Paludicola 14(3):110-121

NEW RECORDS OF EOCENE AND OLIGOCENE SQUAMATES FROM SOUTHWEST MONTANA

Donald Lofgren[1], Debra Hanneman[2], Anthony Runkel[3], Ping Fong[4], Gabriel Hong[4], Josephine Burdekin[4], Michael Chai[4], Yvonne Kan[4], Bailey Jorgensen[1]

[1]Raymond M. Alf Museum of Paleontology, Claremont, California
[2]Whitehall GeoGroup Inc., Whitehall, Montana
[3]Minnesota Geological Survey, Minneapolis, Minnesota
[4]The Webb Schools, Claremont, California

ABSTRACT

Recently recovered specimens from the Chadronian Pipestone Springs Main Pocket (PSMP), Whitneyan strata in the Gravelly Range, and Uintan rocks in the Sage Creek area significantly increase the diversity of squamates known from the Tertiary depositional basins of southwest Montana. At PSMP, most common are the glyptosaurine lizard *Helodermoides tuberculatus* which represents over 60% of dentigerous lizard elements and the boid snake *Calamagras* which is represented by forty-four vertebrae. Four varanid elements, a specimen tentatively referred to the glyptosaurine *Peltosaurus*, and *Calamagras* from PSMP are their first documented occurrences in the Tertiary depositional basins of southwest Montana, as is a miniscule dentary fragment that represents an iguanid smaller than *Aciprion formosum*. A skull of *A. formosum* from the Gravelly Range is the first record of the species from Montana and its first confirmed occurrence from Whitneyan strata. Fragmentary elements from the Uintan Dell beds in the Sage Creek depositional basin indicate the presence of a glyptosaurine and an indeterminate iguanid. These new records of Eocene and Oligocene squamates from Montana are important additions to the temporal and/or paleogeographic ranges of *Calamagras*, *Aciprion formosum*, varanids, and perhaps *Peltosaurus*.

INTRODUCTION

The middle Chadronian Pipestone Springs Main Pocket locality (PSMP) in the Jefferson depositional basin of southwest Montana, is one of the richest late Eocene vertebrate sites in North America and is most notable for yielding a large number of small-bodied mammals, including over 20 holotypes, and mammalian coprolites (Tabrum et al. 1996, 2001; Lofgren et al. 2017). Hundreds of mammalian fossils from other Tertiary depositional basins in southwest Montana have also been described or compiled in faunal lists (Tabrum et al. 1996, 2001; and references therein), but non-mammalian vertebrates from these basins have received less attention. At PSMP, the glyptosaurine *Helodermodies tuberculatus* was described by Douglass (1903) and the presence of both lizards and tortoises was noted by Matthew (1903). Later reports of squamates from PSMP are limited to Kay et al. (1958) who noted the presence of the glyptosaurine *Peltosaurus* and Sullivan (1979) who described additional specimens of *Helodermodies tuberculatus*. Additional squamates reported from other southwest Montana Tertiary depositional basins included "*Ogmophis*" *arenarum* (Barstovian, Flint Creek; Douglass 1903), *Dryinoides oxyrhynchus* (Barstovian, Madison Valley; Auffenberg 1958), "*Glyptosaurus montanus*" (Chadronian, McCartys Mountain; Douglass 1908), and *Calamagras murivorus*, "*Ogmophis*" *arenarum*, "*Glyptosaurus* cf. *montanus*," and *Peltosaurus* (Chadronian-Arikareean, Canyon Ferry; Kay et al. 1958). Here, we describe specimens collected in the past two decades that significantly increase the diversity of squamates known from the Tertiary depositional basins of southwest Montana, including the first record of snakes and varanid lizards from PSMP, a skull of the iguanid *Aciprion formosum* from the Gravelly Range, and fragmentary lizard remains from the Sage Creek depositional basin.

Description of squamates collected since 2003 by RAM crews from PSMP are the main focus of this paper. Recent efforts to recover Tertiary mammalian fossils from the Gravelly Range (Lofgren et al. 2020) and Sage Creek depositional basins (Lofgren et al. in preparation) yielded additional lizard specimens which are included here following the description of the material from PSMP.

Institutional Abbreviations. AMNH, American Museum of Natural History, New York, New York; **CIT,** California Institute of Technology, Pasadena, California (collections now housed at the Natural History Museum of Los Angeles County, Los Angeles, California); **CM**, Carnegie Museum of Natural History, Pittsburgh, Pennsylvania; **LACM**, Natural History Museum of Los Angeles County, Los Angeles, California; **PU**, Princeton University, Princeton, New Jersey (collections now housed at the Yale Peabody Museum, New Haven, Connecticut); **RAM**, Raymond M. Alf Museum of Paleontology, Claremont, California; **USNM**, United States National Museum of Natural History, Washington D.C.

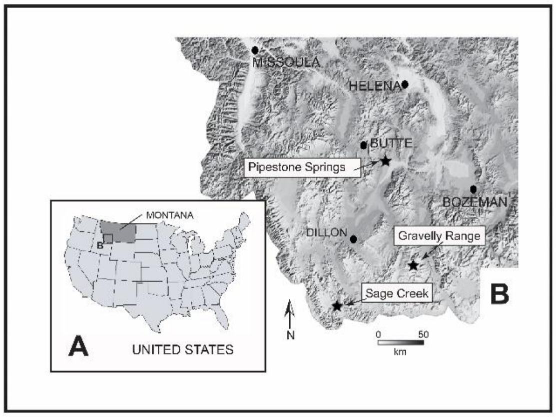

FIGURE 1. Study area location maps. A. Location of study area within the United States and Montana. B. Digital relief image of southwest Montana that includes major cities and the three areas from which taxa were described; Pipestone Springs Main Pocket (PSMP), Gravelly Range, and Sage Creek depositional basin (sourced from the Montana State Library, Natural Resources Information System, 2001 data bank).

PIPESTONE SPRINGS MAIN POCKET

Late Eocene clastic continental strata and pyroclastic rocks at Pipestone Springs, Montana, occur on the west flank of the informally named Whitehall depositional basin. This depositional basin is present within the northern part of the Jefferson Valley (Figure 1), where Cenozoic basin-fill is approximately 760 m thick (Hanneman 1989; Hanneman and Wideman 1991). Contained within a 55 m section of basin-margin strata is Pipestone Springs Main Pocket (PSMP), a middle Chadronian vertebrate locality known for its diverse assemblage of mammals and mammalian coprolites (Tabrum et al. 1996, 2001; Tabrum and Metais 2007; Lofgren et al. 2017). These strata are part of the informal Sequence 2 of Hanneman and Wideman (1991, 2006) and a lithostratigraphic proxy, the Renova Formation, of Kuenzi and Fields (1971). Strata at PSMP represent air-fall ash, slightly reworked air-fall ash, and loessite deposition with the uppermost 15 m of strata yielding the PSMP vertebrate assemblage (Hanneman et al. 2022). Felsic tuffs occur within the basal to upper part of the Pipestone Springs section and have $^{40}Ar/^{39}Ar$ single crystal sanidine ages of 37.50 $\pm$ 0.02 Ma and 36.00 $\pm$ 0.20 Ma, with strata containing PSMP directly overlying the younger felsic tuff. These isotopic age constraints significantly increase the age range of Pipestone Springs strata to include latest Duchesnean-early Chadronian deposits and add additional support that the PSMP vertebrate assemblage is age-correlative to the Chadronian part of the Flagstaff Rim section in central Wyoming (Hanneman et al. 2022).

