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## THE EARLIEST KNOWN FISHER (MUSTELIDAE), A NEW SPECIES FROM THE RATTLESNAKE FORMATION OF OREGON

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**ABSTRACT**—Fishers are elusive carnivorans, with few occurrences in the fossil record. The origin and early evolution of fishers is unclear, but they likely originated in Asia. A new record of *Pekania* from the Rattlesnake Formation of Oregon represents the earliest known occurrence of a fisher, more than 5 million years earlier than other records in North America. This specimen has an unambiguous derived trait shared with other members of the genus, an external median rootlet on the upper carnassial. The age of this new find is inferred to be between 7.05 and 7.3 Ma, through radiometric and magnetostratigraphic dating. This age is supported by the presence of specimens of a shrew, *Sorex edwardsi*, and a rhinoceros, cf. *Teleoceras*, found at the same locality, as well as a rabbit, *Hypolagus* cf. *vetus*, and a tapir nearby, all of which are well known from early Hemphillian deposits. This find indicates that fishers were in both North America and Asia in the late Miocene, around the time of their divergence from other members of the clade as estimated from genetic data. Although it is over 7 million years old, this species shows remarkable similarity to extant *P. pennanti*, highlighting the highly conservative nature of gulonine mustelids. The Rattlesnake specimen is more robust than other fisher species, possibly representing something close to the ancestry of all fishers.

### INTRODUCTION

The extant fisher, *Pekania pennanti*, is an elusive medium-sized mustelid endemic to North America. Fishers are generalized predators and good climbers, favoring forest habitats with continuous canopy (Powell, 1981). The subfamily Guloninae, which includes the fisher, as well as martens, the wolverine, and the tayra, is distributed over much of North America and Eurasia today. This subfamily was formerly referred to as the Martinae, but we follow Sato et al. (2009) in using the name Guloninae, which has priority according to the International Code of Zoological Nomenclature. The gulonine clade of mustelids is known for having conservative morphology (apart from *Gulo*), making morphological studies of their relationships particularly difficult (Anderson, 1970, 1994). Recent genetic studies (Hosoda et al., 2000; Stone and Cook, 2002; Koepfli et al., 2008; Sato et al., 2009; Wolsan and Sato, 2010; Nyakatura and Bininda-Emonds, 2012; Sato et al., 2012) have shown that the fisher (formerly *Martes pennanti*) is more closely related to the tayra (*Eira barbara*) and wolverine (*Gulo gulo*) than to other species of the genus *Martes*, and was thus reclassified in the genus *Pekania* (Koepfli et al., 2008; Sato et al., 2012).

Gulonine mustelids are known from the fossil records of North America and Eurasia, but primarily from fragmentary remains that have been described as local species (including Schlosser, 1924; Zdansky, 1924; Gidley, 1927; Colbert, 1935; Helbing, 1936; Orlov, 1941; Teilhard and Leroy, 1945; Dehm, 1950; Viret, 1951; Ginsburg, 1961; Wilson, 1968; Mein and Ginsburgh, 1997; Stevens and Stevens, 2003; Nagel et al., 2009; Koufos, 2011). Anderson (1994) suggested that the earliest records of this clade include specimens referred to the genus *Martes*, from the early Miocene of Germany (Dehm, 1950). However, Sato et al. (2003) indicated that this '*Martes*' *laevidens* is not a member of that genus. Members of the Guloninae spread across Eurasia, and

may have immigrated to North America from Asia in the late Miocene (Sato et al., 2012). The earliest records of marten-like mustelids in North America include *Dinogale siouxensis* from the late Hemingfordian-aged Sheep Creek Formation of Nebraska (Cook and Macdonald, 1962), '*Martes*' *glareae* from the early Barstovian-aged Olcott Formation of Nebraska (Sinclair, 1915), '*Martes*' *gazini* from the early Barstovian Butte Creek Volcanic Sandstone Formation of Oregon (Hall, 1931), and '*Martes*' *stirtoni* from the Clarendonian-aged Ogallala Formation of Kansas (Wilson, 1968). However, some authors have synonymized these taxa with *Plionictis* or other ischyritines, considering them outside of the Guloninae (Sutton 1977; Anderson, 1994; Baskin, 1998). Anderson (1994) believed many fossil taxa referred to '*Martes*' were not martens and not closely related to the ancestry of extant taxa. She considered the extant American marten, *Martes americana*, to be a late Pleistocene immigrant to North America (Anderson, 1994). Sato et al. (2003) suggested that the oldest true *Martes* known is *Martes wenzensis* from the Pliocene of Poland (Wolsan, 1989).

Fisher fossils are particularly rare. Two species have been described from the late Miocene and Pliocene of Asia, *Martes palaeosinensis* and *M. anderssoni* (Schlosser, 1924; Zdanzky, 1924; Anderson, 1970). Anderson (1994) indicated that both probably represented a single species, although Wang et al. (2012) question whether *M. anderssoni* is truly related to the fisher clade. The earliest fishers known from North America are *M. diluviana* (Cope, 1899) and *M. parapennanti* (Gidley and Gazin, 1933) from the Irvingtonian of the eastern United States, which were later synonymized as *M. diluviana* (Hall, 1936). Both *M. palaeosinensis* and *M. diluviana* were referred by Anderson (1970, 1994) to the subgenus *Pekania*. Given the morphological distinctness of these species from martens (*Martes*), and following the recommendations Koepfli et al. (2008) and Sato et al. (2012) made based upon their genetic divergence, we refer them to the genus *Pekania* as *P. palaeosinensis* and *P. diluviana*, as did Wang et al. (2012).

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The specimen described here, from the late early Hemphillian-aged Rattlesnake Formation of Oregon, represents the earliest dated record of a fisher and predates other known fishers in North America by over 5 million years. This species likely represents an early immigrant from Asia that may be close to the ancestor of other fossil and extant fishers. Given the rarity of fishers in modern ecosystems and in the fossil record, this find greatly improves our understanding of the evolution and biogeography of fishers.

