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First mesonychid from the Clarno Formation (Eocene) of Oregon, USA

Selina V. Robson, Nicholas A. Famoso, Edward Byrd Davis, and Samantha S.B. Hopkins

ABSTRACT

A recently identified left dentary of *Harpagolestes* cf. *uintensis* represents the first mesonychid material known from the Pacific Northwest. The specimen is from the Hancock Quarry (Clarno Unit, John Day Fossil Beds National Monument), which is in the uppermost subunit of the Clarno Formation (middle Eocene, ~40 Ma). The sediments of the Hancock Quarry were deposited by a meandering river system during the middle Eocene when north-central Oregon had a subtropical climate. As with many other mammals from the Hancock Quarry, *Harpagolestes* participated in an Asian-North American faunal interchange; species of *Harpagolestes* are known from the Eocene of both continents. *Harpagolestes* was carnivorous, and members of the genus were likely bone-crushers. Characteristic bone-crushing wear is visible on the occlusal surfaces of the Hancock Quarry specimen's premolars and molars. With the aid of CT scans, it has been determined that the Hancock Quarry *Harpagolestes* contains the alveoli for c1, p1-2, and m3, and preserves the crowns of p3-4 and m1-2. The molariform teeth have a large, conical trigonid with a bulbous talonid. The protoconid of p3 and p4 is tilted posteriorly. This specimen of *Harpagolestes* cf. *uintensis* represents a new large carnivore in the Hancock Quarry ecosystem, adds to the known diversity of the Oregon middle Eocene, and is the only known occurrence of a mesonychid in the Pacific Northwest.

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INTRODUCTION

The Hancock Quarry is a middle Eocene locality in the Clarno Formation of Oregon, equivalent to either the latest Uintan North American Land Mammal Age (NALMA) (Bestland et al., 1999; Lucas et al., 2004) or the early Duchesnean NALMA (Hanson, 1996; Lander and Hanson, 2006) (see Robinson et al., 2004 for a discussion of the Uintan and Duchesnean NALMAS). The locality is bracketed between 42.7 and 39.2 Ma (Bestland et al., 1999). The Hancock Quarry represents one of a few Eocene mammalian localities in the Pacific Northwest (Pratt, 1998; Hanson, 1996; Fremd, 2010) and has produced over 2000 vertebrate specimens (Fremd, 2010), most of which are large-bodied animals estimated to be larger than 10 kg (Pratt, 1998; Hanson, 1996; Fremd, 2010). Taxa reported from the locality include *Eubrontotherium* (Mihlbachler, 2007), *Teletaceras* (Hanson, 1989, 1996), and *Zaisanamynodon* (Lucas, 2006), as well as rarer specimens of *Plesiocolopirus* (Radinsky, 1963; Schoch, 1989) and *Diplobunops* (Hanson, 1996; Emery et al., 2016). Smaller-bodied mammals including the horses *Epihippus* and *Haplohippus* (Hanson, 1996) and unidentified rodents (Hanson, 1996; Samuels and Korth, 2017) are also known from the Hancock Quarry. Previously only two carnivorous mammals, the “creodont” *Hemipsalodon* and an indeterminate nimravid, were known from the Hancock Quarry (Hanson, 1996). A third carnivorous mammal is now recognized: the specimen UOMNH F–36924, from the Lon Hancock field collections, is *Harpagolestes* cf. *uintensis*, a massive bone-cracking mesonychid.

Mesonychia is an order of archaic carnivorous ungulates that roamed the Holarctic during the Paleogene. Mesonychians possess a simplified upper dentition and a specialized lower dentition; their teeth are adapted for carnivory but lack the carnassials that evolved in carnivores and “creodonts” (Szalay, 1969). For many years, mesonychids were thought to be the ancestors or sister group of cetaceans (see Van Valen, 1966; O’Leary, 1998; Luo and Gingerich, 1999; O’Leary and Geisler, 1999; Gatesy and O’Leary, 2001), but mesonychids are now considered to be sister to the artiodactyls (which include cetaceans) (Shoshani, 1986; Gatesy et al., 1996, 2013; Gingerich et al., 2001; Thewissen et al., 2001; Geisler and Uhen, 2003, 2005; Geisler and Theodor, 2009; but see Williamson and Carr, 2007; Spaulding et al., 2009; Tabuce et al., 2011). Within Mesonychia, the family Mesonychidae contains the larger members, including the middle-late Eocene *Harpagolestes*. Species of *Harpagolestes* are known from Asia (*H. leei, H. orientalis, H.*? *koreanicus*) and North America (*H. immanis, H. leotensis, H. macrocephalus, H. uintensis*). Like most North American mesonychids, North American *Harpagolestes* are predominantly found in the continental interior (see Archibald, 1998 for a summary of the distriubtion). The Hancock Quarry *H.* cf. *uintensis* specimen is the first and only mesonychid known from the Pacific Northwest.

