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Source: Acta Palaeontologica Polonica, 56(1) : 1-10

Published By: Institute of Paleobiology, Polish Academy of Sciences

URL: <https://doi.org/10.4202/app.2009.0079>

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An unusual early primate from the Paleocene Paskapoo Formation, Alberta, Canada

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Fox, R.C. 2011. An unusual early primate from the Paleocene Paskapoo Formation, Alberta, Canada. *Acta Palaeontologica Polonica* 56 (1): 1–10.

A new plesiadapiform primate, *Phoxomylus puncticuspis* gen. et sp. nov., is described based on an isolated but well-preserved upper molar from the early Tiffanian (late Paleocene) Cochrane 2 locality, southwestern Alberta, Canada. Although possessing a robust postprotoconal fold, an unambiguous synapomorphy of primates, *Phoxomylus* differs from other plesiadapiforms in its retention of primitive molar features, including acutely pointed major cusps and sharp crests, deep trigon basin, and lack of the bunodont coronal specializations that purportedly marked the transition from insectivorous non-primate ancestors to omnivorous/frugivorous basal primates. Coronal features of the holotype of *P. puncticuspis* imply that during mastication the mandible was adducted in a near-vertical plane, with little capacity for the transverse movement that is already seen in molar morphology of the earliest and most basal plesiadapiform, *Purgatorius*. Instead, molar morphology in *P. puncticuspis* implies emphasis on vertical piercing and shearing, specializations for insectivory unlikely to have been derived via reversal from plesiadapiform ancestors having more bunodont molars adapted for omnivory/frugivory. If that is the case, a long “ghost lineage” must link *P. puncticuspis* to other, basal plesiadapiforms that have yet to be discovered but that had not yet evolved omnivorous adaptations of the dentition.

Key words: Primates, Plesiadapiformes, Paleocene, Alberta, Canada.

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Received 16 June 2009, accepted 14 September 2010, available online 20 September 2010.

Introduction

Ancestral primates are collectively known as plesiadapiforms, a group traditionally accorded the rank of suborder (Plesiadapiformes Simons, 1972) within Primates Linnaeus, 1758 (Silcox and Gunnell 2008; Boyer et al. 2010a), but often considered a paraphyletic assemblage of stem taxa plus Plesiadapoidea Trouessart, 1897; plesiadapoids have been hypothesized to be the sister group of Euprimates Hoffstetter, 1977 or primates of “modern aspect” (Bloch and Silcox 2001, 2006; Bloch and Boyer 2002; Silcox 2003; Bloch et al. 2007; Silcox and Gunnell 2008; Boyer 2009). Plesiadapiforms are best documented by fossils of Paleocene and Eocene age from the Western Interior of North America (Savage and Russell 1983; Woodburne 2004; Rose 2006), but they are also known from Europe, Asia, and perhaps, from Africa (Silcox 2008). The earliest and most basal plesiadapiform is *Purgatorius* Van Valen and Sloan, 1965, a small, shrew-sized early Paleocene mammal documented only by fragmentary jaws and teeth from the middle to late Puercan North American Land Mammal Age (NALMA) in Montana (Van Valen and Sloan 1965; Clemens 1974, 2004; Van Valen 1994; Buckley 1997; Silcox 2008; Silcox and Gunnell 2008), Saskatchewan (Johnston and Fox 1984; Fox and Scott in press), and Alberta (personal observation). Of particular relevance to the present study, however, are

slightly younger but still relatively primitive North American plesiadapiforms that are classified together in the family Palaechthonidae Szalay, 1969, containing two subfamilies, Palaechthoninae Szalay, 1969 and Plesiolestinae Gunnell, 1989, each appearing first in the Torrejonian NALMA (Lofgren et al. 2004). Overall, the record of palaechthonids is an impoverished one, both in regards the incompleteness of the discovered fossil specimens and the limited diversity that these fossils represent. Although recent cladistic analyses radically re-distribute the contents of Palaechthonidae, allying several of the included species separately with other, even distant clades of non-palaechthonid plesiadapiforms (e.g., Silcox 2007, 2008), it is doubtful that the limited quality of the available evidence justifies either the apparent refinement or the certainty in classification required by the results of these analyses. By contrast, Silcox and Gunnell (2008) recognized Palaechthonidae as a monophyletic taxon, the preferable, more conservative, “bookkeeping” option until the group is better known, and the option that is followed in this paper.

The taxon named and described herein, *Phoxomylus puncticuspis* gen. et sp. nov., is based on a single, well-preserved upper molar (UALVP 50991) that displays an unambiguous primate morphology but that has features which, while unexpectedly novel, are most like those of palaechthonids as recently diagnosed by Silcox and Gunnell (2008).

This specimen was collected from Cochrane 2, a locality just east of the village of Cochrane, southwestern Alberta, Canada (Youzwysyn 1988). Cochrane 2 has already yielded a rich mammalian fauna of early late Paleocene age (Youzwysyn 1988; Fox 1990b, 2005; Scott et al. 2002), including the plesiadapiforms *Palaechthon* Gidley, 1923 and *Torrejonia* Gazin, 1968 (Palaechthonidae), *Ignacius* Matthew and Granger, 1921 (Paromomyidae Simpson, 1940), *Elphidotarsius* Gidley, 1923 and *Carpodaptus* Matthew and Granger, 1921 (Carpolestidae Simpson, 1935b), *Picrodus* Douglass, 1908 (Picrodontidae Simpson, 1937), and *Pronothodectes* Gidley, 1923, *Nannodectes* Gingerich, 1975, and *Plesiadapis* Gervais, 1877 (Plesiadapidae Trouessart, 1897) (Youzwysyn 1988; Fox 1990b; Scott and Fox 2005). Besides adding a new, dentally primitive component to plesiadapiform diversity, the discovery of *Phoxomylus* augments the unique composition of the Canadian record of Paleocene plesiadapiforms as further evidence of significant latitudinal differentiation of North American mammals of this age. Moreover, it is becoming increasingly apparent that the Canadian record of Paleocene plesiadapiforms is not an impoverished sample of species otherwise known from correlative beds in the United States, but includes its own unique components that are of interest phylogenetically, paleobiogeographically, and paleoecologically (e.g., Krause 1978; Johnston and Fox 1984; Fox 1984a–c, 1990a, 1991a, b, 2002; Gingerich 1991; Silcox et al. 2001; Scott and Fox 2005; Boyer 2009; Fox et al. 2010; Fox and Scott in press).

