
What's the difference? A multiphasic allometric analysis of fossil and living lions

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Introduction

Differentiating between various species in the fossil record is one of the most vital tasks in paleontology. As such, evaluating the morphological features that we use to make these taxonomic distinctions is critical. Without any confirmation from molecular lines of evidence, morphological analyses are the only option for such studies. Determining the validity and independence of character changes is a major part of that evaluation. Compounding this limitation to morphological analyses is the fact that assembling a significant sample size of fossil specimens for a single taxon is frequently very difficult, if not impossible. Often, paleontologists compare a single fossil specimen with a single specimen of a closely related extant taxon or representatives of several such taxa. Analyses of this nature, while valuable first glimpses, do not account for variation within populations (of either the fossil or the extant groups), and therefore may result in inaccurate conclusions regarding the relationships of the organisms in question. In this chapter, I present an example of a species–status conflict within the pantherine felids and use allometric analyses to evaluate some of the morphological characteristics that have been used as evidence to support arguments in this conflict.

Since its first official use by Pocock (1930), the generic designation of *Panthera* for the clade consisting of the lion (*P. leo*), tiger (*P. tigris*), leopard (*P. pardus*), jaguar (*P. onca*), and now the snow leopard (*P. uncia*) has reached standard usage. However, the attribution of species or subspecies status below the rank of genus has not been so readily settled, especially for fossil groups that seem to show a relationship to one of the extant pantherine cats. One of these fossil groups is the ‘American lion’ (*Panthera leo* cf. *atrox*). There has been some argument regarding the nature of the relationship of *P. atrox* and *P. spelea* (the ‘cave lion’) within *Panthera*, and several authors have maintained a *P. tigris* or

P. onca affinity for *P. atrox* (e.g. Simpson, 1941; Groiss, 1996). However, as the majority of authors have discussed the affinities of *P. atrox* in relation to modern *P. leo*, those will be the comparisons that I will address in this chapter. When using the term 'lion', I am referring to any member of the extant species *Panthera leo* and any known fossil specimen that is more closely related to that species than they are to any other extant species. This definition includes, but is not limited to, specimens attributed to the species *P. atrox* (the 'American Lion') and *P. spelea*.

Palaeogeography of lions

The current geographic distribution of lions is limited to sub-Saharan Africa, with a relic population in northwestern India. This limited range is a fairly recent development as lions are known throughout North Africa and the Middle East as late as the twentieth century (Sunquist and Sunquist, 2002). Prehistorically, however, lions were very widespread indeed. The first lion-like (and lion-sized) species of the genus *Panthera* appears in eastern Africa almost 3.5 Mya ago (Barry, 1987). The earliest fossils that have been attributed to the species *P. leo* come from sediments in the Olduvai Gorge in Tanzania dated at around 1.87–1.7 Mya (Petter, 1973). During the Pleistocene, the lion spread out of Africa and across Eurasia. The earliest lion remains known from North America are found in Alaska and date to roughly 300 Kya ago (Kurtén and Anderson, 1980; Herrington, 1987; Yamaguchi *et al.*, 2004). From there, lions spread south into western North America and South America. Lion fossils have been found as far south in the Americas as the Talara region in northwestern Peru (Lemon and Churcher, 1961). The presence of lions in the Americas persisted until about 10,000 years ago (Harington, 1977; Yamaguchi *et al.*, 2004).

Species-status arguments

Considering the taxonomic arguments that have plagued study of the entire family Felidae (Haas *et al.*, 2005; Bona, 2006), it is not surprising that the species status of fossil lions has been a subject of some debate throughout the years. The American Lion was first described by Leidy (1853) as a separate species (within the genus *Felis*, which, at that time, included all cats). A fuller and more complete description came from Merriam and Stock (1932), who were working with a larger sample of specimens from the La Brea Tar Pits in Los Angeles, California. They, too, chose to designate the American lion as its own species, and proposed that it might be the ancestral stock from which the modern lion and tiger descended. Their conclusions, however, may have

resulted from the information available to them at that time. No lion fossils were known from Siberia or Beringia at that time, and the geographically closest extant *Panthera* species was the tiger (Harington, 1977). Their morphological arguments supported a close relationship with the lion, so it is likely that this paleogeographic consideration prompted their argument for an affinity with *P. tigris*, and perhaps their conclusion that the American lion may be ancestral to both *P. tigris* and *P. leo*.

During much of this early work, species-status was given to these fossils partly because the paleontologists were not entirely certain to which modern *Panthera* species these fossils were most closely related. Most authors agree that the cave lion and the American lion most closely resemble each other (Harington, 1969; Vereshchagin, 1971; Hemmer, 1974; Sotnikova and Nikolskiy, 2006). Simpson (1941) proposed that the American lion was actually an oversized jaguar, although distinct from the extant jaguar (*P. onca*). However, most authors have noted that the American and cave lions shared affinities with modern lions and modern tigers (Leidy, 1853; Pocock, 1930; Merriam and Stock, 1932; Vereshchagin, 1971; Kurtén, 1985; Groiss, 1996; Sotnikova and Nikolskiy, 2006). Aside from Groiss (1996), who felt that braincase similarities were enough to place the cave and American lions within *P. tigris*, most researchers have concluded that the fossil specimens more closely resemble the lion, and that the several tiger-like features are plesiomorphic (Sotnikova and Nikolskiy, 2006). The most promising recent evidence for this conclusion may be the fact that fossil molecular work done on the cave lion placed it as a sister taxon to all modern lions (represented by several subspecies) in an analysis that included both *P. pardus* and *P. tigris* (Burger *et al.*, 2004).

Since the general consensus (although by no means the only possibility) is that the fossil specimens are most closely related to *P. leo*, the main phylogenetic contention has become the status of these groups as separate species (*P. atrox* and *P. spelea*) versus a subspecific designation within *P. leo* (*P. l. atrox* and *P. l. spelea*). This latter assignment has been used by many authors and seems to represent the majority opinion in most of the current literature (e.g. Harington, 1971; Hemmer, 1974, 1979; Kurtén and Anderson, 1980; Haas *et al.*, 2005). There are those who disagree with this assessment, claiming that the fossil lions show synapomorphies separate from modern *P. leo* (Sotnikova and Nikolskiy, 2006). Despite the general agreement that the cave and American lions most closely resemble each other, several authors have pointed out that the American lion is more derived and may be distinct from even the Siberian *P. l. spelea* specimens examined (Kurtén, 1985; Sotnikova and Nikolskiy, 2006). As such, an analysis addressing the differences between fossil and living lions should focus on this most disconnected of the available groups.

