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First occurrences of *Palaeogale* von Meyer, 1846 in the Pacific Northwest, United States

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ABSTRACT
The feliform carnivoran *Palaeogale* von Meyer, 1846 first appears in the Eocene of North America and had a Holarctic distribution in the Oligocene and early Miocene. Despite its large range, *Palaeogale* has not previously been reported from the Pacific Northwest of North America. We report three new specimens from the John Day Basin of Oregon that fill in this geographic gap. The oldest of these is a largely complete cranium from the Turtle Cove Member of the John Day Formation (Oligocene, 30.0-28.9 Ma). The other two specimens are a left and a right dentary from separate individuals, both recovered from the Kimberly Member (Oligocene, 25.3-23.5 Ma). Because *Palaeogale* species are almost entirely distinguished by their lower dentition, the cranium cannot be identified to species. However, the cranium is the oldest occurrence of the genus in the Pacific Northwest. The absence of a posterior accessory cusp on the p4 and of lateral expansion of the m1 protoconid allows the dentaries to be assigned to an endemic North American species, *P. dorothiae* MacDonald, 1963. This is not only the first instance of this species in the Pacific Northwest and outside of South Dakota and Nebraska, but also the last known occurrence of *P. dorothiae*. We expect that these specimens will inform future analyses of phylogenetics, systematics, morphology, and biogeography in *Palaeogale*.

KEY WORDS
Palaeogale,
Oligocene,
Oregon,
John Day Formation,
Kimberly Member,
Turtle Cove Member.

RÉSUMÉ

Premières occurrences de Palaeogale *von Meyer, 1846 dans le Nord-Ouest Pacifique des États-Unis.*

Le carnivore féliforme *Palaeogale* von Meyer, 1846 est apparu pour la première fois à l'Éocène en Amérique du nord et a une distribution holarctique pendant l'Oligocène et le Miocène. Malgré sa distribution étendue, *Palaeogale* n'a pas été reconnu auparavant dans le Nord-Ouest Pacifique d'Amérique du nord. Nous signalons ici trois nouveaux spécimens provenant du bassin John Day dans l'Orégon qui complètent cette lacune géographique. Le plus vieux de ces trois spécimens est un crâne presque complet du Membre Turtle Cove de la Formation John Day (Oligocène, 30,0-28,9 Ma). Les deux autres spécimens sont un dentaire droit et un dentaire gauche issus d'individus différents, tous les deux provenant du Membre Kimberly (Oligocène, 25,3-23,5 Ma). Du fait que les espèces de *Palaeogale* sont presque entièrement différenciées par leur dentition inférieure, le crâne ne peut pas être identifié comme appartenant à une espèce particulière. Cependant, ce crâne représente la plus vieille occurrence du genre dans le Nord-Ouest Pacifique . L'absence d'une cuspide secondaire sur la p4 et d'une expansion latérale du protoconide de m1 permet l'identification des dentaires comme appartenant à une espèce endémique nord-américaine, *P. dorothiae* MacDonald, 1963. Ceci est la première occurrence de cette espèce dans le Nord-Ouest Pacifique (en dehors du Dakota du sud et du Nebraska), et la plus récente occurrence de *P. dorothiae* dans le registre fossile. Ces spécimens seront utiles pour des analyses futures concernant *Palaeogale* (phylogénie, systématique, morphologie et biogéographie).

MOTS CLÉS
Palaeogale,
Oligocène,
Orégon,
Formation de John Day,
Membre Kimberly,
Membre de Turtle Cove.

INTRODUCTION

The enigmatic carnivoran *Palaeogale* von Meyer, 1846 represents a potentially significant case study of dispersal and convergence in the fossil record, but many aspects of its morphology and evolutionary history remain poorly understood. The genus is both temporally and biogeographically widespread. The oldest fossils attributed to the genus are from the Renova and White River formations of Montana and Wyoming (Love *et al.* 1976; Tabrum *et al.* 1996) and date to the Chadronian North American Land Mammal Age (NALMA; late Eocene; Fig. 1). The genus had expanded into a Holarctic distribution by the Oligocene, with specimens recovered from Mongolia (Dashzeveg 1996), China (Wang & Zhang 2015), and multiple localities in Europe and North America (De Bonis 1981). The youngest Asian *Palaeogale* fossils date to at or just above the Oligocene-Miocene boundary (Daxner-Höck & Wu 2003), while the genus persists well into the early Miocene in Europe (Orleanian European Land Mammal Age; Heizmann *et al.* 1980; de Bonis 1981) and North America (Hemingfordian NALMA; Harksen & MacDonald 1967).

