

Prionailurus kurteni (Felidae, Carnivora), a new species of small felid from the late Middle Pleistocene fossil hominin locality of Hualongdong, southern China

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A tiny feline mandibular corpus fragment from the late Middle Pleistocene fossil hominin locality of Hualongdong is reported here as a new species *Prionailurus kurteni*. This species represents the smallest known fossil member of the family Felidae to date, comparable in size to two of the smallest modern cats, *P. rubiginosus* and *Felis nigripes*. It is unique in having a small p4 mesial accessory cuspid, very weak p4 distal cingulid, relatively deep mandibular corpus under m1, and a distally located anterior border of the masseteric fossa. A notable synapomorphy observed in the lineage including *Prionailurus*, *Felis* and *Otocolobus*, is the mesially inclined m1. The identification of *P. kurteni* suggests a potentially high diversity of *Prionailurus* during the prehistorical time, underscoring the significance of revisiting the taxonomy of small Felidae to gain a better understanding of the evolution and diversification of this family.

Introduction

Southeastern Asia and southern China stand out as hotspots of Felidae diversity, especially Felini, with four species of the leopard cat *Prionailurus* (*P. bengalensis*, *P. javanensis*, *P. viverrinus* and *P. planiceps*), two species of the golden cat *Catopuma* (*C. temminckii* and *C. badia*), one species of the marbled cat *Pardofelis* (*Pa. marmorata*), and one species of the wild cat *Felis* (*F. chaus*) (Pocock 1939, Sunquist & Sunquist

2002, Hunter 2015, Kitchener *et al.* 2017, Bellani 2019, Castelló 2020, Zhang *et al.* 2023). While most Felini species share similar dental traits, they exhibit differences in body sizes and ecological niches (Bellani 2019), being an example of mammalian diversification/radiation within forested regions. However, little is known about the evolutionary history of Felini in Southeastern Asia and southern China, due to the relatively rare fossil localities in the forest region, and the fact that Felini are small and bones are



Fig. 1. Position of Hualongdong locality (HLD, red triangle) in southern China.

often fragile, therefore rarely preserved in the fossil record, apart from some isolated teeth, which are not diagnostic in Felini.

The genus *Prionailurus* is the most diverse felid genus in the southern and southeastern forests of Asia, with four (or five) known species, i.e., *Prionailurus bengalensis* (Kerr, 1792) (Kerr 1972: 151), *Prionailurus javanensis* (or *Prionailurus bengalensis javanensis*) (Desmarest, 1816) (Desmarest 1816: 115), *Prionailurus viverrinus* (Bennett, 1833) (Bennett 1833: 68), *Prionailurus planiceps* (Vigors & Horsfield, 1827) (Vigors & Horsfield 1827: 449), and *Prionailurus rubiginosus* (I. Geoffroy Saint-Hilaire, 1831) (Geoffroy-Saint-Hilaire 1831 [1934]: 140) (see also Sunquist & Sunquist 2002, Kitchener et al. 2017, Bellani 2019, Castelló 2020, Zhang et al. 2023). Molecular dating supports a Late Pliocene–Early Pleistocene radiation of the genus (Johnson et al. 2006, Luo et al. 2014, Li et al. 2016). There are however no known fossil species of this genus (all known are extant or *sp. indet.*, often in the genus *Felis*), and the fossils of the genus are extremely rare. Two reasons account for this fact. The first is the rarity of fossil small felines in southern China, mainly represented by cave deposits (Pei 1987), in which the small bones are often rare. The second is the historical assignment of all small felines to *Felis*, without careful study and without revision of these materials.

Here, we describe a new species of *Prionailurus* based on a tiny feline mandibular fragment from the Hualongdong (HLD; Fig. 1) *Homo* Site

(30°06'22.2''N, 117°01'13.0''E), a late Middle Pleistocene locality (Dong et al. 2017, Wu et al. 2019, 2021, 2023, Pei et al. 2022) located in the southernmost part of Anhui Province, not far from the southern bank of the Yangtze River (Dong et al. 2017). Uranium-series dating gives a range between 275 and 331 kyBP for the fossil *Homo* layers, spanning marine isotope stages 9e to 8c (Wu et al. 2019). The fossil feline described in this study was also obtained from this layer. The fauna is a classical *Ailuropoda–Stegodon* fauna, dominated by Artiodactyla, especially bovines, cervids, and *Sus* spp. (Tong et al. 2018, Wu et al. 2019). Apart from the classical members common to this fauna, some northern Chinese components are also present, e.g., brown bear (*Ursus arctos*), and diverse arvicolids, suggesting that the environment was probably colder and more open than those of the typical southern Chinese *Ailuropoda–Stegodon* fauna (Tong et al. 2018).

