Stagodontid marsupials from the Late Cretaceous of Canada and their systematic and functional implications

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Previously undescribed specimens of stagodontid marsupials from Late Cretaceous deposits in Alberta, Canada, reveal new information concerning the upper dentition of *Eodelphis* spp. and the lower dentition of *Didelphodon coyi*. Additionally, an incomplete upper dentition of *D. coyi* from the Scollard Formation extends the range of this species into the Lancian, co-eval with *D. vorax* and *D. padanicus*. Stagodontids are in accord with other North American Late Cretaceous marsupials for which the appropriate parts are known in lacking diastemata between the canines and the molars while possessing well-developed palatal vacuities, implying that these morphologies characterized ancestral marsupials. If so, the diastema between P1 and P2 in the Asian middle Early Cretaceous "metatherian" *Sinodelphys szalayi* is convergent on that in Cenozoic didelphids, and the absence of palatal vacuities in South American Paleogene and Neogene borhyaenids is derived, representing a paedomorphic truncation of development. Claims that the Asian Late Cretaceous "metatherian" *Deltatheridium pretrituberculare* had a marsupial-like dental replacement pattern are tautological, deduced from an a priori acceptance of a marsupial model of replacement to the exclusion of other, no less realistic, alternatives. The new specimens of *Didelphodon coyi* demonstrate that upper and lower premolars occluded broadly, implying that the inflated lingual lobes characteristic of *Didelphodon* premolars evolved primarily as a crushing mechanism, not for passive protection of the gums. Recent speculations that stagodontids were aquatic are not based on credible morphologic or taphonomic evidence and are dismissed, as is speculation that the Judithian species of *Eodelphis* are sexual morphs of a single species. Current knowledge of *Didelphodon* compels correction of numerous errors concerning its morphology as presented in recent analyses of marsupial relationships.

Key words: Mammalia, Marsupialia, Stagodontidae, Cretaceous, Alberta, Canada.

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Introduction

The Stagodontidae are a curious family of early marsupials known from only the Late Cretaceous of North America. The first stagodontid that was described, *Didelphodon vorax* Marsh, 1889a from the Lance Formation, Wyoming (Clemens 1966), is one of the largest North American Late Cretaceous mammals so far discovered and was probably about the size of a small domestic cat (see e.g., Gordon 2003). Geologically earlier stagodontids, classified as species of *Eodelphis* Matthew, 1916 (Fox 1971, 1981), were smaller than *D. vorax* but nonetheless were among the largest mammals in the communities in which they lived. As suggested by dental features, stagodontids were probably predators and/or scavengers: for example, specialized aspects of the premolars of the best known stagodontid, *Didelphodon vorax*, resemble the premolars in the extant Tasmanian devil, *Sarcophilus harrisii* (Boitard, 1841) (see Clemens 1966, 1968), a marsupial that takes both carrion and living prey (Macdonald 1984).

Stagodontid fossils that have been reliably identified taxonomically are strongly biased anatomically, consisting only of isolated teeth and tooth fragments, incomplete dentulous and edentulous jaws, and rare fragmentary skull bones (e.g., Matthew 1916; Smith Woodward 1916; Simpson 1928, 1929; Clemens 1966, 1973; Sahni 1972; Fox 1981; Fox and Naylor 1986; Lofgren 1992; Montellano 1992). Isolated postcranial elements have been referred to stagodontids as well (e.g., Szalay 1994; Kielan-Jaworowska et al. 2004; Longrich 2004; see below), but we emphasize that in the absence of articulation with specimens having dentitions, the taxonomic identification of these elements is impossible to determine, even at the family level. Of undoubted stagodontid fossils, the stratigraphically oldest are a few isolated lower molars from the continental Deadhorse Coulee Member of the Milk River Formation (Meijer Drees and Myhr 1981), southernmost Alberta; Fox (1971) referred these teeth to *Eodelphis* sp. The Deadhorse Coulee Member is of Aquilan or late ?Santonian–earliest Campanian age and was deposited approximately 83.5 Myr before the present (Braman 2001; Payenberg et al. 2002). A somewhat younger and much richer record of *Eodelphis* comes from the Dinosaur Park Formation of southern Alberta. This unit (which was included in the Belly River, Oldman, and Judith River formations of earlier au-

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thors; see Eberth and Hamblin 1993) is Judithian or late Campanian in age, between 76 and 74.5 Myr old (Eberth and Deino 1992; Eberth 1997b). Two species, *E. browni* Matthew, 1916 and *E. cutleri* (Smith Woodward, 1916), which differ somewhat in proportions of the dentary and dentition (Clemens 1966; Fox 1981), occur in the formation. *Eodelphis* is also documented by isolated teeth found at Judithian horizons in northern Montana (e.g., Sahni 1972; Montellano 1992; see Discussion below), and may range into the Edmontonian St. Mary River Formation at Scabby Butte, southwestern Alberta (Sloan and Russell 1974). Archibald (1982) reported that an edentulous mandible from the Lancian Hell Creek Formation, Montana, that he tentatively identified as pertaining to ?*Pediomys* cf. *P. florencae* Clemens, 1966, could with near equal plausibility be referred to *E. browni*.

Didelphodon, the youngest and most derived stagodontid, is best known at Lancian (latest Maastrichtian) horizons. Based initially on fossils collected from the Lance Formation, Wyoming (Marsh 1889a; Clemens 1966, 1973), *Didelphodon* has since been found in the Hell Creek Formation of the Dakotas (Cope 1892; Wilson 1965; Hunter and Pearson 1996) and Montana (Simpson 1927a; Sloan and Van Valen 1965; Clemens 1968; Archibald 1982; Lofgren 1995), the Scollard Formation, Alberta (Lillegraven 1969), and the Frenchman Formation, Saskatchewan (Fox 1989; Storer 1991), all Lancian in age. Two species, *D. vorax* Marsh, 1889a and *D. padanicus* (Cope, 1892), have traditionally been recognized (Clemens 1966, 1973), but in 1986, Fox and Naylor named a third, earlier species, *Didelphodon coyi,* from the Edmontonian (late Campanian/early Maastrichtian) Horseshoe Canyon Formation near Drumheller, Alberta, a unit deposited approximately 73–68 Myr ago (Eberth 1997a). Fox and Naylor (1986) also described isolated teeth from Scabby Butte that possibly belong to yet another species of *Didelphodon*, which they did not name. In as far as is known, stagodontids themselves failed to survive the end-of-Cretaceous extinction event approximately 65 Myr ago and were not ancestral to other marsupials (Clemens 1966; Fox 1981).

Stagodontids possess a unique combination of dental specializations that set them apart from all of their mammalian contemporaries. The molars are of tribosphenic grade, are relatively large, and are massive in their construction. In the lowers, the trigonid is anteroposteriorly compressed, the paraconid high and blade-like and subequal in height with the protoconid, a conspicuous carnassial notch is developed within the paracristid, the metaconid is reduced, and the cristid obliqua meets the posterior wall of the trigonid far labially. In the uppers, the metacone is robust and the postmetacrista long and high, the paracone is small, the preparacrista short, the conules are well developed and closely appressed against the bases of the paracone and metacone, and there is no metacingulum. As a biomechanical consequence of many of these features, the capacity for prevallum/postvallid shear, the primitive pattern in therians (Patterson 1956; Crompton 1971; Fox 1975), was reduced

and that for postvallum/prevallid shear enhanced. This specialized stagodontid shearing pattern was functional in young animals when the molars erupted and were first brought into use, but thereafter the molar cusps and crests were gradually truncated and then erased by horizontal wear; in time, the crowns of the molars were reduced to broad crushing or grinding platforms with no capacity for shear (Fox and Naylor 1995). This pattern proceeded from anterior to posterior along the molar row; moreover, it is widespread among other early marsupials (e.g., *Alphadon* Simpson, 1927b, "*Pediomys*") that lack stagodontid coronal specializations (Fox 1979; Fox and Naylor 1995), suggesting it may be of taxonomic significance in diagnosing early marsupials *versus* other tribosphenic therians contemporary with them. A second, more dramatic feature of the stagodontid dentition is the evolution of large, crushing premolars within the history of the family. The premolars are not known in the Aquilan species, but in the Judithian *Eodelphis cutleri*, P3/p3 had increased in size relative to their counterparts in *E. browni* and more generalized early marsupials (Clemens 1966; Fox 1981). With the advent of *Didelphodon*, all of the premolars displayed inflated crowns, having become highly specialized crushing teeth suitable for breaking up bones or molluscan shells (Clemens 1966, 1968, 1973; Lillegraven 1969; Lofgren 1992).

In addition to the undoubted stagodontids *Eodelphis* and *Didelphodon*, five other taxa have been allied with the Stagodontidae on the basis of certain dental resemblances and are briefly considered here. First among these is *Pariadens kirklandi* Cifelli and Eaton, 1987, founded on a partial lower dentition from the middle Cenomanian (earliest Late Cretaceous) Dakota Formation of Utah. As indicated by the holotype (UCM 54155, an incomplete dentary containing m2?– 4?), however, *P. kirklandi* clearly lacks crucial stagodontid features, including the high blade-like paracristid containing a large, keyhole-like carnassial notch, anteroposterior compression of the lower molar trigonids, and labial position of the cristid obliqua on all of the lower molars (Cifelli and Eaton 1987; Eaton 1993). Cifelli (2004) described a second species of *Pariadens*, *P. mckennai*, based on three isolated lower molariform teeth from the Albian/Cenomanian Cedar Mountain Formation, Utah. Unaccountably, the holotype of this species, a presumed m4 (OMNH 33072), not only lacks diagnostic stagodontid characters [as Cifelli (2004) noted, the trigonid is not compressed anteroposteriorly and the cristid obliqua is lingually positioned, for example, meeting the postvallid wall beneath the protocristid notch], but does not even show closely approximated ("twinned") hypoconulid-entoconid cusps, unlike m4 in undoubted stagodontids (Clemens 1966; Fox 1981) and indeed, m4 in all other early marsupials known to us. Based on these considerations, we do not include *Pariadens* in the Stagodontidae and find *P. kirklandi* best classified as "Marsupialia, incertae sedis" [*contra* Cifelli et al. (2004) and Kielan-Jaworowska et al. (2004)]. From the available evidence, "*P.*" *mckennai* shows no special resemblances to stagodontids nor to Marsupialia

more generally, and seems best classified as incertae sedis among therians of tribosphenic grade.