MATERIALS AND METHODS

The Hancock Quarry specimen (UOMNH F-36924) still has plaster and burlap from the initial bedding jacket adhering to the specimen. Plaster on the lingual and occlusal surfaces was removed with deionized water and dental tools to expose the morphology while the buccal side remains jacketed to preserve the integrity of the specimen.

Computed tomography (CT) scanning was employed to reveal the covered surface and internal morphology, such as mineralized teeth. The specimen (UOMNH F-36924) was scanned with a Philips Brilliance 64 scanner at Oregon Imaging Centers in Eugene, Oregon. The scan was performed at an energy of 140 kV and an intensity of 997 μA. A filter detail was used to reduce noise, and some orthogonal reconstructions were done post-scan. An image stack of 797 slices with a slice thickness of 0.9 mm and resolution of 512 x 512 was produced. The stack was imported into Amira 5.3 for Mac OS X (Visage, Inc., Chelmsford, MA; http://www.visage.com) where elements were digitized and a three-dimensional (3D) reconstruction of the teeth was created with the LabelFields module. Scans of the specimen and the reconstructed teeth are available on MorphoSource under the project heading “Robson et al. *Harpagolestes* project” (DOIs: https://doi.org/10.17602/M2/M49061; https://doi.org/10.17602/M2/M49067; https://doi.org/10.17602/M2/M65700).

TABLE 1. Dental measurements of *Harpagolestes* cf. *uintensis* (UOMNH F-36924) compared to other *Harpagolestes* specimens. Measurements of the other *Harpagolestes* specimens are taken from the literature. In some cases, these measurements were reported in millimeters rather than tenths of millimeters. All alveolar measurements are at the bottom of the table.

Species		c1	p1	p2	p3	p4	m1	m2	m3
H. cf. *uintensis* (UOMNH F–36924)	L				27.8	25.1	31.5	24.0	
	W				12.5	14.2	14.1	16.5	
H. uintensis (YPM-PU 11659)* (Scott and Osborn, 1889)	L			14		28	31	29	18
	W						15	15	
H. uintensis (YPM 10072) (Thorpe, 1923)	L			20.7	28.0	27.5	31.5	23.0	19.0
	W								
H. uintensis (CM 2961) (Gustafson, 1986)	L			21.0	26.0	30.0	29.0		
	W			13.0	15.0	16.5	15.5		
H. uintensis (AMNH 1878) (Gustafson, 1986)	L			16.7	28.3	30.0	24.3		
	W								
H. cf. *uintensis* (TMM 40498-3 left) (Gustafson, 1986)	L					31.5			
	W					16[b]			
H. cf. *uintensis* (TMM 40498-3 right) (Gustafson, 1986)	L	31.8	11.3		29.4	31[b]			
	W	22.0	8.4		15.5	16.9			
H. brevipes (YPM 13098)* (Jin, 2005)	L				31.5	34.0	37.0		
				13.8	15.7	14.8			
H. immanis (AMNH 13143)* (Szalay and Gould, 1966)	L	28.2		21.7	30.4	32.8	30.2	31.5	21.7
	W	19.3		10.8	15.1	16.3	15.8	15.3	11.0
H. leotensis (CM 11778)* (Peterson, 1931)				20		30	30	26	

Measurements of the Hancock Quarry specimen were taken with Pittsburgh digital calipers to the nearest 0.1 mm. Additional measurements were made from CT scans of the specimen. The CT-based measurements were taken from scaled images with ImageJ (https://imagej.nih.gov/ij/) (Table 1).

Institutional Abbreviations. AMNH, American Museum of Natural History, New York, New York, USA; CM, Carnegie Museum of Natural History, Pittsburg, Pennsylvania, USA; IVPP, Institute of Vertebrate Paleontology and Paleoanthropology, Beijing, China; TMM, Texas Memorial Museum, Austin, Texas, USA; UCMP, University of California Museum of Paleontology, Berkeley, California, USA; UOMNH, University of Oregon Museum of Natural and Cultural History, Eugene, Oregon, USA; YPM, Yale Peabody Museum of Natural History, New Haven, Connecticut, USA.

