is closely related to an animal's auditory capabilities. While the relationship between middle ear morphology and hearing frequency has been explored in living carnivorans, the size and shape of ossicles in fossil carnivorans have been sparsely documented. In this study, we present the first morphological data on four iconic carnivoran taxa from the Rancho La Brea Tar Pits: *Smilodon fatalis*, *Panthera atrox*, *Canis dirus*, and *Arctodus simus*. These data are contextualized with samples of extant felids, canids, and ursids to determine the extent to which the ossicles of these iconic fossil taxa resemble their living relatives. Six, five, and seven linear measurements were taken from the malleus, incus, and stapes, respectively. Comparisons of geometric means reveal that the ossicles of fossil canids and felids are similar in size to living analogs, but those of *A. simus* are significantly larger than those of any living ursid. Further, principal components analyses demonstrate close morphological affinities between fossil and extant taxa within canids and felids, and again, a greater disparity between fossil and extant ursids. Canids and ursids occupy distinct regions of the morphospace, yet both overlap the morphological range spanned by felids. While some elements—for example, the stapes—require further specimens to facilitate more nuanced interpretations of variation, our findings underscore the need for concerted efforts towards identifying and preserving these bones within fossil assemblages.

## KEYWORDS

acoustics, *Arctodus simus*, fossil, *Panthera*, *Smilodon fatalis*

## 1 | INTRODUCTION

The mammalian middle ear, which includes three articulated bones (i.e., the malleus, incus, and stapes, collectively known as the auditory ossicles), is a highly specialized system adapted to transmit sounds across a broad range of frequencies (Allin, 1975; Hopson, 1966; Manley, 2010; Mason, 2013; Nummela, 1995). Several aspects of ossicular morphology impact sound transmission, including the size, shape, and stiffness of individual bony components (Malkemper et al., 2020; Mason, 2013, 2016; Nummela, 1995). Together, these factors control the vibrational response that transmits sounds from the tympanic membrane to the oval window and inner ear. The morphology (and thus the auditory performance) of the ossicles is intimately connected to body mass: as ossicular volume scales closely with body size (Nummela, 1995) and smaller ossicles are easier to excite with high frequency vibrations, smaller animals are generally strong at detecting high frequency sounds (Heffner, 1983; Heffner et al., 2001, 2006; Hemila et al., 1995; Huang et al., 2000; Nummela, 1995). By contrast, the middle ear of larger-bodied animals are typically characterized by an increase in ossicular (and middle ear cavity) volume, and by reduced rigidity between the malleus and the skull, both of which better suit low frequency sound transmission (Fleischer, 1978; Mason, 2013, 2016). The impact of body size on the hearing abilities of Carnivorans was most comprehensively analyzed by Huang et al. (2000), who experimentally tested acoustic admittance in vivo across 11 felid species ranging in size from 3 to 180 kg. Sensitivity to low frequency sounds increased with body size, suggesting that the window of auditory sensitivity shifts towards lower frequencies in larger-bodied animals. One major outlier to this trend, however, was the sand cat (*Felis margarita*, i.e., a taxon that was highly sensitive to low frequency sounds despite their diminutive size; Huang et al., 2000).

Despite a relatively strong understanding of the relationship between ossicular morphology and the bounds of hearing frequency, the size and shape of ossicles in fossil Carnivorans have been poorly documented. This is likely because of a multitude of factors, including the small size of the ossicular chain itself, making its constituent elements both prone to taphonomic destruction and difficult to detect paleontologically. However, the exceptional conditions of preservation at the Rancho La Brea (RLB) Tar Pits (Los Angeles, California) present a unique opportunity to study the ossicles of extinct carnivoran taxa identified with certainty to not only the taxonomic level, but to the specific individual crania from which they are removed. Several recent studies have highlighted the potential of these deposits to preserve other small, understudied skeletal elements, including clavicles (Hartstone-Rose et al., 2012), bacula (Hartstone-Rose et al., 2015), and hyoid bones (Flores et al., 2020). Within this study, we present the first morphological data on some of RLB's most iconic fossil carnivorans—*Smilodon fatalis*, *Panthera atrox*, *Canis dirus*, and *Arctodus simus*—alongside contextual data on morphological variation in the ossicles of extant felids, canids, and ursids. In so doing, we provide a framework within which to compare the hearing frequencies of these fossil taxa to their extant counterparts.

### 1.1 | The carnivorans of RLB

The tar pits of RLB are famous as a “predator trap” deposit, at which an abundance of carnivorans were attracted to trapped, dying herbivores and ultimately ensnared alongside them (Merriam, 1911; Shaw & Quinn, 1986; Stock & Harris, 1992). Among the most important assemblages of fossil mammal remains, the late Pleistocene specimens—spanning the last few tens of thousands of years of the last ice age—form the standard for the Rancho La Brea Land Mammal Age of North American vertebrate paleontology (Savage, 1951; Savage et al., 1954). In total, more than 3000 individual carnivoran skeletons have been identified, with a particular wealth of larger-bodied taxa. This demographic is ascribed by Carbone et al. (2009) to a carcass domination scenario, in which larger, more social predators would be most capable of defending carcasses of trapped prey from other predators and, by extension, were most likely to become trapped and preserved themselves (Carbone et al., 2009; McHorse et al., 2012).

Represented by more than a thousand specimens, the extinct dire wolf (*C. dirus*), is the most abundant carnivore found at RLB (Christiansen & Harris, 2005; Janczewski et al., 1992). With an estimated body mass of 59 kg, *C. dirus* is interpreted to be ~25% larger (Anyonge & Roman, 2006) than the extant gray wolf (*C. lupus*), which it closely resembles in morphology (Prevosti, 2010) but from which it diverged approximately 5.7 million years ago (MYA; Perri et al., 2021). The second most prevalent carnivoran at RLB is the sabertooth cat (*S. fatalis*). With an estimated body size of 150–280 kg, this taxon is comparable in body size to the range occupied by modern lions and tigers (Christiansen & Harris, 2005; Janczewski et al., 1992). Also present at RLB, however, is the North American lion (*P. atrox*)—among the largest felids with an estimated body mass of up to 450 kg (Wheeler & Jefferson, 2009). Though less well represented than either *S. fatalis* or *C. dirus*, more than 80 fossil specimens are currently attributed to this taxon, including eight ossicular samples (Stock & Harris, 1992). Finally, the short-faced bear (*A. simus*) is one of the rarest fossil taxa at RLB (Figueirido et al., 2017), as well as the largest. With an estimated body mass of 700–800 kg (Christiansen, 1999), this taxon exceeds the average body masses of extant ursids, with only the polar bear (~650 kg average body mass; Wilson, Mittermeier, Cavallini, 2009) of comparable stature. Only four preserved ossicular specimens have thus far been recovered from *A. simus*.