## METHODS

Measurements of the teeth, to the nearest 0.1 mm, were made using Mitutoyo Absolute digital calipers. Measurements were taken at the enamel dentine junction surface of the teeth and included anteroposterior length and transverse breadth; descriptions of measurements are provided in Appendix 1. Comparisons were made with specimens of extant *Pekania* and *Martes* species from the United States National Museum of Natural History, Natural History Museum of Los Angeles County, and Donald R. Dickey Collection of the University of California, as well as photographs and measurements in several publications (including Zdansky, 1924; Gidley and Gazin, 1933; Anderson, 1970; Wang et al., 2012).

**Specimen Repositories**—**JODA**, John Day Fossil Beds National Monument, Kimberly, Oregon; **LACM**, Natural History Museum of Los Angeles County, Los Angeles, California; **UCLA**, Donald R. Dickey Collection of the University of California, Los Angeles, Los Angeles, California; **USNM**, United States National Museum of Natural History, Washington, D.C.

## GEOLOGICAL SETTING

John Day Fossil Beds National Monument (JODA) was created to help protect key fossil deposits within the John Day Basin of eastern Oregon. The John Day Basin contains hundreds of fossil localities spanning the late Eocene through the end of the Miocene; the stratigraphically highest unit exposed in the monument is the Rattlesnake Formation. The area south of Picture Gorge and west of Dayville, Oregon (Fig. 1) was first examined by Merriam (1901), and made the type area of the Rattlesnake Formation by Merriam et al. (1925). This area was later studied by Enlows (1976) and Martin (1983, 1996). When the Hemphillian Land Mammal Age was originally designated, the

Rattlesnake Formation was chosen as a reference fauna (Wood et al., 1941). The Hemphillian age of the Rattlesnake fauna has been confirmed by several studies (Martin, 1983, 1996; Fremd et al., 1994; Tedford et al., 2004; Samuels and Zancanella, 2011). In the area west of Dayville, the Rattlesnake Formation unconformably overlies the Mascall Formation, which is of Barstovian (middle Miocene) age.

The Rattlesnake Formation type area geology consists mainly of fluvial deposits, including siltstones, sandstones, and conglomerates (Enlows, 1976; Martin, 1996; Martin and Fremd, 2001). Specimens described here were found as surface float on a small exposure of reddish-brown siltstone, on the east face of a gently sloping northeast-trending ridge. The Rattlesnake Formation has many small isolated exposures with little exposed stratigraphy, making it difficult to correlate their precise position within a stratigraphic section. The prominent Rattlesnake Ash Flow Tuff (RAFT), which is widely distributed across central Oregon, has been  $Ar_{40}/Ar_{39}$  dated to  $7.05 \pm 0.01$  Ma (Streck and Grunder, 1995). Although the RAFT is not exposed in the Rattlesnake type area, regional correlation confirms this site lies well below that unit. The site lies just above a second marker bed within the lower Rattlesnake Formation, an undated white vitric tuff ("Ted's Tuff"). This tuff, which lies approximately 16 m above the base of the section (Retallack, 1999; Retallack et al., 2002), is exposed on a small exposure 70 m southeast of where the specimens were found. Prothero et al. (2006) did a paleomagnetic stratigraphy study of the type Rattlesnake section, correlating it with magnetic Chrons C3Bn to C3Br2n (6.9–7.3 Ma). Multiple lines of evidence thus confirm a late early Hemphillian age for the entire formation (Martin, 1983, 1996; Prothero et al., 2006).

Based upon Merriam's description of the type Rattlesnake area, Enlows (1976) divided the Formation into three members: a lower fanglomerate member, the Rattlesnake Ash Flow Tuff (called Rattlesnake Ignimbrite), and an upper fanglomerate member. Walker (1979, 1990) redefined the Rattlesnake Formation as only including the Rattlesnake Ash Flow Tuff, effectively orphaning the upper and lower fanglomerate members, and the biostratigraphically important associated fauna (Wood et al., 1941). More recent authors have suggested treatment of the Rattlesnake Formation as including three members (Martin, 1996) or elevating it to group status with three formations (Martin and Fremd, 2001). Like a variety of other recent studies (e.g., Retallack et al., 2002; Prothero et al., 2006; Samuels and Zancanella, 2011), we use the broader definition of Rattlesnake Formation suggested by Martin (1996).

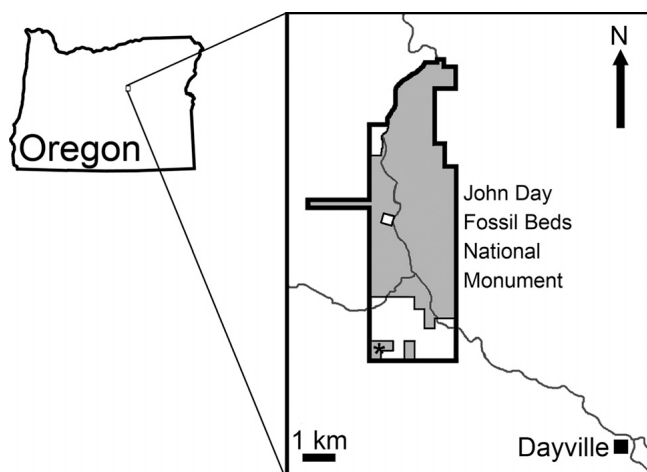


FIGURE 1. Map showing the Sheep Rock unit of John Day Fossil Beds National Monument, Grant County, Oregon. The area where the specimen described here was found is indicated by an asterisk.

## SYSTEMATIC PALEONTOLOGY

Class MAMMALIA Linnaeus, 1758  
 Order CARNIVORA Bowditch, 1821  
 Family MUSTELIDAE Fischer von Waldheim, 1817  
 Subfamily GULONINAE Gray, 1825  
 Genus *PEKANIA* Gray, 1865

**Type Species**—*Pekania pennanti* Erxleben, 1777.

**Included Species**—*P. occulta*, new species; *P. diluviana* (Cope, 1899); *P. palaeosinensis* (Zdansky, 1924); *P. pennanti* Erxleben, 1777.

**Emended Diagnosis**—A synapomorphy that unites species of *Pekania* is a P4 with a prominent exposed external median rootlet (Anderson, 1970).

**Distribution**—Early Hemphillian (late Miocene) of Oregon; late Miocene and Pliocene of China and Mongolia; Irvingtonian of Arkansas, Colorado, Pennsylvania, Maryland, and West Virginia; Rancholabrean (late Pleistocene) of eastern United States; historic range included northern forests of North America, extending south in the Appalachian mountains and Pacific Coast range, Cascades, and Rocky Mountains.