The third purported stagodontid is *Boreodon matutinus* Lambe, 1902, established on a large isolated premolar, NMC 1887, from the Dinosaur Park Formation, Alberta. We consider *B. matutinus* to be a *nomen dubium*: NMC 1887 is of uncertain premolar position and lacks taxonomically diagnostic features (see Russell 1952; Clemens 1966; Sahni 1972; Fox 1981). We have similar doubts about the fourth purported stagodontid record, that by Rigby and Wolberg (1987): they described several fragmentary teeth from the Kirtland Shale [?late Campanian (Cifelli et al. 2004)], New Mexico, referring them to "cf. *Eodelphis*", but in the absence of well-preserved specimens (and the original fossils were not illustrated), this record is considered no further in this paper. Finally, McKenna and Bell (1997: 52) included *Delphodon* Simpson, 1927a in the Stagodontidae; Clemens (1966: 107, 109) had earlier concluded that this genus contained species founded on teeth that probably pertain to the early marsupials *Pediomys* sp. or *Alphadon* sp. as then recognized, and that view is followed here.

The present paper describes incomplete jaws with teeth of *Eodelphis* and *Didelphodon* that preserve features not known in stagodontids before, thereby increasing understanding of stagodontid anatomy and inferences of relationship based on it. Moreover, the new information about dental and gnathic structure allows better insight into dental function in stagodontids than was previously possible; functional inferences can be a valid primary source of evidence as to relationships (e.g., Fox 1979; O'Keefe and Sander 1999; Vermeij 1999, 2001; Shu et al. 2004) as well as enhancing interpretation of the ways of life of long-extinct organisms. Finally, the specimens on which this paper is based compel correction of important errors made in stagodontid character descriptions in recent analyses of marsupial evolution (e.g., Luo et al. 2003).

Institutional abbreviations.—AMNH, American Museum of Natural History, New York, USA; LACM, Los Angeles County Museum, Los Angeles, USA; MAE, Mongolian Academy of Sciences–American Museum of Natural History Expeditions; NMC, Canadian Museum of Nature (previously the National Museum of Canada), Ottawa, Canada; OMNH, Oklahoma Museum of Natural History, Norman, USA; PSS, Paleontology and Stratigraphy Section (Geological Institute), Mongolian Academy of Sciences, Ulaanbaatar, Mongolia; TMP, Royal Tyrrell Museum of Palaeontology, Drumheller, Canada; UALVP, Laboratory for Vertebrate Paleontology, University of Alberta, Edmonton, Canada; UCM, University of Colorado Museum, Boulder, USA; UCMP, Museum of Paleontology, University of California, Berkeley, USA.

Other abbreviations.—L = length; W = width; WTri = width of the trigonid; WTal = width of the talonid; AW = anterior width; PW = posterior width. The terms "Lancian", "Edmontonian", "Judithian", and "Aquilan" refer to North American Land Mammal Ages, which are biochrons, i.e., intervals of time defined by the mammalian species that lived during those intervals (Lillegraven and McKenna 1986; Woodburne 2004). The traditional convention of designating the primitive dental complement of adult marsupials as I1–5/1–4, C1/1, P1–3/1–3, M1–4/1–4 is followed here, while acknowledging that teeth at the anteriormost two premolar loci are probably retained deciduous teeth lacking successors (Clemens 1966; Luckett 1993; Cifelli et al. 1996). All measurements are in millimeters; measurements in square brackets indicate that the tooth in question is damaged and the measurement compromised to a minor degree.

Systematic paleontology

Cohort Marsupialia Illiger, 1811

Remarks.—At present, little consensus exists as how best to classify marsupials (compare, e.g., Aplin and Archer 1987; Reig et al. 1987; Marshall et al. 1990; Szalay 1994; McKenna and Bell 1997; Kielan-Jaworowska et al. 2004; Case et al. 2004). Moreover, some recent authors (Rougier et al. 1998; Luo et al. 2003; Horovitz and Sánchez-Villagra 2003; Asher et al. 2004) have preferred to limit the name "Marsupialia" to the crown clade, i.e., living marsupials, their last common ancestor, and all descendants of that last common ancestor. As a consequence, many major fossil groups of what for over a century have been considered marsupials by paleontologists and mammalogists have been relegated to a non-marsupial category informally termed "stem-Metatheria" or "basal Metatheria." This revision is not owing to the anatomical characters that these "stem-" or "basal-metatherians" may or may not share with "crown marsupials", but merely as a consequence of the crown clade definition being based on the occurrence of species in an arbitrarily selected time horizon, the Recent (Holocene). In actual practice, however, the scope of crown Marsupialia is sometimes even more limited than this, denoting only living species: contrary to the implications of crown-clade definitions, none of the four papers cited above include in their analyses characters of extinct groups that descended from the "last common ancestor" of the crown clade. As an example of the consequences of such omissions, Luo et al. (2003) included loss of conules as an unambiguous synapomorphy of crown Marsupialia, while ignoring the well-documented presence of conules in Herpetotheriinae (Korth 1994; Johanson 1996a, b). Herpetotheriines are Tertiary opossum-like marsupials that are near universally accepted as included in Didelphidae (e.g., Simpson 1945; Fox 1983; Marshall 1987; Reig et al. 1987; Marshall et al. 1990; Korth 1994; Johanson 1996b; McKenna and Bell 1997) and, hence, are crown clade marsupials even though extinct. The obvious fallacy here is that "commonness" in the living species was typologically assumed to be primitive for the crown clade and therefore must have characterized its last common ancestor and all descendants of that ancestor.

Regardless of the practices of individual paleontologists, however, the basic conceptual weakness of crown-group taxa is that they are defined by extinction events (Lucas 1990; Miao 1991), an objection mostly ignored but valid nonetheless. By definition, crown-group taxa are those that have survived to the Recent, a criterion that muddles the distinction between adaptation of the organisms concerned and their descent relationships, yet it is the latter that furnishes the basis for classification in modern biology. Moreover, crown-group nomina are defined by reference to other nomina (definition by extension, i.e., a listing of items to which the definition applies), which in themselves have no material substance, leaving their reality impossible to demonstrate or refute. We believe that in order to be useful and subject to critical examination, membership in the units that are named, and hence the reality of those units and the utility of their definitions, can only be by reference to the material characters that they possess (definition by intension, i.e., by a list of properties required of all individuals included in the definition). In other words, for the working systematist, marsupials are marsupials because of the material features that allow their recognition and testify to their evolutionary history, not because of the taxonomic nomina that the name "Marsupialia" subsumes (see e.g., Kielan-Jaworowska et al. 2004). That being the case, the recent claim that no marsupials are known from the Cretaceous (Rougier et al. 1998: 462) is based only on semantics, i.e., "language used to have a desired effect as in advertising or political propaganda" (Mish 1983: 1068), not on the distribution of material characters that imply relationships among real organisms.

Suborder Archimetatheria Szalay, 1993
Family Stagodontidae Marsh, 1889b
Genus *Eodelphis* Matthew, 1916
Eodelphis browni Matthew, 1916
Fig. 1A.

Holotype: AMNH 14169, left dentary, symphyseal region of right dentary, and fragments of the skull. Judithian Land Mammal Age (late Campanian), Sand Creek, Red Deer River Valley, Alberta.

New material.—TMP 85.53.3, an incomplete left maxilla, containing P1–2 and M1, and alveoli for C (incomplete), P3 and M2; from Dinosaur Park Formation, Dinosaur Provincial Park, Alberta.

Description

Maxilla and upper dentition.—In TMP 85.53.3 (Fig. 1A), the preserved part of the maxilla extends from the canine alveolus to the posterolabial alveolus of M2. P1–2 and M1 are in place, whereas the canine, P3, and M2 are represented only by their alveoli. A rounded notch in the broken dorsal border of the facial process of the maxilla is the remnant of the infraorbital foramen above P3; the foramen opens above M1 in *Didelphodon* (see below) and above P2 or between P2 and P3 in uncatalogued specimens of the Virginia opossum, *Didelphis virginiana* Kerr, 1792, at hand and available for

comparison. A finished edge on the palatal process of the maxilla opposite M1 indicates the presence of a palatal vacuity in this specimen; the anterior extremity of the palatal vacuity is commonly opposite M1 in *D. virginiana*.

The canine alveolus is incomplete but obviously was large originally, and it is substantially larger than the alveoli more posteriorly in the specimen, as is the case in *D. virginiana*. In TMP 85.53.3, the maxilla probably furnished much of the walls of the canine alveolus. As preserved, this bone extends further anteriorly on the medial side of the alveolus than laterally, but this may be only an artifact. By comparison, in the Virginia opossum the maxilla furnishes the entire lateral wall of the canine alveolus but the bone there is very thin; had the maxilla a similar configuration in TMP 85.53.3, the lateral wall of the canine alveolus doubtless would not have been preserved. The canine alveolus displays no evidence of subdivision, leading to the conclusion that the upper canine of *Eodelphis browni*, like that of *Didelphodon vorax* (Lillegraven 1969; Lofgren 1992), was single-rooted.