Despite this broad temporal and geographic range, *Palaeogale* has long been an evolutionary and taxonomic conundrum. Simpson (1946) considered it a mustelid, but subsequent work has not supported this assessment. Flynn & Galiano (1982) suggested that not only was *Palaeogale* not a mustelid, but it was not a caniform at all, instead sharing numerous dental synapomorphies with feliforms. They further suggest that a large postglenoid foramen located posteroexternally on the postglenoid process of the squamosal, a trait shared by *Palaeogale* and *Viverravus* Marsh, 1872, indicate that *Palaeogale* may have been a member of the extinct family Viverravidae Wortman & Matthew, 1899. Martin & Lim (2001) likewise identify *Palaeogale* as a feliform, citing a reduced internal carotid, the presence of a septum bulla, and an enlarged parastyle as evidence of its feliform ancestry. However, they assigned it not to the Viverravidae, but to a new family, the Palaeogalidae Martin & Lim, 2001 that also includes the genus *Cryptailurus* Martin & Lim, 2001. A phylogenetic analysis by Wang & Zhang (2015) that included specimens from China supported the interpretation of *Palaeogale* as a basal feliform, but did not support its inclusion in Viverravidae, which they suggest are basal carnivoromorphs. The placement of a monophyletic Viverravidae at the stem of Carnivoramorpha is also supported in the stem-sample heavy analyses of Wesley-Hunt & Flynn (2005).

Taxonomy within the genus *Palaeogale* has a similarly convoluted history. Simpson (1946) noted that, despite the relatively small number of specimens known from North America at the time, variation within those specimens was great enough that they might represent as many as five species. However, he suggested that much of this variation might be due to sexual dimorphism, in which case all North American specimens might be attributed to just one or two species. The most rigorous taxonomy of *Palaeogale* is that of de Bonis (1981), which recognizes four species: *P. sectoria* Gervais, 1848, *P. dorothiae* Macdonald, 1963, *P. minuta* Gervais, 1848, and *P. hyaenoides* Dehm, 1950. More recently, a fifth species has been described from the early Miocene of Germany, *P. praehyaenoides* Morlo, 1996 which is smaller than *P. hyaenoides* but larger than the other three recognized species (Morlo 1996). Baskin (1998) indicated a sixth species from eastern Wyoming, *P. sanguinarius* Loomis, 1932, was recombined out of *Plionictis* and into *Palaeogale* and is equivalent in age and slightly larger than *P. dorothiae*. The genus *Palaeogale* is defined by de Bonis (1981) in part based on upper dentition, specifically the presence of a well-developed parastyle on the P4 and M1,

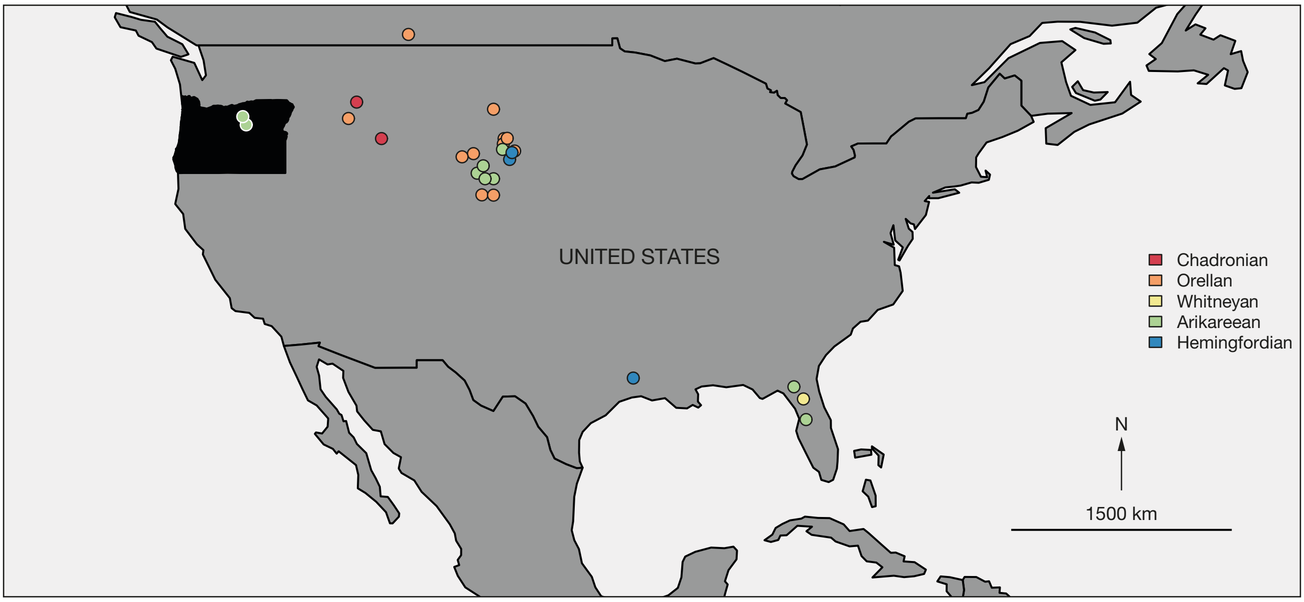

Fig. 1. — Map of distributions of North American *Palaeogale* von Meyer, 1846 specimens both published and from museum records. Localities are colour coded by North American Land Mammal Age. Black shaded area represents Oregon. Distribution data downloaded from Paleobiology Database (https://paleobiodb.org/) and iDigBio (https://www.idigbio.org/) on 23 April 2020. The Texas occurrence is reported in Albright (1996).

an M1 with a paracone larger than the metacone, and a narrowed lingual portion of the M1. However, all the traits used to differentiate the four species of *Palaeogale* are from the lower dentition. This has proven taxonomically problematic, as in many specimens, including those described here, skulls and dentaries are not regularly found in association with one another. Taphonomic processes have also precluded the association of postcranial material further complicating taxonomy and phylogenetic analysis.