GEOLOGIC CONTEXT

The Hancock Quarry is from the top of the Clarno Formation (Figure 1) and is geographically located within the Clarno Unit of John Day Fossil Beds National Monument. The quarry consists of tan siltstones, mudstones, and cobble conglomerate units and is about 5 m below the unconformable contact with the John Day Formation (Bestland et al., 1999; Hanson, 1996). These sedimentary units are 10 m thick while the bone-bearing deposits of the main locality are only 5.3 m thick, representing a normal grading sequence (Hanson, 1996). The Hancock Quarry is bracketed between Stony Tuff dated at 42.7 ± 0.3 Ma (Bestland et al., 1999) and Member A Ignimbrite at the base of the Big Basin Member of the John Day Formation dated at 39.22 ± 0.03 Ma (Bestland et al., 1999).

TABLE 1 (continued).

H. leotensis (CM 2961)	L			21	26	30	29	27	19
(Peterson, 1931)				12	13	16	13		
H. macrocephalus (YPM	L					27.0	30.4	30.1	24.3
11901)* (West, 1981)							14.3	15.4	14.0
H. orientalis (IVPP V 13646)	L	20.5	10.7	17.7	21.6	23.2	26.9		
(Jin, 2005)		13.8	5.8	9.2	9.8	11.0	12.2		
H. orientalis (IVPP V 13647)	L			17.9					
(Jin, 2005)				9.9					
H.? koreanicus (repository					20.5	20.8			
unknown) (Shikama, 1943)					9.0	9.8			
Alveolar Measurements									
H. cf. *uintensis* (UOMNH F–	L	15.6	10.4[a]	29.0[a]					16.5[a]
36924)	W	9.7	7.3[a]	10.5[a]					7.5[a]
H. cf. *uintensis* (TMM 40498-3	L			23.7			28.7		
right) (Gustafson, 1986)	W								

All measurements are in millimeters.
[a] Measurement is taken from the CT scan
[b] Measurement estimated (see Gustafson, 1986)
* Type specimen
Measurement abbreviations: **L,** anteroposterior length of tooth; **W,** transverse width of tooth

SYSTEMATIC PALEONTOLOGY

Order MESONYCHIA Matthew, 1937
Family MESONYCHIDAE Cope, 1875
Genus HARPAGOLESTES Wortman, 1901

Type species. *Harpagolestes macrocephalus* Wortman, 1901, by original designation

Harpagolestes cf. *uintensis* (Scott, 1888)
Figures 2-4, Appendix 1

Referred specimen. UOMNH F-36924, left dentary with partial crowns of p2-m2 and alveoli of c1, p1, and m3 (Figures 2-4, Appendix 1).
Occurrence. UO 2473 (JDNM-13, UCMP V75203), Hancock Quarry, Wheeler County, Oregon, Clarno Formation. Precise locality information available to qualified researchers upon request.
Age. Late middle Eocene, either latest Uintan NALMA (Bestland et al., 1999; Lucas et al., 2004) or early Duchesnean NALMA (Hanson, 1996;

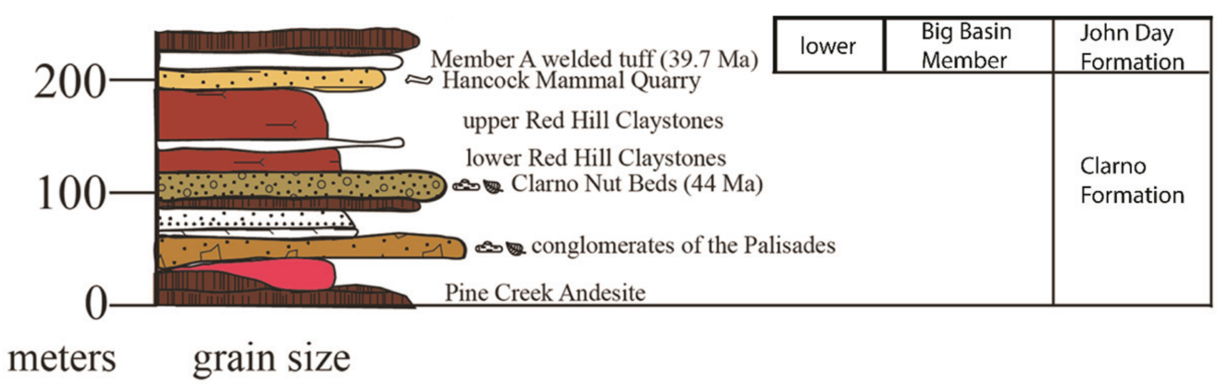

FIGURE 1. Stratigraphic column of the Clarno Formation with known fossil localities' stratigraphic positions indicated. Figure provided by the U.S. National Park Service.

