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A new species of the basal plesiadapiform *Purgatorius* (Mammalia, Primates) from the early Paleocene Ravenscrag Formation, Cypress Hills, southwest Saskatchewan, Canada: further taxonomic and dietary diversity in the earliest primates

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A new species of the basal plesiadapiform *Purgatorius* (Mammalia, Primates) from the early Paleocene Ravenscrag Formation, Cypress Hills, southwest Saskatchewan, Canada: further taxonomic and dietary diversity in the earliest primates

Craig S. Scott, Richard C. Fox, and Cory M. Redman

Abstract: The fossil record of the earliest primates, purgatoriid plesiadapiforms, has become increasingly well documented during the past two decades, but their dietary preferences remain poorly understood. While the available evidence, which consists mostly of isolated teeth and incomplete jaws with teeth, suggests that purgatoriids were insectivorous to omnivorous, we describe here a new species of *Purgatorius*, *Purgatorius pinecreeensis* sp. nov., that extends the range of purgatoriid dental disparity toward greater omnivory than had been known before. *P. pinecreeensis* sp. nov., from the early Paleocene (Puercan) Ravenscrag Formation of southwestern Saskatchewan, differs from other species of *Purgatorius* in having slightly lower

47 crowned teeth with a lower trigonid relative to talonid, blunter and more swollen major cusps,
48 more transverse lower molar paracristids, and m3 with a more robustly developed posterior lobe.
49 Taken together, these specializations enhanced the capacity for crushing and grinding at the
50 expense of orthal shear, and represent the first instance of a modest degree of bunodonty in the
51 family. The discovery of *P. pinecreeensis* sp. nov., along with other recently reported basal
52 plesiadapiforms from the Puercan and Torrejonian of the northern Western Interior, lends
53 additional support to the notion of a significant primate radiation soon after the Cretaceous–
54 Paleogene extinction event.

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56 **Résumé:**

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58 Key words: Primates, Plesiadapiformes, *Purgatorius*, Paleocene, Saskatchewan, Canada
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Introduction

Of the mammals that diversified immediately after the end-of Mesozoic extinctions ca. 66 Mya, plesiadapiform primates rank among the least well known, with both their systematics and paleoecology poorly understood. Like many of their mammalian contemporaries, earliest Paleocene (Puercan) plesiadapiforms are documented nearly exclusively by isolated teeth or, more rarely, incomplete jaws with teeth, a limited body of evidence that makes determination of relationships to later plesiadapiforms and other primates difficult (Van Valen 1994; Silcox 2001; Silcox and Gunnell 2008; Ni et al. 2013; Chester et al. 2015). From present evidence, Puercan plesiadapiforms can be distinguished from their small-bodied eutherian contemporaries, such as cimolestids and leptictids, by the possession of lower-crowned molars having somewhat swollen cusps and blunt crests, enlarged protocones, and concordantly expanded talonid basins (Van Valen and Sloan 1965; Clemens 1974; Szalay and Delson 1979; Silcox 2007; Fox and Scott 2011). These features of the dentition have been thought to reflect the results of an adaptive shift from reliance on insects as a primary food resource toward a greater incorporation of plant tissues, such as fruit and seeds, in the diet (Szalay 1968, 1969; Kay and Cartmill 1977; Silcox and Gunnell 2008). The timing of this shift is uncertain: traditionally, it has been thought to occur soon after the K–Pg extinction horizon, but with increased knowledge of the diversity of primitive plesiadapiforms and the ghost lineages that this diversity requires, it seems likely to have already begun in the Late Cretaceous (Clemens 2004; Fox 2011; Fox and Scott 2011; Fox et al., 2015). Moreover, the recent discovery of several isolated, possible plesiadapiform tarsals from the early Paleocene of Montana suggests that the change from an insectivorous to a more omnivorous diet may have occurred concurrently with adaptation to an arboreal environment (Chester et al. 2015)

83 For many years, the record of the earliest and most basal plesiadapiforms consisted only
84 of *Purgatorius unio* Van Valen and Sloan, 1965, based on a small sample of isolated teeth from
85 the late Puercan (Pu3) Purgatory Hill locality of Montana. A second species, *P. ceratops* Van
86 Valen and Sloan, 1965, from the Lancian/early Puercan (La-Pu1) Harbicht Hill locality of
87 Montana, was founded on a single, poorly preserved and non-diagnostic lower molar. The poor
88 preservation and uncertain age of the type and only specimen of *P. ceratops* has led to questions
89 regarding its referral to *Purgatorius* (Buckley 1997; Clemens 2004; Fox and Scott 2011), and as
90 such it will be considered no further here. Van Valen (1994) significantly expanded knowledge
91 of Puercan plesiadapiform diversity with description of a second purgatoriid (see Gunnell 1989),
92 *Purgatorius janisae*, from late Puercan (Pu3) channel deposits of the Garbani Quarry, Montana,
93 and a purported basal plesiadapid, *Pandemonium dis*, from the late Puercan Purgatory Hill
94 locality, Montana. The discovery of *Purgatorius coracis* Fox and Scott, 2011, documented by a
95 small sample of isolated teeth and a single incomplete dentary with teeth from the Ravenscrag
96 Formation, Medicine Hat Brick and Tile Quarry, southwestern Saskatchewan, pushed the record
97 of primates back further into the Puercan: Ravenscrag strata at this locality were deposited
98 during magnetic polarity chron 29R (Lerbekmo 1985), i. e., within the first several hundred
99 thousand years after the K–Pg extinction horizon (Ogg 2012; Sprain et al. 2014; Ickert et al.
100 2015). Knowledge of early plesiadapiform diversity has continued to increase modestly since:
101 the Purgatoriidae now include three, or possibly four, species of *Purgatorius* (Buckley 1997;
102 Silcox and Gunnell 2008; Fox and Scott 2011), plus the recently described ‘large-bodied’
103 *Ursolestes perpetior* Fox, Scott, and Buckley 2015. Further, *Pandemonium* is now known from
104 a second species, *P. hibernalis* Fox, Rankin, Scott, and Sweet, 2014, from the middle Puercan
105 (Pu2) of southern Alberta, although the relationships of this genus are uncertain.

We report here on a new species of *Pugatorius* from mid- to late Puercan deposits of the Ravenscrag Formation, southwestern Saskatchewan, a unit that also documents the oldest primate known (Fox and Scott 2011; O’Leary et al. 2013). This new species possesses a more bunodont dentition than in other species of *Purgatorius*, reflecting expansion of the dietary range in even the initial stages of primate evolution.

Geological setting and localities

The fossils described in this paper were discovered in strata of the Ravenscrag Formation at Pine Cree Regional Park, southwestern Saskatchewan, Canada (Fig. 1). The Ravenscrag Formation is a richly fossiliferous unit of terrestrial rock that crops out extensively in southwestern Saskatchewan, but also occurs sporadically in southeastern Alberta, and across southern Saskatchewan eastward to near the border with Manitoba (Dawson 1875; McLearn 1929; Russell 1974; Krause 1977; McIver and Basinger 1993; Redman et al. 2015). The formation is Paleocene in age, and has long been known to preserve mammals and other vertebrates of Puercan age in southern Saskatchewan (Russell 1974; Krause 1977, 1978; Naylor 1978; Johnston 1980; Naylor and Krause 1981; Johnston and Fox 1984; Fox 1990, 2002; Fox and Scott 2011; Fox et al. 2010), includes the oldest known primate, *Purgatorius coracis* (Fox and Scott 2011). The Pine Cree Park locality occurs in Pine Cree Regional Park, 12 km northeast of Eastend and approximately 30 km northeast of the Rav W-1 locality at the Medicine Hat Brick and Tile Quarry (Russell 1974; Redman et al. 2015). The locality occurs at a cutbank of a minor unnamed creek near the south end of the park; vertebrate fossils from Pine Cree Park occur in fine- to very fine grained sandstone along with siltstone clasts and the broken shells of mollusks (Redman et al. 2015). Prior to the present study, fossil mammals from Pine Cree Park consisted

only of the holotype of the chriacid ‘condylarth’ *Carcinodon aquilonius* Russell 1974, and two unidentified multituberculate teeth (Russell 1974; Fox 1990). A large sample was obtained from the locality by the Royal Tyrrell Museum of Palaeontology in 2012, resulting in discovery of the specimens described here, as well as significant new mammal material, to be described elsewhere (Scott et al. in prep.). The Pine Cree Park locality is provisionally considered middle Puercan (Pu2) based on the mammal assemblage and recently analyzed palynomorphs (Redman et al. 2015).