The long-standing uncertainty surrounding the phylogenetic position of *Palaeogale* and the relationship and diagnosis of species within the genus is due in part to a paucity of specimens. While the European record of the genus is fairly robust (Heizmann *et al.* 1980; De Bonis 1981), its North American occurrences (Fig. 1) are limited to the Gulf Coast (Albright 1996; Hayes 2000), the Northern Great Plains (Simpson 1946; Storer 1996), and the adjacent Rocky Mountains (Love *et al.* 1976; Tabrum *et al.* 1996). Here we present a description of three previously undescribed specimens of *Palaeogale* (two partial dentaries and a mostly complete skull with upper dentition) from the Oligocene John Day Formation of Oregon. These specimens represent the first reported occurrence of *Palaeogale* in the Pacific Northwest of North America and may be valuable tools for addressing long-standing questions about palaeogalid taxonomy and paleobiology.

MATERIAL AND METHODS

Measurements

Measurements of the specimens at John Day Fossil Beds National Monument (JODA) were taken with a Mitutoyo Absolute Solar Digimatic CD-54"c digital caliper (error ±0.02mm). All measurements were taken as close to the enamel-dentine junction as possible and at the widest points of each tooth for both the anterior-posterior length (APL) and the transverse width (TW). Some scaled figures and photographs of non-Oregon specimens were measured in ImageJ (https://imagej.nih.gov/ij/). JODA 13221 was collected in July 2007, JODA 6177 in April 1997, and JODA 5893 was collected in November 1995.

Geologic context

The John Day Formation is distributed throughout eastern and central Oregon and is currently subdivided into seven members: Big Basin, Turtle Cove, Kimberly, Haystack Valley, Balm Creek, Johnson Canyon, and Rose Creek (Retallack *et al.* 2000; Hunt & Stepleton 2004; Albright *et al.* 2008). This study focuses on the Oligocene Turtle Cove (30.8-25.9 Ma) and Kimberly (25.9-24.2 Ma) members (Albright *et al.* 2008). The Turtle Cove and Kimberly consist of *c.* 500 m of section that Albright *et al.* (2008) divided into 16 lithostratigraphic subunits (A-M). Included within the Turtle Cove Member are several dated tuffs and the Picture Gorge ignimbrite – a super-volcanic event related to the Yellowstone hotspot (Seligman *et al.* 2014). The faunas of the Turtle Cove Member are assigned to the Whitneyan (Wh2) and Arikareean (Ar1 and Ar2) NALMAs while the fauna of the Kimberly Member is only assigned to the Arikareean (Ar3) NALMA (Albright *et al.* 2008). In the Lonerock area, there are small and visually unimpressive exposures of the Kimberly Member (Fremd & Whistler 2009). The exact stratigraphic position of these exposures within the Kimberly Member have not yet been determined (Fremd & Whistler 2009).

TABLE 1. — Measurements of upper dentition: Abbreviations: **APL**, anterior-posterior length; **TW**, transverse width; **–**, not available. All measurements are in mm. **†**, measured scaled figure or photo in ImageJ.

		P2		P3		P4		M1		
Specimen	**ID**	**APL**	**TW**	**APL**	**TW**	**APL**	**TW**	**APL**	**TW**	**Reference**
JODA 13221 Right	*Palaeogale* sp.	2.36	0.86	2.78	1.13	5.11	2.52	2.51	3.43	This paper
JODA 13221 Left	*Palaeogale* sp.	–	–	2.76	1.31	5.03	2.62	–	3.55	This paper
BADL 18581/SDSM 7118 Right †	*Palaeogale* sp.	3.16	1.37	3.71	2.33	6.26	3.72	2.96	4.42	Benton *et al.* 2015
BADL 18581/SDSM 7118 Left †	*Palaeogale* sp.	3.08	1.28	4.35	2.02	5.97	3.31	2.88	3.91	Benton *et al.* 2015
UF 163536	*Palaeogale minuta*	–	–	2.96	1.59	–	–	–	–	Hayes 2000
Brooksville mean (UF)	*Palaeogale minuta*	–	–	–	–	4.06	1.99	–	–	Hayes 2000
LSUMG V-2246 †	*?Palaeogale*	–	–	–	–	4.37	–	–	–	Albright 1996
IVPP V 19325.3	*Palaeogale sectoria*	–	–	–	–	6.40	3.50	2.70	5.50	Wang & Zhang 2015
IVPP V 19328	*Palaeogale sectoria*	–	–	–	–	5.80	3.00	2.30	4.40	Wang & Zhang 2015

