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RESEARCH ARTICLE

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The roar of Rancho La Brea? Comparative anatomy of modern and fossil felid hyoid bones

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Abstract

Animal vocalization is broadly recognized as ecologically and evolutionarily important. In mammals, hyoid elements may influence vocalization repertoires because the hyoid apparatus anchors vocal tissues, and its morphology can be associated with variation in surrounding soft-tissue vocal anatomy. Thus, fossil hyoid morphology has the potential to shed light on vocalizations in extinct taxa. Yet, we know little about the hyoid morphology of extinct species because hyoid elements are rare in the fossil record. An exception is found in the Rancho La Brea tar pits in Los Angeles, California, where enough hyoids have been preserved to allow for quantitative analyses. The La Brea Tar Pits and Museum houses one of the largest and most diverse collections of carnivore fossils, including hyoid elements from the extinct felids *Smilodon fatalis* and *Panthera atrox*. Here, we found that extant members of Felinae (purring cats) and *Panthera* (roaring cats) showed characteristic differences in hyoid size and shape that suggest possible functional relationships with vocalization. The two extinct taxa had larger and more robust hyoids than extant felids, potentially reflecting the ability to produce lower frequency vocalizations as well as more substantial muscles associated with swallowing and respiration. Based on the shape of the hyoid elements, *Panthera atrox* resembled roaring cats, while *Smilodon fatalis* was quite variable and, contrary to suggestions from previous research, more similar overall to purring felids. Thus *P. atrox* may have roared and *S. fatalis* may have produced vocalizations similar to extant purring cats but at a lower frequency. Due to the confounding of vocalization repertoire and phylogenetic history in extant Felidae, we cannot distinguish between morphological signals related to vocalization behavior and those related to shared evolutionary history unrelated to vocalization.

KEYWORDS

functional morphology, *Panthera atrox*, *Smilodon fatalis*, vocal apparatus

1 | INTRODUCTION

To generate sound, animals must produce some sort of vibration using morphological structures. These vibrations may be generated in a number of ways, including percussion (Arcadi et al., 1998; Schaller, 1963), cavitation (Koukouvinis et al., 2017), and stridulation (Norris & Evans, 1988); however, many terrestrial air-breathing animals produce vibrations for vocalization by forcing air from the respiratory system through a valve. In terrestrial mammals, this valve is called the glottis or vocal cords. This structure along with associated muscles and cartilage are part of the larynx. The movement and configuration of these structures impact the quality of the produced sound (e.g., Hast, 1986, 1989).

A species' vocalization repertoire is known to have ecological and evolutionary importance through social, sexual, competitive, and predator–prey interactions (e.g., Searcy & Nowicki, 2005) making this an important variable for fossil behavioral reconstructions. While the soft tissues responsible for many vocalizations are rarely preserved in the fossil record, fossils of the bony hyoid apparatus that acts to anchor these vocal tissues in many taxa are sometimes found. While most morphological descriptions of fossil hyoids have not focused on functional implications of hyoid morphology for vocalization (e.g., Pérez et al., 2010; Werdelin et al., 2018), the relationship between the vocalization repertoire of species and hyoid morphology has been applied to reconstruct vocalizations in fossil taxa (e.g., Flores et al., 2020).

In mammals, the hyoid apparatus is a midline structure, usually composed of several bones, located in the ventral neck. The hyoid acts as a skeletal support for the base of the tongue and the upper vocal tract. The generalized mammalian hyoid apparatus consists of nine elements (Figure 1): paired bilateral stylohyoid, epihyoid, ceratohyoid, and thyrohyoid elements as well as an unpaired midline basihyoid (Pérez et al., 2010). The thyrohyoid extends caudally from the basihyoid, where it connects to the cricoid cartilage of the larynx (Weissengruber et al., 2002). Because of this interaction with the larynx and vocal folds, the hyoid potentially plays an important role in acoustic production and has been a central component of discussions of functional anatomy of acoustic capabilities (e.g., Capasso et al., 2008; D'Anastasio et al., 2013; Evans, 1959; Flores et al., 2020; Lieberman et al., 1992; Milovancev et al., 2014; Pérez et al., 2010; Peters & Hast, 1994; Pocock, 1916; Weissengruber et al., 2002).

For nearly two centuries, functional anatomists have ascribed iconic differences in sound production abilities within Felidae to morphological differences in the configuration of the hyoid apparatus

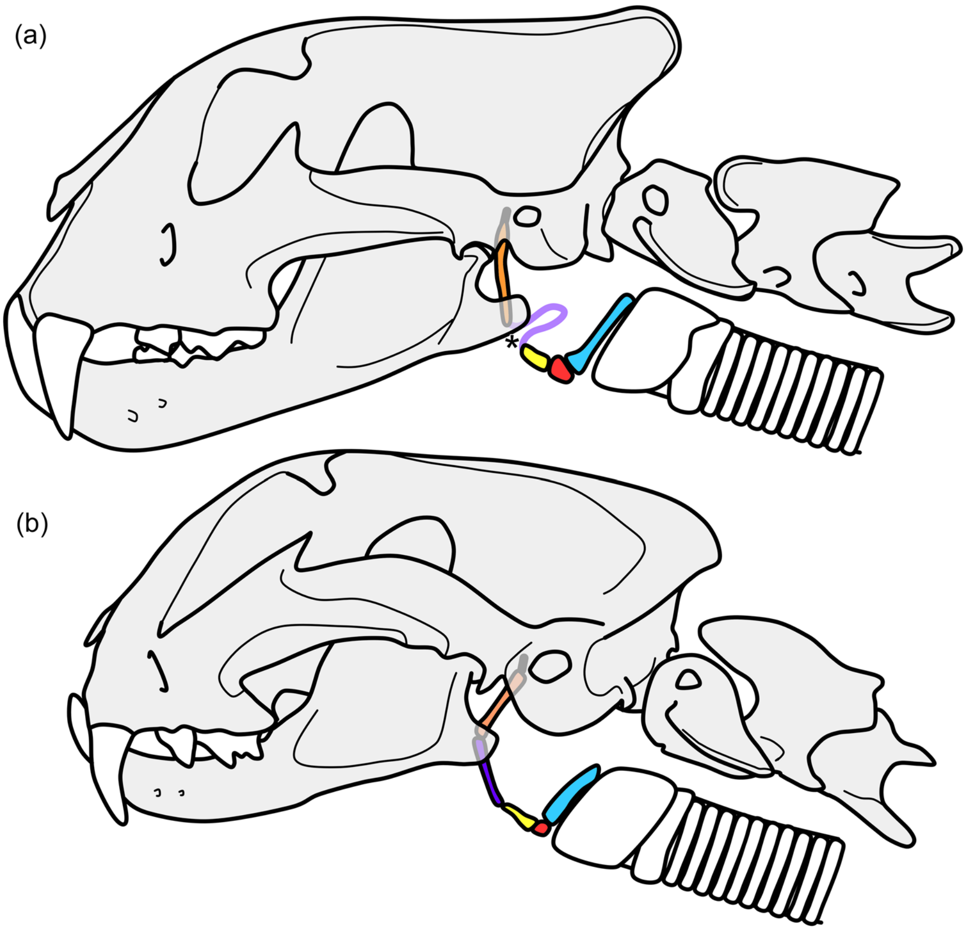

FIGURE 1 Schematic of felid hyoid anatomy in situ in (a) *Panthera tigris* and (b) *Caracal caracal*. Stylohyoid is orange, epihyoid (* = ligamentous in *Panthera*) is purple, ceratohyoid is yellow, basihyoid is red, and thyrohyoid is cyan.

and its associated soft tissue (Hast, 1989; Owen, 1834; Peters & Hast, 1994; Pocock, 1916; Shaw, 2018; Weissengruber et al., 2002): the vocalizations of members of Felidae have been categorized as either "purring" or "roaring," generally restricted to the sister subfamilies Felinae and Pantherinae, respectively. Within Felidae, the first anatomical examination of the hyoid postulated that the differences in vocal capacities between felids were related to differences in the ligamentous attachment of the hyoid to the cranium (Owen, 1834). Later work has suggested that the degree of ossification of the epihyoid may relate to differences in vocalization capabilities between species (e.g., Pocock, 1916; Weissengruber et al., 2002). Within Pantherinae, four of the five *Panthera* species (*Panthera leo*, *Panthera tigris*, *Panthera onca*, and *Panthera pardus*) exhibit an epihyoid that is an elastic ligament rather than ossified bone and can produce roaring rather than purring vocalizations. Weissengruber et al. (2002) have suggested that this elastic ligament may allow for a lower laryngeal position, which is correlated with lower frequency vocalizations in other species (Tecumseh Fitch & Reby, 2001). Despite having a similarly unossified epihyoid, the fifth member of the monophyletic genus, *Panthera uncia*, is unable to either purr or roar; this has been attributed to differences in other soft-tissue anatomy (Assar et al., 2021; Hast, 1989; Peters & Hast, 1994). All cats within the subfamily Felinae, are able to purr and have fully ossified epihyoid bones (Peters & Hast, 1994; Peters, 2002). Unossified elements, such as elastic ligaments, largely are not preserved in the fossil record and infrequent preservation of hyoid elements in general may make it difficult to make presence/absence determinations about the epihyoid in fossil taxa.