Methods, terminology, and abbreviations

Dental nomenclature follows Van Valen (1966) as modified by Szalay (1969). Dental measurements follow Clemens (1966) and were taken using digital calipers under a microscope. Institutional abbreviations: LACM, Los Angeles County Museum (now Natural History Museum of Los Angeles County), Los Angeles, California, U.S.A; RSM, Royal Saskatchewan Museum, Regina, Saskatchewan, Canada; TMP, Royal Tyrrell Museum of Palaeontology, Drumheller, Alberta, Canada; UALVP, University of Alberta Laboratory for Vertebrate Paleontology, Edmonton, Alberta, Canada; UM, University of Michigan Museum of Paleontology, Ann Arbor, Michigan, U.S.A.; UMVP, University of Minnesota Vertebrate Paleontology Collection, Minneapolis, Minnesota, U.S.A.

Other abbreviations: L/R, left/right; Lg, anteroposterior length; M/m, upper/lower molar; P/p, upper/lower premolar; Ta, talonid; Tr, trigonid; W, labiolingual width. The terms “Puercan” and “Torrejonian” refer to the first two North American Land Mammal Ages (NALMAs) of the Paleocene, respectively; NALMAs are biochrons, units of relative time defined by mammalian taxa that lived during those intervals (Woodburne 2004).

Systematic paleontology

Order	Primates Linnaeus, 1758
Suborder	Plesiadapiformes Simons, 1972
Family	Purgatoriidae Gunnell, 1989
Genus	<i>Purgatorius</i> Van Valen and Sloan, 1965

TYPE SPECIES: *Purgatorius unio* Van Valen and Sloan, 1965.

Purgatorius pinecreeensis sp. nov.

Figs. 2–3

ZOOBANK LSID: zoobank.org/pub:339FBC06-6C4B-4F86-A9A0-B2B5F9266C40

DIAGNOSIS: Differs from *Purgatorius janisae* in having significantly smaller and slightly lower crowned lower molars, with shorter trigonid relative to talonid, more gracile coronal morphology, and in having relatively more swollen lower molar cusps. Differs further from *P. janisae* in having better-developed posterior lobe on m3. Differs from *Purgatorius coracis* and *P. unio* (including *P. titusi*) in having lower molars slightly lower crowned, with shorter trigonid relative to talonid, paraconid more inflated and distinct from longer and more transversely directed paracristid, and usually more lingual in position, and in having protoconid and metaconid with more swollen walls. Differs further in hypoconulid of m1–2 being more robust and swollen, entoconid and hypoconid of m1–2 more anteriorly positioned and posterior rim of talonid more arcuate (posteriorly convex), and in posterior lobe of talonid of m3 more sharply distinct from remainder of talonid, and hypoconulid of m3 more strongly developed.

174 HOLOTYPE AND LOCALITY: RSM P3195.1, incomplete right dentary having m1-3 and alveoli for
175 p1-4. Measurements: m1: Lg = 1.75, Tr W = 1.20; Ta W = 1.25; m2 : Lg = 1.85, Tr W = 1.45;
176 Ta W = 1.40; m3: Lg = 2.00; Tr W = 1.30; Ta W = 1.10. Pine Cree Park locality (RSM locality
177 72F10-0012), Ravenscrag Formation, southwestern Saskatchewan, Canada. Pine Cree Park is
178 provisionally considered Pu2 in age, a conclusion based on the limited mammalian evidence, in
179 conjunction with palynomorph data (Redman et al. 2015).

180 REFERRED SPECIMENS: RSM P3195.2, LP4 (Lg = 1.62; W = 1.76); RSM P3195.3, LM1 (W =
181 2.20); RSM P3195.4, RM1 (Lg = 1.53; W = 2.08); RSM P3195.5, Lp4 (Lg = 1.33; W = 0.81);
182 RSM P3195.6, Rm1. All specimens included in this paper were collected under Saskatchewan
183 Provincial Heritage Permit 12-001P.

184 AGE AND DISTRIBUTION: Type locality only.

185 DESCRIPTION: *P4*: The P4 of *Purgatorius pinecreeensis* is documented by RSM P3195.2, an
186 isolated tooth from the left side (Fig. 2A–C). It is not well preserved, exhibiting diagenetic
187 dissolution/erosion of the enamel, plus a minor amount of breakage of the enamel near the base
188 of the crown, and in-life occlusal wear, especially along the postmetacrista and postprotocrista.
189 Nonetheless, many of the crucial features of the specimen are preserved. RSM P3195.2 is
190 premolariform, having a well-developed paracone and robust lingual protocone. An acute
191 parastylar process arises anterior to the paracone and bears a small, subconical, parastylar cusp.
192 Labially, an ectocingulum extends posteriorly from the parastylar process to the posterolabial
193 corner of the crown, but disappears over a short interval at the base of the paracone; there is no
194 stylocone or stylar shelf. The paracone is tall, somewhat compressed labiolingually, and
195 separated from the parastylar cusp by a transverse groove, which received the protoconid of p4
196 during mastication; the anterior face of the paracone is rounded, i.e., there is no preparacrista and

hence no capacity for shear in this part of the crown. The apex of the paracone was probably acute, but it is presently incomplete posteriorly, leaving its original configuration somewhat in doubt; however, it probably was not bluntly rounded. Arising from the posterior side of the paracone is a tall crest that descends as it curves to the posterolabial corner of the crown. Posterior to the apex of the paracone, the continuity of the cutting edge of this crest is interrupted by a faint notch, which we interpret as marking the position of an incipient metacone; leading to this notch along the lingual face of the crest is a weak sulcus in the position of the division between the paracone and metacone if the latter cusp had been fully developed; a similar sulcus is developed on the opposite, labial side of the crest. More posteriorly, the postparacrista is increasingly worn towards its termination at the posterolabial corner of the crown. Anteriorly, a paracingulum extends a short distance lingually from the parastylar process before fading away as it approaches the labialmost parts of the protocone. The protocone is strongly developed, subconical, about one-third the height of the paracone, and somewhat deflected anteriorly. A short postprotocone crista descends posteriorly and slightly lingually from the apex of the protocone but fades away shortly before meeting the postcingulum. The postcingulum is well developed and labially grades into the metacingulum, which continues labially to the posterolabial corner of the crown. There is presently no evidence of a hypocone, but the postcingulum/metacingulum is deeply worn, so if a lingual cuspule was present originally, evidence of it no longer remains.

M1: M1 of *Purgatorius pinecreeensis* is represented by RSM P3195.4, a well-preserved tooth from the right side (Fig. 2D–F). This specimen has a remnant of the maxilla still adhering to it, but too little of the bone is present to provide any useful information concerning its anatomy.

220 We identify RSM P3195.4 as an M1, as evidenced by the configuration of its labial
221 margin: this margin slants obliquely from posterolabial to anterolingual, reflecting the
222 asymmetrical development of the stylar shelf. The shelf is narrow anteriorly and the parastylar
223 lobe is not swollen labially. Posterior to the ectoflexus, which is very shallow, the shelf widens
224 increasingly to the posterolabial corner of the crown, where it is widest. If RSM P3195.4 were
225 an M2, the parastylar and metastylar lobes would be more nearly symmetrical relative to the
226 ectoflexus.

227 The parastylar process of RSM P3195.4 projects anterior to the main body of the crown,
228 is narrow but rounded anteriorly, and is wide, extending nearly as far lingually as does the base
229 of the paracone. Whether the process supported a parastyle cannot be determined owing to poor
230 preservation. A deep labiolingual groove crosses the occlusal surface of the process, the
231 consequence of wear by the tip of the protoconid of m1 during mastication. A low, narrow
232 ectocingulum arises posteriorly from the parastylar process and thereafter borders the stylar shelf
233 along the entire length of the crown. A low, acute stylocone arises from the ectocingulum
234 anterolabial to the paracone; no other ectocingular cuspules are present. The stylar shelf
235 opposite the stylocone is undeveloped, leaving the ectocingulum abutting the base of the
236 paracone. Posterior to the level of the paracone, the width of the shelf gradually increases,
237 achieving its greatest width posterolabial to the metacone.

238 The paracone and metacone of RSM P3195.4 are subconical, narrow but rounded at their
239 apices, which are slightly worn, and separate at their bases. The paracone is taller than the
240 metacone and vertical in orientation, whereas the metacone leans somewhat posteriorly. The
241 preparacrista is weakly developed, arising from the side of the paracone and becoming more
242 elevated closer to the base of the cusp, where it turns anterolabially toward the stylocone;

whether the crest reached the stylocone, however, cannot be determined owing to wear reflected by the protoconid groove crossing the parastylar process. The postparacrista and premetacrista form a straight line (i.e., are not deflected labially), and their summits have been worn deeply enough from occlusion with the hypoconid, cristid obliqua, and hypocristid of m1 to expose dentine. Although their original heights, therefore, cannot be determined, together these crests form a broadly open, V-shaped centrocrista notch, a configuration that probably has not been altered significantly by the wear that the crests now exhibit. The postmetacrista arises from the entire height of the metacone, from its apex to its base; it decreases in height as it curves towards the posterolabial corner of the crown, where it meets the ectocingulum and walls off the stylar shelf posteriorly.