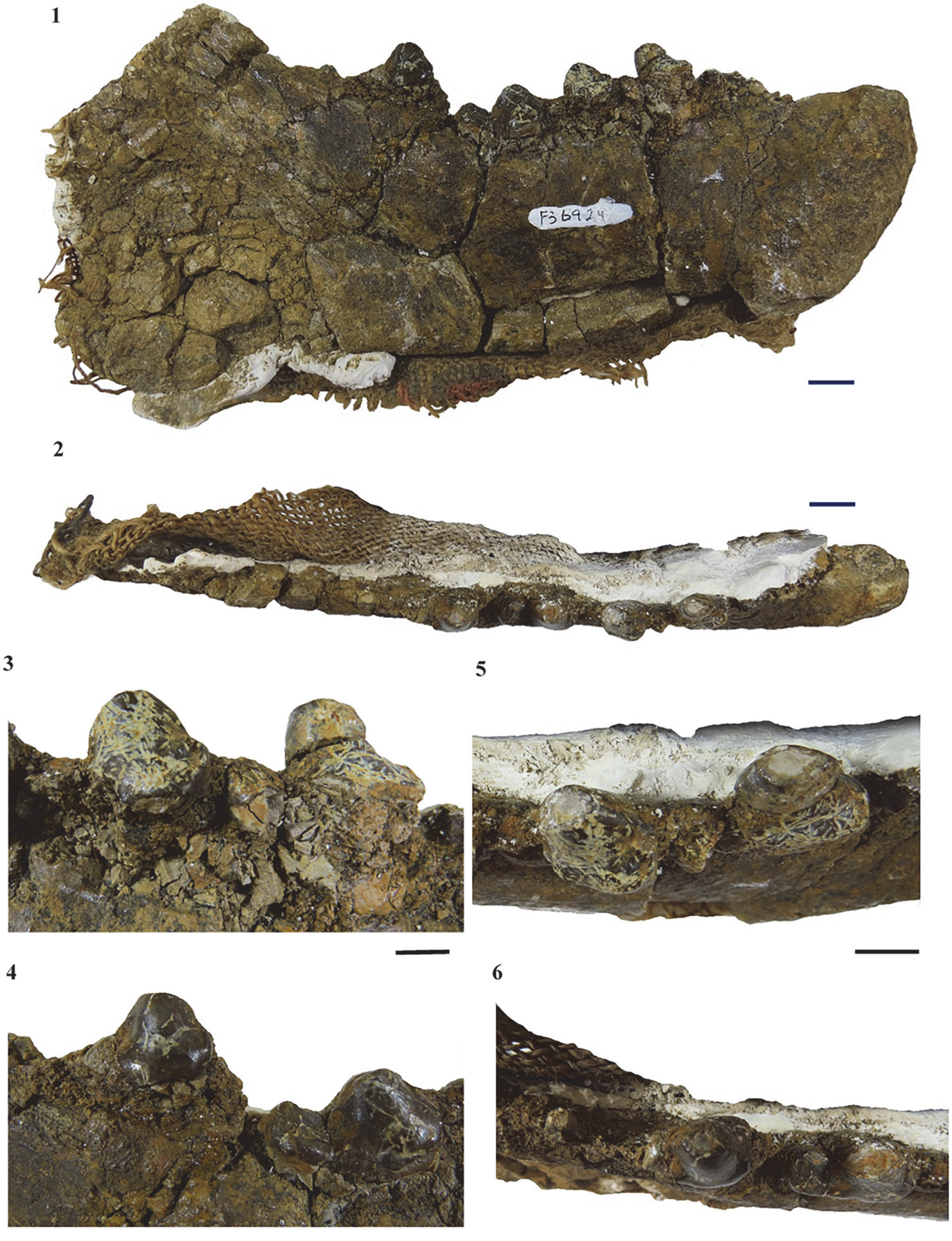

FIGURE 2. *Harpagolestes* cf. *uintensis* (UOMNH F-36924). **1,** lingual view of full specimen; **2,** occlusal view of full specimen; **3,** lingual view of p3-p4; **4,** lingual view of m1-m2; **5,** occlusal view of p3-p4; **6,** occlusal view of m1-m2. Anterior is facing toward the right. Scale bars equal 10 mm.

