# Evidence for unusual size dimorphism in a fossil ailurid

## Ethan L. Fulwood and Steven C. Wallace

### ABSTRACT

A second nearly complete skeleton of the fossil ailurid *Pristinailurus bristoli* was recently recovered from the Hemphillian (late Miocene) Gray Fossil Site of northeast Tennessee. It appears to be significantly larger than the previously known skeleton of *P. bristoli*, which was surprising as the living red panda *Ailurus fulgens* is thought to be generally monomorphic, including between sexes. Here the presence of significant size difference in the geometric means of cranial and postcranial measurements and canine area in the two specimens of *P. bristoli* is tested relative to the distribution of size differences in intersex and intrasex pairs of *A. fulgens*. The presence of sexual dimorphism in these dimensions is also assessed in *A. fulgens* using t-tests. We report the first evidence of sexual dimorphism in both upper and lower canine area in *A. fulgens*. We also found evidence of significantly greater body size difference in the two specimens of *P. bristoli* than that present in *A. fulgens*. This could reflect a variety of causes, including the presence of multiple species or subspecies, a greater range of ecologically driven variability, or the presence of sexual dimorphism. We argue tentatively for sexual dimorphism as the most plausible explanation for the apparent size range of *P. bristoli*.

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## INTRODUCTION

*Pristinailurus bristoli* Wallace and Wang, 2004 is known from the Late Hemphillian (7–4.5 Ma) Gray Fossil Site in northeast Tennessee (Wallace and Wang, 2004; Wallace, 2011a, 2011b), and is currently represented by numerous isolated teeth and bones and two relatively complete skeletons, which constitute the first associated skeletons from a fossil ailurine (Figure 1). Body mass estimates for
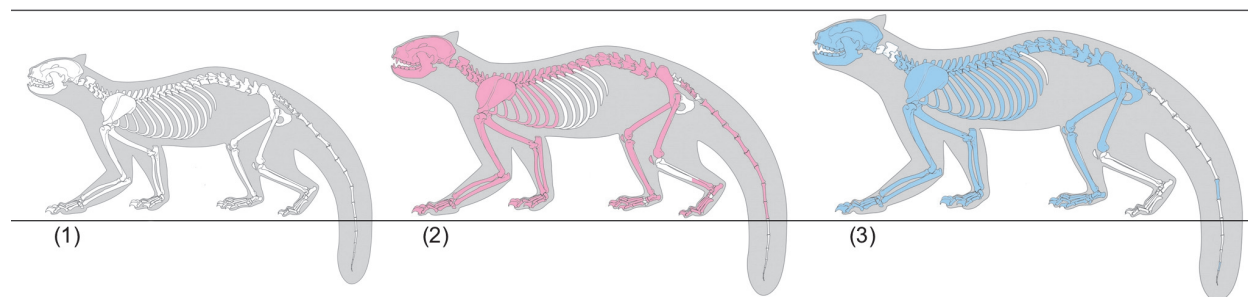
**FIGURE 1.** Size differences between *Ailurus fulgens* (1) and the two known skeletons *of Pristinailurus bristoli* (ETMNH 3596, 2; ETMNH 15000, 3). Shaded bones represent recovered elements from the two fossil skeletons.

the two specimens, calculated from the minimum breadth of the humerus following Christiansen and Harris (2005), differ by 52%. The smaller of the two specimens (ETMNH 3596), a fully mature individual showing dental wear indicative of advanced age, is reconstructed at 8.25 kg. Its skeleton is roughly 95% complete (Figure 1.2). The larger specimen (ETMNH 15000), a mature young adult with largely unworn teeth, is estimated at 15 kg. It is roughly 75% complete (Figure 1.3). These two individuals do not therefore appear to indicate separate steps in an ontogenetic sequence. They also occur in relatively close stratigraphic and spatial proximity, and share diagnostic characters of the upper first molar (as defined by Wallace and Wang, 2004; see also Wallace, 2011a, 2011b). These include a first molar with length less than width; metaconule enlarged, strongly crest-like and isolated from the protocone; metastylar and parastylar cusps poorly developed to lacking; absence of both a mesostylar cusp and a discrete accessory cusp on posterior cingulum between the metastyle and metaconule; and retention of a lingual cingulum that merges with the hypocone at its posterior end.