ABBREVIATIONS

AMNH — American Museum of Natural History, New York, New York;
BADL — Badlands National Park, United States National Park Service, Interior, South Dakota;
IVPP — Institute of Vertebrate Palaeontology and Palaeoanthropology, Chinese Academy of Sciences, Beijing;
JDNM — Locality number for John Day Fossil Beds National Monument;
JODA — John Day Fossil Beds National Monument, United States National Park Service, Kimberly, Oregon;
LSUMG — Museum of Geosciences, Louisiana State University, Baton Rouge, Louisiana;
SDSM — Museum of Geology, South Dakota School of Mines and Technology, Rapid City, South Dakota;
SMF — Senckenberg Research Institute and Natural History Museum, Frankfurt;
UF — Florida Museum of Natural History, University of Florida, Gainesville, Florida.

SYSTEMATICS/RESULTS

Order CARNIVORA Bowdich, 1821
Suborder FELIFORMIA Kretzoi, 1945
Family PALAEOGALIDAE Martin & Lim, 2001

Genus *Palaeogale* von Meyer, 1846

Bunaelurus Cope, 1873: 8. — Type species: *B. lagophagus*.

TYPE SPECIES. — *Palaeogale minuta* Gervais, 1848 (synonym of *Mustela*) by original designation.

GENUS DIAGNOSIS. — "An early mustelid with cheek tooth formula 1.4/1-3.2-1/2. P1 and M2 vestigial or absent. P4 with small protocone, directed forward, large, somewhat recumbent main blade separated by a deep cleft from the strong metastylar blade. M1 strongly transverse, short and wide, triangular, with sharply projecting parastyle, small, simple protocone, not expanded anteroposteriorly and without cingulum. P2 procumbent, with long, shearing heel. M1 compressed, without metaconid, heel unbasined, with longitudinal shearing crest. M2 small but functional, elongate oval in outline, with weak longitudinal crest, without metaconid or basined talonid but with three vague cusps in series. No postorbital processes. No ossified auditory meatus. Palate ending at level of M1. Pterygoid crests converging posteriorly. Cerebellar region long and bounded externally by a distinct groove posterior to the cerebral region. Stylomastoid foramen lateral, near porus. Foramen ovale posterior to level of postglenoid processes. Carotid foramen small and nearly confluent with posterior lacerate foramen. Sagittal crest single throughout. Paroccipital process free, small." (Simpson 1946: 12)

Palaeogale sp.
(Fig. 2; Table 1)

REFERRED SPECIMEN. — JODA 13221, Skull; Braincase broken on both sides, exposing endocase. Posterior sagittal crest absent. Zygomatic arches absent. Incisors and left premolar absent. Tympanic bulla broken exposing endocast.

LOCALITY. — JDNM-7B, North Foree, Grant County, Oregon, USA. Unit E2, Turtle Cove Member, John Day Formation. Precise locality information available to qualified researchers upon request.

AGE. — Middle Oligocene in the Early Arikareean (Ar1) NALMA, between A/B tuff (30.0 Ma) and Blue Basin Tuff (28.9 Ma) (Albright *et al.* 2008).

DESCRIPTION

JODA 13221 is a mostly complete skull. The braincase is broken on both sides, exposing endocase. Posterior sagittal crest is broken, and the zygomatic arches are broken. The tympanic bulla is broken, exposing the endocast. All Incisors are broken in the alveoli. The canines are missing but the alveoli are present and filled with matrix. Both P1s are missing and some matrix and dentine are present in the alveoli. The left P2 is broken at the roots which are lodged in the alveoli. The crown of the left P4 is damaged as is that of the left M1. The protocone of both the left and right M1s are present but are heavily worn.

Dentition

In the P4, the protocone is small and rounded. In the M1, the protocone is small but is worn so other characters are unknown. However, the M1 is triangular, transverse, short and wide, with a sharply projecting parastyle. Alveoli are present for both right and left P1. M2 is absent. See Table 1 for measurements.

Cranium

The skull is elongate (total length of 50.63 mm; max skull height of 14.76 mm) while the muzzle is short (14.50 mm from the naris to the orbit) making up about 29% of the total skull length. Tympanic bullae are elongate and rounded. The sagittal and occipital crests are damaged.