### 1.2 | Ossicles within the fossil record

The fossil record of mammalian ossicles is extraordinarily sparse; indeed, despite the anatomy of the middle ear serving as a defining characteristic of the mammalian lineage, only a handful of studies have described ossicular size or morphology in extinct taxa. When preserved and identified, however, ossicles have greatly enhanced our understanding of both the phylogeny and auditory function of early mammals. Only a single fossil ossicle is

described, namely an incus attributed to *Hyaenodon* (Bastl et al., 2017). It is relatively small, with a compact body slim processes, while morphological features of incudomalleolar facet are similar to those of felids and nandiinids and distinct from canids (Bastl et al., 2017). Among cetaceans, the morphology of an incus attributed to *Pakicetus* (~50 MYA) demonstrated a close affinity to extant, terrestrial artiodactyls (Thewissen & Hussain, 1993). Yet, ossicles in the more aquatically derived *Remingtonocetus* (~45 MYA) exhibit morphology consistent with underwater hearing (Kumar & Sahni, 1986; Nummela et al., 2004). These data would eventually facilitate comprehensive morphological analyses tracking changes in the Cetacean middle ear across the land-to-water transition (e.g., Nummela et al., 2007). Fossilized ossicles have further clarified our ecological understanding of some of the earliest true mammals, such as *Liaconodon* (Meng et al., 2011), as well as the auditory capacity

of our recent hominid ancestors (e.g., Moggi-Cecchi & Collard, 2002; Quam et al., 2013; Rak & Clarke, 1979).

### 1.3 | Aims and predictions

Within this study, we test the overarching hypothesis that the ossicles of RLB's fossil carnivorans are distinct in size and/or morphology from their modern-day relatives. Ossicular size has been related to a species' auditory range, and has been demonstrated to vary as a product of body size. However, ossicular morphology is reported to be relatively conservative within ecomorphologically similar taxa. As such, we assess the following predictions:

**Prediction 1.** The ossicles of *Canis dirus*, *Panthera atrox* and *Arctodus simus* will be larger than the equivalent ossicles in their closest living counterparts (namely *C. lupus*, *P. leo/tigris*, and *Ursus americanus/arctos/maritimus*). Meanwhile, the ossicles of *Smilodon fatalis* will be similar, or slightly smaller, in size than *P. leo/tigris*.

**Prediction 2.** In terms of shape, fossil felid, ursid, and canid ossicles will fall within the range of variation defined by their extant relatives.

**TABLE 1** Regression statistics following ordinary least squares (OLS) regressions of ossicle geometric mean against body mass, with each species represented as a single point denoting its taxon average

Element	Family	Slope (95% CIs)	Intercept	R <sup>2</sup>
Malleus	Canidae	0.29 (0.15–0.43)	0.34	0.63
	Felidae	0.49 (0.39–0.59)	0.23	0.90
	Ursidae	0.06 (–0.53 to 0.65)	0.42	0.01
Incus	Canidae	0.37 (0.27–0.48)	0.18	0.84
	Felidae	0.53 (0.46–0.60)	0.14	0.96
	Ursidae	0.09 (–0.23 to 0.40)	0.36	0.07
Stapes	Canidae	0.59 (–0.43 to 1.61)	–0.02	0.24
	Felidae	0.40 (0.30–0.49)	–0.06	0.91
	Ursidae	N/A	N/A	N/A

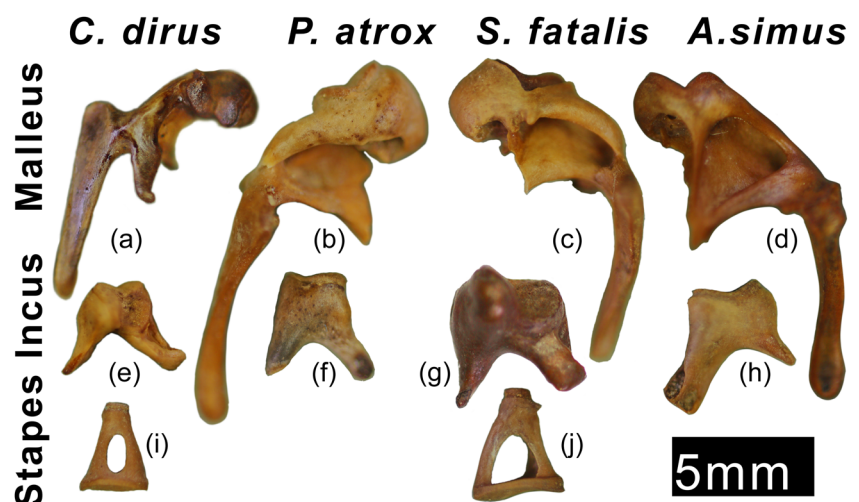
Note: Both variables linearized and log-transformed before analysis such that isometry is represented by a slope of 1.

Abbreviation: CI, confidence interval.

## 2 | MATERIALS AND METHODS

A total of 106 carnivoran ossicles from the La Brea Tar Pits and Museum were compared to those of modern analogs, including both specimens from the comparative collection also housed at RLB and the Functional Morphology and Comparative Anatomy Research Lab collection housed at North Carolina State University (see Supporting Information online Material, Supporting Information: Table 1). Because all fossil and modern ossicular specimens were extracted directly from the crania of known specimens, their taxonomic affiliations are confirmed. The RLB fossil sample consisted of ossicles from *C. dirus* ( $n = 47$ ), *S. fatalis* ( $n = 47$ ), *P. atrox* ( $n = 8$ ) and *A. simus* ( $n = 4$ ). A single ossicle from a fossil coyote (*C. latrans*) has also been

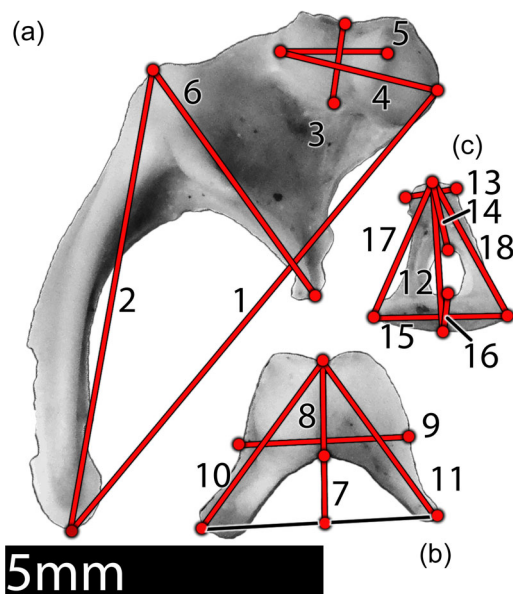
**FIGURE 1** Representative ossicles of the four RLB carnivoran taxa analyzed herein (i.e., *Smilodon fatalis*, *Panthera atrox*, *Canis dirus*, and *Arctodus simus*). Stapes unknown for *P. atrox* and *A. simus*. Specimen numbers: (a) HC 142810; (b) HC 142823; (c) R 48602; (d) HC 142834; (e) R 53697; (f) HC 142825; (g) R 24996; (h) R 63766; (i) R 32459; (j) R 11194.



recovered from the site and was also included in analyses. The extant comparative sample comprised 36 specimens from 11 canid species (including both *C. lupus* and *C. latrans*), 54 specimens from 18 different felid species including all members of *Panthera*, and 11 ursid specimens representing all 6 species of extant ursid (i.e., all living bears with the exceptions of the giant panda and the sloth bear). To avoid issues of pseudoreplication, ossicles from only one side of each animal's skull were included for analysis (see Supporting Information online Material, Supporting Information: Table S1).