Post-depositional erosion dissected strata at PSMP resulting in development of a 100 m wide gully separating the two main stratal accumulations which historically have been labeled as distinct localities, Main Pocket or North Section, and South Pocket or South Section (Kay et al. 1958; Garcia 1992; Tabrum et al. 1996). In keeping with the stratal separation, vertebrate fossils from the two sections were curated separately. Middle Chadronian assemblages from both sections were referred to as the Pipestone Spring Main Pocket (PSMP) assemblage (Lofgren et al. 2017), and the two sites (RAM localities V2003001 and V2003022) are demonstrably stratigraphically correlative (Hanneman et al. 2022). At PSMP, all squamate specimens were recovered on the outcrop surface as isolated elements, except for articulated and associated vertebrae of *Calamagras*.

Order Squamata Merrem 1820
Family Anguidae Gray 1825
Subfamily Glyptosaurinae McDowell and Bogert 1954
Tribe Glyptosaurini Sullivan 1979
Helodermoides Douglass 1903
Helodermoides tuberculatus Douglass 1903
Figure 2A-F

Glyptosaurus montanus Douglass 1908
Glyptosaurus tuberculatus Gilmore 1928
Glyptosaurus giganteus Gilmore 1928

Holotype—CM 707 nearly complete left frontal and anterior part of right frontal, anterior part of left dentary, and skull fragments with osteoderms, PSMP, Montana (Douglass 1903, fig. 10a-b).

Referred Specimens—Caudal vertebrae: RAM 23905-06, RAM 23908-11, RAM 23921-23, RAM 23925-27, RAM 23932-33, RAM 23939, RAM 23941; Sacral vertebrae: RAM 23928-31; Dorsal vertebrae: RAM 23913-18, RAM 23920; Maxillae: RAM 17815 (edentulous), RAM 17813 (right), RAM 17818 (left); Dentaries: RAM 17816 (left), RAM 23900 (right); RAM 26219 (left), RAM 23901 (left), RAM 23902 (left); Skull Fragment: RAM 17817; Osteoderms: RAM 25816, RAM 23942-48, RAM 23950-57.v

Description-Discussion — *Helodermoides tuberculatus* is the best known glyptosaurin (Sullivan 2019) and its holotype (CM 707) was recovered from PSMP (Douglass 1903). Soon thereafter, Douglass (1908) described "*Glyptosaurus? montanus*" based on a partial skull from McCartys Mountain, another Chadronian site about 70 km south of PSMP. Two decades later, Gilmore (1928) synonymized

Helodermoides with *Glyptosaurus* (CM 707 became *Glyptosaurus tuberculatus*) and erected "*Glyptosaurus giganteus*" based on a frontal from Chadronian strata in Nebraska. Later, Sullivan (1979) resurrected *Helodermoides* and included "*Glyptosaurus giganteus*" and "*G. montanus*" within *Helodermoides tuberculatus*, because additional specimens of *H. tuberculatus* included the variation in cephalic osteoderms and body size that was the basis of the diagnosis of the other two species. Some characteristics diagnostic for *Helodermoides* are cephalic osteoderms bulbous with numerous tubercles, teeth subconical with posterior ones slightly recurved, maxilla straight, and dentary moderately slender (Sullivan 1979), features evident in RAM specimens recovered since 2003. Since PSMP is the type locality of *H. tuberculatus* (Douglass 1903) there is little doubt that the RAM specimens represent this taxon. However, Smith (2006) referred a glyptosaurine parietal fragment from Chadronian strata in North Dakota to *Helodermoides* sp. nov.? because of variation demonstrated in the closure of the supratemporal fenestra, a feature diagnostic of *H. tuberculatus* (Sullivan 1979). Thus, there may be greater specific diversity within the sample of *Helodermoides* in North America.

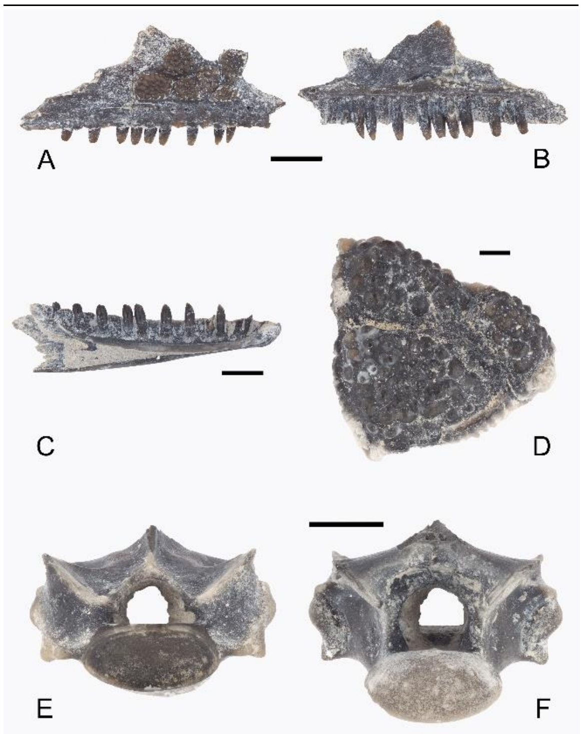

FIGURE 2. *Helodermoides tuberculatus* from PSMP. RAM 17818, left maxilla, A) labial view and B) lingual view (scale bar equals 5 mm). RAM 26219, left dentary C) lingual view (scale bar equals 5 mm). RAM 25816, osteoderm D) dorsal view (scale bar equals 1 mm). RAM 23916, dorsal vertebra E) anterior view, F) posterior view (scale bar equals 3 mm).

The most complete RAM elements of *Helodermoides tuberculatus* from PSMP are a maxilla with tuberculate osteoderms (Figure 2A-B) and a nearly complete dentary (Figure 2C). Osteoderms of *H. tuberculatus* are the most common vertebrate elements found at PSMP and are usually well preserved (Figure 2D). Many dorsal, sacral, and caudal vertebrae about the expected size of *H. tuberculatus* were also recovered (Figure 2E-F) and caudals were the most numerous. Limb elements of *H. tuberculatus* were not confidently identified. Based on dentigerous elements in the RAM collections, those of *H. tuberculatus* comprise about 60% of lizard remains recovered from PSMP.

Helodermoides tuberculatus is known from other Chadronian sites in Montana, South Dakota, Colorado, Nebraska, and Wyoming (Douglass 1908; Gilmore 1928; Sullivan 1979, 2019; Maddox and Wall 1998), with a few occurrences in Orellan strata in Nebraska and Wyoming (Gilmore 1938a; Sullivan and Holman 1996), although the Orellan occurrences may actually be from latest Chadronian strata (Sullivan 2019). If indeed restricted to the Chadronian, *H. tuberculatus* would be an excellent index fossil as it is relatively widespread and is commonly found at sites that also yield mammals, like PSMP. If there is an additional species of *Helodermoides* in North America (see Smith 2006), the biostratigraphic utility of *H. tuberculatus* would require revaluation.

Tribe Melanosaurini Sullivan 1979
Peltosaurus? Cope 1873b
Figure 3A-B

Referred Specimen—RAM 17844 right maxilla with nine tooth positions, six of which are occupied.

Description-Discussion—RAM 17844 has four complete pleurodont teeth and two others with slight basal damage (Figure 3A-B). Teeth are hollow and transversely compressed with wedged shaped apices, and expansions along the base of each tooth do not exhibit striations. RAM 17844 is questionably referred to *Peltosaurus* based on its transversely compressed teeth with wedge shaped crowns. Based on size, RAM 18744 is within the range of variation expected for *Peltosaurus* as six teeth occupy a space of 6.1 mm, and in the holotype of *P. granulosus* (AMNH 1610) six teeth occupy a space of 7.8 mm (Gilmore 1928), a difference of 22%.