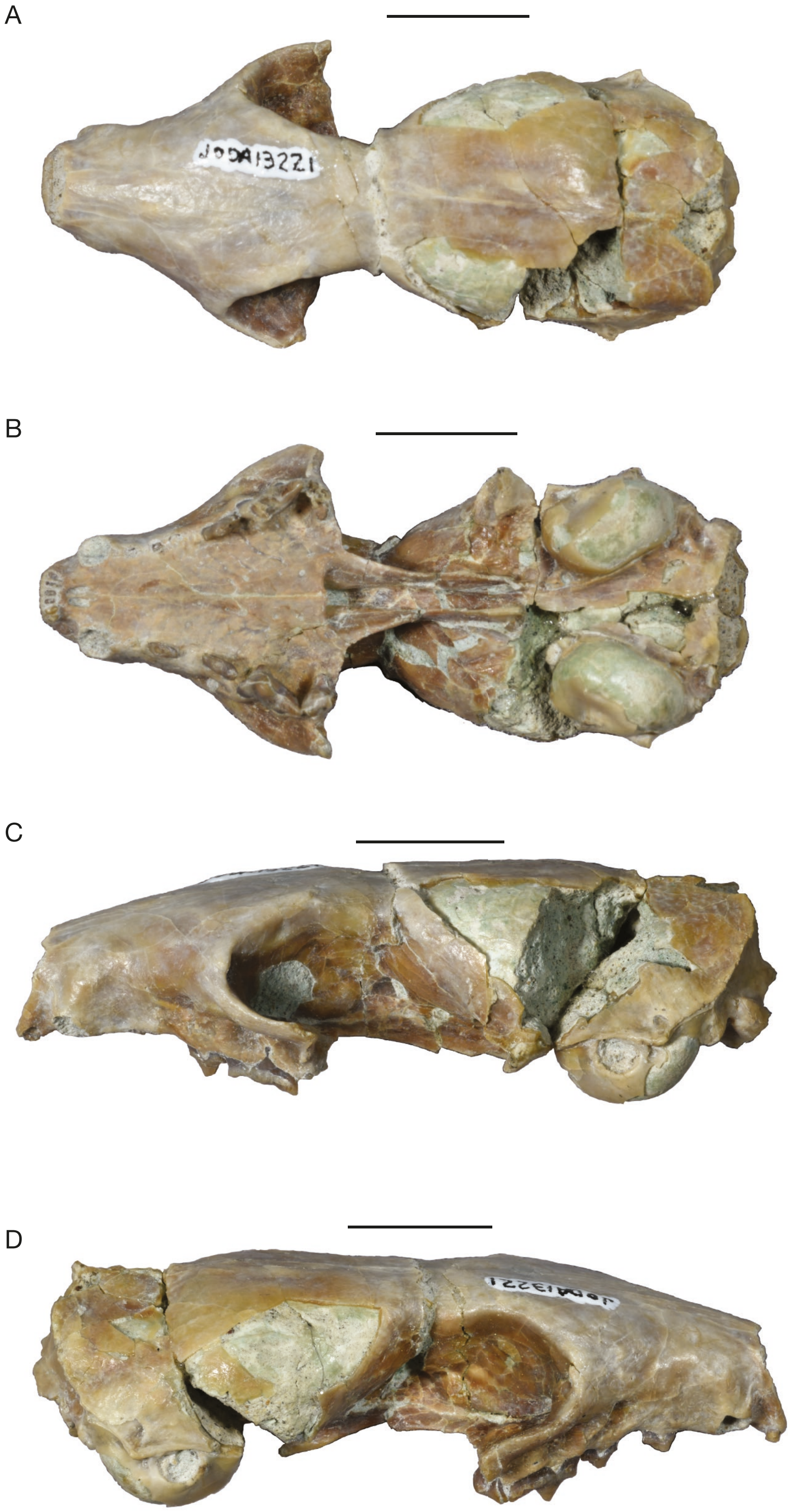

Fig. 2. — Skull of *Palaeogale* sp. (JODA 13221): **A**, dorsal view; **B**, ventral view; **C**, left lateral view; **D**, right lateral view. Scale bars: 1 cm.

Comparison

There are no species level characters that are identified on the skull making a species level diagnosis impossible. Inference based on size is possible, but it lacks the rigor to justify a species-level diagnosis. It is likely that this specimen belongs to *P. sectoria* based on the size (Wang & Zhang 2015), but it also overlaps in size with *P. minuta* (Hayes 2000). This specimen could be attributed to *P. sectoria*

Table 2. — Measurements of the lower dentition. Abbreviations: **APL**, anterior-posterior length; **TW**, transverse width; **–**, not available; *****, type specimen. All measurements are in mm. **†**, measured scaled figure or image in ImageJ.