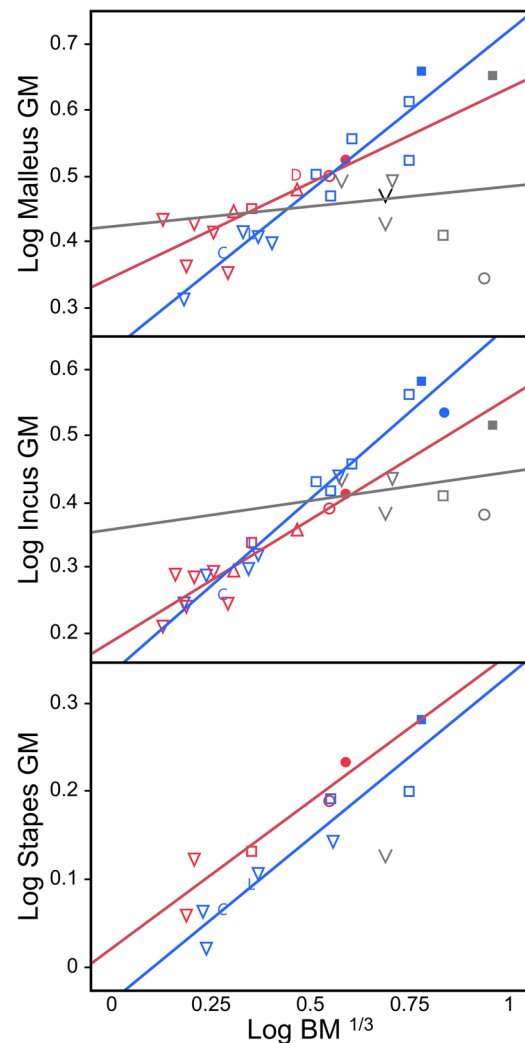
Six, five, and seven linear measurements were taken to the nearest 0.01 mm on the malleus, incus, and stapes, respectively (Figure 1), using Image J v1.8 (National Institute of Health) and photographs taken with a Canon 5DSR EF equipped with 180 mm Macro lens (Figure 1). These measurements followed the protocol outlined by (Gürbüz et al., 2019) in a morphometric assessment of canid ossicles, but with the addition of three additional measurements to further describe the morphology of the malleus head and neck (see measurements 3, 5 and 6 in Figure 2).

Data for each bony element were analyzed individually using JMP (SAS Institute Inc. version 10.0.2). Morphological variation was examined using Principal Component Analysis, and Tukey's honestly significant different tests were applied to the geometric means (GM) of each element to compare the sizes of ossicles in each fossil taxon to those of its extant relatives (two separate GM were calculated for the malleus: one including all measurements and one including only measurements of the malleus head, measurements 3–5 in Figure 2). The overall scaling of the ossicular chain relative to body size was



**FIGURE 2** Linear measurements used for morphological analyses. (a) malleus, (b) incus, and (c) stapes. 1. maximal length of malleus, 2. manubrium length, 3. facet width, 4. head length, 5. facet length, 6. process length, 7. maximal length of incus, 8. body length, 9. body width, 10. long crus length, 11. short crus length, 12. maximal length of stapes, 13. head width, 14. head length, 15. base length, 16. base height, 17. rostral crus length, and 18. caudal crus length.

also assessed using reduced major-axis (RMA) regressions of log-transformed GM against log-transformed body masses. Body mass data for extant carnivores was sourced from Wilson, Mittermeier, Cavallini, (2009). Citations for body mass estimates of fossil taxa can be found alongside the full specimen list in Supporting Information online Material, Supporting Information: Table S1.



**FIGURE 3** Ordinary least squares (OLS) regressions of ossicle geometric mean (mm) versus body mass (kg). Both variables linearized and log<sub>10</sub> transformed before analysis. Colors: red = canids, blue = felids, gray = ursids. Key as follows: closed red circles = *Canis dirus*, closed red squares = fossil *C. latrans*, closed red triangles = fossil *U. cinereoargenteus*, open red circles = *C. lupus*, open red squares = *C. latrans*, D = extant *C. lupus familiaris* (dalmatian), open red triangles = extant canid (non-fox), open red inverted triangles = extant fox. Closed blue circles = *Panthera atrox*, solid blue squares = *Smilodon fatalis*, open blue squares = extant *Panthera*, L = *Lynx* sp., C = *F. catus domesticus*, open inverted triangles = other felid. Closed gray circles = *Arctodus simus*, open gray circles = *Ursus maritimus*, open gray inverted triangles = *U. americanus*, V = other ursid. Points represent a species mean for any taxon represented in the sample by more than one specimen (see Supporting Information online Material, Supporting Information: Table S1 for full specimen list).