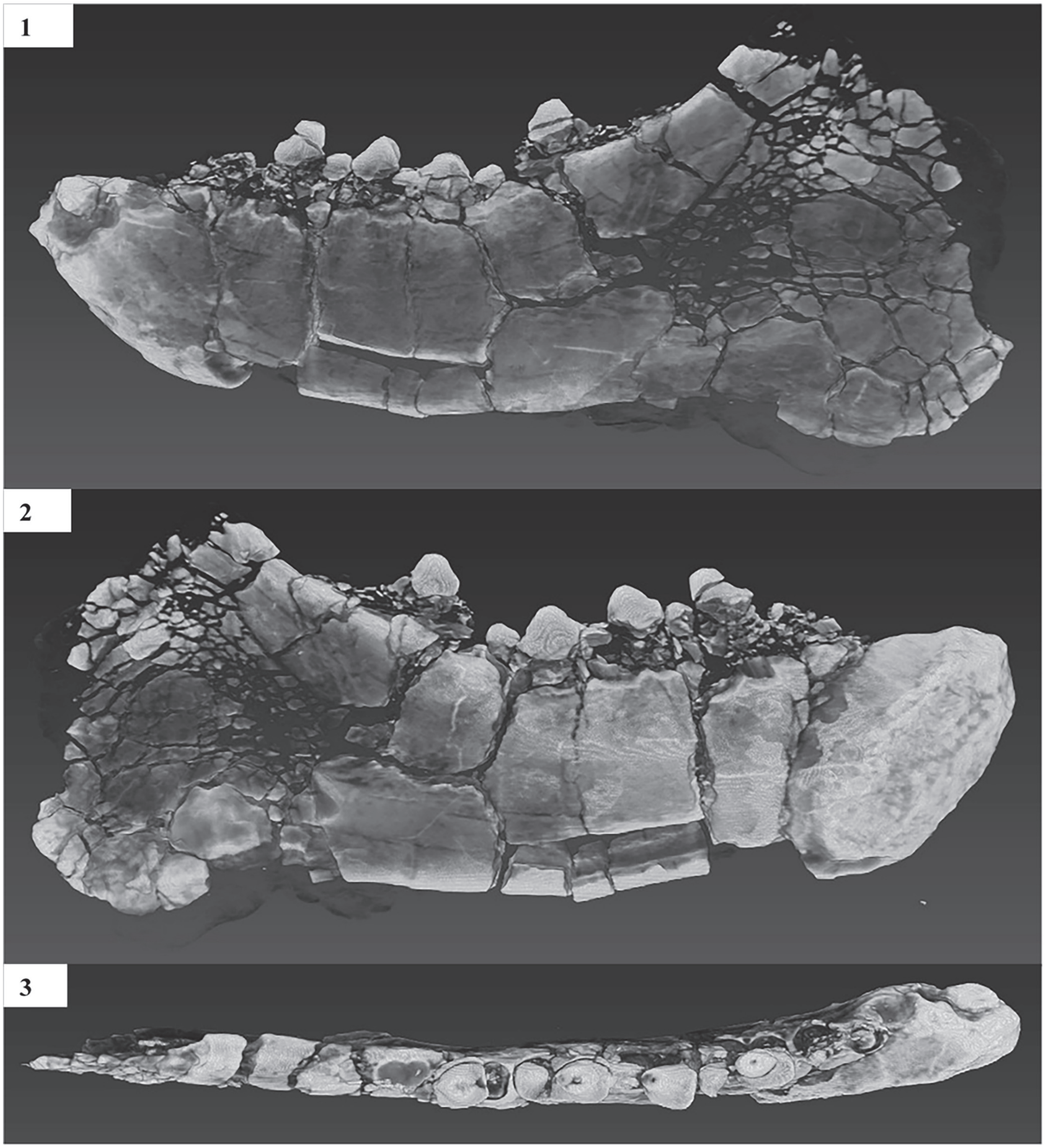

FIGURE 3. CT image of *Harpagolestes* cf. *uintensis* (UOMNH F-36924). **1,** buccal view; **2,** lingual view; **3,** occlusal view. Anterior is facing towards the left in **1**. Anterior is facing towards the right in **2-3**. Scale bar equals 10 mm.

Lander and Hanson, 2006). Bracketed between the Stony Tuff dated at 42.7 ± 0.3 Ma (Bestland et al., 1999) and the Member A Ignimbrite dated at 39.22 ± 0.03 Ma (Bestland et al., 1999).

Genus diagnosis. *"Harpagolestes* has a dental formula of 3.1.3(4).2/3.1.4.3 P3 is double-rooted; metacone is present on P4; parastyle on M1 is well developed while metastyle may be reduced; M2 is considerably wider than long, with a paracone subequal to the protocone and while metacone vestigial or absent; buccal cingulum is absent on P4-M2; p1 is greatly reduced; metaconids are absent from m1-3; lacrimal-nasal contact is present in several species" (Zhou, 1995, p. 115).