Institutional abbreviation.—UALVP, University of Alberta Laboratory for Vertebrate Paleontology, University of Alberta, Edmonton, Canada.

Other abbreviations.—L, length; M, molar, NALMA, North American Land Mammal Age; P, premolar; W, width.

Geological setting

The Paskapoo Formation consists of continental sediments eroded from highlands to the west and deposited in the Alberta Foreland Basin during Paleocene time. Today, this unit comprises surface bedrock in western and central parts of the Alberta Plains, exposed at river banks, steep hillsides, road and railway cuts, and mines. The formation consists predominantly of interbedded sandstones, siltstones, and shales, but coal beds are locally common and some are of commercial importance. Paskapoo sediments were deposited in the channels and floodplains of small to moderate-sized rivers, and in ponds, lakes, and swamps. The Paskapoo landscape probably had little topographic relief and appears to have been thickly vegetated. The warm-temperate, humid coastal plain of the southeastern United States probably furnishes a realistic modern analogue of the Paskapoo environment.

At Cochrane 2, mammalian fossils occur intermittently along about 30 m of strike, within an interval ranging from a few centimeters to a meter or so in thickness (Fox 1990b). The

fossiliferous layers consist of poorly bedded grayish-green siltstones, rich in broken bivalve and gastropod shells that are accompanied by bits of coalified wood and occasional well-rounded pebbles. Disarticulated skeletal parts of lepisosteid and amiid fish, small teleosts, albanerpetontid allocaudates, batrachosauroidid and scapherpetontid salamanders, trionychid turtles, *Champsosaurus* sp., and *Leidyosuchus*-like crocodylians accompany the mammalian fossils at Cochrane 2.

References to this locality in the published literature have had a confusing history. Regrettably, Lofgren et al. (2004), although meant to be authoritative, ignored nomenclature published by Canadian workers familiar with Cochrane 2 (Fox 1990b; Scott et al. 2002) and referred to this locality as Cochrane “II”, thereby maintaining the basis for confusion with the name Cochrane “11”, also given to this locality but sometimes erroneously interpreted as designating a separate locality having a different age (e.g., Savage and Russell 1983; Gunnell 1989). Cochrane 2 is the unambiguous name for this important locality (i.e., Cochrane II and Cochrane 11 are its synonyms) and is used here on that account. Moreover, the formation name applied to the beds at Cochrane 2 has differed among authors: in some literature (e.g., Youzwysyn 1988; Fox 1990b), these beds have been considered to be part of the Porcupine Hills Formation (Carrigy 1970, 1971; Lofgren et al. 2004), but recent revisions to the lithostratigraphy of the continental Paleocene in southwestern Alberta refer them to the Paskapoo Formation (Lerbekmo and Sweet 2000), as had Tozer (1956) and Russell (e.g., 1958) before; I follow these revisions here.

Systematic paleontology

Conventions.—In measuring angles of occlusal surfaces of isolated upper molars, I have oriented the base of the crown lingual to the paracone/metacone in the horizontal plane, which approximates the orientation of plesiadapiform upper molars when articulated in the maxilla.

Order Primates Linnaeus, 1758

Suborder Plesiadapiformes Simons, 1972

Family ?Palaechthonidae Szalay, 1969

Subfamily ?Plesiolestinae Gunnell, 1989

Genus *Phoxomylus* nov.

Type species: *Phoxomylus puncticuspis* gen. et sp. nov.; see below.

Etymology: From Greek *phoxos*, pointed or peaked and Greek *mylos*, grinder, molar.

Diagnosis.—As for the type and only species.

Phoxomylus puncticuspis sp. nov.

Fig. 1.

Etymology: From Latin *punctus* and *cuspis*, in reference to the tall, acute major cusps on the holotype.

Holotype: UALVP 50991, left upper molar, probably M1 (only known specimen).

Type locality: Cochrane 2, 0.5 km east of Cochrane, Alberta, in SE1/4, S1, T26, R4, W5, at approximately 1059 m above sea level (Youzwyshyn 1988; Fox 1990b). The holotype was quarried by Gordon P. Youzwyshyn on 10 July 1988.

Type horizon: Paskapoo Formation, late Paleocene, earliest Tiffanian NALMA (*Plesiadapis praecursor*/*P. anceps* Lineage Zone [Ti1] of Archibald et al. [1987] and Lofgren et al. [2004]).

Diagnosis.—A plesiadapiform primate most closely resembling plesiolestine palaeotheriids in upper molar structure but differing from upper molars of all known plesiolestines by the following unique combination of characters: significantly larger size and more robust coronal proportions; tall, uninflated major cusps having acute apices; protocone lacking anterior inflection and posterior “twist”; strongly developed ectocingulum; wide, gutter-like paracingulum; deep trigon basin, not expanded lingually; precingulum and postcingulum extending labially to meet paracingulum and meta- cingulum, respectively; short but prominent postprotoconal fold joining with postcingulum to enclose narrow but well-defined talon basin; no hypocone developed.

Stratigraphic and geographic range.—Type locality and type horizon only.

Description.—UALVP 50991 (L = 3.7 mm; W = 4.8 mm) is subtriangular in occlusal view, with its anteroposterior length at the level of the paracone and metacone somewhat greater than more lingually, at the levels of the conules and protocone (Fig. 1). The anterior and posterior sides are subequal in length; the crown is slightly constricted at the conules and narrows further at the protocone, which is, nonetheless, stout and bluntly rounded lingually. The labial edge of the crown forms two weakly convex lobes that are nearly symmetrical in relation to the ectoflexus, but the metastylar lobe extends slightly more labially. The shallow ectoflexus is deepest just anterior to the level of the centrocrista notch. The ectocingulum is unusually robust for a plesiadapiform, forming a faintly crenulated, elevated ridge above the plane of the stylar shelf; the shelf itself is narrow. There is no mesostyle, although a weak ridge in the position of this cusp crosses the stylar shelf from the deepest part of the ectoflexus to the base of the postparacrista.