While the association between hyoid bone shape and specific vocal abilities has not previously been empirically established in felids, when these bones are found in the fossil record, it may be possible to make inferences relative to the abilities of other closely related taxa; for instance, the Rancho La Brea (RLB) tar pits in Los Angeles, California preserve so many rare and understudied bones that it is possible to study their comparative morphology quantitatively unlike perhaps any other fossil sample in the world (Flores et al., 2020; Hartstone-Rose et al., 2012; Hartstone-Rose et al., 2015), and among these rare and delicate bones are carnivoran hyoids. Recently, Flores et al. (2020) described the hyoid bones of the dire wolves *Aeocyon dirus* and fossil coyotes (*Canis latrans*) in comparison to those of modern large canids and concluded that both of these ancient species might have howled at lower frequencies than modern wolves (*Canis lupus*) and coyotes, respectively. Similarly, hyoid bones of the sabertooth, *Smilodon fatalis*, exist in large enough samples in RLB to quantitatively compare to those of modern felids. This investigation empirically evaluates the relationship between hyoid morphology and vocalization across modern felids and examines whether *S. fatalis* hyoid morphology is similar enough in shape to modern felines or pantherines to suggest whether they might have been capable of purring or roaring.

The asphalt deposits of RLB preserve a remarkably detailed late Pleistocene (40,000–11,000 years ago) terrestrial fossils sample (Merriam & Stock, 1932; Shaw & Quinn, 1986; Shaw et al., 2007). The quality of preservation and quantity of fossils at this site are in part due to the presence of asphalt at the site (Shaw et al., 2007). Plants and animals are hypothesized to have become entrapped by the sticky surface of the asphalt surrounding active oil vents; upon submersion, asphalt saturates the remains, in some instances preserving even very delicate tissues (Quinn et al., 1992; Shaw & Quinn, 1986). While early excavations at the site primarily recovered large fossil bones, particularly craniodental material and limb bones, more recent excavations have produced large collections of well-preserved smaller fossils (Shaw, 1982). The quantity and quality of preservation provide a unique opportunity for the quantitative examination of the functional morphology of small fossils, including clavicles (Hartstone-Rose et al., 2012), bacula (Hartstone-Rose et al., 2015), canid hyoids (Flores et al., 2020), and auditory ossicles (Dickinson et al., 2022).

Smilodon fatalis is found abundantly within the RLB tar pits. Although a preliminary description of its hyoid morphology (namely the lack of ossified epihyoids found in the sample) has pointed to the ability of *S. fatalis* to roar (Shaw, 2018), no quantitative shape analysis has been carried out to support this hypothesis. Molecular data suggest that *S. fatalis* is a stem felid within the subfamily Machairodontinae, meaning that all extant felids (i.e., both the purring and roaring modern subfamilies) are more closely related to each other than they are to *S. fatalis* (Barnett et al., 2005). While it is likely that the plesiomorphic trait in felids is an inability to roar, recent molecular analyses suggest that roaring may have evolved multiple times within the lineage (Pecon-Slattery et al., 2004). As such, the vocalization behavior of *S. fatalis* is unknown. *S. fatalis* was similar in size to the largest modern felid *P. tigris tigris* with an estimated body mass ranging from 160 to 280 kg (Christiansen & Harris, 2005). As all large extant felids are able to roar, previous work based on visual examination of *S. fatalis* hyoid fossils found that *S. fatalis* hyoid morphology was qualitatively similar to that of large modern felids (Shaw, 2018) and suggested that *S. fatalis* may have also been able to roar. *Panthera atrox*, another extinct felid which has been preserved in the RLB tar pits, has been estimated to weigh on average 178 kg for females and 251 kg for males, only slightly more than modern lions (Wheeler & Jefferson, 2009). The evolutionary relationship of *P. atrox* to other members of the genus *Panthera* had been debated (Barnett et al., 2009; Christiansen, 2008; King & Wallace, 2014), but recent molecular data suggests *P. atrox* is closely related to *P. leo*, a roaring felid (Barnett et al., 2009). As such, we expect that the hyoid morphology of *P. atrox* will be similar to that of *P. leo*, pointing to similar vocalization behaviors.

In this study, we first quantitatively analyzed the size and shape of hyoid bones from six large modern felid species (*Panthera leo*, *Panthera tigris*, *Panthera pardus*, *Panthera onca*, *Puma concolor*, and *Acinonyx jubatus*) and three smaller modern felid species (*Caracal caracal*, *Leptailurus serval*, and *Leopardus pardalis*) with known vocalization capabilities. We then compared hyoid morphology of *S. fatalis* and *P. atrox* to these modern taxa in the context of felid vocalization. Because previous research has attributed differences in vocalization behaviors to the degree of ossification of the epihyoid (e.g., Pocock, 1916; Weissengruber et al., 2002), we hypothesized that the morphological differences driving vocalization capabilities in extant felids will primarily involve the stylohyoid and ceratohyoid as these bones surround the epihyoid. Additionally, as Shaw (2018) found in a preliminary analysis that *Smilodon* hyoid morphology is more similar to *Panthera* than Felinae, we hypothesized that *S. fatalis* hyoid morphology will be more similar to *Panthera* than Felinae in our analysis as well. If we can accurately distinguish between roaring and purring species based on hyoid morphology, then it may be possible to infer the vocalization behaviors of *S. fatalis* and *P. atrox* based on their hyoid morphology.

2 | MATERIAL AND METHODS

Our modern comparative sample consisted of all of the felid hyoid bones available from several collections: the Smithsonian National Museum of Natural History (USNM; Washington, D.C), the American Museum of Natural History (AMNH; New York, NY), and the Hartstone-Rose laboratory (AHR; Raleigh, NC). Unfortunately, as these bones are more closely associated with soft-tissue structures that are usually discarded during the skeletal preparation process than the more substantial osteological elements, they are very limited in these collections. The modern comparative sample consisted of four species of *Panthera*—five specimens of *P. leo*, seven specimens of *P. tigris*, three specimens of *P. pardus*, and one specimen of *P. onca*—and five species from Felinae—two specimens of *Puma concolor*, one specimen of *Acinonyx jubatus*, two specimens of *Caracal caracal*, two specimens of *Leptailurus serval*, and two specimens of *Leopardus pardalis* (Table 1). We compared these modern analogs to our felid fossil hyoid sample (Table 1 and Supporting Information: Supplement 1) consisting of 106 *S. fatalis* and 1 *P. atrox* isolated hyoid specimens curated at RLB Tar Pits and Museum, part of the Natural History Museum of Los Angeles County (LSCM; Los Angeles, California). Due to the nature of preservation and perturbation in the tar, these elements were not associated with each other or other skeletal elements. All elements included were complete, unbroken, and from adults.

Measurements for each hyoid element (Figure 2) were taken using digital calipers to the nearest 0.01 mm following Flores et al. (2020). On each stylohyoid, epihyoid, and thyrohyoid, seven measurements were taken: width and thickness at each end (cranial and caudal), width and thickness at the midshaft, and overall length (Figure 2). Similar measurements were taken for the more irregular ceratohyoid; however, neck width and thickness were measured in place of midshaft width and thickness (Figure 2). For the roughly symmetrical basihyoid which exists in the midline, inner chord length, and height were measured in addition to width and thickness at each end (left and right), width and thickness at the midshaft, and overall length for a total of nine measurements (Figure 2). The epihyoid was excluded from analyses because only members of Felinae have fully ossified epihyoids. While the presence of an ossified epihyoid has been thought by some to be indicative of vocalization capacities, the fossil record is inherently incomplete so that the absence of an epihyoid does not necessarily reflect the presence of an unossified epihyoid though the fact that there is no clear ossified epihyoid among the 106 *S. fatalis* hyoid elements preserved at RLB would be

TABLE 1 Sample sizes of specimens examined for hyoid morphology across 11 felid species.

