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Blaine W. SCHUBERT and Joshua X. SAMUELS (2026) Revised age of early short-faced bears (Tremarctinae, *Plionarctos*) in the fossil record

Cover: UCMP 22462, left dentary overlaying an image of the weathered and eroded Rattlesnake Formation where Merriam and Stock made classic collections of the fauna. Ridges in the background are capped by the Rattlesnake Ash Flow Tuff; below that are fossiliferous strata of the Rattlesnake Formation on top of the lighter colored Mascall Formation. Specimen photo by B.W. Schubert and landscape photo by J.X. Samuels.

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Revised age of early short-faced bears (Tremarctinae, *Plionarctos*) in the fossil record

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A carnivoran partial dentary with m2 from the late Miocene Rattlesnake Formation of Oregon was originally published as either an amphicyonid or ursid, and more recently as the tremarctine bear, *Plionarctos*. This identification represents the oldest purported record for short-faced bears, setting their biochronologic appearance at ~7 million years ago. Our re-assessment of this specimen indicates the m2 is morphologically consistent with Ursidae, but the fossil material cannot be confirmed as *Plionarctos* or even Tremarctinae. Based on this, the oldest unambiguous tremarctine is currently from the Eden Formation of California, and dates to ~5.6 Ma (late Miocene).

Keywords: Neogene, Mammalia, Carnivora, Ursidae, California, Oregon

INTRODUCTION

During the first quarter of the 20th century the University of California collected vertebrate fossils from the Rattlesnake Formation of Oregon, and the mammalian fauna was subsequently reported by Merriam et al. (1916, 1925). Among the diverse assemblage, one specimen (UCMP 22462) was particularly enigmatic for the researchers, a carnivoran partial dentary with a complete but worn molar "situated immediately in advance of the base of the coronoid process" (Merriam et al. 1925, pp. 60-61). Although the authors considered the tooth to be "strikingly similar" to the lower second molar of bears, the specimen was identified as an m2 or m3, with a taxonomic assignment of "Amphicyonid or Ursid sp." The current condition of UCMP 22462 (Fig. 1) appears to be identical to that depicted in Merriam et al., 1925.

The Rattlesnake Formation amphicyonid or ursid specimen seems to have gone unnoticed in the literature for most of the 1900s, and then near the turn of the century it is reported as the oldest record of the short-faced bear group by Hunt (1998) and Tedford and Martin (2001). Hunt (1998) designated short-faced bears as a tribe (Tremarctini) while Tedford and Martin (2001) followed earlier researchers (e.g., Merriam and Stock, 1925; Kurten, 1967) who grouped them as the subfamily Tremarctinae. In addition, Hunt (1998) and Tedford and Martin (2001) identified UCMP 22462 as *Plionarctos* Frick, 1926, with an age of ~7 million years. Hunt (1998) is even more specific, referring the fossil to *Plionarctos edensis* Frick, 1926, which was originally reported from the Eden Formation of California. These identifications have now served as the first appearance date of short-faced bears (Tremarctinae or Tremarctini) for ~25 years in the scientific literature. Further, *Plionarctos* has been referenced as a characterizing taxon for the medial or late early Hemphillian (Hh2) North American Land Mammal Age (NALMA) (e.g., Hunt 1998, Janis et al. 1998 p.84, fig.

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4.6A, Jiangzuo and Wang 2023), as a divergence point for phylogenetic research (e.g., Mitchell et al. 2016), and as a biochronologic marker for dating fossil sites in North America (e.g., Wallace and Wang 2004).

To date, short-faced bears are only known from the Americas, with *Plionarctos* considered to be the ancestral form (Tedford and Martin 2001). *Tremarctos* Gervais, 1855, *Arctodus* Leidy, 1854 and *Arctotherium* Burmeister, 1879 are generally considered to be descendants of *Plionarctos*, with *Tremarctos* appearing earlier than *Arctodus* and *Arctotherium*. Both *Tremarctos* and *Arctodus* appear in North America, and *Arctodus* is only known from this continent throughout its existence. *Arctotherium* is recorded exclusively from South America until the end of the Pleistocene, when the smallest form (*A. wingei* Ameghino, 1902) is also found as far north as the Yucatan Peninsula of Belize and Mexico (Schubert et al. 2019). *Arctodus* and *Arctotherium* became extinct near the end of the Pleistocene while *Tremarctos* disappears from North America in the late Pleistocene and appears in South America during the early Holocene as *T. ornatus,* the only living species of the group (Soibelzon 2004, Schubert 2010, Soibelzon and Schubert 2011, Schubert et al. 2019).