Peltosaurus has a broad temporal and geographic distribution in North America as occurrences have been reported from Saskatchewan and the Rocky Mountain and Great Plains states south to Texas, Florida and California, in strata that range from Eocene to the early Miocene (Gilmore 1928, 1942; White 1942; Holman 1976; Golz and Lillegraven

1977; Albright 1994; Sullivan and Holman 1996; Maddox and Wall 1998; Smith 2006). However, Estes (1983) followed Meszoely (1970) by noting that only Oligocene specimens from Colorado, Nebraska, Wyoming, and South Dakota were properly referred to *Peltosaurus*. Later, Sullivan and Holman (1996) noted that putative Miocene and pre-Oligocene occurrences were misidentified and that *Peltosaurus* was restricted with certainty to Orellan-early Arikareean strata in North America. More recently, Scarpetta (2019) documented *Peltosaurus granulosus* from the early Arikareean of South Dakota. If confirmed, the PSMP occurrence would extend the temporal range of *Peltosaurus* to Chadronian strata and its paleogeographic range to southwest Montana.

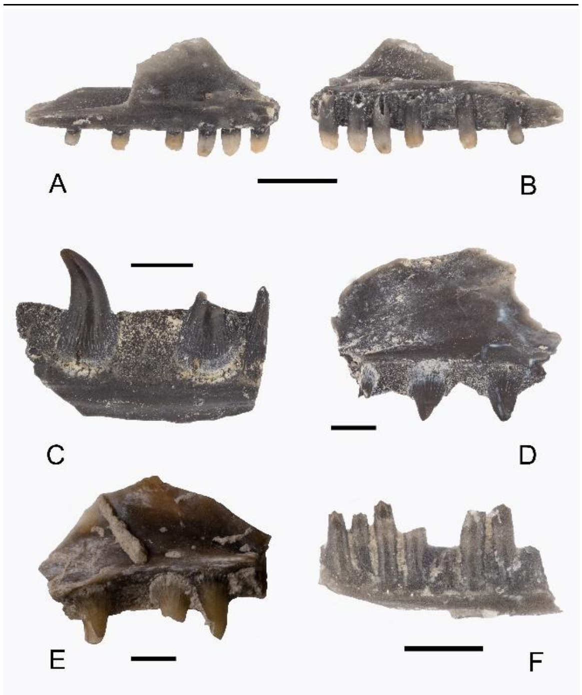

FIGURE 3. Various squamate taxa from PSMP. RAM 17844, right maxilla of *Peltosaurus*? A) labial view, B) lingual view (scale bar equals 3 mm). RAM 17845, left dentary fragment of Varanidae genus indeterminate C) lingual view (scale bar equals 3 mm). RAM 26220, maxilla fragment of Varanidae genus indeterminate D) lingual view (scale bar equals 3 mm). E) RAM 27764, maxilla fragment of Varanidae genus indeterminate, lingual view (scale bar equals 3 mm). RAM 23904, dentary fragment of unidentified iguanid (scale bar equals 1 mm).

Family Varanidae Gray 1827
Genus indeterminate
Figure 3C-E

Referred Specimens—RAM 17845 left dentary fragment with a complete tooth, another missing its crown, and the base of a third, RAM 26220 maxilla fragment with two complete teeth and a fragment of a third, RAM 23903 dentary fragment with the bases of two teeth, RAM 27764 maxilla fragment with a complete tooth, another lacking the crown apex, and a third with the basal half of the crown.

Description-Discussion—These four fragmentary dentaries and maxillae were not found in association. Of the two dentaries RAM 17845 has the only complete tooth which is 4.6 mm in height and has a prominent recurved crown (Figure 3C). The base of this tooth and the broken teeth in both RAM 17845 and RAM 23903 are expanded and strongly striated and have a single lingual basal foramen located equal or slightly distal to the anteroposterior mid-point of each tooth. Tooth bases in both specimens are 3 mm in diameter, as are spaces between teeth (Figure 3C). The striated part of the complete tooth in RAM 17845 is less than half the height of the crown.

RAM 26220 is a maxilla fragment with two complete conical teeth that are 3.8 mm in height (Figure 3D). Both teeth have broad striated bases that are 2.7 mm in diameter, with the striated part of each tooth exceeding half of its height. A single lingual basal foramen is located equal to the anteroposterior mid-point of both teeth in RAM 26220 and spaces between teeth are 3 mm (Figure 3D). Features of the teeth in RAM 27764 are similar to those in RAM 26220 except for size. In RAM 27764, the one complete conical tooth is 3.4 mm in height, tooth bases are all 2.2 mm in diameter, and the space between teeth is 2.3 mm (Figure 3E).

The four varanid specimens from PSMP are similar in size and morphology and probably represent a single species, which represents the only known record of varanids from the Tertiary depositional basins of southwest Montana. Varanid taxonomy is often based on vertebrae (Gilmore 1928; Brattstrom 1955; Estes 1983) and a varanid vertebra has not been identified from the RAM collections. Varanid specimens referred to *Saniwa* are known from Wasatchian to Unitan strata in California, Colorado, New Mexico, North Dakota, Utah, and Wyoming (Gilmore 1928; Jepsen 1963; Golz and Lillegraven 1977; Estes 1983; Sullivan and Lucas 1988; Stucky et al. 1996; Sullivan and Holman 1996), but the only reported occurrence in Chadronian strata is *S. edura* from the Chadron Formation of North Dakota (Smith 2006). Thus, the fragmentary RAM specimens constitute a second Chadronian occurrence of varanids. Prior to description of *S. edura*, *Saniwa* was represented by eight species, but only *S. ensidens* was adequately known (Sullivan and Holman 1996). A comparison based on size indicated that *S. edura* was larger than *S. ensidens* as three dentary teeth in the holotype of *S. edura* occupy 12 mm (Smith 2006) and three teeth in the dentary of the holotype of *S. ensidens* occupy 11 mm (Gilmore 1928). In RAM 17845, a dentary with spaces between teeth, two teeth and the space between occupy less than 10 mm. Thus, if the RAM specimens represent *Saniwa*, they appear to be more similar in size to *S. ensidens*. In any case, these PSMP specimens are important additions to the record of varanids in North America based on their location and age.

Family Iguanidae Oppel 1811 sensu Torres-Carvajal et al. 2020
Genus indeterminate
Figure 3F

Referred Specimen—RAM 23904, dentary fragment with four complete teeth, two with damaged crowns, and another with the tooth base.

Description/Discussion—An iguanid affinity of RAM 23904 is suggested by the relatively low tricuspid crowns on the four complete teeth where the lateral denticles are distinctly set apart from a larger median cusp (Figure 3F). The tallest complete tooth has a height of 1.2 mm. Antero-posteriorly, the seven teeth of RAM 23904 occupy a space of 2 mm. If that tooth to length ratio is scaled to 5 mm, the space would occupy approximately 17-18 teeth. Thus, RAM 23904 represents an unidentified iguanid smaller than *Aciprion formosum*, because the number of teeth occupied by 5 mm in *A. formosum* varies from 8-12 (Table 1).