In addition to its greater size, ETMNH 15000 exhibits greater robusticity in all long bone elements, with a humeral width/length ratio of 0.11 and femoral W/L ratio of 0.09 compared to ratios of 0.098 and 0.074 for ETMNH 3596, respectively. ETMNH 15000 displays a broader and deeper rostrum than ETMNH 3596, a trait often associated with sexual dimorphism in male musteloids and likely related to canine root depth (Ritke, 1990; Gittleman and Valkenburgh, 1997). ETMNH 15000 also displays wider and more massive zygomatic arches, associated with greater canine bite strength (Ritke, 1990).

We explore the magnitude of the apparent size difference between these two specimens by reference to the size distribution of the modern red panda, *Ailurus fulgens*, using pairwise comparisons of *A. fulgens* individuals. The fossil skeletal sample size of two is insufficient for robust inferential statistical analyses, but the percentage of randomly drawn pairs of *A. fulgens* as dimorphic as the two fossil specimens may be provisionally suggestive of the pattern present in *Pristinailurus bristoli*. If the two known specimens of *P. bristoli* differ more in size dimensions than > 95% of pairs of *A. fulgens*, this may suggest that the difference between ETMNH 3596 and ETMNH 15000 is biologically significant. This could reflect higher size variability in this fossil species than is present in the living ailurid, including variability due to sexual dimorphism, or indicate two size-differentiated species or subspecies present at the Gray site in the Hemphillian.

## METHODS AND MATERIALS

### Sample

Following Stefen and Heidecke (2012), standard cranio- and osteometric measurements were taken on 11 male and 11 female specimens of *Ailurus fulgens* (Field Museum of Natural History and Smithsonian National Museum of Natural History) and two specimens of *Pristinailurus bristoli* (East Tennessee State University and General Shale Brick Natural History Museum). Not all measurements were recordable on some specimens due to damage (see Table 1), so the total sample had to be subsampled for some measurements to calculate mean values.

### Institutional Abbreviations

ETMNH – East Tennessee State University and General Shale Brick Museum of Natural History, Gray, Tennessee; FMNH – Field Museum of Natural History, Chicago, Illinois.

**TABLE 1.** Table of *p* values from each pairwise comparison by measurement and geometric mean. Asterisks indicate significant values (< 0.05). Bolded measurements indicate those discussed and interpreted in the text

| Measurements | Intersex *p* | Intrafemale *p* | Intramale *p* | Male *n* | Female *n* |
|---|---|---|---|---|---|
| Cranial length | 0.1111 | 0.125 | 0* | 9 | 8 |
| Basal length | 0.121 | 0.149 | 0.0741 | 9 | 11 |
| Zygomatic breadth | 0* | 0.0165* | 0* | 8 | 11 |
| Upper carnassial length | 0.0505 | 0.0744 | 0.0988 | 9 | 11 |
| Lower carnassial length | 0.0404* | 0.0496* | 0* | 9 | 11 |
| Upper canine mesiodistal breadth | 0.515 | 0.116 | 0.173 | 9 | 11 |
| Upper canine buccolingual breadth | 0.354 | 0.0744 | 0.148 | 9 | 11 |
| Lower canine mesiodistal breadth | 0.192 | 0.0413* | 0.0494* | 9 | 11 |
| Lower canine buccolingual | 0.182 | 0.0331* | 0.0370* | 9 | 11 |
| Facial length | 0.633 | 0.633 | 0.633 | 7 | 7 |
| Bicanine breadth | 0.025* | 0* | 0.0313* | 8 | 10 |
| Biorbital breadth | 0* | 0* | 0* | 8 | 10 |
| Skull height | 0.0313* | 0.0625 | 0* | 8 | 8 |
| Mandible length | 0.152 | 0.124 | 0.0988 | 9 | 11 |
| Coronoid height | 0.152 | 0.174 | 0.0123* | 9 | 11 |
| Mandible height | 0.0556 | 0.04* | 0* | 9 | 10 |
| Humerus length | 0* | 0.08 | 0* | 7 | 5 |
| Humerus breadth | 0.0571 | 0.04* | 0* | 7 | 5 |
| Femur length | 0.0286* | 0.12 | 0* | 7 | 5 |
| Femur breadth | 0* | 0* | 0* | 7 | 5 |
| **Upper canine area** | **0.404** | **0.0826** | **0.148** | **9** | **11** |
| **Lower canine area** | **0.152** | **0.0248*** | **0.0494*** | **9** | **11** |
| **Cranial geometric mean** | **0.0667** | **0.0278*** | **0*** | **5** | **6** |
| **Postcranial geometric mean** | **0*** | **0.04*** | **0*** | **7** | **5** |