While most work discerning the various subspecies in extant *P. leo* uses soft tissue and molecular data (Hemmer, 1974; Dubach *et al.*, 2005; Haas *et al.*, 2005), fossil specimens generally provide only skeletal morphology for examination. Therefore, the designation of species status with regard to these fossil groups has relied heavily on this morphology in conjunction with the geographic distribution of the specimens. However, given that the fossil record is somewhat capricious and arbitrary in the amount and types of information it provides, statistical samples of fossil features can be difficult to attain. In this chapter, I will present several skeletal features of the skull that have been proposed by various authors as distinguishing between the extinct *P. l. atrox* and the extant *P. leo*. These characteristics will be quantitatively examined using a multiphasic allometric methodology that allows for a population-level analysis of these features as distinguishing taxonomic characters.

Methods

Proposed phenotypic differences between the crania of *P. l. leo* and *P. l. atrox*

The species-status arguments regarding *P. l. atrox* are based upon numerous phenotypic differences with relation to the modern *P. leo* that have been proposed. The larger size of *P. l. atrox* has been noted by most authors and remains uncontested. In order to address the question of species-status in the American lion, I analysed measurements obtained from *P. l. atrox* specimens and compared them to similar measurements from extant lion specimens. These measurements are solely from the exterior of the skull, so analysis is necessarily restricted to cranial features that are externally visible. While some arguments regarding separation of these groups based on hide pattern (Harington, 1977), mane presence/absence (Yamaguchi *et al.*, 2004), and brain endocast morphology (Groiss, 1996) have been made, these are not features that can be statistically analysed from the samples available. Fortunately, there are multiple external cranial features that are different between *P. l. atrox* and modern *P. leo* and have been used as diagnostic characters. The features addressed in this chapter can be seen in Figure 6.1.

The size of the braincase in *P. l. atrox* relative to modern lions has been described in several studies, some of which say it is larger (Kurtén and Anderson, 1980), while others claim that it is smaller (Merriam and Stock, 1932; Harington, 1969; Martin and Gilbert, 1978; Sotnikova and Nikolskiy, 2006). Groiss (1996) argued that brain size was irrelevant for taxonomic assignment, apparently in an effort to focus on brain morphology. Most of these studies refer to endocasts of the braincase, as opposed to external measurements of the skull. Due to this,

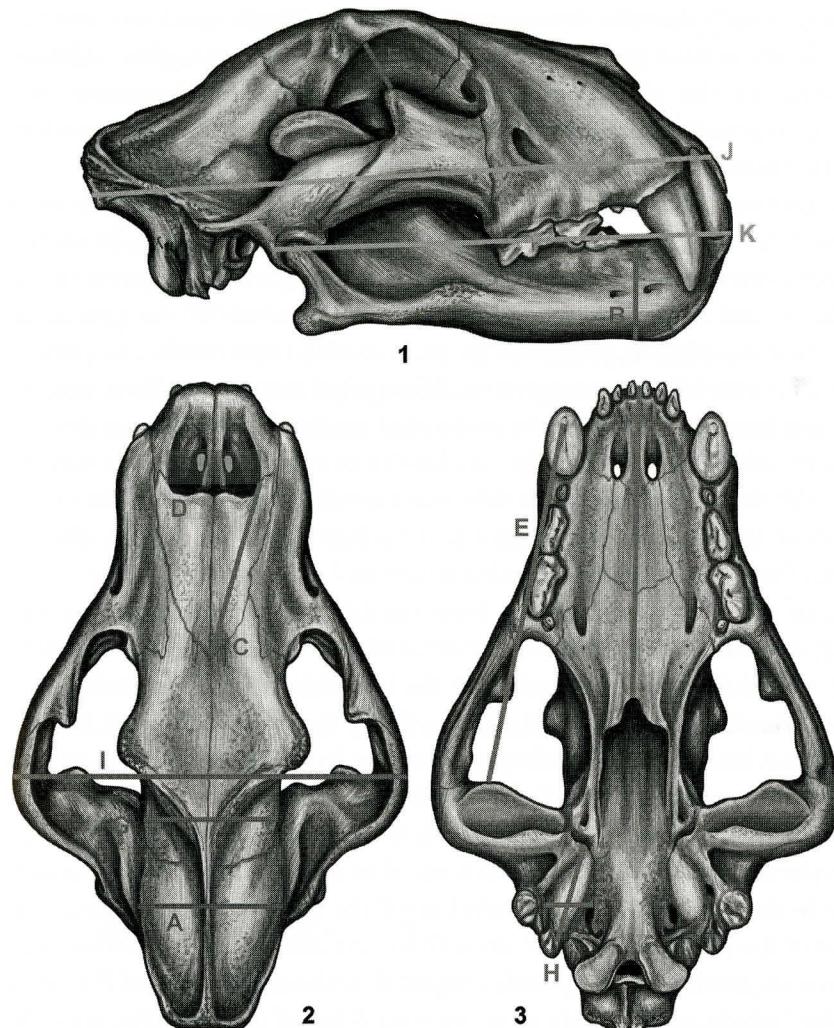


Figure 6.1 For colour version, see Plate 8. Measurements analysed for multiphasic analyses. A, Braincase width (BCW); B, mandibular flange (i.e. symphyseal) depth (MFD); C, nasal bone length (NBL); D, external narial area (NRA); E, facial length measured by length of the palate (PLL) and the length from the glenoid to the tip of the canine (GCL); F, orbit size measured by the distance between the left or right postorbital processes of the frontal and zygoma (LRPP); G, postorbital constriction width (POC); H, auditory bulla size measured as anteroposterior length (TBL) and mesiolateral width (TBW); I, zygomatic arch width measured as the greatest distance across the skull at the zygomatic arches (ZAW); J, skull length (SKL); K, mandible length (GML). The measurements are colour-coded based on whether that measurement should be larger (red), smaller (blue), or ambiguous (purple) in the American lion, according to descriptions in the literature as discussed above. The baseline measurements are shown in green. GML is the allometric baseline for MFD analyses. Skull of *P. l. atrox* illustrated by Emma Schachner, redrawn from Merriam and Stock (1932). Skulls are drawn in 1. lateral, 2. dorsal, and 3. ventral views.

they generally only describe one or two specimens. Single specimen analyses between closely related groups with natural levels of morphological variation may account for this discrepancy in the literature regarding braincase size. For this study, external braincase width (BCW) is the measurement used to address this feature.