Serpentes Linnaeus 1758
Constrictores *incertae sedis* sensu Smith and Georgalis 2022
Calamagras sp. indeterminate
Figure 4A-F

Genotype—AMNH 1603, six articulated trunk vertebrae, Cedar Creek Locality, White River Formation, Colorado (Gilmore 1938b, fig. 14).

Referred Specimens—RAM 23786-88, 23791-92, 23794-98, 23800-01, 23803-07, 23958-63, 23965-66, 25732-34 middle trunk vertebrae (MTV), RAM 23789 nine associated MTV, RAM 23802 two associated MTV, RAM 23964 two associated MTV, RAM 23799 anterior trunk vertebra articulated with two MTV; identification of vertebral regions follows Laduke (2019).

Description-Discussion—The sample of snake vertebrae from PSMP consists of 28 isolated MTV, and one anterior and 15 additional MTV based on articulated and associated occurrences (RAM 23802, RAM 23789, RAM 23964, RAM 23799) that likely represents a single species based on the similarity in size and morphology of the MTV. Exemplified by the two in RAM 23799 (Figure 4A-F), PSMP MTV share these features: hemal keel present, centrum short, thick and short neural spine occupying less than half of length of vaulted neural arch, neural canal smaller than cotyle, zygosphene wider than cotyle, zygosphenal articular facets steeply inclined, prezygapophyseal articular facets slightly inclined, and prezygapophyseal accessory process absent. RAM 23799 also preserves the terminal anterior trunk vertebra which has a narrow and well developed hypapophysis that occupies half the length of the hemal keel, with a vertical face on the posterior end of the hypapophysis that diminishes in height anteriorly to merge with the hemal keel (Figure 4A, C-D). These vertebral features align with the diagnosis of *Calamagras* and its genotypic species *C. murivorus* established by Gilmore (1938b) and modified by Holman (2000). In comparison to trunk vertebrae referred to *C. murivorus*, *C. angulatus* is relatively larger, has a shorter hemal keel, and a less vaulted neural arch, *C. floridanus* has a sharper hemal keel, *C. platyspondyla* has a more depressed vertebral form and wider hemal keel, and *C weigeli* apparently has a relatively wider hemal keel (Sullivan and Holman 1996; Holman 2000).

TABLE 1. Measurements in mm of the dentaries and skull of RAM 25624 from the Gravelly Range compared to two skulls with dentaries and a dentary of *Aciprion formosum*, USNM 16566 (Gilmore 1941), LACM 4893 (CIT uncatalogued in Brattstrom 1958) and PU 10015 (Gilmore 1928) from the Brule Formation of Colorado and Wyoming.

	RAM 25624	USNM 16566	PU 10015	LACM 4893
Length of dental border of dentary	9.6	—	11.5	—
Number of dentary teeth in 5 mm	12.0	10.5	9.0	8.0
Length of dental border of maxillary	10.0	12.4	—	12.9
Depth of dentary	1.9	2.2	3.0	2.8
Greatest length of ramus	18.1	—	27.3	27.6
Greatest width of skull across jugals	11.4	14.6	—	—
Length of nasal	3.6	3.6	—	—
Length of frontal	7.2	7.0	—	—

The sample of *Calamagras* MTV from PSMP is large but smaller than the 88 vertebrae of *C. weigeli* from Medicine Pole Hills in North Dakota described

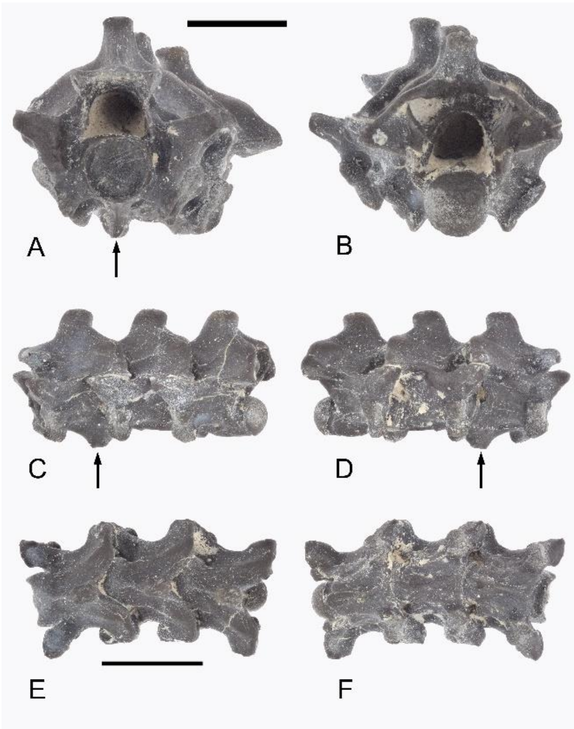

FIGURE 4. RAM 23799 three articulated vertebrae (terminal anterior trunk and two anterior MTV) of *Calamagras* sp. indeterminate from PSMP. A) anterior view, B) posterior view (scale bar equals 3 mm); C) left lateral view, D) right lateral view, E) dorsal view, F) ventral view (scale bar equals 5 mm). Location of hypapophysis noted by arrows.

by Smith (2013) and the three articulated skeletons of "*Ogmophis*" and/or *Calamagras* from Wyoming described by Breithaupt and Duvall (1986); the assertion that "*Ogmophis*" and *Calamagras* may represent a single taxon (Rage 1984; Sullivan and Holman 1996) was documented by Caldwell et al. (2007; but see Smith 2013, Smith and Georgalis 2022). The sample of MTV of *C. weigeli* from Medicine Pole Hills exhibit elongation of the MTV based on the centrum length (CL)/neural arch width (NAW) ratio, which if ≥ 1.1 aligns with extant dwarf boas (Ungaliophiinae) (Smith 2013). This ratio is 1.1 for the holotypes of *C. murivorus* and *C. angulatus* and the sample of *C. weigeli* from Medicine Pole Hills, while the same ratio for "*C. talpivorus*" is .92, suggesting the latter is not in the same clade (Smith 2013); "*C. talpivorus*" was synonymized with *C. murivorus* by Sullivan and Holman (1996). The CL/NAW ratio of only 20 MTV from PSMP could be determined because many specimens had a damaged neural arch and/or centrum. Ratios varied from .85 to 1.1, with five having a ratio of 1.1. Thus, the taxonomic affinity of MTVs from PSMP is unclear because 75% of CL/NAW ratios apparently align with "*C. talpivorus*" and 25% with *C. murivorus*, *C. angulatus*, or *C. weigeli*. This is not surprising because the utility of using trunk vertebrae to identify a species of Tertiary snake can be problematic (Smith 2013; Smith and Georgios 2022) and study of the entire vertebral column along with cranial elements is most effective (Smith 2013). Detailed study of the snake skeletons from Wyoming referred to *Calamagras* and "*Ogmophis*" (Breithhaupt and, Duvall 1986) should aid in elucidating the systematic affinity of MTV previously referred to *Calamagras* (Smith and Georgalis 2022). Until those results become available, we refer the vertebrae from PSMP to *Calamagras* sp. indeterminate.

Calamagras weigeli is known from Chadronian strata in North Dakota (Smith 2013) and Saskatchewan (Holman 1972). The presence of *Calamagras* sp. indeterminate at PSMP is an additional Chadronian occurrence and the first documented record of *Calamagras* from the Tertiary depositional basins of southwest Montana.

Considering that 44 vertebrae of *Calamagras* were collected at PSMP by RAM crews since 2003, it is surprising that there were no prior reports of snakes because the site has been prospected numerous times since the early 1900s. Thus, it is likely other collections from PSMP contain unreported snake vertebrae.