Both conules are well developed, arising from the base of the paracone and metacone, respectively; the paraconule extends slightly more lingually than the metaconule, with both extending about half the distance between the protocone and the paracone and metacone. The preparaconule crista is robust and fades into the paracingulum, which forms a wide crest extending labially along the anterior side of the crown to the base of the parastylar process. The postparaconule crista and premetaconule crista are both trenchant crests, which together with the bases of the paracone and metacone define the walls of the trigon basin. The postmetaconule crista+metacingulum is robust and extends labially to the level of the metacone, where it fades away on the posterior side of the crown, not joining with either the postmetacrista or ectocingulum.

The protocone is well developed; it has straight (i.e., non-swollen) sides, and is nearly vertical in orientation, not leaning anteriorly. There is no evidence of a posterior protocone shift (Van Valen 1994) relative to the more labial parts of the crown; consequently, the pre- and

postprotocone cristae are subequal in length. A postprotocone fold is not developed. The protocone cingula are prominent, especially the postcingulum, which is squarish lingually and supports a small hypocone at the junction between its posterior and lingual 'limbs'. The protocone cingula do not meet on the lingual face of the protocone.

RSM P3195.3 is a heavily worn left M1; the crown is incomplete, with the parastylar process having been broken off prior to burial (Fig. 2G–I). The crown shows deep wear, with a continuous, strap-like labial facet in which dentine is broadly exposed, affecting the preparacrista, apex of the paracone, centrocrista, apex of the metacone, and the postmetacrista. A second facet extends from the deepest part of the centrocrista notch lingually on to the floor of the trigon basin. A third facet has nearly erased the paraconule and its cristae, continues lingually along the preprotocone crista, truncates the apex of the protocone, and then turns labially along the postprotocone crista, postmetaconule crista, and metacingulum. As a consequence of this wear, much of the detailed coronal morphology of this specimen has been lost. In the parts that can be compared, RSM P3195.3 closely resembles RSM P3195.4, differing only in the postmetacrista being higher and forming a more continuous crest curving posterolabially from the metacone, without a notch intervening along its length, as is seen in RSM P3195.4.

Dentary: RSM P3195.1 is an incomplete right dentary with m1–3 and alveoli for several anterior teeth (Fig. 2M–N). RSM P3195.1 is now in two parts, an anterior fragment that contains m1 and more anterior alveoli, and a posterior fragment that contains m2–3 and the base of the coronoid process. A short piece of bone between m1 and m2 was lost during the collecting process, so there is at present no fit between the anterior and posterior parts of the specimen. However, owing to the same pale brown color of the two bone fragments, including yellowish

root markings on each, and the virtually identical dark brown color exhibited by m1 and m2, with morphological differences only owing to occupancy of different loci, there is no doubt that the two fragments pertain to the same individual; accordingly, they have been catalogued as such in the RSM collections, and they are described as such here.

The anterior fragment of RSM P3195.1 is slender throughout but deepens gradually posteriorly. Seven complete or nearly complete alveoli anterior to m1 open dorsally in the fragment. We interpret these as having housed two-rooted p2–4, and a single-rooted p1. The anterior side and most of the labial side of the p1 alveolus have been broken away, but from the parts that remain, it appears that this alveolus was slightly longer anteroposteriorly than the alveolus holding the anterior root of p2. The alveolus for p1 is oriented obliquely, at a weak posteroventral angle, implying that the crown was somewhat procumbent. Anterior to the alveolus for p1, most of the dentary has been broken away, but a small part of the posterolingual wall of a relatively large alveolus remains, which we interpret as being the remnant of the alveolus for the lower canine. How large the lower canine might have been, however, cannot be determined, as none of the dentary more anteriorly is preserved; hence, nothing can be determined concerning the lower incisors of RSM P3195.1. The premolar alveolar openings posterior to the p1 locus increase gradually in size posteriorly to m1, with the posterior alveolus of each pair being slightly larger than the anterior alveolus at that position. If we have identified the empty alveoli of RSM P3195.1 correctly, the lower post-incisor dental formula of *Purgatorius pinecreeensis* is c, p1–4, m1–3, as in other species of *Purgatorius* where this information is known (Clemens 2004) and in *Ursolestes* (Fox et al. 2014). A large mental foramen, directed somewhat anterodorsally, opens ventral to the level of the posterior alveolus for p3.

p4: The collection from Pine Cree Park includes one p4 (RSM P3195.5) that we tentatively refer to *Purgatorius pinecreeensis* (Fig 2J–L). This tooth, from the left side, is not well preserved: overall, it has undergone a degree of erosion/corrosion of the enamel, erasing fine morphological details, and the enamel near the base of the crown has been spalled away both labially and lingually, probably during the washing/screening process. As such, the measurements recorded for this specimen (Lg = 1.33; W = 0.81) are underestimations, and do not reflect the original dimensions of the crown. RSM P3195.5 is premolariform, dominated by a tall protoconid, with a small talonid more posteriorly; it is two-rooted, and hence is in keeping with the two alveoli identified as having contained p4 in the dentary fragment, RSM P3195.1, described above. Anteriorly on RSM P3195.5, there is a small irregularity of the enamel in the position of a paraconid, but this surface has been deeply corroded and what its original morphology might have been cannot be determined. The talonid is about two-fifths the height of the protoconid. The narrow occlusal surface of the talonid slopes steeply lingually, but the enamel has been spalled away and the original size and position of any talonid cusps is impossible to determine as no trace of these cusps remains. In its major features, the crown of RSM P3195.1 more closely resembles p4 than it does p3, a tooth that is presently known only for *P. janisae* among species of *Purgatorius* (e.g., Clemens 1974, 2004). Although the crown of p3 and p4 is premolariform, the p3 in *P. janisae* is shorter relative to its length, and the protoconid is nearly vertical in its orientation, rather than slightly recurved. Further, the talonid is lower, and the talonid basin is both narrower and shorter on p3 of *P. janisae*. Although we refer RSM P3195.5 to *P. pinecreeensis* on the basis of its resemblance in its major features to p4 in *P. unio*, we recognize that our lack of knowledge of its fine structure lends a degree of uncertainty to our identification of the specimen.

m1: The m1 of *Purgatorius pinecreeensis* is represented by two specimens, one contained in the anterior fragment of RSM P3195.1, the other (RSM P3195.6), an isolated tooth and less well preserved (Fig. 2M–P). In RSM P3195.1, m1 has suffered no damage and is but very slightly worn, with only the tips of the major cusps having been abraded during life, except for the entoconid, which is unworn. In overall occlusal outline, the crown is subrectangular; the trigonid is about equal to the talonid in length, but is narrower in width, and is weakly deflected anteriorly.

The paraconid is the smallest trigonid cusp; it is inset labially from the most lingual extent of the trigonid wall and is low, subconical, with swollen walls. It leans somewhat anteriorly, and with the protoconid and metaconid, forms a trigonid angle of about 50°. Labially, the sides of the paraconid grade smoothly into those of the paracristid; posteriorly, the base of the paraconid is separated from that of the metaconid by a narrow valley. The paracristid is a robust crest that descends a short distance from the apex of the paraconid and then extends transversely across the anterior side of the trigonid to the protoconid, where it turns sharply posterodorsally, rising along about half the height of that cusp and then fading away. The transverse arm of the paracristid leans anteriorly, and both it and the protoconid arm are faintly crenulated along their cutting edges. The precingulid begins beneath the junction of the two arms of the paracristid and curves ventrolabially to its termination on the anterolabial side of the trigonid near its base. The protoconid is about three times the height of the paraconid and is stoutly built; it tapers dorsally to a bluntly rounded apex. In cross section, this cusp is subtriangular, with anterolabial and lingual walls that are somewhat swollen and a posterior wall that is flat. The metaconid is more massive than the protoconid, although subequal to it in height; its apex, like that of the protoconid, is bluntly rounded. Its lingual and anterolabial walls

are significantly swollen, whereas its posterior wall is nearly flat, but is slightly inflated lingually. Overall, the postvallid wall from labial to lingual is weakly posteriorly oblique. The protocristid is low and its two arms are weakly convex dorsally; at their ventral junction, they form a narrow, slit-like notch.