As part of an ongoing effort to better understand the evolutionary history of the short-faced bear lineage, we reexamined the earliest reported record, UCMP 22462 from the Rattlesnake Formation. As such, we test the identification hypotheses of previous researchers, specifically that this specimen can be classified as Ursidae, Tremarctinae, *Plionarctos*, and *P. edensis*. We follow Tedford and Martin (2001) and Kurtén (1967) using Tremarctinae rather than Tremarctini for the short-faced bear group; use of Tremarctinae is also the classification presented by a wide range of recent studies (e.g., Mitchell et al. 2016, Kumar et al. 2017, Arnaudo et al. 2019, Hassanin et al. 2021, Vela-Vargas et al. 2021). Our assessment: 1) includes an updated description and identification of UCMP 22462; 2) discusses characters used for identification; and 3) provides a revised temporal foundation for interpreting early tremarctine bears.

SETTING AND AGE

The Rattlesnake Formation was first described by Merriam (1901) with additional early studies by Hay (1903), Merriam and Sinclair (1906) and Merriam et al. (1916, 1925). These studies were later supplemented by additional research that further characterize the fauna (e.g., Shotwell 1955, Martin 1983, 1996, Samuels and Zancanella 2011, Samuels and Cavin 2013, Stilson et al. 2016, Orcutt and Calede 2021). The formation is widely distributed through central and eastern Oregon, with its type area being adjacent to Picture Gorge, west of Dayville. The fauna from that area was chosen as a reference fauna when the Hemphillian NALMA was originally designated (Wood et al. 1941). Several more recent studies have confirmed the Hemphillian age of the Rattlesnake fauna (Martin 1983, 1996, Fremd et al. 1994, Martin and Fremd 2001, Tedford et al. 2004, Samuels and Zancanella, 2011).

Though represented by small collections and relatively little studied, the Rattlesnake fauna is quite diverse. To date, over 40 mammal species have been recognized from the fauna (Fremd 2010). In particular, the fauna has a very high level of carnivoran diversity (Merriam et al. 1916, 1925, Martin 1996, Tedford and Martin 2001, Bredehoeft and Samuels 2015). The Rattlesnake Formation contains some of the earliest North American occurrences of immigrant taxa from Asia, such as *Castor* Linnaeus, 1758, *Indarctos* Pilgrim, 1913, *Lutravus* Furlong, 1932, *Machairodus* Kaup, 1833, *Pekania* Gray, 1865, and *Simocyon* Wagner, 1858 (Qiu 2003, Woodburne 2004, Samuels and Zancanella 2011, Samuels and Cavin 2013).

MATERIALS AND METHODS

Measurements were taken with Mitutoyo Absolute Digimatic calipers to the nearest 0.1 mm, and include standard length and width measurements of the m2. The dentary (UCMP 22462) was scanned using a high-resolution X-ray computed tomography scanner, Skyscan 1273 (Bruker, USA), College of Arts & Sciences, East Tennessee State University. Pixel resolution was 42 µm. During acquisition, 1200 equiangular radiographs were taken over 360° using an adjustable range of accelerating voltage of 130 kV and a beam current of 300 µA with a 2.0 mm Cu filter. CT reconstruction was performed using NRECON (Bruker, USA). Segmentation was performed with Amira 2023.1 (Thermo Fisher Scientific, USA). Specimens were photographed using a Nikon DSLR D7000 with a Micro Nikkor 60 mm lens and figures were created in Adobe Photoshop. The CT image series and reconstructed mesh models of the specimen are available at MorphoSource at the following links:

https://n2t.net/ark:/87602/m4/886755 mesh
https://n2t.net/ark:/87602/m4/886759 mesh of molar
https://n2t.net/ark:/87602/m4/886751 image series

Abbreviations—UC, University of California; **UCMP**, Museum of Paleontology, University of California, Berkeley, California; **NALMA**, North American Land Mammal

Age; **Hh2**, late early Hemphillian NALMA; **Hh4**, latest Hemphillian NALMA

SYSTEMATIC PALEONTOLOGY

MAMMALIA Linnaeus, 1758
CARNIVORA Bowdich, 1821
URSIDAE Fischer von Waldheim, 1817
URSIDAE sp. indet.
Figs. 1-4; Table 1

Referred Specimen—UCMP 22462, partial left dentary with m2.