Species diagnosis. "Large size; paraconid is reduced on lower molars; there are diastemata

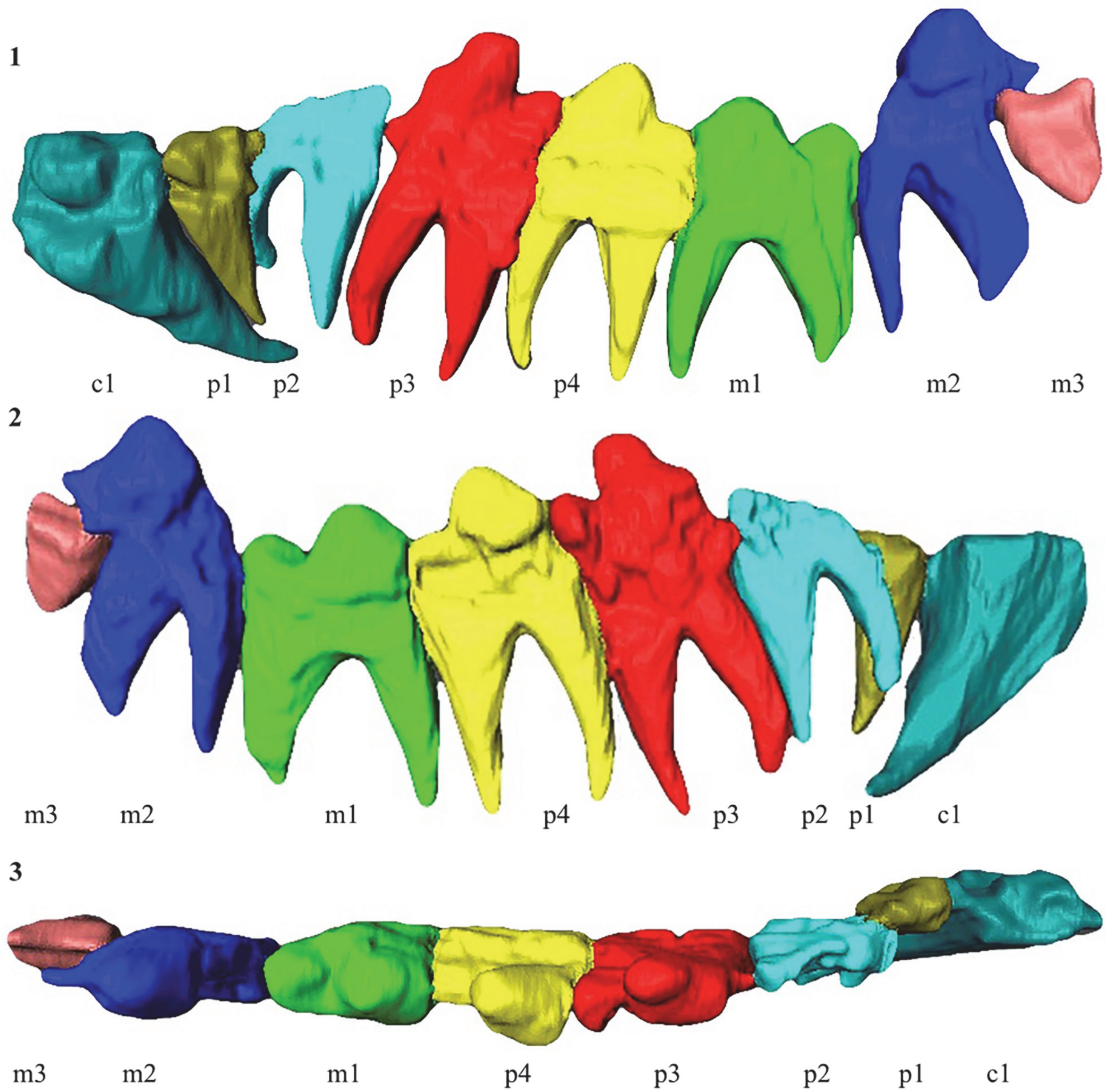

FIGURE 4. Three-dimensional reconstruction of *Harpagolestes* cf. *uintensis* (UOMNH F-36924) crowns and roots. **1,** buccal view; **2,** lingual view; **3,** occlusal view. Anterior is facing towards the left in **1**. Anterior is facing towards the right in **2-3**. Colors indicate tooth position. Scale bar equals 10 mm.

between P1 and P2 and between P2 and P3" (Zhou, 1995, p. 118).

Description. UOMNH F-36924 is a left dentary that has been taphonomically deformed, mostly through anteroposterior compression. Much of the dentary is broken because of this deformation, and the portion anterior to c1 is missing. The premolars have been shifted lingually from their natural position (Figure 3). The mandibular symphysis is intact, steep, and roughly oval in shape. The symphysis extends from the anterior breakage point to the posterior of p2. The horizontal ramus is deep, but the depth cannot be accurately determined because of deformation. Similarly, the ventral margin of the horizontal ramus appears to be slightly convex, but this convexity may be a result of deformation; the unbroken section of the ventral margin under m2 is straight. The angular process of the dentary is severely crushed, and the specimen is broken at the base of the ascending ramus. No foramina are visible on the specimen.

