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Research Paper

Borophagine canids of the Monarch Mill Formation (Middle Miocene), Nevada, U.S.A. ☆

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ABSTRACT

The non-marine Middle Miocene Monarch Mill Formation (Nevada, U.S.A.) outcrops in the Middlegate Basin and preserves fossil mammals that lived during the establishment of the present-day basin and range topography in central Nevada. The Monarch Mill Formation and its mammal fauna overlie the Middlegate Formation and its flora, and together the biota provides an informative window into ecosystem composition at the geographic crossroads between the Great Plains and the coastal regions of North America during the Middle Miocene. Here we report on previously undescribed and/or unfigured canids from the Monarch Mill Formation. To the previously known borophagine *Tomarctus brevirostris* and the fox-like canine *Leptocyon* we add two borophagine genera to the Eastgate Local Fauna of the Monarch Mill Formation. Specimens of the hypocarnivores *Paracynarctus* and *Cynarctus* are described and provide an enhanced understanding of the Middlegate Basin canid assemblage, now comprising at least four genera. Together with floral evidence, this canid assemblage is indicative of mesocarnivore-sustaining vegetation and locally limited open environments, with no hypercarnivorous canid occurrences. Rapid regional subsidence was an overarching factor in the shift towards present-day hyper- and mesocarnivore dominated canid assemblages in the Basin and Range Province, and the appearance of hypercarnivores in post-Barstovian times may reflect contemporaneous regional topographic shifts in the Great Basin at large.

1. Introduction

The Monarch Mill Fm. in central Nevada (Fig. 1) is a nearly 800 m thick sequence of tuffaceous clay, siltstone, sandstone, and conglomerates of Miocene age in the Middlegate Basin, which is part of the Basin and Range Province (Smith et al., 2014). The first vertebrate fossils were interpreted by Axelrod (1985) as occurring in the lowest unit of the Monarch Mill, within layers of sedimentary breccia and conglomerate. Subsequent investigations recovered several other fossil mammal localities, all of which are south of Highway 50, which runs through the Middlegate Basin (Smith et al., 2014). The exact stratigraphic relationships among the fossil mammal localities have not been resolved. The age control for the fossil mammal fauna (referred to as the Eastgate Local Fauna [LF] by Smith, 2002; Smith et al., 2014) is limited to a maximum age of ~15.95–15.5 Ma based on $^{40}Ar/^{39}Ar$ dates obtained from the Middlegate Fm., which underlies the Monarch Mill Fm. (Swisher, 1992; Smith et al., 2014). Smith (2002) conducted a study of the fossil mammals known to date and assigned the Eastgate LF to the early Barstovian North American Land Mammal Age.

The comprehensive faunal review conducted by Smith (2002) lists the presence of fish, amphibians, reptiles, birds, as well as 60 species of mammals from the Monarch Mill Fm. The diverse mammal fauna includes 25 families of insectivores, bats, lagomorph, rodents, carnivorans, artiodactyls, and perissodactyls. Smith et al. (2006) described a new genus of eomyid rodent, and Smith et al. (2014) described most of the carnivoran material from the Monarch Mill Fm. This report adds to this body of work on the Eastgate LF by reviewing its borophagine canid assemblage and its implications for regional paleozoogeography.

2. Material and methods

Specimen measurements were taken with Mitutoyo digital calipers to the nearest 0.01 mm. Specimen CT image stacks were generated using a Phoenix Nanotom M microCT system in the

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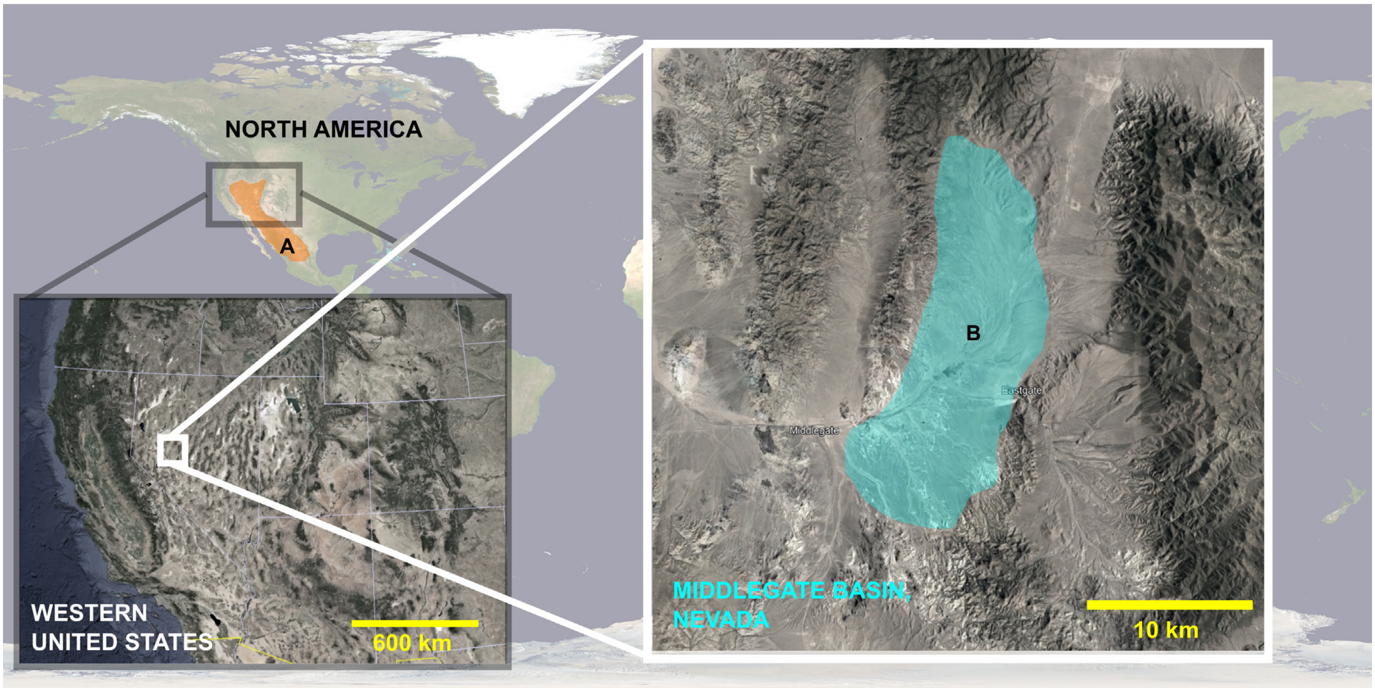