Locality—UCMP locality 3045, described in the UCMP records as "Reddish colored, weathered, material and white ash of Rattlesnake exposed for most part on low hills N. of wagon road and approximately 1 mi. W from Cottonwood Creek". Rattlesnake Formation, Grant County, Oregon. Tedford and Martin (2001) list the Rattlesnake Formation as being in Wheeler County, Oregon, but that is incorrect.

Description—UCMP 22462 consists of a fragmentary left dentary with m2. The horizontal ramus is broken anterior and ventral to the m2 exposing a portion of the posterior alveolus of m1. This alveolus is centrally located on the dorsal surface of the ramus but descends ventrally at an angle towards the lingual side (Fig. 1A). The horizontal ramus is robust, lacks a premasseteric fossa, and has an ascending ramus located close (9.5 mm) to the posterior margin of the m2 (Fig. 1B). The anterior margin of the masseteric fossa on the ascending ramus

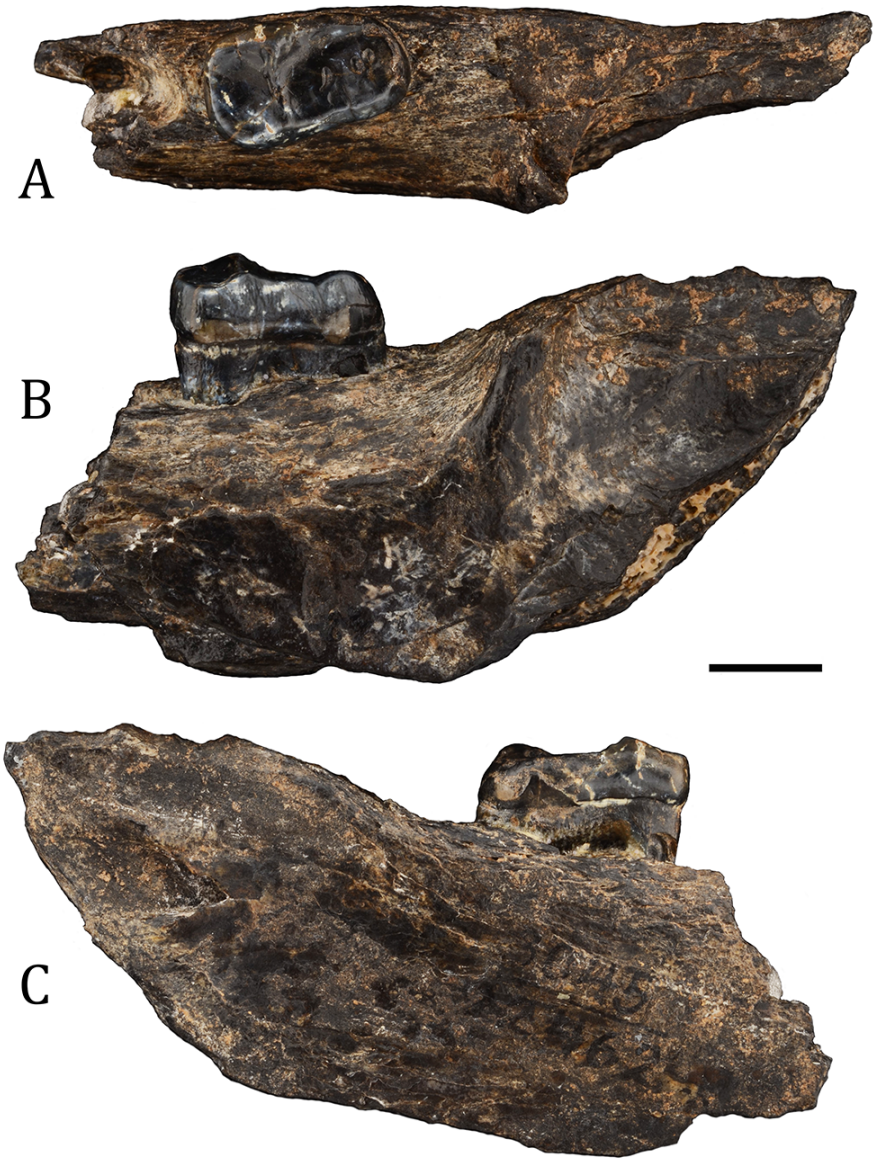

Figure 1. Ursidae indet. partial left dentary (UCMP 22462) in occlusal view (A), lateral view (B), and medial view (C). Scale bar = 1 cm.

