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Paleoecological and biogeographical implications of late Pleistocene noble marten (*Martes americana nobilis*) in eastern Washington State, USA

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ABSTRACT

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Keywords: Biogeography Eastern Washington State Extinct mammal Marmes Rockshelter Noble marten Paleoecology A mandible identified as noble marten (*Martes americana nobilis*) recovered from sediments dating to 11,800 cal yr BP and a humerus identified as *M. a.* cf. *nobilis* recovered from sediments dating from 13,100 to 12,500 cal yr BP at the Marmes Rockshelter archaeological site in southeastern Washington represent the first record of this taxon in the state. Mammalian taxa associated with the Marmes Rockshelter noble marten represent a diversity of open mesic habitats corroborating earlier analyses of other records of the noble marten in the western United States and exemplify how paleozoologists determine the ecology and environmental predilections of extinct taxa. The recovery site represents the topographically lowest record of this species in western North America and the farthest north record in the United States. Future research should examine known late-Quaternary *Martes* spp. remains from British Columbia and Alberta to fill in the 2200-km geographic gap in the known distribution of this taxon between a record in the northern Yukon and those in the western United States, and to refine our knowledge of noble marten paleoecology.

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Introduction

In 1926, mammalogist E. Raymond Hall (1926) suggested that what were believed to be late Pleistocene-age fossils of a marten recovered from two sites in northern California represented a distinct subspecies that he named noble marten (Martes caurina nobilis). Hall (1936) later suggested that the fossils did not differ sufficiently from extant martens to warrant unique taxonomic status. Paleobiologist Elaine Anderson (1970) studied the same fossils as Hall (1926) plus those from two other sites in the western United States and concluded that indeed the fossils were sufficiently distinct from extant martens (by then, western martens were given the taxonomic name Martes americana [Wright, 1953]) and fishers (M. pennanti), and an extinct marten (M. diluviana) to warrant designation as a distinct species (Martes nobilis). Youngman and Schueler (1991) later argued that the differences between the fossils and modern skeletons concerned size, and because in their opinion size was a poor taxonomic criterion, the fossils-those studied by Anderson (1970), plus others that had subsequently been identified as noble marten-should be considered M. americana. Paleobiologists in turn suggested subspecies designation (M. a. nobilis) was appropriate (Grayson, 1993; Anderson, 1994; Graham and Graham, 1994; Hughes, 2009). Most recently, geometric morphometric analysis of crania of the fossils and numerous modern specimens of extant Martes spp. indicates that noble marten are sufficiently morphometrically distinct from extant Martes to warrant

taxonomic distinction, perhaps at the species level (Meyers, 2007). Here I follow the conservative route of subspecific designation; future geometric morphometric analyses of noble marten mandibles may corroborate, or contradict, the analysis of crania of this marten.

The extinct noble marten (*Martes americana nobilis*) has previously been recorded at 18 fossil localities in western North America (Hughes, 2009). Specimens date from the late Pleistocene (ca. 20,000 ¹⁴C yr BP to as young as 2550 ¹⁴C yr BP; Grayson, 1984a). Most localities are in the western United States, but one is in the Yukon (Fig. 1). The distribution of sites producing remains of noble marten in the U.S. is: California–2; Colorado–1; Idaho–4; Nebraska–1; Nevada–4; Wyoming–5 (Table 1). Here I report the first record of the taxon from Washington State. The record is made up of a mandible identified as *Martes americana nobilis*, and a humerus identified as *M. a. cf. nobilis*. Both specimens were recovered from Marmes Rockshelter (45FR50) in southeastern Washington State (N46°36.924', W118°12.093'), adjacent to the Palouse River approximately 3 km upstream from its confluence with the Snake River (Fig. 1).

In this paper I describe the morphometry of the Marmes Rockshelter remains assigned to noble marten, compare them to other noble marten specimens as well as modern pine marten and fisher bones and teeth, present evidence on the age of the Marmes noble marten specimens, summarize the paleoecological implications of the mammalian fauna associated with the Marmes noble marten, and describe how our knowledge of this extinct taxon's ecological predilections, elevational distribution, and geographic range have increased over time. The noble marten exemplifies how paleozoologists grapple with the taxonomy and ecological significance of extinct taxa.

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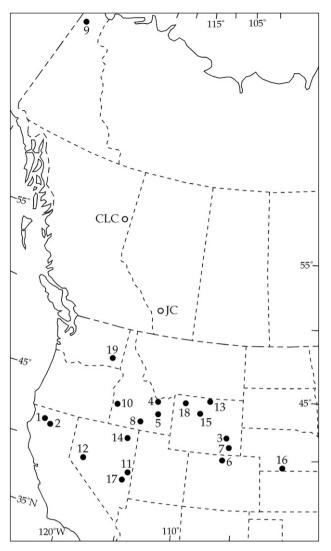


Figure 1. Sites that have produced remains of noble marten (filled circles). CLC, Charlie Lake Cave; JC, January Cave. See Table 1 for key to numbers.