P1 [L = (1.8); W = (1.5)] is a small, two-rooted tooth in TMP 85.53.3, and is located directly behind the canine, without a diastema intervening. Indeed, the anterior root of P1 is partly exposed in the posterolabial wall of the canine alveolus. The same tight spacing between the upper canine and P1, including the exposure of the anterior root in the posterolabial wall of the canine alveolus, is seen in *Didelphis virginiana*. Most of the crown of P1 in TMP 85.53.3 has been eroded away, leaving little useful information about its morphology. From the outline of its base, however, the crown was stout, somewhat wider posteriorly than anteriorly, but longer than wide overall. Its long axis is oblique, from anterolabial to posterolingual, and the anteriormost extremity of the crown and the anterior root are labial to the midline of the canine alveolus, as in *D. virginiana*, although P1 in the Virginia opossum extends still further anterolabially relative to the canine. In TMP 85.53.3, the posterior root of P1, which is substantially larger in cross section than the anterior root, is immediately adjacent to the anterior root of P2, with space for only a thin wall of bone between their respective alveoli; hence, it is clear that there was no diastema between P1 and P2 in this specimen, with the short gap between the crowns of the two teeth as preserved being due to breakage and erosion of P1 posteriorly and erosion of P2 anteriorly. The anterior root of P1 is vertical, not angled obliquely posteriorly, nor does the remnant of the crown lean anteriorly. The posterior root slants posterolingually and probably passes lingual to the anterior root of P2 within the maxilla, but in lateral view the posterior root is nearly vertical, not angled strongly posteriorly as in *D. virginiana*; its proportions do not suggest that it supported an expanded lingual lobe of the crown. In *Didelphodon vorax*, P1 is single rooted and there are no diastemata between the upper canine, P1, and P2 (Lofgren 1992: fig. 1). A procumbent P1 and a diastema between P1 and P2 have been claimed to be diagnostic for "metatherians" (Rougier et al. 1998: fig. 5; see below).
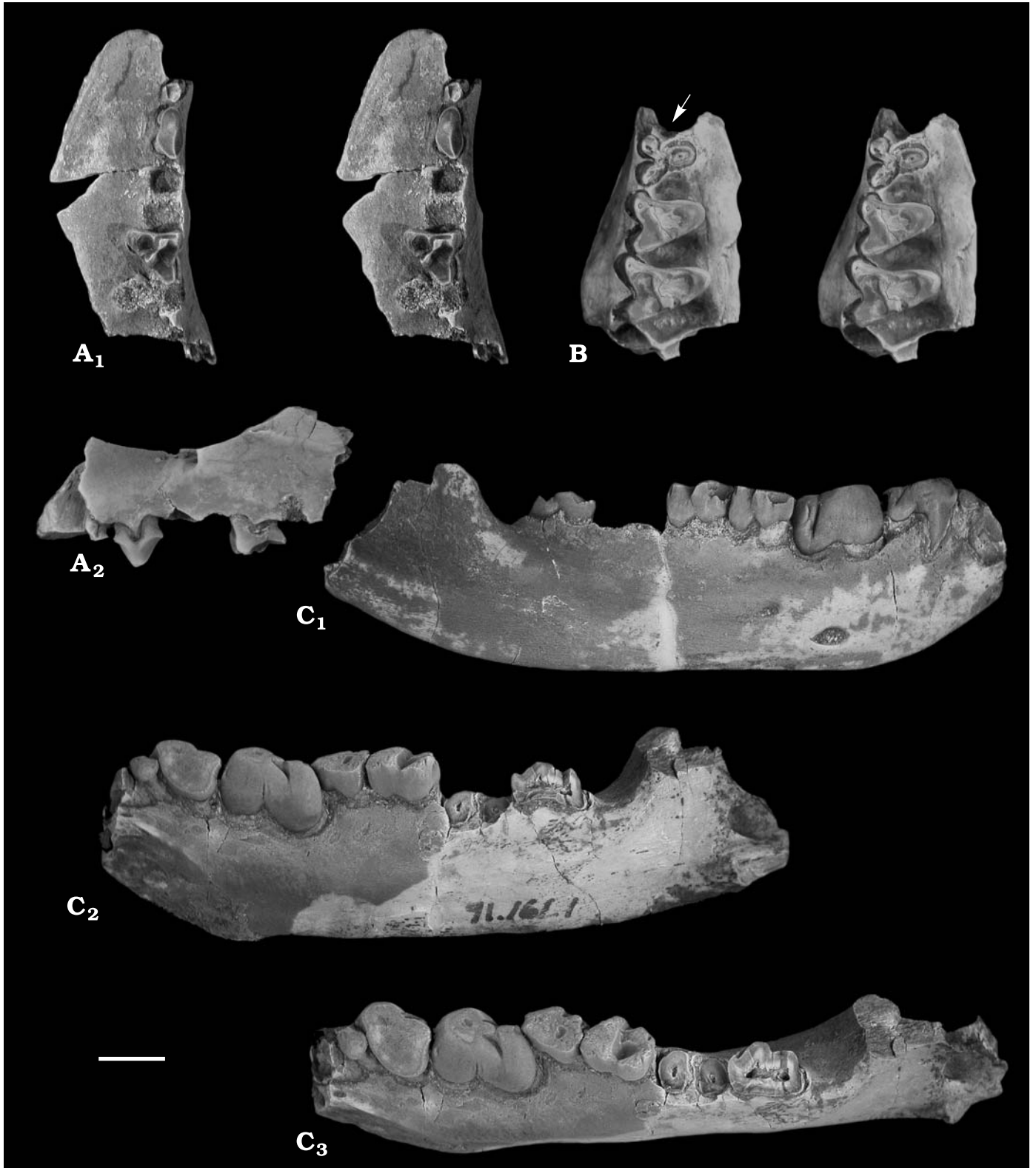
Fig. 1. **A**. *Eodelphis browni* Matthew, 1916, incomplete left maxilla, TMP 85.53.3, from the Dinosaur Park Formation, Judithian Land Mammal Age (late Campanian), Dinosaur Provincial Park, Alberta, containing P1–2, M1 in occlusal (A$_1$) and labial (A$_2$) views. **B**. *Eodelphis cutleri* (Smith Woodward, 1916), incomplete right maxilla, UALVP 7031, from the Dinosaur Park Formation, Judithian Land Mammal Age (late Campanian), mouth of Sand Creek, Dinosaur Provincial Park, Alberta, containing M1 (broken), M2–3 in occlusal view; arrow shows posterior alveolus of P3. **C**. *Didelphodon coyi* Fox and Naylor, 1986, incomplete right dentary, TMP 91.161.1, from the Horseshoe Canyon Formation, Edmontonian Land Mammal Age (early Maastrichtian), Paintearth Creek, Alberta, containing i2–3 (broken), c (broken), p1–3, m1–2, m3–4 (broken) in labial (C$_1$), lingual (C$_2$), and lingually oblique (C$_3$) views. A$_1$ and B stereophoto pairs. Scale bar 5 mm.

In TMP 85.53.3, P2 (L = 3.3; AW = 1.4; PW = 1.8) is substantially larger than P1. P2 is two-rooted, premolariform, bilaterally compressed, and has a single main cusp, the paracone. The outermost surface of enamel has been eroded from over most of the crown, but little loss of morphological detail has resulted. In lateral profile, the crown nearly forms an isosceles triangle but the posterior side is slightly longer and slightly less steep than the anterior side. A faint anterior ridge extends from the apex of the paracone to the base of the crown; this ridge curves gently labially along its length. A stronger ridge is present posteriorly and curves lingually from the apex of the paracone to the base of the crown. A basal cingulum is developed anteriorly; a second, wider cingulum is developed posteriorly and terminates posteriorly in a small cusp; the two cingula fail to meet either labially or lingually, but curve apically as they approach one another. The sides of the crown above the cingula are slightly hollowed out, more so above the posterior cingulum than anteriorly, and the crown is moderately expanded posteriorly, especially on its lingual side. In all of these features, P2 of TMP 85.53.3 closely resembles P2 in *Didelphis virginiana*, except that the anterior cingulum is better developed in the fossil specimen. The tooth displays no trace of a swollen lingual lobe as is present on P2 of *Didelphodon vorax* (Clemens 1966: fig. 49; Lofgren 1992: fig. 1) and probably P2 of *Didelphodon coyi*, as discussed below.

P3 in TMP 85.53.3 is represented by its two alveoli; the anterior alveolus contains a broken root. The alveoli are larger than those for P2 and more widely spaced from one another anteroposteriorly, implying that P3 was larger than P2, undoubtedly the primitive proportions of these teeth in opossum-like marsupials generally (*contra* Luo et al. 2003). The P3 alveoli are subcircular; the posterior alveolus is slightly wider than the anterior alveolus (anterior alveolus: W = 2.1; posterior alveolus: W = 2.4), but it is narrower than the coronal width of M1, in contrast to *E. cutleri*, in which the posterior alveolus alone of P3 is wider than the crown of M1 (see UALVP 7031: Fig. 1B, arrow).

In TMP 85.53.3, the surface features of M1 (L = 3.4; AW = 3.4; PW = 3.9) are somewhat eroded diagenetically, but nonetheless the tooth displays the characteristic specializations of M1 in stagodontids: the stylar shelf is wide, especially posterior to the ectoflexus, the stylocone and protocone are robust, the paracone is reduced and smaller than the metacone, the conules are closely appressed to the lingual bases of the paracone and metacone, and there is no metacingulum.