The incisors are absent because the dentary is broken anterior to c1. The canine is broken at the base of the crown, with the root present. The shape of the root suggests that the canine was a large, anteroposteriorly compressed tooth (Figure 4, Appendix 1).

The p1 is not visible on the specimen. A CT scan has revealed that a small, single rooted p1 was present, but the tooth is now missing and the alveolus is infilled with sediment (Figures 3-4, Appendix 1).

A relatively large, double-rooted p2 sits posterior to the p1 alveolus. Most of the p2 crown has been shattered and lost; the few remaining fragments indicate that the tooth had a large trigonid and a relatively narrow talonid. The anterior root is bent lingually (Figure 4, Appendix 1.2). Whether this was a result of premolar crowding or postmortem deformation cannot be determined.

The p3 has a robust trigonid dominated by a conical protoconid. The tip of the protoconid is flattened from extensive occlusal wear. The trigonid is mostly intact and inclined posteriorly. However, the top of the trigonid was broken off and then reattached after collection. The angle of reattachment may not reflect the original orientation. Taphonomic deformation has resulted in the anteriormost portion of the trigonid being broken. Thus, the presence of a paraconid on p3 cannot be determined. The p3 talonid is present and appears to have had a single cusp, but damage precludes a more extensive description. Like the p2, the p3 is double-rooted.

The p4 is slightly larger than p3, but size is difficult to determine because of the postmortem anteroposterior compression and the anterior breakage of p3. The CT scan shows that the anterior enamel of the p4 trigonid remains intact and that only the anterior root has been damaged (Appendix 1.2). Thus, the p4 lacks a paraconid and the large, posteriorly tilted trigonid is composed entirely of the conical protoconid. Like the p3, the p4 protoconid exhibits extensive wear on its occlusal surface. The p4 talonid, which is narrower than the trigonid, has extensive damage to its occlusal surface; little can be said about its morphology.

The double-rooted m1 is the most intact of the teeth. The m1 trigonid is dominated by a robust, conical protoconid that has an occlusal surface flattened by wear. Anterior breakage makes the presence of a paraconid impossible to determine, although a small protrusion on the anterolingual side suggests that a paraconid may have initially been present. The trigonid is wider than the talonid. There is a single cusp at the center of the talonid and a posterobuccal protrusion on the heel. A lingual cingulum extends from the anterior face of the protoconid to the posterior of the talonid.

Taphonomic distortion of the jaw has resulted in the m2 being elevated above the rest of the toothrow, and the trigonid has been forced into the space the talonid originally occupied. The trigonid is anteriorly damaged, but the occlusally worn conical protoconid is intact. There is a lingual cingulum and a slight anterolingual swelling that suggests a paraconid may have existed. The talonid has been broken, but the posterior root is still present. The remaining outline of the talonid is triangular with a narrow heel.

The m3 crown is missing, but the CT scan confirms that the tooth was originally present (Figure 3, Appendix 1.2). The scan shows a single alveolus which appears to be for a fused or partially fused double root. The size of the alveolus indicates that m3 was smaller than the other molars (Table 1).

DISCUSSION

Comparison

The Hancock Quarry specimen was compared to all species of *Harpagolestes*. *Harpagolestes orientalis, H.? koreanicus,* and *H. leei* are all smaller than the Hancock Quarry specimen (Table 1) (Jin, 2005, 2012). The only lower dentition of *H. macrocephalus* is a dentary with all teeth highly worn except for m3 (Wortman, 1901). Thus, no diagnostic morphological characters are available for *H. macrocephalus* lower dentition. However, the m3 of *H. macrocephalus* is relatively large (24.3 mm) compared to the Hancock Quarry specimen (16.5 mm) (West, 1981). *Harpagolestes brevipes* is larger than the Hancock Quarry specimen and has a symphysis that extends more posteriorly (Thorpe, 1923; Zhou, 1995). *Harpagolestes leotensis* and *H. immanis* share many features with *H. uintensis*, and these taxa may be conspecific (Szalay and Gould, 1966; West, 1981; Gustafson, 1986). However, the species have not been formally synonymized. Both specimens of *H. leotensis* lower dentition (CM 117778; CM 2961) have a distinct paraconid on p4 while the Hancock Quarry specimen has a vestigial one (Peterson, 1931; Zhou, 1995). Szalay and Gould (1966, p. 144) note that, for *H. immanis*, “the teeth of the lower jaw are virtually identical with those of *H. uintensis*. The scarcity of specimens precludes further analysis.” We attribute the Hancock Quarry specimen to *H.* cf. *uintensis* because the description of *H. uintensis* best matches the Hancock Quarry specimen. We have chosen to use the designation *H.* cf. *uintensis* rather than *H. uintensis* because some fea-