The fossil material described in this study is housed at IVPP. Specimens of fossil and living Felidae species housed at AMNH, USNM, IVPP, IOZ, and KIZ were checked for comparison.

The craniodental measurements follow Jiangzuo et al. (2022), see Fig. 2 for details. The classification system of modern Felidae follows Zhang et al. (2023). We use upper-case letters to describe upper tooth loci (e.g. M1, P4) and lower-case letters to describe lower tooth loci (e.g. m1, p4).

Institutional abbreviations used in the text are as follows: AMNH M = mammal collection of the American Museum of Natural History, New York, USA; IOZ = Institute of Zoology, Chinese Academy of Science, Beijing, China; IVPP = Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences, Beijing, China; KIZ = Kunming Institute of Zoology, Chinese Academy of Sciences, Kunming, China; and USNM = Smithsonian National Museum of Natural History, Washington DC, USA.

Systematic palaeontology

Order: Carnivora Bowdich, 1821
Family: Felidae Batsch, 1788

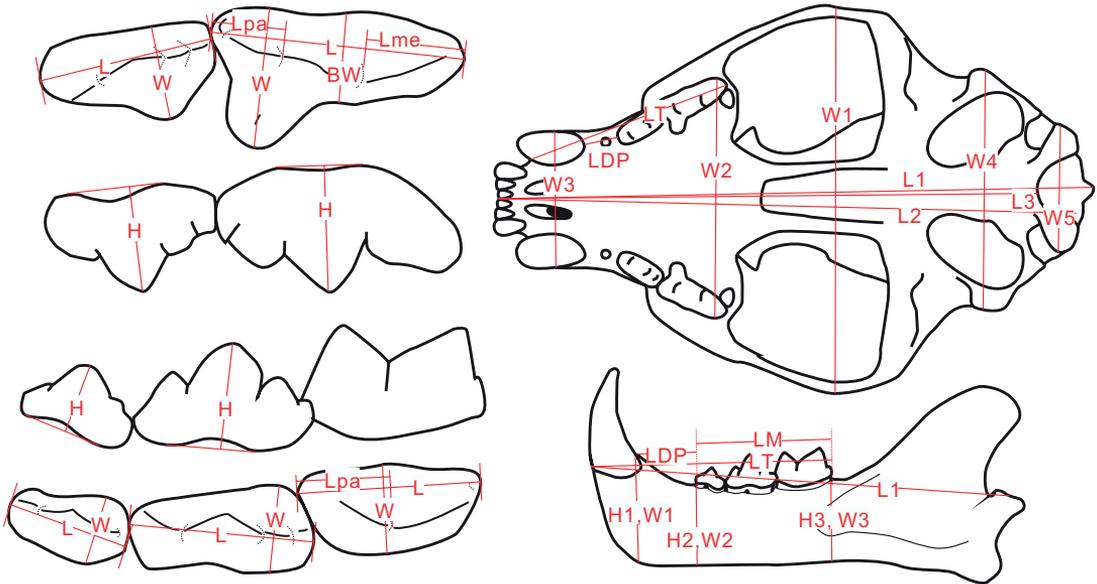


Fig. 2. Measurements of Felidae skull and teeth: BW = blade width of the P4 (width across the paracone distal to the protocone), H = tooth height, H1 = mandibular height behind c, H2 = mandibular height in front of p3, H3 = mandibular height behind m1, L = tooth length, LDP = postcanine diastema length, LM = tooththrow length from p3 to m1, Lme = metacone/metastyle length, Lpa = paracone/paraconid length, LT = tooththrow length from c to m1, W = tooth width, W1 = mandibular width behind c, W2 = mandibular width in front of p3, W3 = mandibular width behind m1, W4 = width of cranium across mastoid process, W5 = width of condyle.

Subfamily: Felinae Batsch, 1788

Genus: *Prionailurus* Severtzov, 1858

***Prionailurus kurteni* sp. nov.** (Fig. 3)

HOLOTYPE: IVPP V33075, a partial mandible with p4 and m1.

HYPODIGM: Holotype only.

STRATIGRAPHIC AND GEOGRAPHIC PROVENANCE: Found only in Hualongdong Cave No. I (HLD1) *Homo* Site (30°06'22.2"N, 117°01'13.0"E), a late Middle Pleistocene locality in the southernmost part of Anhui Province, China.