Marmes Rockshelter

Initially excavated in 1962-1964, discovery in 1968 of terminal Pleistocene human remains in a stratigraphic trench excavated through the Palouse River floodplain below and in front of Marmes Rockshelter resulted in emergency excavations during the last several months of 1968 prior to inundation of the site by a man-made reservoir originating on the Snake River. The 1968 excavations focused on the Pleistocene-Holocene transition (PHT, hereafter) era floodplain sediments, and the deepest strata in the rockshelter that were also thought to be of PHT age (see Hicks, 2004 for additional historical details). Gustafson (1972) analyzed a sample of mammalian remains recovered from the entire Holocene stratigraphic sequence within Marmes Rockshelter, and mentioned the occurrence of two noteworthy species among the faunal remains recovered from the floodplain-a mandible of what he identified as a "pine marten" (Martes americana), and a single skull fragment of an arctic fox (Alopex lagopus). Caulk (1988) later identified a small sample of remains recovered from the floodplain PHT sediments, and reported additional specimens of arctic fox. Most recently Gustafson and Wegener (2004) identified another small sample of remains recovered from the floodplain but did not restudy either the Martes mandible or the arctic fox skull fragment originally reported by Gustafson (1972). I am studying the complete PHT mammalian fauna from the site, both those remains recovered from within the rockshelter and those recovered from the adjacent floodplain; as of mid-2010 about 25% of the collection has been studied. Examination of the *Martes* mandible reported by Gustafson (1972) indicates that it is a noble marten.

Taxonomic identification

Gustafson (1972) identified the pine marten mandible about the same time that Anderson (1970) published morphometric criteria that she believed distinguished modern pine marten and fisher from the noble marten. Thus not only had the noble marten been very recently (relative to Gustafson's work) suggested to be a valid taxon, but the morphometric criteria Anderson (1970) proposed were not well known among paleomammalogists working in North America. Gustafson (1972) likely did not know of Anderson's (1970) work (he did not reference it in his 1972 dissertation) and hence his identification of the Marmes mandible as pine marten rather than noble marten is not unexpected.

Following Anderson (1970), I identified the Marmes floodplain mandible (Washington State University Museum of Anthropology [WSU] Inventory Number 17531) as noble marten based on the total length of the m1 relative to the length of the m1 trigonid (Table 2). The Marmes mandible's m1 falls on the trend line defined by other specimens of m1 that have been identified as noble marten; the noble marten trend line is distinct from the trend lines defined by modern pine marten and fisher m1s (Fig. 2). Anderson (1970) found that the trigonid is shorter relative to the total length of the m1 in noble marten than in American marten, and the tooth overall is smaller than in modern fishers. Anderson's (1970) trend lines describing the relationship of the two dimensions provide not only an indication of size but also of shape, precisely because they illustrate the relationship of m1 total length relative to the m1 trigonid length.

Comparisons of each of the two m1 dimensions as documented by Youngman and Schueler (1991) among various *Martes* taxa reveal that the Marmes m1 length is different from modern pine martens (Student's t=2.783, one-tailed p<0.01) but not different from previously identified noble martens (t=0.433, one-tailed p>0.3) (Fig. 3). The Marmes m1 trigonid length is not significantly different from either pine martens (t=1.225, one-tailed p>0.1) or other noble martens (t=0.985, one-tailed p>0.15). Interestingly, the Marmes m1 total length is not different from modern female fishers (t=0.329, one-tailed p>0.3) but the m1 trigonid length is different from modern female fishers (t=2.683, one-tailed p<0.01).

The depth of the Marmes mandible between m1 and m2 compares favorably with previously measured mandibles attributed to noble marten (Table 2), but it also compares favorably with modern female fishers as measured by Youngman and Schueler (1991) (Fig. 3). The Marmes mandible's depth is significantly different than the average of that dimension as documented by Youngman and Schueler (1991) for modern pine marten (t=4.883, one-tailed p<0.0001) and noble martens (t=2.268, one-tailed p<0.02) but is not statistically significantly different than modern female fishers (t=0.106, onetailed p>0.4). The weight of the morphometric evidence, however, suggests the mandible is not that of a female fisher.

The complete humerus of a *Martes* recovered from PHT sediments within Marmes Rockshelter (WSU Inventory Number 16114) is smaller than the range observed in four dimensions of female fisher humeri (Table 3). It falls within the size range of both modern pine marten and previously identified noble martens as documented by Youngman and Schueler (1991). It is, however, larger than the mean of three of four dimensions of pine marten humeri measured by Anderson (1970) (Fig. 4, Table 2). Anderson (1970) measured humeri of 30 male and 26 female pine martens of *M. a. actuosa* whereas Youngman and Schueler (1991) measured 36 males and 6 females; given the marked sexual dimorphism of martens, it is likely that the differences in observed means and ranges between investigators are a

Table 1

List of sites that have produced remains assigned to noble marten. The list is in the chronological order of reporting the identification. Site numbers correspond to Figure 1.

Site	Noble marten identified	Age (¹⁴ C yr BP)	NISP
1. Potter Creek Cave, CA	Hall, 1926; Anderson, 1970	Late Pleistocene	18
2. Samwell Cave, CA	Hall, 1926; Anderson, 1970	Late Pleistocene	7
3. Jaguar Cave, ID	Anderson, 1970; Kurtén and Anderson, 1972	11,580-7000	48
4. Little Box Elder Cave, WY	Anderson, 1970, 1974	24,000-10,000	39
5. Moonshiner Carnivore Trap, ID	Hager, 1972; Anderson, 1974; White et al., 1984	Early Holocene	?(25+)
6. Chimney Rock (Animal Trap), CO	Hager, 1972; Kurtén and Anderson, 1972	Late Pleistocene-early Holocene	47
7. Bell Cave, WY	Anderson, 1974; Zeimans and Walker, 1974	13,500-10,000	?
8. Wilson Butte Cave, ID	Bryan, 1975	~10,000	1?
9. Old Crow, Yukon	Harington, 1977	Late Pleistocene	?
10. Dry Creek Rockshelter, ID	Webster, 1978	3270-2550	1
11. Smith Creek Cave, NV	Miller, 1979	13,000-11,000	1
12. Hidden Cave, NV	Grayson, 1984a, 1985	>7500; 3700-3600?	2
13. Natural Trap Cave, WY	Gilbert and Martin, 1984	20,250-14,670	?
14. Bronco Charlie Cave, NV	Grayson, 1987	3500	1
15. Little Canyon Creek Cave, WY	Walker, 1987	Late Pleistocene	?
16. North Cove, NE	Stewart, 1987	Late Pleistocene-early Holocene	?
17. Snake Creek Burial Cave, NV	Mead and Mead, 1989	15,100–9460	?
18. Mummy Cave, WY	Hughes, 2003, 2009	6400	1
19. Marmes Rockshelter, WA	This report	11,200–9840	2

Table 2

Metrics (mm) of modern martens and fishers, compared to noble martens and Marmes Rockshelter mandible.