*PEKANIA OCCULTA*, sp. nov.  
(Figs. 2, 3)

**Holotype**—JODA 15214 (Figs. 2, 3): left maxilla with partial P3, P4, and M1, isolated partial left P2 and right I3. The maxilla was collected by J. Cavin on 8 December 2011; the M1 and a portion of the P3, which had broken off of the maxilla, were collected on 13 January 2012 by J. Samuels and C. Schierup.

**Type Locality**—Lower fanglomerate member of the Rattlesnake Formation, west of Dayville, Grant County, Oregon; approximately 793 m above mean sea level. This area lies within the type area of Merriam, on land administered by the National Park Service within the Sheep Rock Unit of John Day Fossil Beds National Monument (Fig. 1). Precise locality information, including GPS (global positioning satellite) data, is on file at JODA.

**Referred Specimens**—Known from holotype only.

**Diagnosis**—*Pekania occulta* has several features that distinguish it from other members of the genus: more robust dentition; enlarged P4 protocone, anteriorly positioned with weak inflection between protocone and parastyle; reduced M1 metacone and posteroexternal cingulum; distinct M1 shape characterized by narrow external lobe and broad internal lobe.

**Distribution**—Type locality only, early Hemphillian of Oregon.

**Etymology**—From the Latin, *occulta*, meaning ‘hidden’ or ‘secret,’ in reference to the long hidden origin of extant fishers and their elusive nature.

**Description and Comparisons**—The specimens consist of a left maxilla (Figs. 2, 3), which has an incomplete P3 and complete P4 and M1, as well as a partial left P2 and right I3 found nearby (Fig. 2). The teeth show little wear, suggesting that this was a young adult individual; however, there is some substantial erosion to the tooth enamel, particularly in the M1. The maxilla is similar to that of the extant *Pekania pennanti*, with a round infraorbital foramen 5.6 mm in diameter (*P. pennanti* mean = 5.09 mm). The base of the orbit is preserved, lying directly above

the infraorbital foramen and anterior root of the P4; the orbit is slightly elevated compared with *P. pennanti* and *P. palaeosinensis*. The maxillary portion of the zygomatic arch rises sharply above the M1, suggesting strongly curved arch more like *P. pennanti* than *P. palaeosinensis*.

The isolated right I3 has a broken surface, precluding detailed description of its morphology. The isolated left P2 is missing the anterior portion of the tooth, but clearly double-rooted. There is a weak cingulum at the posterior margin of the P2, along with a small but distinct ridge running down the midline of the tooth. Although incomplete, the posterior portion of the P3 in the maxilla is intact enough to observe that it has two roots and a single primary cusp. Like the P2, there is a cingulum at the posterior margin of the P3 and a distinct ridge running down the midline of the tooth. The preserved portions of the P2 and P3 in *Pekania occulta* are relatively robust, noticeably more robust than the narrow premolars of *P. palaeosinensis* (Table 1).

The P4 is very robust, with a prominent exposed external median rootlet, as is characteristic of the genus *Pekania* (Anderson, 1970) (Figs. 2, 3). This rootlet is mostly missing, but the broken base and exposed alveolus clearly indicate its presence. The P4 protocone is large compared with other species of *Pekania*, and anteriorly positioned relative to *P. pennanti*, extending as far anteriorly as the parastyle. The shape of the anterior portion of the tooth is similar to *P. palaeosinensis* and the Pleistocene *P. diluviana*, which also have an anteriorly positioned protocone. However, both of those species have a deeper inflection of the anterior portion of the tooth between the parastyle and protocone; the inflection is weak in *P. occulta* and the posterior portion of the P3 essentially occupies this space. This position of the P3 between the P4 parastyle and protocone is also seen in individuals of *P. palaeosinensis* (Zdansky, 1924), as well as *Martes martes*, *M. flavigula*, and *Gulo gulo*. In *P. pennanti*, *P. diluviana*, and *Martes americana*, the posterior portion of the P3 is adjacent to the P4 parastyle. The P4 proportions of the Rattlesnake specimen are more robust than is seen in other *Pekania* species, with a