The anterior parastylar process (parastylar wing of Kielan-Jaworowska et al. 2004) projects weakly anteriorly and is broadly rounded, not acute or hook-like; the postero- labial corner of the crown is still more rounded and does not jut posteriorly. The paracone and metacone are tall and massive, but with uninflated sides. They are subequal in height, with the paracone slightly taller, and are separate at their bases. The paracone is erect and subtriangular in cross section. Its labial side is weakly convex, its anterolingual side nearly flat, and its posterolingual side, facing the trigon basin, shallowly concave; labially, a low ridge extends from near the apex to the base of the cusp. The apex of the metacone, which is virtually unworn, is acute, suggesting that the paracone apex was acute as well, although in UALVP 50991 it has been slightly blunted by wear. The preparacrista is faint near the apex of the paracone, but becomes higher and more robust to-

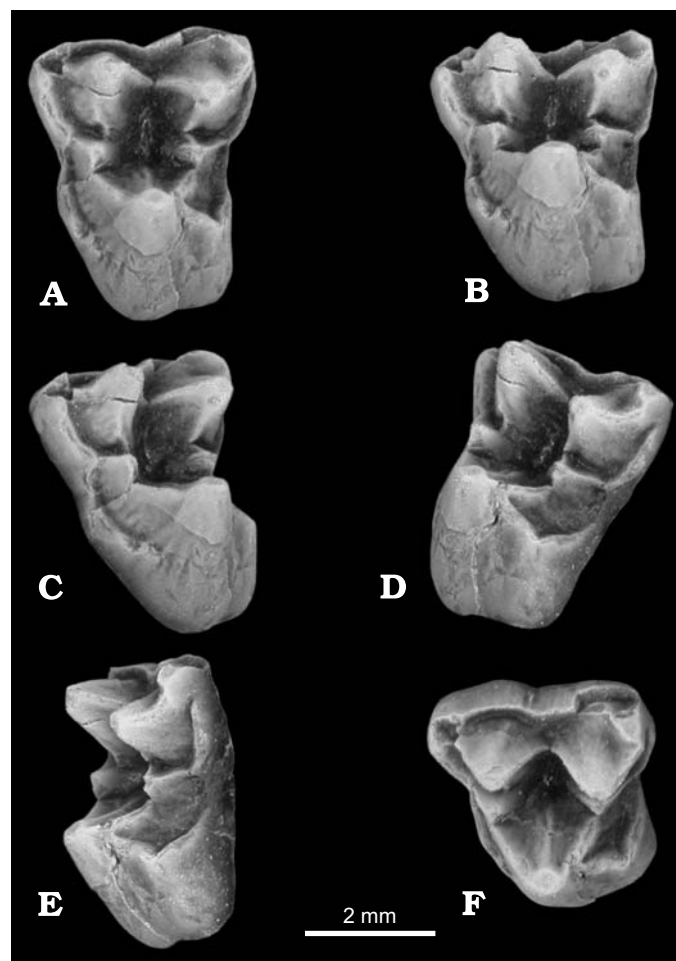


Fig. 1. The plesiadapiform primate *Phoxomylus puncticuspis* gen. et sp. nov., UALVP 50991 (holotype), left M1, from Cochrane 2, Paskapoo Formation, early Tiffanian (late Paleocene) (Youzwyshyn 1988; Fox 1990b), Alberta, Canada, in occlusal (A), lingually oblique (B), anteriorly oblique (C), posterolingually oblique (D), posteriorly oblique (E), and labially oblique (F) views.

wards the base of the cusp, where it curves on to the antero- labial corner of the crown. Its full extent there and the height of the parastylar cusp (see below) cannot be determined because of breakage during collection of the specimen. The postpara- crista is higher and sharper than the preparacrista and is almost blade-like along its extent from the apex of the paracone to the deepest part of the V-shaped centrocrista notch, where it meets the premetacrista.

The base of the metacone is directly posterior to the base of the paracone, but the metacone leans lingually, bringing its apex to a more lingual position than that of the paracone; the base of the metacone extends more lingually as well, and is larger overall. The premetacrista is sharp and about equal to the postparacrista in length and height. In labial or lingual view, the two crests are steep and form a symmetrical centro- crista notch, but because of the lingual inclination of the metacone, the premetacrista leans somewhat lingually in occlusal view. There is no dilambdodont-like deflection of the centrocrista, as in, e.g., many plesiadapids. The cross sec-

tion of the metacone is virtually the mirror image of that of the paracone: it is subtriangular, with a slightly convex labial side (but lacking a labial ridge), a shallowly concave anterolingual side facing the trigon basin, and a moderately convex posterolingual side. The postmetacrista is short and high; it turns sharply labially to meet the ectocingulum, where it is greatly thickened and elevated.

The paraconule and metaconule are robust and set close to the base of the paracone and metacone respectively, relatively far from the protocone, and their apices are narrowly pointed and substantially higher than the flat, more labial part of their occlusal surfaces, which slope steeply labially. The paraconule is slightly larger than the metaconule. The two cusps appear to have been subequal in height originally, but the apex of the metaconule is incomplete, having been damaged during collection. The preparaconular crista is sharp and labially joins the paracingulum. The junction between these crests is unusually clear because the paracingulum is substantially thicker than the preparaconular crista. The paracingulum is robust and defines a shallow gutter between its raised anterior edge and the base of the paracone. From the elongate oval shape of several wear facets along its length, the paracingulum was irregularly crenulate or cuspidate originally. Labially, the paracingulum becomes increasingly elevated as if terminating at a parastylar cusp, but as already noted, damage has made the original height of the structure here impossible to determine. The postparaconular crista is short and its cutting edge somewhat rounded. It meets the base of the paracone at an acute notch and then rises towards the apex of the cusp as a narrower, anteriorly convex ridge, the hypoparacrista (Szalay and Delson 1979).