Fig. 1. Satellite imagery of the locality area. **A.** Approximate extent of the Great Basin taphrogen (after Dickinson, 2006). **B.** The approximate boundary of the Middlegate Basin. Base world map courtesy of the National Aeronautics and Space Administration (U.S.A.); close-up maps from Google Earth.

Functional Anatomy and Vertebrate Evolution Laboratory in the Department of Integrative Biology at the University of California, Berkeley. The CT images were imported into 3D Slicer (Fedorov et al., 2012) and thresholded, and 3D meshes were then saved and imported into Geomagic Wrap (3D Systems Corp., Rock Hill, South Carolina, U.S.A.) and reoriented to a standardized cartesian coordinate system for producing figures. Data for all described borophagine canid specimens from the Monarch Mill are also available as 3D PDFs on FigShare (https://doi.org/10.6084/m9.figshare.26485528.v1), and photographs showing texture and color of fossil preservation are included in Fig. S1 (Appendix A). Dental anatomy terminology follows those in Wang et al. (1999) unless otherwise indicated.

We estimated the body mass (in kg) of the carnivoran taxa described in this study using linear regression equations developed by Van Valkenburgh (1990) based on lower first molar lengths (m1L). Linear regression equations based on all-Carnivora and all-Canidae were first used to derive a preliminary body mass estimate for fossil taxa, and subsequently a size class specific body mass estimate was made based on size-class equations chosen using the all-Carnivora and all-Canidae body mass estimates (Table S1; Appendix A). Finally, a mean body mass estimate was calculated from all three linear equations for each fossil taxon. Body mass estimates for extant species used in comparison were derived from the University of Michigan Museum of Zoology's Animal Diversity database (https://animaldiversity.org, accessed in August 2024).

Additionally, we assessed the degree to which the Middlegate borophagine assemblage has an even distribution along a size gradient. We used lower first molar length as the trait of interest and calculated the Clark-Evans index (R), a measure of whether a series of values is clustered in distribution ($R < 1$) or more evenly distributed ($R > 1$). In addition to the Middlegate assemblage, we calculated and compared the Clark-Evans index for seven other borophagine assemblages in the Great Basin, including the early Barstovian Yermo Quarry, Second Division, First Division, and Green Hills assemblages of the Barstow Fm., the Caliente Fm., and the Clarendonian Dove Spring Fm. The Quaternary Nevada canid assemblage is used as a recent-day reference point. Mean molar length measurements for the above assemblages were extracted from Wang et al. (1999) (Table S2; Appendix A), and the Clark-Evans index was calculated using the *spatstat* package in the R programming environment (Baddeley et al. 2015).

Institutional abbreviations: OMNH, Oklahoma Museum of Natural History, Norman, Oklahoma, USA; UCMP, University of California Museum of Paleontology, Berkeley, California, USA.

3. Systematic paleontology

Class Mammalia Linnaeus, 1758
Order Carnivora Bowdich, 1821
Family Canidae Fischer von Waldheim, 1817
Subfamily Borophaginae Simpson, 1945
Genus ***Cynarctus*** Matthew, 1902
Cynarctus cf. *C. saxatilis*
Figs. 2(G–I), 3(E, I, J)

2014. *Tomarctus brevirostris* (Cope, 1873) – Smith et al., p. 235 (in part).

Material: UCMP 141916, right m2.

Locality: UCMP V70147, "Nevaxel XI", Monarch Mill Fm., Churchill County, Nevada.

Age: Barstovian North American Land Mammal Age.

Measurements: See Table 1.

Description: This taxon is represented in the Monarch Mill Fm. by an isolated m2 preserved in pristine condition. The specimen is larger in size and similar in morphology to the m2 on a complete hemimandible of *Cynarctus saxatilis* from the Valentine Fm. of Nebraska (UCMP 29891). Both specimens share diagnostic characteristics for the species, including small m2 protoconid contrasted with an extremely well-developed m2 metaconid. Both also exhibit a substantial anterolabial cingulum. UCMP 141916 additionally preserves a strong m2 metastylid.