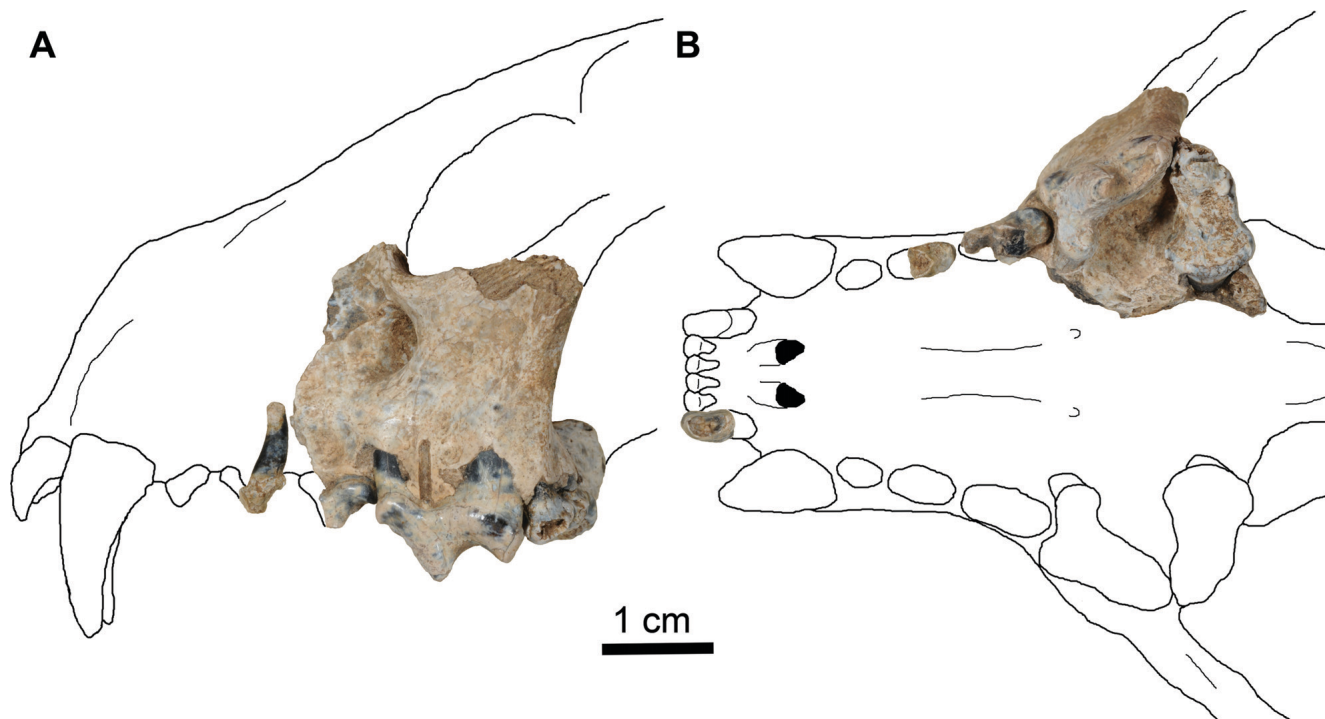


FIGURE 2. Holotype of *Pekania occulta* (JODA 15214) from the Rattlesnake Formation, Oregon. Specimen consists of a left maxilla with partial P3, P4, and M1, and partial left P2 and right I3. **A**, left lateral view; **B**, occlusal view. Scale bar equals 1 cm (Color figure available online).

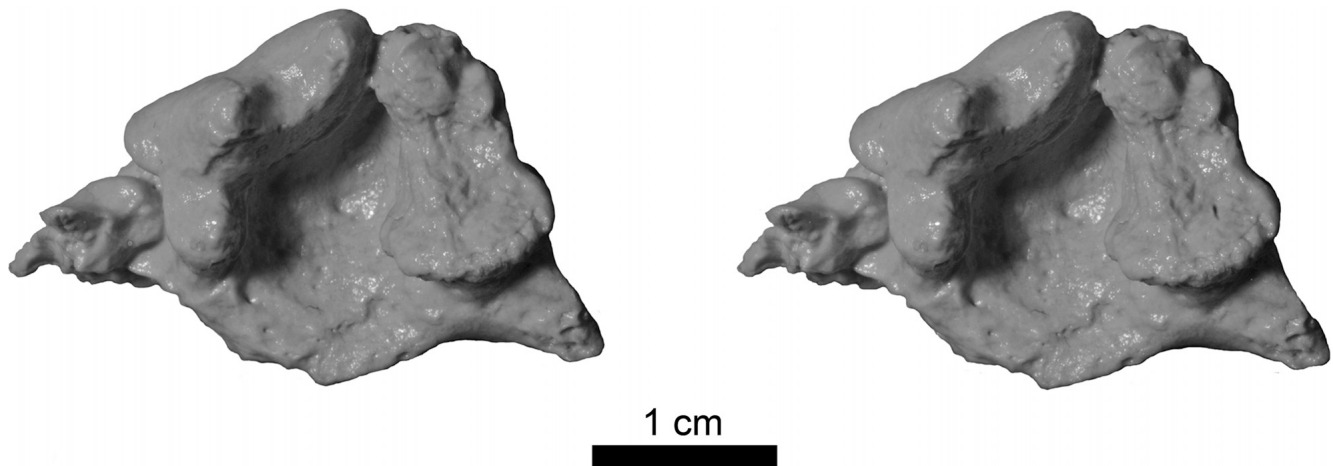


FIGURE 3. Stereophotograph of grayscale cast of *Pekania occulta* holotype (JODA 15214). Scale bar equals 1 cm.

particularly large protocone and wide paracone and metacone (Table 1). There is a slightly worn shear facet between the P4 paracone and metacone, but this is the only real evidence of tooth wear in this individual.

The M1 shape is similar to other gulonines, with the expanded inner lobe characteristic of *Martes* and *Pekania* (Figs. 2, 3). The M1 external roots are distinctly separated, with the posterior root located medially relative to the anterior root; this is more similar to the characteristics of *P. palaeosinensis* and *P. pennanti* than *P. diluviana*. The M1 of *P. occulta* is anteriorly constricted between the inner and outer lobes, and the inner lobe is rounded as in *P. pennanti*, rather than having a hypocone with a square shape as is seen in *P. palaeosinensis*. The surface of the M1 is eroded and pitted, but the paracone and metacone are small; there is an expanded cingular shelf labial to both cusps, larger anteriorly. Compared with *P. pennanti*, the metacone is reduced, as is the posteroexternal cingulum. The protocone ridge is crescentic in shape and much narrower than the rounded and expanded hypoconal cingulum. The orientation of the M1 in *P. occulta* also differs slightly from *P. pennanti* and *P. palaeosinensis*, with its occlusal surface parallel to that of the other maxillary teeth. In the later taxa, the posterior portion of the M1 is elevated, resulting in

a more acute angle between the occlusal surfaces of the M1 and P4. The M1 proportions of *P. occulta* differ from other *Pekania* species, with a particularly narrow external lobe and wide internal lobe (Table 1). The ratio of internal to external lobe length ( $M1L_{int}/M1L_{ext}$ ) for *P. occulta* is 0.65, whereas all other *Pekania* sampled have values between 0.76 and 0.91.

#### DISCUSSION

The fisher from the Rattlesnake Formation is only represented by a single specimen, but is readily differentiable from known specimens of extant and extinct species of *Pekania*. The morphologies of the teeth in *P. occulta* are distinct, most notably the robust P4 protocone and shape of the M1. Additionally, the proportions of the teeth in *P. occulta* fall outside the range of variation for extant *P. pennanti* for nearly all measurements. *P. occulta* shows particularly robust teeth when compared with extant *Pekania* and *Martes*, potentially reflecting similarity to a shared ancestor with the wolverine clade (*Gulo*).

This find represents the earliest known and dated occurrence of *Pekania* in the world, predating the former earliest record of the genus in North America by more than 5 million years.

TABLE 1. Dental measurements (in mm) of *Pekania* and *Martes* species.