Although smaller than the paraconule, the metaconule extends slightly more lingually owing to the greater lingual extent of the base of the metacone compared to that of the paracone. The premetaconular crista is damaged but from the parts that remain, was originally sharper than the postparaconular crista. The premetaconular crista meets the lingual face of the metacone near its base forming a narrow, slit-like notch, and then continues on to the metacone as the hypometacrista (Szalay and Delson 1979), rising partway towards the apex of the cusp. The postmetaconular crista, which has a shearing edge, curves posterolabially to meet the metacingulum posterolingual to the metacone, adjacent to its base. The junction between these crests is marked by the greater thickness of the metacingulum. The metacingulum, which is weaker than the paracingulum, then continues past the metacone where it fades away, failing to meet the postmetacrista or ectocingulum more labially.

The trigon basin is subovate in occlusal outline, not developed as a somewhat elongate labiolingual trough, as in many plesiadapiforms, including *Purgatorius* (Fig. 2). It is crisply defined by the concave, basin-facing surfaces of the paracone, metacone, and centrocrista, by the steeply sided internal “wings” of the conules, and by the nearly vertical labial side of the protocone (at approximately 75° from the horizontal); moreover, the junction between the postparacrista

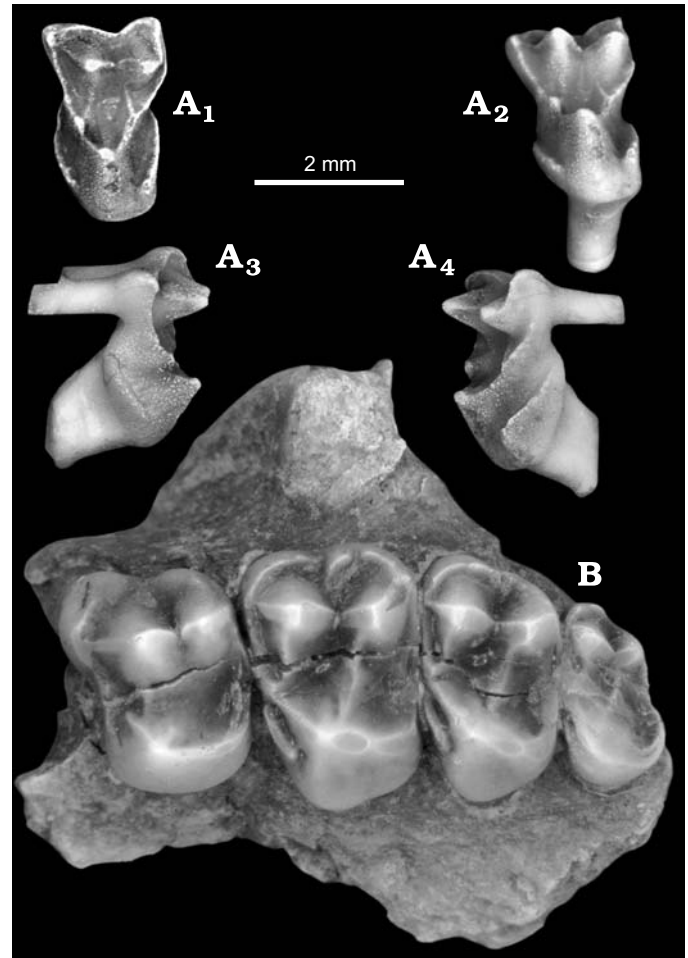


Fig. 2. Comparative upper molar structure in plesiadapiform primates. **A.** *Purgatorius* sp., UALVP 51021, left M2, from Medicine Hat Brick and Tile Quarry, Rav W-1 horizon, Ravenscrag Formation, early Puercan (early Paleocene) (Johnston and Fox 1984; Fox and Scott in press), Saskatchewan, Canada, in occlusal (**A₁**), lingually oblique (**A₂**), anterior (**A₃**), and posterior (**A₄**) views. **B.** *Phenacolemur* sp. (Paromomyidae, Plesiadapiformes), UALVP 51028, incomplete left maxilla containing P4, M1–3, from Gao Mine, Paskapoo Formation, late Tiffanian (late Paleocene) (Fox 2005), Alberta, Canada, in occlusal view. These specimens illustrate a shallow, transverse trigon basin and substantial capacity for ectental movement of the lower molars on the uppers during the power stroke in a basal (**A**) and a derived (**B**) plesiadapiform; both are in marked contrast to upper molar structure and its implications in *Phoxomylus puncticuspis* (see text).

and premetacrista forms an elevated labial wall (at about 65° from the horizontal) that separates the basin from the stylar shelf. The area of the trigon basin is roughly equal to that in M1 of the latest Tiffanian bunodont plesiadapid *Plesiadapis fodinatus* Jepsen, 1930, which has similar length/width dimensions of the crown (see Gingerich 1976: tables A-10, A-11; based on calculations in Boyer et al. 2010b, these dimensions suggest that *P. fodinatus* was an omnivore). The basin in UALVP 50991, however, is differently shaped and is very much deeper than in *P. fodinatus* or in any other plesiadapid, with steep, as opposed to gently sloping, sides. These proportions imply that the occluding lower molar cusp in *Phoxomylus*, the hypoconid, was tall, sharply pointed, and

accompanied by strong, high crests (cristid obliqua and hypocristid) leading to its apex.

The protocone of UALVP 50991 is massive but its walls are uninflated, and its apex, although lightly worn, is narrow and was probably sharply pointed originally. If the base of the crown is held horizontally, the protocone is tall, subequal in height to the paracone, and slightly taller than the metacone. The height of the protocone is additional evidence that the talonid basin on the occluding lower molar was deep owing to the necessity of the protocone in centric occlusion to fit within the basin in tribosphenic molars, with the basin contrasting markedly with its usual shallow dimensions in plesiadapiforms (see, e.g., Fig. 2). In lingual view, the apex of the protocone is at a level that is posterior to the apex of the paracone but anterior to the deepest parts of the centrocrista notch. In this view, the protocone is vertical in orientation: it neither leans anteriorly nor exhibits a posteriorly directed protocone “twist” (Van Valen 1994) relative to the labial parts of the crown, common specializations of the protocone among plesiadapiforms. The base of the protocone is substantially more lingual than the apex, and the lingual face of the protocone slopes steeply labially. Owing to the position of the protocone at a level near the mid-length of the crown and the vertical orientation of the cusp, the preprotocrista and postprotocrista are nearly equal in length (the preprotocrista is slightly shorter, straighter, and not shifted anteriorly); although the postprotocrista is more heavily worn, both crests were well developed originally. A low, rounded ridge extends from the apex of the protocone towards the deepest parts of the trigon basin, where it fades away.