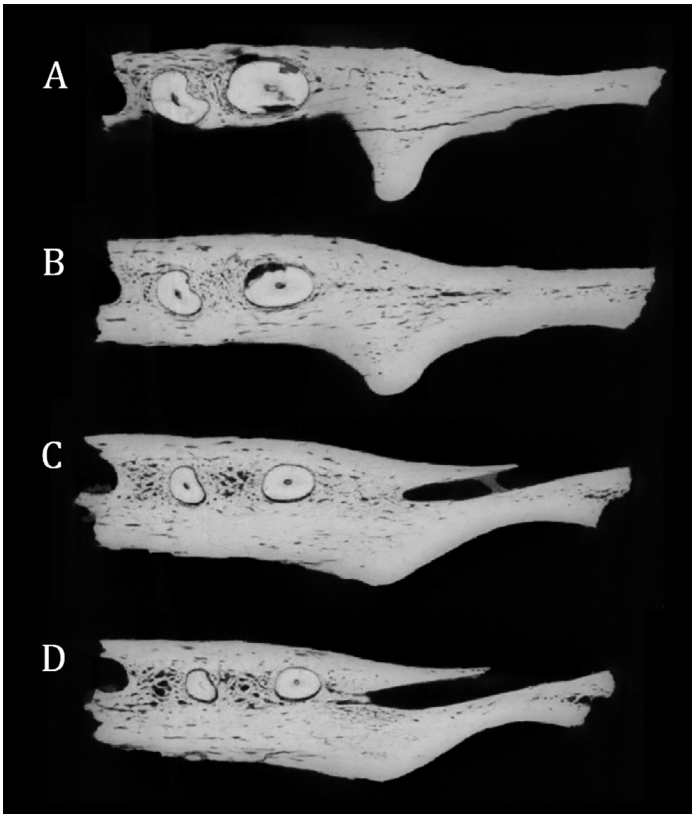

Figure 2. CT slices and internal morphology of UCMP 22462 in dorsal view. A - D are transverse slices that depict increasing depth into the dentary, with A being the most dorsal slice, and D being the most ventral slice. All images are approximately the same scale, and anterior is to the left.

is marked by a prominent ridge and the preserved portion of the fossa is deeply depressed and rugose. There is no m3, and it seems there never was one based on: 1) the lack of an alveolus for m3, and 2) a CT image series and reconstructed mesh model that showed no evidence for m3 development or retention in the ramus (Fig. 2). There is a large mandibular foramen on the medial side of the dentary posterior to the m2 and opposite the masseteric fossa. The internal mandibular canal is large (Fig. 2D) posterior to the m2, further demonstrating a lack of space and bone for an m3.

The m2 of UCMP 22462 is mostly intact (Fig. 1, Fig. 3), though it is heavily worn and enamel is missing from portions of the lingual and distal margins of the talonid. As preserved, the m2 trigonid is slightly wider than the talonid, and the missing enamel is unlikely to have altered the outline of the tooth significantly in occlusal view. The enamel of the m2 crown is thin and smooth on the occlusal surface, a consequence of wear, and more rugose where intact on the labial and lingual surfaces of the crown. Wear has exposed dentine within a low ridge that extends transversely from the protoconid to the metaconid. The trigonid includes a small crescentic cuspid in the anterolingual corner, which is separated distally from the larger metaconid by a small notch and labially from the preprotocristid by a small depression. The protoconid is broad and triangular in shape, with a low, but elevated, preprotocristid extending anteriorly along the labial and mesial margins of the trigonid. Anterolabially, the trigonid appears to have accessory cuspules, however, under a microscope, these light-colored