### 3 | RESULTS

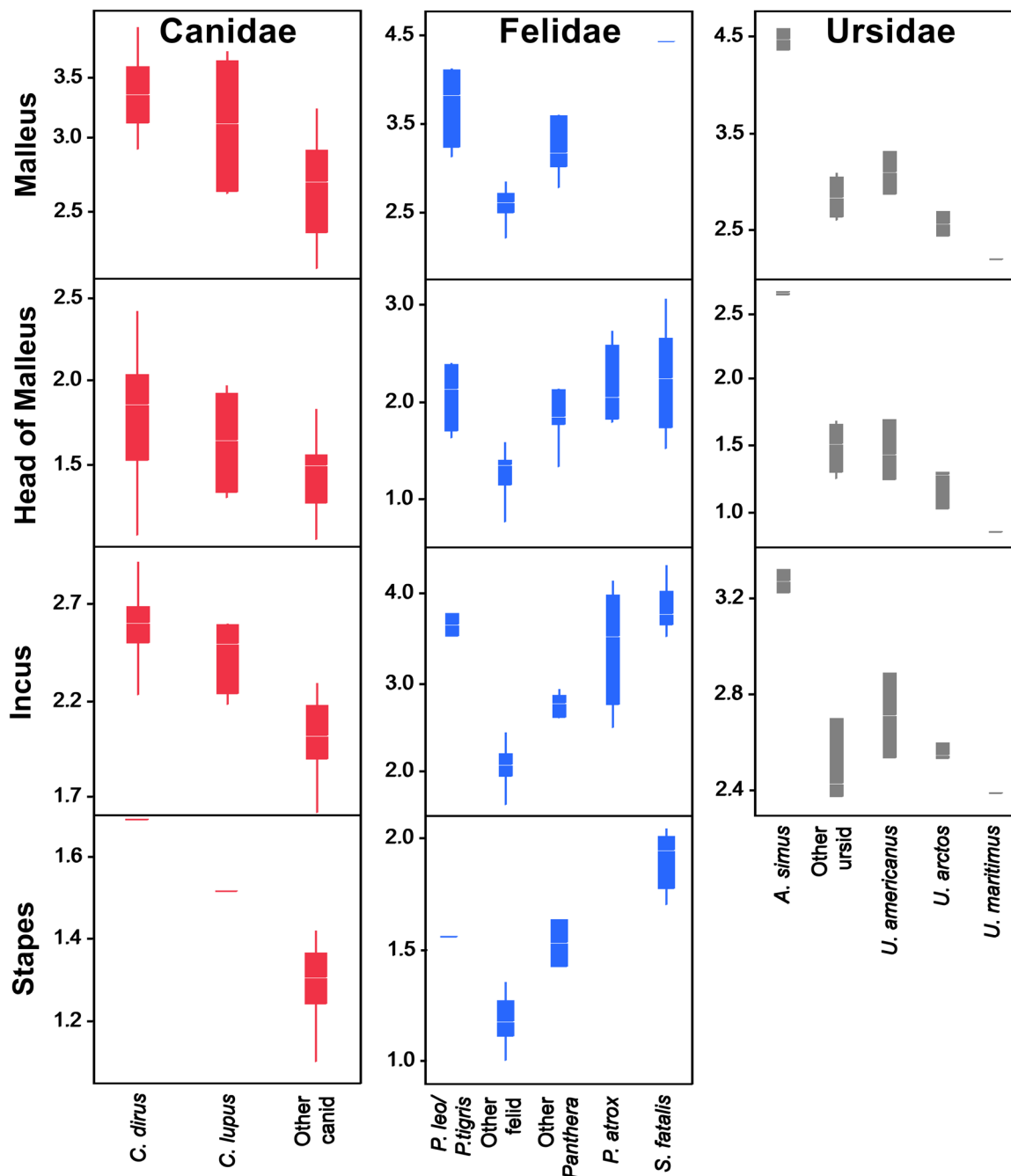
#### 3.1 | Scaling of ossicular size

RMA regressions of ossicular GM against body mass within canids, felids, and across the sample as a whole reveal a consistently negatively allometric relationship (Table 1, Figure 3). The scaling of the stapes also exhibits towards negative allometry in felids and across the sample as a whole, but 95% confidence intervals (CIs) cannot exclude the possibility of isometry within canids. Sample sizes

for the stapes in ursids were too small to assess CIs and thus infer scaling relationships.

#### 3.2 | Comparisons of size between fossil and extant taxa

The ossicles of *C. dirus* and *C. lupus* are equivalent in size in both the malleus ( $p = .60$ ), head of malleus ( $p = .46$ ) and incus ( $p = .26$ ), while the low number of preserved fossil stapes precludes comparison

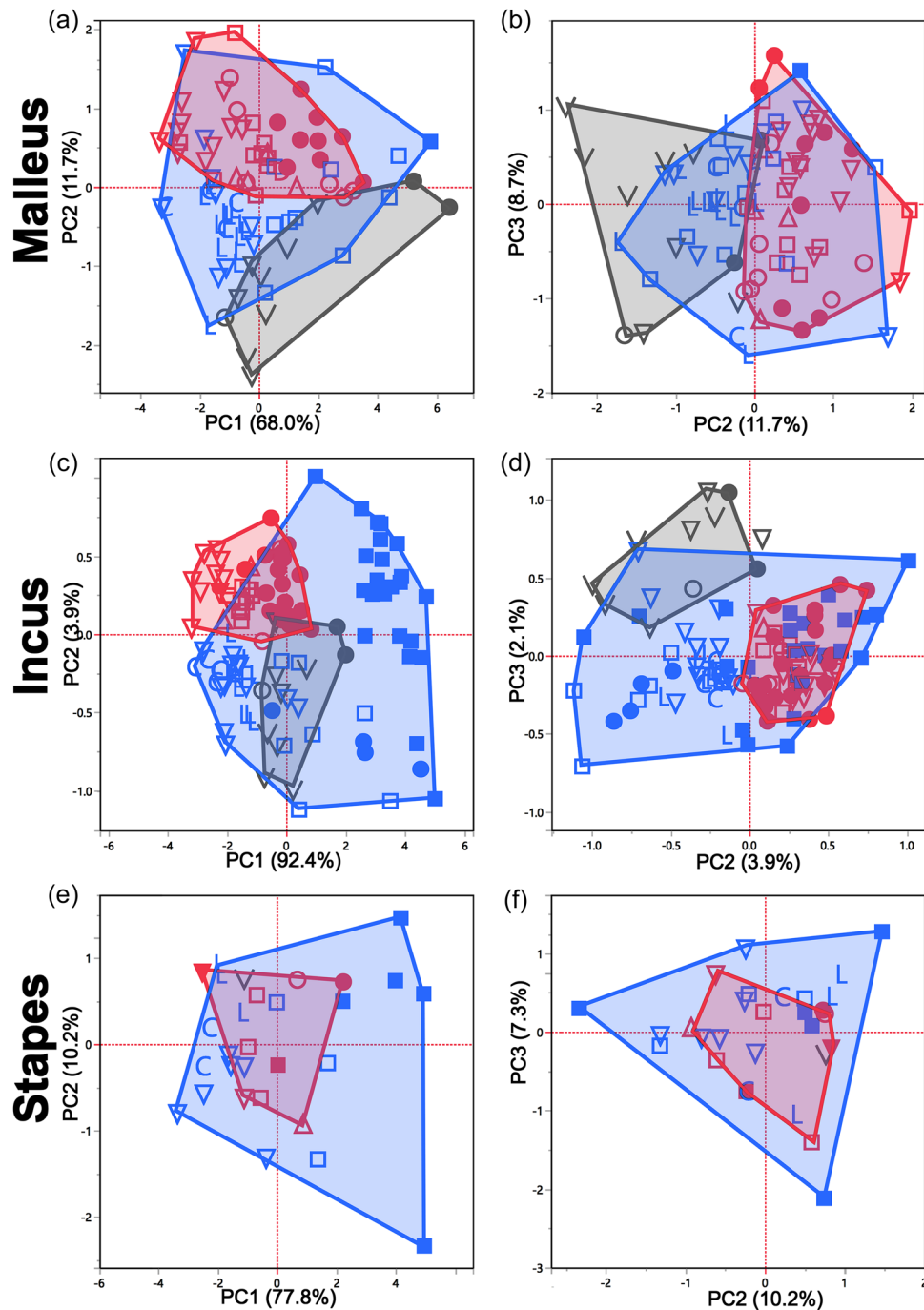


**FIGURE 4** Boxplots comparing geometric mean of individual ossicles across the four fossil taxa (i.e., *Smilodon fatalis*, *Panthera atrox*, *Canis dirus*, and *Arctodus simus*) and select extant species (i.e., I, I, I, I, and I). All other extant species are grouped within family.