GRAVELLY RANGE

Tertiary strata that yield vertebrate fossils are exposed at high elevation (approximately 3,000 m) in the south-central part of the Gravelly Range (Figure 1). These rocks are also part of the informal Sequence 2 of Hanneman and Wideman (1991, 2006). Uintan to Whitneyan vertebrates were recovered from these strata (Gutmann et al. 1989; Luikart 1997; Wahlert et al. 2006; Lofgren et al. 2020). Extrusive volcanics interbedded with fossil bearing strata provide age constraints on the Whitneyan vertebrate assemblage at Lion Mountain (Gutmann et al. 1989; Lofgren et al. 2020). The section exposed at Lion Mountain is approximately 270 m thick and is comprised of channel, floodplain, and loessite deposits (Lofgren et al. 2020, fig. 2). The uppermost 20 m of the Lion Mountain section yields well preserved Whitneyan mammals referred to as the Lion Mountain High assemblage, whose strata are capped by a 25 m thick basalt that has a K-Ar age of 30.8 ± 0.7 Ma (Gutmann et al. 1989; Lofgren et al. 2020). A tuff exposed on the east side of Lion Mountain is stratigraphically below the position of the Lion Mountain High assemblage and has a sanidine single crystal ^{40}Ar/^{39}Ar age of 31.7 ± 0.02 Ma (Lofgren et al. 2020, fig. 2). The lizard skull described here (RAM 25624) was recovered in situ from Lion Mountain High (RAM locality V2018039) in 2018.

Family Iguanidae Oppel 1811 sensu Torres-Carvajal et al 2020
Aciprion Cope 1873a
Aciprion formosum Cope 1873a
Figure 5A-D, Table 1

Aciprion majus Gilmore 1928

Holotype—AMNH 1609 nearly complete dentary with seven teeth, Oreodon Beds (Oligocene), White River Formation, Colorado (Cope 1873a; Gilmore 1928, pl. 20, fig. 10-10a).

Referred Specimen—RAM 25624, partial skull with articulated mandibles.

Description—RAM 25624 is a nearly complete skull and sutures between skull elements are visible (Figure 5A-C). Because the rear of RAM 25624 was eroded prior to discovery, the skull lacks the parietal, squamosals, paroccipitals, and the left postorbital and quadrate. Also, the left mandible is missing most of the angular and surangular. About 20 teeth are visible in both the left and right maxillary, and anterior maxilla and dentary teeth are small and unicuspid, while posterior teeth are larger and tricuspid (Figure 5A, D). Several anterior teeth are missing in both the lower and upper dentition, but nearly all posterior teeth are present. Dentary teeth are difficult to count and only 15 are evident on each mandible because posterior dentary teeth are obscured by maxillary teeth (Figure 5D). Maxillary teeth are higher crowned than the dentary teeth that can be seen. Selected measurements of the skull and dentary of RAM 25624 are given in Table 1.

Discussion—Cope (1873a) briefly described *Aciprion formosum* based on a dentary (AMNH 1609) and Gilmore (1928) described a second dentary of *A. formosum* (USNM 10962) and also erected *A. majus* based on PU 10015, a dentary whose teeth were larger than those of *A. formosum*. The cranial anatomy of *A. formosum* was later described and illustrated by Gilmore (1941, fig. 30-31) based on a nearly complete skull (USNM 16566). Later, Brattstrom (1958) referred an uncatalogued CIT skull with mandible (now LACM 4893) to *A. formosum* and concluded that size differences separating *A. formosum* and *A. majus* were insignificant and proposed the synonymy of the species, an opinion shared by Estes (1983).

RAM 25624 compares closely with USNM 16566. The nasals and frontals of RAM 25624 and USNM 16566 are nearly equal in length, while the latter is wider across the jugals (Table 1). The transition from unicuspid to tricuspid crowns is also similar in RAM 25624 and USNM 16566 and the teeth of each are similarly spaced in both the maxillaries and dentaries. Estes (1983) noted that *A. formosum* had approximately 20 maxillary teeth and Gilmore (1941) listed 20 for USNM 16566. RAM 25624 has about 20. The dentaries of RAM 25624 are slightly smaller than most known dentaries of *Aciprion formosum* (Table 1), but size differences like this were not considered significant concerning *Aciprion* (e.g. Brattstrom 1958; Estes 1983).

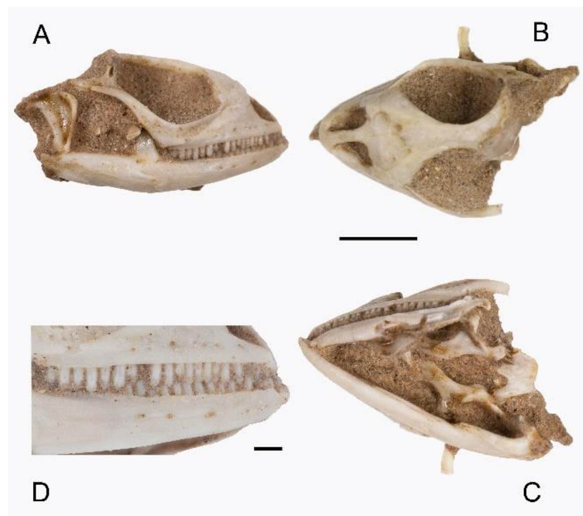

FIGURE 5. RAM 25624 skull and mandibles of *Aciprion formosum* from the Gravelly Range. A) labial view, B) dorsal view, C) ventral view (scale bar equals 5 mm), and D) labial view of right dentition (scale bar equals 1 mm).

In RAM 25624, maxillary teeth are higher crowned than dentary teeth (Figure 5D). In labial view, dentary teeth appear to be higher crowned than maxillary teeth in both USNM 16566 and PU 10015 (see Gilmore 1928, plate XX, fig. 11 and Gilmore 1941, fig. 31). *Cypressaurus* is a Chadronian iguanid known from Saskatchewan and North Dakota whose maxillary and dentary teeth are high crowned (Holman 1972; Smith 2006, 2011) which differs from *Aciprion* in having higher crowned and much less closely spaced teeth (Holman 1972). RAM 25624 differs from *Cypressaurus* because only its maxillary teeth are high crowned and dentary/maxillary teeth are closely spaced. However, the crown height of the maxillary teeth in RAM 25624 apparently differs from known specimens of *Aciprion formosum* and thus could have considerable taxonomic import.

Aciprion formosum is known from Orellan rocks in Colorado, Wyoming, and Nebraska (Cope 1873a; Gilmore 1928, 1941; Brattstrom 1958; Sullivan and Holman 1996) and has been tentatively identified from Whitneyan strata in Colorado (Holman 1989) and Chadronian rocks in North Dakota (Smith 2006).

Thus, RAM 25624 represents the first record of *A. formosum* from Montana and the first confirmed specimen recovered from Whitneyan strata.