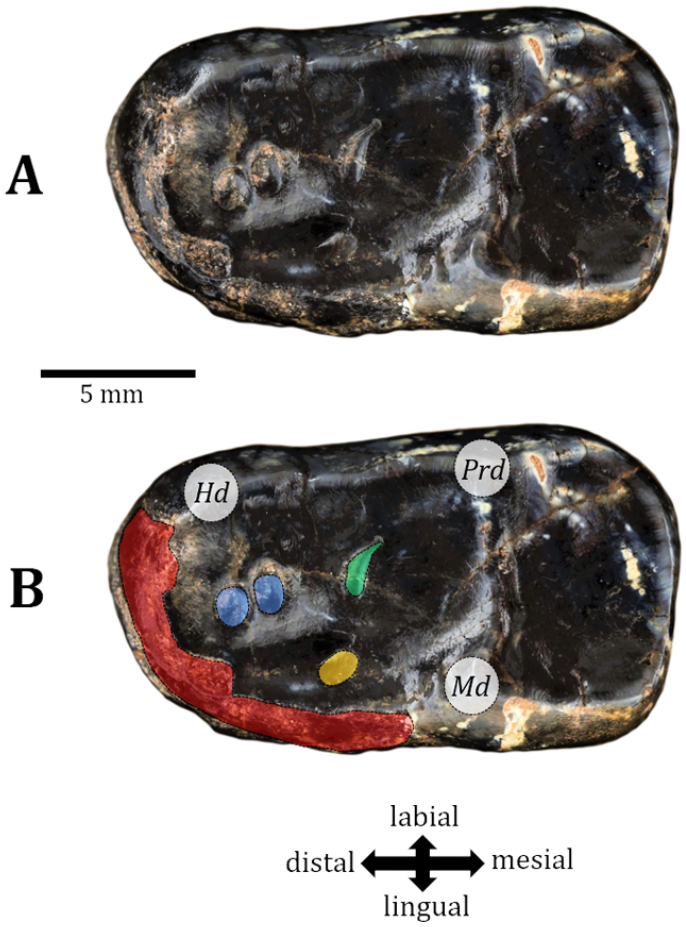

Figure 3. Occlusal views of left m2 (UCMP 22462) without (A) and with (B) marked features. Metaconid (Md), protoconid (Prd), and hypoconid (HD) indicated by gray circles. Green = worn cristid exposing dentine; blue = pair of oval cuspules worn into dentine; orange = additional oval depression into dentine; red = area where enamel is missing as a result of postmortem fragmentation.

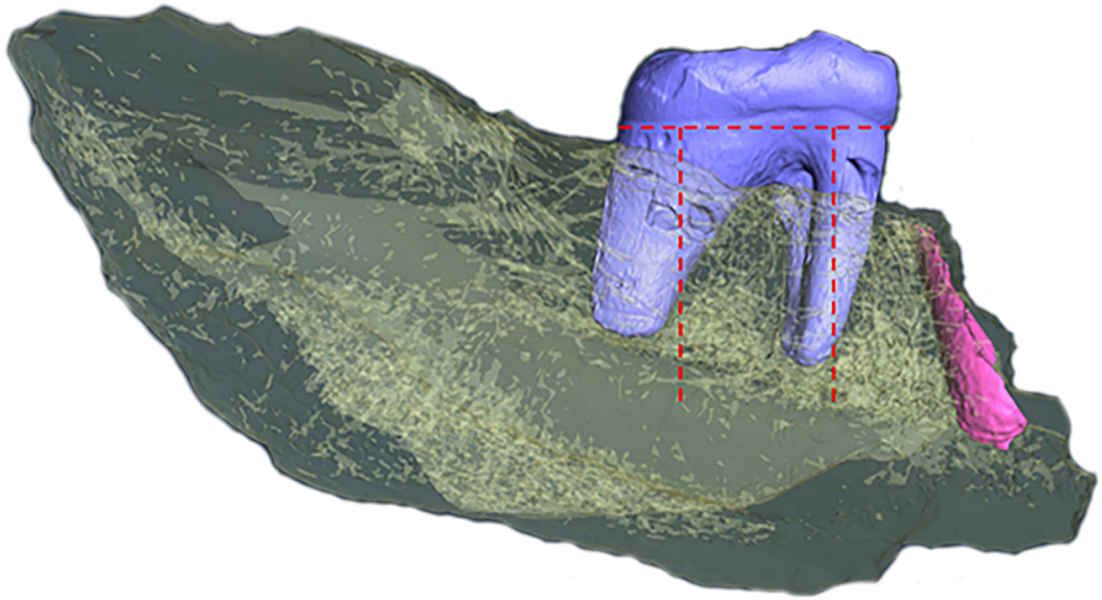

Figure 4. CT reconstruction of UCMP 22462 showing orientation of roots. The m2 is shown as purple and the posterior alveolus of m1 is pink. Red dashes compare the ventral margin of the m2 crown (enamel dentine junction) in horizontal position to perpendicular lines that are offset from the roots.