Species	Subfamily	Sample Size	Date	Vocalization
Panthera leo	Pantherinae	5	Modern	Roar[a]
Panthera tigris	Pantherinae	7	Modern	Roar[b]
Panthera pardus	Pantherinae	3	Modern	Roar[a]
Panthera onca	Pantherinae	1	Modern	Roar[a]
Puma concolor	Felinae	2	Modern	Purr[c]
Acinonyx jubatus	Felinae	1	Modern	Purr[d]
Caracal caracal	Felinae	2	Modern	Purr[e]
Leptailurus serval	Felinae	2	Modern	Purr[a]
Leopardus pardalis	Felinae	2	Modern	Purr[f]
Panthera atrox	Pantherinae	1	Fossil	—
Smilodon fatalis	Machairodontinae	106	Fossil	—

Note: A complete list of specimens with catalog numbers is available in Supporting Information: Table S1.

[a] Peters and Hast (1994).

[b] Ji et al. (2013).

[c] Peters, (1978).

[d] Sissom et al. (1991).

[e] Peters, (1983).

[f] Murray and Gardner (1997).

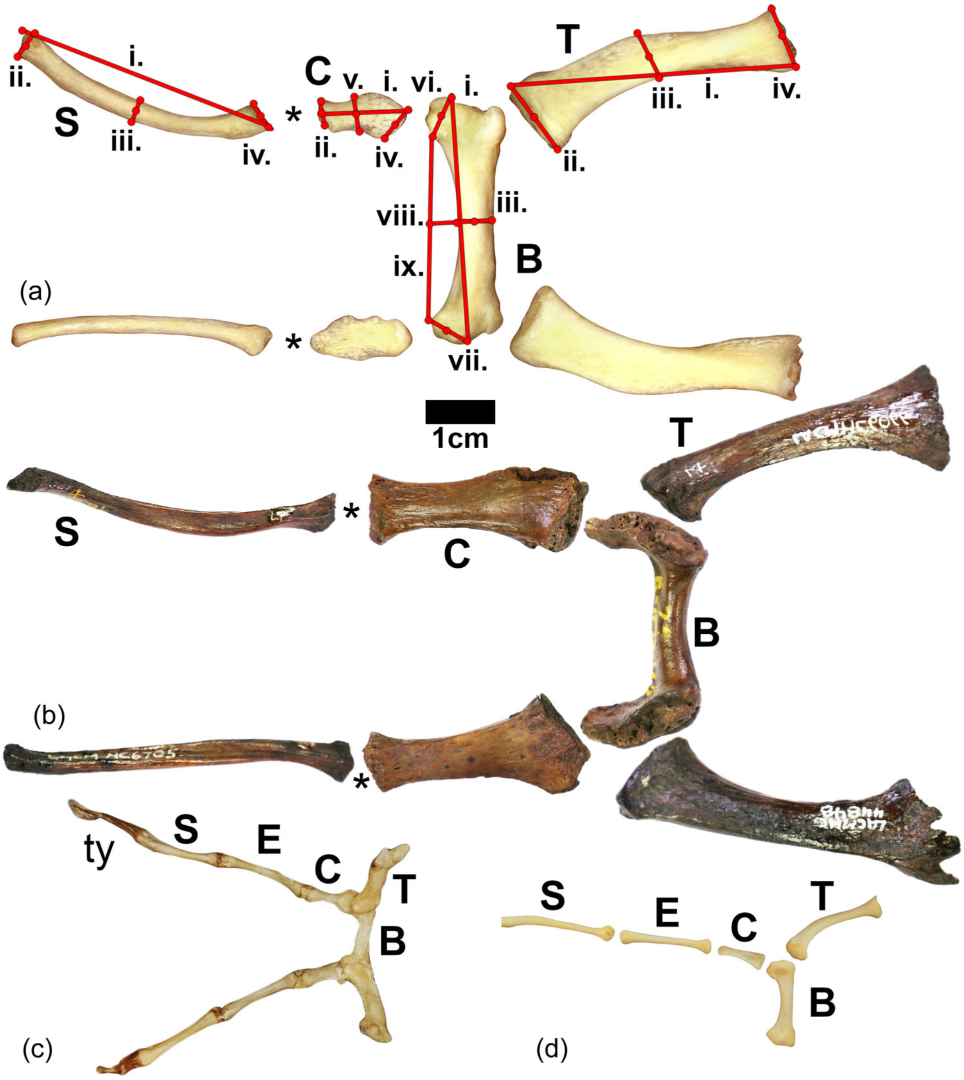

FIGURE 2 Hyoid elements of (a) *Panthera tigris* (AHR 202118; dorsal view), (b) *Smilodon fatalis* (composite of unassociated specimens; dorsal view), (c) *Leptailurus serval* (AHR 202101; dorsal view held in articulation by ligaments with thyrohyoid coming out of page plane), and (d) *Caracal caracal* (AHR 202148; dorsal view). Rostral to the left. Stylohyoid (S), epihyoid (E), ceratohyoid (C), basihyoid (B), thyrohyoid (T), and ligamentous tympanohyoid (ty; in C). Unrepresented or unossified epihyoid elements are marked by *. Measurement indications are i. maximal length, ii. cranial end width and thickness, iii. midshaft width and thickness, iv. caudal end width and thickness, v. neck width and thickness, vi. left end width and thickness, vii. right end width and thickness, viii. inner chord height, and ix. inner chord length.

remarkably coincidental given the representation of all other elements if, indeed, *Smilodon* did have an ossified epihyoid.

We conducted all principal component analyses (PCAs) and analyses of variance (ANOVAs) using JMP software (SAS Institute Inc. version 17.0.0). PCAs using correlation matrices were used to reduce dimensionality and explore morphological trends within these data. We retained the first three PC axes in each case. Analyses were conducted for each bone independently allowing the geometric relationship between the variables to be explored for each bone individually. Two separate PCAs were conducted for each bone, one using raw measurements to assess overall form that includes size and shape, and one using size-adjusted measurements to more directly assess bone *shape*. In all cases, we conducted PCAs using extant taxa only, and then projected fossil hyoid elements onto the PCs for each element using the PCA equations (i.e., fossils were excluded from the *generation* of the shape space, though their metrics were then used to calculate where they fell on the extant-based PCA shape space). For the size-adjusted PCA, we used "sheared" variables: we regressed all raw measurements on the PC1 scores derived for that bone and saved size-adjusted residuals (Humphries et al., 1981; PC1 reflected overall bone size in all cases, see Section 3). Again, PCAs using correlation matrices for sheared residuals included only extant taxa, while fossil taxa were projected onto these PCs. We conducted ANOVAs to test for differences in PC values between roaring and purring cats and used Tukey post hoc tests to evaluate differences between *S. fatalis* and either vocalization group.

PCAs of variables combined across multiple hyoid elements were performed to assess morphological trends across the hyoid more broadly. Because hyoid elements are rare both in osteological samples and fossil assemblages, all hyoid elements were not represented for many individuals within the sample. Species means were calculated to account for missing elements so that analyses could be performed on combinations of elements. As stylohyoid elements were missing from several species means it was excluded from this combined analysis as was *Acinonyx jubatus* as no thyrohyoid is represented in this sample. Raw measurement as well as sheared PCAs were performed on the combined ceratohyoid, basihyoid, and thyrohyoid elements.

To assess the ability to discriminate between taxa that roar and purr based on multivariate hyoid morphology, we conducted multivariate analyses of variance (MANOVAs) in JMP for raw measurements and sheared residuals for each bone. If we observed significant differences between roaring and purring taxa for a bone in the MANOVA, we then followed this with linear discriminant function analyses (DFA) using jackknife cross validation using the R package MASS (Venables & Ripley, 2002). We assessed the accuracy of our DFAs in predicting the vocalization behavior of extant taxa (i.e., percent correctly classified), and then evaluated DFA predictions of vocalization behavior for extinct taxa.