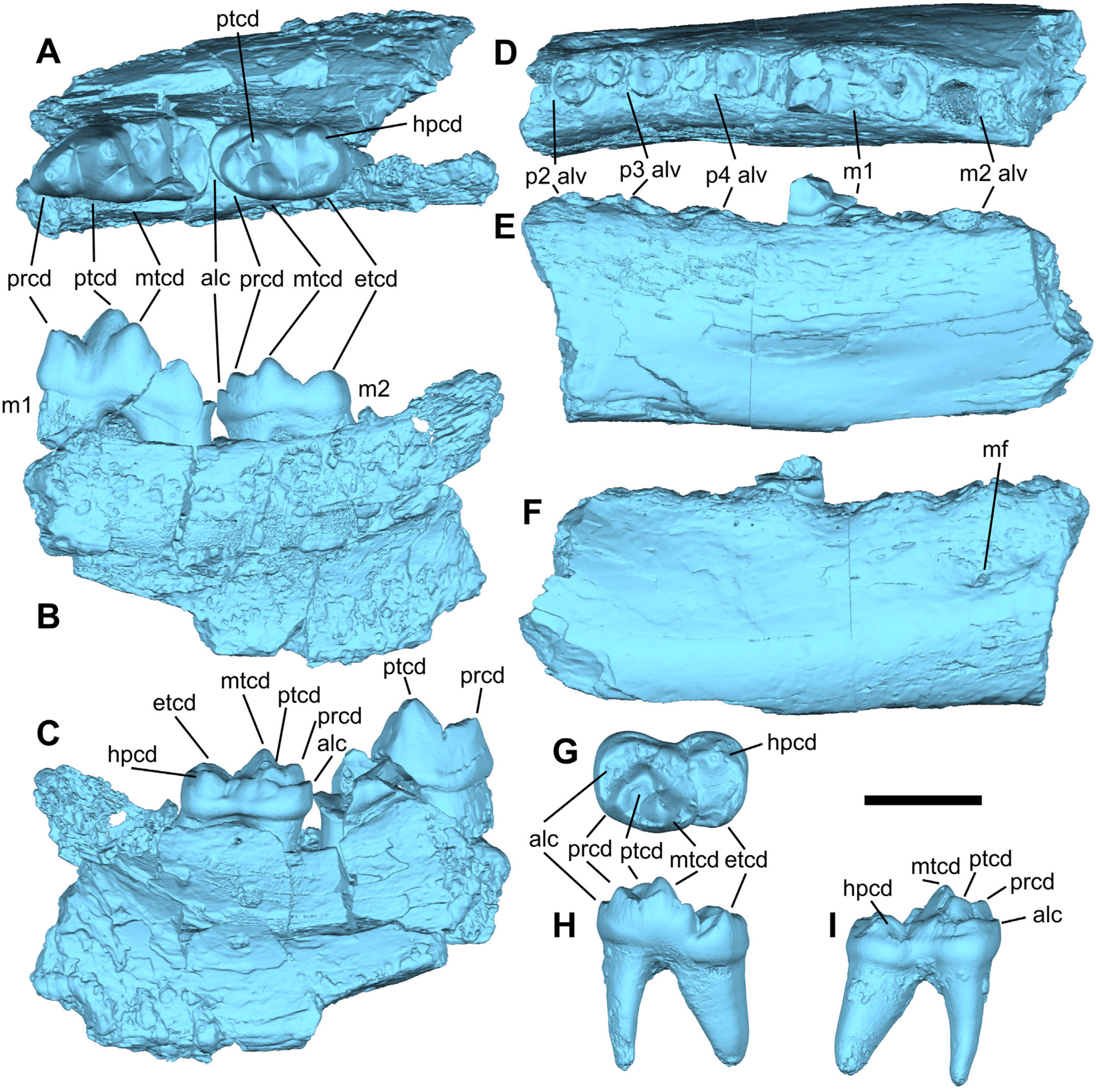

Fig. 2. Cynarctinan borophagine canids from the Monarch Mill Formation. **A–C.** *Paracynarctus kelloggi*, UCMP 136037 in occlusal/dorsal (A), lingual (B) and labial (C) views. **D–F.** *Paracynarctus* cf. *P. kelloggi*, UCMP 80400 in occlusal/dorsal (D), lingual (E) and labial (F) views. **G–I.** *Cynarctus* cf. *C. saxatilis*, UCMP 141916 in occlusal (G), lingual (H) and labial (I) views. Abbreviations: prcd, paraconid; ptcd, protoconid; mf, mental foramen; mtcd, metaconid; alc, anterolabial cingulum; etcd, entoconid; hpcd, hypoconid; p2-p4, second to fourth lower premolar; m1-m2, first and second lower molar; alv, alveolus. Scale bar: 10 mm.

Remarks: UCMP 141916 is minimally 30% longer than all other m2 specimens known from the Monarch Mill Fm. The m2 in the *Paracynarctus kelloggi* specimen from Monarch Mill (UCMP 136037) shows a smaller anterolabial cingulum than UCMP 141916; the metaconid is also relatively less developed compared to the protoconid in the *P. kelloggi* specimen compared to UCMP 141916. The well-preserved m2 in one of the *Tomarctus brevirostris* specimens from the Monarch Mill (UCMP 141908) is 30% smaller than UCMP 141916. Furthermore, the m2 protoconid and metaconid are equal in size in UCMP 141908 whereas the protoconid is much smaller compared to the metaconid in UCMP 141916 (Fig. 4). For these reasons, here we reassign UCMP 141916 to *Cynarctus* rather than *Tomarctus brevirostris* as originally described in Smith et al. (2014). Despite m2 morphology and size both being consistent with *C. saxatilis*, given the paucity of available material from the Monarch Mill Fm., we tentatively identify this specimen as *Cynarctus* cf. *C. saxatilis*. A more confident assignment awaits the discovery of additional diagnostic dentition, especially those that preserve upper P4 to M2 characteristics as well as lower premolar diastema.

Table 1
Specimen measurements and CT scanning parameters. Abbreviations: kV, kilovolts; µA, microAmperes; µm, micrometers; mm, millimeters.