		p2		p3		p4		m1		m2		
Specimen	**ID**	**APL**	**TW**	**APL**	**TW**	**APL**	**TW**	**APL**	**TW**	**APL**	**TW**	**Reference**
JODA 5893	*Palaeogale dorothiae*	2.92	1.32	–	–	3.92	1.65	–	–	–	–	This paper
JODA 6177	*Palaeogale dorothiae*	–	–	–	–	3.78	1.78	5.36	2.32	–	–	This paper
SDSM 53326 *	*Palaeogale dorothiae*	–	–	–	–	3.60	1.40	4.50	2.00	1.90	1.10	MacDonald 1963
UF 163550	*Palaeogale minuta*	–	–	2.47	1.00	2.72	1.28	3.95	1.41	–	–	Hayes 2000
UF 163549	*Palaeogale minuta*	–	–	2.10	–	2.92	1.28	4.32	1.51	–	–	Hayes 2000
UF 163548	*Palaeogale minuta*	–	–	–	–	–	–	3.81	1.47	1.05	0.62	Hayes 2000
Brooksville mean (UF)	*Palaeogale minuta*	–	–	–	–	–	–	3.99	1.35	–	–	Hayes 2000
Mongolian Mean (AMNH)	*Palaeogale sectoria*	2.30	0.90	3.50	1.40	3.90	1.50	5.80	2.10	2.30	1.30	Lange-Badre & Dashzeveg 1989
BADL 63558 †	*Palaeogale sectoria*	–	–	–	–	4.60	2.78	6.11	2.75	2.31	1.75	Boyd & Welsh 2014
IVPP V 19325.1	*Palaeogale sectoria*	2.80	1.10	3.70	1.50	4.50	2.10	6.60	2.60	2.70	1.50	Wang & Zhang 2015
IVPP V 19325.2	*Palaeogale sectoria*	–	–	3.70	1.50	–	2.30	6.50	2.70	2.80	1.60	Wang & Zhang 2015
IVPP V 19326	*Palaeogale sectoria*	–	–	–	–	–	–	5.60	2.20	2.10	1.30	Wang & Zhang 2015
IVPP V 19327	*Palaeogale sectoria*	–	–	2.70	1.20	3.30	–	–	–	–	–	Wang & Zhang 2015
IVPP V 19329	*Palaeogale sectoria*	–	–	–	–	–	–	–	–	2.70	1.70	Wang & Zhang 2015
IVPP V 10528.1	*Palaeogale sectoria*	2.90	1.10	2.70	1.40	3.80	2.00	3.10	2.50	–	–	Wang & Zhang 2015
IVPP V 10528.2	*Palaeogale sectoria*	–	–	–	–	–	–	4.90	1.80	2.10	1.10	Wang & Zhang 2015
IVPP V 10528.3	*Palaeogale sectoria*	–	–	–	–	–	–	4.80	1.70	–	–	Wang & Zhang 2015
SMF M 5755 * †	*Palaeogale praehyaenoides*	4.00	2.00	4.60	2.20	5.60	2.80	7.10	3.20	–	–	Morlo 1996

because of the presence of the P1s, but it is on the smaller end of the body size distribution. However, the presence of the P1s has been shown to be a plastic character in this genus (Simpson 1946). Additionally, *P. sectoria* is traditionally known from the Oligocene while *P. minuta* is known from the Miocene (de Bonis 1981) further suggesting this specimen could be *P. sectoria*. However, this is called into question by the presence of *P. sectoria* in the Miocene of South Dakota (Harksen & MacDonald 1967) and reference to specimens of this species from the Eocene (Baskin & Tedford 1996; Boyd & Welsh 2014). The morphology of JODA 13221 also closely resembles a skull from the Oligocene White River Badlands of South Dakota (BADL 18581/SDSM 7118) which has also not been assigned to a specific species of *Palaeogale* (Benton *et al.* 2015). The teeth of JODA 13221 are not robust or large enough to be *P. hyaenoides* (Fejfar *et al.* 2003), or *P. praehyaenoides* (Morlo 1996). The skull clearly cannot belong to *Cryptailurus*, the other genus putatively in the Palaeogalidae, because the muzzle is narrow, P4 protocone is less developed, and the bullae are inflated and less flattened ventrally (Martin & Lim 2001).

Palaeogale dorothiae MacDonald, 1963
(Fig. 3; Table 2)

Referred specimens. — JODA 6177 left fragmentary dentary with p4-m1. JODA 5893 right fragmentary dentary with p2 and p4.

Occurrence. — JDNM-140, Lonerock, Gilliam County, Oregon, USA. Kimberly Member, John Day Formation. Precise locality information available to qualified researchers upon request.

Age. — Late Oligocene in the Late Arikareean (Ar3) NALMA, between the Tin Roof Tuff (25.3 Ma) and the UNSM JD-BC-3 tuff (23.5-23.8 Ma) (Fremd & Whistler 2009).

Species diagnosis. — The p4 is without a posterior accessory cusp and the protoconid of the m1 is not expanded laterally (MacDonald 1963).

Description

JODA 5893 has no posterior accessory cusp on p4; however, there is a small enamel anomaly on the posterior edge. There is an alveolus for p3. The p2 crown is stretched forward with an upturned posterior heel. JODA 6177 is broken behind the c, and there is no p2 alveoli. There is no p4 accessory cusp. The m1 protoconid is not expanded laterally. See Table 2 for measurements of both specimens.

Comparison

Both specimens match the species diagnosis in the absence of the p4 accessory cusp. They are both too large to be *P. minuta*. In JODA 5893, the morphology of the p4 is similar to *P. sectoria* (Lange-Badre & Dashzeveg 1989; Wang & Zhang 2015). The size of JODA 6177 is comparable to *P. sectoria* from Mongolia but the protoconid of the m1 is not expanded (Lange-Badre & Dashzeveg 1989; Wang & Zhang 2015). The type specimen is from the Sharps Formation of South Dakota which is 30-28.6 Ma (MacDonald 1963; McConnell & DiBenedetto 2012). Swisher (1982) states that this species is also known from the Brown Siltstone Beds or Whitney Member of the Brule Formation (*c.* 31-30 Ma) and the Unit B Member of the Gering Formation (28.26-28.11 Ma) both of Nebraska (Tedford *et al.* 1996, 2004). This makes the Lonerock specimens, which are between 25.3 and 23.8 Ma, the latest known occurrences of this species.