3 | RESULTS

3.1 | Stylohyoid

Among the four individually examined hyoid elements—the stylohyoid, the ceratohyoid, the basihyoid, and the thyrohyoid—the first principal component (PC1) for the stylohyoid accounted for the lowest amount of morphological variation (56.74%; Table 2). For the stylohyoid, PC1 was driven positively by size, driven primarily by midshaft width, caudal end dimensions, and maximal length (Table 3). PC2 accounted for 23.30% of the variation (Table 2) and was driven primarily by cranial end dimensions and inversely midshaft width and caudal end thickness (Table 3). PC3 accounted for only 7.41% of the variation (Table 2) and was driven primarily by midshaft thickness versus caudal end thickness and maximal length (Table 3). The morphospaces of purring and roaring cats overlapped along all PCs thus these groups could not be distinguished based on the shape-space morphology of this bone by ANOVA ($p = 0.05$, 0.32, and 0.20 for PC1, PC2, and PC3, respectively; Table 4; Figure 3a,b). Despite having slightly more purring cat stylohyoids in the sample, roaring cats occupied a larger volume of morphospace (Figure 3a,b). *Smilodon fatalis* had minimal overlap with the morphospaces of modern taxa. Along PC1, *S. fatalis* stylohyoids were large; however, they overlapped with both modern purring and roaring cats (Figure 3a). PC2 and PC3 of *S. fatalis* differed significantly from PCs of both purring and roaring cats. Based on a MANOVA, roaring and purring felids did not differ based on this morphology ($F_{7,6} = 0.90$, $p = 0.56$).

In PCA of sheared residuals of stylohyoid measurements, PC1 (41.75%; Table 5) was driven by cranial end dimensions and caudal end width and inversely midshaft width (Table 6). PC2 (27.05%; Table 5) was driven by an inverse relationship between midshaft thickness and maximal length versus caudal end thickness (Table 6). PC3 (13.34%; Table 5) was driven by an inverse relationship between cranial end thickness and midshaft width (Table 6). This analysis suggests that when size is adjusted for through shearing, roaring, and purring cats occupy similarly sized morphospaces. In Tukey post hoc tests, *Smilodon fatalis* differed significantly from purring cats based on PC1 ($p < 0.01$) and PC2 ($p < 0.02$; Table 4); however, purring and roaring cats did not differ significantly from each other (Figure 4a,b). Based on a MANOVA, roaring and purring felids again did not differ based on this morphology ($F_{7,6} = 0.59$; $p = 0.75$).

TABLE 2 Principal component eigenvalues for each of the four examined hyoid elements based on raw measurements of extant species.

	Eigenvalue	Percent	Cumulative percentage
Stylohyoid			
PC1	3.97	56.74	56.74
PC2	1.63	23.30	80.04
PC3	0.52	7.41	87.45
Ceratohyoid			
PC1	4.43	63.35	63.35
PC2	1.01	14.46	77.80
PC3	0.63	8.97	86.77
Basihyoid			
PC1	8.03	89.20	89.20
PC2	0.36	4.00	93.20
PC3	0.26	2.88	96.07
Thyrohyoid			
PC1	5.99	85.64	85.64
PC2	0.42	5.99	91.63
PC3	0.30	4.28	95.90

Abbreviation: PC, principal component.

3.2 | Ceratohyoid

In ceratohyoid, PC1 accounted for the next lowest amount of morphological variation (63.35%; Table 2) and was driven positively by size. For the ceratohyoid, PC2 only accounted for 14.46% of variations (Table 2) and was driven by an inverse relationship between cranial end thickness and neck thickness (Table 3). PC3 (8.97%; Table 2) was driven by an inverse relationship between cranial end thickness and neck width. The morphospaces of purring and roaring felids overlapped along PCs 1, 2, and 3 and cannot be distinguished based on this morphology (Figure 3c,d). *Smilodon fatalis* occupied morphospace far outside of modern taxa along PC1, having much larger ceratohyoids (Figure 3c). Along PC2 and PC3, *S. fatalis*

TABLE 3 Eigenvectors for the first three principal components of each of the four examined bones based on raw measurements of extant specimens.

Variables	PC1	PC2	PC3
Stylohyoid			
Cranial end width	0.18	0.67	−0.02
Cranial end thickness	0.22	0.61	0.07
Midshaft width	0.45	−0.21	0.14
Midshaft thickness	0.38	−0.18	0.80
Caudal end width	0.42	0.17	−0.05
Caudal end thickness	0.45	−0.21	−0.35
Maximal length	0.44	−0.17	−0.45
Ceratohyoid			
Cranial end width	0.43	−0.06	0.32
Cranial end thickness	0.36	−0.28	0.70
Neck width	0.40	0.25	−0.42
Neck thickness	0.17	0.89	0.24
Caudal end width	0.43	−0.18	−0.33
Caudal end thickness	0.36	−0.18	−0.28
Maximal length	0.42	0.05	−0.05
Basihyoid			
Left end width	0.34	−0.06	−0.45
Left end thickness	0.33	−0.48	0.13
Right end width	0.34	−0.15	−0.36
Right end thickness	0.33	−0.48	0.32
Midshaft width	0.34	0.17	−0.12
Midshaft thickness	0.33	0.00	0.55
Maximal length	0.34	0.32	0.04
Inner chord length	0.32	0.60	0.30
Inner chord height	0.34	0.10	−0.38
Thyrohyoid			
Cranial end width	0.37	−0.21	0.52
Cranial end thickness	0.34	0.76	0.42
Midshaft width	0.39	−0.42	−0.10
Midshaft thickness	0.38	0.29	−0.53
Caudal end width	0.39	−0.22	0.14
Caudal end thickness	0.38	0.12	−0.48
Maximal length	0.40	−0.23	0.08

overlapped with variation in both purring and roaring felids (Figure 3d). PC2 of *S. fatalis* differed significantly from PC2 of both purring and roaring cats (both $p < 0.01$; Table 4). MANOVA found that roaring and purring felids did not differ based on this morphology ($F_{7,10} = 1.69$; $p = 0.22$).

In the PCA of sheared residuals of ceratohyoid measurements, PC1 (33.22%; Table 5) was driven inversely by neck dimensions and maximal length versus cranial end dimensions (Table 6). PC2 (25.69%; Table 5) was driven by an inverse relationship between cranial end dimensions and caudal end dimensions (Table 6). PC3 (15.11%; Table 5) was driven inversely by neck thickness and maximal length (Table 6). The sheared morphospaces of purring and roaring felids were largely overlapping; however, PC1 by PC2 provided moderate separation with roaring and purring felids being statistically different along PC2 based on an ANOVA ($p = 0.02$; Table 4; Figure 4). While there were few *S. fatalis* ceratohyid elements in this sample, their morphospace largely overlapped with modern purring and roaring felids along PCs 1, 2, and 3 (Figure 4c,d). *S. fatalis* was not statistically distinguishable from modern purring or roaring cats based on sheared PCs in Tukey post hoc tests (Table 4). MANOVA again revealed that roaring and purring felids did not differ in ceratohyoid morphology ($F_{7,10} = 1.10$; $p = 0.43$).

3.3 | Basihyoid

PC1 for the basihyoid accounted for 89.20% (Table 2) of variation and was driven positively by size. PC2 (4.00%; Table 2) was driven by inner chord length and inversely left and right end thicknesses (Table 3). PC3 (2.88%; Table 2) was driven by an inverse relationship between midshaft thickness versus right and left end widths and inner chord height (Table 3). Roaring and purring felids were largely separable along PC1 with roaring felids having larger basihyoids based on an ANOVA ($p < 0.01$; Table 4). In PC1 by PC3, extant roaring cats occupied a larger morphospace than extant purring cats, with purring felids falling inside of roaring felid morphospace (Figure 3e,f). *Smilodon fatalis* occupied morphospace at the extreme positive end of PC1, having larger basihyoids than most modern taxa, including extant felids of a similar body size (Figure 3e). In PC1 by PC2 and PC2 by PC3 plots, *S. fatalis* and extant felids were almost entirely nonoverlapping (Figure 3e,f). Based on ANOVA and Tukey post hock tests, *Smilodon fatalis* PC3 differed significantly from both roaring ($p < 0.01$) and purring ($p < 0.01$) felids; however, roaring and purring felids did not differ significantly from each other based on PC3 ($p = 0.38$; Table 4).

MANOVA uncovered significant differences in basihyoid morphology between roaring and purring felids ($F_{9,12} = 4.95$; $p < 0.01$). DFA with leave-one-out cross-validation was able to distinguish extant roaring and purring felids with 77.3% accuracy; however, *S. fatalis* did not clearly fall into one of these vocalization categories with a 50% prediction of roaring and a 50% prediction of purring.