Dimension	M. caurina ¹	M. americana ¹	Noble marten ¹	Marmes	<i>M. pennanti</i> female ²	<i>M. pennanti</i> male ²
Mandible depth, mean	7.3 ± 0.7	7.3 ± 0.6	8.8 ± 0.7	10.42	10.63 ± 0.56	14.11 ± 1.13
Mandible depth, range	6.0-8.7	6.0-8.4	7.9-11.0	-	9.5-11.8	12.0-16.4
m1 length, mean	9.4 ± 0.7	9.6 ± 0.5	10.8 ± 0.5	11.02	11.16 ± 0.42	13.01 ± 0.64
m1 length, range	8.1-10.9	8.5-10.2	9.8-11.8	-	10.4-12.0	11.6-14.0
m1 trigonid length, mean	6.9 ± 0.5	6.9 ± 0.4	7.8 ± 0.4	7.40	8.27 ± 0.32	9.47 ± 0.40
m1 trigonid length, range	6.2–7.8	5.9-7.4	6.9-8.7	-	7.6–9.1	8.6-10.1

¹ Data from Youngman and Schueler, 1991.

² Data from Anderson, 1970.

result of the difference in the proportion of males in each sample. Thus Anderson's data are likely to provide a more accurate representation of the mean size of pine marten remains regardless of sex. Granting that, the Marmes humerus more closely resembles noble marten than pine marten (Fig. 4), and that prompts my assignment of the humerus to *M. a.* cf. *nobilis*, pending study of other specimens. Hereafter I assume the humerus indeed represents a noble marten.

Because the two dimensions as graphed in Figure 2 reflect shape, they warrant taxonomic distinction of the mandibles assigned to noble marten relative to those of pine marten and fisher, although whether at the subspecies level or species level is unclear. The noble

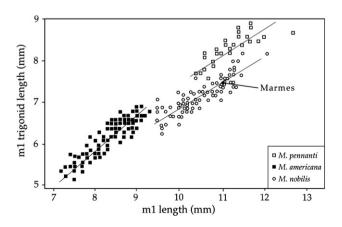


Figure 2. Scatter plot of m1 length against m1 trigonid length produced by Elaine Anderson (after Hager, 1972) showing the distinction of extinct noble marten from extant pine marten (*M. americana*) and fisher (*M. pennanti*). Noble marten m1 specimens from Hidden Cave (Grayson, 1985) and Mummy Cave (Hughes, 2009) have been added.

marten is yet one more form of Quaternary mammal that exemplifies some of the difficulties of assigning remains of morphologically and/ or metrically unique faunal remains to taxon (e.g., Mead et al., 2000; Graham, 2001; Mead and Spiess, 2001).

Age of Marmes noble marten

The Marmes noble marten mandible was recovered from the stratigraphic unit known as the Harrison horizon, radiocarbon dated to 11,800 cal yr BP (average of two dates; 9840 ± 110^{-14} C yr BP, W-2212; $10,130 \pm 300^{-14}$ C yr BP, W-2218 [Hicks, 2004]; calibration

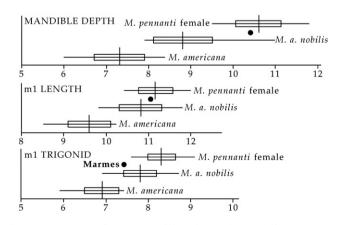


Figure 3. Measurements of *Martes* sp. mandibles and m1s as documented by Youngman and Schueler (1991) compared to the Marmes mandible and m1 (black dot). All measurements are in mm; vertical line is the mean; box is one standard deviation; horizontal line is the range.

Metrics (mm) of modern martens and fishers, compared to noble martens and Marmes Rockshelter humerus.						
Dimension	M. caurina ^a	M. americana ^a	Noble marten ^a	Marmes	<i>M. pennanti</i> female ^b	M. pennanti m
Greatest L, mean	61.3 ± 4.2	67.6 ± 4.3	65.4 ± 4.5	68.98	83.55 ± 2.31	97.11 ± 3.63
Greatest L, range	54.8-70.3	55.8-73.5	57.3-72.4	-	78.3-87.9	90.8-101.7
Proximal BR, mean	10.6 ± 0.8	11.8 ± 0.9	11.5 ± 0.9	12.06	15.36 ± 0.57	18.51 ± 0.98
Proximal BR, range	8.9-12.3	9.6-13.2	9.7-12.9	-	14.2-16.2	17.1-20.6
Distal BR, mean	12.8 ± 1.0	14.2 ± 1.1	14.2 ± 1.3	14.02	19.13 ± 0.59	23.43 ± 0.94
Distal BR, range	10.8-15.1	11.7-15.8	12.2-16.0	-	18.0-20.0	21.8-24.7
Least shaft width, mean	4.1 ± 0.4	4.4 ± 0.4	4.6 ± 3.2	4.82	5.65 ± 0.25	6.95 ± 0.64
Least shaft width, range	3.4-4.7	3.5-5.0	3.9-5.0	-	5.3-6.1	5.9-8.4