SAGE CREEK DEPOSITIONAL BASIN

Eocene strata that yield vertebrate fossils in the Sage Creek depositional basin (Figure 1) comprise the earliest record of sedimentation in southwest Montana after Sevier-Laramide compression ended (Hanneman and Wideman 1991). The Sage Creek Formation of Wood (1934) is Bridgerian and is unconformably overlain by the Uintan-age Dell beds (Tabrum et al. 1996, 2001; Robinson et al. 2004; Schwartz and Graham 2017), an informal unit introduced by Fields et al. (1985). Both stratigraphic units are part of Sequence 1 of Hanneman and Wideman (1991, 2006). The unconformity between the Sage Creek Formation and the Dell beds is estimated at three million years or less based on geochronology and vertebrate fossils (Schwartz and Graham 2017). Early studies of mammalian fossils from the Sage Creek Formation and Dell beds (Douglass 1903, Wood 1934, Hough 1955, 1958) were supplemented by the efforts of Alan Tabrum, culminating in recognition of an early Bridgerian and a middle-late Bridgerian fauna in the Sage Creek Formation and two late Uintan assemblages from the Dell beds, the Douglass Draw and Hough Draw local faunas (Tabrum et al. 1996, 2001). Fragmentary lizard specimens were recovered from the Dell beds in 2020-21 from RAM localities V2018034 (screen washing sample) and V2020006 (surface sample) in strata equivalent to those that yielded the Hough Draw local fauna.

Family Anguidae Gray 1825
Glyptosaurin indeterminate
Figure 6A-E

Referred Specimens—RAM 28101 partial left frontal, RAM 28559 partial parietal, both from RAM locality 2020006; RAM 28549, RAM 28552, RAM 28577, RAM 28088, RAM 28550, RAM 28098, RAM 28554 osteoderms, all from RAM locality V2018034.

Discussion—RAM 28101 appears to be broken along the median suture, which connects the left and right frontal and osteoderms present are subequal, hexagonal, and arranged in a concentric ring pattern (Figure 6A-B). Parietal osteoderms of RAM 28559 are more rounded, smaller, and less distinctly hexagonal and protrude higher above the surface of the skull in comparison to the osteoderms of RAM 28101 (Figure 6C-D), differences that might be taxonomically significant. Hexagonal shaped skull osteoderms are a feature of glyptosaurines, a lizard clade poorly known from Uintan strata (Sullivan 1979, 2019). RAM 28088 (Figure 6E) and other glyptosaurine osteoderms were generated by screen washing sediments of the Dell beds. These osteoderms and the skull fragments demonstrate that glyptosaurines are present in the late Uintan Dell beds. Recovery of more complete specimens would be a significant addition to glyptosaurine taxonomy.

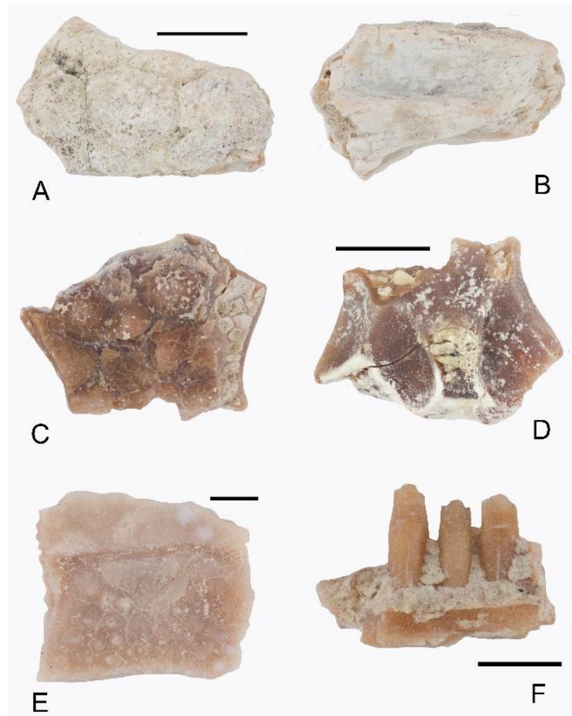

FIGURE 6. Lizards from RAM localities V2020006 and V2018034, Dell beds, Sage Creek depositional basin. RAM 28101 left frontal of unidentified glyptosaurine A) dorsal view, B) ventral view (scale bar equals 5 mm). RAM 28559 parietal of unidentified glyptosaurine C) dorsal view, D) ventral view (scale bar equals 5 mm). RAM 28088 glyptosaurine osteoderm E) dorsal view (scale bar equals 1 mm). RAM 28087 tooth bearing fragment of indeterminate iguanid F) lingual view (scale bar equals 1 mm).

Family Iguanidae Oppel 1811 sensu Torres-Carvajal et al 2020
Iguanid genus indeterminate
Figure 6F

Referred Specimen—RAM 28087 dentary fragment with three complete teeth from RAM locality 2018034.

Discussion—Tricuspid teeth of RAM 28087 (Figure 6F) suggest an iguanid affinity.

Squamata indeterminate

Referred Specimens—RAM 28551 dentary fragment with broken tooth, RAM 28666 dentary fragment with three partial teeth, RAM 28553 dentary fragment with two damaged teeth, all from RAM locality V2018034; RAM 28565 vertebra fragment from RAM locality V2020006.

Discussion—These specimens are too fragmentary to be identified to family.

DISCUSSION AND SUMMARY

Specimens recovered from the Gravelly Range, Sage Creek depositional basin, and PSMP over the past two decades significantly increase the diversity of squamates known from the Tertiary depositional basins of southwest Montana. Including these new records, squamates listed by ascending North American Land Mammal Age from these basins are:

Sage Creek Depositional Basin (Uintan)
Glyptosaurin indeterminate
Iguanidae genus indeterminate
Squamata indeterminate

Pipestone Spring Main Pocket, Jefferson Depositional Basin (Chadronian)
Helodermodies tuberculatus (also known from Chadronian sites McCarty's Mountain and Little Pipestone Creek; Douglass 1903, 1908; Sullivan 1979).
Calamagras sp. indeterminate
Peltosaurus?
Varanidae genus indeterminate
Iguanid genus indeterminate

Gravelly Range (Whitneyan)
Aciprion formosum

Barstovian of southwest Montana
"*Ogmophis*" *arenarum* (Flint Creek; Douglass 1903).
Dryinoides oxyrhynchus (Madison Valley; Auffenberg 1958).

Helodermoides tuberculatus is the most common squamate at PSMP and most elements recovered represent isolated osteoderms. No other squamates were described from PSMP even though various museums made extensive collections throughout the 20th century. The identification of *Peltosaurus* from PSMP is based on a questionably referred fragmentary maxilla which if confirmed, would extend the temporal and geographic range of *Peltosaurus* to Chadronian strata in Montana. Four fragmentary specimens represent the only known record of varanids from the Tertiary depositional basins of southwest Montana and the second known occurrence of varanids in Chadronian strata. A probable iguanid dentary fragment from PSMP is too fragmentary for generic identification but represents a species smaller than *Aciprion formosum*. Based on articulated, associated, and isolated occurrences totaling 44 trunk vertebrae, the snake *Calamagras* is relatively common at PSMP. This large sample represents the third record of *Calamagras* from Chadronian strata in North America and the first report of the genus from the Tertiary depositional basins of southwest Montana. The high number of MTV recovered at PSMP suggests that unreported snake vertebrae may be present in other museum collections.

The skull with mandibles of *Aciprion formosum* from the Gravelly Range is similar to specimens referred to *A. formosum* except its maxillary teeth are higher crowned. The Gravelly Range specimen represents the first confirmed occurrence of *A. formosum* in Whitneyan strata and the first record from Montana.

Uintan squamates from the Dell beds in the Sage Creek depositional basin consist of osteoderms and skull/dentary fragments that indicate the presence of a glyptosaurine and a probable iguanid.

Besides increasing the diversity of squamates known from the Tertiary depositional basins of southwest Montana, these new records of Eocene-Oligocene squamates are important additions to the temporal and/or paleogeographic ranges of *Calamagras*, *Aciprion formosum*, varanid lizards, and perhaps *Peltosaurus*.