When basihyoid measurements were sheared to account for the effects of size, PC1 accounted for 42.62% (Table 5) of variation and was driven by an inverse relationship between left end and midshaft width versus right end dimensions and maximal length (Table 6). PC2 (26.22%; Table 5) was driven by an inverse relationship between inner chord height versus left and right end thicknesses (Table 6). PC3 (12.47%; Table 5) was driven by midshaft width and inversely inner chord length (Table 6). *Smilodon fatalis* occupied a larger basihyoid morphospace than modern felids. Along PC2 and PC3, *S. fatalis*

TABLE 4 ANOVA and Tukey post-hoc test results for first three PCs of raw hyoid element measures as well as sheared residuals.

		Extant ANOVA			Full Sample ANOVA			Tukey vs *S. fatalis*	
		p value	*F* Ratio	*DF*	*p* value	*F* Ratio	*DF*	Purring *p* value	Roaring *p* value
Raw measurements									
Stylohyoid	PC1	0.05	4.66	1,12	<0.001*	13.19	2,24	<.0001*	0.06
	PC2	0.32	1.07	1,12	<0.001*	21.03	2,24	<0.001*	<0.001*
	PC3	0.20	1.85	1,12	<0.001*	22.32	2,24	<0.001*	<0.01*
Ceratohyoid	PC1	<0.01*	10.82	1,16	<0.001*	267.05	2,19	<0.001*	<0.001*
	PC2	0.74	0.12	1,16	<0.001*	10.89	2,19	<0.001*	<0.001*
	PC3	0.19	1.85	1,16	0.30	1.27	2,19	0.83	0.32
Basihyoid	PC1	<0.001*	28.69	1,20	<0.001*	150.85	2,51	<0.001*	<0.001*
	PC2	0.45	0.59	1,20	0.07	2.89	2,51	0.41	0.07
	PC3	0.38	0.80	1,20	<0.001*	29.02	2,51	<0.001*	<0.001*
Thyrohyoid	PC1	<0.001*	58.67	1,17	<0.001*	140.97	2,71	<0.001*	<0.001*
	PC2	0.61	0.27	1,17	0.89	0.11	2,71	0.94	0.96
	PC3	0.38	0.80	1,17	0.12	2.23	2,71	0.79	0.10
Sheared residuals									
Stylohyoid	PC1	0.07	4.01	1,12	<0.01*	7.27	2,24	0.30	<0.01*
	PC2	0.65	0.21	1,12	0.02*	4.64	2,24	0.02	0.12
	PC3	0.68	0.18	1,12	0.19	1.77	2,24	0.20	0.47
Ceratohyoid	PC1	0.19	1.83	1,16	0.53	0.67	2,19	0.99	0.63
	PC2	0.02*	0.68	1,16	0.09	2.76	2,19	0.77	0.50
	PC3	0.58	0.32	1,16	0.90	0.10	2,19	1.00	0.94
Basihyoid	PC1	<0.001*	31.06	1,20	<0.001*	14.71	2,51	<0.001*	<0.001*
	PC2	0.50	0.47	1,20	0.41	0.91	2,51	0.84	0.39
	PC3	0.55	0.38	1,20	0.67	0.40	2,51	0.98	0.65
Thyrohyoid	PC1	0.27	1.33	1,17	0.52	0.65	2,71	0.50	1.00
	PC2	0.01*	9.44	1,17	<0.01*	5.14	2,71	0.70	0.01*
	PC3	0.60	0.29	1,17	0.12	2.22	2,71	0.78	0.10

Note: Reported ANOVAs test for differences between extant roaring and purring felids (Extant ANOVA) and *S. fatalis*, extant roaring felids, and extant purring felids (full sample ANOVA). F ratio, degrees of freedom, and *p* value are reported for ANOVAs. For Tukey post hoc tests, *p* values for comparisons of each vocalization group with Smilodon fatalis are reported.

Abbreviation: ANOVA, analysis of variance.

*quick visual reference, significant values are represented with an asterisk.

overlapped entirely with both roaring and purring felids; however, while purring and roaring felids differed significantly along PC1 ($p < 0.01$), and roaring felids differed significantly from *S. fatalis* ($p < 0.01$), purring felids did not differ significantly from *S. fatalis* (Figure 4e).

MANOVA revealed that roaring and purring felids differed in the shape of the basihyoid ($F_{9,12} = 4.77$; $p < .01$). DFA with leave-one-out cross-validation could distinguish between purring and roaring felids based on sheared residuals of basihyoid measurements with an accuracy of 81.8%. Based on this DFA, 78.1% of *S. fatalis* individuals were predicted to be purring felids with an average prediction probability assigned to each individual of 75.2%.

3.4 | Thyrohyoid

For the thyrohyoid, PC1 accounted for 85.64% (Table 2) of variation and was positively driven by size (Table 3). PC2 (5.99%; Table 2) was driven by an inverse relationship between cranial end thickness and midshaft width (Table 3). PC3 (4.28%; Table 2) was driven by an inverse relationship

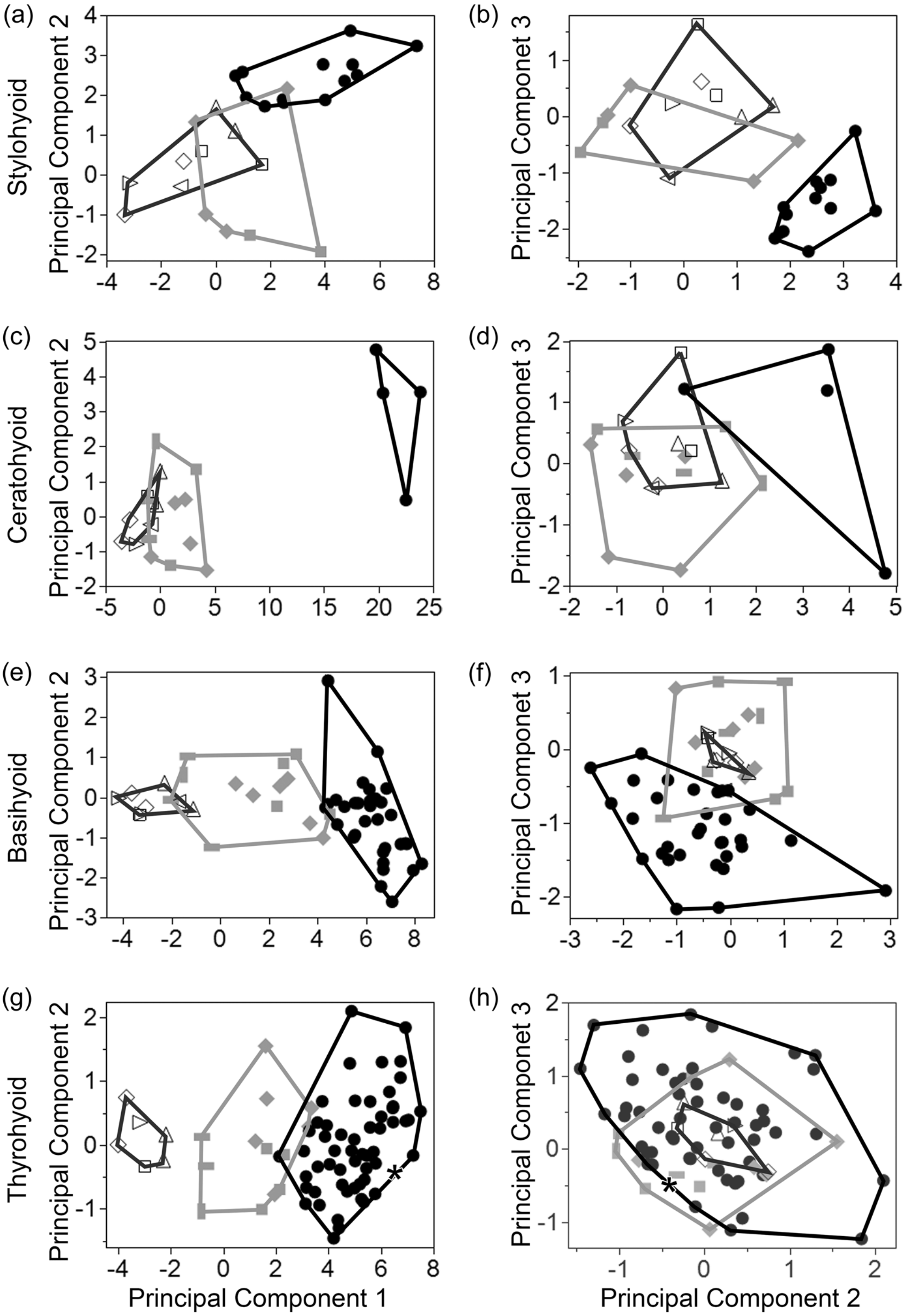

FIGURE 3 Principal components plots representing morphological variation in the stylohyoid (a, b), ceratohyoid (c, d), basihyoid (e, f), and thyrohyoid (g, h). Each graph has points and convex hulls for *Smilodon fatalis* (black circles) *Panthera atrox* (asterisk), *Panthera spp*. (gray shapes), and Felinae *spp*. (open shapes). PC space is generated from extant values. Species are indicated as follows: *Panthera leo* = gray square, *Panthera tigris* = gray diamond, *Panthera pardus* = gray horizontal rectangle, *Panthera onca* = gray vertical rectangle, *Puma concolor* = open upward triangle, *Acinonyx jubatus* = open left-pointing triangle, *Caracal caracal* = open right-pointing triangle, *Leptailurus serval* = open diamond, and *Leopardus pardalis* = open square.