Table 3 M

Data from Youngman and Schueler, 1991.

b Data from Anderson 1970

from Reimer et al. 2009). The Martes humerus recovered from the rockshelter was found in sediments (probably stratum Ib; field records are unclear) in one of the deepest units excavated in the site, some 1.6 m below two radiocarbon dates (from Stratum I, which overlies Stratum Ib) indicating an age of 9900 cal yr BP (8700 ± 300^{14} C yr BP, W-2208; 9010 ± 300^{-14} C yr BP, W-2207 (Hicks, 2004)). The oldest radiocarbon date yet obtained from within the rockshelter is 13,100 cal yr BP $(11,230 \pm 50^{14}$ C yr BP, Beta 156698) (Hicks, 2004), and stratigraphically it lays on the contact between what is believed to be Glacier Peak volcanic tephra and underlying "lacustrine" deposits (Huckleberry and Fadem, 2007). The "lacustrine" deposits represent one of the last, if not the last, catastrophic Spokane floods that carved the Channeled Scablands of eastern Washington's Columbia Basin and also carved Marmes Rockshelter (Fryxell and Keel, 1969:39-40); the last Spokane flood occurred about 15,500 cal yr BP (Huckleberry et al., 2003). Glacier Peak volcanic tephra is thought to have been deposited about 13,100 cal yr BP (Foit et al., 1993). Given present understanding of rockshelter stratigraphy, I suggest the Martes humerus dates between 12,500 and 13.100 cal vr BP.

The Marmes site noble marten remains fall well within the documented temporal range of this taxon. Some of the previously studied specimens of this marten have associated radiocarbon dates; these range from about 28,700 cal yr BP to 3250 cal yr BP. The majority of the deposits that have produced remains of noble marten specimens that have associated radiocarbon ages date between 15,000 and 11,500 cal yr BP. The latter is likely because of a greater tendency of researchers to obtain radiocarbon dates on what are believed to be terminal Pleistocene artifacts and faunal remains rather than a reflection

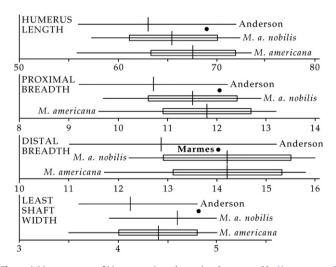


Figure 4. Measurements of Martes americana humeri as documented by Youngman and Schueler (1991) and by Anderson (1970), and M. nobilis humeri as documented by Youngman and Schueler (1991), compared to the Marmes humerus (black dot). All measurements are in mm; vertical line is the mean; box is one standard deviation; horizontal line is the range. Anderson (1970) measured very few pine martens, and distinguished them by sex, precluding calculation of an overall standard deviation.

of peak abundances of noble martens on the landscape at this time (e.g., Meltzer and Mead, 1983).

Geographic distribution

The geographic location of the Marmes site noble martens begins to fill a considerable gap in the known distribution of this taxon (Fig. 1). Prior to identification of the Marmes specimens, the approximate distance between the record from Old Crow, Yukon, and the nearest records of Dry Creek Shelter and Jaguar Cave in southcentral Idaho was 2700 km. The Marmes record shortens that distance by about 500 km. It is likely that as the PHT and Holocene mammalian record of the Canadian Rockies and adjacent areas becomes better known, the gap between the Old Crow record and the Marmes record will shrink. For example, deposits in January Cave in southwestern Alberta (Fig. 1) date between 33,000 and 23,000 $^{14}\mathrm{C}$ yr BP and have produced remains attributed to Martes americana (Burns, 1991). Although older than the age of known noble martens, the marten remains from January Cave warrant restudy.

Another site with the potential to produce remains of noble marten is Charlie Lake Cave in northeastern British Columbia (Fig. 1). It contains a depositional record spanning the last 11,000 ¹⁴C yr BP and has produced remains of both fisher and pine marten dating between 4000 and 1500¹⁴C yr BP (Driver, 1988, 2001; Driver et al., 1996). I reexamined the Martes remains identified by Driver (1988, 2001; Driver et al., 1996), and confirmed his original identifications. Of the four specimens that were measureable and for which comparative size data are available, all clearly fall within the size range of modern pine marten. These four specimens are a right mandible (with m1), proximal right tibia, and two distal left humeri. The m1 dimensions clearly do not represent noble marten but instead the pine marten; those dimensions are: total length = 8.38 mm, and trigonid length = 6.12 mm. The Charlie Lake Cave Martes mandible falls well within the scatter of points in Figure 1 derived from modern pine marten and well outside of that for modern fisher and that for extinct noble marten.

Few sites like January Cave and Charlie Lake Cave are presently known, but others are sure to eventually be found in the Canadian Rockies (Driver, 1998). Until that time, it would be worthwhile to reexamine all marten and fisher remains thus far recovered from sites located in eastern British Columbia and western Alberta. Like the "pine marten" mandible from the Marmes site, some of those Canadian remains may prove to represent the noble marten. Given the unique geographic locations of such remains, we likely would learn much about the paleoecology of noble martens by study of the taxa associated with them

Paleoecological significance

Identifying the Marmes Rockshelter Martes mandible as pine marten and given that species' modern habitat preferences, Gustafson (1972:73) found that the mandible "suggests an environment dominated by coniferous forest." He discounted the possibility that it might represent

pennanti male^b

an individual whose hide was transported by PaleoIndians to the site from distant montane forests "because mandibles normally would be removed during the skinning process unless the entire carcass was brought to the site before skinning." In his conclusions Gustafson (1972:115) hesitated to infer nearby coniferous forests and instead stated the mandible "could have been carried by humans or water to the site from a forested region." There is no evidence on the specimen of transport by either agent such as butchering marks or sediment abrasion and rounding, respectively. This does not, however, mean the mandible was not transported by either of these agents or by a raptor or carnivore (in which case digestive corrosion might be displayed). But there is a much simpler explanation for this seemingly ecologically anomalous specimen, and it concerns the (paleo) ecology of the noble marten as it is now understood.