(Figure 4). Among felids, the ossicles of both *S. fatalis* and *P. atrox* are similar in size to those of extant lions and tigers in the malleus head ( $p = .91$  and  $.99$ , respectively) and incus ( $p = .89$  and  $.94$ , respectively), and could not be compared in the stapes or full malleus body (Figure 4). Finally, the malleus and incus of *A. simus* are consistently larger than those in either *U. arctos*, *U. maritimus*, or *U. americanus*

( $p < .05$  in all cases). As in canids, the paucity of fossilized stapes precluded analysis. Thus, prediction 1 was supported only among ursids, and rejected in both canids and felids.

Among extant taxa, the malleus and incus of *C. lupus* is larger than those of other extant canids ( $p = .02$  and  $p < .01$ , respectively). However, no differences are observed in the malleus head or the



**FIGURE 5** Interfamilial morphospaces (canids, red; felids, blue; ursids, gray) following principal components analysis of linear measurements from each ossicle. (a, b) show PC1 versus PC2 and PC2 versus PC3 for the malleus; (c, d) show PC1 versus PC2 and PC2 versus PC3 for the incus; (e, f) show PC1 versus PC2 and PC2 versus PC3 for the stapes. Light red = *Canis dirus*, dark red = *C. lupus*. Medium blue—modern *Panthera*, dark blue = *Smilodon fatalis*. Light gray = *Ursus maritimus*, *U. arctos* and *U. americanus*, dark gray = *Arctodus simus*. For symbols see caption of Figure 2.



stapes. Among felids, the malleus, malleus head, and stapes of *P. leo/tigris* are larger than in non-*Panthera* species, but similar to other *Panthera*. The incus of *P. leo/tigris*, however, is larger than both other species of *Panthera* and non-*Panthera*. All extant ursids were statistically indistinguishable in all ossicular elements.

### 3.3 | Ossicular morphology: Interfamilial differences

Across all elements, the widest proportion of morphospace (Figure 5) is occupied by felids (blue) and, in most cases, felids span most, or in some cases all, the range of size and shape occupied by canids (red). In the malleus and incus, canids and ursids are largely separated on the basis of both size (Principal Component [PC1]) and shape (PC2 and PC3). Ursids are not, however, strongly distinguished from felids. The absence of ursid stapes precludes comparison of this element against those of canids and felids but, as before, the morphospace occupied by canids is completely conscribed within the range of that of felids.

Exploring specific morphological traits, malleus PC2 (11.7%) describes an inverse relationship of process length versus facet width and manubrium length (Table 2). Malleus PC3 (8.7%) is similarly driven by facet length versus manubrium length but also more

strongly reflects variation in maximal length, facet width, and head length. Within the incus, PC2 (3.9%) is largely driven by body width while PC3 (2.1%) strongly reflects short crus length (Table 2). Finally, stapes PC2 (10.2%) is strongly driven by base height, while PC3 (7.3%) describes an inverse relationship between head length and base height versus head width (Table 2).

### 3.4 | Morphology of the malleus: Intrafamilial differences

Among canids, PC1 accounts for 70.6% of total variation and reflects roughly isometric scaling of all variables (i.e., total malleus size). PC2 (11.8%) is driven by an inverse relationship between facet size (i.e., facet width and facet length) versus manubrium length and maximal length. PC3 (10%) is driven by facet morphology (specifically, an inverse relationship between facet width and facet length). Extant *C. lupus* and fossil *C. dirus* occupy similar portions of the morphospace (Figures 6–7; Table 3).

In felids, PC1 (74.7%) is similarly reflective of overall malleus size. PC2 (10.1%) describes an inverse relationship between process length and manubrium/maximal length (Table 3), while PC3 (7.5%) is driven by an inverse relationship between facet size (i.e., facet width and facet length) versus manubrium length and maximal length (similar to PC2 in canids). Due to a lack of intact felid mallei, morphological comparisons between fossil and extant taxa cannot be made.

Similarly, PC1 (74.8%) in ursids is driven by size, whereas PC2 (12.1%) reflects an inverse relationship between facet length and manubrium length (Table 3). Finally, PC3 (7.2%) is driven by an inverse relationship between process length and manubrium/maximal length. While differences in morphology are suggested between *A. simus* and extant bears (Figures 6, 7), the small number of fossil specimens ( $n = 2$ ) preclude meaningful interpretation.