between cranial end dimensions versus midshaft and caudal end thickness (Table 3). Along PC1, purring and roaring felids were nonoverlapping, and *S. fatalis* occupied a morphospace at the extreme positive end of PC1 overlapping only slightly with roaring felids (Figure 3g). Along PC2 and PC3, all three groups were largely overlapping (Figure 3). *Panthera atrox* fell outside of extant pantherines along PC1 and was significantly different from extant *Panthera* ($p < 0.01$); however, it fell inside pantherine morphospace on PC2 and PC3 (Figure 3h).

Based on MANOVA, roaring and purring felids clearly differed in thyrohyoid morphology ($F_{7,11} = 17.91$; $p < 0.001$). DFA with leave-one-

TABLE 5 Principal component eigenvalues for sheared residuals of each of the four examined hyoid elements in extant specimens.

	Eigenvalue	Percent	Cumulative percentage
Stylohyoid			
PC1	2.92	41.75	41.75
PC2	1.89	27.05	68.80
PC3	0.93	13.34	82.15
Ceratohyoid			
PC1	2.33	33.22	33.22
PC2	1.80	25.69	58.91
PC3	1.06	15.11	74.02
Basihyoid			
PC1	3.84	42.62	42.62
PC2	2.36	26.22	68.84
PC3	1.12	12.47	81.31
Thyrohyoid			
PC1	2.49	35.53	35.53
PC2	1.71	24.41	59.94
PC3	1.48	21.15	81.09

Abbreviation: PC, principal component.

out cross-validation distinguished between purring and roaring felids with 100% accuracy. The *P. atrox* individual was predicted to roar with a 100% probability. DFA also predicted that all *S. fatalis* belonged to the roaring group, with an average assignment probability of 100%.

When thyrohyoid measurements were sheared to adjust for size, PC1 accounted for 35.53% of variation (Table 5) and was driven by an inverse relationship between maximal length and caudal end and midshaft width versus midshaft, caudal end, and cranial end thickness (Table 6). PC2 accounted for 24.41% of variation (Table 5) and was driven by an inverse relationship between caudal end thickness and cranial end width (Table 6). PC3 accounted for 21.15% of variation (Table 5) and was driven by midshaft width and inversely cranial end thickness and caudal end width. Groups were most significantly separated along PC2. While purring and roaring felids differed significantly along PC1 ($p = 0.04$), and roaring felids differed significantly from *S. fatalis* ($p = 0.01$), purring felids did not differ significantly from *S. fatalis* (Figure 4g). *P. atrox* fell at the periphery of extant pantherine space in PC2 by PC3; however, it fell solidly within pantherine morphospace in PC1 by PC2 space (Figure 4g,h).

MANOVA also indicated that roaring and purring felids differed in the shape of the thyrohyoid ($F_{7,11} = 3.66$; $p = 0.03$). DFA with leave-one-out cross-validation distinguished between purring and roaring felids with 83.3% accuracy. *Panthera atrox* was again predicted to be roaring with a 100% assignment probability. Using sheared variables, DFA classified 54.6% of *S. fatalis* individuals as purring, with an average assignment probability of 89.4%.

TABLE 6 Eigenvectors for the first three principal components of sheared residuals of each of the four examined bones in extant specimens.

Variables	PC1	PC2	PC3
Stylohyoid			
Cranial end width	0.51	0.14	0.17
Cranial end thickness	0.45	−0.05	0.44
Midshaft width	−0.42	−0.34	−0.23
Midshaft thickness	−0.28	−0.51	0.36
Caudal end width	0.37	−0.11	−0.76
Caudal end thickness	−0.28	0.53	−0.08
Maximal length	−0.26	0.55	0.11
Ceratohyoid			
Cranial end width	−0.39	0.38	0.22
Cranial end thickness	−0.36	0.48	−0.26
Neck width	0.52	−0.22	−0.05
Neck thickness	0.35	0.22	0.71
Caudal end width	−0.27	−0.54	−0.22
Caudal end thickness	−0.27	−0.41	0.35
Maximal length	0.43	0.24	−0.45
Basihyoid			
Left end width	0.42	0.28	−0.19
Left end thickness	0.23	−0.48	0.21
Right end width	0.43	0.18	−0.13
Right end thickness	0.22	−0.53	0.04
Midshaft width	−0.33	0.12	0.58
Midshaft thickness	−0.32	−0.33	−0.17
Maximal length	−0.45	0.14	0.08
Inner chord length	−0.30	0.19	−0.61
Inner chord height	0.19	0.44	0.40
Thyrohyoid			
Cranial end width	0.11	−0.66	0.29
Cranial end thickness	−0.37	−0.37	−0.45
Midshaft width	0.33	0.06	0.63
Midshaft thickness	−0.46	0.31	0.01
Caudal end width	0.45	0.18	−0.38
Caudal end thickness	−0.34	0.46	0.31
Maximal length	0.45	0.30	−0.27

Abbreviation: PC, principal component.

3.5 | Combined species means

PCs analysis of species means for the combined ceratohyoid, basihyoid, and thyrohyoid revealed distinct Felinae, *Panthera*, and