ETYMOLOGY: Named in memory of Björn Kurtén, one of the most influential figures in Finnish palaeontology, who made significant contributions to the study of Carnivora, including Felidae.

DIAGNOSIS. Smallest known felid, with weak p4 accessory cusp, very weak p4 distal cingulid, m1 slightly mesially inclined; caudally located masseteric fossa.

DIFFERENTIAL DIAGNOSIS. Differs from *Prionailurus bengalensis* and *P. javanensis* in smaller size, distinctly weaker p4 mesial accessory cuspid, weaker p4 distal cingulid, and more caudally located masseteric fossa. Further differs from *P. planiceps* by more robust dentition. Dif-

fers from *Felis* spp. by weaker p4 mesial accessory cuspid and distal cingulid and less mesially inclined m1. Differs from *Pardofelis marmorata* and *Catopuma* spp. by much smaller size, and slightly mesially inclined m1.

MEASUREMENTS: p4 length 5.54 mm, p4 width 2.79 mm, p4 height 4.45 mm, m1 length 6.37 mm, m1 paraconid length 3.23 mm, m1 width 3.08 mm, mandibular depth behind the m1 9.81 mm.

DISTRIBUTION AND AGE: So far known only from Hualongdong Cave I, southern China, 0.3 Ma.

DESCRIPTION. A mandibular fragment with p4 and m1 is preserved. The horizontal ramus is relatively deep for a small Felini. The anterior border of the masseteric fossa is located distinctly distal to the distal border of the m1. The p4 is high-crowned, with distinct but relatively small mesial and distal accessory cuspid. The mesial and distal cuspid are roughly the same size. The distal cingulid is very weak, only developed at the postero-lingual corner of the tooth, not forming a distal platform or cuspid distal to the distal accessory cuspid. The m1 is

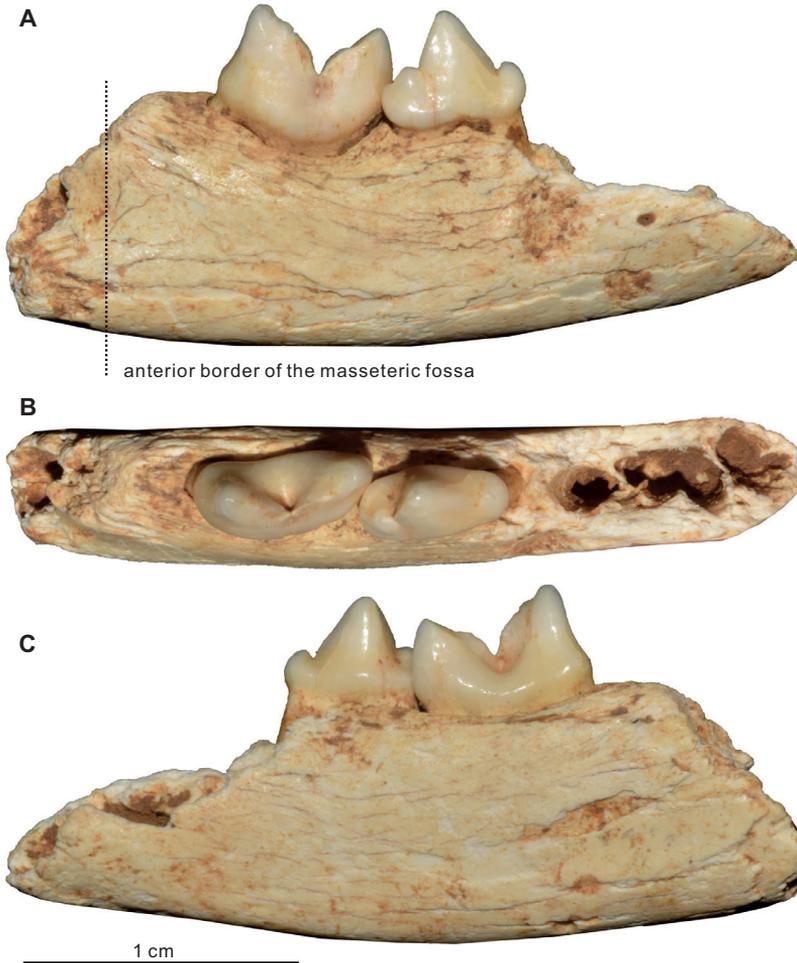


Fig. 3. *Prionailurus kurteni* *sp. nov.*, IVPP V33075 from Hualongdong. A. lateral view; B. occlusal view; C. medial view.

slightly mesially inclined, but the mesial border of the paraconid is still slightly distally inclined. The paraconid and protoconid are roughly the same length. The widest part of the tooth is located at or very slightly distal to the carnassial notch. There is no metaconid or talonid.