Species	Specimen no.	Locality	I3		P2	P3	P4			M1		
			L	W	W	W	L	W <sub>pro</sub>	W <sub>met</sub>	L <sub>ext</sub>	L <sub>int</sub>	W
<i>Pekania occulta</i>	JODA 15214	Oregon	4.8	2.4	3.0	4.1	13.3	8.8	5.3	5.6	8.5	12.8
<i>P. pennanti</i>	Mean ( $\sigma$ , n = 12)	Various	4.1	2.4	3.0	3.4	12.2	7.4	4.6	6.2	7.4	10.9
	Min.		3.8	2.1	2.8	3.3	11.7	6.8	4.3	5.8	7.0	10.1
	Max.		4.4	2.7	3.2	3.6	13.4	7.9	4.9	6.5	7.8	11.5
	Mean ( $\varphi$ , n = 10)		3.6	2.0	2.6	3.0	10.7	6.5	3.7	5.3	6.1	9.2
	Min.		3.3	1.6	2.0	2.8	10.0	5.8	3.3	4.9	5.5	8.4
	Max.		3.8	2.1	3.0	3.4	11.1	7.2	3.9	5.9	6.4	9.5
<i>P. diluviana</i>	USNM 8010 <sup>a</sup>	Maryland					10.2	6.0	3.9	5.0	6.0	9.5
<i>P. palaeosinensis</i>	PMU 3793	China	3.2	1.9	2.0	2.9	11.0	6.4	4.0	5.7	6.5	10.4
	Min. <sup>b</sup>				1.9	2.6	9.0	4.6			5.2	8.5
	Max. <sup>b</sup>				2.5	3.7	11.5	6.7			7.6	10.9
<i>Martes americana</i>	Mean ( $\sigma$ , n = 3)		2.3	1.8	2.1	2.6	9.0	5.7	3.4	4.3	6.5	9.3
<i>M. martes</i>	LACM 74508		2.7	1.7	2.8	3.8	9.3	6.1	3.4	4.7	7.8	9.6
<i>M. flavigula</i>	LACM 8229		2.5	2.1	2.6	3.4	10.1	6.4	3.5	4.0	5.3	9.6

**Abbreviations:** L, anteroposterior length; W, transverse width; **pro**, at protocone; **met**, at metacone; **ext**, external lobe; **int**, internal lobe. Detailed definitions of dental measurements are provided in Appendix 1.

<sup>a</sup>Gidley and Gazin (1933); <sup>b</sup>Zdansky (1924).

Because many of the early Eurasian species previously referred to 'Martes' likely do not belong to the Guloninae (Anderson, 1994; Sato et al., 2003), *Pekania occulta* also represents the earliest known well-dated gulonine. The position of this locality within the Rattlesnake Formation, relative to a dated ash bed and magnetostratigraphy, indicates a late early Hemphillian age, between 7.3 and 7.05 Ma. The presence of a shrew dentary, *Sorex edwardsi*, and rhinocerotid tooth fragments, cf. *Teleoceras*, at the site supports a Hemphillian age. Additionally, several other taxa well known from Hemphillian-aged deposits were found on exposures nearby, including a nearly complete rabbit dentary, *Hypolagus cf. vetus*, and a partial tapir tooth. *Teleoceras* and *Hypolagus* are both commonly found within Rattlesnake Formation deposits (Merriam et al., 1925; Martin, 1983, 1996). Although none of these taxa are restricted to the Hemphillian, the occurrence of all of these taxa within the same horizon as *P. occulta* supports the inferred early Hemphillian age of the site.

This record from Oregon indicates that fishers were in North America by at least 7.05 Ma, either evolving here or emigrating from Asia. *Pekania occulta* is morphologically distinct from other fisher species in North America and Asia, with both *P. palaeosinensis* and *P. diluviana* more similar to the extant *P. pennanti* (Anderson, 1970, 1994; Wang et al., 2012). This suggests that *P. occulta* did not directly lead to *P. pennanti* in North America, but probably displays features close to the ancestor of all fishers. Ancestral-state reconstructions based on molecular data (Koepfli et al., 2008; Sato et al., 2012) suggest an Old World origin for this clade. Sato et al. (2012) inferred Asia as the ancestral area for the clade through parsimony and Bayesian inference, whereas maximum likelihood favored Asia and North America. Given the presence of other marten-like mustelid fossils earlier in Europe and Asia (Dehm, 1950; Sotnikova, 1995; Qiu, 2003; Nagel, 2009; Wang et al., 2012), it is likely that *Pekania* evolved somewhere in Eurasia and *P. occulta* represents an early immigrant to North America. Most records of *P. palaeosinensis* from Asia are not well dated, but a new record from the Baodean-aged Baogeda Ula Fauna of Mongolia is likely similar in age to *P. occulta* from the Rattlesnake Formation (Wang et al., 2012). Although that fauna has not been directly dated, that region of Mongolia has a number of dated basalt layers and one that may cap the Baogeda Ula Fauna may be  $7.11 \pm 0.48$  Ma (Wang et al., 2012). This is roughly the same age (or slightly younger) than the Rattlesnake Formation, clearly indicating that *Pekania* was present on both continents in the late Miocene.

In the late early Hemphillian, when *Pekania* may have dispersed to North America, several other carnivorous species immigrated to North America from Asia (Tedford et al., 1987; Qiu, 2003; Tedford et al., 2004; Woodburne, 2004). Another mustelid (*Lutravus*), as well as a bear (*Indarctos*) and an ailurid (*Simocyon*), have all been found in the Rattlesnake Formation (Merriam et al., 1916, 1925; Thorpe, 1921), and are known from similar-aged (Baodean) deposits in Asia (Zdansky, 1924; Qiu, 2003). The Baogeda Ula Fauna from Mongolia has *Hipparion* and *Dipoides* co-occurring with *Pekania* (Wang et al., 2012); both of these taxa are common in the Rattlesnake Formation (Merriam et al., 1925). The beaver, *Castor*, was also recently found in the Rattlesnake Formation, illustrating its arrival on this continent at the same time (Samuels and Zancanella, 2011). Oregon has some of the Hemphillian-aged sites located nearest to the land bridge between North America and Asia, therefore, similarity to Asian faunas and early records of immigrant taxa from Oregon should not be surprising (Shotwell, 1956).

Several recent molecular studies have estimated the divergence dates of the Guloninae from other mustelids. In a study using an extensive sampling of 22 gene segments, Koepfli et al. (2008) estimated that this clade diverged from other mustelids around 11.0 Ma (95% confidence interval [CI]: 9.4–12.5 Ma) and *Pekania* diverged around 6.4 Ma (95% CI: 4.7–8.0 Ma). Yu et al.