Because the noble marten is a taxon that went extinct prior to its study by zoologists and ecologists, its ecology (as well as its taxonomic status) has been the subject of some discussion. It was originally suggested that noble marten remains indicated cool climates (Anderson, 1970; Kurtén and Anderson, 1980). As the number of find locations increased and more faunas stratigraphically associated with noble marten became known, it was suggested that noble marten had occupied a variety of environments (Grayson, 1982, 1984a). Gustafson (1972) was thus caught in this conundrum. If the Marmes *Martes* mandible was, as Gustafson (1972) thought, indeed pine marten, it made no sense ecologically relative to other paleoecological data from the site; those data indicated the cool mesic closed forests preferred by pine marten did not exist at the site in PHT times.

It has long been suggested that although it is tenuous to infer the ecology of extinct taxa, there are techniques to do so (Findley, 1964; Lundelius, 1964). The analyst can assume the ecology of the extinct taxon is similar to that of its closest living relative, or assume that the morphometry of a key anatomical element, especially teeth, indicate something of the ecology of the extinct taxon, such as presuming mammoths were grazers whereas mastodons were browsers (Findley, 1964). There are problems with these particular techniques (Graham and Semken, 1987). A third technique provides a robust way to infer the ecology of an extinct taxon (Lundelius, 1964; Grayson, 1981). It involves consulting the (usually extant) taxa with known ecological and environmental tolerances that are stratigraphically associated with the extinct taxon. Once sufficient faunas have been studied and the extinct taxon's ecology is established, future discoveries of its remains can contribute to determining prehistoric environmental conditions.

Here I follow Hughes (2009) and assign mammalian taxa associated with the Marmes noble marten mandible, that is, recovered from the Harrison horizon, to life zone and also to preferred habitat. Because analysis of the Marmes PHT mammalian fauna is not yet complete, I compiled data from Caulk (1988) and Gustafson and Wegener (2004) on the mammalian fauna from the Harrison horizon. Several taxa identified only to genus, or deemed relatively ecologically ubiquitous, were not included. The excluded taxa are: ground squirrel (Spermophilus sp.), deer mouse (Peromyscus maniculatus), coyote (Canis latrans), bobcat (Lynx rufus), deer (Odocoileus sp.), and pronghorn (Antilocapra americana). The identification of a single specimen as Clethtrionomys sp. was said to be "tentative" (Gustafson and Wegener, 2004:274) and hence it is not included in the analyses of associated mammalian taxa. One specimen of Reithrodontomys sp. was identified by Gustafson and Wegener (2004); this specimen makes up less than 1% of the Harrison horizon mammalian fauna and was represented by a single incisor, the identification of which is questionable, thus I omit it from my analysis. Finally, two specimens identified as Martes americana by Caulk (1988)a proximal ulna and a distal tibia-have been reexamined and found to more closely resemble mink (Mustela vison) than marten; these remains are excluded from analysis here. The mammalian taxa from the Harrison horizon, and frequency data for each are summarized in Table 4; frequency data are numbers of identified specimens (NISP), where a specimen is a bone or tooth or fragment thereof (Grayson, 1984b; Lyman, 2008a).

Table 4

Frequency of remains (NISP) of mammalian taxa from the Harrison horizon of Marmes Rockshelter and stratigraphically associated with the noble marten mandible, and their preferred habitat and life zone (after Hughes, 2009).

Taxon	NISP	Habitat	Life zone
Sylvilagus sp.	4	Open	Hudsonian–Canadian
Lepus sp.	27	Grass	Hudsonian–Canadian
Marmota flaviventris	15	Rocky meadow	Hudsonian–Canadian
Spermophilus columbianus	5	Rocky meadow	Hudsonian–Canadian
Thomomys talpoides	38	Meadow	Other
Perognathus parvus	33	Sagebrush	Sonoran
Castor canadensis	1	Riparian	Hudsonian–Canadian
Neotoma cinerea	12	Rocky	Hudsonian–Canadian
Microtus spp.	30	Meadow	Hudsonian–Canadian
Lemmiscus curtatus	3	Sagebrush-grass	Sonoran
Alopex lagopus	6	Open	Tundra
Vulpes fulva	19	Open-edge	Hudsonian–Canadian
Mustela frenata	3	Open-Riparian	Other
$\Sigma =$	196	- *	

As originally conceived by Merriam (1894, 1898), life zones were discontinuous communities dictated by climate, particularly temperature. Now recognized as continuous and influenced by a host of climatic and nonclimatic variables (e.g., Whittaker, 1975), assigning species to one or more life zones allows determination of the general climatic conditions of particular mammalian taxa (e.g., Bailey, 1936; Hoffmeister, 1964). Mammal taxa represented among the remains recovered from the Harrison horizon at the Marmes site represent three life zones. As used here the Hudsonian–Canadian life zone refers to cool-moist climates rather than the more typical characteristics of boreal or montane closed forests. The Sonoran life zone is relatively warm and dry. The Tundra (or Arctic-Alpine) life zone is characterized by year-long cool temperatures. Habitat preferences were derived from references on each species (e.g., Ingles, 1965; Verts and Carraway, 1998).