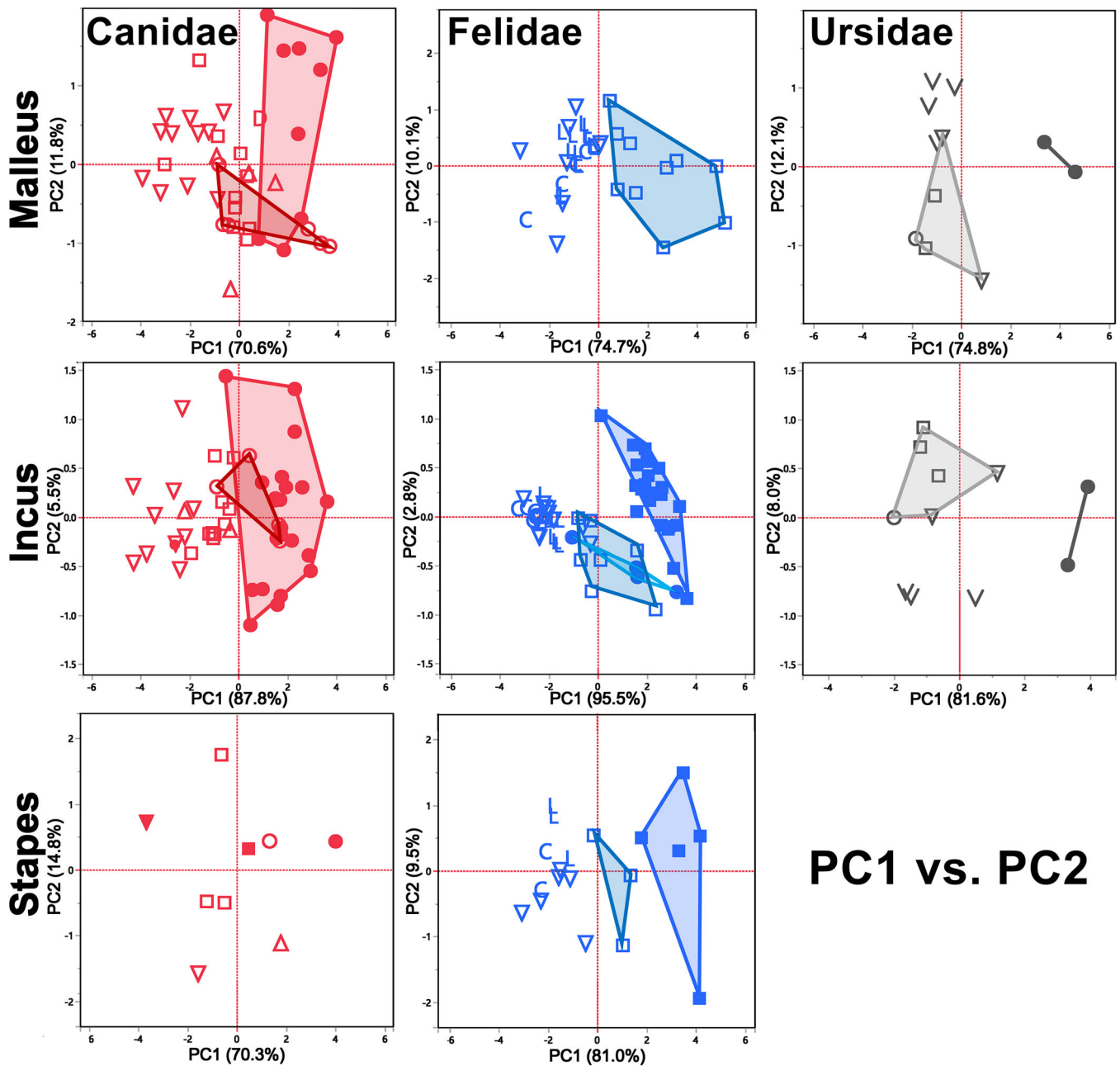
**TABLE 2** Eigenvectors following principal components analysis of morphological variables within the malleus, incus, and stapes across our entire sample

Element	Measurement	PC1	PC2	PC3
Malleus	Maximal length	0.44	-0.12	-0.39
	Manubrium length	0.39	0.47	-0.53
	Facet width	0.37	0.60	0.29
	Head length	0.45	-0.20	0.21
	Facet length	0.40	-0.08	0.64
	Process length	0.38	-0.60	-0.21
Incus	Maximal length	0.46	-0.26	0.00
	Body length	0.45	-0.45	0.08
	Body width	0.43	0.82	0.30
	Long crus length	0.45	-0.21	0.45
	Short crus length	0.45	0.14	-0.83
Stapes	Maximal length	0.42	-0.06	-0.01
	Head width	0.35	0.25	-0.61
	Head length	0.34	-0.35	0.66
	Base length	0.42	-0.06	-0.11
	Base height	0.27	0.86	0.40
	Rostral crus width	0.41	-0.19	-0.09
	Caudal crus width	0.42	-0.17	-0.07

### 3.5 | Morphology of the incus: Intrafamilial differences

In canids, PC1 (87.8%) describes isometric scaling of incus size, while PC2 (5.5%) is strongly driven by body length alone (Table 4). PC3 (4.2%) describes an inverse relationship between body width and short crus length. As in the malleus, *C. lupus* and *C. dirus* occupy similar portions of the morphospace (Figures 6, 7, Table 4).

Among felids, PC1 (95.5%) describe the size of the incus, while PC2 (2.8%) describes overall incus robusticity (i.e., an inverse relationship of body width versus body length and maximal length). PC3 (0.9%) describes long crus length versus short crus length. The incus of *S. fatalis* (solid squares and medium blue) appears to be distinguished from both *P. atrox* (solid circles and light blue), extant *Panthera* (open squares and dark blue) and other extant felids with regard to PC1, but these differences do not extend to subsequent principal components (Figures 6, 7, Table 4).



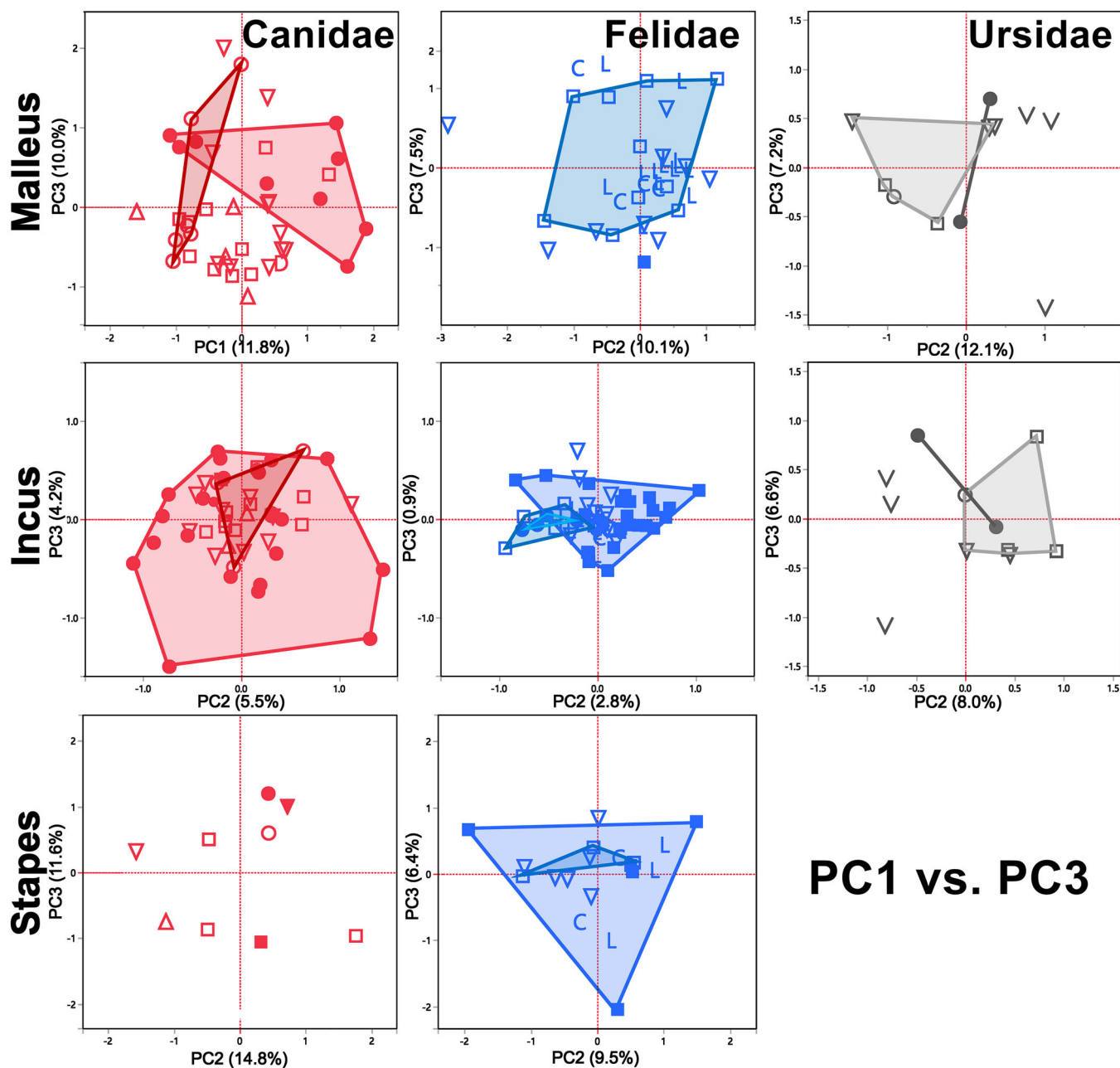
**FIGURE 6** Intrafamilial morphospaces following principal components analysis of linear measurements from each ossicle. PC1 and PC2 shown on X and Y axes respectively. Light red = *Canis dirus*, dark red = *C. lupus*. Light blue = *Panthera atrox*, medium blue—modern *Panthera*, dark blue = *Smilodon fatalis*. Light gray = *Ursus maritimus*, *U. arctos* and *U. americanus*, dark gray = *Arctodus simus*. Symbols and morphospace visualization same as in Figures 2 and 4.