circular features are just discolorations in the enamel. The trigonid basin completely lacks accessory cuspules. The metaconid is bulbous and slightly larger and higher than the protoconid. In labial view (Fig. 1B), the postprotocristid slopes gradually from the protoconid without any apparent apices. However, in occlusal view (Fig. 3), the postprotocristid intersects a cristid along its lingual border, which forms a low triangular cuspule-like pattern at their intersection. This cristid extends in a posterolingual direction and is heavily worn, exposing a depression of dentine within the talonid basin (Fig. 3). Further, this cristid is separated by a small notch from the triangular hypoconid. Lingual to the hypoconid are a pair of small oval cuspules in the talonid basin evinced by raised enamel edges that surround worn depressions into dentine. Anterior to these cuspules is an additional depression into dentine, but there is no evidence that a cuspule was present. Posterior to the metaconid, the entoconid region appears to be relatively horizontal and flat, however, microscopic examination reveals that the enamel is completely removed from the lingual margin of the talonid, as well as most of the posterior margin (Fig. 3). Because no wear occurs along the fractured enamel surfaces, this enamel loss is considered to be postmortem.

Based on CT image series and reconstructed mesh model (Fig. 4), the ventral margin of the crown at the enamel dentine junction is oblique in lingual and labial views when compared to the orientation of the roots. This contrasts with modern ursid comparative specimens, where the roots are more perpendicular to the crown in these views. Root morphology of UCMP 22462 indicates they are either posteroventrally oriented or the anterior half of the crown is more dorsal than the posterior half. The m2 roots are deep with the posterior root being larger than the anterior root. The posterior root is oval in cross-section, whereas the anterior root has a posterolingual groove that extends dorsoventrally (Fig. 2). In dorsal view, the m2 roots are offset, descending ventrolingually. In comparison, the m1 posterior root alveolus is deeper and more angled ventrolingually (Fig. 2, Fig. 4).

Some measurements of UCMP 22462 were previously provided by Merriam et al. (1925) and Tedford and Martin (2001). Here we list their m2 measurements and ours for descriptive purposes (Table 1).

DISCUSSION

Below we address each descriptive character of Merriam et al. (1925) and Tedford and Martin (2001), and discuss morphological characters and identifications in light of new data. While Merriam et al. (1925) and Tedford and Martin (2001) describe UCMP 22462 in some detail, this is not the case for Hunt (1998) who referred the specimen to *Plionarctos edensis* in a summary chapter that reviewed North American carnivorans. Though Hunt

Table 1. Measurements (in mm) of UCMP 22462 m2 by different researchers

Measurement dimensions	Merriam et al. 1925	Tedford & Martin 2001	Schubert & Samuels this paper
Antero-posterior length	18.8	19.0	19.1
Antero-posterior length of trigonid	12.1	---	12.8
Antero-posterior length of talonid	6.7	---	6.3
Greatest trigonid width	10.5	11.0	11.1
Greatest talonid width	---	10.3	10.0

(1998: pp. 184-185) does list some general characteristics of short-faced bears, it is unclear which features were used to support the identification of this specimen.

Although Merriam et al. (1925) considered the UCMP 22462 tooth to be morphologically consistent with an ursid m2, the lack of an m3 led to a search for alternative explanations. As such, they discuss the possibility of the tooth being an amphicyonid m3 rather than an ursid m2 and suggest a potential affinity with *Amphicyon amnicola* Matthew and Cook, 1909, which was described from the Snake Creek Beds of Nebraska by a single lower jaw with m1, m2, and vacant alveoli for a "double-rooted" m3 (Matthew and Cook 1909:368-370). In particular, Merriam et al. (1925) note that the Snake Creek specimen had a large m3 with dimensions close to the material from the Rattlesnake Formation, and end their paper by stating it "is necessary to await the discovery of additional material before forming a final judgement as to the affinities of this form." Over the years as additional material became available, *A. amnicola* was synonymized within another amphicyonid taxon, *Cynelos sinapius* Matthew, 1902. With more complete material it also became apparent that *C. sinapius* and other similar amphicyonids have round to oval shaped m3s with short talonids (see Matthew 1924:105, Peigné and Heizmann 2003:18), in contrast to the UCMP 22462 molar and typical ursid m2s, which are more rectangular with elongated talonids. As a note, *C. sinapius* is known from the early Barstovian age Mascall fauna of Oregon (Stock 1930), which lies directly below the Rattlesnake Formation but has very different fossil preservation (Maguire et al. 2018).