The talonid of m1 in RSM P3195.1 is slightly wider than the trigonid and about equal in length, and is slightly over half the height of the trigonid. The labial wall of the talonid descends steeply posteroventrally, well below the ventralmost margins of the posterior or lingual walls. The hypoconid is the tallest, most massive talonid cusp, with somewhat swollen labial sides but shallowly concave lingually, facing the talonid basin. The cristid obliqua extends between the hypoconid and the postvallid wall, which it meets directly beneath the protocristid notch and then ascends a short distance on the wall, terminating ventrolingually to the deepest part of the notch. The cristid obliqua is slightly elevated midway along its length, but a mesoconid is not developed. Together with the postvallid wall, the cristid obliqua and anterolabial side of the hypoconid form a deep, narrow hypoflexid; a small cuspule arises from the floor of the hypoflexid. The hypoconulid, the lowest talonid cusp, is a transversely oriented, cuspidate (rather than tab-like) structure on the posterior rim of the talonid; it is oriented posterodorsally and is located just lingual to the central axis of the crown, closer to the entoconid than to the hypoconid but not twinned with the lingual cusp. Both the hypocristid (between the hypoconid and hypoconulid) and posteristid (between the hypoconulid and entoconid) are shallowly concave dorsally. The entoconid is located slightly posterior to the level of the hypoconid; it is somewhat compressed anterolabially-posterolingually. The entocristid, arising from the anterior side of the entoconid, descends into the moderately deep talonid notch. The postcingulid arises from the labial side of the hypoconulid and descends ventrolabially, continuing as a faint crest to

near the base of the crown, where it fades away. Wear facets from tooth-on-tooth occlusion during the power stroke phase of mastication are most evident on the anterior side of the protoconid, the postvallid wall labial to the protocristid notch, the posterior side of the cuspsule at the base of the hypoflexid, and the labial side of the hypoconid.

m2: The m2 of *Purgatorius pinecreeensis* is preserved in the posterior fragment of RSM P3195.1, which also contains m3 (Fig. 2M–P, 3L). It has suffered no damage and its crown is virtually unworn, with the tips of the protoconid, metaconid, and hypoconid showing small, circular cavitations of the enamel from contact with food during the mastication process. The crown of m2 is subrectangular in overall occlusal outline, with somewhat swollen sides; the trigonid is slightly longer and wider than the talonid. The trigonid is low and is deflected weakly anteriorly. The paraconid is the smallest and lowest trigonid cusp; it is subconical, with swollen sides and bluntly rounded apex. Posteriorly, the paraconid abuts the anterior side of the metaconid at its base, but is not appressed against it; instead, the paraconid leans anteriorly, away from the metaconid. The paracristid is a short, low, robust crest that arises from the labial side of the paraconid, is deflected anteriorly, and extends transversely and slightly posteriorly across the trigonid to the base of the protoconid; the apex of the paraconid is slightly taller than the summit of the paracristid adjacent to it. At the base of the protoconid, the paracristid turns posterodorsally, where it is a substantially weakened crest that ascends to nearly the apex of the protoconid. The precingulid arises from the anterior side of the paraconid where it descends vertically for a short distance, then swings labially to cross the anterior face of the trigonid along a dorsally shallow concave arc that met the posterior side of the talonid of m1, as indicated by an interdental wear facet. Past this facet, the precingulid curves ventrolabially along the labial side of the trigonid towards its base, where it terminates adjacent to the hypoflexid. The protoconid is

approximately four times the height of the paraconid and is substantially larger overall. In cross section, the protoconid is subtriangular, somewhat compressed anteroposteriorly, with a convex anterolabial side, a flat posterior side, and a swollen anterolingual side facing the trigonid basin. Its apex, presently slightly truncated by wear, is narrow but was probably bluntly rounded originally. The metaconid, subequal in height with the protoconid, is otherwise the more massive cusp; at its base, it is wider than long anteroposteriorly, its lingual and anterolabial sides are swollen, but its posterior side is flat (Fig. 3L). The postvallid wall is nearly transverse, but from labial to lingual is it weakly posteriorly oblique. The posteristid is a low crest; its protoconid and metaconid arms meet at an angle of about 60 degrees.

The talonid of m2 is about two-thirds the height of the trigonid, and is slightly longer and narrower. The major talonid cusps are each well developed, with the hypoconid the tallest and most massive; its labial sides are weakly swollen, whereas its lingual side, facing the talonid basin, is shallowly concave. The cristid obliqua meets the postvallid wall beneath the deepest part of the protoconid notch and ascends the wall for a short distance before fading away. The crest is somewhat elevated midway along its length, but a mesoconid is not developed. Along with the posterior side of the trigonid, the cristid obliqua forms a moderately deep and narrow hypoflexid. The hypoconulid is the lowest talonid cusp; it is a transverse, tab-like elevated segment of the posterior rim of the talonid that projects weakly posterodorsally and is located slightly lingual to the midline axis of the crown. It is closer to the entoconid than to the hypoconid, but is not twinned with the entoconid. Both the hypocristid and posteristid are shallowly concave dorsally. The entoconid is subconical and positioned just posterior to the level of the hypoconid. The entocristid slopes anteriorly from the entoconid into a moderately

426 deep talonid notch. The talonid basin is deep and ovate in outline, being wider than long. A
427 short postcingulid extends ventrolabially from the labial side of the hypoconulid.

428 In comparison with m1, the m2 differs in being larger overall, and is somewhat higher
429 crowned. The trigonid is relatively wider than on m1, being about subequal to the talonid in
430 width, and is more compressed anteroposteriorly and is slightly less deflected anteriorly. The
431 paraconid on m2 is in a more lingual and posterior position, closer to the metaconid, and leans
432 less anteriorly, and the paracristid is longer and more transverse in its orientation. The
433 precingulid is substantially longer, extending farther both lingually and ventrolabially. The m2
434 protoconid and metaconid are larger than those on m1, with more swollen walls, and are farther
435 apart labiolingually; the protocristid is longer and the protocristid notch is accordingly broader
436 absolutely and relative to its depth, which is about equal in the two teeth. The talonid basin, and
437 talonid cusps and crests are all of greater dimensions than in m1 but they retain their relative
438 proportions to one another as seen in the more anterior tooth, and the postcristid extends further
439 ventrally.

440 m3: The m3 of RSM P3195.1 is pristinely preserved (Fig. 2M–P). The tooth is narrower
441 but longer than m2, the greater length owing to the expanded posterior lobe. Although the
442 trigonid is roughly twice the height of the talonid, it is nevertheless low crowned, with slightly
443 swollen walls, and is vertically oriented.

444 The paraconid is smallest and lowest trigonid cusp, subconical, and with a swollen
445 posterior side that abuts the anterior side of the metaconid at its base but is not appressed against
446 it. The paraconid is somewhat more labial in position than the most lingual parts of the trigonid
447 more posteriorly, and leans weakly anteriorly. The apex of the paraconid has been shallowly
448 cavitated by wear, but probably was bluntly rounded originally, as in m2. The paracristid is

449 slightly narrower than the paraconid, with its sides grading smoothly from the cusp, with no
450 abrupt demarcation between cusp and crest. The crest is low, stout, and in anterior view slopes
451 ventrolabially as it crosses the trigonid to the base of the protoconid; there it swings sharply
452 posterodorsally to ascend the anterior face of the protoconid as a weak crest to near the apex of
453 the cusp, where it disappears. The paraconid and protoconid arms of the paracristid are about
454 equal in length and faintly crenulated along their cutting edges. A well-developed precingulid
455 slopes posteroventrally from the middle of the paracristid to the base of the trigonid on its labial
456 side. The posterior wall of the m2 meets the anterior face of the m3 trigonid immediately lingual
457 to the lingualmost extent of the precingulid. The protoconid is roughly 2.5 times the height of
458 the paraconid, is substantially more massive, and is stout overall. At its base, the protoconid is
459 wider than long; in cross section, it is subtriangular, with a convex anterolabial side, a flat
460 posterior side that is nearly transverse but lingually turns weakly posteriorly, and a swollen
461 lingual side that faces the trigonid basin. The apex of the protoconid has been worn away,
462 leaving a small, circular cavitation, but from the parts that remain, it seems clear that the apex,
463 although narrow, was bluntly rounded originally, not sharply acute. The metaconid is the tallest
464 trigonid cusp, slightly exceeding the protoconid in height, but like the protoconid, is stoutly
465 constructed; at its base, the length and width of the metaconid are subequal. The base of the
466 metaconid abuts the paraconid, but more dorsally, the opposing sides of the two cusps diverge
467 strongly from one another. The lingual side of the metaconid is significantly swollen, its labial
468 side less so, and its posterior side, contributing to the lingual half of the postvallid wall, is nearly
469 flat; this part of the wall is oriented more obliquely posterolingually than the labial half, beneath
470 the protoconid, and slopes less steeply. The protocristid is a low crest, with the two subequal
471 arms forming a V-shaped notch of about 80 degrees.