The precingulum arises lingually from the anterior side of the protocone and then flexes sharply ventrally (as oriented in anatomical position) to meet the paracingulum at its junction with the preparaconular crista. The precingulum is narrow but robust, and although worn, was originally crenulated and irregularly pitted along its length; the adjacent parts of the protocone wall are marked by several irregular, low, vertical ridges and shallow grooves. Posteriorly, the postprotoconal fold, an unambiguous primate synapomorphy (Bloch et al. 2007; Silcox et al. 2007), arises near the apex of the protocone but apparently not from the apex itself, although the enamel here has been damaged and the precise relationship between the two features is accordingly uncertain. The postprotoconal fold rapidly increases in height, becoming a short but robust crest that in posterior view is nearly vertical on the posterior wall of the protocone. At a level slightly less than half the height of the protocone, the postprotoconal fold meets the postcingulum, which is wider and more robust than the precingulum and slopes steeply labially. The postcingulum does not extend lingually beyond the postprotoconal fold in contrast to some plesiadapiforms (e.g., the micromomyid *Tinimomys graybulliensis* Szalay, 1974; the plesiadapid *Platychoerops* Charlesworth, 1855) and basal euprimates. Labially, the postcingulum meets the metacingulum at its junction with the postmetaconular crista, turning sharply ventrally to do so. Together, the postprotoconal fold and postcingulum enclose a

narrow, labiolingually elongate talon basin that contrasts with the broad talon basin in, e.g., paromomyids (Fig. 2) and plesiadapids. Dorsal to this basin in UALVP 50991, the crown expands into a moderately swollen lobe partly differentiated from the base of the protocone. There is no evidence of a hypocone, even incipiently.

Discussion

Comparisons with upper molars of other plesiadapiforms.

—UALVP 50991 is probably an M1: it is not markedly transverse relative to its length, although the nearly symmetrical stylar lobes defining the ectoflexus more closely resemble M2 than M1 in many plesiadapiforms

In comparison to anterior upper molars (M1–2) of basal plesiadapiforms, UALVP 50991 most resembles those of the family Palaechthonidae (superfamily Paromomyoidea Simpson, 1940). Silcox and Gunnell (2008: 220) diagnosed the Palaechthonidae in part as having “upper molars with strong conules and well-demarcated postprotocingula that enclose a distolingual basin”, features seen in UALVP 50991 and that provide the main basis for tentative referral of *Phoxomylus* to this family. As in palaechthonids, the talon basin in UALVP 50991 is narrow, unlike the broad basin in, e.g., paromomyids and plesiadapids. Two subfamilies, Palaechthoninae and Plesiolestinae, comprise the Palaechthonidae (Silcox and Gunnell 2008); palaechthonine genera include *Palaechthon*, *Palenochtha* Simpson, 1935a, and *Premnoides* Gunnell, 1989. Upper molars of *Premnoides* are unknown, but the available dental evidence indicates that palaechthonines were all significantly smaller in body size than *Phoxomylus* (for estimates of body size in extinct primates, see Gingerich et al. 1982; Fleagle 1999). In *Palenochtha*, the protocone “twist” is strongly developed and in *Palenochtha* and *Palaechthon*, the molar protocones are canted at least somewhat anteriorly, the preprotocrista has shifted anteriorly, and the trigon basin is shallow and transversely wide (see Szalay and Delson 1979: figs. 14, 17), contrasting with these features in UALVP 50991. Moreover, the postprotoconal fold in palaechthonines is much weaker than in UALVP 50991, and the major cusps are usually lower, with more swollen sides and rounded apices. Even in *Palenochtha minor* (Gidley, 1923; see Szalay and Delson 1979: fig. 17), in which the paracone and metacone are relatively tall and acute, the protocone is in an anterior position and is inclined anteriorly, the protocone “twist” is pronounced, the preprotocrista is anteriorly placed, and the trigon basin is shallow and broad. Moreover, *P. minor* was tiny relative to *Phoxomylus*.

From dental dimensions, the Plesiolestinae were larger than palaechthonines and, at least in that respect, more comparable to *Phoxomylus*. *Talpothenach torrejonius* Kay and Cartmill, 1977 (= ?*Palaechthon nacimienti* Wilson and Szalay, 1972), from the Torrejonian of New Mexico, having an average length of M2 of 2.45 mm (Silcox and Gunnell 2008) and being large among palaechthonids, appears none-

theless to have been significantly smaller than *Phoxomylus*. Anterior upper molars of *Torrejonia sirokyi* (Szalay, 1973), the largest known plesiolestine, are comparable to UALVP 50991 in transverse width (see, e.g., dimensions in Youzwyshyn 1988; Webb 1996), but are significantly shorter anteroposteriorly. Additionally, the upper molars of both *Talpohenach* and *Torrejonia* are much lower crowned than UALVP 50991, with lower, blunter major cusps, a much shallower and more transverse trigon basin, more anteriorly canted protocone, and weaker postprotoconal fold + postcingulum complex. Furthermore, in *Talpohenach*, a hypocone is developed (Wilson and Szalay 1972). Upper molars referred to *Anasazia williamsoni* Van Valen, 1994 are wider relative to their length than UALVP 50991 and exhibit a marked protocone “twist”. Upper molars of smaller plesiolestines, such as *Plesiolestes* spp., show many of these same differences, with lower, more swollen major cusps, more transverse crowns, anteriorly inflected protocones, protocone “twist”, and a weaker postprotoconal fold + postcingulum complex (e.g., Szalay and Delson 1979: fig. 16).

Among other primitive plesiadapiforms relevant for comparison is *Pandemonium dis* Van Valen, 1994 from the late Puercan of Montana and hence a contemporary of *Purgatorius* through part of its temporal range. *P. dis* was first classified as a basal plesiadapid and thought to be an intermediate between *Purgatorius* and *Pronothodectes* (Van Valen 1994), the most primitive plesiadapid. A cladistic analysis by Silcox (2001, 2008; Silcox and Gunnell 2008), however, suggested that the affinities of *Pa. dis* were probably with Palaechthonidae. In light of these conflicting opinions, which remain unresolved, Silcox and Gunnell (2008) classified *Pandemonium* incertae sedis within Plesiadapiformes. Regardless, the upper molars of *Pandemonium* are already bunodont, with a shallow, transversely wide trigon basin in marked contrast to UALVP 50991, even though the occurrences of *P. dis* significantly antedate UALVP 50991 at Cochrane 2.