Taxon	Specimen	kV	µA	Voxel size (µm)	Tooth	Length (mm)	Width (mm)
Cynarctus cf. *C. saxatilis*	UCMP 141916	110	100	33.40	Rm2	13.30	8.45
Paracynarctus kelloggi	UCMP 136037	110	100	41.75	Rc1	8.68	7.08
					Rm1	15.22	7.00
					Rm2	11.34	6.62
Paracynarctus cf. *P. kelloggi*	UCMP 80400	110	100	33.40	Rp2 (alveoli)	5.79	3.73
					Rp3 (alveoli)	6.66	3.98
					Rp4 (alveoli)	8.20	4.58
					Rm1 (alveoli)	13.87	6.62
Tomarctus brevirostris	UCMP 141836	110	110	38.41	Rm1 (partial)	18.29	8.05
					Rm2	10.11	6.47
	UCMP 141908	110	100	41.75	Lp2	8.10	4.66
					Lp4	11.36	7.01
					Lm1 (partial)	20.64	8.30
					Lm2	9.43	6.37
	UCMP 141920	110	100	36.74	Rm1 (partial)	21.76	9.09
					Rm2 (alveoli)	8.92	5.15
	UCMP 148257	110	100	13.36	RM2 (partial)	6.47	11.21
	UCMP 177909	110	100	25.05	Lp4 (partial)	–	5.57
					Lm1	19.56	8.10
Comparative material							
Cynarctus saxatilis	UCMP 29891	110	100	46.76	Lc1	8.60	6.86
					Lp1	4.21	2.75
					Lp2	7.64	4.05
					Lp3	9.05	4.46
					Lp4	10.68	5.41
					Lm1	16.96	7.78
					Lm2	11.61	7.46
					Lm3	6.85	5.38
Paracynarctus kelloggi	UCMP 11474	110	110	46.76	Rp1	4.19	2.98
					Rp2	7.15	3.90
					Rp3 (alveoli)	8.17	3.93
					Rp4 (partial)	10.58	5.38
					Rm1 (partial)	17.24	6.99
					Rm2	11.26	6.40

Genus ***Paracynarctus*** Wang et al., 1999.

Paracynarctus kelloggi (Merriam, 1911)

Fig. 2(A–C)

Material: UCMP 136037, right dentary fragments with c, partial m1, m2.

Locality: UCMP V88079, "Hanson's Dog", Monarch Mill Fm., Churchill County, Nevada.

Age: Barstovian North American Land Mammal Age.

Measurements: See Table 1.

Description: The specimen was collected in several pieces, the most diagnostic fragment of which is a mandibular fragment with m1 trigonid and m2. The m1 trigonid preserves all three main cuspids, with similarly sized paraconid and metaconid. The talonid is missing except for a portion of the lingual wall that would have connected the metaconid to the entoconid. The missing portion of m1 is roughly 30% of the total length of that tooth. The m2 is well-preserved, with a strong anterolingual cingulum and a well-developed metaconid. The m2 hypoconid and entoconid are similar in size and connected distally by a smooth cingulum.

Remarks: The morphology of the m2 in UCMP 136037 matches those of *P. kelloggi* (UCMP 11474, Fig. 3, and holotype UCMP 11562, not figured here) from the contemporaneous Virgin Valley Fm. in northwest Nevada. In all *P. kelloggi* specimens examined, the m2 metaconid and anterolabial cingulum are both less developed than those in *Cynarctus saxatilis*, including UCMP 141916.

cf. *Paracynarctus kelloggi*

Fig. 2(D–F), 3(A, D, F)

Material: UCMP 80400, right edentulous dentary fragment with p2-m2 alveoli.

Locality: UCMP V67245, "Eastgate 2", Monarch Mill Fm., Churchill County, Nevada.

Age: Barstovian North American Land Mammal Age.

Measurements: See Table 1.

Description: The specimen is a mandibular ramus fragment with a small portion of m1 trigonid preserved. A mental foramen is preserved and sits ventral to the position of p3.

Remarks: The depth of the ramus, position of the mental foramen, and the closely-set arrangement of cheek tooth alveoli are all consistent with those observed in the Virgin Valley *P. kelloggi* (UCMP 11474, Fig. 3, and holotype UCMP 11562, not figured here). *Cynarctus saxatilis*, in contrast, has a more spaced-out distribution of the premolars, with mental foramina sitting in between premolars at the position of the interdental diastemae (Fig. 3). The overall size of UCMP 80400 is similar to compared material of *P. kelloggi*, but smaller than Monarch Mill *Tomarctus* specimens and larger than *Cynarctus saxatilis* (Table 1). Given the lack of additional morphological characteristics, we tentatively assign this specimen to cf. *Paracynarctus kelloggi*.

As the most basal member of the cynarctinan clade, *Paracynarctus kelloggi* displayed initial tendencies toward hypocarnivory. In dental measurements, these tendencies are often shown as enlargements of the posterior molars relative to M1 or m1 (Wang et al., 1999: fig. 53), i.e., increasing grinding areas of the dentition. The m2/m1 length ratio for UCMP 80400 is ca. 0.75 (alveolar measurements), compared to an average ratio of 0.69 for *P. kelloggi* (as provided by Wang et al., 1999 based on dental measurements of samples across the species' paleogeographic range, and so would translate to even smaller values if measured from alveoli), showing that the Eastgate specimen is clearly trending toward hypocarnivory.