The talonid of m3 is longer but narrower than the trigonid. Each of the three major talonid cusps is well developed, and their apices are slightly worn. The hypoconid is the lowest talonid cusp but the most massive, with somewhat swollen labial and lingual walls. The cristid obliqua extends from the apex of the hypoconid to the posterior wall of the trigonid, which it meets directly beneath the deepest part of the protocristid notch, then ascends a short distance on the wall. The crest curves slightly labially along its length; the crest adjacent to the hypoconid is swollen and elevated, and a small apical wear facet here suggests the development of an incipient mesoconid. The hypoflexid is narrow and deep. The talonid is expanded posteriorly to form a robust and enlarged lobe on which is developed a vertically oriented, subconical hypoconulid, which, although low, is the tallest talonid cusp. The hypoconulid is located just lingual to the anteroposterior midline of the crown, closer to the entoconid than to the hypoconid, but the two cusps are not twinned. An anterodorsally facing wear facet has truncated the apex of the hypoconulid, so its original height cannot be determined. The hypocristid curves labially and anteriorly from the hypoconid apex, contributing to the enlarged posterior lobe; the crest is interrupted along its length by a deep slit-like notch that extends lingually into the basin, imparting a somewhat furrowed appearance to the talonid. The postcristid, between the hypoconulid and entoconid, is very broadly U-shaped (i.e., broadly open dorsally), with no notch developed along its length. The entoconid is taller than the hypoconid, is labiolingually compressed, and very slightly posterior to the level of the labial cusp. The entocristid slopes anteriorly into a shallow, dorsally concave talonid notch. The moderately deep talonid basin is ovate in outline, somewhat longer than wide, with shallowly concave sides except for the lingual wall of the hypoconid, which is swollen and hence convex. Labially, a short, anteroventrally steep postcingulid separates the posterior lobe of the talonid from the hypoconid. Although the

495 roots of m3 are mostly concealed within their alveoli, the posterior root is clearly the longer
496 anteroposteriorly in support of the elongated talonid, its usual configuration in the ultimate lower
497 molar of plesiadapiforms.

498 The m3 differs from the m2 of *Purgatorius pinecreeensis* as follows: it is longer, but
499 narrower; it is lower crowned (both trigonid and talonid); each of the trigonid cusps and the
500 hypoconid and entoconid are smaller and less robust than in m2, but the hypoconulid is more
501 strongly developed, and arises from within an enlarged posterior lobe of the talonid;
502 the precingulid is longer ventrally, curving to the base of the trigonid on its labial side; the
503 paraconid is less distinctly set off from the paracristid, melding more smoothly into the crest than
504 in m2; the paraconid is slightly more inset labially from the lingualmost extent of the trigonid
505 wall, beneath the metaconid; the talonid is narrower and longer; the hypoflexid is shallower and
506 wider; the hypoconulid is further from the hypoconid and entoconid owing to the expanded
507 posterior lobe of the talonid from which it arises; the entoconid is lower and more labiolingually
508 compressed; and the talonid notch is longer and shallower.

509

510 **Comparison with other species of *Purgatorius***

511 When compared with other Puercan plesiadapiforms, the dentition of *Purgatorius pinecreeensis*
512 most closely resembles those of species of *Purgatorius*, leaving little doubt of its proper
513 inclusion in the Purgatoriidae, and as a species of *Purgatorius* in particular. As noted previously,
514 the dentitions of the various species currently included in *Purgatorius* are distinguished from one
515 another primarily by subtle differences in premolar and molar anatomy; in this sense, *P.*
516 *pinecreeensis* continues the trend, but the teeth display differences that suggest a departure from
517 the more insectivorous-omnivorous dentitions of other *Purgatorius* species. Here, we compare

the dentition of *P. pinecreeensis* to those of other species of *Purgatorius*. Following Silcox and Gunnell (2008), we accept for the purposes of this comparison that *P. titusi* Buckley, 1997 from Simpson Quarry, Montana, is a junior synonym of *P. unio* Van Valen and Sloan, 1965 from Purgatory Hill, Montana.

Purgatorius unio: *P. unio* is known from the hypodigm from Purgatory Hill, eastern Montana, as well as from a significantly larger sample from the Pu2/3 Simpson Quarry of southern Montana (Van Valen and Sloan 1965; Buckley 1994, 1997; Van Valen 1994; Fox et al. 2015). With respect to the upper dentition, comparisons can presently only be made with M1, the only locus known for both taxa. The M1 of *P. unio*, from both Purgatory Hill and Simpson Quarry, differs from that of *P. pinecreeensis* in several ways. The tooth is larger overall [M1, *P. unio* mean Lg = 1.75, mean W = 2.67 (Buckley 1997) versus M1, *P. pinecreeensis* Lg = 1.53, mean W = 2.14], the parastylar process is less acute (more rounded), and the stylar shelf is wider. The protocone is larger in *P. unio*, more strongly deflected anteriorly, exhibiting a strong postprotocone shift, is more lingually extending at its base, and its lingual face slopes more steeply labially. Further, the pre- and postcingula are more robust in *P. unio*, and an incipient hypocone is present on some specimens. As noted previously, we have tentatively referred an isolated p4 from the Pine Cree Park locality to *P. pinecreeensis*, and although this tooth closely resembles p4 of *P. unio* from Simpson Quarry in its major features (e.g., both are premolariform, with the crown supporting a tall protoconid and a small talonid, and both bear two roots), the p4 of *P. unio* differs in several respects. For example, UM 90167 displays a small but distinct paraconid, positioned at about two-thirds the height of the protoconid and facing anterolingually (this is also true of the single p4 referred to *P. unio* from Purgatory Hill, UMVP 1616; Van Valen 1994) (an irregularity of the enamel in this position is present in RSM P3195.5, but no

541 cusp remains, perhaps as a consequence of the diagenetic corrosion that this tooth has
542 undergone). Further, the talonid in UM 90167 is roughly half the height of the protoconid,
543 thereby being somewhat taller relatively than in RSM P3195.5, and is incomplete, being open
544 lingually, and bears what are likely an entoconid and a smaller hypoconid (see Fox et al. 2015)
545 posteriorly. The occlusal surface of the talonid in RSM P3195.5 is similarly developed to that in
546 UM 90167, but as already noted no trace of talonid cusps, if present originally, remains on the
547 specimen. The lower molars of *P. unio* are well represented in the collections from Simpson
548 Quarry and show consistent differences from those of *P. pinecreeensis*, irrespective of locus
549 (Fig. 3). Overall, the lower molars of *P. unio* differ from those of *P. pinecreeensis* in being
550 slightly larger (length and width) and slightly higher crowned, and the trigonid is taller relative to
551 the talonid (Fig. 3A, D). They have a weaker developed paraconid that is positioned more
552 anteriorly, farther from the metaconid, and in some specimens is indistinguishable from the
553 paracristid. The molar paracristid is longer and more robust in *P. unio*, and together with the
554 paraconid is deflected more anteriorly. The walls on the protoconid, metaconid, and hypoconid
555 are notably less swollen in *P. unio*, and the metaconid is larger relative to the protoconid (Fig.
556 3J). On m1 and m2, the talonid basin is both narrower and deeper, the hypoconulid is more
557 cuspidate, and on m3 the posterior lobe is considerably less lobate, with a taller and more finger-
558 like hypoconulid and a taller and more cuspidate entoconid. In some features, there is some
559 overlap between the species, for example: in UM 90197 (m2), the walls of the protoconid and
560 metaconid are about equally inflated as in m2 of RSM P3195.1, but the other differences cited
561 above nonetheless pertain.

562 *Purgatorius janisae*: *P. janisae* is represented by large samples from the Pu3 Garbani
563 Channel localities of northeastern Montana (Clemens 2004), and is to date the best-known

species of *Purgatorius*. The P4 of *P. janisae* (figured in Kielan-Jaworowska et al. 1979) differs from RSM P3195.2 in being substantially larger and in the more robust development of the major cusps and crests. The crown is longer relative to its width, displays a distinct, well-developed metacone arising from the posterior ‘shoulder’ of the paracone, a stronger paracingulum+preprotocrista, an inflection in the position of a paraconule, and a protocone that is both taller relative to the height of the paracone and deflected anteriorly. The M1 of *P. janisae* is substantially larger than that of *P. pinecreeensis* [M1, *P. janisae* Lg = 1.95, W = 2.6 (estimated from LACM 28128, incomplete left maxilla with P4, M1-2, as figured in Kielan-Jaworowska et al. 1979, fig. 12-21) versus M1, *P. pinecreeensis* Lg = 1.53, mean W = 2.14] and its coronal features are considerably more robust. The crown is anteroposteriorly longer relative to width than is M1 of *P. pinecreeensis*, especially those parts of the crown lingual to the paracone and metacone, resulting in a relatively narrower trigon basin in *P. janisae*. Further, the pre- and postcingula are more robust in *P. janisae*, with the latter displaying at least an incipient hypocone. With regard to the lower dentition, the p4 of *P. janisae* differs most notably from that of *P. pinecreeensis* in being larger and in having a well-developed paraconid arising from relatively high on the protoconid; it further differs in having a relatively better developed and taller talonid that generally bears one or two distinct cusps (although there is significant variation in this feature, see Silcox, 2001). The lower molars of *P. janisae* are larger and slightly higher crowned than those of *P. pinecreeensis*, the trigonid is taller relative to the talonid, and the major cusps are more acute. In many respects the molars of *P. janisae* differ from those of *P. pinecreeensis* in ways similar to those of *P. unio*. For example, the trigonid leans farther anteriorly, and the paraconid is generally taller (i.e., arising from higher on the metaconid) but is much less distinct from the paracristid, and the paraconid+paracristid is oriented more

transversely (as opposed to having an anterior protoconid arm and a transverse paraconid arm). The protoconid, metaconid, and hypoconid are much less swollen; as a result, the protocristid notch is wider (i.e., the angle is less acute), resulting at least in part from the apices of the protoconid and metaconid being farther apart (also a measure of how swollen the cusp bases are in *P. pinecreeensis*), and the hypoflexid is longer and deeper. Further, the talonid is wider relative to length, especially that on m2, and the basin deeper, the entoconid is more posterior, and the posterior lobe on m3 is much less lobate.