DISCUSSION

These specimens expand the geographic range of *Palaeogale* to include the Pacific Northwest of the United States. The mandibles of *P. dorothiae* also represent a temporal range

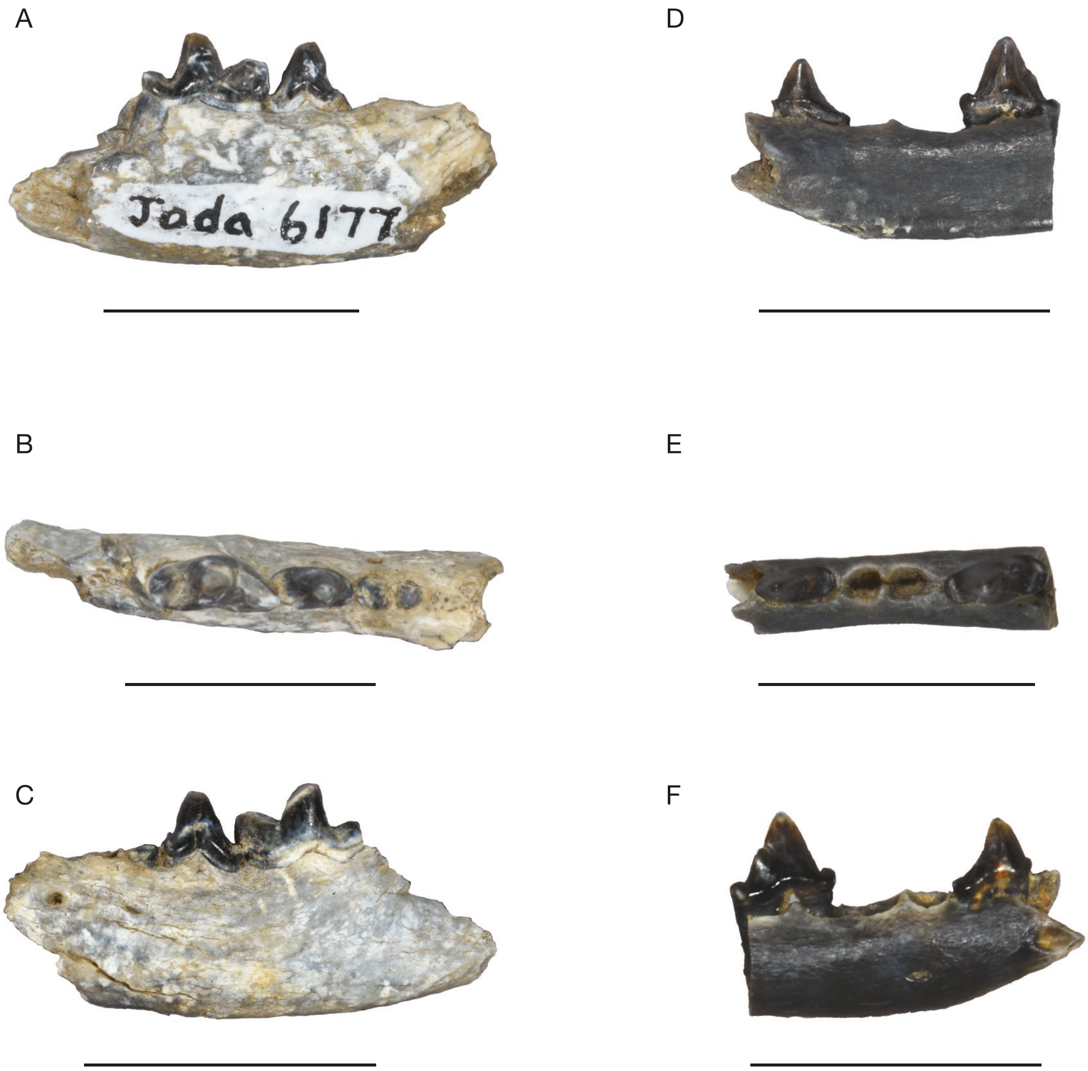

Fig. 3. — Dentaries of *Palaeogale dorothiae* MacDonald, 1963: **A**, lingual view (JODA 6177); **B**, occlusal view (JODA 6177); **C**, buccal view (JODA 6177); **D**, lingual view (JODA 5893); **E**, occlusal view (JODA 5893); **F**, buccal view (JODA 5893). Scale bars: 1 cm.