## Calculations

Geometric means of all cranial and postcranial measurements and the basal areas of the upper and lower canines (mesiodistal breadth x buccolingual breadth) were calculated for both the fossil and modern samples. To test for sexual dimorphism in *Ailurus fulgens*, the cranial and postcranial geometric means and upper and lower canine areas for each sex were compared using Welch's *t*-tests. One unusually robust female specimen, FMNH 60452, was more than 1.5 times above the interquartile range of the female sample in both upper and lower canine areas (Figure 2). Removing this individual from the analysis increased the significance of the *t*-tests, but as this did not impact the direction of the findings, analyses with FMNH 60452 included are reported.

A pairwise distance operation was employed to test for significantly greater dimorphism in *Pristinailurus bristoli* than in *Ailurus fulgens*, following approaches that have been used to test for multiple species in the hominin fossil record (Kramer et al., 1995). Dimorphism in each of the three measures used was quantified using a log transformed ratio of the values for each pair of specimens drawn, following the recommendation for quantifying dimorphism made by (Smith, 1999). Log ratios were calculated for every possible intersex and intrasex pair of *A. fulgens.* The percentage of the *A. fulgens* ratios as great as the log ratio between ETMNH 15000 and ETMNH 3596 was then determined and this percentage interpreted as a *p* value. Significance was set at a < 5% probability of sampling two individuals as different as ETMNH
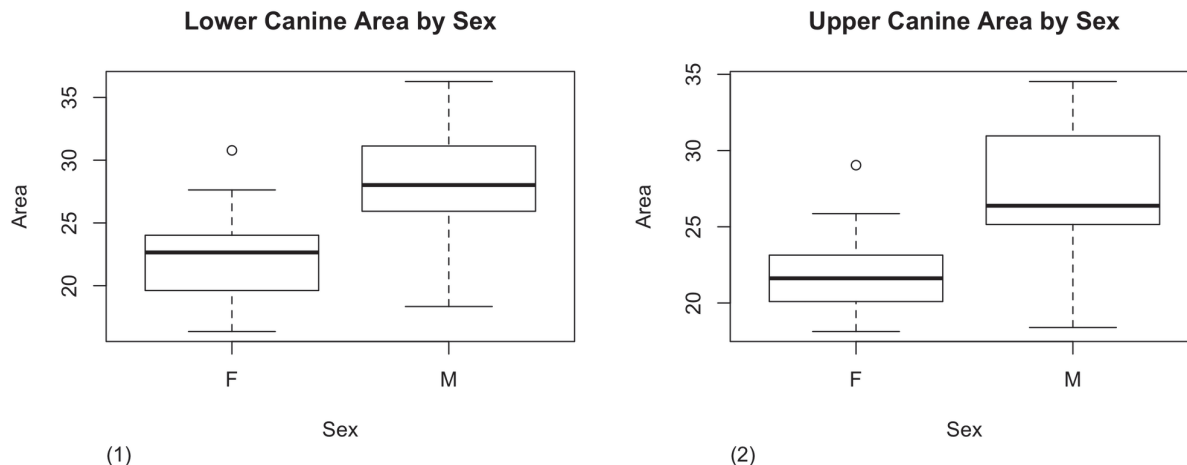
**FIGURE 2.** (1) Boxplot of *Ailurus fulgens* lower canine area by sex. (2) Boxplot of *A. fulgens* upper canine area by sex. Horizontal bars indicate the median, boxes represent middle quartiles, and error bars extend 1.5 times the interquartile range. Open circles beyond these bars indicate outliers.