Purgatorius coracis: Perhaps the most relevant comparison is between the dentitions of *P. pinecreeensis* and *P. coracis* (Fig. 3): both species are known from the Puercan of southwestern Saskatchewan (Pine Cree Park and Rav W-1, the type locality for *P. coracis*, are approximately 30 km from one another), although *P. coracis* is slightly older (Fox and Scott 2011; Redman et al. 2015). As regards the upper dentition, UALVP 51003, a left P4 of *P. coracis* is slightly larger than RSM P3195.2 and more robust. It lacks a parastyle, has an interconnected paracingulum and preprotocrista, a narrow precingulum, a better developed postprotocrista, and the protocone is anteriorly deflected. UALVP 51002 displays many of these features, but possesses a parastylar cusp, an incipient metacone and a postprotocrista that joins with the postcingulum. However, it resembles RSM P3195.2 more closely than does UALVP 51003 in being more gracile, and is transversely wider relative to its length. The M1 of *P. coracis* is known from an incomplete specimen (UALVP 51019), but in the parts that can be compared, differs from M1 of *P. pinecreeensis*. UALVP 51019 is wider and less gracile (more robust) in coronal features when compared with RSM P3195.4. The metacone is lower relative to the height of the paracone, the ectoflexus is somewhat more posterior in position, and both the paracone and metacone are lower relatively than in *P. pinecreeensis* and more robust (although

610 the walls of these cusps are not swollen, a condition also seen on the several M2s referred to *P.*
611 *coracis*, e.g., UALVP 51021). The protocone is more strongly deflected anteriorly in *P. coracis*,
612 and a postprotocone shift is evident, and the pre- and postcingula are more robust and extend
613 farther lingually, lending a 'squarish' occlusal outline to the lingual margin of the crown. The
614 sample of lower molars of *P. coracis* is small but includes more than one specimen at each locus,
615 with all but one specimen consisting of isolated teeth (Fox and Scott 2011; Fig. 3). The lower
616 molars of *P. coracis* are slightly higher crowned, with less swollen major cusps, and the trigonid
617 is taller relative to the talonid (Fig. 3B, E, K). The paraconid is smaller, less distinct from the
618 paracristid, and the paracristid is shorter and tends to be more oblique anterolingually (and the
619 occlusal outline of the trigonid more triangular on that account). The molar paraconid is in a
620 more labial position in *P. coracis*, although in this feature there is a degree of individual
621 variation, at least on m1 and m2: for example, in UALVP 51009, a left m1, the paraconid is in a
622 lingual position, even more lingual than in m1 of RSM P3195.1, and in UALVP 51014, a right
623 m2, the paraconid is also in a lingual position and the paracristid long, resembling m2 of *P.*
624 *pinecreeensis*, but in other features the differences from the lower molars of *P. pinecreeensis* are
625 maintained. The protoconid and metaconid are taller, less inflated, and the protocristid notch is
626 deeper in *P. coracis*, and like the lower molars of *P. janisae*, the apical width between
627 protoconid and metaconid is more nearly equal to the width of the trigonid at its base (Fig. 3K).
628 The talonid basin on m1-2 is longer and wider, with the posterior rim being more 'squared off'
629 (i.e., less convex posteriorly), the hypoconulid is weaker, and a faint ectocingulid, connecting
630 precingulid and postcingulid, is commonly present. Comparison of the m3 of *P. coracis* and
631 RSM P3195.1 adds locus- specific features not seen in m1 and m2. The paraconid in m3 of *P.*
632 *coracis* is still more labially positioned than in m1 and m2 of this species, and the paracristid

shorter and more strongly oblique anterolingually (lending a still more triangular occlusal outline to the trigonid), all in contrast to their counterparts on m3 in RSM P3195.1. Moreover, the talonid basin of m3 is shallower in *P. coracis*, and the posterior lobe of the talonid is not so sharply differentiated from the remainder of the talonid as in RSM P3195.1.

Conclusion

The earliest primates, to date represented principally by purgatoriids, have been characterized as having been primarily insectivorous, although their relatively lower crowned molars and less acute cusps suggest a diet that was likely more varied than those of contemporaneous, more strictly insectivorous eutherians (Van Valen 1994; Silcox and Gunnell 2008). The dentition of *Purgatorius pinecreeensis* represents a departure from that seen in other purgatoriids: the slightly lower crowned molars, with notably swollen cusps, blunter crests, and expanded m3 talonid are specializations that enhanced the capacity for crushing and grinding at the expense of orthal shear (Kay and Hiiemae 1974; Lucas 1979, 2004; Strait 1997). Taken together, these features represent the advent of a modest degree of bunodonty in the family, and suggest that whatever the dietary preferences of *P. pinecreeensis* might have been, they probably included more resistant food items, such as seeds. Bunodonty is a relatively common dental specialization found in several plesiadapiforms, in some cases first occurring in the basalmost members and characterizing the family (e.g., Picrodontidae Simpson, 1937) (Scott and Fox 2005), in others developing at some point within the evolutionary history of the family (e.g., Palaechthonidae Szalay, 1969 and Micromomyidae Szalay, 1974) (Silcox and Gunnell 2008; Chester and Bloch 2013). While the dentition of *P. pinecreeensis* does not exhibit bunodonty to the same degree as many stratigraphically younger plesiadapiforms, the teeth are distinct from those of

contemporaneous purgatoriids, with several of the dental specializations paralleling those features seen in the Puercan plesiadapiform *Pandemonium* (e.g., trigonid and talonid more nearly equal in height, cusp inflation, expanded m3 talonid posterior lobe; Van Valen 1994; Fox et al. 2014). The specializations for bunodonty in *P. pinecreeensis* are combined with an otherwise primitive dentition, resulting in a mosaic of characters, a condition that, given recent discoveries, seems to characterize several of the earliest primates, including *P. coracis* and *Ursolestes* (Fox and Scott 2011; Fox et al. 2015). For example, the dentition of *P. pinecreeensis* includes p1 and relatively lingual molar paraconids, both primitive characters among eutherians generally; in contrast, the lower molar trigonid, inflated cusps, and enlarged and more lobate m3 talonid are almost certainly derived relative to their alternatives in other *Purgatorius* species (Silcox 2001; Silcox and Gunnell 2008; Fox and Scott 2011). We contend that the modest bunodonty seen in the teeth of *P. pinecreeensis* represents a derived condition among purgatoriids and early primates generally, and this hypothesis is valid irrespective of whether the ancestral primate dentition was characterized by omnivorous adaptations, as has been the traditional view, or as recently proposed, by a dentition that was adapted more for orthal shear (Silcox and Gunnell 2008; Fox 2011).

The discovery of *P. pinecreeensis* doubles the number of purgatoriid species from the Puercan of southwestern Saskatchewan; a third purgatoriid, known from several specimens from the ?Pu2 Croc Pot locality, located approximately 1.5 km southwest of the Rav W-1 locality at the former Medicine Hat Brick and Tile Quarry, is currently under study and will be published elsewhere (Spivak 1997; Scott and Fox, in prep.). These occurrences, combined with newly discovered purgatoriids and other basal plesiadapiforms from Puercan, and possibly early Torrejonian deposits in Alberta and Montana (Rankin and Fox 2007; Clemens and Wilson 2009;

Fox and Scott 2011; Fox et al. 2014; Fox et al. 2015) suggest that a significant primate radiation occurred during the earliest parts of the Paleocene in the northern parts of the Western Interior, and that this radiation was already well under way by Pu2/3 time. As has been suggested previously, given the occurrence of purgatoriids in the early Puercan in sediments that have been interpreted as being in magnetochron 29r, the origin of plesiadapiforms, and potentially their immigration into the more northern parts of the Western Interior, almost certainly occurred in the Late Cretaceous (Clemens 2004; Silcox 2008; Fox and Scott 2011).