extension for the species. The youngest previously described individuals of *P. dorothiae* are from the Early Arikareean Gering Formation of Nebraska (Swisher 1982). Having now been reported from the John Day Formation, *Palaeogale* is known to be present in the Arikareean of the Pacific Northwest, the Great Plains (Simpson 1946; de Bonis 1981), and the Gulf Coast (Albright 1996; Hayes 2000). Notably, the genus has not yet been reported from the rich Arikareean faunas of southern California (Stock 1932; Deméré 1988). Whether this represents a genuine absence or a paucity of research is unclear, but reconstructing range shifts in *Palaeogale* is of considerable biogeographic interest. By the late Oligocene, *Palaeogale* had already spread into Asia (Dashzeveg 1996; Wang & Zhang 2015) and Europe (De Bonis 1981), meaning that the Oregon specimens were members of a genus with a Holarctic distribution. Any range extension of *Palaeogale* has the potential to shed light on what drove the remarkable expansion and eventual extinction of the genus.

While they represent a geographic and temporal range extension for *P. dorothiae*, these specimens may not be the youngest palaeogalids in the Pacific Northwest. Barrett *et al.* (2020) recently described *Cryptailurus* from the Hemingfordian NALMA of the Crooked River Basin in central Oregon. The Crooked River specimen was uncovered below the 16.22 Ma Hawk Rim Tuff, and this gap of up to 9 million years suggests that palaeogalids either persisted into the mid-Miocene in the region or recolonized it during or prior to the Hemingfordian. However, Barrett *et al.* (2020) suggest that the Palaeogalidae is polyphyletic. Therefore, a more expansive analysis of basal feliform relationships is necessary before any definitive conclusions can be drawn about the persistence in or migration to the Northwest by *Palaeogale* and its relatives.

While these specimens provide new insight into the geographic and temporal range of *Palaeogale*, much remains unclear about its biostratigraphic utility, its phylogenetic relationships, the timing of the dispersal events leading to its Holarctic distribution, or its ecological relationships to

Fig. 4. — Bivariate plot of anterior-posterior length (**APL**) and transverse width (**TW**) of *Palaeogale* carnassials: **A**, upper fourth premolar (P4); **B**, lower first molar (m1). Points are colour coded by species and labelled with their specimen numbers. All measurements are in mm and can be found in Tables 1 and 2.

other Oligo-Miocene organisms. The challenge of diagnosing species in the fossil record is not unique to *Palaeogale*, as species concepts can be difficult to apply to fossil taxa and morphological differences due to intraspecific variation, age, sex, and preservation can artificially inflate estimates of species diversity. Another John Day Formation mammal, the equid *Miohippus* Marsh, 1874, illustrates this difficulty: eight species of *Miohippus* had been described from the formation, but morphological variation was consistent with, at most, two species (Famoso 2017). *Palaeogale* has proven to be especially problematic taxonomically because species have historically been diagnosed based on size or age, rather than on dental or skeletal characters. Notably, size is used by Morlo (1996) as one of the primary traits differentiating *P. praehyaenoides* from other European species, while Baskin (1998) cites size as the sole trait distinguishing *P. sanguinarium* from *P. dorothiae*. This tendency to use size to distinguish between species has much deeper roots, though, as Simpson (1946) addresses it in his review of the genus. Given the prevalence of sexual dimorphism in many small carnivorans, he suggests that large and small coeval "species" are more likely to be males and females of a single species. Whether the size variation observed within *Palaeogale* is consistent with what would be expected in a sexually dimorphic carnivoran remains an unanswered question. The John Day specimens have been plotted alongside other specimens in Fig. 4. There is clear overlap is size between *P. dorothiae* and *P. sectoria* (Fig. 4). Simpson (1946) underscores a second problematic theme in *Palaeogale* systematics when he notes that two North American species recognized at the time, *Palaeogale lagophaga* Cope, 1873 and *Palaeogale infelix* Matthew, 1903 were differentiated only by geologic age, not by morphology. Without a more rigorous, character-based taxonomy of *Palaeogale* it is difficult to say whether such temporal distinctions are biologically valid or whether they arbitrarily split long-lived species. The skull described here illustrates the shortcomings of a taxonomy so dependent on age and body size. It is consistent in its size and age with *P. sectoria* and *P. minuta* and without clearly defined diagnostic traits it is impossible to assign it to either species.

The dearth of diagnostic traits characterizing *Palaeogale* species is compounded in specimens such as JODA 13221 that lack lower dentition. While several characters of the upper P4 and M1 are diagnostic for the genus *Palaeogale*, the four species recognized by de Bonis (1981) are differentiated solely on characters of their lower dentition. While some aspects of *Palaeogale* dentition are evidently highly variable (for example, the m2 is frequently absent in individuals of *P. dorothiae* and *P. sectoria*; de Bonis 1981), future geometric morphometric and phylogenetic analyses of palaeogalids would do much to clarify the true diversity of the family and to identify diagnostic traits. This in turn would facilitate analyses of many aspects of the paleobiology of these enigmatic and fascinating feliforms, notably their widespread dispersal across the Northern Hemisphere and their apparent strong convergence with mustelids.

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