Discussion

TMP 85.53.3 is the first known specimen of *Eodelphis* in which the maxilla extends anteriorly as far as the canine alveolus, thereby preserving evidence of the configuration of the upper premolars and of the size, at least, of the upper canine. This specimen is relevant to several related issues as follows:

Spacing of the upper premolars.—Luo et al. (2003: 1934–1935) claimed that in Late Cretaceous "metatherians" and Cenozoic "didelphid-like" marsupials, P1 "is procumbent and close to the upper canine, followed by a large diastema behind", derived features that purportedly unite these groups with the then-new middle Early Cretaceous "basal metatherian" *Sinodelphys* Luo et al. 2003 from China [as noted above, Rougier et al. (1998: 462) had earlier cited these same characters as diagnostic of "Metatheria", including "marsupials"]. In fact, these features are hardly known at all in North American Late Cretaceous marsupials, the richest source of information about early marsupial diversity and dental evolution. Nonetheless, the evidence that the available specimens provide plainly conflicts with the aspects of the anterior upper premolars that Rougier et al. (1998) and Luo et al. (2003) have cited as diagnostic for metatherians. For example, Clemens (1966: fig. 27) illustrated an incomplete maxilla (UCMP 52094) of *Pediomys hatcheri* (Osborn, 1898) in which P1 is indeed separated from P2 by a "large" diastema, but P1 is also separated from the upper canine by a diastema that from spacing of the alveoli, appears nearly as long as that between P1 and P2 (because the crown of P1 is missing from this specimen whether or not it was procumbent cannot be determined). In no other specimens of the Lance marsupials that Clemens (1966, 1973) described are these parts preserved. Lillegraven (1969: fig. 14.3b) illustrated UALVP 2389, an incomplete maxilla of *Alphadon marshi* Simpson, 1927b (or *A. jasoni* Storer, 1991; see Johanson 1996a) preserving P2–3, M1 from the Lancian Scollard Formation, Alberta, but in this specimen the posterior root of P1 is present as well and shows that this tooth was not separated from P2 by a diastema. None of the other marsupial specimens in Lillegraven's (1969) description of the Trochu local fauna are preserved this far anteriorly. Lofgren (1992) demonstrated that in *Didelphodon vorax* the alveolus for P1 is close behind the canine, but from the spacing of their alveoli, P1 and P2 were not separated by a diastema. As described above in the earlier and more primitive stagodontid *Eodelphis browni*, P1 is close behind the canine, probably was not procumbent, and there is no diastema between P1 and P2. Given this pattern in *Eodelphis*, the lack of diastemata in the anterior upper postcanine dentition in *Didelphodon* cannot be explained away as a peculiarity restricted to that genus, i.e., a feature that is a correlate to the shortening of the jaws and specialized crowding of the anterior postcanine dentition that *Didelphodon* exhibits. Another, previously unpublished, example preserving the anterior upper dentition in early marsupials agrees with those cited above: reconstruction of the maxillary dentition of a Late Cretaceous *Alphadon*-like didelphoid, TMP 95.178.26 (Fig. 3D) from the Judithian Devil's Coulee locality, Alberta, to be described elsewhere, indicates that in this species P1 was erect (not procumbent) and there was no diastema between P1 and P2. Additional direct evidence as to the spacing of the upper premolars in early marsupials is provided by a well-preserved maxilla (UALVP 43007) of a new Paleocene species of *Peradectes* Matthew and Granger, 1921 from locality DW-2

(Fox 1990) also to be described elsewhere: this specimen contains the alveolus for the canine and P1, and P2–3, M1–4 are in place: P1 was single-rooted and (from the slope of its alveolus), not procumbent and there are no diastemata anywhere along the tooth row.

In sum, the spacing between the upper premolars considered diagnostic by Rougier et al. (1998) and Luo et al. (2003: 1934–1935) in "Late Cretaceous metatherians" (= Late Cretaceous marsupials of this paper) is known to occur in only a single specimen of *P. hatcheri*, but because of the diastema between the upper canine and P1, this resemblance is incomplete. More importantly, the lack of a diastema between P1 and P2 in *Didelphodon* is not a peculiar specialization limited to this genus but has a wider distribution, including occurrences in at least four genera of dentally less specialized early marsupials. From these facts, we suggest that contrary to Rougier at al. (1998) and Luo et al. (2003), the primitive condition in marsupials is one in which P1 is vertical (not procumbent) and there are no diastemata along the tooth row between the upper canine and the molars. If so, the resemblances between *Sinodelphys* and Cenozoic "didelphid-like" marsupials involving a procumbent P1 and a diastema between P1 and P2 are convergent, in keeping with the virtual certainty that living didelphids share a more recent common ancestry with known North American Late Cretaceous opossum-like marsupials than with the Asian middle Early Cretaceous *Sinodelphys* (see, e.g., Case et al. 2004 for discussion of paleobiogeography of early marsupials).

Palatal vacuities.—In 1995, Fox and Naylor described the first evidence of vacuities (fenestrae) in the secondary palate of North American Late Cretaceous marsupials, including the stagodontids *Eodelphis cutleri* and *Didelphodon vorax*. As noted above, TMP 85.53.3 displays a rounded, finished edge along the medial side of the maxilla opposite M1, which extends the evidence of palatal vacuities in Late Cretaceous marsupials to *E. browni*. Palatal vacuities were cited as a synapomorphy of "crown group Marsupialia" by Horovitz and Sánchez-Villagra (2003: fig. 1, appendix B), who evidently were unaware of the by-then well-documented occurrence of these structures in diverse Late Cretaceous marsupials—perhaps reflecting a widespread view among neontologists that incomplete fossils and the literature describing them contain no useful anatomic and, hence, phylogenetic information. Palatal vacuities in generalized early marsupials also occur in *Andinodelphys cochabambensis* Marshall and Muizon, 1988 from the early Paleocene Tiupampa deposits of Bolivia (Muizon et al. 1997); this species was based on a well-preserved skull but was also omitted from Horovitz and Sánchez-Villagra's (2003) analysis. Evidence of palatal vacuities occurs additionally in the new species of *Peradectes* from the Paleocene Paskapoo Formation of Alberta.

Marshall et al. (1995) and Muizon (1998) contended that because palatal openings occur sporadically throughout Mammalia (e.g., in some multituberculates, in carpolestid plesia *Erinaceus* Linnaeus, 1758, etc.), they contain little phylogenetic information in regards marsupials. We dis-

agree: we do not accept that the independent acquisition of a character among unrelated clades furnishes valid information as to the homology (or not) of that character as it occurs within a clade (see Vermeij 1999, 2001; Van Valen 2004). Marshall et al. (1995) and Muizon (1998) further argued that because palatal openings develop by the resorption of bone in marsupial pouch-young already having a complete secondary palate (i.e., one lacking these openings), these openings cannot constitute a marsupial synapomorphy, a derived character arising at the origin of marsupials. We acknowledge that the late appearance of palatal openings in marsupial ontogeny is at least consistent with a complete palate being primitive for marsupials (as for mammals generally), but we note that the early establishment of a complete palate ontogenetically may instead be related to precocious suckling by the developing pouch young (de Beer 1937) and hence convey no phylogenetic signal. In any case, the timing of development of palatal openings in extant marsupials can tell us nothing about when during marsupial geological history these openings originated or the pattern of their distribution in extinct species thereafter. That information can be supplied only by the fossil record.

The fossil record reveals that palatal vacuities occur in all North American Late Cretaceous marsupials for which the appropriate parts have been discovered, from Judithian to Lancian horizons, in both dentally generalized (e.g., *Alphadon*) and specialized (e.g., Stagodontidae) species, including basal marsupials (Stagodontidae, "Pediomyidae") (Fox and Naylor 1995). The taxonomic and temporal distributions of these specimens agrees with the long-standing hypothesis that palatal vacuities are a marsupial synapomorphy (Simpson 1947; Tyndale-Biscoe 1973; Reig et al. 1987; Fox and Naylor 1995), with absence of vacuities, as in Paleogene and Neogene South American borhyaenids, being a derived condition, reflecting truncation of palatal development in geologically younger species (Reig et al. 1987: 30). While the precise source of Cenozoic marsupials among their Cretaceous predecessors is not known, it probably is still most closely approximated by taxa having an *Alphadon*-like dentition (Clemens 1966, 1979; Case et al. 2004) and hence likely having palatal vacuities, as documented by specimens already collected from the North American Western Interior.

Sexual dimorphism in Eodelphis.—Montellano (1992: 84) suggested that the two nominal Judithian species of *Eodelphis* could well be sexual dimorphs of a single species. We reject this interpretation: the qualitative differences in the dentition between *E. browni* and *E. cutleri* (see Fox 1981), with the enlarged posterior premolars in the latter antecedent at least phenetically to those of *Didelphodon*, imply very different food niches, to a degree that would be unexpected between the sexes of a single mammalian species. Moreover, dental differences of this magnitude are without parallel known to us within single species of extant opossum-like marsupials, the nearest living analogue to Late Cretaceous stagodontids.

Genus *Didelphodon* Marsh, 1889a

Didelphodon coyi Fox and Naylor, 1986

Figs. 1C, 2, 3A, B.

Holotype: TMP 84.64.1, incomplete right dentary containing p3, m3–4 (Fox and Naylor 1986: figs. 3, 4). Edmontonian Land Mammal Age (early Maastrichtian), Michichi Creek, Alberta.

New material.—TMP 91.166.1, an incomplete right dentary containing p1–3, m1–2, m4 (broken), and roots of the canine, two incisors, and m3 contained in their alveoli, from Paintearth Creek, Alberta; TMP 90.12.29, an incomplete left dentary with heavily worn and broken p3, alveoli for m1–4, the canine, p1? and p2, from the type locality, Michichi Creek, Alberta (Fox and Naylor 1986) (both of these localities are in the Horseshoe Canyon Formation, with exact coordinates on file at the Royal Tyrrell Museum of Palaeontology); TMP 94.125.125, incomplete right maxilla with P3, M1 and damaged M2, from the latest Cretaceous (latest Maastrichtian; Lancian) Scollard Formation at KUA-1 [see Lillegraven (1969) for description of the locality and Archibald (1982) for account of the Trochu local fauna; see Fox (1974) and Fox and Naylor (2003) for important additions to this local fauna].

Although the dentary TMP 90.12.29 was found at the type locality and is from the opposite side of the jaw than the holotype, the two specimens are clearly from different individuals as evidenced, for example, by the deep wear exhibited on p3 of TMP 90.12.29 and the virtually unworn p3 of the holotype.

Description

Dentary.—Of the two new dentaries of *Didelphodon coyi*, TMP 91.166.1 (Figs. 1C, 2A) is the better preserved, but it is broken and missing from the base of the canine anteriorly, and posteriorly from just beyond the level of the mandibular foramen; nonetheless, it displays several features more extensively than does the holotype or other available specimens of this species.