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References

Archibald, J. D. and D. L. Lofgren. 1990. Mammalian zonation near the Cretaceous-Tertiary boundary. *In* Dawn of the Age of Mammals in the Northern Part of the Rocky Mountain Interior, North America. *Edited by* T. M. Bown and K. D. Rose. Geological Society of America Special Paper, **243**: 31–50.

- 702 Bloch, J. I., M. T. Silcox, D. M. Boyer, and E. J. Sargis. 2007. New Paleocene
703 skeletons and the relationship of plesiadapiforms to crown-clade primates. Proceedings of
704 the National Academy of Sciences of the United States of America, **104**: 1159–1164.
- 705 Buckley, G. A. 1994. Paleontology, geology, and chronostratigraphy of Simpson Quarry
706 (early Paleocene), Bear Formation, Crazy Mountains Basin, south-central Montana.
707 Unpublished Ph. D. dissertation, Department of Geology, Rutgers, The State University
708 of New Jersey, New Brunswick, New Jersey.
- 709 Buckley, G. A. 1997. A new species of *Purgatorius* (Mammalia; Primatomorpha) from
710 the lower Paleocene Bear Formation, Crazy Mountains Basin, south-central Montana.
711 Journal of Paleontology, **71**: 149–155.
- 712 Chester, S. G. B. and J. I. Bloch. 2013. Systematics of Paleogene Micromomyidae (Euarchonta,
713 Primates) from North America. Journal of Human Evolution, **65**: 109–142.
- 714 Chester, S. G. B., J. I. Bloch, D. M. Boyer, and W. A. Clemens. 2015. Oldest known euarchontan
715 tarsals and affinities of Paleocene *Purgatorius* to Primates. Proceedings of the National
716 Academy of Science, **112**: 1487–1492.
- 717 Clemens, W.A. 1966. Fossil mammals of the type Lance Formation, Wyoming. Part II.
718 Marsupialia. University of California Publications in Geological Sciences, **62**: 1–122.
- 719 Clemens, W. A. 1974. *Purgatorius*, an early paromomyid primate. Science, **184**: 903–
720 905.
- 721 Clemens, W. A. 2004. *Purgatorius* (Plesiadapiformes, Primates?), a Paleocene
722 immigrant into northeastern Montana: stratigraphic occurrences and incisor proportions.
723 Bulletin of Carnegie Museum of Natural History, **36**: 3–13.

- 724 Clemens, W. A. and G. P. Wilson. 2009. Early Torrejonian mammalian local faunas from
725 northeastern Montana, U.S.A. *In* Papers on Geology, Vertebrate Paleontology and
726 Biostratigraphy in Honor of Michael O. Woodburne. *Edited by* L. B. Albright II. Museum
727 of Northern Arizona Bulletin, **65**: 111–158.
- 728 Dawson, G. M. 1875. Report on the geology and resources in the vicinity of the Forty-ninth
729 parallel, from the Lake of the Woods to the Rocky Mountains. British North American
730 Boundary Commission, Montreal, 387 pp.
- 731 Fox, R. C. 1990. The succession of Paleocene mammals in western Canada. *In*
732 Dawn of the Age of Mammals in the Northern Part of the Rocky Mountain Interior,
733 North America. *Edited by* T. M. Bown and K. D. Rose. Geological Society of America
734 Special Paper, **243**: 51–70.
- 735 Fox, R. C. 2002. The oldest Cenozoic mammal? *Journal of Vertebrate Paleontology*, **22**: 456–
736 459.
- 737 Fox, R. C. 2011. An unusual early primate from the Paleocene Paskapoo Formation,
738 Alberta, Canada. *Acta Palaeontologica Polonica*, **56**: 1–10.
- 739 Fox, R. C., and C. S. Scott. 2011. A new, early Puercan (earliest Paleocene) species of
740 *Purgatorius* (Plesiadapiformes, Primates) from Saskatchewan, Canada. *Journal of*
741 *Paleontology*, **85**: 537–548.
- 742 Fox, R. C., C. S. Scott, B. D. and Rankin. 2010. New early carnivoran specimens from the
743 Puercan (earliest Paleocene) of Saskatchewan, Canada. *Journal of Paleontology*, **84**:
744 1035–1039.

- 745 Fox, R. C., C. S. Scott, and G. F. Buckley. 2015. A 'giant' purgatoriid (Plesiadapiformes) from
746 the Paleocene of Montana, USA: mosaic evolution in the earliest primates.
747 *Palaeontology*, 58: 277–291.
- 748 Fox, R. C., C. S. Scott, B. D. Rankin, and A. R. Sweet. 2014. Second known occurrence of the
749 early Paleocene plesiadapiform *Pandemonium* (Mammalia: Primates), with description of
750 a new species. *Canadian Journal of Earth Sciences*, **51**: 1059–1066.
- 751 Ickert, R. B., S. R. Mulcahy, C. J. Sprain, J. F. Banaszak, and P. R. Renne. 2015. Chemical and
752 Pb isotope composition of phenocrysts from bentonites constrains the chronostratigraphy
753 around the Cretaceous-Paleogene boundary in the Hell Creek region, Montana.
754 *Geochemistry, Geophysics, Geosystems*, **16**: 2743–2761.
- 755 Johnston, P. A. 1980. Late Cretaceous and Paleocene mammals from southwestern
756 Saskatchewan. Unpublished M.Sc. thesis, Department of Geology, The University of
757 Alberta, Edmonton, Alberta.
- 758 Johnston, P. A., and R. C. Fox. 1984. Paleocene and Late Cretaceous mammals from
759 Saskatchewan, Canada. *Palaeontographica A*, **186**: 163–222.
- 760 Kay, R. F. and K. M. Hiiemae. 1974. Jaw movement and tooth use in recent and fossil primates.
761 *American Journal of Physical Anthropology*, **40**: 227–256.
- 762 Kay, R. F. and M. Cartmill. 1977. Cranial morphology and adaptations of *Palaechthon*
763 *nacimienti* and other Paromomyidae (Plesiadapoidea, ?Primates), with a description of a
764 new genus and species. *Journal of human Evolution*, **6**: 19–53.
- 765 Kielan-Jaworowska, Z., T. M. Bown, and J. A. Lillegraven. 1979. Eutheria. *In* Mesozoic
766 mammals: The first two-thirds of mammalian history. *Edited by* J. A. Lillegraven, Z.

- 767 Kielan-Jaworowska, and W. A. Clemens. University of California Press, Berkeley. pp.
768 221–258.
- 769 Krause, D.W. 1977. Paleocene multituberculates (Mammalia) of the Roche Percée local fauna,
770 Ravenscrag Formation, Saskatchewan, Canada. *Palaeontographica Abt. A*, **159**: 1–36.
- 771 Krause, D. W. 1978. Paleocene primates from western Canada. *Canadian Journal of Earth*
772 *Sciences*, **15**: 1250–1271.
- 773 Lerbekmo, J. F. 1985. Magnetostratigraphic and biostratigraphic correlations of Maastrichtian to
774 early Paleocene strata between south-central Alberta and southwestern Saskatchewan.
775 *Bulletin of Canadian Petroleum Geology*, **33**: 213–226.
- 776 Linnaeus, C. 1758. *Systema naturae per regna tria naturae, secundum classes, ordines,*
777 *genera, species cum characteribus, differentiis, synonymis, locis. Editio decima,*
778 *reformata, I: Regnum animale. Laurentii Salvii, Stockholm.*
- 779 Lofgren, D. L., J. A. Lillegraven, W. A. Clemens, P. D. Gingerich, and T. E.
780 Williamson. 2004. Paleocene biochronology: the Puercan through Clarkforkian
781 land mammal ages. *In* *Cenozoic Mammals of North America. Edited by* M. O.
782 Woodburne. University of California Press, Berkeley. pp. 43–105.
- 783 Lucas, P. W. 1979. The dental-dietary adaptations of mammals. *Neues Jahrbuch für Geologie*
784 *und Paläontologie*, **8**: 486–512.
- 785 Lucas, P. W. 2004. *Dental functional morphology*. Cambridge University Press, New York.
- 786 McIver, E.E., and Basinger, J.F. 1993. *Flora of the Ravenscrag Formation (Paleocene),*
787 *southwestern Saskatchewan, Canada. Palaeontographica Canadiana*, **10**: 1–167.
- 788 McKenna, M.C., and Bell, S.K. 1997. *Classification of Mammals Above the Species Level*.
789 Columbia University Press, New York, 631 pp.