UALVP 50991 shows no striking resemblances to upper molars of other known plesiadapiforms, which either lack a strongly developed postprotoconal fold (e.g., Microsypidae Osborn and Wortman, 1892; Micromomyidae Szalay, 1974) or, if one is present, have lower, more bunodont, subrectangular upper molar crowns (Paromomyidae: Fig. 2; all Plesiadapoidea). Whereas the unique morphology of UALVP 50991 might well imply that the species to which it pertains represents a new, previously unknown plesiadapiform family, that conclusion, while attractive, must await the advent of more evidence concerning its morphology than is presently available.

Function.—As documented above, UALVP 50991 differs from upper molars of palaechthonids sensu Silcox and Gunnell (2008) not only in its large size and length/width proportions, but also in the unique morphology of its major coronal features. Besides their systematic implications, these features have paleobiological consequences that are unexpected in the context of early primate evolution as presently under-

stood and accordingly are of heightened interest. These consequences relate to diet of the Cochrane species and in turn, to dietary factors that are often hypothesized to have driven the transition from the non-primate ancestors of plesiadapiforms to plesiadapiforms and thereby to primates (e.g., Szalay 1968; Butler 1973; Silcox et al. 2007).

Many of the differences in occlusal morphology that distinguish UALVP 50991 from upper molars of palaechthonids also distinguish it from upper molars of *Purgatorius* (Fig. 2). *Purgatorius* is generally considered to be the dentally most primitive known primate, living or extinct, i.e., the taxon that is basal to the primate radiation as presently reconstructed from the fossil record (e.g., Silcox et al. 2007; Silcox 2008; Silcox and Gunnell 2008). While the upper molars of *Purgatorius* (e.g., Kielan-Jaworowska et al. 1979: fig. 12-21; Johnston and Fox 1984: pl. 5: 4, 5; Van Valen 1994: pls. 4, 5; Buckley 1997: fig. 2; Fox and Scott in press) are smaller and more gracile than UALVP 50991, they also differ in occlusal features long known to have important functional implications: the paracone and metacone have mildly inflated sides and rounded apices; the postparacrista and premetacrista are much lower and less trenchant; neither hypoparacrista nor hypometacrista is developed; the protocone is significantly lower relative to the paracone and metacone; the trigon basin is proportionally wider transversely, narrower, and much shallower, with lower, more gently sloping walls; the conules are lower, more lingually extending platforms with but weakly elevated apices and long, subhorizontal cristae; the labial side of the protocone facing the trigon basin is moderately inclined, not nearly vertical in orientation; the protocone is more anterior in position, leans anteriorly, and the protocone “twist” is clearly developed; the preprotocrista is shifted anteriorly and is shorter than the postprotocrista; the postprotoconal fold, when present, is faint; there is no talon basin.

Because tooth shape in mammals determines the direction of jaw movement (e.g., Hiiemäe and Kay 1973), the list of the above features implies that lower jaw adduction in *Purgatorius* followed an obliquely transverse (ectental) trajectory as the lower molars were brought into occlusion with the uppers, with less capacity for vertical (orthal) piercing and shear than in the insectivorous ancestors of primates. In a pioneering study concerning evolution of mammalian molar function, Butler (1972: fig. 3) was the first to suggest this pattern for *Purgatorius*: he estimated from wear striations on lower molars of *P. unio* Van Valen and Sloan, 1965 that these teeth moved obliquely across the uppers at a 40–45° angle. He was unable to measure this angle exactly, however, because his study specimens were isolated teeth and their precise orientations when articulated in the dentary unknown. Moreover, Butler (1972) lacked upper molars of *Purgatorius* to complement his conclusions from the lowers. He (1972: fig. 1) assumed that *Purgatorius* lower molars were vertically oriented, but specimens of *Purgatorius* sp. nov., the geologically earliest species of *Purgatorius* yet discovered (Fox and Scott in press), show that they lean lingually at an angle of about 20° from the vertical, decreasing

by that amount the apparent steepness of the wear striations that Butler (1972) recorded. In the present study, I manually brought upper and lower molars of *Purgatorius* sp. nov. into occlusion under 10–40 magnifications and found that the occlusal pattern between these teeth requires additional of Butler's (1972) conclusions to be modified as well. My results apply not only to *Purgatorius* sp. nov., but also to the other species of *Purgatorius*: none display significant differences in the features of interest here.

In his study of early primates, Butler (1973) focused on detailed movement of the lower jaws, which in each chewing cycle brings the lower molars into occlusion with the uppers. He recognized buccal and lingual phases of the power stroke (Crompton and Hiimäe 1970), with direction of jaw movement evidenced by parallel wear striae incised in the enamel of the opposing teeth (Mills 1955; Butler and Mills 1959; Butler 1973). My observations of molar occlusion in *Purgatorius* indicate that movement of the lower molars on the uppers was more complex, with a greater ectental component, than Butler (1972, 1973) had supposed. My study shows that in *Purgatorius* the buccal phase itself consisted of three stages: (i) an initial stage, in which movement of the lower molar on the upper was dorsolingual, at an angle of approximately 20° from the horizontal; (ii) a middle stage, in which the lower molar followed an arced trajectory on the upper ranging from 40 to 20° depending on the dorsolingual position of the lower molar along the arc; (iii) and a final stage, in which movement of the lower molar on the upper was lingual and approximately horizontal, bringing the teeth into final or centric occlusion.