ACKNOWLEDGEMENTS

We thank Gregory Liggett and Shannon Gilbert of the Dillon and Billings offices of the Montana Bureau of Land Management and Dale Olson and Erik Torgerson from the Beaverhead-Deer Lodge National Forest of the United States Forest Service for permits, and Krister Smith and Robert Sullivan for very helpful reviews. We gratefully acknowledge the Malcolm C. McKenna Research Fund and the Augustyn Family Fund of the RAM and the David B. Jones Foundation for financial support, Robert Sullivan for discussions on lizards, Samuel McCloud for information concerning LACM 4893, and Andrew Farke, Jared Heuck, and Gabe Santos at the RAM for general assistance. Our appreciation is also extended to Chuck Wideman, Duncan Everhart, Steve Johnson, David Mirkin, Karen Piacentini, Dan Gluckstein, Akemi Chang, Page Thibodeaux, students at The Webb Schools, and many others who assisted in fieldwork at PSMP, the Gravelly Range, and/or the Sage Creek depositional basin.

LITERATURE CITED

Albright, L.B. 1994. Lower vertebrates from an Arikareean (earliest Miocene) fauna near the Toledo Bend Dam, Newton County, Texas. Journal of Paleontology 68:1131–1145.

Auffenberg, W. 1958. A new genus of colubrid snake from the upper Miocene of North America. American Museum Novitates 1874:1–16.

Brattstrom, B.H. 1955. New snakes and lizards from the Eocene of California. Journal of Paleontology 29:145–149.

Brattstrom, B.H. 1958. Two Oligocene Lizards. Herpetologica 14:43–44.

Breithaupt, B.H. and D. Duvall. 1986. The oldest record of serpent aggregation. Lethia 19:181–185.

Caldwell, M., B. Breithaupt, and B. Bamforth. 2007. The Oligocene erycine snakes, *Ogmophis* and *Calamagras*: new material clarifies vertebral-form species. Journal of Vertebrate Paleontology Abstracts with Programs 27A:55.

Cope, E.D. 1873a. Synopsis of New Vertebrata from the Tertiary of Colorado, obtained during the summer of 1873. Pp. 3–19, in Hayden, F.V., The Seventh Annual Report of the United States Geological Survey of the Territories. Government Printing Office, Washington.

Cope, E.D. 1873b. Second notice of extinct Vertebrata from the Tertiary of the plains. Palaeontological Bulletin 15:1–6.

Douglass, E. 1903. New Vertebrates from the Montana Tertiary. Annals of the Carnegie Museum 2:145–199.

Douglass, E. 1908. Some Oligocene lizards. Annals of the Carnegie Museum 4:278–285.

Estes, R. 1983. Sauria terrestria, Amphisbaenia. Handbuch der Paläoherpetologie 10A. Gustav Fischer Verlag, Stuttgart.

Fields, R.W., D.L. Rasmussen, A.R. Tabrum, and R. Nichols. 1985. Cenozoic rocks of the intermontane basins of western Montana and eastern Idaho. Pp. 9–36, in*:* R.M. Flores and S.S. Kaplan (eds.), Cenozoic paleogeography of the west central United States. Society of Economic Paleontologists and Mineralogists, Tulsa, Oklahoma.

Garcia, D. 1992. Fossil Mammalia from the Pipestone Creeks Region, late Eocene and Oligocene (Chadronian and Orellan), Jefferson County, Montana. Ph.D. Thesis, University of California-Berkeley, Berkeley, California. 215 pp.

Gilmore, C.W. 1928. Fossil lizards of North America. Memoir of the National Academy of Sciences 22:1–201.

Gilmore, C.W. 1938a. Descriptions of new and little-known fossil lizards from North America. Proceedings of the United States National Museum 86:11–26.

Gilmore, C.W. 1938b. Fossil snakes of North America. Geological Society of America Special Paper 9:1–96.

Gilmore, C.W. 1941. Some little-known fossil lizards from the Oligocene of Wyoming. Proceedings of the United States National Museum 91:71–76.

Gilmore, C.W. 1942. Paleocene faunas of the Polecat Bench Formation, Park County, Wyoming. Part II Lizards. Proceedings of the American Philosophical Society 85:159–167.

Golz, D.J., and J.A. Lillegraven. 1977. Summary of known occurrences of terrestrial vertebrates from Eocene strata of southern California. Contributions to Geology, University of Wyoming 15:43–64.

Gray, J.E. 1825. A synopsis of the genera of Reptiles and Amphibia, with a description of some new species. Annals of Philosophy 10:193–217.

Gray, J.E. 1827. A synopsis of the genera of saurian reptiles, some new genera are indicated and others reviewed by actual examination. The Philosophical Magazine 2:54–58.

Gutmann, J.T., P.D. Pushkar, M.C. McKenna. 1989. Late Cretaceous and Tertiary history and the dynamic crushing of cobbles, Black Butte area, southwestern Montana. Engineering Geology 27:413–431.

Hanneman, D.L. 1989. Cenozoic basin evolution in a part of southwestern Montana. Ph.D. Thesis, University of Montana, Missoula, Montana. 347pp.

Hanneman, D.L., and C.J. Wideman. 1991. Sequence stratigraphy of Cenozoic continental rocks. Geological Society of America Bulletin 103:1335–1345.

Hanneman, D.L., and C.J. Wideman. 2006. Calcic pedocomplexes—regional sequence boundary indicators. Pp. 1–15, in A.M. Alonso-Zarza and L.H. Tanner (eds.), Paleoenvironmental Record and Applications of Calcretes and Palustrine Carbonates, Geological Society of America Special Paper 416, Geological Society of America, Denver, Colorado.

Hanneman, D.L., D. Lofgren, S.T. Hasiotis, and W.C. McIntosh. 2022. Late Eocene (Priabonian) chronostratigraphy, depositional environment, and paleosol-trace fossil associations, Pipestone Springs, southwest Montana. Acta Palaeontological Polonica 67:5–20.

Holman, J. A. 1972. Herpetofauna of the Calf Creek local fauna (lower Oligocene: Cypress Hills formation) of Saskatchewan. Canadian Journal of Earth Sciences 9:1612-1631.

Holman, J.A., 1976. Cenozoic herpetofaunas of Saskatchewan. Pp. 8–92, in R. S. Churcher (ed.), Athlon Essays on Palaeontology in honour of Loris Shano Russell. Royal Ontario Museum Life Sciences Miscellaneous Publications.

Holman, J.A. 1989. Some amphibians and reptiles from the Oligocene of northeastern Colorado. Dakoterra 3:16–21.

Holman, J.A. 2000. Fossil snakes of North America: Origin, Evolution, Distribution, Paleoecology. Indiana University Press, Bloomington and Indianapolis. 357 pp.

Hough, J.R. 1955. An Upper Eocene fauna from the Sage Creek area, Beaverhead County, Montana. Journal of Paleontology 29:22–36.

Hough, J.R. 1958. Tertiary Beds of the Sage Creek area, Beaverhead, County, Montana. Pp. 41–45, in Fields, R.W. (ed.), Western Montana, Guidebook, Eighth Field Conference Society of Vertebrate Paleontology. Montana State University Press, Missoula, Montana.

Jepsen, G.L., 1963. Eocene vertebrates, coprolites, and plants in the Golden Valley Formation of western North Dakota. Geological Society America Bulletin 74:673–684.