While discussing the affinity of *P. l. atrox* to modern *P. leo*, Martin and Gilbert (1978) stated that the orbits in *P. l. atrox* were large and forward-facing. However, they made no mention as to whether they considered this to be in excess of the already large and forward-facing orbits of most members of the genus. In general, their description seems to be in line with their desire to portray *P. l. atrox* as a cursorial cat convergent on *Acinonyx* (or more likely *Miracinonyx*). The distance between the tips of the postorbital processes (LRPP) on either the left or right side, depending on the availability of measurement, was used to examine orbit size variations. While this measurement is expressly chosen to test the variation hypothesised by Martin and Gilbert (1978), it should also be indicative of any other variation in orbit structure.

In one of the earliest descriptions from the La Brea tar pits, Merriam and Stock (1932) report that mandible of *P. l. atrox* had a sharp chin. While in extant lions the ventral surface slopes back from the lower incisors, they reported that American lion mandibles dropped sharply down from the incisors to a more abrupt corner before the ventral surface swept back under the rest of the toothrow. The measurement of the dorsoventral depth of the mandibular ramus at the postcanine diastema (MFD) is used here to analyse this feature.

The external nares of *P. l. atrox* open somewhat dorsally, as in *P. leo*, although not quite to the same extent. The rostral tip of the nasal suture is closer to the rostral tip of the premaxillae in *P. l. atrox* (Merriam and Stock, 1932). However, this difference contrasts slightly with a report that the nasal bones of *P. l. atrox* are shorter (which would imply that the rostral tip of their suture might be farther away from that of the premaxilla) (Martin and Gilbert, 1978). However, Martin and Gilbert (1978) also described a shorter face and larger nareal area in *P. l. atrox*, which may have resulted from their observations regarding the nasal bones. Several measures were chosen to analyse these two features (craniofacial length and narial orientation). The distance from the glenoid to the canine (GCL), the palate length (PLL), and the nasal bone length (NBL) are informative with regard to the shortness of the preorbital face. The external nareal area (NRA) and the length of the nasal bone (NBL) are informative with regard to the external nareal opening.

The postorbital constriction of *P. l. atrox* is reportedly 'less pronounced', as a result of the posterior skull (including the braincase) being fuller and more robust (Merriam and Stock, 1932). More recent work has also reported that the

cave lion is also less constricted than the modern lion (Sotnikova and Nikolskiy, 2006). These same researchers, however, note that the La Brea specimens have still greater breadth across the constriction, which is important when considering this analysis (see 'Sampling effects' below). The width of the skull at the postorbital constriction (POC) is informative with regard to this feature. A 'less pronounced' constriction shows up as a wider measurement.

Several reports have claimed that the auditory bullae in *P. l. atrox* are relatively small, although most authors have not designated whether they are small for a lion of that size or whether they are absolutely smaller than those of extant *P. leo* (Martin and Gilbert, 1978). Interestingly, Merriam and Stock (1932) did not note these small bullae in their first description of the skull, possibly because they did not feel that this feature was helpful in determining whether *P. l. atrox* had a closer affinity to *P. leo* or *P. tigris*. Two bullar measurements were used in this study: total bullar length (TBL) and total bullar width (TBW).

Finally, Merriam and Stock (1932) reported that the American lion had two phenotypes, one of which had very wide zygomatic arches, the other having more narrow arches. A specimen from northern Alaska was also described as having a large zygomatic arch breadth (Harington, 1969). However, Sotnikova and Nikolskiy (2006) claimed that the modern lion is derived in having 'strongly arched zygomata'. Unfortunately, they gave no indication whether they mean broader zygomata or simply zygomata that are arched in a different shape (rounder arching in the dorsal view). In order to examine this feature, the width across the zygomatic arches (ZAW) was examined.

Measurement acquisition

To obtain the measurements for this study, I visited the paleontological and osteological collections of several museums. The majority of extant *P. leo* measurements in this study were obtained from specimens in the Mammalogy Department at the American Museum of Natural History (AMNH) in New York City. Their extensive collection provided over 90 *P. leo* skulls that were complete enough for measurement. *P. atrox* measurements were obtained from specimens at the Canadian Museum of Nature (CMN) in Ottawa, ON and the Page Museum at the La Brea Tar Pits, which is a branch of the Los Angeles County Museum of Natural History (LACMNH) in Los Angeles, CA.

The specimens were measured using a Microscribe G2X digitiser. The digitiser provided a quick, accurate, and efficient method for taking multiple measurements from a large quantity of specimens quickly with little handling of the specimens themselves. The range of the arm is 127 cm (50 in), which was easily large enough to obtain measurements from every felid skull encountered.

The precision of the digitizer was 0.23 mm (0.009 in), which is less than most calipers would provide. However, the measurements taken were large enough that the digitiser precision was acceptable.

When taking the measurements for this study, each skull was mounted using clay so that it would not be able to move during the measurement session. In order to obtain all of the measurements, most skulls had to be mounted in three separate positions: skull (without mandibles) upright, skull upside-down, and mandibles upright. After taking the locations of each of the measurement endpoints available, the skull was examined for damage or deformation that could skew or invalidate the measurements.