The dentary in TMP 91.166.1 is robustly constructed but is slightly smaller than the holotype dentary, a difference of no significance taxonomically. The alveolar and ventral margins of the horizontal ramus are nearly parallel with each other, except anteriorly from beneath p3, where the ventral margin rises steeply at the level of the symphysis. In TMP 91.166.1, two mental foramina penetrate the outer side of the ramus, the larger and more ventral one opening beneath p3, the other beneath m1, matching their relative size and position in the holotype; a faint sulcus extends anteriorly from the anterior foramen. However, as in the holotype, there is no evidence within the masseteric fossa of the "labial mandibular foramen" that has been reported in the early marsupials *Kokopellia juddi* Cifelli, 1993a and *Alphadon eatoni* Cifelli and Muizon, 1998a (see also Cifelli and Muizon 1997, 1998b).

On the medial side of TMP 91.166.1, the symphyseal boss is the most prominent feature of the horizontal ramus; it is better preserved and dorsoventrally shallower than in the holotype. It forms a raised, elongate oval of bone that slopes posteroventrally to beneath p3, which in TMP 91.166.1 is at the deepest part of the ramus (the holotype is deepest beneath m4). The articulating surface of the boss is covered by broad, shallow pits that give it an irregularly pock-marked texture. If this surface is held in the vertical plane, its presumed orientation in life when in full articulation with its counterpart on the left side, the horizontal ramus at the level of the symphysis leans laterally, causing the premolars to lean laterally as well (Fig. 2A$_2$); more posteriorly, the dentary gradually becomes more vertical and the molars are vertically emplaced. This peculiar orientation of the lower premolars has unusual functional implications that have not been recognized before and these are discussed below.

In TMP 91.166.1, a medial shelf on the horizontal ramus extends posteriorly from the upper margin of the symphyseal boss, beginning below p1. This shelf slopes ventromedially, becoming steeper posteriorly; it is more prominent in this specimen than in the holotype. The ventral limits of the shelf are provided by a faint, narrow ridge that may be the mylohyoid line, which marks the origin of the mylohyoid muscles, although in the Virginia opossum, *Didelphis virginiana*, these muscles are reported to originate much more ventrally on the medial face of the dentary (Hiiemae and Jenkins 1969); beneath m4 in TMP 91.166.1, this ridge curves dorsally towards the raised anterior margin of the pterygoid fossa. Although little of the pterygoid fossa is preserved in TMP 91.166.1, the mandibular foramen has not been damaged and opens into the fossa just anterior to the broken posterior edge of the specimen, well anterior to its position in *D. virginiana* and directly above the anteriormost extremity of the inflected angular process; in living didelphids, the foramen carries the inferior alveolar branch of the mandibular nerve and blood vessels that accompany it (Wible 2003: 177). Anterior to the foramen in TMP 91.166.1 (as in the holotype: Fox and Naylor 1986: fig. 1C), there is no evidence of an internal mandibular groove (holding postdentary elements; e.g., Meng et al. 2003) or even a mylohyoid groove as seen in, e.g., *D. virginiana* [this groove marks the passage of the mylohyoid vessels and nerve (Bensley 1902)].

The second new specimen, TMP 90.12.29 (Figs. 2B, 3A), is in poorer condition overall than TMP 91.166.1, but it includes a more extensively preserved coronoid process, a complete dentary peduncle or condylar process, the condyle, and part of the angular process. In TMP 90.12.29, the anterior margin of the coronoid process slopes at about 104 degrees relative to the alveolar border, approximately at the same angle as in the holotype (Fox and Naylor 1986: fig. 3). What remains of the angular process in TMP 90.12.29 is inflected and forms a broad, medially directed shelf that is flat on its ventral side; the shelf is broken both medially and anteriorly, so its full extent cannot be determined. The posteromedial margin of the shelf, however, is complete and curves smoothly anteriorly; at least in the parts that remain, it does not form a posteriorly directed notch and acute posterior process, as in *D. virginiana* and the short-tailed opossum, *Mono-*

Fig. 2. *Didelphodon coyi* Fox and Naylor, 1986 from the Horseshoe Canyon Formation, Edmontonian Land Mammal Age (early Maastrichtian). **A**. TMP 91.161.1, Paintearth Creek, Alberta, incomplete right dentary, containing 12-3 (broken), c (broken), p1–3, m1–2, m3–4 (broken) in occlusal (A_1) and anterior (A_2) views. **B**. TMP 90.12.29, Michichi Creek (type locality), Alberta, incomplete left dentary, containing p3 (broken) in occlusal (B_1) and labial (B_2) views. A_1 and B_1 stereophoto pairs. Scale bars 5 mm.

delphis brevicaudata (Erxleben, 1777) (Wible 2003). At the anteriormost extent of this margin, the shelf turns abruptly medially a short distance before reaching a now-broken

edge: perhaps a shallow notch and posterior process were developed more medially here, although if so, they would have been well medial to their position in *D. virginiana*. In the
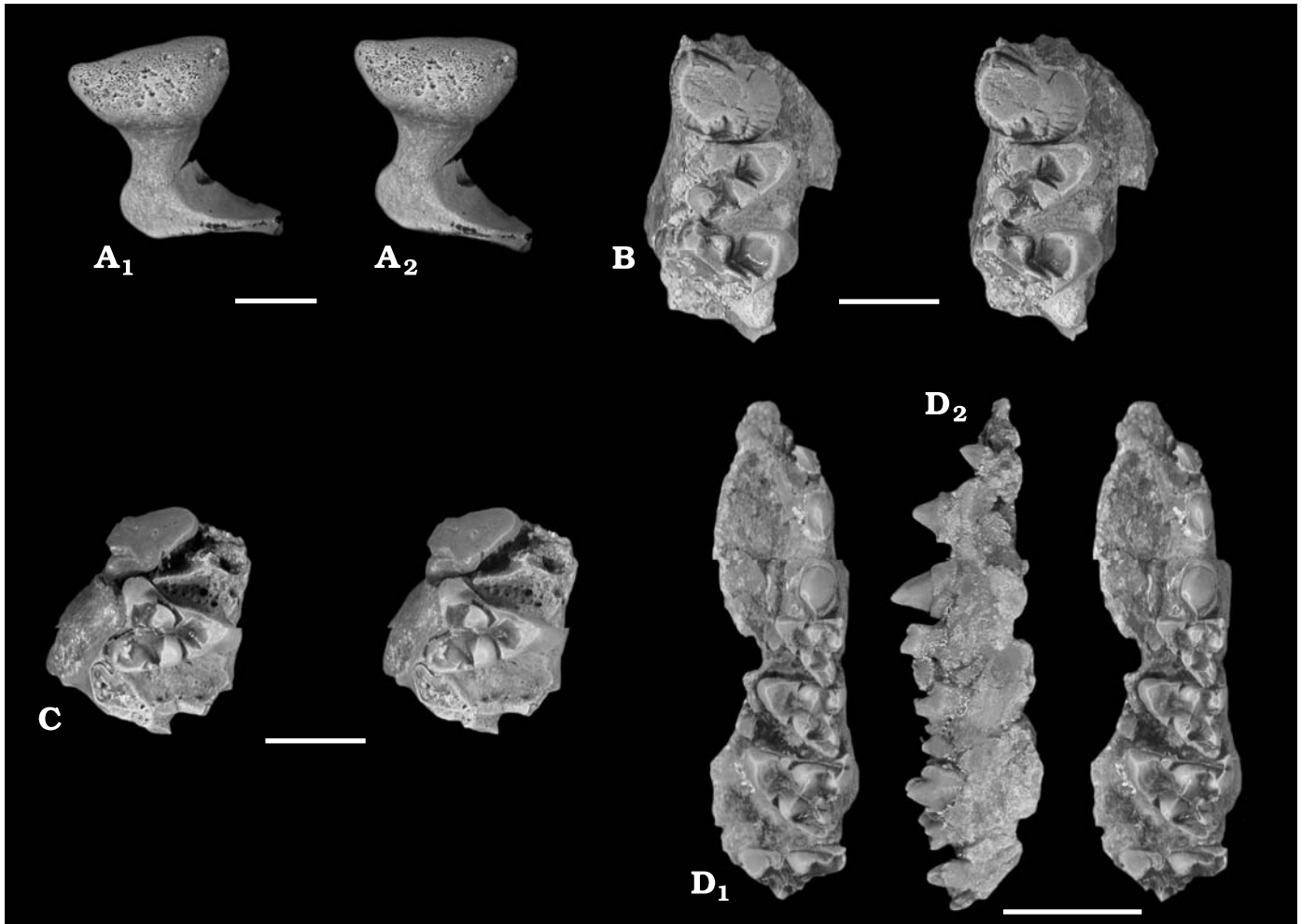
Fig. 3. **A**. *Didelphodon coyi* Fox and Naylor, 1986, condyle and inflected angle of TMP 90.12.29, from the Horseshoe Canyon Formation, Edmontonian Land Mammal Age (early Maastrichtian), Michichi Creek (type locality), Alberta, in posterior view with ventral surface of inflected angle horizontal (A_1) and dorsal surface of condyle horizontal (A_2). **B**. *Didelphodon coyi* Fox and Naylor, 1986, incomplete right maxilla, TMP 94.125.125, from the Scollard Formation, Lancian Land Mammal Age (late Maastrichtian), KUA-1 locality, Red Deer River Valley, Alberta, containing P3, M1, M2 (broken) in occlusal view. **C**. *Eodelphis cutleri* (Smith Woodward, 1916), incomplete right maxilla, UALVP 43005, from the Dinosaur Park Formation, Judithian Land Mammal Age (late Campanian), Onetree Creek, Dinosaur Provincial Park, Alberta, containing M2–3 in occlusal view. **D**. Undescribed *Alphadon*-like marsupial, incomplete left maxilla, TMP 95.178.26, from the Oldman Formation, Judithian Land Mammal Age (late Campanian), Devil's Coulee, Alberta, containing P1–3, M1–4 in occlusal (D_1) and labial (D_2) views. B, C, and D_1 stereophoto pairs. Scale bars 5 mm.

holotype and TMP 91.166.1, the shelf reaches slightly anterior to the level of the mandibular foramen, almost as far anteriorly as the base of the coronoid process above and well anterior to the anteriormost extent of the shelf in the Virginia opossum. Crompton and Lieberman (2004) associated the inflected angle in living marsupials with insertion of a neomorphic superficial division of the medial pterygoid musculature not seen in extant eutherians; we conclude that this muscle was present in *Didelphodon*, as well.