The Marmes site mammalian fauna from the Harrison horizon (Table 4) largely corroborates Hughes's (2009) conclusions regarding the paleoecology and paleoenvironment of the extinct noble marten. Eight of the 13 genera represented in the Harrison horizon fauna occupy the Hudsonian–Canadian life zone, and of the total 196 NISP, 113 (58%) imply that life zone. Many of the taxa represented implicate meadows or grasslands; 115 NISP (59%) of the remains are from species that occupy grassy habitats. All taxa occupy open habitats; none occupy closed forests typical of modern pine marten. Hughes (2009) found that mammalian faunas associated with previously reported noble marten remains indicate mesic, cool life zones, in particular, the Hudsonian-Canadian life zone. Indicated habitats are dominated by open types. The Marmes noble marten from the Harrison horizon suggests the paleoecology of this taxon surmised by Hughes (2009) is accurate. But in one respect the Marmes record of noble marten also is unique from other records of the taxon, and thus it adds significantly to our knowledge of this extinct taxon's paleoecology.

The Marmes noble marten is in an exceptionally low topographic setting at 165 m above mean sea level. The mean elevation of sites that have produced remains of late Pleistocene noble marten is 1501 ± 714 m (range = 380 to 2410 m; data from Hughes, 2009). The Marmes noble marten is from a statistically significant lower elevation than the previously observed mean elevation (Student's t = 1.798, p = 0.05). The low elevation of the Marmes Rockshelter noble marten strengthens Hughes's (2009) observation that during the late Pleistocene and Holocene pine marten occupied higher elevations than noble martens, though the records for the two taxa dating to the late Pleistocene are not statistically significantly different, likely because of the few samples available for comparison. Thus far no *Martes* remains from the Marmes site can unequivocally be attributed to pine marten or to fisher. Other mammalian data from the Harrison horizon sediments at Marmes Rockshelter indicate that the climate at the time was cooler than at

present (Lyman, 2008b), and this may have allowed the noble marten to occupy the elevationally low area near the site that today is extremely warm during summer months.

Conclusions

The Marmes Rockshelter noble marten corroborates the earlier conclusion that this extinct marten was not geographically sympatric with extant pine martens or fishers, nor was it ecologically like those extant taxa. This observation strengthens the suggestion that the noble marten is taxonomically distinct from modern pine marten and fisher. It lends credence to conclusions as to the taxonomic uniqueness of fossils attributed to noble marten based on morphological and metric attributes of their remains. And finally, when their remains are found, noble martens can now be confidently argued to represent open mesic grasslands of foothills and not the dense closed forests typical of mountains and occupied by modern martens and fishers.

The noble marten, whether worthy of designation as a distinct species or an extinct subspecies, is now known from 19 localities in western North America. It is probable that more geographically distinct records of this form of marten will eventually be reported from the geographic gap between the northwestern U.S. and the Yukon. Previously reported records of noble marten with associated faunal data suggest this marten occupied a wider variety of more open habitats and lower topographic settings than the modern pine marten. The new record of noble marten from Marmes Rockshelter in southeastern Washington corroborates and strengthens these earlier findings, and also significantly lowers the known elevation range of the taxon and extends the geographic range within the contiguous 48 states north about 500 km. The history of research on the noble marten also exemplifies how paleozoologists grapple with learning about how and where and when extinct taxa lived.

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References

- Anderson, E., 1970. Quaternary evolution of the genus Martes (Carnivora, Mustelidae). Acta Zoologica Fennicae 130, 1–132.
- Anderson, E., 1974. A survey of the late Pleistocene and Holocene mammal fauna of Wyoming. In: Wilson, M.V. (Ed.), Applied Archaeology and Geology: The Holocene History of Wyoming: Wyoming Geological Survey Reports of Investigations 10, Laramie, pp. 78–87.
- Anderson, E., 1994. Evolution, prehistoric distribution, and systematics of *Martes*. In: Burkirk, S.W., Harestad, A.S., Raphael, M.G., Powell, R.A. (Eds.), Martens, Sables, and Fishers: Biology and Conservation. Cornell Univ. Press, Ithaca, NY, pp. 13–25.
- Bailey, V., 1936. The mammals and life zones of Oregon. North American Fauna 55, 1–416.
- Bryan, A.L., 1975. Paleoenvironments and cultural diversity in Late Pleistocene South America: A rejoinder to Vance Haynes and a reply to Thomas Lynch. Quaternary Research 5, 151–159.
- Burns, J.A., 1991. Mid-Wisconsinan vertebrates and their environment from January Cave, Alberta, Canada. Quaternary Research 35, 130–143.
- Caulk, G.H., 1988. Examination of Some Faunal Remains from the Marmes Rockshelter Floodplain. Unpublished Master of Arts thesis, Department of Anthropology, Washington State Univ., Pullman.
- Driver, J.C., 1988. Late Pleistocene and Holocene vertebrates and palaeoenvironments from Charlie Lake Cave, northeast British Columbia. Canadian Journal of Earth Sciences 25, 1545–1553.

Driver, J.C., 1998. Human adaptation at the Pleistocene/Holocene boundary in western Canada, 11, 000 to 9000 BP. Quaternary International 49/50, 141–150.