(2011) used 17 nuclear gene segments and mitochondrial genome data, yielding estimates for the origin of the Guloninae of 5.97 Ma (95% CI: 3.39–8.90 Ma) and 10.91 Ma (95% CI: 7.82–14.37 Ma), respectively. Sato et al. (2012) examined nine nuclear genes and one mitochondrial gene, estimating divergence of the Guloninae from other mustelids at 12.65 Ma (95% CI: 10.83–14.72 Ma) and divergence of *Pekania* at 7.90 Ma (95% CI: 6.41–9.64 Ma) using Multidivtime analysis. The age of *Pekania occulta* is very close to these estimates based on molecular data, and the inclusion of *P. occulta* as a calibration point in future studies would help yield better estimates of the timing of splits within the Mustelidae. Late Miocene records of *Pekania* correspond well with the timing of diversification within multiple groups of carnivores based upon molecular estimates (Koepfli et al., 2008; Eizirik et al., 2010; Sato et al., 2012); 7.3 Ma was actually estimated to be a peak in net diversification rate for carnivores by Nyakatura and Bininda-Emonds (2012).

Today, fishers (*Pekania pennanti*) occur across the northern United States and southern Canada. Fishers strongly prefer dense forests with continuous canopy (Powell, 1981). Oregon in the Hemphillian has been interpreted as representing tall grassland and shrubland with faunas typical of open habitats (Fremd et al., 1994). Retallack et al. (2002) studied paleosols in the Rattlesnake Formation, interpreting the base of the section as riparian woodlands and meadows, and, following aridification through the section, a shift to tall grassland and semiarid wooded shrubland environments. Commonly found cursorial grazers (equids: *Pliohippus* and *Hipparion*; antilocaprids: *Sphenophalos*) and burrowing mammals (*Spermophilus* and *Scapanus*) (Merriam et al., 1925; Martin, 1996) support reconstruction of the Rattlesnake Formation with open paleoenvironments. However, boreal organisms such as *Pekania* and rare petrified wood fragments (*Quercus* sp.) suggest the persistence of a heterogeneous environment, with some extensive forested areas. These may have existed in riparian areas, which were common, as indicated by paleosol evidence and large root traces (Retallack et al., 2002) and the abundance of the beaver *Dipoides stirtoni* in Rattlesnake Formation deposits.

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#### LITERATURE CITED

- Anderson, E. 1970. Quaternary evolution of the genus *Martes* (Carnivora, Mustelidae). *Acta Zoologica Fennica* 130:1–132.
- Anderson, E. 1994. Evolution, prehistoric distribution and systematics of *Martes*; pp. 13–25 in S. W. Buskirk, A. S. Harestad, M. G. Raphael, and R. A. Powell (eds.), *Martens, Sables and Fishers: Biology and Conservation*. Cornell University Press, Ithaca, New York.
- Baskin, J. A. 1998. Mustelidae; pp. 152–173 in C. M. Janis, K. M. Scott, and L. L. Jacobs (eds.), *Evolution of Tertiary Mammals of North America, Volume 1: Terrestrial Carnivores, Ungulates, and Ungulate-like Mammals*. Cambridge University Press, Cambridge, U.K.