In TMP 90.12.29, a low ridge extends from the base of the angular process to the ventromedial margin of the condyle. In the holotype, the condyle is damaged, with its medial end missing (Fox and Naylor 1986: fig. 3B). In TMP 90.12.29, the complete condyle is a transversely expanded subcylindrical body 11.6 mm long that in posterior view is slightly deeper at its medial end than laterally (Fig. 3A). Re-

construction of the posterior part of the dentary based on TMP 90.12.29 and the holotype together demonstrates that most of the condyle in *D. coyi* is lateral to the vertical plane of the coronoid process. By contrast, in *Didelphis virginiana*, the condyle projects further laterally than medially relative to this same plane but projects further medially than in *D. coyi*.

On the lateral side of TMP 90.12.29, the posterior part of the masseteric shelf that ventrally borders the masseteric fossa is still in place. As in the holotype (Fox and Naylor 1986: fig. 3), the shelf narrows posteriorly to a low crest that extends along the ventrolateral edge of the dentary peduncle to the lateral extremity of the condyle; in *Didelphis virginiana*, this shelf remains wide posteriorly to its junction with the condyle. The articulating surface of the condyle is well defined, especially dorsally, and presumably was covered by

a thin layer of cartilage in life: in dorsal aspect, the articulating surface extends slightly more anteriorly on the lateral side of the condyle than medially; in its curvature around the posteroventral aspect of the condyle it narrows from either side as in *D. virginiana*. If the dentary is held so that the ventral surface of the inflected angular process is horizontal, the condyle slants obliquely (Fig. 3A$_1$), from dorsomedial to ventrolateral; alternatively, if the condyle is held horizontally (Fig. 3A$_2$), the angular process slants ventromedially. These same relative orientations between condyle and angular process are seen in some adults of *D. virginiana*. Until better preserved specimens of *D. coyi* are collected, however, the actual orientation of these structures in life cannot be determined in this species.

Lower dentition.—TMP 91.166.1 is incomplete anteriorly but its cleanly broken anterior surface reveals the roots of the canine and incisors still within their alveoli (Fig. 2A$_2$). The lower canine, not known previously in *Didelphodon coyi*, was well developed as indicated by the dimensions of its broken cross section (depth = 4.6; W = 3.8), which show the tooth to have been slightly compressed bilaterally. In TMP 90.12.29, the canine is missing but its alveolus extends posteriorly to beneath p3. In addition to these aspects of the canine, something of its orientation can be determined as well: if TMP 91.166.1 is held so that its symphyseal surface is vertical, a line through the greatest depth of the canine leans laterally at approximately 30 degrees from the vertical. In *Didelphis virginiana*, the snout at the level of the canines is wider than the mandible and the lower canines are splayed, allowing their tips to slide dorsally past the ventral margin of the maxillae into the maxillary fossae when the mandible is elevated and the postcanine teeth brought into occlusion. Perhaps the orientation of the lower canines in *D. coyi* is related to similar differences in the relative widths of the upper and lower jaws.

In TMP 91.166.1, two small incisor alveoli are exposed in cross section near the canine (Fig. 2A$_2$). The larger of the two is ventromedial in position, between the canine and the symphyseal surface; the root that it contains is ovate in cross section, being somewhat compressed bilaterally (depth = 1.7; W = 1.2), and is substantially less than the diameter of the canine root. This alveolus is clearly the homologue of the ventromedial incisor alveolus preserved in the holotype (Fox and Naylor 1986: fig. 4). The second incisor alveolus, not evident in the holotype, is ventral to the canine and ventrolateral to the medial incisor; it is nearly circular in cross section and the root is less than half the diameter of that of the medial incisor, appearing to have been broken very near its end (depth = 0.5; W = 0.5). There is no indication of a third or fourth incisor alveolus in TMP 91.166.1 (for our assessment of the homologies of the lower incisors in *D. coyi*, see Discussion below).

In TMP 91.166.1, p1 [L = (2.4); W = 2.8] is located directly behind the canine and is closely appressed to it. Clemens (1966) identified isolated p1s of *Didelphodon vorax*, and two alveoli for this tooth are present in dentaries of this species, UCMP 54462 and LACM 15433 (Clemens 1966, 1968),

but p1 of *Didelphodon* has not previously been known from a tooth articulated in the lower jaw. The crown of p1 in TMP 91.166.1 is anteroposteriorly compressed and oriented nearly transversely across the summit of the dentary, from a labial and slightly anterior position to a lingual and slightly posterior position. Accordingly, the crown is wider than anteroposteriorly long; in *D. vorax*, the position of its alveoli indicates that p1 was probably oriented more anteroposteriorly (Clemens 1966: fig. 37, 1968: fig. 1), although in USNM 2136, a dentary that Clemens (1966: fig. 36) referred to *D. vorax* but that may pertain to *D. padanicus* (Archibald 1982: 158), the alveoli of p1 are nearly opposite one another across the jaw. In occlusal view of p1 in TMP 91.166.1, the middle parts of the crown are weakly constricted, with the anterior surface of the resulting "waist" fitting tightly over the convex posterior side of the canine and the posterior surface of the "waist" receiving a swollen anterobasal cusp on p2. The labial part of the p1 crown has been lost but the lingual side is unbroken: it is expanded into a small lobe and supports a steeply sloping wear facet in which the enamel has been abraded away and the dentine exposed; deep irregular scratches are incised into the dentine. Labial to the wear facet, a few irregular enamel ridges border the broken surface. A short cingulid is posteriorly adjacent to the wear facet; this cingulid may have extended further lingually but if so, it was worn away before death.

In TMP 91.166.1, p1 is two-rooted; both roots are stout and descend on either side of the root of the canine; they are nearly opposite to one another across the jaw, with the labial root only slightly more anterior in position. The lingual root is angled steeply posteriorly, parallel to the side of the canine root; the labial root is more nearly vertical and passes labial to the canine root; no accessory roots of p1 are visible in the specimen. In the holotype of *Didelphodon coyi*, there appears to be a single alveolus for p1, implying that the tooth was single-rooted in that specimen (Fox and Naylor 1986); if so, p1 in *D. coyi* is polymorphic for the number of roots. In TMP 90.12.29, there is a single small circular alveolus that opens between the posterior root of p2 and the canine alveolus, but whether this was for one of two roots or if p1 was single rooted cannot be determined owing to the poor condition of the specimen.

In TMP 91.166.1, p2 is well preserved and crowded against p1. In occlusal outline, its crown (L = 5.5; W = 5.0) is over four times as large in areal dimensions as that of p1. It is narrow anteriorly, expands into a greatly widened posterolingual lobe, and is oriented obliquely across the alveolar border of the dentary, so that its anteriormost parts project anterolabially beyond the posterior margin of p1; unlike p1, the crown of p2 is slightly longer than wide. In LACM 15433, the dentary of *D. vorax* described by Clemens (1968), p2 is in place but this tooth has not previously been known in *D. coyi*, being represented only by alveoli in the holotype. Like p1, p2 in TMP 91.166.1 is deeply worn: all of its original cuspation has been worn away, exposing dentine across most of the remaining surface. Like that on p1, the wear sur-

face slopes steeply lingually, faces dorsolingually, and is faintly convex from its labial to lingual side. From comparison to p2 on LACM 15433, this wear surface encompasses the main cusp (protoconid) and the swollen posterolingual lobe. In TMP 91.166.1, the lobe is worn down to nearly its base, leaving little of the lingual wall of the crown remaining. On the anterior side of p2, two small basal cusps are developed, the more lingual of which fits into the hollow on the posterior side of p1; the labial basal cusp is free, not contacting p1. The enamel on the labial side of p2 forms exodaenodont lobes above the anterior and posterior roots, respectively. A short, deep, nearly vertical furrow is formed by the enamel on the side of the posterior lobe; by comparison with p3, in which a longer furrow is developed in this position, this furrow marks the junction between the talonid or "heel" and the main body of the crown (protoconid) and corresponds to the molar hypoflexid. In its turn, the talonid is partly divided into two lobes on its posterior side. The more lingual of these projects posteriorly from the worn occlusal surface and probably represents the hypoconulid. Two roots are visible on p2; because the crown fits closely to the dentary, the complete dimensions of the roots cannot be determined, but alveoli on the holotype indicate that the anterior root of p2 is small, circular in cross section, and in a labial position; the posterior root is greatly widened transversely, extending across much of the alveolar border of the dentary as in the holotype (Fox and Naylor 1986) and confirmed by the broken roots of p2 in TMP 90.12.29. There is no evidence from these specimens that p2 possessed an accessory root as Clemens (1966) reported on a p2 of *D. vorax*.

The p3 in TMP 91.166.1 is greatly enlarged (L = 7.3; W = 4.7), with swollen coronal walls as is characteristic of p3 of *Didelphodon* (Clemens 1966, 1968; Fox and Naylor 1986); it closely resembles p3 on the holotype of *D. coyi* but is slightly smaller. The crown is divided into a tall, massive protoconid and a lower, bulbous, unicuspid, unbasined talonid; there is no evidence of anterobasal cusps. A strong ridge is developed posteriorly on the protoconid and terminates ventrally at the heel, separated from it by a shallow notch; the heel is also demarcated from the protoconid by deep furrows, one each on the labial and lingual sides of the crown. A very short basal cingulid is present anterolingually, and immediately labial to this, the anterior face of the protoconid is shallowly concave, fitting against the posterior side of p2. Towards its base, the crown is subdivided labially and lingually into two lobes at the anterior and posterior roots; the lingual lobes extend further ventrally and are more swollen than those on the labial side. On the labial side of the talonid a vertical ridge is developed that approximates the position of the posterior cingulid on the molars.