Allometric analysis

Nearly all authors have commented upon the fact that *P. l. atrox* is larger than the modern *P. leo*. Despite this broad agreement, very little research has aimed to statistically distinguish which of the cranial features described above correspond with allometric trends in *P. leo*. In order to do this, I used multiphasic allometric analyses of various measurements of the skulls of *P. leo* and *P. l. atrox* (see below for the procedural details). Multiphasic allometric analysis involves analysing shape and size proxies with an eye on the possibility that their relationships are different at different size ranges. Multiphasic regression analysis fits different regression lines to different sections of the data, finding the best statistical fit. When applied intraspecifically, regression analyses of this type allow for the recognition of ontogenetic allometries consisting of more than one growth phase, illuminating periods of ontogenetic development where the trait is developing faster or slower. In this way, multiphasic allometric analysis allows a researcher to discover more complex allometric relationships without relying on age determination (see Figure 6.2 for a comparison of multiphasic and monophasic allometric analyses). This feature of multiphasic analyses is particularly important for the comparison of modern *P. leo* with fossil *P. l. atrox*. In most wild felids, tooth eruption is the most reliable form of age determination. However, the teeth of most felids finish erupting before the organism has completed its developmental growth. As mentioned below, most museum specimens of large pantherine felids have little to no age data. In the absence of these data, multiphasic allometry allows a researcher to find developmental growth phases based on the size of the organism.

Having designated these periods of different allometric relationships, one can compare these patterns with other groups (subspecies or closely related species) and see if interspecific size differences account for perceived shape differences. For the comparison of postorbital constriction widths of *P. leo*

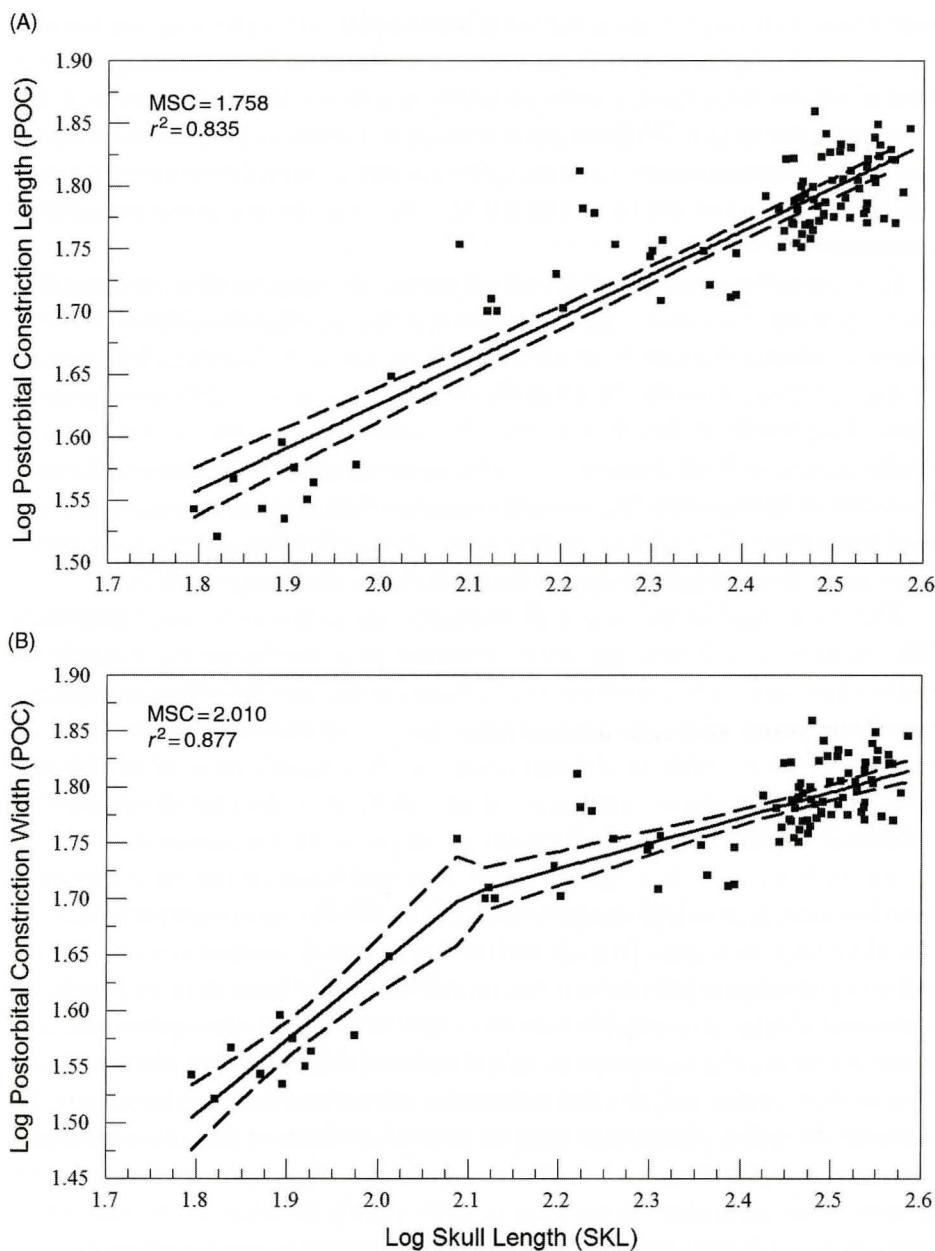


Figure 6.2 Comparison of monophasic and multiphasic allometries. Data plots for the logged postorbital constriction width measurements of the *P. leo* specimens plotted against logged skull length. All scale units are \log_{10} millimetres. Fit statistics r^2 and MSC are given for each regression. A, Monophasic (simple) allometric regression through the data showing 95% confidence intervals. B, Multiphasic allometric regression through the same data showing 95% confidence intervals. This regression is a two-phase regression with a phase change at 2.1 (the value of X_{pi} in Equation 1) on the x -axis.

(see Figure 6.2) and *P. l. atrox*, the use of a monophasic (simple) regression would not reflect the biphasic growth pattern seen in the data. As such, comparison of that allometry with the *P. l. atrox* allometry would not be representative of this more complex nature. Without many juvenile *P. l. atrox* specimens available (see below), the determination of the final phase of ontogenetic development for each trait in *P. leo* became even more important, as that was the only phase available for comparison in *P. l. atrox*.