Comparisons and discussion

The small feline from Quaternary deposits of China has long been assigned to *Felis microtis* (type near Beijing) or *Felis sinensis* (type probably from Guangzhou), both of which are synonyms of the modern leopard cat, *P. bengalensis* (Gao 1987). In China, records come from many localities, e.g., Zhoukoudian, Beijing (Pei 1934, 1940), Longtan Cave, Hexian (Huang & Zheng

2001), and Hualongdong (Tong *et al.* 2018). However, materials assigned to this species are clearly heterogeneous, including specimens of very different sizes. This is due to the difficulty of distinguishing small Felini based on the dentition, which is the most commonly preserved part in the fossils. A revision of these materials is outside the scope of this study, but we can point out here that the HLD specimen is smaller than those records, whatever species they may actually belong to.

The small size and mesially inclined m1 points to an affinity with the lineage that includes *Prionailurus*, *Otocolobus* and *Felis* (Johnson *et al.* 2006, Li *et al.* 2016). This lineage was never recognized by morphology (Weigel 1956, Hemmer 1978, Herrington 1986, Salles 1992), probably due to the repeated divergence and

convergence of morphology within Felini. Our observations suggest two characters that are relevant. The first is the small size. The two smallest extant felines, i.e., *P. rubiginosus* and *F. nigripes*, are both from this lineage (Sunquist & Sunquist 2002, Bellani 2019, Castelló 2020). Some species of *Leopardus* are also very small (Sunquist & Sunquist 2002, Bellani 2019, Castelló 2020), but their restricted distribution make them easy to discount in comparisons with other felines. However, there is also a size overlap between the species in the *Prionailurus-Otocolobus-Felis* lineage and other genera, so size can only be used as a starting point. A second character is the mesially inclined m1. When orienting the cheek tooththrow horizontally, the carnassial notch of this lineage is often mesially inclined (Fig. 4), whereas in other felines the notch is mostly vertical or distally inclined. As a result, the paraconid and protoconid are also somewhat mesially inclined, and the anterior border of the paraconid is close to vertical. This kind of inclination is most distinct in *Felis*, and moderate in *Otocolobus* and *Prionailurus*. In *Felis*, the anterior border of the paraconid is generally vertical or even slightly mesially inclined. The situation in the HLD specimen is closer to *Prionailurus*, and considering the geographic distribution and general environment (forest dominant/open forest), the HLD specimen is assigned to *Prionailurus*.

The teeth of the HLD specimen are smaller than those of any modern felid species other than *P. rubiginosus* and *F. nigripes*. The m1 length (6.4 mm) is less than in two samples of *P. rubiginosus* (6.7–6.8 mm) and within the lower bound of four samples of *F. nigripes* (6.36–6.94 mm) (Fig. 5), and also within the range of *P. rubiginosus* (6–7 mm) given by Pocock (1939), or 5.9–7.2 mm measured by Kurtén (unpubl. data). On the other hand, the mandibular depth under the m1 is deep relative to size, as the ratio of m1 length/mandibular depth behind the m1 is smaller than in any modern species of *Prionailurus* and *Felis* (see Fig. 5). The p4 is unique in having rather small accessory cusps, and near absence of the distal cingulid. In all modern species of *Prionailurus*, the mesial accessory cuspid is larger, and the distal cingulid always forms a short platform behind the distal accessory cuspid. In this regard, the HLD specimen

is different from all modern species. Another unique trait is the rather caudally located masseteric fossa. In *P. bengalensis*, *P. javanensis* and *P. rubiginosus*, the anterior border of the masseteric fossa is always located at or slightly anterior to the m1 distal border. In *Felis*, the masseteric fossa is sometimes located more distally, but never at such a large distance as is seen in the HLD specimen. In summary, the HLD specimen represents a unique small feline species, with traits most referable to *Prionailurus*. It possesses several unique dental and mandibular traits that fall out of the range of variation observed in modern species, and is here erected as a new species, *Prionailurus kurteni*.