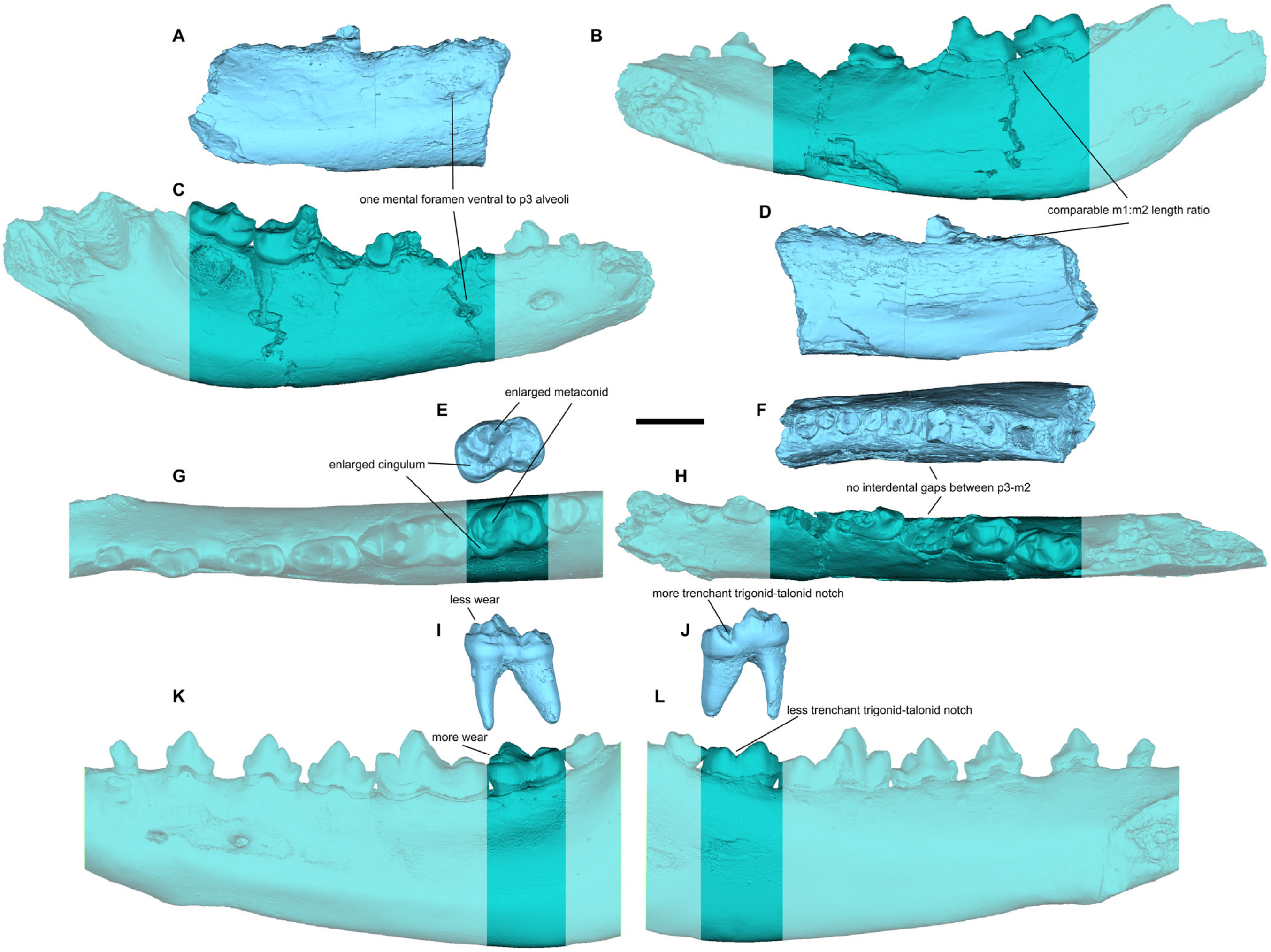

Fig. 3. Comparison of referred cynarctinan specimens. **A**. Lateral/labial view of UCMP 80400 (*Paracynarctus* cf. *P. kelloggi*). **B**. Medial/lingual view of UCMP 11474 (*P. kelloggi*). **C**. Lateral/labial view of UCMP 11474. **D**. Medial/lingual view of UCMP 80400. **E**. Mirrored occlusal view of UCMP 141916 (*Cynarctus* cf. *C. saxatilis*). **F**. Occlusal view of UCMP 80400. **G**. Dorsal/occlusal view of UCMP 29891 (*C. saxatilis*). **H**. Dorsal/occlusal view of UCMP 11474. **I**. Mirrored labial view of UCMP 141916. **J**. Mirrored lingual view of UCMP 141916. **K**. Lateral/labial view of UCMP 29891. **L**. Medial/lingual view of UCMP 29891. Scale bar: 10 mm.

Genus ***Tomarctus*** Cope, 1873

Tomarctus brevirostris Cope, 1873

Fig. 4.

2014. *Tomarctus brevirostris* (Cope, 1873) – Smith et al., p. 235, fig. 3 (in part).

Material: UCMP 141836, right mandibular fragment with m1 trigonid and worn m2; UCMP 141908, left mandibular fragment with p2, p4, m1 talonid, and m2; UCMP 141920, right mandibular fragment with partial m1 and alveoli of m2; UCMP 148257, isolated partial RM2; UCMP 177909, left mandibular fragment with partial p4, complete m1; OMNH 54975, left edentulous dentary fragment.

Localities: UCMP V70147 (UCMP 141836, 141908, 141920, OMNH 54975), “Nevaxel XI”; UCMP V70140 (UCMP 148257), “Nevaxel 5”; UCMP V87139 (UCMP 177909), “V-3”. All are within the Monarch Mill Fm., Churchill County, Nevada.

Age: Barstovian North American Land Mammal Age.

Measurements: See Table 1.

Description: Of the five Monarch Mill specimens referred to *T. brevirostris*, only UCMP 141908 was previously figured and described (Smith et al., 2014). Those details are not repeated here. Two of the remaining referred specimens provide additional morphological information not preserved on UCMP 141908: UCMP 177909 and UCMP 148257. UCMP 177909 preserves a complete m1 in an early stage of wear, with protoconid being the tallest cuspid on the tooth. The m1 paraconid and metaconid are equal in height, and m1 hypoconid and entoconid are also comparable in size and height. A small protostylid is present on the labial ridge leading up to the tip of the protoconid, and a small entoconulid is present on the boundary between the trigonid and talonid regions of m1. UCMP 148257 is a right M2 preserving all major cusps but missing the labial edge; the protocone and hypocone are moderately worn into broad ridges. The paracone and metacone are less worn and still maintain cusps; the former is taller than the latter. A small metaconule is present in the form of a ridge that is connected rostrally to the protocone. The two remaining referred specimens are dentary fragments that reinforce the morphological traits already observed in the aforementioned specimens. UCMP 141836 preserves a worn m1 trigonid showing a taller protoconid and a shorter paraconid; it also preserves a worn m2 that is consistent in overall morphology and size to that in UCMP 141908. UCMP 141920 preserves a partial m1 trigonid and m2 alveoli, both of which are similar in size and proportion to those preserved in UCMP 141908.