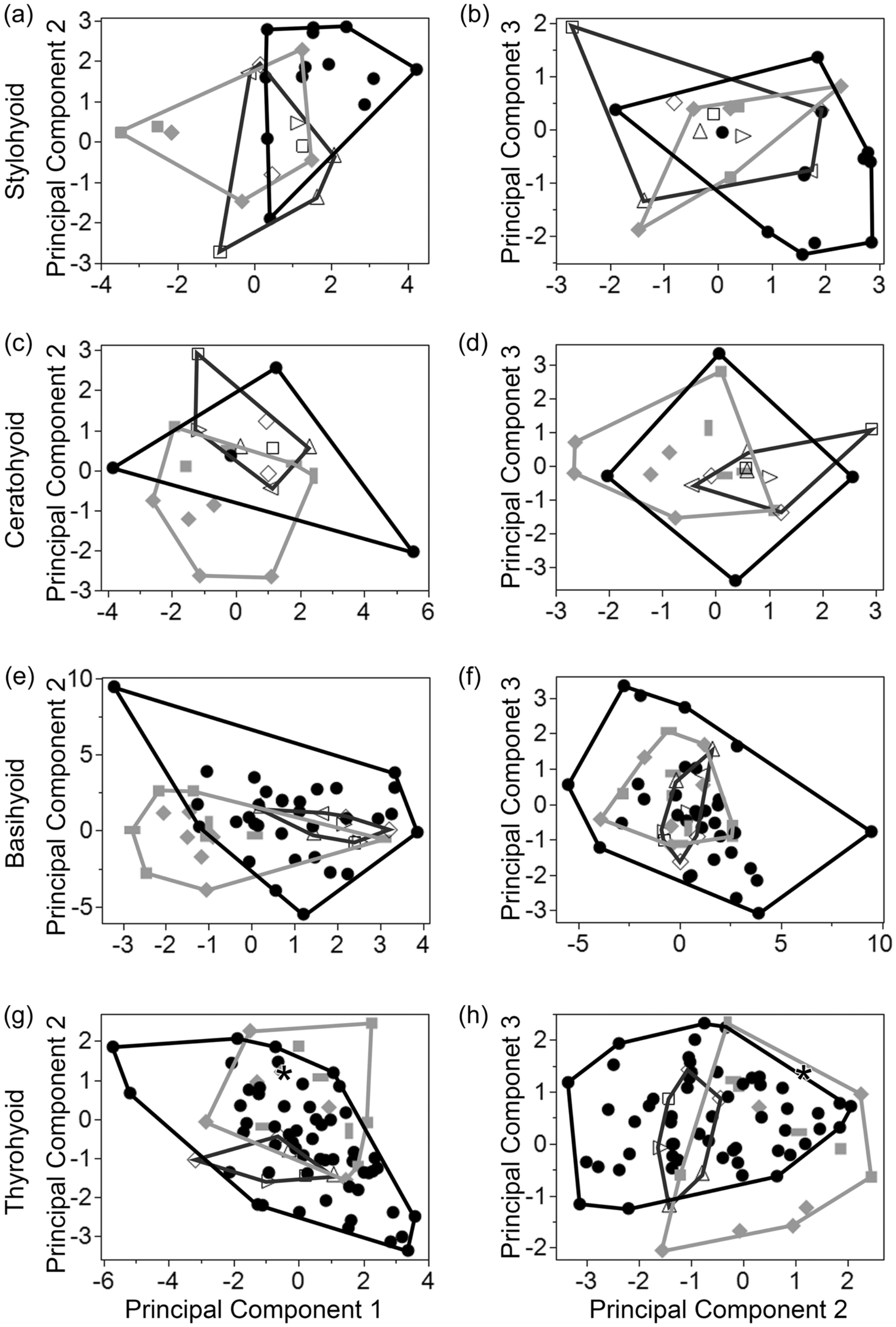

FIGURE 4 Principal components plots representing morphological variation in the sheared residuals of stylohyoid, ceratohyoid, basihyoid, and thyrohyoid measurements. See Figure 3 caption for key. PC space is generated from extant values.

S. fatalis groups in PC1 by PC2 and PC2 by PC3 space, with *P. pardus* (leopard) and *P. onca* (jaguar) clustering closer to Felinae than *P. leo* (lion) and *P. tigris* (tiger) in PC1 by PC2 (Figure 5a). DFA with leave-one-out cross-validation differentiated between roaring and purring felids with only 37.5% accuracy, worse than by random chance alone. This poor performance was likely due to inadequate sample size or that the combination of all the bones overwhelms any potentially important variation. PCs analysis of sheared residuals again had three distinct clusters in PC1 by PC2 space; however, all three groups overlapped in PC2 by PC3 space (Figure 5d). Due to the small sample size, there was not enough power for a MANOVA for these combined variables.

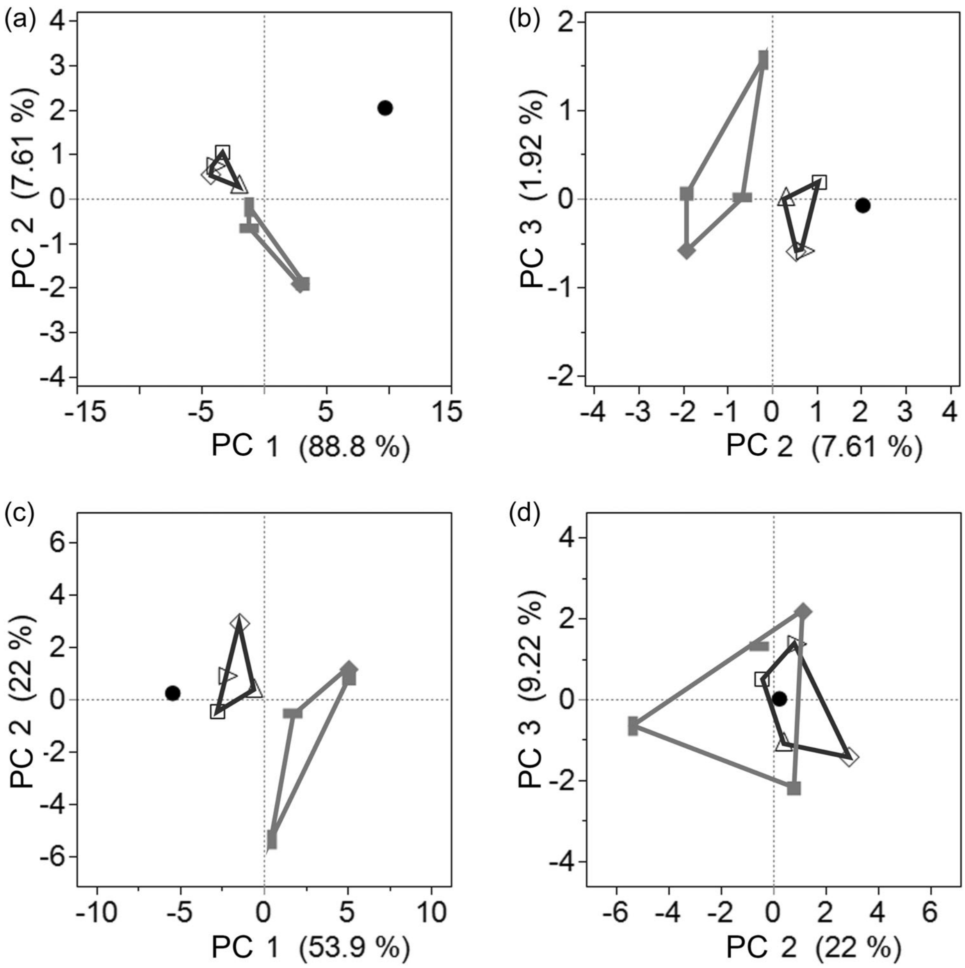

FIGURE 5 Principal components plot of species means derived from raw (a, b) and sheared (c, d) ceratohyoid, basihyoid and thyrohyoid measurements. See Figure 3 caption for species key.

4 | DISCUSSION

Despite being integrally attached to vocal tissues, hyoid morphology has remained largely understudied in the context of acoustic repertoire (Pérez et al., 2010; Pocock, 1916; Werdelin et al., 2018; but see e.g., Flores et al., 2020). Indeed, although the roaring/purring difference within the Felidae has often been attributed to differences in this osteology, more work needs to be done to demonstrate that functional link. As vocalization repertoires are an important evolutionary and ecological variable (e.g., Searcy & Nowicki, 2005), these capabilities are important for reconstructing behavior and social structures in extinct species. Given that soft tissue is largely unpreserved in the fossil record, the examination of hyoid morphology may be essential for understanding fossil species. However, to reconstruct the relationship between hyoid morphology and vocalizations in extinct species, we must first examine this relationship in extant taxa. Because of their anatomical position and isolation from other bones, hyoids are often discarded during skeletonization and are poorly represented in modern skeletal collections. As such, to our knowledge, this is the first quantitative examination of extant felid hyoid morphology.

In contrast to our a priori hypotheses based on prior research, we did not find that roaring and purring cats were distinguished based on the stylohyoid and ceratohyoid morphology. Instead, we found that Felinae have substantially different basihyoid and thyrohyoid elements from the *Panthera* taxa in this sample not only based on raw measurements but also when adjusted for their smaller body size. These consistent shape differences suggest that the *shape* of these elements, not only their *size*, may be functionally important. Stylohyoid and ceratohyoid morphologies may not differ between roaring and purring felids because these elements are farther from the vocal apparatus and less involved in vocalizations. Although it is not possible to understand this pattern separately from phylogenetic patterns (these are two separate monophyletic clades and therefore the influence of the phylogeny cannot be removed from potential functional signals), the fact that the two bones that clearly distinguished roaring from purring felids were caudal bones closely associated with the thyroid cartilage, and hence associated with the vocal folds, suggests that this difference may reflect functional differences in vocal capabilities. With that said, although there is this seemingly correlative relationship, the true functional relationship between any of the hyoid bones and the soft tissues of the vocal apparatus requires much further exploration. As the vocal folds are more closely related with the laryngeal cartilages, if there is a functional relationship between vocalization and hyoideal morphology, it is likely related to some developmental processes common to the anatomical region.

While felid vocal differences have traditionally at least in part been attributed to the level of ossification of the epihyoid (Owen, 1834; Pocock, 1916; Weissengruber et al., 2002), the position of the epihyoid away from the vocal apparatus and between the stylohyoid and ceratohyoid—two bones that we found were not morphologically different between purring and roaring cats—suggests to us that a lack of epihyoid ossification may instead be a synapomorphic trait shared by *Panthera* unrelated to their acoustic production repertoire. This interpretation of epihyoid ossification as a phylogenetic signal unrelated to behavior is aligned with that of Peters (1978) and Peters and Hast (1994), who suggested that *Panthera uncia*'s inability to roar despite having an unossified epihyoid, while all cats that purr have a fully ossified epihyoid demonstrates a lack of correlation between this trait and behavior. Our sample does not include any hyoid elements from *Panthera uncia* or *Neofelis*, the sister taxon to *Panthera* which displays ossified epihyoids; however, future examination of these taxa could help disentangle roaring from unrelated phylogenetic trends—potentially using a radiographic approach to determine exactly which osteological movements (if any) occur during roaring and purring.