I compared the cranial measurements of statistically viable numbers of extant *P. leo* ($n = 93$) and *P. l. atrox* ($n = 46$) in order to examine whether the differences in the features outlined above are the result of simple extension of allometries (ontogenetic scaling) resulting from the American lion's greater size or truly different characters derived separately within that taxon. This analysis allows for an evaluation of independence of these characters from the size difference noted between the taxa. I compared the two taxa using two different types of allometric analysis: monophasic and multiphasic. In order to analyse these allometric relationships, each cranial measurement was logged and plotted against the log skull length (SKL).

The use of skull length as the allometric baseline deserves some explanation. The skull of vertebrates has been identified as a developmental module for quite some time. The pattern of skull growth from early in ontogeny separates the development of the skull from that of the rest of the body (Jacobson, 1993), apparently as a result of differentiation of the neural crest (Langille and Hall, 1993). Therefore, treatment of the skull as a distinct developmental module is justified. Using skull length as the proxy for the size of that module is appropriate, as it is a measurement that encompasses the entire module. Furthermore, a principal components analysis (PCA) was performed on all of the skull measurements. In such analyses of biological entities, the first principal component generally reflects the overall size of the body or body part being measured (McKinney and McNamara, 1991), provided the first principal component explains the vast majority of the variance (Hammer and Harper, 2006). In the PCA performed, the first principal component accounted for 98% of the variance, and all loadings were positive, strongly indicating that this component represents overall size. SKL had the highest loading (0.56) on the first component, indicating that its variance is more closely correlated with the overall size of the skull than any other measurement. Based on these arguments, skull length was deemed appropriate for use as the allometric baseline of this study.

I performed linear best-fit analyses on these bivariate plots to determine the allometric parameters for each measurement. Three different types of best-fit line were employed: original least squares (OLS or linear regression), major axis (MA), and standardised major axis (SMA, or reduced major axis). The best fits for each taxon were then compared (discussed below). Monophasic allometric

analyses produced and compared single best-fit lines for the entire specimen sample of each taxon, including skulls of the youngest cubs available (some only a week or two old). Multiphasic allometric analyses, however, required the determination of the final growth phase of development in the taxa for comparison.

To compare multiphasic allometric relationships, I first performed a multiphasic allometric analysis on the *P. leo* sample, determining the optimum number of regression segments and their location. To perform these regressions, I used the following equation from Vrba (1998):

$$Y = \beta_1 X + \alpha_1 + \sum_{i=2}^n I_i \beta_i (X - X_{P(i-1)}) \quad (1)$$

where Y is the log of the feature measurement; X is log skull length; β_i is the regression coefficient (line slope) for the i th phase; α_1 is the Y -intercept of the first phase (P_1) line; I_i is an indicator variable such that $I_i = 0$ if $X < X_{P(i-1)}$ and $I_i = 1$ if $X > X_{P(i-1)}$; X_{P_i} is log skull length value at the end of growth phase i . In order to determine which model (number of phases) fit the data best, I used the Model Selection Criterion (MSC) in PSI-Plot (2002), which is an adaptation of the Akaike Information Criterion (AIC) (Akaike, 1974). The MSC evaluates the correlation between the best-fit line and the data, but penalises best-fit formulae for each parameter they contain. Therefore, while the correlation will likely go up with the number of phases allowed in the regression formula, the MSC will be lower for models that use too many phases for a relatively small increase in correlation.

Ontogenetic age designations were almost never available on the museum tag for the *P. leo* specimens. Therefore, for this group, age determinations were performed using the calendar of Smuts *et al.* (1978) for tooth eruption. Because these determinations used only tooth eruption schedules, all individuals with fully erupted adult dentition are referred to as adults. However, one should note that fully erupted adult dentition occurs well before sexual adulthood and the end of ontogenetic development in lions. Error in age estimation based on tooth eruption increases with age. Based on this methodology, age class estimates were established for the *P. leo* population. The distribution of specimens in the various age classes can be seen in Table 6.1. As one would expect, the majority of specimens are classified as 'adult' (meaning that their adult dentition have fully erupted); however, there is a relatively good representation of each age class through development. There were no prenatal specimens in these analyses.

For *P. l. atrox*, very few young juvenile specimens were preserved in the fossil record, reducing the overall spread of ages sampled. There are juveniles in the sample, however, the use of the Smuts *et al.* (1978) calendar would not be

Table 6.1 Distribution of specimens of *P. leo* and *P. l. atrox* by age class as determined using the Smuts *et al.* (1978) tooth eruption calendar. As discussed in the text, this calendar is not appropriate for *P. l. atrox* and is used here only to show the dearth of very young specimens of this group.

Smuts <i>et al.</i> (1978) age class	No. of <i>P. leo</i> specimens	No. of <i>P. l. atrox</i> specimens
0–7 days	7	0
7–21 days	4	0
1–2 months	3	0
2–3 months	3	0
4–8 months	4	0
9–11 months	3	1
12–14 months	4	1
14–17 months	3	1
18–24 months	1	0
2–3 years	2	0
>2–3 years ('Adult')	59	43

appropriate for designation of ontogenetic age, because it is based on modern *P. leo* specimens and cannot be extrapolated to other *Panthera* species (and presumably not to extinct subspecies either). One should note that the *P. l. atrox* juveniles are not the very young juveniles that were available for the extant sample (see Table 6.1). Analyses of the *P. l. atrox* specimens showed that there were no multiphasic allometries discernible from the sample. Because of this, all *P. l. atrox* allometries in this study are monophasic, encompassing the final phase of ontogenetic allometry. Therefore, comparison of *P. l. atrox* allometries were performed only with the final phase of the multiphasic *P. leo* allometries. Using monophasic allometric analyses of *P. leo* does not account for the complexity of development, and lumps all variation into the single regression line provided. However, the use of multiphasic allometric analysis to determine the final developmental phase allowed for the most inclusive, late-developmental growth phases to be accurately compared between the taxa, allowing a comparison that is more appropriate and informative.