Remarks: Comparisons of the lower dentition of Monarch Mill *Tomarctus brevirostris* were provided in Smith et al. (2014) and

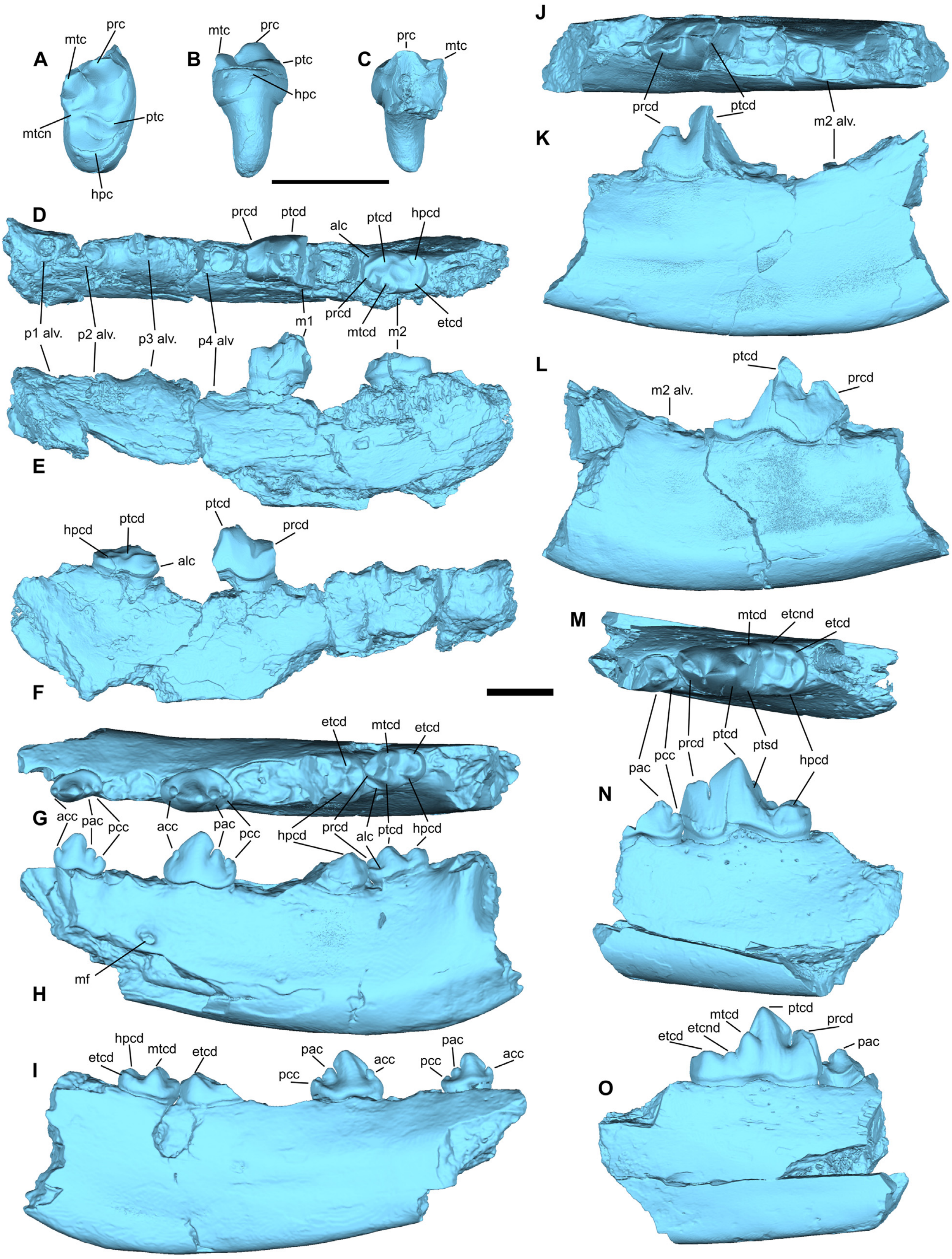

Fig. 4. *Tomarctus brevirostris* specimens from the Monarch Mill Formation. **A–C.** UCMP 148257 in occlusal (A), lingual (B) and labial (C) views. **D–F.** UCMP 141836 in dorsal/occlusal (D), medial/lingual (E) and lateral/labial (F) views. **G–I.** UCMP 141908 in dorsal/occlusal (G), lateral/labial (H) and medial/lingual (I) views. **J–L.** UCMP 141920 in dorsal/occlusal (J), medial/lingual (K) and lateral/labial (L) views. **M–O.** UCMP 177909 in dorsal/occlusal (M), lateral/labial (N) and medial/lingual (O) views. Abbreviations: acc, anterior cingular cuspid; hpc, hypocone; pac, posterior accessory cuspid; pcc, posterior cingular cuspid; prc, paracone; ptc, protocone; ptsd, protostylid; mtc, metacone; mtcn, metaconule; other abbreviations as in Fig. 2. Scale bar: 10 mm.

are not repeated here. The only new element of this taxon added in this study, the M2, shows similar morphology to the M2 of AMNH 18246 (early Barstovian Olcott Fm., Nebraska) illustrated by Wang et al. (1999): the paracone and metacone are similar in size, the large protocone connected distally to a much smaller metaconule, and a ridge-like hypocone that is shorter rostro-distally than the labial length of the tooth. In contrast, the M2 specimens of *Paracynarctus kelloggi* from early Barstovian Tesuque Fm. of New Mexico (F:AM 27487, 50137, illustrated in Wang et al., 1999) show a more elongate hypocone ridge that is similar in extent to the labial length of the tooth. The general dimensions of M2 in *Cynarctus saxatilis* are closer to a square (mean length: 10.15 mm, mean width: 11.45 mm; Wang et al., 1999) whereas UCMP 148257 is more rectangular (length: 6.47 mm, width: 11.21 mm; Table 1).