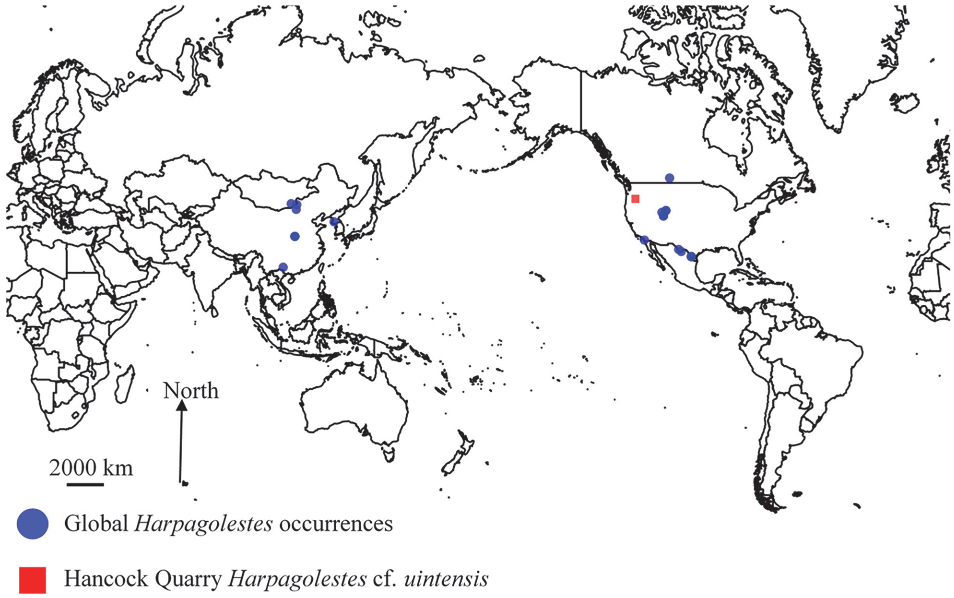

FIGURE 5. Map of global *Harpagolestes* occurrences. Occurrence data were obtained from Shikama (1943), Kay (1957), Szalay and Gould (1966), Chow et al. (1973), Gazin (1976), Golz and Lillegraven (1977), Zheng and Chi (1978), Storer (1984), Gustafson (1986), Tomida and Lee (2004), Jin (2005, 2012).

tures of the specimen are ambiguous as a result of deformation.

Paleogeography

The Hancock Quarry specimen is a significant addition to the global distribution of mesonychids. North American mesonychids have been predominantly recovered from the Rocky Mountain and Great Plains regions (with one indeterminate mesonychid known from California), and no mesonychids were known from the limited Eocene fossil records of the Pacific Northwest (Archibald, 1998). Zhou (1995) suggested that many Eocene mesonychid genera originated in North America and migrated to Asia; however, there are coeval occurrences of *Harpagolestes* on both continents (e.g., Sazaly and Gould, 1966; Zhou, 1995; Jin, 2005), leaving the geographic origination of this genus indeterminable at present. Asian species of *Harpagolestes* are known from both the middle and late Eocene: *H. leei* and *H. orientalis* are from the middle Eocene of China and Mongolia, while *H.*? *koreanicus* is from the late Eocene of the Korean peninsula (Figure 5). Unfortunately, more precise stratigraphic ranges are not available for the Asian species.

Unlike the Asian *Harpagolestes*, all North American species are from the middle Eocene. The earliest occurrence is *H. macrocephalus* from the Wyoming Bridgerian NALMA (Gazin, 1976) (Figure 5). Most North American species are from the Uintan NALMA, including *H. uintensis* (Archibald, 1998). *Harpagolestes uintensis* has been found in Texas and Utah; coeval specimens of *Harpagolestes* are reported from Texas, Utah, Wyoming, California, and Saskatchewan (Figure 5). The latest known North American occurrence is an indeterminate *Harpagolestes* from the Duchesnean NALMA of Texas (Gustafson, 1986). The Hancock Quarry specimen is the first mesonychid described from the Pacific Northwest, adding to the known distribution of mesonychids. While the geographic origination still cannot be determined, the Hancock Quarry specimen does support the idea of mesonychid migration through the Bering region.

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APPENDIX 1.

Interactive 3-dimensional reconstruction of *Harpagolestes* cf. *uintensis* (UOMNH F-36924). **1,** Reconstruction of scanned surface; **2,** Reconstruction of volumized toothrow. Available as a PDF only at https://palaeo-electronica.org/content/2019/2585-first-mesonychid-from-oregon.