Kay, J.L., R.W. Fields, and J. Orr. 1958. Faunal lists of Tertiary vertebrates from western and southwestern Montana. Pp. 33–39, in R.W. Fields (ed.), Western Montana Guidebook, Eighth Field Conference, Society of Vertebrate Paleontology, Montana State University, Missoula, Montana.

Kuenzi, W.D., and R.W. Fields. 1971. Tertiary stratigraphy, structure and geologic history, Jefferson Basin, Montana. Geological Society of America Bulletin 82:3374–3394.

LaDuke, T.C. 1991. The fossil snakes of Pit 91, Rancho la Brea, California. Contributions in Science, Natural History Museum of Los Angeles County 424:1–28.

Lofgren, D.L., C.Y. Shen, N.N. Buday, C.A.C. Ylagan, K.K. Lofgren, R. Lai, D.D. Santana-Grace, A.R. Tabrum. 2017. Coprolites and Mammalian Carnivores from Pipestone Springs, Montana, and their Paleoecological Significance. Annals of the Carnegie Museum 84:265–285.

Lofgren, D., D.L. Hanneman, J. Bibbens, L. Gerken. F. Hu, A. Runkel, I. Kong, A. Tarakji, A. Helgeson, I. Gerard, R. Li, S. Li, and Z. Ji. 2020. Eocene and Oligocene mammals from the Gravelly Range of southwest Montana. Paludicola 12: 263–297.

Luikart, E.J. 1997. Syn-and post-Laramide geology of the south-central Gravelly Range, southwestern Montana. M.S Thesis, Montana State University Boseman, Montana. 96pp.

Maddox, D., and W.P. Wall. 1998. A systematic review of the fossil lizards and snakes (Squamata) from the White River Group of Badlands National Park. National Park Service Paleontological Research Vol. 3 Technical Report NPS/NRGRD/GRDTR-98/1, pp. 4–7.

Matthew, W.D. 1903. The fauna of the *Titanotherium* beds at Pipestone Springs, Montana. Bulletin of the American Museum of Natural History 19:197–226.

McDowell, S.B., and C.M. Bogert. 1954. The systematic position of *Lanthanotus* and the affinities of the anguinomorphan lizards. Bulletin of the American Museum of Natural History 105:1–142.

Meszoely, C.A.M. 1970. North American fossil anguid lizards. Bulletin of the Museum of Comparative Zoology 139:87–149.

Oppel, M. 1811. Die Ordnung.en, Familien, und Gattungen der Reptilien. Munich.

Parmley, D., and J.A. Holman. 2009. Erycine boids from the Early Oligocene of the South Dakota badlands. Georgia Journal of Science 67:61–66.

Rage, J.C. 1984. Serpentes, in Wellnhofer, P. (ed.), Encyclopedia of Paleoherpetology, Part II. Gustav Fischer, Stuttgart, New York, 80p.

Robinson, P., G.F. Gunnell, S.L. Walsh, W.C. Clyde, J.E. Storer, R.K. Stucky, D.J. Froehlich, I. Ferrusquia-Villafranca, and M.C. McKenna. 2004. Wasatchian through Duchesnean Biochronology. Pp. 106–155, in M. O. Woodburne (ed.), Late Cretaceous and Cenozoic Mammals of North America. Columbia University Press, New York, New York.

Scarpetta, S. G. 2019. *Peltosaurus granulosus* (Squamata, Anguidae) from the middle Oligocene of Sharps Corner, South Dakota, and the youngest known chronostratigraphic occurrence of Glyptosaurinae. Journal of Vertebrate Paleontology 39:3, DOI: 10.1080/02724634.2019.1622129.

Schwartz, T.M., and S.A. Graham. 2017. Depositional history and provenance of Paleogene strata in the Sage Creek Basin, southwestern Montana. Geosphere 13:1285–1309.

Smith, K.T. 2006. A diverse new assemblage of Late Eocene squamates (Reptilia) from the Chadron Formation of North Dakota, U.S.A. Palaeontologia Electronica 9 (5A):1–44.

Smith, K.T. 2011. The evolution of mid-latitude faunas during the Eocene: Late Eocene lizards of the

Medicine Pole Hills reconsidered. Bulletin of the Peabody Museum of Natural History 52: 3-105.

Smith, K.T. 2013. New constraints on the evolution of the snake clades Ungaliophiinae, Loxocemidae and Colubridae (Serpentes), with comments on the fossil history of erycine boids in North America. Zoologischer Anzeiger 252:157-182.

Smith, K.T., and G. Georgalis. 2022. The diversity and distribution of Palaeogene snakes: A review, with comments on vertebral sufficiency. Pp. 55-84 in D. Gower & H. Zaher (eds.). The Origin and Early Evolutionary History of Snakes (Systematics Association Special Volume 90). Cambridge University Press, Cambridge, United Kingdom.

Stucky, R.K., D.R. Prothero, W.G. Lohr, and J.R. Snyder. 1996. Magnetic stratigraphy, sedimentology, and mammalian faunas of the early Uintan Washakie Formation, Sand Wash Basin, northwestern Colorado. Pp. 40–51 in D. R. Prothero and R. J. Emry (eds.), The Terrestrial Eocene-Oligocene Transition in North America. Cambridge University Press, New York.

Sullivan, R.M. 1979. Revision of the Paleogene genus *Glyptosaurus* (Reptilia, Anguidae). Bulletin of the American Museum of Natural History 163:1–72.

Sullivan, R.M. 2019. The taxonomy, chronostratigraphy, and paleobiogeography of glyptosaurine lizards (Glyptosaurinae, Anguidae). Comptes Rendus Palevol 18:747–763.

Sullivan, R.M., and J.A. Holman. 1996. Squamata. Pp. 354–372, in Prothero, D.R., and R.J.

Emry (eds.), The Terrestrial Eocene-Oligocene Transition in North America. Cambridge University Press, New York.

Sullivan, R.M., and S.G. Lucas, 1988. Fossil Squamata from the San Jose Formation, Early Eocene, San Juan Basin, New Mexico. Journal of Paleontology 62:631–639.

Tabrum, A.R. and G. Métais. 2007. *Pipestoneia douglassi*, a new genus and species of selenodont artiodactyl from the Pipestone Springs area, Jefferson County, Montana. Bulletin of Carnegie Museum of Natural History 39:83–96.

Tabrum, A.R., D.R. Prothero, and D. Garcia. 1996. Magnetostratigraphy and biostratigraphy of the Eocene-Oligocene transition, southwestern Montana. Pp. 278–311, in Prothero, D.R. and R.J. Emry (eds.), The Terrestrial Eocene-Oligocene Transition in North America. Cambridge University Press, New York.

Tabrum, A.R., R. Nichols, and A.D. Barnosky. 2001. Tertiary paleontology of southwest Montana and adjacent Idaho. SVP Guidebook, Mesozoic and Cenozoic paleontology in the western plains and Rocky Mountains. Museum of the Rockies Occasional Papers 3:93–112.

Torres-Carvajal, O., K. de Queiroz, and J.A. Schulte. 2020. Iguanidae. Phylonyms: A Companion to the PhyloCode.

Wahlert, J.H., W.W. Korth, and M.C. McKenna. 2006. The skull of *Rapamys* (Ischyromyidae, Rodentia) and description of a new species from the Duchesnean (late Middle Eocene) of Montana. Palaeontographica Abt. A 2877:39–51.

White, T.E. 1942. The Lower Miocene mammal fauna of Florida. Bulletin of the Museum of Comparative Zoology 92:1–49.

Wood, H.E. 1934. Revision of the Hyrachyidae. Bulletin of the American Museum of Natural History 67:181–295.