Dental measurements (Table 1) of this taxon in Middlegate are largely consistent with those of *Tomarctus brevirostris*. However, the m1 in UCMP 177909 (19.56 mm in length) falls short of the smallest individual of *T. brevirostris* (21.0–24.8 mm in length; total number of individuals: 36; Wang et al., 1999), but within the range of *T. hippophaga* (16.5–22.5 mm) and other contemporaneous borophagines. Morphologically these two species are difficult to distinguish based on isolated teeth, and chronologically both are present in the early Barstovian.

4. Discussion

As open-terrain adapted, pursuit predators, canids are well represented in the open habitats in mid-latitudes, where the best terrestrial sediment records are located. To the extent that our knowledge of Cenozoic vertebrate evolution is heavily biased toward the mid latitude arid regions, fossil canids have an excellent record in North America, better than any other group of carnivorans. Canid records thus not only afford insights into their evolution but also may be sensitive to the opening of landscapes in which they occur.

Our treatment of the Eastgate LF borophagine canids brings new information to bear on Miocene canid paleozoogeography. For one, *Cynarctus saxatilis* was previously only known in the late Barstovian of Colorado and Nebraska. Its occurrence in the Middlegate Basin of Nevada thus represents the first record in the Great Basin west of the Rockies. *C. saxatilis* is the first representative of the advanced species of *Cynarctus* with prominent hypocarnivorous adaptations such as enlargement of the m2, high-crowned metaconid, and enlarged anterior and labial cingulum. The Middlegate m2 is larger than any known records of *Cynarctus* (Wang et al., 1999).

More generally, the previously described occurrence of the canine *Leptocyon* from the Monarch Mill Fm. (Smith et al., 2014), together with the referred borophagine specimens in this study, bring the total diversity of canids from the Middlegate Basin to four genera (one canine, three borophagines). This canid assemblage is doubled in taxonomic diversity from the most recent treatment and is noteworthy for the addition of hypocarnivorous taxa to the two previously known mesocarnivorous canids (Fig. 5). Based on first molar derived body mass estimates, this moderately diverse assemblage of meso- and hypocarnivores largely mirrors the body size range of the extant canid assemblage in the Basin and Range biogeographic province, but the extant canid assemblage does not contain hypocarnivorous canids. Another notable difference is the absence of large hypercarnivores in the Eastgate LF. Large hypercarnivores in Neogene North American fossil localities tend to preserve better because of their robust teeth and jaws, and are thus less likely to be missed due to traditional collections bias. Such an absence during the initial Barstovian diversification of the larger, bone-cracking borophagine genera elsewhere in the Great Basin region, namely southern Nevada and southern California (Wang et al. 1999), may reflect regional differences in proportion of open versus closed habitats. The paleoenvironment in which the Eastgate LF canid assemblage lived can be approximated by the geologically slightly older Middlegate and Eastgate floras, which suggest a chaparral habitat and mixed conifer-deciduous forest, respectively (Smith et al., 2014). The proportion of open habitats typically associated with hypercarnivorous borophagines such as *Aelurodon* may have represented only a minor component in ecological landscape of the Middlegate Basin during the Barstovian, and the subsequent arrival and spread of *Aelurodon* and *Epicyon* in the basin and range region of Nevada during the Clarendonian (~12–8.5 Ma) may reflect a broadening distribution of open habitats (Wang et al., 1999). Additionally, analyses of the paleobotanical evidence in central and western Nevada suggest a local paleoaltitude of more than 3,000 m in the early Barstovian, followed by rapid subsidence to half that altitude in as little as two million years of time (Wolfe et al., 1997; Bahadori et al., 2018). It is possible that high altitude during the Barstovian may have discouraged more cursorial, hypercarnivorous borophagines from dispersing to the area; this hypothesis is partially supported by the local first appearance of both *Aelurodon* and *Epicyon* in central and northern Nevada's post-subsidence Clarendonian deposits (Wang et al., 1999).

This inferred spatial and temporal heterogeneity in borophagine assemblage composition during the Barstovian is in part supported by estimates of molar size distribution evenness across Great Basin. The Middlegate borophagine assemblage represents a moderately evenly distributed set of taxa by molar size (Table 2). Some early Barstovian assemblages in the Barstow Fm. in the southern part of the Great Basin exhibit higher evenness than the Quaternary canid assemblage in Nevada (used here as a baseline comparison), but other Barstow assemblages show comparable degrees of evenness to Middlegate borophagines. The mid-range value of Clark-Evans evenness index in the Middlegate assemblage does not indicate that uneven or biased sampling explains the absence of larger bone-cracking taxa in the fauna. A broader analysis of the vertebrate faunas in these localities are necessary to further reveal potential environmental differences across the Great Basin during the Barstovian NALMA, but such an undertaking is beyond the scope of the present study.

Finally, it is worth noting that Nevada is situated near the northern margin of the greater Basin and Range taphrogen (Dickinson, 2006), and tectonic activities leading to the establishment of present day western North American topography reconfigured the entire taphrogen from Nevada down to central Mexico during the late Cenozoic (Henry and Aranda-Gomez, 1992). Therefore, the topographic transformations along the north–south axis of the Great Basin may have affected not only local canid and other mammal dispersal in the Basin and Range Province in and around Nevada, but also the broader distribution of fossil mammals in western North America. The lower-latitude dispersal to Mexico of otherwise widespread mid-latitude borophagine canids such as *Borophagus* did not occur until the Hemphillian NALMA (~8.5 to 4.9 Ma; Wang et al. 1999), suggesting that the timing and extent of crustal extension may be in part responsible for the successive stages of range expansion of hypercarnivorous borophagine canids (e.g., *Borophagus, Epicyon*) in the Great Basin during post-Barstovian times. A possible scenario suggests an initial dispersal north into Nevada from lower mid-latitudes during the Clarendonian, and subsequently south towards even lower latitudes into Mexico during the Hemphillian. Certainly, such a continental-scale paleozoogeographic scenario requires rigorous testing with additional occurrence data from elsewhere in the Great Basin, of not only borophagines but other mammal taxa as well.