Comparing best-fit lines

Until recently, best-fit lines have only been statistically comparable if they were OLS regressions compared using an analysis of covariance (ANCOVA). OLS regression (and therefore ANCOVA) is not always appropriate for use with

allometric data, although it is commonly used. For a review of these conditions, please refer to Sokal and Rohlf (1995) or Warton *et al.* (2006). Recently, however, software has been developed to allow for statistical comparison of both MA and SMA regression lines (Warton *et al.*, 2006). I used this software (Standardised Major Axis Tests & Routines, SMATR) to determine and compare the best-fit lines for the various allometric relationships using all three best-fit techniques (OLS, MA, and SMA). The software utilises an algorithm that is comparable to a likelihood analysis, because it tests statistical compatibility through iterative testing (Warton and Weber, 2002; Warton *et al.*, 2006). SMATR allows for comparison of allometric slopes, elevational shifts in allometries (same slope, but significantly different y -intercepts), and shifts along allometries (an extension of an allometry into a larger size range).

There is often argument about the applicability or usefulness of MA vs. SMA for various data sets, so results from both analyses are provided to accommodate such discussion. OLS comparisons are also presented so that the regressions discussed here may be compared with previous studies that may have used that methodology to determine allometric relationships.

Culling measurements

Measurements were culled from analyses based on the sample size, the coefficient of determination (COD or r^2), or the feasibility of the allometric slope obtained. Sample sizes of less than five were considered useless for analyses, because their confidence intervals were too broad to allow for any meaningful interpretation. If the COD was too low (accounting for less than 30% of the variance), then the results for that measurement were rendered ambiguous and removed from comparison. If the slope of the allometry was extremely unlikely to represent the natural condition (i.e. if it was a negative value), then the measurement was considered untenable for analysis.

Sampling effects

The vast majority of American lion specimens which I measured were from the La Brea Tar Pits in Los Angeles. These specimens are housed at the Page Museum at the La Brea Tar Pits and were collected under the auspices of the Los Angeles County Museum of Natural History (LACMNH). The mode of entrapment in the tar pits was one that favoured the preservation of carnivores. A prey animal, such as a mammoth, would get stuck in the tar. Its distress calls or general scent would attract carnivores, often represented in the pits by dire wolves (*Canis dirus*), sabre-toothed cats (in this case *Smilodon*

fatalis), and the American lion. These carnivores would also get trapped in the tar. Attesting to this scenario, the Page Museum at the La Brea Tar Pits is full of the remains of carnivores and scavengers, yet contains relatively few herbivorous taxa.

While *P. l. atrox* remains are not nearly as plentiful in the tar pits as those of *S. fatalis* and *C. dirus*, they are substantially more abundant there than at any other Pleistocene site in the Americas. The American lion is rare at most sites, and, if found, is usually represented by a few teeth or a mandibular fragment, such as the type specimen described by Leidy (1853). Due to this preservational constraint, in order to examine the properties of the crania of these animals in a statistical manner, I was forced to rely on a large percentage of samples (100% for many measurements) from a single fossil locality. While previous morphometric analyses on the mandibles and dentition of the American lion have determined that there is no significant difference between specimens from La Brea and those from other localities across the Americas (Kurtén, 1985), the danger of local ecological or preservational bias is still present.

The sampling for extant lions should produce no bias. The skulls measured are housed at the American Museum of Natural History (AMNH) in New York City. These specimens were collected from all over Africa as well as from several zoos. Due to this diverse sampling, the variation found in extant lions should prove to be higher than would be expected for any subspecific group that may be within extant *P. leo*. As such, there should be no subspecific bias in the measurements for the extant lions used in this study.

Results and discussion

Previous comparative descriptions have resulted mainly from the analysis of one or a few skulls of each group (e.g. Martin and Gilbert, 1978; Groiss, 1996; Sotnikova and Nikolskiy, 2006). There has been some statistical analysis with regard to fossil and extant lions. Kurtén (1985) examined metric characters of various fossil lions from across Eurasia and the Americas. However, his analysis, while recognising some difficulties with including young specimens, did not analyse them allometrically, but merely compared the averages of dental and mandibular measurements. Hemmer (1974) performed an allometric analysis on extinct lions, although the measurements he analysed did not address the features outlined above. Hemmer's analysis also examined only adult specimens with a simple linear regression, which cannot detect multiphasic ontogenetic allometric relationships that might exist between the groups.

Every one of the measurements examined for this study exhibited multiphasic allometry in extant *P. leo*, as determined by MSC values. All of the

measurements showed biphasic allometric relationships in *P. leo*, except for braincase width (BCW), which had a triphasic allometric regression. The slopes and r^2 values of all analyses (mono- and multiphasic) for both taxa can be seen in Table 6.2. The intertaxon comparisons of these parameters are presented in Tables 6.3. and 6.4, respectively. Glenoid–canine length (GCL) and left/right postorbital process gap (LRPP) measurements did not produce sample sizes or correlations (r^2) that allowed for allometric analyses. As such, statements about species status based on these features should be considered tentatively.

The multiphasic comparisons showed different significance patterns for several of the measurements taken. In general, the use of multiphasic allometric analysis found lower F -statistics and higher p -values for the slope comparisons. For the analysis of palate length (PLL), the monophasic OLS regression indicated significantly different slopes between the two taxa. However, when the phasic nature of the development of this feature was taken into account, all three best-fit analyses indicated no significant difference in either the slope or the elevation (y -intercept). In the multiphasic analyses, the only measurement to show a significant difference in slope was postorbital constriction width (POC). This measurement demonstrated poor correlation with skull length in both taxa ($r^2 = 0.54$ and 0.46 for *P. leo* and *P. l. atrox*, respectively), which may account for this result. However, it should be noted that the POC values for *P. l. atrox* were consistently larger than for extant *P. leo*.

Elevation shifts (which can be detected if the slopes are not significantly different) were statistically detected in mandibular flange depth (MFD), nareal area (NRA), bullar length (TBL), and zygomatic arch width (ZAW). MFD and NRA both showed an elevational increase in *P. l. atrox*, while TBL and ZAW showed drops in elevation in this taxon relative to extant lions. POC also displayed an increase in elevation in *P. l. atrox* for the OLS analysis (the only one to find no significant difference in slope). Bullar width (TBW) showed a significant increase in elevation in only the MA and SMA analyses, with OLS showing no significant difference. The reverse is found in the braincase width analyses, with OLS showing a barely significant increase elevation in *P. l. atrox*.