Merriam et al. (1925) and Tedford and Martin (2001) both note the absence of an m3 is characteristic of simocyonine ailurids, like *Simocyon*. However, these researchers acknowledge that *Simocyon* has a different m2 morphology. We agree with this assessment, and although the overall occlusal outline of *Simocyon* m2s is somewhat similar to ursids, the cusp morphology and crown height is distinctly different. The absence of an m3 also occurs in the enigmatic arctoid *Kolponomos* Stirton, 1960, as well as some amphicyonids, like the late Miocene *Magericyon* Peigné et al., 2008, of Europe. However, none of these taxa have occlusal morphologies similar to UCMP 22462 or members of the Ursidae (both simocyonines and *Magericyon* have trenchant talonids, while *Kolponomos* has radically different m2 morphology).

We agree with Tedford and Martin (2001) in assigning UCMP 22462 as an ursid m2. In all views, and intact morphological features, this tooth is like typical ursids, and unlike other carnivorans. Merriam et al. (1925) also agreed with this assessment, but the complete lack of an m3 or corresponding alveolus resulted in their cautionary identification. Our observations of the internal morphology based on CT image slices and reconstructed mesh models further support the original assessment of Merriam et al. (1925) in the lack of m3, showing there are no remnants of an unerupted m3, an alveolus, or any signs that an m3 once occurred in the dentary (Fig. 3). Tedford and Martin (2001:319) acknowledge the absence of m3 but contend that the lack of this tooth "seems to be a developmental anomaly known to occur in ursids rather than a feature of phylogenetic importance." While this may be the case, the current authors have viewed many ursid dentaries and have never observed this anomaly.

Thus, we recognize the possibility that UCMP 22462 could represent an unknown ursid taxon that lost its m3 as part of its evolutionary history.

Although Tedford and Martin (2001) are confident that UCMP 22462 represents an ursid, with an m2, the degree of certainty in their classification level varies in different sections of the paper. In the abstract they note that the Rattlesnake Formation specimen is "recognized as a tremarctine bear, thus extending the earliest record of the group into the early part of the late Miocene." Within their Systematic Paleontology section, the specimen is identified to a more specific level, *Plionarctos* sp., yet the first line for that section states that "Tremarctinae may extend backward into the medial Hemphillian (earlier late Miocene)" as indicated by the Rattlesnake material; thus, even the tremarctine assignment seems uncertain here. However, on the following page the specimen is again identified as *Plionarctos* sp. (Tedford and Martin 2001:320, table 2).

In support of their tremarctine identification, Tedford and Martin (2001) note that the "m2 is strikingly similar to *Plionarctos*" in a number of features. This includes the "proportions of trigonid to talonid length (2:3)" which indicates the talonid is considered to be ~66.7% of the overall tooth length. However, this proportional difference depends on where the borders of the trigonid and talonid are measured, which varies among researchers. Regardless of the ratio or percentage, the talonid is certainly elongated in UCMP 22462, but not to the same degree as that of *Tremarctos*, or some specimens previously described as *Plionarctos* by Tedford and Martin (2001).

Next, the authors note that the specimen is like *Plionarctos* in the "presence of a high preprotoconid cristid so that the trigonid does not slope anteriorly in lateral view". While the aforementioned cristid is indeed high, the trigonid of UCMP 22462 does slope anteriorly in lateral view (Fig. 1B). The relatively high cristid occurs in other extinct and extant non-tremarctine taxa, with varying degrees of an anterior slope. This character needs to be further evaluated to better assess its variability and utility in morphological identifications.