In TMP 91.166.1, the apex of the protoconid of p3 has been truncated by wear, although much less deeply than on p1 or p2. The protoconid wear facet, in which dentine is already exposed, slopes lingually but less steeply than the wear facets on the more anterior premolars. The apex of the talonid displays the first stages of wear: two subcircular facets

are developed there, one anterior, which is larger, and a substantially smaller facet posterior to it, immediately above the dorsal end of the posterior cingulid; this facet may mark the position of the hypoconulid. Much of the enamel covering the unworn parts of the crown is weakly wrinkled, especially on the lower parts of the labial wall. The entire crown is set more deeply into the dentary than are the crowns of the adjacent teeth, as if its eruption had not been fully completed at the time of death (see Discussion below).

In TMP 91.166.1, m1 and m2 are in place (they are missing from the holotype); the crown of m3 has been lost, although its roots are contained in their alveoli, whereas m4 is represented by only the base of the crown and the roots, its occlusal surface having been broken off before the specimen was collected. As in the holotype of *D. coyi* (Fox and Naylor 1986) and in *D. vorax* (Clemens 1966, 1968), the lower molar row in TMP 91.166.1 crosses the summit of the dentary obliquely, from anterolabial to posterolingual; hence, the long axis of m1 (L = 4.8; WTri = 3.2; WTal = 3.5) is oblique relative to the long axis of the dentary. The crown of m1 is deeply worn; what remains of the trigonid has been abraded down to the same level as the talonid, which is also worn. Together, these two parts of the crown form a nearly flat occlusal surface; dentine is broadly exposed over all of this surface, except at the center of the talonid basin, where a small, circular patch of enamel remains. The trigonid of m1 is narrower but longer than the talonid. A strongly curved cingulid is present on the anterolabial wall of the trigonid and may have terminated anterodorsally in a distinct cuspule, although the uppermost parts of the cingulid have been worn away. The anterolingual side of what remains of the paraconid projects anterolabially beyond the swollen posterolingualmost parts of p3 to meet the talonid of p3 along a very faint vertical groove in its posterior wall beneath the hypoconulid. This overlap was already suggested by the position of the empty alveoli of m1 relative to p3 in the holotype and in TMP 83.33.7 (Fox and Naylor 1986: figs. 3B, 6A). Posteriorly on m1, the tip of the hypoconulid has been truncated by wear but its base juts posteriorly, inserted into a notch on m2 formed by the base of the paraconid and the anterior end of the basal cingulid in a tight interlock between the two teeth. A short posterior cingulid descends labially from the hypoconulid and blends into a series of rounded, irregular vertical ridges on the labial face of the talonid. By contrast, the enamel covering the lingual side of the crown is smooth. The posterior labial cingulid and hypoconulid of m1 form a shallow notch that receives the anterior cingulid of m2, enhancing the interlock between the two molars.

In TMP 91.166.1, m2 (L = 5.1; WTri = 3.7; WTal = 3.8) is slightly longer and wider than m1 and is in line with it, so it too is oriented obliquely relative to the long axis of the dentary. The tooth is deeply worn, but less so than m1: the occlusal surface of the trigonid has been worn flat but the trigonid remains slightly higher than the talonid. The talonid is slightly wider than the trigonid and the trigonid is more anteroposteriorly compressed than that of m1. The rim of the

talonid is worn, but the cristid obliqua meets the posterior wall of the trigonid in a labial position (a stagodontid feature). The hypoconulid is still recognizable as a distinct cusp; a posterolingual furrow marks the division between the hypoconulid and entoconid, which were "twinned" posterolingually on the rim of the talonid, with the hypoconulid posterolabial to the entoconid. On the lingual side of m2, swellings marking the base of the paraconid and metaconid indicate that the paraconid was substantially larger than the metaconid, as in stagodontids generally. The anterolabial cingulid is massively constructed, incompletely enclosing a shallow pocket on the anterolabial wall of the protoconid. The cingulid ends lingually at a cuspule that is labially adjacent to the hypoconulid of m1; labially, the cingulid terminates in a cuspule on the side of the protoconid, near its base, and two smaller cuspules are developed along its length. The posterior cingulid is short but prominent. The posterior wall of the talonid is marked by a broad interdental wear facet that extends over much of its surface as evidence of the close interlock between m2 and m3. Nothing can be observed of the crown morphology of m3 or m4, except that on m4, the anterior cingulid is strongly developed and subdivided into small cuspules, not evident on m4 of the holotype owing to wear. A line passing through the long axis of m3–4 would unambiguously extend medial to the coronoid process, as in the holotype. The roots of the canine, premolars, and molars are heavily invested with cement. Further posteriorly, the mandibular corpus twists increasingly into a vertical orientation carrying the molar row with it. Interestingly, a similar trend in orientation of the lower tooth row is seen in *Didelphis virginiana*, although it is not as strongly developed.

Maxilla and upper dentition.—TMP 94.125.125 (Fig. 3B) is an incomplete right maxilla containing P3, M1, and a broken M2. The maxilla itself preserves little of anatomical interest except for a notch along the broken dorsal edge of the facial process. This notch marks the position of the infraorbital foramen, which opened above M1, as in *Didelphodon vorax* (Clemens 1973).

Whereas TMP 94.125.125 clearly pertains to *Didelphodon*, it is significantly smaller than specimens of *D. vorax* in dental dimensions that can be compared (see Clemens 1966: table 13). Moreover, when held manually, M1–2 of TMP 94 125.125 occlude readily with m1–2 on TMP 91.166.1, the specimen of *D. coyi* that has the most extensively preserved lower dentition now known. Conversely, the teeth of TMP 94.125.125 are too small to fit with the lower dentition of *D. vorax* as preserved in, e.g., a cast of LACM 15433, left dentary of *D. vorax* from the Hell Creek Formation cited above (Clemens 1968), or UALVP 1985, an incomplete right dentary with c and m2 of *D. vorax* from the Scollard Formation (Lillegraven 1969). Hence, TMP 94.125.125 is referred to *D. coyi* and furnishes the first evidence of the upper dentition of this species.

In TMP 94.125.125, P3 is a large tooth (L = 5.0; W = 5.4) and the tallest on the specimen; it has an inflated crown consisting of a labial cusp (paracone) and a swollen lingual lobe.

The crown, which is bean-shaped in occlusal outline, is wider transversely than anteroposteriorly long. Its anterior side is slightly concave, presumably meeting the convex posterior side of P2, an intuition corroborated by an interdental wear facet incised into the enamel within the deep part of the concavity. A narrow anterior cingulum extends along the base of the main cusp and continues around the anterolabial corner, where it breaks up into a labial patch of irregular cuspules. The anterolabial corner of P3, although rounded, projects somewhat anteriorly. A small cusp is present here, at the junction of a crest from the paracone and the cingulum; by comparison with the molars, this cusp is the stylocone and the crest, the preparacrista. The posterolabial corner of P3 is smoothly rounded and lacks a labial or posterior projection; a poorly defined vertical crest or postparacrista is developed on the posterior wall of the paracone. A short, rugose posterior cingulum meets the posterior crest at a raised cuspule, and lingually it divides into two ridges that curve towards the apex of the main cusp; the cingulum abuts the anterior side of M1 at the level of the paracone. The lingual side of P3 is expanded into a low but inflated lobe. Wear has truncated the apex of the paracone, producing a flat, subovate facet in which dentine is widely exposed, but the facet had not extended onto the lingual lobe by the time of death. Much of the enamel that remains is wrinkled, especially on the labial side of the crown.

M1 is well preserved, although moderately deeply worn. It closely resembles M1 of *Didelphodon vorax*, but on a smaller scale (L = 4.0; AW = 4.6; PW = 5.5). The crown is wider transversely than long anteroposteriorly and has prominent, rounded parastylar and metastylar lobes separated by a narrow but deep ectoflexus; the metastylar lobe projects far labially, as in M1 of *D. vorax* (Clemens 1966: fig. 52). Wear has truncated stylar cusps A and B (stylocone), preparacrista, and paracone, but from the proportions that remain, stylar cusp B was robust, as in *D. vorax*; whether a paracingulum was developed cannot be determined owing to wear. No cusp is present at the C position, and cusp D is massive and low, distinguishing features of M1–3 of *Didelphodon*. A low crest descends posteriorly from the apex of the D cusp to the posterolabial corner of the crown, but whether a small E cusp might have been present there is unclear. The postmetacrista is a high crest that extends from the posterolabial corner of the crown to the base of the metacone, from which it is separated by a carnassial notch; a narrow, strap-like wear facet extends along the crest, exposing dentine through much of its length. Most of the metacone has been worn away but from the parts that remain, it was distinctly larger than the paracone, as in *D. vorax* and other stagodontids; there is no metacingulum. The conules are clearly developed structures that are appressed closely to the bases of the paracone and metacone, respectively, as in other stagodontids. The protocone is anteroposteriorly short and transversely wide, as in *D. vorax*, but on this specimen its occlusal surface has been deeply worn. There are no protoconal cingula.

M2 (AW = 5.5) is little worn but its posterolabial corner,

including the ectoflexus, stylar cusp D, the postmetacrista, and much of the metacone, are not preserved. The parastylar lobe extends anteriorly as a hook-like structure that meets the posterolabial side of M1. What remains of the labial border of the parastylar lobe projects strongly labially, and the stylocone, although worn at its apex, is a massive cusp. The paracone is reduced and is smaller than the stylocone; as noted above, reduction of the paracone is a characteristic feature of the upper molars of stagodontids (Clemens 1966). The size of the remnant of the metacone indicates that it was larger than the paracone originally, and the conules are appressed to the base of the paracone and metacone. The paracingulum extends from the preparaconule crista to stylar cusp A. The protocone is unworn and is a prominent, tall cusp, as in *D. vorax* (it fits tightly into the talonid of m2 on TMP 91.166.1). There are no protoconal cingula.