By comparison to the hyoid elements of the extant felids in our sample, *S. fatalis* hyoid elements are much larger in size and more robust relative to their body size. *Smilodon fatalis* is estimated to be similar in size to modern *P. leo* and *P. tigris* (Christiansen & Harris, 2005), yet, based on PC1 of nonsize-adjusted measurements, which reflects scaling, *S. fatalis* ceratohyoids, basihyoids, and thyrohyoids are significantly different from all of the extant felids, and their stylohyoids are significantly different from extant purring cats but not roaring cats. Because of the close association between the hyoid bones and laryngeal tissues, this likely reflects a larger larynx, which has been found to correlate with lower frequency vocalizations (Bergman et al., 2016; Titze et al., 2016), suggesting that *S. fatalis* was capable of producing lower frequency vocalizations than extant felids.

Hyoid size may also relate to feeding and respiration. The hyoid provides rigid support for the airway and anchors muscles involved in upper airway dilation (van Lunteren et al., 1987a, 1987b; Wiegand & Latz, 1991) and swallowing (Thexton & McGarrick, 1994). Larger hyoid elements provide larger potential attachment area for these muscles suggesting that the muscles involved in swallowing and respiration may have been greater in volume relative to body size in *S. fatalis* than in extant cats.

While the sizes of *S. fatalis* hyoid elements were larger than those of extant taxa, the shape of their bones when adjusted for size tended to be more similar to Felinae hyoid elements. This was opposite to our a priori hypothesis derived from prior research, likely because previous studies rarely considered *shape* variation. Only the basihyoid and thyrohyoid reflected significant shape differences between *Panthera* and Felinae, and for both of these elements, *S. fatalis* differed significantly from *Panthera* but not Felinae, suggesting that if these differences do reflect features of vocalization, *S. fatalis* may have been capable of producing vocalizations more similar to those of Felinae. These findings run contrary to preliminary findings from Shaw (2018), which suggest that *S. fatalis* hyoid elements are morphologically similar to those of *Panthera*.

When species means were analyzed to understand morphological differences between groups across multiple elements, similar size and shape trends were reflected. Because of the small sample size in these combined analyses, no additional statistical tests were able to be performed.

Panthera atrox was only represented by a single thyrohyoid element. Despite being nested within the genus *Panthera*, this element was significantly larger and more robust than extant *Panthera*. This, however, is to be expected, as *P. atrox* is estimated to be larger than extant pantherines (Christiansen, 2008). Similar to *S. fatalis*, this substantial size difference may reflect a lower vocalization frequency (Titze et al., 2016) as well as larger muscle volumes associated with swallowing (Thexton & McGarrick, 1994) and respiration (van Lunteren et al., 1987b, 1987a). The shape of this bone did not differ from those of extant *Panthera*, potentially suggesting that *P. atrox* was capable of producing vocalizations similar to modern pantherines, including having the ability to roar.

A clearly substantial difference between the *Panthera* and Felinae is epihyoid ossification. Of the fossil 106 *S. fatalis* hyoid elements in the RLB collection at the time of this data collection, only one element was classified as an epihyoid. PCA of sheared residuals place this element squarely within the morphospace of Felinae epihyoids; however, our measurements fail to capture the unique s-curve present in the bone (Figure 6), which is not characteristic of Felinae epihyoid bones. This uncharacteristic morphology may suggest that this bone has been misclassified as a *S. fatalis* epihyoid. Furthermore, as epihyoids represent more than 22% of modern Felinae hyoid bones (i.e., two of the nine ossified hyoid elements in each individual), it is statistically highly unlikely that there would be a taphonomic reason to bias the sample so substantially to result in them being less than 1% of the RLB *S. fatalis* hyoid sample.

While preservation of these elements is uncommon even within the RLB site, preservation of context is even less likely. This reflects a larger problem with this sample and paleontological interpretations in general. These hyoid elements have been found in isolation. While experts have identified elements and assigned them to taxonomic

FIGURE 6 Possible *Smilodon fatalis* epihyoid (RLB R33114). The fracture at the center of the shaft does not show signs of healing and likely occurred postmortem. Pathology cannot be ruled out. Scale = 1 cm.

designations, we do not have hyoid elements associated with specific *S. fatalis* or *P. atrox* crania or more complete skeletons to compare them to. While an unossified epihyoid in *S. fatalis* would not be parsimonious with felid phylogenetics because both Felinae and the first members to branch off within Pantherinae, *Neofelis*, have ossified epihyoids, ossification is developmentally controlled and has been lost then gained in other lineages (Schultz et al., 2016; Zhu, 2014). The underrepresentation may instead be reflective of larger trends within this sample. Caudal elements are better represented than rostral elements. It is possible that preservation differences are related to as yet undetected differences in the degree of ossification (e.g., possibly affecting density) across all hyoid elements in addition to known variation in epihyoid ossification. Future research may further investigate this potential trend.

Hyoid elements are rare in the fossil record and as such have rarely been studied. Because of this, little is known about the evolutionary history and functional morphology of hyoid elements. While Felidae has received the majority of focus in the discussion of the relationship between hyoid shape and size and vocalizations because of the purported roaring/purring divide, previous studies have focused largely on the presence or absence of epihyoid elements (e.g., Pocock, 1916), a feature that cannot be assessed in the already sparse fossil record and may not relate to acoustic capabilities (e.g., Hast, 1986; Peters & Hast, 1994). This study instead quantitatively examined the relationship between hyoid morphology and vocalization amongst modern felids. This kind of approach has been applied in canids (Flores et al., 2020), xenarthrans (Pérez et al., 2010) and now felids; however, it is essential to examine the relationship between vocalizations and hyoid morphology in more diverse taxa to better understand this important ecological variable in the past. Due to phylogenetic constraints in extant Felidae, it is currently difficult or impossible to distinguish between morphological similarities related to vocalization behavior and those related to shared evolutionary history unrelated to vocalization. This could be remedied through detailed functional investigations, including experimental approaches that examine the role of hyoid bones and their associated soft tissue anatomy in vocalization for felids as well as the relationship between soft tissue anatomy and the morphology of the hyoid elements themselves.

Despite sampling and phylogenetic limitations, the quantitative examination of extant and extinct felid hyoid morphology revealed interesting trends related to felid evolution as well as behavioral reconstruction of *S. fatalis*. Although the signal could be driven predominantly by phylogenetic relationships, the elements that most define the morphological differences between purring and roaring cats are elements most closely associated with the vocal tissues of the larynx: the basihyoid and ceratohyoid. Thus, the ossification of one of the more cranial bones, epihyoid, which has traditionally been attributed to felid vocal differences (Owen, 1834; Pocock, 1916; Weissengruber et al., 2002), may be merely a synapomorphic trait in *Panthera* rather than a true indicator of vocal behaviors. When projecting fossil taxa onto these extant differences, basihyoid and thyrohyoid shape morphology in *S. fatalis* is more similar to that of purring cats than roaring cats, but their hyoid elements are significantly larger than those of extant felids, suggesting that *S. fatalis* may have produced vocalizations similar to members of Felinae but at a lower pitch; however, given some of the morphological uniqueness and combination of size and shape morphology, and the lack of empirical evidence that major vocal differences within Felidae are significantly influenced by this osteology at all, it is alternatively possible that *S. fatalis* produced vocalizations wholly different from those produced by modern felids.

AUTHOR CONTRIBUTIONS

Ashley R. Deutsch: Conceptualization; investigation; writing—original draft; methodology; validation; visualization; writing—review & editing; formal analysis; data curation. **R. Brian Langerhans**: Methodology; writing—review & editing; formal analysis; validation. **Deanna Flores**: Conceptualization; writing—review & editing; investigation; visualization; formal analysis. **Adam Hartstone-Rose**: Conceptualization; investigation; funding acquisition; writing—review & editing; visualization; methodology; validation; project administration; data curation; supervision.

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DATA AVAILABILITY STATEMENT

The data that support the findings of this study are openly available in Dryad at https://doi.org/10.5061/dryad.j6q573nkp.

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