15000 and ETMNH 3596 from the sample of *Ailurus fulgens.* All analyses were performed in the statistical programing environment R (R Development Core Team, 2011).

## RESULTS

Measurements are reported in Table 1. In *Ailurus fulgens*, both upper and lower canine areas were significantly different between sexes (Figure 2). No other measurements demonstrated significant sexual dimorphism. The geometric mean of the postcranial measurements of *Pristinailurus bristoli* was significantly more dimorphic than in the *A. fulgens* intersex (p = 0) and intrasex (male p = 0, female p = 0.04) pairs (Table 1, Figure 3). Dimorphism in the cranial means of *P. bristoli* approached significance in comparison with the intersex pairs of *A. fulgens* (p = 0.0667) and was significant in comparison with the intrasex pairs (male p = 0, female p = 0.0278). Upper canine area was not significantly more different in *P. bristoli* than in *A. fulgens* in any of the comparisons. Lower canine area in *P. bristoli* was significantly more dimorphic than the intrasex pairs of *A. fulgens* (male p = 0.0494, female p = 0.0248). This likely reflects the presence of sexual dimorphism in these traits in *A. fulgens* and not necessarily monomorphism in *P. bristoli*.

## DISCUSSION

This study presents the first evidence of significant canine sexual dimorphism in *Ailurus fulgens*. It supports, however, earlier suggestions that body size dimorphism is absent or negligible in this species (Roberts and Gittleman, 1984). As *A. fulgens* is known to exhibit a noncompetitive, promiscuous mating system in which male-male competition is rare or absent (Roberts and Gittleman, 1984), significant canine dimorphism is difficult to explain functionally. Canine dimorphism has been found to exhibit a strong phylogenetic correlation in other carnivorans (Gittleman and Valkenburgh, 1997), which may be the case here as well. Ailurids are nested within the Musteloidea (Schmidt-Kittler, 1981; Wolsan, 1993; Wang, 1997; Delisle and Strobeck, 2005; Sato et al., 2006; Fulton and Strobeck, 2006, 2007; Arnason et al., 2007; Yonezawa et al., 2007; Finarelli, 2008; Yu et al., 2008, 2011), the other families of which (Mustelidae, Mephitidae, and Procyonidae) are noted for their relatively high degree of canine sexual dimorphism (Weckerly, 1998). It may be probable that ailurids retained canine sexual dimorphism from a highly dimorphic last common ancestor with their sister clade, variously interpreted as procyonidae (Wang, 1997), or a larger clade of musteloids (Schmidt-Kittler, 1981; Wolsan 1993; Delisle and Strobeck, 2005; Sato et al., 2006; Fulton and Strobeck, 2006, 2007; Arnason et al., 2007; Yonezawa et al., 2007; Finarelli, 2008; Yu et al., 2008).