- Bowditch, T. E. 1821. An Analysis of the Natural Classifications of Mammalia for the Use of Students and Travelers. J. Smith, Paris, France, 151 pp.
- Burmeister, G. 1850. Verzeichnis der im Zoologischen Museum der Universität Halle-Wittenberg aufgestellten Säugethiere, Vögel und Amphibien. Halle, Friedrichs-Universität, 84 pp.
- Colbert, E. H. 1935. Siwalik mammals in the American Museum of Natural History. Transactions of the American Philosophical Society, Philadelphia, New Series 26:1–401.
- Cook, H. J., and J. R. Macdonald. 1962. New Carnivora from the Miocene and early Pliocene of western Nebraska. Journal of Paleontology 36:560–567.
- Cope, E. D. 1899. Vertebrate remains from Port Kennedy bone deposit. Journal Academy of Natural Sciences of Philadelphia, 11:193–267.
- Dehm, R. 1950. Die Raubtiere aus dem Mittel-Miocän (Burdigalium) von Winstershof-West bei Eichstätt in Bayern. Abhandlungen der Bayerischen Akademie der Wissenschaften, Mathematisch-naturwissenschaftliche Klasse, Neue Folge 58:1–141.
- Enlows, H. E. 1976. Petrography of the Rattlesnake Formation at the type area, central Oregon. Department of Geology and Mineral Industries, State of Oregon, Oil and Gas Investigations 25:1–34.
- Eizirik, E., W. J. Murphy, K. P. Koepfli, W. E. Johnson, J. W. Dragoo, R. K. Wayne, and S. J. O'Brien. 2010. Pattern and timing of diversification of the mammalian order Carnivora inferred from multiple nuclear gene sequences. Molecular Phylogenetics and Evolution 56:49–63.
- Erxleben, J. C. P. 1777. Systema Regni Animalis, per Classes, Ordines, Genera, Species, Varietates, cum Synonymia et Historia Animalium. Classis I, Mammalia. Weygand, Leipzig, 636 pp.
- Fischer von Waldheim, G. 1817. Adversaria zoologica. Mémoires de la Société Impériale des Naturalistes de Moscou 5:357–472.
- Fremd, T. J., E. A. Bestland, and G. J. Retallack. 1994. John Day Basin paleontology field trip guide and road log. Society of Vertebrate Paleontology, 1994 Annual Meeting. Seattle, Northwest Interpretive Association, 80 pp.
- Gidley, J. W. 1927. A true marten from the Madison Valley (Miocene) of Montana. Journal of Mammalogy, 8:239–242.
- Gidley, J. W., and C. L. Gazin. 1933. New Mammalia in the Pleistocene Fauna from Cumberland Cave. Journal of Mammalogy 14:343–357.
- Ginsburg, L. 1961. La faune des carnivores Miocènes de Sansan (Gers). Mémoires du Muséum National d'Histoire Naturelle Série C Géologie 9:1–187.
- Gray, J. E. 1821. On the natural arrangement of vertebrate animals. The London Medical Repository Monthly Journal and Review 15:296–310.
- Gray, J. E. 1865. Revision of the genera and species of Mustelidae contained in the British Museum. Proceedings of the Zoological Society of London 1865:100–154.
- Helbing, H. 1936. Die carnivoren des Steinheimer beckens, A. Mustelidae. Palaeontographica Beiträge zur Naturgeschichte der Vorzeit 5:1–56.
- Hemprich, W. 1820. Grundriss der Naturgeschichte für höhere Lehranstalten. Berlin, August Rucker, 432 pp.
- Hosoda, T., H. Suzuki, M. Harada, K. Tsuchiya, S.-H. Han, Y.-p. Zhang, A. P. Kryukov, and L.-K. Lin. 2000. Evolutionary trends of the mitochondrial lineage differentiation in species of genera *Martes* and *Mustela*. Genes & Genetics Systems 75:259–267.
- Koepfli, K.-P., K. A. Deere, G. J. Slater, C. Begg, K. Begg, L. Grassman, M. Lucherini, G. Veron, and R. K. Wayne. 2008. Multigene phylogeny of the Mustelidae: resolving relationships, tempo and biogeographic history of a mammalian adaptive radiation. BMC Biology 6:10.
- Koufos, G. D. 2011. The Miocene carnivore assemblage of Greece. Estudios Geológicos 67:291–320.
- Kurtén, B. 1970. The Neogene wolverine *Plesiogulo* and the origin of *Gulo* (Carnivora, Mammalia). Acta Zoologica Fennica 131:1–22.
- Kurtén, B., and E. Anderson. 1980. Pleistocene Mammals of North America. Columbia University Press, New York, 442 pp.
- Linnaeus, C. 1758. Systema naturae per regna tria naturae, secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis, locis. Vol. 1: Regnum animale. Editio decima, 1758. Societas Zoologicae Germanicae, Stockholm.
- Martin, J. E. 1983. Additions to the early Hemphillian (Miocene) Rattlesnake Fauna from central Oregon. Proceedings of the South Dakota Academy of Science 62:23–33.
- Martin, J. E. 1996. Investigation of the late Miocene (Hemphillian) Rattlesnake Formation on lands administered by the Bureau of Land Management, Picture Gorge area, central Oregon. Unpublished report, Bureau of Land Management, Prineville District Office, 22 pp.
- Martin, J. E., and T. J. Fremd. 2001. Revision of the lithostratigraphy of the Hemphillian Rattlesnake units of central Oregon. PaleoBios 21:89.
- McKenna, M. C., and S. K. Bell. 1997. Classification of Mammals above the Species Level. Columbia University Press, New York, 631 pp.
- Mein, P., and L. Ginsburg. 1997. Les mammifères du gisement miocène inférieur de Li Mae Long, Thaïlande: systématique, biostratigraphie et paléoenvironnement. Geodiversitas 19(4):783–844.
- Merriam, J. C. 1901. A contribution to the geology of the John Day Basin. University of California, Publication of Department of Geological Sciences 2(9):269–314.
- Merriam, J. C., C. Stock, and C. L. Moody. 1916. An American Pliocene bear (Rattlesnake beds, John Day region, Oregon). University of California Publications, Bulletin of the Department of Geology 10:87–109.
- Merriam, J. C., C. Stock, and C. L. Moody. 1925. The Pliocene Rattlesnake Formation and fauna of eastern Oregon, with notes on the geology of the Rattlesnake and Mascall deposits. Carnegie Institution of Washington, Contributions to Palaeontology 347:43–92.
- Nagel, D. 2009. The early Vallesian vertebrates of Atzelsdorf (Late Miocene, Austria). 10. Carnivora. Annalen des Naturhistorischen Museums in Wien 111A:605–618.
- Nagel, D., C. Stefen, and M. Morlo. 2009. The carnivoran community from the Miocene of Sandelzhausen (Germany). Paläontologische Zeitschrift 83:151–174.
- Nyakatura, K., and O. R. P. Bininda-Emonds. 2012. Updating the evolutionary history of Carnivora (Mammalia): a new species-level supertree complete with divergence time estimates. BMC Biology 10:12.
- Orlov, J. A. 1941. Tertiary Carnivora of West Siberia, III: Mustelidae; pp. 30–39 in J. A. Orlov (ed.), Tertiary Mammalia and Localities of Their Remains. Travaux de l'Institut Paleontologique, Académie des Sciences de l'Union des Républiques Soviétiques Socialistes 8.
- Powell, R. 1981. *Martes pennanti*. Mammalian Species 156:1–6.
- Prothero, D. R., J. M. Hoffman, and S. E. Foss. 2006. Magnetic stratigraphy of the upper Miocene (Hemphillian) Rattlesnake Formation, central Oregon. PaleoBios 26:37–42.
- Qiu, Z.-X. 2003. Dispersals of Neogene carnivorans between Asia and North America; pp. 18–31 in L. J. Flynn (ed.), Vertebrate Fossils and Their Context: Contributions in Honor of Richard H. Tedford. Bulletin of the American Museum of Natural History 279.
- Retallack, G. J. 1999. Paleosols and Paleoenvironments of the Rattlesnake Formation (late Miocene) near Dayville, Oregon. Final report, National Park Service, John Day Fossil Beds National Monument, no. 1443-PX9325-99-005, 61 pp.
- Retallack, G. J., S. Tanaka, and T. Tate. 2002. Late Miocene advent of tall grassland paleosols in Oregon. Palaeogeography, Palaeoclimatology, Palaeoecology 183:329–354.
- Samuels, J. X., and J. Zancanella. 2011. An early Hemphillian occurrence of *Castor* (Castoridae) from the Rattlesnake Formation of Oregon. Journal of Paleontology 85:930–935.
- Sato, J. J., T. Hosoda, M. Wolsan, K. Tsuchiya, M. Yamamoto, and H. Suzuki. 2003. Phylogenetic relationships and divergence times among mustelids (Mammalia:Carnivora) based on nucleotide sequences of the nuclear interphotoreceptor retinoid binding protein and mitochondrial cytochrome *b* genes. Zoological Science 20:243–264.
- Sato, J. J., M. Wolsan, S. Minami, T. Hosoda, M. H. Sinaga, K. Hiyami, Y. Yamaguchi, and H. Suzuki. 2009. Deciphering and dating the red panda's ancestry and early adaptive radiation of Musteloidea. Molecular Phylogenetics and Evolution 53:907–922.
- Sato, J. J., M. Wolsan, F. J. Prevosti, G. D'Elia, C. Begg, K. Begg, T. Hosoda, K. L. Campbell, and H. Suzuki. 2012. Evolutionary and biogeographic history of weasel-like carnivorans (Musteloidea). Molecular Phylogenetics and Evolution 63:745–757.
- Schlosser, M. 1924. Tertiary vertebrates from Mongolia. Palaeontologia Sinica, Series C 1:1–132.
- Sotnikova, M. V. 1995. Extinct wolverine from the former USSR: review of the genus *Plesiogulo* (Carnivora: Mustelidae). Lutetia 6:1–8.