- Driver, J.C., 2001. Paleoecological and archaeological implications of the Charlie Lake Cave fauna, British Columbia, 10,500 to 9,500 B.P. People and Wildlife in Northern North America: Essays in Honor of R. Dale Guthrie: In: Gerlach, S.C., Murray, M.S. (Eds.), British Archaeological Reports International Series 944, Oxford, pp. 13–22.
- Driver, J.C., Handly, M., Fladmark, K.R., Nelson, D.E., Sullivan, G.M., Preston, R., 1996. Stratigraphy, radiocarbon dating, and culture history of Charlie Lake Cave, British Columbia. Arctic 49, 265–277.
- Findley, J.S., 1964. Paleoecological reconstruction: vertebrate limitations. The Reconstruction of Past Environments: Proceedings. In: Hester, J.J., Schoenwetter, I. (Eds.). Fort Burgwin Research Center Publication 3. Taos. NM. pp. 23–25.
- Foit Jr., F.F., Mehringer Jr., P.J., Sheppard, J.C., 1993. Age, distribution, and stratigraphy of Glacier Peak tephra in eastern Washington and western Montana, United States. Canadian Journal of Earth Sciences 30, 535–552.
- Fryxell, R., Keel, B.C., 1969. Emergency Salvage Excavations for the Recovery of Early Human Remains and Related Scientific Materials from the Marmes Rockshelter Archaeological Site, Southeastern Washington. Washington State Univ. Department of Anthropology, Final Report to U.S. Army Corps of Engineers, Walla Walla District, Washington.
- Gilbert, B.M., Martin, L.D., 1984. Late Pleistocene fossils of Natural Trap Cave, Wyoming, and the climatic model of extinction. In: Martin, P.S., Klein, R.G. (Eds.), Quaternary Extinctions: A Prehistoric Revolution. Univ. of Arizona Press. Tucson, pp. 138–147.
- Graham, R.W., 2001. Comment on "Skeleton of extinct North American sea mink (*Mustela macrodon*)" by Mead et al. Quaternary Research 56, 419–421.
- Graham, R.W., Graham, M.A., 1994. Late Quaternary distribution of Martes in North America. In: Buskirk, S.W., Harestad, A.S., Raphael, M.G., Powell, R.A. (Eds.), Martens, Sables, and Fishers: Biology and Conservation. Cornell Univ. Press, Ithaca, NY, pp. 26–58.
- Graham, R.W., Semken Jr., H.A., 1987. Philosophy and procedures for paleoenvironmental studies of Quaternary mammalian faunas. Late Quaternary Mammalian Biogeography and Environments of the Great Plains and Prairies: In: Graham, R.W., Semken Jr., H.A., Graham, M.A. (Eds.), Illinois State Museum Scientific Papers 22. Springfield, IL, pp. 1–17.
- Grayson, D.K., 1981. A critical view of the use of archaeological vertebrates in paleoenvironmental reconstruction. Journal of Ethnobiology 1, 28–38.
- Grayson, D.K., 1982. Toward a history of Great Basin mammals during the past 15,000 years. Man and Environment in the Great Basin: In: Madsen, D.B., O'Connell, J.F. (Eds.), Society for American Archaeology Papers No. 2, pp. 82–101.
- Grayson, D.K., 1984a. Quantitative Zooarchaeology. Academic Press, Orlando.
- Grayson, D.K., 1984b. Time of extinction and nature of adaptation of the noble marten, Martes americana nobilis. Contributions in Quaternary Vertebrate Paleontology: A Volume in Memorial to John E. Guilday: In: Genoways, H.H., Dawson, M.R. (Eds.), Carnegie Museum of Natural History Special Publication No. 8, Pittsburgh, pp. 233–240.
- Grayson, D.K., 1985. The mammals. The Archaeology of Hidden Cave, Nevada: In: Thomas, D.H. (Ed.), American Museum of Natural History Anthropological Papers 61(1), New York, pp. 125–161.
- Grayson, D.K., 1987. The biogeographic history of small mammals in the Great Basin: observations on the last 20, 000 years. Journal of Mammalogy 68, 359–375.
- Grayson, D.K., 1993. The Desert's Past: A Natural Prehistory of the Great Basin. Smithsonian Institution Press, Washington, DC.
- Gustafson, C.E., 1972. Faunal Remains from the Marmes Rockshelter and Related Archaeological Sites in the Columbia Basin. Unpublished doctoral dissertation, Department of Zoology, Washington State Univ., Pullman.
- Gustafson, C.E., Wegener, R.M., 2004. Faunal remains. In: Hicks, B.A. (Ed.), Marmes Rockshelter: A Final Report on 11, 000 Years of Cultural Use. Washington State Univ. Press, Pullman, pp. 253–317.
- Hager, M.W., 1972. A late Wisconsin–Recent vertebrate fauna from the Chimney Rock Animal Trap, Larimer County, Colorado. Wyoming Contributions to Geology 2, 63–71.
- Hall, E.R., 1926. A new marten from the Pleistocene caves of California. Journal of Mammalogy 7, 127–130.
- Hall, E.R., 1936. Mustelid mammals from the Pleistocene of North America with systematic notes on some recent members of the genera *Mustela*, *Taxidea*, and *Mephitis*. Carnegie Institute of Washington Publication 73, 41–119.
- Harington, C.R., 1977. Pleistocene Mammals of the Yukon Territory. Unpublished doctoral dissertation, University of Alberta, Edmonton, Alberta.
- Hicks, B.A. (Ed.), 2004. Marmes Rockshelter: A Final Report on 11, 000 Years of Cultural Use. Washington State Univ. Press, Pullman.
- Hoffmeister, D.F., 1964. Mammals and life zones: time for re-evaluation. Plateau 37, 46–55. Huckleberry, G., Fadem, C., 2007. Environmental change recorded in sediments from
- the Marmes Rockshelter archaeological site, southeastern Washington State, USA. Ouaternary Research 67, 21–32.
- Huckleberry, G., Lenz, B., Galm, J., Gough, S., 2003. Recent geoarchaeological discoveries in central Washington. Western Cordillera and Adjacent Areas: In: Swanson, T.W. (Ed.), Geological Society of America Field Guide 4. Boulder, CO, pp. 237–249.
- Hughes, S.S., 2003. Beyond the Altithermal? The Role of Climate Change in Prehistoric Human Adaptations at Mummy Cave, northwestern Wyoming. Unpublished doctoral dissertation, Univ. of Washington, Seattle.
- Hughes, S.S., 2009. Noble marten (Martes americana nobilis) revisited: Its adaptation and extinction. Journal of Mammalogy 90, 74–92.
- Ingles, L.G., 1965. Mammals of the Pacific States: California, Oregon, Washington. Stanford University Press, Stanford, CA.
- Kurtén, B., Anderson, E., 1972. The sediments and fauna of Jaguar Cave, II, the fauna. Tebiwa 15, 21–45.
- Kurtén, B., Anderson, E., 1980. Pleistocene Mammals of North America. Columbia Univ. Press, New York.