The previously reported *Felis microtis* maxilla from HLD is clearly too large to be assigned to the same species (Tong et al. 2018), and may be assigned to *Catopuma* based on size and morphology (Jiangzuo et al. 2018). Two mandibular fragments from Longtan Cave, not far from Hualongdong, were assigned to *Felis microtis* by Huang and Zheng (2001). The age of Longtan Cave is probably earlier in the early Middle Pleistocene, as it includes the presence of *Pachycrocuta* and *Homotherium*. The size of the Longtan Cave specimen is distinctly larger than that of the HLD specimen, and the m1 does not incline mesially. The size of the Longtan Cave specimen fits that of both *P. bengalensis* and *Paradofelis marmorata*, and the morphology seems to be close to the latter species, but as we have not seen the original specimen, we cannot provide a further identification of that specimen.

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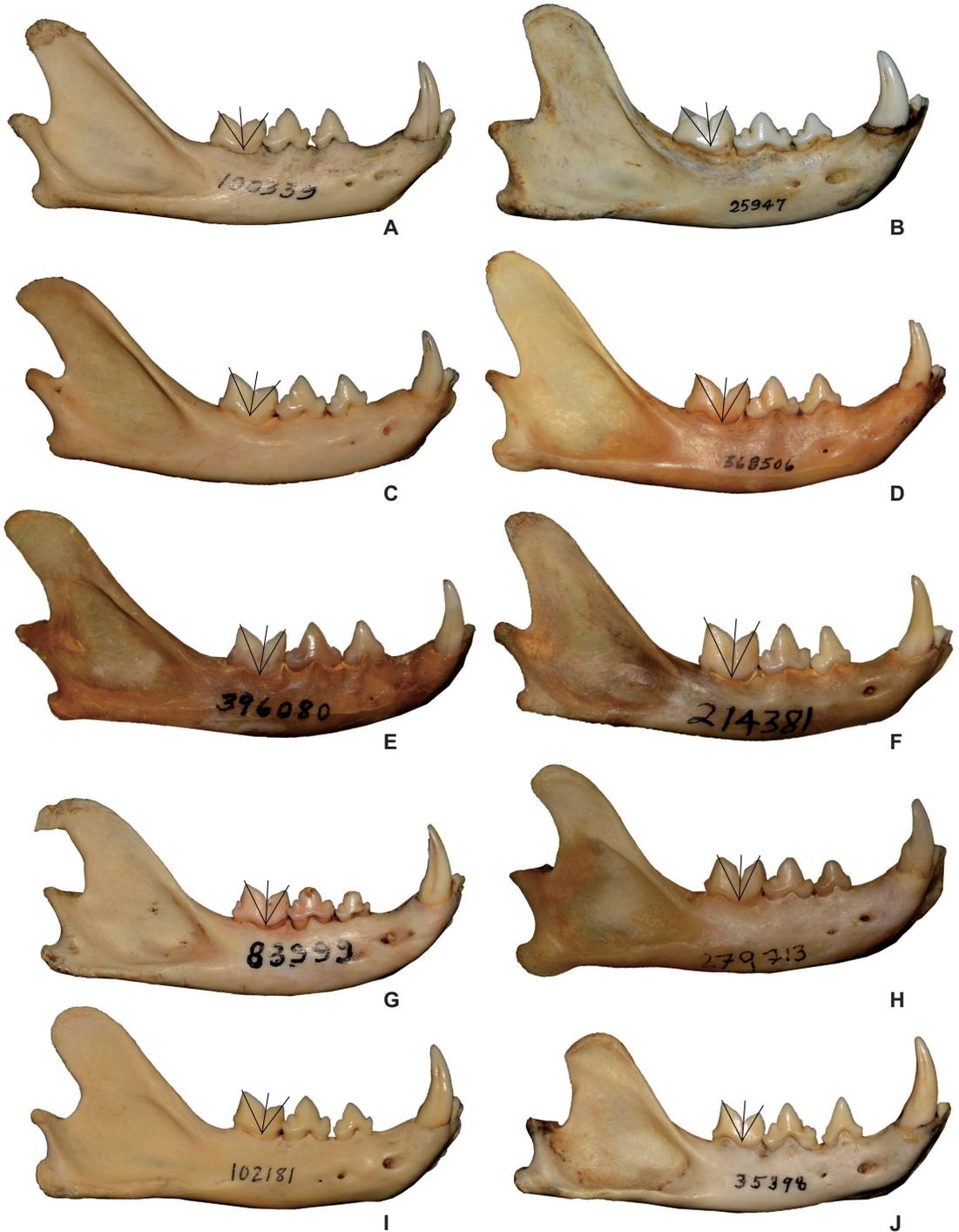