- Streck, M. J., and A. L. Grunder. 1995. Crystallization and welding variations in a widespread ignimbrite sheet; the Rattlesnake Tuff, eastern Oregon, U.S.A. *Bulletin of Volcanology* 57:151–169.
- Tedford, R. H., M. S. Skinner, R. S. Fields, J. M. Rensberger, D. P. Whistler, T. Galusha, B. E. Taylor, J. R. Macdonald, and S. D. Webb. 1987. Faunal succession and biochronology of the Arikarean through Hemphillian (late Oligocene through earliest Pliocene Epochs) in North America; pp. 153–210 in M. O. Woodburne (ed.), *Cenozoic Mammals of North America*. University of California Press, Berkeley, California.
- Tedford, R. H., L. B. Albright III, A. D. Barnosky, I. Ferrusquia Villafranca, R. M. Hunt Jr., J. E. Storer, C. C. Swisher III, M. R. Voorhies, S. D. Webb, and D. P. Whistler. 2004. Mammalian biochronology of the Arikarean through Hemphillian interval (late Oligocene through early Pliocene Epochs); pp. 169–231 in M. O. Woodburne (ed.), *Late Cretaceous and Cenozoic Mammals of North America*. Columbia University Press, New York.
- Teilhard de Chardin, P., and P. Leroy. 1945. Les Mustélidés de Chine. *Publications de l'Institut de Géobiologie* 12:1–56.
- Thorpe, M. R. 1921. Two new fossil Carnivora. *American Journal of Science* 1:477–483.
- Viret, J. 1951. Catalogue critique de la faune des mammifères miocènes de la Grive Saint-Alban. *Nouvelles Archives du Muséum d'Histoire Naturelle de Lyon* 3:1–104.
- Wagner, A. 1858. *Geschichte der Urwelt, mit besonderer Berücksichtigung der Menschenrassen und des mosaïschen Schöpfungsberichtes* (Second Edition). Leopold Voss, Leipzig, 528 pp.
- Walker, G. W. 1979. Revisions to the Cenozoic stratigraphy of Harney Basin, southeastern Oregon. *Bulletin U.S. Geological Survey* 1475:1–35.
- Walker, G. W. 1990. Miocene and younger rocks of the Blue Mountains region, exclusive of the Columbia River Basalt Group and associated mafic lava flows; pp. 101–118 in G. W. Walker (ed.), *Geology of the Blue Mountain Region of Oregon, Idaho and Washington: Cenozoic Geology of the Blue Mountains Region*. U.S. Geological Survey, Professional Paper 1437.
- Wang, X., Z. J. Tseng, and G. T. Takeuchi. 2012. Zoogeography, Molecular Divergence, and the Fossil Record—the Case of an Extinct Fisher, *Pekania palaeosinensis* (Mustelidae, Mammalia), from the Late Miocene Baogeda Ula Formation, Inner Mongolia. *Vertebrata Palasiatica* 50:293–307.
- Wolsan, M. 1989. Drapieżne—Carnivora; pp. 177–196 in K. Kowalski (ed.), *Historia i ewolucja łądowej fauny Polski, Folia Quatern* 59–60.
- Wolsan, M., and J. J. Sato. 2010. Effects of data incompleteness on the relative performance of parsimony and Bayesian approaches in a supermatrix phylogenetic reconstruction of Mustelidae and Procyonidae (Carnivora). *Cladistics* 26:168–194.
- Wood, H. E., Jr., R. W. Chaney, J. Clark, E. H. Colbert, G. L. Jepsen, J. B. Reeside Jr., and C. Stock. 1941. Nomenclature and correlation of the North American continental Tertiary. *Bulletin Geological Society of America* 52:1–48.
- Woodburne, M. O. 2004. Global events and the North American mammalian biochronology; pp. 315–343 in M. O. Woodburne (ed.), *Late Cretaceous and Cenozoic Mammals of North America*. Columbia University Press, New York.
- Yu, L., D. Peng, J. Liu, P. Luan, L. Liang, H. Lee, M. Lee, O. A. Ryder, and Y. Zhang. 2011. On the phylogeny of Mustelidae subfamilies: analysis of seventeen nuclear non-coding loci and mitochondrial complete genomes. *BMC Evolutionary Biology* 11:92.
- Zdansky, O., 1924. Jungtertiäre Carnivoren Chinas. *Palaeontologia Sinica, Series C* 2(1):1–149.

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#### APPENDIX 1. Definitions of dental measurements presented in Table 1.

Measurement	Definition
I3 length (I3L)	Maximum anteroposterior diameter of upper third incisor.
I3 width (I3W)	Maximum transverse diameter of upper third incisor.
P2 width (P2W)	Maximum transverse diameter of upper second premolar.
P3 width (P3W)	Maximum transverse diameter of upper third premolar.
P4 length (P4L)	Maximum anteroposterior diameter of upper fourth premolar, taken from the parastyle to the metastyle.
P4 width at protocone (P4W <sub>pro</sub> )	Maximum transverse diameter of upper fourth premolar at the protocone.
P4 width at metacone (P4W <sub>met</sub> )	Maximum transverse diameter of upper fourth premolar at the metacone.
M1 length (M1L <sub>ext</sub> )	Maximum anteroposterior diameter of upper first molar, taken along the labial border of the tooth.
M1 length (M1L <sub>int</sub> )	Maximum anteroposterior diameter of upper first molar, taken along the lingual border of the tooth.
M1 width (M1W)	Maximum transverse diameter of upper first molar, taken from the labial (hypoconal) cingulum to the lingual border between the paracone and metacone.