In ursids, PC1 (81.6%) again reflects isometric scaling of incus size. PC2 (8.0%) is driven by an inverse relationship between body width and short crus length (similar to PC3 in canids), while ursid PC3 (6.6%) describes general robusticity (i.e., an inverse relationship of body width vs. body length), similar to PC2 in felids (Table 4). As in the malleus, differences in morphology are suggested between *A. simus* and extant bears. Again, however, the small number of fossil specimens ( $n = 2$ ) preclude meaningful interpretation.

### 3.6 | Morphology of the stapes: Intrafamilial differences

While intact stapes are rare within the fossil record of RLB, basic morphological comparisons could be conducted within canids and felids. Within canids, PC1 (70.3%) again describes size, but appears to be principally driven by changes in maximal length, base length, rostral crus width and caudal crus width (Table 5). PC2 (14.8%) describes an inverse relationship between head width and head





## PC1 vs. PC3

**FIGURE 7** Intrafamilial morphospaces following principal components analysis of linear measurements from each ossicle. PC2 and PC3 shown on X and Y axes respectively. Symbols same as in Figure 2. Minimum convex hulls represent, among the canids, *Canis lupus* and *C. dirus* (conscripting open and closed circles, respectively), among the felids *S. fatalis*, extant *Panthera* and *P. atrox* (conscripting closed and open squares, respectively) and, among the ursids, *Ursus* (open symbols) with the two *Arctodus simus* specimens of each bone connected by a line.

length, whereas PC3 (11.6%) describes an inverse relationship between head width and base height. Due to the small number of fossil canid stapes, the extent of morphological similarity or difference between *C. dirus* and *C. lupus* cannot be ascertained.

Among felids, PC1 describes largely isometric scaling of stapes size, while PC2 (9.5%) is strongly driven by base height alone (Table 5). Finally, PC3 (6.4%) describes head morphology, reflecting an inverse relationship between head width and head length. As in the incus, *S. fatalis* is distinguished from extant *Panthera* and other

extant felids along PC1, but differences cannot be observed in PC2 or in PC3 (Figures 6, 7).

## 4 | DISCUSSION

Morphologically preserved ossicles are exceptionally rare within the fossil record, particularly within carnivorans, a paucity which likely reflects their taphonomic vulnerability and also the ease with which

**TABLE 3** Eigenvectors following principal components analysis of morphological variables within the malleus of canids, felids, and ursids

Family	Measurement	PC1	PC2	PC3
Canids	Maximal length	0.45	-0.30	0.24
	Manubrium length	0.42	-0.45	0.10
	Facet width	0.35	0.52	0.67
	Head length	0.44	0.29	-0.10
	Facet length	0.36	0.47	-0.64
	Process length	0.41	-0.37	-0.25
	Felids	Maximal length	0.43	-0.30
Manubrium length		0.42	-0.42	0.42
Facet width		0.39	-0.22	-0.66
Head length		0.43	0.18	-0.09
Facet length		0.43	0.08	-0.36
Process length		0.35	0.80	0.26
Ursids		Maximal length	0.43	-0.11
	Manubrium length	0.41	-0.45	-0.34
	Facet width	0.44	-0.06	0.29
	Head length	0.45	0.09	-0.06
	Facet length	0.31	0.87	-0.10
	Process length	0.40	-0.13	0.73

**TABLE 4** Eigenvectors following principal components analysis of morphological variables within the incus of canids, felids, and ursids

Family	Measurement	PC1	PC2	PC3
Canids	Maximal length	0.46	-0.35	0.16
	Body length	0.42	0.86	0.27
	Body width	0.44	0.05	-0.80
	Long crus length	0.46	-0.18	-0.12
	Short crus length	0.45	-0.32	0.50
Felids	Maximal length	0.45	-0.33	0.25
	Body length	0.45	-0.32	0.03
	Body width	0.43	0.88	0.10
	Long crus length	0.45	-0.13	0.46
	Short crus length	0.45	-0.07	-0.85
Ursids	Maximal length	0.46	-0.19	0.33
	Body length	0.45	0.00	-0.69
	Body width	0.42	0.73	0.43
	Long crus length	0.47	0.12	-0.35
	Short crus length	0.43	-0.64	0.33

**TABLE 5** Eigenvectors following principal components analysis of morphological variables within the stapes of canids and felids

Family	Measurement	PC1	PC2	PC3
Canids	Maximal length	0.44	0.08	0.07
	Head width	0.30	0.52	-0.56
	Head length	0.28	-0.74	0.02
	Base length	0.44	-0.01	-0.11
	Base height	0.25	0.38	0.81
	Rostral crus width	0.43	-0.16	0.07
	Caudal crus width	0.44	0.00	-0.12
	Felids	Maximal length	0.42	-0.07
Head width		0.38	0.12	-0.56
Head length		0.35	-0.22	0.78
Base length		0.41	-0.07	-0.14
Base height		0.27	0.92	0.21
Rostral crus width		0.40	-0.21	-0.13
Caudal crus width		0.41	-0.18	-0.03

Note: The absence of ursid stapes precludes comparisons within this family.

such small bones can be overlooked when excavating even if they do survive fossilization. In this study, we present the first analysis of ossicular size and shape within the famous carnivoran assemblage of RLB, and compare these smallest bones recovered from this site to those of a range of extant relatives.