Fig. 4. Comparison of mandibles of several extant felids (not to scale). — **A:** *Caracal caracal* AMNH M100339. — **B:** *Catopuma temminckii* IOZ25947. — **C:** *Felis chaus* AMNH163607. — **D:** *Felis silvestris* USNM368506. — **E:** *Felis margarita* USNM396080. — **F:** *Felis nigripes* AMNH M214381. — **G:** *Prionailurus bengalensis* AMNH M83999. — **H:** *Prionailurus rubiginosus* AMNH M279713. — **I:** *Prionailurus viverrinus* AMNH M102181. — **J:** *Prionailurus planiceps* AMNH M35398. The three lines in each m1 represent the line of carnassial notch (middle one); the lines connecting the base of crown at middle line, and the tips of paraconid and protoconid, respectively.

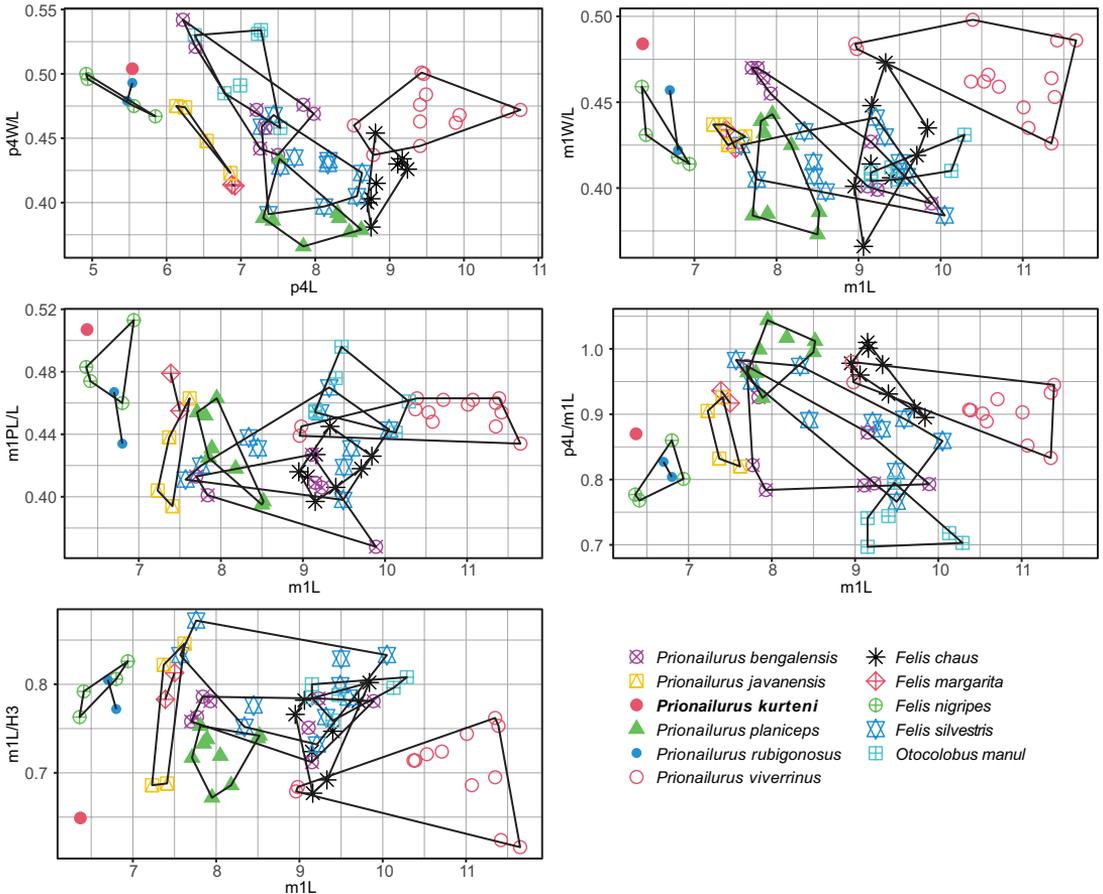


Fig. 5. Metrics and ratios of *Prionailurus kurteni* and members of modern *Prionailurus*, *Felis* and *Otocolobus*. Note the small size and relatively deep mandible of the new species. L. length; W. width; PL. m1 paraconid length; H3. mandibular depth a behind m1.

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