Almost every measurement exhibited a shift in *P. l. atrox* that extended the allometry of modern lions into larger ranges. This result is unsurprising, as the increased size of *P. l. atrox* has already been noted across the board. This shift was detected for all but one of the measurements which also exhibited an elevational change. TBW showed no significant shift for the MA and SMA analyses. These analyses showed a significantly lower elevation for the *P. l. atrox* allometry, which may have affected their ability to detect a shift.

Arguments regarding the species status of *P. l. atrox* have been morphological in nature, but most fail to account for variation in the population and allometric

Table 6.2 Results of allometric regressions for *P. leo* and *P. l. atrox*. The beginning of the final phase of multiphasic regressions (Final Phase Start) is given as the value of the logged baseline measurement (SKL or GML) at the start of that phase.

Meas. analysis	<i>Panthera leo</i>				<i>Panthera leo atrox</i>					
	Monophasic			Multiphasic						
	r^2	Slope	y-intercept	r^2	# of phases	Final phase start	Final phase slope	r^2	Slope	y-intercept
BCW	0.97			0.98	3	2.43		0.71		
OLS	0.540	0.644					0.591		0.442	0.905
MA	0.544	0.634					0.688		0.473	0.824
SMA	0.550	0.621					0.741		0.525	0.692
MFD	0.95			0.95	2	2.14		0.45		
OLS	0.904	-0.540					0.669		0.670	0.091
MA	0.927	-0.593					0.898		1.00	-0.703
SMA	0.929	-0.597					0.925		1.00	-0.701
NBL	0.98			0.99	2	2.20		0.65		
OLS	1.123	-0.827					1.006		0.964	-0.450
MA	1.133	-0.852					1.051		1.254	-1.191
SMA	1.132	-0.849					1.049		1.200	-1.053
NRA	0.99			0.99	2	2.46		0.90		
OLS	1.069	-0.987					0.761		1.159	-1.196
MA	1.077	-1.005					0.989		1.236	-1.392
SMA	1.076	-1.004					0.992		1.223	-1.358
PLL	0.98			0.99	2	1.94		0.88		
OLS	1.077	-0.533					1.016		0.850	0.042
MA	1.091	-0.567					1.023		0.898	-0.081
SMA	1.090	-0.564					1.022		0.904	-0.096

POC	0.835		0.88	2	2.10		0.53	
OLS	0.344	0.939				0.226	0.579	0.402
MA	0.351	0.922				0.239	0.727	0.025
SMA	0.376	0.862				0.332	0.790	-0.136
TBL	0.95		0.96	2	2.32		0.49	
OLS	0.922	-0.601				0.627	0.600	0.158
MA	0.946	-0.660				0.839	0.806	-0.370
SMA	0.948	-0.664				0.882	0.860	-0.508
TBW	0.88		0.93	2	2.25		0.53	
OLS	0.787	-0.513				0.225	0.715	-0.367
MA	0.830	-0.616				1.207	0.971	-1.024
SMA	0.839	-0.639				1.042	0.979	-1.044
ZAW	0.99		0.99	2	1.94		0.70	
OLS	1.033	-0.255				1.062	0.658	0.682
MA	1.037	-0.265				1.071	0.751	0.444
SMA	1.037	-0.265				1.070	0.786	0.354

Table 6.3 Comparison of monophasic allometric analyses of *P. l. atrox* and *P. leo*.

Measurement analysis	Slope F-test	Slope P-value	Elevation WALD	Elevation P-value	Shift WALD	Shift P-value
BCW						
OLS	0.952	0.330	3.571	0.059	47.181	0.000*
MA	0.423	0.518	2.884	0.089	50.002	0.000*
SMA	0.060	0.806	2.211	0.137	52.611	0.000*
MFD						
OLS	2.452	0.121	54.127	0.000*	47.933	0.000*
MA	0.127	0.722	44.745	0.000*	69.535	0.000*
SMA	0.261	0.609	44.405	0.000*	71.714	0.000*
NBL						
OLS	0.266	0.609	5.204	0.023*	38.958	0.000*
MA	0.103	0.751	5.874	0.015*	32.712	0.000*
SMA	0.052	0.823	5.808	0.016*	33.541	0.000*
NRA						
OLS	0.238	0.624	7.043	0.008*	32.830	0.000*
MA	0.716	0.394	6.243	0.012*	35.264	0.000*
SMA	0.677	0.409	6.299	0.012*	35.152	0.000*
PLL						
OLS	4.077	0.039*	N/A	N/A	N/A	N/A
MA	2.373	0.122	1.255	0.263	46.886	0.000*
SMA	2.499	0.114	1.186	0.276	46.921	0.000*
POC						
OLS	1.492	0.222	51.488	0.000*	47.848	0.000*
MA	2.780	0.094	49.629	0.000*	55.967	0.000*
SMA	7.420	0.006*	N/A	N/A	N/A	N/A
TBL						
OLS	2.284	0.132	37.430	0.000*	42.083	0.000*
MA	0.233	0.629	41.507	0.000*	27.500	0.000*
SMA	0.173	0.679	41.997	0.000*	26.497	0.000*
TBW						
OLS	0.109	0.745	11.494	0.001*	42.083	0.000*
MA	0.256	0.615	15.737	0.000*	31.166	0.000*
SMA	0.461	0.499	17.231	0.000*	28.429	0.000*
ZAW						
OLS	1.982	0.157	7.746	0.005*	46.073	0.000*
MA	0.781	0.372	8.199	0.004*	43.829	0.000*
SMA	0.818	0.365	8.179	0.004*	43.938	0.000*

Note: * Significant at $p < 0.05$.

Table 6.4 Comparison of multiphasic allometric analyses of *P. l. atrox* and *P. leo*.