- 790 McLearn, F.H. 1929. Southern Saskatchewan. Canada Geological Survey Summary Report
791 1928, Part B: 30–45.
- 792 Naylor, B. G. 1978. The earliest known *Necturus* (Amphibia, Urodela) from the Paleocene
793 Ravenscrag Formation of Saskatchewan. *Journal of Herpetology*, **12**: 565–569.
- 794 Naylor, B. G. and D. W. Krause. 1981. *Piceoerpeton*, a giant early Tertiary salamander from
795 western North America. *Journal of Paleontology*, 55: 507–523.
- 796 Ni, X.-J., D. L. Gebo, M. Dagosto, J. Meng, P. Tafforeau, J. J. Flynn, and K. C.
797 Beard. 2013. The oldest known primate skeleton and early haplorhine evolution. *Nature*,
798 **498**: 60–64.
- 799 Ogg, J. G. 2012. The Geomagnetic Polarity Time Scale. *In* The Geologic Time Scale 2012.
800 Edited by F. M. Gradstein, J. G. Ogg, M. D. Schmitz, and G. M. Ogg. Elsevier,
801 Philadelphia. pp. 85–113.
- 802 O’Leary, M. A., J. I. Bloch, J. J. Flynn, T. J. Gaudin, A. Giallombardo, N. P.
803 Giannini, S. L. Goldberg, B. P. Kraatz, Z.-X. Luo, J. Meng, X. Ni, M. J. Novacek, F. A.
804 Perini, Z. S. Randall, G. W. Rougier, E. J. Sargis, M. T. Silcox, N. B. Simmons, M.
805 Spaulding, P. M. Velazco, M. Weksler, J. R. Wible, and A. L. Ciranello. 2013. The
806 placental mammal ancestor and the post-K–Pg radiation of placentals. *Science*, **339**: 662–
807 667.
- 808 Rankin, B. D. and R. C. Fox. 2007. A new early Paleocene mammal locality from southern
809 Alberta. *Journal of Vertebrate Paleontology*, **27** (supplement to 3): 132A.
- 810 Redman, C. M., J. D. Gardner, C. S. Scott, and D. R. Braman. 2015. Geological setting of
811 vertebrate microfossil localities across the Cretaceous-Paleogene boundary in
812 southwestern Saskatchewan, Canada. *Canadian Journal of Earth Sciences*, **52**: 846–862.

- 813 Russell, L.S. 1974. Fauna and correlation on the Ravenscrag Formation (Paleocene) of
814 southwestern Saskatchewan. Royal Ontario Museum Life Sciences Contribution, **102**: 1–
815 52.
- 816 Scott, C. S., and R. C. Fox. 2005. Windows on the evolution of *Picrodus*
817 (Plesiadapiformes: Primates): morphology and relationships of a species complex from
818 the Paleocene of Alberta. *Journal of Paleontology*, **70**: 635–662.
- 819 Silcox, M. T. 2001. A phylogenetic analysis of Plesiadapiformes and their relationship to
820 Euprimates and other archontans. Unpublished Ph. D. dissertation, School of Medicine,
821 The Johns Hopkins University, Baltimore, Maryland.
- 822 Silcox, M. T. 2007. Primate taxonomy, plesiadapiforms, and approaches to primate origins. *In*
823 *Primate Origins and Adaptations: A Multidisciplinary Perspective*. Edited by M. J.
824 Ravosa and M. Dagosto. Springer, New York. pp.143–178.
- 825 Silcox, M. T. 2008. The biogeographic origins of Primates and Euprimates: east, west, north, or
826 south of Eden? *In* *Mammalian Evolutionary Morphology: A Tribute to Frederick S.*
827 *Szalay. Edited by* E. J. Sargis and M. Dagosto. Springer, Dordrecht, Germany. pp. 199–
828 231.
- 829 Silcox, M. T., and G. F. Gunnell. 2008. Plesiadapiformes, *In* *Evolution of Mammals of*
830 *North America. Edited by* C. M. Janis, G. F. Gunnell, and M. D. Uhen. Cambridge
831 University Press, Cambridge, U. K. pp. 207–238.
- 832 Simons, E. L. 1972. *Primate Evolution: An Introduction to Man's Place in Nature*. The
833 Macmillan Company, New York.
- 834 Simpson, G. G. 1937. The Fort Union of the Crazy Mountain Field, Montana, and its mammalian
835 faunas. *Bulletin of the United States National Museum*, **169**: 1–287.

- 836 Spivak, D. N. 1997. Early Paleocene (Puercan) mammals from the Ravenscrag Formation,
837 Saskatchewan, Canada. *Journal of Vertebrate Paleontology*, **17** (supplement to 3): 78A.
- 838 Sprain, C. J., P. R. Renne, G. P. Wilson, and W. A. Clemens. 2014. High-resolution
839 chronostratigraphy of the terrestrial Cretaceous-Paleogene transition and recovery
840 interval in the Hell Creek region, Montana. *Geological Society of America Bulletin*, **127**:
841 393–409.
- 842 Strait, S. G. 1997. Tooth use and the physical properties of food. *Evolutionary Anthropology*, **5**:
843 199–211.
- 844 Szalay, F. S. 1968. The beginnings of primates. *Evolution*, **22**: 19–36.
- 845 Szalay, F. S. 1969. Mixodectidae, Microsyopidae, and the insectivore-primate transition. *Bulletin*
846 *of the American Museum of Natural History*, **140**: 193–330.
- 847 Szalay, F. S. and E. Delson. 1979. *Evolutionary History of the Primates*. Academic Press, New
848 York, 580 pp.
- 849 Van Valen, L. 1966. Deltatheridia, a new order of mammals. *Bulletin of the American Museum*
850 *of Natural History*, **132**: 1–126.
- 851 Van Valen, L. M. 1994. The origin of the plesiadapid primates and the nature of
852 *Purgatorius*. *Evolutionary Monographs*, **15**: 1–79.
- 853 Van Valen, L. M. and R. E. Sloan. 1965. The earliest primates. *Science*, **150**: 743–745.
- 854 Woodburne, M.O. (ed.) 2004. *Late Cretaceous and Cenozoic Mammals of North America*.
855 University of California Press, Berkeley, USA, 391 pp.
- 856
- 857

858 Figure Captions

859

860 Fig. 1. Map of the Ravenscrag-Eastend-Shaunavon area of southwestern Saskatchewan, Canada
861 showing the Medicine Hat Brick and Tile Quarry Rav W-1 horizon and Pine Cree Park localities.

862

863 Fig. 2. *Purgatorius pinecreeensis* sp. nov. from the middle Puercan (?Pu2) Pine Cree Park
864 locality, Ravenscrag Formation, southwestern Saskatchewan. RSM P3195.2, LP4 in (A) labial,
865 (B) lingual, and (C) occlusal views. RSM P3195.4, RM1 in (D) labial, (E) lingual, and (F)
866 occlusal views. RSM P3195.3, LM1 in (G) labial, (H) lingual, and (I) occlusal views. RSM
867 P3195.5, Lp4 in (J) labial, (K) lingual, and (L) occlusal views. RSM P3195.1, holotype,
868 incomplete right dentary (in two parts) with m1-3 and alveoli for c (partial), p1-4 in (M) labial,
869 (N) lingual, and (O) occlusal views; posterior part of RSM P3195.1 with m2-3 in (P) occlusal
870 view, rotated slightly lingually and posteriorly. Scale bar = 2 mm.

871

872 Fig. 3. *Purgatorius unio* from the middle/late (Pu2/3) Simpson Quarry, Bear Formation,
873 Montana, *Purgatorius coracis* from the middle Puercan (Pu2) Rav W-1 locality, Ravenscrag
874 Formation, southwestern Saskatchewan, and *Purgatorius pinecreeensis* sp. nov. from the middle
875 Puercan (?Pu2) Pine Cree Park locality, Ravenscrag Formation, southwestern Saskatchewan. *P.*
876 *unio*, composite lower dentition (UM 90180, Rm1, UM 90198, Lm2 [reversed from original],
877 UM 90202, Rm3) in (A) labial, (D) lingual, and (G) occlusal views. *P. coracis*, composite lower
878 molar dentition (UALVP 51009, Rm1, UALVP 51012, Rm2, and UALVP 51018, Rm3) in (B)
879 labial, (E) lingual, and (H) occlusal views. *P. pinecreeensis*, sp. nov., RSM P3195.1, holotype,
880 incomplete right dentary (in two parts) with m1-3 and alveoli for c (partial), p1-4 in (C) labial,

881 (F) lingual, and (I) occlusal views. Enlarged anterior view of (J) UM 90198, Lm2 [reversed
882 from original], *P. unio*, (K) UALVP 51012, Rm2, *P. coracis*, and (L) RSM P3195.1, Rm2
883 (remainder of holotype digitally cropped), *P. pinecreeensis*. Scale bar = 2 mm.

Draft

Figure 2
236x308mm (300 x 300 DPI)

Figure 3
236x308mm (300 x 300 DPI)