Lundelius Jr., E., 1964. The use of vertebrates in paleoecological reconstructions. The Reconstruction of Past Environments: Proceedings. In: Hester, J.J., Schoenwetter, J. (Eds.), Fort Burgwin Research Center Publication 3. Taos, NM, pp. 26–31.

Lyman, R.L., 2008a. Quantitative Paleozoology. Cambridge Univ. Press, Cambridge.

- Lyman, R.L., 2008b. Climatic implications of latest Pleistocene and earliest Holocene mammalian sympatries in eastern Washington state, USA. Quaternary Research 70, 426–432.
- Mead, E.M., Mead, J.I., 1989. Snake Creek Burial Cave and a review of the Quaternary mustelids of the Great Basin. Great Basin Naturalist 49, 143–154.
- Mead, J.I., Spiess, A.E., 2001. Reply to Russell Graham about *Mustela macrodon*. Quaternary Research 56, 422–423.
- Mead, J.I., Spiess, A.E., Sobolik, K.D., 2000. Skeleton of extinct North American sea mink (Mustela macrodon). Quaternary Research 53, 247–262.
- Meltzer, D.J., Mead, J.I., 1983. The timing of late Pleistocene mammalian extinctions in North America. Quaternary Research 19, 130–135.
- Merriam, C.H., 1894. Laws of temperature control of the geographic distribution of terrestrial animals and plants. National Geographic Magazine 6, 229–238.
- Merriam, C.H., 1898. Life zones and crop zones of the United States. USDA Biological Survey Bulletin 10, 1–79.
- Meyers, J.I., 2007. Basicranial Analysis of Martes and the Extinct Martes nobilis (Carnivora: Mustelidae) Using Geometric Morphometrics. Unpublished Master's of Science thesis, Department of Geosciences, Northern Arizona Univ., Flagstaff.
- Miller, S.G., 1979. The fauna of Smith Creek Canyon. The Archaeology of Smith Creek Canyon, Eastern Nevada: In: Tuohy, D.R., Randall, D.L. (Eds.), Nevada State Museum Anthropological Papers 17, Carson City, pp. 272–329.
- Reimer, P.J., Baillie, M.G.L, Bard, E., Bayliss, A., Beck, J.W., Blackwell, P.G., Bronk Ramsey, C., Buck, C.E., Burr, G.S., Edwards, R.L., Friedrich, M., Grootes, P.M., Guilderson, T.P., Hajdas, I., Heaton, T.J., Hogg, A.G., Hughen, K.A., Kaiser, K.F., Kromer, B., McCormac,

- F.G., Manning, S.W., Reimer, R.W., Richards, D.A., Southon, J.R., Talamo, S., Turney, C.S.M., van der Plicht, J., Weyhenmeyer, C.E., 2009. Intcal90 and Marine09 radiocarbon age calibration curves, 0–50, 000 cal BP. Radiocarbon 51, 1111–1150.
- Stewart, J.D., 1987. Prehistoric and Historic Cultural Resources of Selected Sites at Harland County Lake, Harland County, Nebraska; Final Report. Unpublished report on file, U.S. Army Corps of Engineers, Kansas City, MO.
- Verts, B.J., Carraway, L.N., 1998. Land Mammals of Oregon. Univ. of California Press, Berkeley.
- Walker, D.N., 1987. Late Pleistocene/Holocene environmental changes in Wyoming: the mammalian record. Late Quaternary Mammalian Biogeography and Environments of the Great Plains and Prairies: In: Graham, R.W., Semken, H.A., Graham, M.A. (Eds.), Illinois State Museum Scientific Papers 22, Springfield, pp. 334–393.
- Webster, G.S., 1978. Dry Creek Rockshelter: cultural chronology in the western Snake River region of Idaho ca. 4, 150–1, 300 BP. Tebiwa 15, 1–35.
- White, J., McDonald, H.G., Anderson, E., Soiset, J.M., 1984. Lava blisters as carnivore traps. Contributions in Quaternary Vertebrate Paleontology: A Volume in Memorial to John E. Guilday: In: Genoways, H.H., Dawson, M.R. (Eds.), Carnegie Museum of Natural History Special Publication No. 8, Pittsburgh, pp. 241–256.
- Whittaker, R.H., 1975. Communities and Ecosystems, 2nd edition. Macmillan, New York.
- Wright, P.L., 1953. Intergradation between Martes americana and Martes caurina in western Montana. Journal of Mammalogy 72, 567–577.
- Youngman, P.M., Schueler, F.W., 1991. Martes nobilis is a synonym of Martes americana, not an extinct Pleistocene–Holocene species. Journal of Mammalogy 72, 567–577.
- Zeimans, G., Walker, D., 1974. Bell Cave, Wyoming: preliminary archaeological and paleontological investigations. Applied Archaeology and Geology: The Holocene History of Wyoming: In: Wilson, M.V. (Ed.), Wyoming Geological Survey Reports of Investigations 10, Laramie, pp. 88–90.