While Merriam et al. (1925) state that UCMP 22462 lacks a paraconid, Tedford and Martin (2001) disagree and state the specimen is like *Plionarctos* in having a paraconid on the anterolingual corner of the tooth. While protoconid, metaconid, hypoconid, and entoconid are commonly used to describe cusps on the m2 of ursids, the use and placement of the paraconid varies among researchers. This includes labeling an apex on the anterolingual corner the paraconid (e.g., Tedford and Martin 2001), anterobuccal corner the paraconid (e.g., Jiangzuo and Flynn 2020), or avoidance of the term paraconid altogether for ursid m2s. UCMP 22462 does have a small but distinct enamel incision separating the metaconid from a raised region on the anterolingual corner (Fig. 1A, C), but we do not consider this to be a paraconid. The separation of the metaconid from a more anterior apex, or apices with a dividing incision, occurs in several ursid taxa and is not a defining characteristic of tremarctines.

Next, Tedford and Martin (2001) state the specimen is like *Plionarctos* in the following features: "talonid rimmed by a crest containing a weakly differentiated cuspule on the crista obliqua, hypoconid and a low and elongate entoconid". We interpret this statement to indicate that the talonid has a crest around it, there is a weakly differentiated cuspule on the cristid obliqua, the hypoconid connects with the crest, and the entoconid region of the crest is low and elongate. We infer their "crista obliqua" as indicating the crest between the protoconid and the hypoconid, and their "weakly differentiated cuspule" as the intersection of the postprotocristid with the lingually oriented cristid (Fig. 1, Fig. 3). This feature is common in ursid m2s. The referenced "low and elongate entoconid" noted by Tedford and Martin (2001) cannot be interpreted or supported because that entire region of the tooth is missing the enamel.

Further, Tedford and Martin (2001) state that the molar is like *Plionarctos* based on "the presence of cuspules (some worn to dentine) filling the talonid basin". Indeed, multiple cuspules in the talonid basin is a characteristic exemplified by tremarctines, but it should be noted that there are only two visible cuspules in this basin of UCMP 22462 (Fig. 3), and talonid basin cuspules may occur in other bears as well. In addition to dental characteristics, Tedford and Martin (2001) also note that the "masseteric fossa is deeply indented anteriorly at the level of the tooth row as in tremarctines", however, this can also occur in other extinct and extant ursid taxa.

Ultimately, Tedford and Martin (2001) only note "one significant difference" between UCMP 22462 and *Plionarctos*, that "the talonid is slightly narrower than the trigonid, even adjusting for the enamel broken posteriorly and lingually." However, it is actually common in bears to have a talonid that is narrower than the trigonid, and this does occur in some specimens currently referred to *Plionarctos*. So, in this case, the potential difference listed by Tedford and Martin (2001) doesn't actually negate the possibility that it is a tremarctine.

In sum, we find that the m2 and dentary morphology of UCMP 22462 are sufficient for assignment to Ursidae, but based on the fragmentary and worn nature of the specimen, lack of defining characters, and its unusual features, we assert the specimen cannot be confidently assigned to either the subfamily Tremarctinae or genus *Plionarctos*. UCMP 22462 has a number of features that are not typical of *Plionarctos*, Tremarctinae, or Ursidae in general, specifically the lack of m3 (and evidence for any m3 alveolus), an ascending ramus located relatively close to the posterior margin of m2, an atypical orientation of the m2 roots compared to the enamel dentine juncture, and an unusually oriented posterior m1 root. Ultimately, these features mean we cannot rule out the possibility that UCMP 22462 represents a previously unknown member of the family. We also cannot rule out the possibility that the specimen is a tremarctine, or that the unusual atypical features are the result of pathologies or developmental anomaly.

Our referral of UCMP 22462 to Ursidae rather than *Plionarctos* and Tremarctinae (or Tremarctini) is particularly important as it alters the temporal range of the short-faced bear group as a whole. With this revision, there are no definite records of the subfamily known from the late early Hemphillian (Hh2). The oldest described record of *Plionarctos* is the record of *P. edensis* from the Mt. Eden Local Fauna, which dates to the latest Hemphillian (Hh4) around 5.6 Ma (chron C3r, Albright, 1999). However, undescribed material in the American Museum of Natural History collection from the Ash Hollow Formation of Nebraska could represent Tremarctinae and is likely from the late Hemphillian, Hh3 (Voorhies 1990), and material from the Bone Valley Formation of Florida could be slightly older (Tedford and Martin 2001).

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