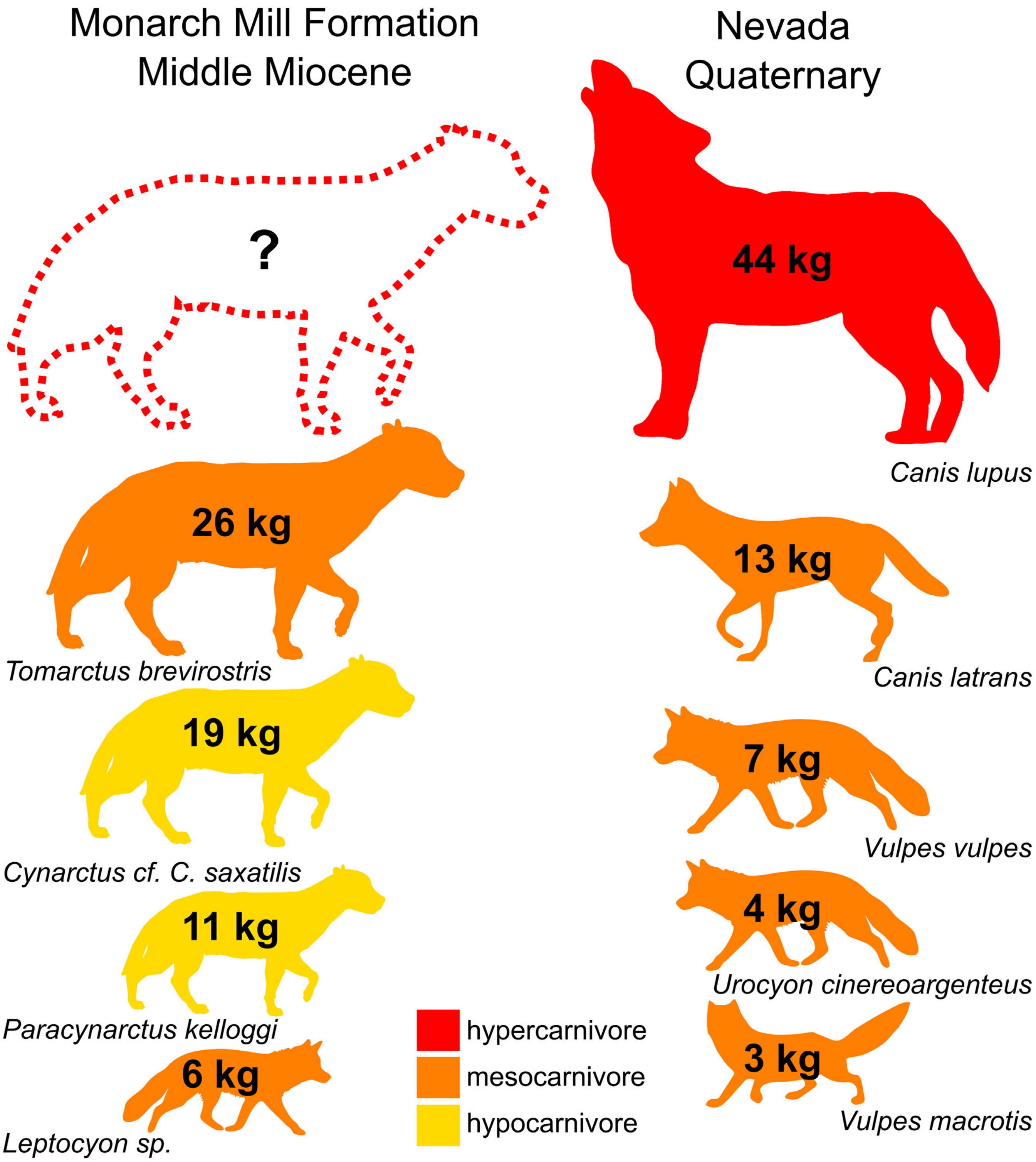

Fig. 5. Comparison of canid assemblages. Average body mass for Quaternary/extant species taken from Van Valkenburgh (1990) and Animal Diversity Web (https://animaldiversity.org/, accessed July 26, 2024). Body masses for Monarch Mill canids estimated from m1 length using clade-specific regression equations in Van Valkenburgh (1990) (for specific equations and measurements used, see Table S1; Appendix A). Dietary category is assigned based on Animal Diversity Web (extant taxa) or Wang et al. (1999) and Tedford et al. (2009) (extinct taxa). Dotted outline indicates the absence of large-bodied hypercarnivores in the Monarch Mill Formation, and more generally their rarity in Barstovian deposits in the northern Basin and Range Province. Silhouettes modified from phylopic.org.

Table 2

Clark-Evans index (R) of evenness for molar lengths in Great Basin canid assemblages. R/nb. taxa is the ratio between R and number of taxa counted in each assemblage.

Geologic Age	Fauna	Clark-Evans Index R	R/nb. taxa
Quaternary	Nevada	2.89	0.58
Clarendonian	Dove Spring	2.17	0.72
Barstovian	*Middlegate*	1.35	0.45
Early Barstovian	Caliente	1.12	0.56
Early Barstovian	Green Hills – Barstow	1.20	0.30
Early Barstovian	First Division – Barstow	1.17	0.23
Early Barstovian	Second Division – Barstow	3.72	0.53
Early Barstovian	Yermo Quarry – Barstow	3.50	1.17

CRediT authorship contribution statement

Z. Jack Tseng: Writing – review & editing, Writing – original draft, Visualization, Resources, Project administration, Methodology, Investigation, Funding acquisition, Formal analysis, Conceptualization. **Xiaoming Wang:** Writing – review & editing, Writing – original draft, Investigation, Funding acquisition, Formal analysis.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary information

Supplementary information (including Fig. S1 and Tables, S1, S2) associated with this article can be found, in the online version, at https://doi.org/10.1016/j.geobios.2024.11.011.

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