Final phase comparison	Slope F-test	Slope P-value	Elevation WALD	Elevation P-value	Shift WALD	Shift P-value
BCW						
OLS	1.622	0.203	4.946	0.026*	15.665	0.000*
MA	2.469	0.114	1.411	0.235	19.863	0.000*
SMA	2.663	0.101	0.323	0.57	22.657	0.000*
MFD						
OLS	0.000	0.995	87.315	0.000*	23.773	0.000*
MA	0.197	0.653	47.915	0.000*	53.047	0.000*
SMA	0.222	0.639	52.001	0.000*	71.864	0.000*
NBL						
OLS	0.019	0.891	2.359	0.125	21.108	0.000*
MA	0.306	0.582	3.484	0.062	15.507	0.000*
SMA	0.272	0.607	3.456	0.063	15.800	0.000*
NRA						
OLS	2.986	0.081	10.765	0.001*	4.614	0.032*
MA	1.258	0.260	6.669	0.010*	6.818	0.009*
SMA	1.364	0.245	7.972	0.005*	6.810	0.009*
PLL						
OLS	2.413	0.119	0.005	0.944	40.705	0.000*
MA	1.142	0.287	0.014	0.904	42.878	0.000*
SMA	1.165	0.279	0.013	0.909	42.846	0.000*
POC						
OLS	3.039	0.081	60.903	0.000*	34.6000	0.000*
MA	4.205	0.041*	N/A	N/A	N/A	N/A
SMA	9.141	0.003*	N/A	N/A	N/A	N/A
TBL						
OLS	0.017	0.899	19.100	0.000*	22.345	0.000*
MA	0.013	0.908	26.015	0.000*	8.431	0.004*
SMA	0.011	0.915	32.231	0.000*	6.000	0.014*
TBW						
OLS	3.096	0.078	0.515	0.473	8.606	0.003*
MA	0.083	0.762	4.823	0.028*	3.419	0.064
SMA	0.054	0.815	8.042	0.005*	3.348	0.067
ZAW						
OLS	2.216	0.135	8.968	0.003*	37.715	0.000*
MA	0.919	0.334	9.650	0.002*	35.406	0.000*
SMA	0.995	0.314	9.604	0.002*	35.631	0.000*

Note: *Significant at $p < 0.05$.

relationships. The results presented here indicate that such considerations are warranted. Of the eight major features examined here that have been argued as distinguishing of *P. l. atrox*, only five showed unambiguous differences when multiphasic allometric analyses were applied. Braincase width showed very little difference between the taxa, although OLS did show a weakly significant difference between the taxa. As mentioned in the methods section, however, OLS, while the most commonly used form of regression, is rarely applicable to allometric data. In the analyses done here, MA and SMA were consistent with regard to significant differences, with any inconsistency (which was rare) coming from OLS. At best, BCW seems to be ambiguous with regard to its independence of size.

The depth of the mandibular symphysis did show significant allometric differences. The elevated allometry of MFD for *P. l. atrox* indicates that the character noted by Merriam and Stock (1932) is indeed valid and allows for some level of distinction between the groups independent of size. The sharper chin resulting from this feature is not surprising in a felid coming from the Hollywood area and may indicate that this region of the country was a celebrity haven some tens of thousands of years ago just as it is today.

The shorter face of *P. l. atrox* does not seem to be a feature that is independent of the size change. The nasals show no allometric difference, indicating that *P. l. atrox* nasals are exactly the length that one should expect from a lion of that size. The length of the palate, another indicator of facial length, also showed no allometric deviation. The only other indicator of this feature (GCL) provided no information due to low sample size. There is, therefore, little evidence that the shorter face observed by some researchers in *P. l. atrox* is independent of the size difference of this organism.

The more dorsal opening of the external nares may have some validity as a feature distinct from size that distinguishes *P. l. atrox* from modern *P. leo*. While the nasals showed no difference, as mentioned above, the overall measure of nareal area did show significant allometric elevation in *P. l. atrox*. The fact that this feature, which is very much a product of the shape of the front of the face, shows deviation when those associated with the face 'shortness' showed no such difference may indicate that the shape of the nareal opening is altered such that it opens more dorsally.

The postorbital constriction of *P. l. atrox* from the La Brea region is definitely more robust than that found in extant lions. Even without strong allometries discernible in either taxon, the POC measurements of *P. l. atrox* were clearly higher, despite their poor correlation with size.

The auditory bullae's lower allometric elevation in *P. l. atrox* is both striking and intriguing. The bullae were absolutely about the same size as one would expect in modern lions (although in the lower end of that spectrum). It is

possible that the sound waves that were important in the life of an American lion were shorter than those that are important in modern lions. However, this speculation requires a great deal of further investigation. Nonetheless, the auditory bullae measurements show independence from the size difference between modern and American lions.

The zygomatic arches of *P. l. atrox* are narrower than those of *P. leo*; a feature that, according to the allometric analyses, is independent of the size difference. This result runs counter to the previous literature, which has indicated more strongly arching or wider zygomatic arches. The nature of this feature would not have been discernible without an allometric perspective. The significant difference of zygomatic arch width independent of the size difference supports the argument for species status for *P. l. atrox*. Contrary to previous argument, however, the width across the zygomas is narrower in *P. l. atrox* than it is in *P. leo*.

Conclusions

Assigning fossil specimens to extant taxa is a tricky business. The size difference between *P. l. atrox* and modern *P. leo* has led to several misidentifications of distinguishing features, because the differences between the taxa were not considered allometrically. The features examined in this study revealed that while many of the characteristics used to argue for/against species status are allometrically distinct in the two taxa, several are not. Braincase width and the facial shortness should not be considered differences between the taxa that are independent of size. When measured indirectly through the gap between postorbital processes, orbit size is too variable to be used as a distinguishing character, though other orbital measurements may be of value. Arguments based on such traits only serve to confuse and confound paleontological inquiry. The research presented here does not disprove the hypothesis that the American lion and modern lions are separate species. However, the argument for this hypothesis is weakened by broadly sampled, multiphasic, allometric analyses of these character traits. With the extensive museum collections we have accumulated and the ever-increasing computer power available, investigations into the allometry and variability of diagnostic characters will help refine our understanding of past species and their relationships to extant relatives.

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