Initially in the buccal phase, the angle of lingual movement of the lower molar is governed by the slope of the anterior parastylar process of the upper, which received the tip of the protoconid; the protoconid is the tallest and first lower molar cusp to make contact with the opposing tooth. With lingual movement of the lower molar at the beginning of occlusion, the protoconid incised a labiolingual groove containing parallel wear striae just anterior to the paracone at its base (e.g., UALVP 51020, 51021). This groove is the anterior part of facet 2 that Butler (1973: fig. 4) identified in the palaeochthonid *Palenochtha minor* as representative of primitive primates. In *Purgatorius*, this groove rises at an angle of approximately 20° from the horizontal, and determined the trajectory of movement of the lower molar on the upper as long as contact with the tip of the protoconid was maintained. As the protoconid tip moved lingually along this groove, the labial arm of the protocristid sheared past the preparacrista, generating wear striae on the anterior side of the paracone that parallel the slope of the groove (UALVP 51020) and that represent the posterolabial part of Butler's (1973: fig. 4) upper molar facet 2.

Once the protoconid passes lingual to the anterior parastylar process, the lower molar is free to move more dorsally, the beginning of the intermediate stage. With this more dorsal movement, the labial arm of the protocristid sheared past the paracingulum (the posterolingual part of facet 2; Butler 1973: fig. 7), while the hypoconid, cristid obliqua, and hypocristid entered the centrocrista notch, shearing past the edges

of the postparacrista and premetacrista along their lingual sides (facets 6 and 7; Butler 1973: fig. 4). During this stage, the lower molar trajectory is governed by the contours of the valley between the paracone and metacone; the valley receives the hypoconid, its crests (cristid obliqua, hypocristid), and the labial wall of the talonid. If this valley in *Purgatorius* were straight, at a constant oblique angle along its length, the angle of lower molar movement would have been dorso-lingually along a straight path, the trajectory that Butler (1972: fig. 2) attributed to a diversity of early tribosphenic mammals. The paracone-metacone valley in *Purgatorius*, however, is not straight but transcribes an evenly curved arc (e.g., UALVP 51022, an unworn M2), which is steepest labially (at about 40°), gradually becomes less so lingually, and is virtually horizontal at its lingualmost extent in the trigon basin. Because the hypoconid and labial wall of the talonid fitted closely within this valley, as confirmed by matching parallel wear striae on the talonid wall and valley surfaces in *Purgatorius* sp. nov. (e.g., UALVP 51020, M2; UALVP 51012, m2) that Butler (1973) recorded as facets 6 and 7 in other early primates, the lower molar is physically constrained to follow the curvature of the valley as the tooth is elevated, i. e., it followed an arcuate, increasingly ectental trajectory during this stage of the power stroke.

The final stage of the buccal phase of the power stroke is simple and also was unrecognized by Butler (1972, 1973); it consists of ectental movement of the lower molar lingually a short distance beyond the end of the paracone-metacone valley, thereby bringing the lingually-facing wall of the hypoconid into centric occlusion with the parallel, labially-facing wall of the protocone.

The second or lingual phase of the power stroke in early primates carried the lower molar ventrolingually out of centric occlusion, with the lingual wall of the hypoconid gliding over the opposing wall of the protocone (Butler 1973). The angle of movement in this phase is determined by the angle of these surfaces, and a grinding interaction is generated between them. Lacking upper molars of *Purgatorius*, Butler (1972, 1973) was unable to investigate the lingual phase of the power stroke at the purported base of the primate radiation. In *Purgatorius* sp. nov., the labial wall of the protocone is at an angle of about 50° from the horizontal (UALVP 51022). The apex of this cusp is very narrow and was quickly worn away, with the steepness of this slope reduced and the capacity for greater ectental movement of the lower molar accordingly increased (e.g., UALVP 50121). Butler (1973: figs. 5, 6) also showed that the lingual phase of the power stroke in, e.g., *Palenochtha* included a significant anterior (propalinal) component, arising from lateral rotation of the mandible on the condyles (Mills 1955). This component affected the lingual phase in *Purgatorius* as well, evidenced by the direction of wear striae in the trigon basin (UALVP 50121, 51027). In the propalinal component of lower jaw movement, the hypoconid moved obliquely anterolingually and crossed the preprotocrista between the apices of the paraconule and protocone, as in *Palenochtha* (Butler 1973: fig. 6).

Implications.—What implications does the reconstructed pattern of jaw movement in *Purgatorius* hold for understanding of the paleobiology and relationships of *Phoxomylus*? The central point is that except for its tribosphenic coronal structure and postprotoconal fold, UALVP 50991 shares no important aspects of upper molar coronal morphology with *Purgatorius* and few with other plesiadapiforms. Although UALVP 50991 seems more advanced in some respects than *Purgatorius* (e.g., symmetry of the parastylar and metastylar lobes, rounded anterolabial and posterolabial corners of the crown, labial extension of pre- and postcingulum, robust postprotoconal fold, talon basin), it shows no evidence of the greater bunodonty and capacity for ectental movement and lingual phase grinding that are already evident in *Purgatorius* (Fig. 2) and that purportedly marked the transition from insectivory to omnivory in primate origins (e.g., Szalay 1968; Szalay and Delson 1979; Silcox et al. 2007; Silcox and Gunnell 2008). In the perspective of Hiimäe and Kay's (1973) precept relating occlusal morphology to jaw movement, *Phoxomylus* had no capacity for substantial ectental movement of the lower molars on the uppers. Instead, movement of the lower molars during the power stroke in *Phoxomylus* was more strictly orthal, in both buccal and lingual phases. Lingual surfaces of the paracone and metacone that occluded with the labial side of the lower molar talonid during the buccal phase are steep, initially at an angle of approximately 65–70° from the horizontal, but lessening near centric occlusion. Capacity for ectental movement is very limited owing to the steepness (at approximately 75°) of the labial side of the protocone, which serves as the lingual wall of the trigon basin, guiding movement of the lower molar in the lingual phase of the power stroke. Emphasis on orthal, not ectental, movement of the lower molars is consistent with the clearly more punctate and sectorial cusps and crests of UALVP 50991, including the robust preparacrista and postmetacrista, high and steep postparacrista and premetacrista, strongly developed hypocristae, elevated and sharply pointed apices of the conules, steeply sloping conular cristae, and the narrow notches at the junctions between several major shearing crests. These features unambiguously point to insectivorous/faunivorous habits.