The postcranial geometric mean was significantly more dimorphic in the *Pristinailurus bristoli* pair than in both inter- and intra- sex pairs of *Ailurus fulgens*. This supports the presence of a significant body size difference between these two individuals, outside of the normal range of the modern red panda. The evidence for dimorphism pre-
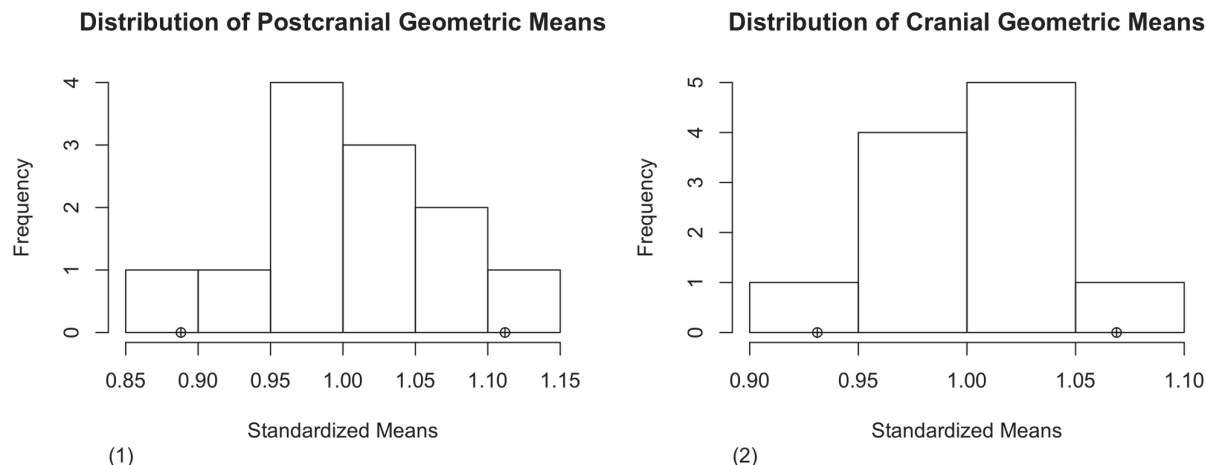
**Distribution of Postcranial Geometric Means**

**Distribution of Cranial Geometric Means**



**FIGURE 3.** (1) Position of the standardized postcranial geometric means of the *Pristinailurus bristoli* within the standardized postcranial geometric mean distribution of a modeled *Ailurus fulgens* population. (2) Position of the standardized cranial geometric means of the *P. bristoli* pair within the standardized cranial geometric mean distribution of a modeled *A. fulgens* population.

sented here is necessarily tentative because of the small sample size and the limitations of the method employed. However, recent recovery (June 2013) of an isolated tibia that appears to fall within the size range of ETMNH 15000 and metatarsals closer to the size range of ETMNH 3596, but from different individuals, would appear to support the interpretation of two distinct morphotypes within this species.

The extent and causes of this dimorphism would likely be better resolved through the employment of traditional inferential statistics on body and canine size characters from a larger sample of *Pristinailurus bristoli*, which must await future discovery. We believe the close temporal and spatial relationship of these two specimens and the large number of shared traits argues against the presence of two species or subspecies, however. It is possible that *P. bristoli* exhibited a broader, but normally distributed, range of variation in size traits than *Ailurus fulgens*, perhaps for ecological reasons. However, the nature of the differences between the two specimens, in particular the depth of the rostrum and breadth of the zygomatics, suggest the strong possibility that the difference between the two specimens represents sexual dimorphism in body size in *P. bristoli* to a degree absent in the living red panda. Results from the lower canine comparisons may further support this hypothesis. These were non-significant intersexually but significant intrasexually. This pattern also prevailed in comparisons of upper canine breadth, although all of the *p* values were > 0.05. This sug-

gests that the two individuals of *P. bristoli* differ from each other in canine cross-sectional area to a degree most comparable with a pair of male and female *A. fulgens*, which are shown here to be sexually dimorphic in this trait. Presence of sexual dimorphism in *P. bristoli* might suggest elevated levels of male intrasexual competition and could be related to the presence of a polygynous mating system, more typical of carnivorans than the promiscuous mating behavior reported for *A. fulgens* (Roberts and Gittleman, 1984; Gittleman and Van Valkenburg, 1997). More specimens of *P. bristoli* demonstrating a clear bimodal distribution in size would be necessary to confirm this hypothesis, however.

As the best-known fossil ailurine, *Pristinailurus bristoli* offers a unique opportunity to better understand the past diversity in body size variability of the Ailuridae, particularly if it does prove to demonstrate body size sexual dimorphism absent in the living species. This would better contextualize the evolution of the relatively unusual social system of *Ailurus fulgens* and support its interpretation as a derived character, perhaps related to its specialist arboreal, hypocarnivorous niche.

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