Ossicles consistently appear to scale with negative allometry relative to body size, a relationship that is unsurprising given the nonload-bearing nature of bones in the middle ear. As such, despite body size being a relatively strong predictor of auditory range, increases in body size are proportionally larger than the associated increase in ossicle size across all carnivoran families (Figure 3). While a relationship between ossicle size and high-frequency hearing ranges has been suggested (Hemila et al., 1995), it is important to note that many other morphological factors impact hearing range, including the volume of the middle ear cavity (which has been shown to impact low frequency hearing responses; Ravicz et al., 1992) and ossicular stiffness (which modulates the vibrational response; Mason, 2016). Thus, morphological data alone is insufficient to fully infer auditory capabilities from the ossicular chain.

Interfamilial comparisons of ossicular morphology (Figure 5) demonstrate that, while ursids and canids share a closer phylogenetic affinity than either do to felids (Agnarsson et al., 2010), the ossicles of ursids and canids are typically distinct, with each falling into separate ends of the morphological range defined by felids. Thus, among Carnivora, it would seem that ossicular morphology is defined by more than simply phylogenetics alone.

On a familial level, ossicles from both fossil felids (*S. fatalis* and *P. atrox*) and canids (*C. dirus*) are similar in size to those of their extant counterparts (modern *P. tigris*, *P. leo* and *C. lupus*, respectively). This is surprising, given body estimates place both *P. atrox* and *C. dirus* at larger sizes than any modern congeners, while *S. fatalis* occupies a similar body mass range to modern lions and tigers. Thus, despite differences in body size estimates between living and extinct taxa, auditory range is predicted to have been broadly equivalent between these animals.

One possible explanation for this result is a similar high-frequency hearing response between extinct and extant taxa. If, as suggested by Hemila et al. (1995), ossicle size correlates to high frequency hearing performance sensitivity across carnivorans, then it might be possible to infer that the retention of similarly-sized ossicles across a range of body sizes is indicative of a requirement to focus hearing sensitivity toward similar frequencies—that is to say, despite differences in body size between the extinct North American lion (~325 kg) and modern lions (~175 kg), auditory transmission capabilities may have been comparable between taxa. Data on the hearing ranges of extant, terrestrial carnivorans are somewhat limited (and do not extend to the full range of taxa sampled herein), some interesting trends can be observed. For instance, while a general relationship exists between body size and hearing ranges (Huang et al., 2000), the relative upper hearing limit of domestic cats (~79 kHz; Fay, 1988) is reported to be much higher than domestic dogs (~44 kHz; Heffner, 1983) wild red foxes (~48 kHz; Malkemper et al., 2015), or least weasels (~44 kHz), all of whom are similar in range. Experimental data suggest that high frequency hearing limits in bears are significantly lower: experimental data demonstrate an upper frequency hearing limit of ~20 kHz in polar bears (Owen & Bowles, 2011), though preliminary data on the giant panda suggests a frequency ceiling that exceeds 31.5 kHz (Owen, Keating, et al., 2011). Future work is required, however, to further elucidate the acoustic environments inhabited across the body size range of modern carnivores.

It is also interesting to note that, unlike canids and felids, a significant difference in ossicular size is noted between the fossil taxon *A. simus* and any extant ursid. Indeed, the relative size of the middle ear bones in this taxon are larger than would be expected even for an animal of its enormous size (~750 kg), as evidenced by comparison to modern *U. maritimus* (~650 kg). However, the small number of preserved ossicular elements from *A. simus* (which is represented by only four elements at RLB) makes defining the range of ossicular size in this taxon difficult, and as such inferences as to the auditory capabilities of this taxon would be highly speculative.

Finally, from the perspective of morphology, we report a general similarity between fossil carnivorans and their extant analogs. However, as is the case for overall size, *A. simus* appears distinct from extant ursids—consistently occupying regions of the morphospace beyond the range of modern bears. While small sample sizes hinder nuanced interpretation of these observations, our data strongly underscore the need for further analysis of the middle ear of this taxon. Given the extended geographic (Richards et al., 1996; Schubert, Hulbert, et al., 2010; Voorhies & Corner, 1982) and temporal (Kurten & Anderson, 1980; Schubert, 2010) ranges of *A. simus*, with over 100

fossil localities across North and Central America, the potential to expand the ossicular assemblage associated with this taxon is theoretically high. However, as ossicles have historically been overlooked within fossil assemblages, a concerted effort is necessary to identify and preserve these elements for future studies.

## AUTHOR CONTRIBUTIONS

**Edwin Dickinson:** Conceptualization (equal); data curation (equal); formal analysis (lead); investigation (equal); methodology (equal); project administration (equal); supervision (equal); visualization (equal); writing—original draft (lead); writing—review and editing (equal). **Erin E. Elminowski:** Conceptualization (equal); data curation (equal); formal analysis (equal); funding acquisition (equal); investigation (equal); methodology (equal); project administration (equal); visualization (equal); writing—original draft (equal); writing—review and editing (equal). **Deanna Flores:** Conceptualization (supporting); funding acquisition (supporting); investigation (equal); methodology (equal); visualization (equal); writing—review and editing (equal). **Emma I Eldridge:** Conceptualization (supporting); funding acquisition (supporting); investigation (equal); methodology (equal); visualization (equal); writing—review and editing (equal). **Michael C. Granatosky:** Funding acquisition (supporting); supervision (supporting); writing—review and editing (equal). **Adam Hartstone-Rose:** Conceptualization (lead); data curation (equal); formal analysis (equal); funding acquisition (lead); investigation (equal); methodology (equal); project administration (equal); resources (equal); supervision (lead); visualization (equal); writing—original draft (equal); writing—review and editing (lead).

## ACKNOWLEDGMENTS

We are grateful to the managing Editor and two anonymous reviewers for their helpful feedback, which greatly improved and clarified an earlier version of this manuscript. We also thank the La Brea Tar Pits and Museum and all members of the staff, especially Aisling Farrel, Gary Takeuchi, and Stephanie Potze, for allowing access to their collections. We are similarly grateful to Marissa Boettcher, Kaitlyn Leonard, Antonio Meza, and Abby Blume for help with data collection and paper revisions.

## DATA AVAILABILITY STATEMENT

All data are available on our lab website.

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**How to cite this article:** Dickinson, E., Elminowski, E. E., Flores, D., Eldridge, E. I., Granatosky, M. C., & Hartstone-Rose, A. (2022). A morphological analysis of carnivoran ossicles from Rancho La Brea. *Journal of Morphology*, 283, 1337–1349. <https://doi.org/10.1002/jmor.21506>