Given this context, the molar morphology of *Phoxomylus* must represent either: (i) a derived condition, modified from an ancestor already possessing molar adaptations to the more omnivorous diet that accompanied the transition to primates; or (ii) a primitive condition, retained from an ancestral primate that had not yet evolved omnivorous molar adaptations, implying that the origin of primates was not accompanied by significant dietary change. Although evidence of the molar morphology of *Phoxomylus* is admittedly limited, I conclude that the second hypothesis is the more likely to be correct, partly because the first would be without precedent: no known lineage of early primates has reverted to a tribosphenic insectivorous molar dentition from a more bunodont omnivorous dentition, a history that the first hypothesis requires. Two reviewers of this paper, however, proposed that the extant haplorhine *Tarsius* Storr, 1780 supplies the missing precedent and that ac-

cordingly, *Phoxomylus* could well represent descent from a more omnivorous ancestor, and on that account hold no implications at all concerning the insectivore-primate transition.

Extant *Tarsius*, an inhabitant of a number of islands in the southwest Pacific (Walker 1975), is a highly specialized insectivore and carnivore, eating a wide variety of arthropods and small vertebrates (Niemitz 1984). Tarsiers have a sparse fossil history, but the earliest tarsiids known, from the middle Eocene of China, closely resemble modern representatives in their molar morphology, with one species even classified as a species of *Tarsius* itself on the basis of dental remains (Beard et al. 1994; Beard 1998; Jablonski 2003). Small early Tertiary primates of the family Omomyidae, best known from North America, are usually considered to be the nearest fossil relatives of tarsiids (Rose 2006), but while omomyids are often characterized as omnivorous, the family includes insectivorous species, as well (Strait 2001). That being the case, *Tarsius* would not necessarily furnish an example of a reversal from a more omnivorous ancestor merely by virtue of its descent from an omomyid, if that in fact occurred.

Probably more germane for assessing the history of *Phoxomylus* than speculations about tarsiid/omomyid phylogeny are studies by Jablonski and Crompton (1994) on mastication in *Tarsius* itself. These authors concluded that the molar structure of *Tarsius*, although modified from an omnivorous ancestor, does not represent a reversal toward a primitive insectivorous pattern: "... the dentition of the tarsier has departed significantly from the primitive tribosphenic configuration characteristic of many Insectivora [...] The molars [of *Tarsius*] bear crowns of relatively high relief, but the cusps are low relative to those of Insectivora, the trigon and talonid basins are relatively wide, and distinct tipcrushing as well as grinding surfaces are evident. In most members of the Insectivora, movements of the jaws during chewing are said to be predominantly orthal [...] with a relatively small transverse or Phase II [i.e., lingual phase of Butler 1973] component of the power stroke [...] The molars of tarsiers, however, bear distinctive, Phase II grinding surfaces with transversely or anteromedially oriented striations... these features of wear clearly define a masticatory apparatus that has departed significantly from a scissor-like *en echelon* shearing mechanism that characterizes insectivores with a classic tribosphenic dentition" (Jablonski and Crompton 1994: 47–49). From this account, the faunivorous molar adaptations of *Tarsius* were indeed imposed as modifications on a more omnivorous occlusal pattern, in apparent agreement with the reservations of the reviewers noted above. In spite of this apparent agreement, however, tarsiid dental history does not effectively challenge the hypothesis that *Phoxomylus* had descended from a basal insectivorous plesiadapiform: in marked contrast to the molars of *Tarsius*, UALVP 50991 exhibits no evidence of modification from a more omnivorous occlusal pattern, i.e., one having blunter, more swollen cusps, weaker crests with less capacity for orthal shear, shallower and more transverse trigon basin, and greater potential for ectental movement of the lower molars across the uppers during both the buccal and lingual phases of the power

stroke—a suite of structural and functional features already established in *Purgatorius* (Butler 1972, 1973; this paper).

If the lineage of descent of *Phoxomylus* was not from an ancestral omnivorous plesiadapiform as is represented by *Purgatorius*, then *Phoxomylus* is the evolutionary outcome of a ghost lineage that extends back from the early Tiffanian, the age of *Phoxomylus* at Cochrane 2 (Fox 1990b), to at least the earliest Puercan, the age of *Purgatorius* sp. nov. (Fox and Scott in press), and very probably beyond, into the Late Cretaceous. If that is the case, present knowledge of the origin and earliest evolution of primates is markedly incomplete, with the anatomy, systematics, paleobiology, and temporal and geographic distribution of the species that participated in the transition to primates from non-primate ancestors still to be discovered. Expressed from a different perspective, we presently know nothing of the actual sequence and pattern in which novel characters (synapomorphies) of the earliest primates arose, an essential requisite for evaluating euprimate-like cranial and postcranial characters that have been recently described from exceptionally preserved plesiadapiform specimens of late Paleocene/Eocene age (e.g., Bloch et al. 2007). Although these discoveries have added significantly to discussions concerning early primate history, the single known tooth of *Phoxomylus* indicates that many fundamental aspects of this history can still be learned.

Acknowledgements

I thank Mary T. Silcox (University of Winnipeg, Winnipeg, Canada) for supplying me with a copy of her Ph. D. dissertation, casts of teeth of *Purgatorius unio* and *Pandemonium dis*, and copies of her published papers, including a preprint of Silcox and Gunnell (2008). I also thank Gregory A. Buckley (Roosevelt University, Chicago, USA), Gregg F. Gunnell (University of Michigan, Ann Arbor, USA), David W. Krause (Stony Brook University), and Douglas M. Boyer (Stony Brook University, Stony Brook, USA), who collectively facilitated the loan for my study of the hypodigm of *Purgatorius titusi*. Gordon P. Youzwyshyn (Grant McEwen University, Edmonton, Canada) collected UALVP 50991 from Cochrane 2, prepared it in the laboratory, and noted its unusual coronal morphology. I am grateful to Brian D. Rankin (University of Calgary, Calgary, Canada), who took the photographs for this paper and generously provided other technical help, and to Mark V.H. Wilson (University of Alberta, Edmonton, Canada), for use of photographic equipment. I thank the Geosciences Grant Selection Committee, Natural Sciences and Engineering Research Council of Canada (NSERC), for their vision in necessitating Emersonian self-reliance in funding support for my continuing, original research on Cretaceous and Paleocene mammals from Canada.

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