Discussion

Lillegraven (1969) first documented the occurrence of *Didelphodon* in the Lancian Trochu local fauna from the lower (i.e., uppermost Cretaceous) parts of the Scollard Formation, Red Deer River Valley, Alberta. He referred the stagodontid specimens of his study to *D. vorax*; *contra* Fox and Naylor (2003), however, none of these specimens came from KUA-1, the locality that has yielded most of the Trochu local fauna. Hence, TMP 94.125.125 constitutes the first record of *Didelphodon* at KUA-1 and is also the first record of *D. coyi* at a Lancian horizon, all previous discovered occurrences being in the Edmontonian Horseshoe Canyon Formation (Fox and Naylor 1986; this paper). From the dimensions of its known parts, *D. coyi* appears to have been somewhat smaller in body size than *D. vorax*, although the p3 is more specialized than in the younger species, being relatively larger and having a more complex coronal structure (Fox and Naylor 1986; this paper). The new specimens of *Didelphodon coyi* described above contribute new information concerning several other issues, as follows:

Lower incisors.—Matthew (1916) recorded three lower incisors, the second of which is enlarged, in *Eodelphis browni* (Matthew 1916: figs. 1, 2; pls. II–IV; Simpson 1929: fig. 48; Clemens 1966: 58). If there were three lower incisors in *D. coyi* and if they had the same relative sizes and positions as in *E. browni,* then the small medial incisor, i1 (of the three), is not preserved in TMP 91.166.1. Alternatively, this tooth may have been lost evolutionarily, leaving only two lower incisors in at least TMP 91.166.1 (and perhaps in the species generally), with the more medial being the larger of the two. Clemens (1966: 58, 60) reported evidence of three lower incisor alveoli of subequal size in a dentary of *Didelphodon vorax* (UCMP 54462), and a second, undescribed, dentary of *D. vorax* appears to have three incisor alveoli, as well (personal communication 2003, Shane Ziemmer, Childrens' Museum, Indianapolis, Indiana). The primitive number of lower incisors in marsupials is at least four [see discussion in Cifelli and Muizon (1998)].

Hershkovitz (1982, 1995) cited *Eodelphis browni* as an early marsupial in which i2 (his i3) is "staggered", i.e., offset lingually and supported labially by a high bony buttress, a purported synapomorphy of didelphimorphian marsupials; by contrast, Cifelli and Muizon (1998: 536; and see Muizon et al. 1997: 488) stated that although i2 is enlarged in *E. browni* it is not "staggered", a view supported by Matthew's illustration of the holotype of *E. browni,* AMNH 1416 (*contra* Hershkovitz 1982: 193, 1995: 165). The more dorsal (lingual?) position of the larger incisor in TMP 91.166.1 (Fig. 2A$_2$) resembles that of the "staggered" i2 in *Didelphis virginiana*, implying homology with that locus; if so, the smaller incisor in TMP 91.166.1 is presumably i3. If *D. coyi* had but two unequally-sized lower incisors, it could not have been part of the ancestry of *D. vorax*, barring a reversal in the number and size of lower incisors for which there is no evidence.

Orientation of upper premolars.—At the time of Clemens' (1966) monograph on marsupials from the Lance Formation, Wyoming, *Didelphodon vorax* was known only from isolated upper and lower premolars and molars, several incomplete dentaries with teeth, and fragments of the otic region of the skull. The crowns of the upper premolars consist of a large main cusp (paracone) and a prominent basal lobe; lacking direct evidence from articulated dentitions, Clemens suggested that the lobes arise from the labial side of the crowns. In 1968, he re-addressed the orientation of the upper premolars in *D. vorax* based on premolar morphology and wear in LACM 15433, a previously undescribed left dentary of *D. vorax* containing p2–3, m3–4. He concluded that the basal lobes on the upper premolars are lingual in position, corresponding to the expanded lobes on the lowers, which extend lingually in LACM 15433. By matching the roots of isolated premolars to the alveoli of incomplete maxillae of *D. vorax*, Clemens (1973) and Lofgren (1992) strengthened the evidence that the lobes on the upper premolars are lingual in position. However, TMP 94.125.125, the maxilla of *D. coyi* described above, is the first discovered specimen of *Didelphodon* having an upper premolar in place in the maxilla and thus demonstrates conclusively that P3s having the coronal morphology of the isolated P3s referred to *D. vorax* do indeed pertain to *Didelphodon* and that in these teeth, the basal lobe is expanded lingually. In this light, and given the morphology and wear pattern of p1 and p2 in TMP 91.166.1, the crowns of P1 and P2 in *D. coyi* must have been expanded lingually, as well.

Premolar replacement pattern.—Although largely overlooked since, Clemens (1966: 62, fig. 37) presented the first definitive evidence showing that the replacement pattern of the postcanine dentition in Mesozoic marsupials is the same as in living species [in postnatal marsupials, but not other extant mammals, functional deciduous teeth are replaced at only the third premolar locus (Luckett 1993)]. Clemens discovered an incomplete crown of a developing p3 deep within its crypt in a dentary of a juvenile individual of *Didelphodon vorax* (UCMP 54462; Clemens 1966: 37); two alveoli open-

ing into the crypt from the alveolar margin demonstrate that the double-rooted deciduous premolar at this locus had been in place at the time of death. Alveoli for two double-rooted teeth open between the canine alveolus and the p3 locus in this specimen; in-life erosion of the alveolar margin of the dentary at the second postcanine locus indicates that this tooth was incompletely erupted (Clemens 1966: 62). No crypts or other evidence of replacing teeth are present at the anterior premolar loci in this juvenile individual, implying that these teeth were dp1 and dp2. Posterior to the p3 locus, alveoli show that m1 and m2 had already erupted, m3 partly so, and that m4 in this specimen was still mostly in its crypt with its roots only incompletely formed at death (Clemens 1966). In modern opossums, p3 and m4 are the last lower postcanine teeth to erupt (Luckett 1993; Cifelli and Muizon 1998a, b), a pattern matched by UCMP 54462. A later discovery of this same pattern in an early marsupial was subsequently reported by Cifelli et al. (1996; Cifelli and Muizon 1998a, b) in a dentary (OMNH 27380) of the Late Cretaceous *Alphadon eatoni*, thereby extending the generality of the pattern to another major lineage of Mesozoic marsupials.

With this as background, how do the specimens of *D. coyi* add to knowledge of postcanine tooth replacement in *Didelphodon*? In TMP 91.166.1, the crowns of p1 and p2 are deeply worn but that of p3 only slightly so. Moreover, the base of the p3 crown is set much more deeply into the alveolar border of the dentary than that of p1, p2, or the molars Fig. 1C); hence p3 appears to have been incompletely erupted at death, coming into occlusion with upper teeth only after p1–2 and at least m1–2 were in use. This suggests that p3 had been preceded by a deciduous tooth but that p1 and p2 had no functional predecessors, the pattern implied by Clemens' specimen UCMP 54462 (*D. vorax*) and seen in marsupials generally. Moreover, because the little-worn dorsal occlusal surface of p3 is virtually at the same plane as the occlusal plane of the adjacent premolars and molars, which are deeply worn, p3 in *D. coyi* must have continued to erupt after it first became functional (i.e., after it first began to occlude with upper teeth). Perhaps its rate of eruption compensated for the rate of wear that increasingly truncated its crown. Indeed, in the second new dentary of *D. coyi*, TMP 90.12.29, the base of p3 is much more elevated, close to level of the alveolar border of the anterior premolars and the molars (Fig. 2B$_2$), but the unbroken parts of its crown have been almost completely worn away, deeply enough to expose the posterior root canal. The late eruption of p3 in *D. coyi* is substantiated by the holotype: p3 is unworn, whereas m3 exhibits moderate and m4 only slight wear (m1–2 and the anterior premolars are missing in this specimen). Hence, from the evidence provided by specimens of *Didelphodon* (*D. vorax*, *D. coyi*) and *Alphadon* (Clemens 1966; Cifelli et al. 1996; this paper), the unique pattern of postcanine tooth replacement in early marsupials had been established in all pertinent details at least by Edmontonian time, approximately 74 Myr ago (Eberth 1997a). In arriving at this conclusion, we have assumed that the pattern of replacement in

the upper dentition of *Didelphodon* matched that in the lower, as is commonly the case in extant therian mammals (e.g., Slaughter et al. 1974: table 1).

Rougier et al. (1998) argued that the marsupial pattern of replacement has a taxonomic distribution beyond marsupials and that this pattern also characterizes the Deltatheroida, a group of non-marsupial mammals that are purported to be "stem metatherians" (although for a still-cogent, but largely ignored, dissenting opinion, see Cifelli 1993b) from the Late Cretaceous of East Asia and North America. Deltatheroidans resemble marsupials in postcanine dental formula, having three premolariform and four molariform teeth in each jaw, but the molars are significantly more primitive in structure and occlusal function than those of marsupials, never having achieved a fully tribosphenic grade of evolution (Fox 1975; Cifelli 1993b) and possessing no synapomorphies exclusively with marsupial molars. Rougier et al.'s (1998) conclusion concerning the replacement pattern in deltatheroidans was based on a juvenile specimen of *Deltatheridium pretrituberculare* Gregory and Simpson, 1926 (PSS-MAE 132), in which teeth at the p1–2 loci are in place and the tooth at the p3 locus had not completely erupted at the time of death. Invoking the marsupial model, Rougier et al. (1998) postulated that these teeth are dp1–2 and p3, and then deduced that because deltatheroidans have a marsupial-like pattern of tooth replacement, deltatheroidans and marsupials have a special relationship with each other! From the actual evidence that PSS-MAE 132 presents, however, the only valid conclusion that can be drawn is that the teeth in place at the p1–2 loci had erupted earlier than that at the p3 position: absent circular reasoning, whether the anterior two premolars had been preceded by deciduous teeth (the primitive pattern in therians), or instead are themselves deciduous teeth lacking successors (the marsupial pattern), cannot be determined from the specimen (and see Kielan-Jaworowska et al. 2004: 438, who arrived at this conclusion independently). It may be that deltatheroidans are "stem metatherians", but the evidence from eruption of the premolars is only permissive in that regard and is open to other, no less realistic, interpretations.

Premolar function.—In reconstructing the orientation of the upper premolars of *Didelphodon vorax*, Clemens (1968) hypothesized that the expanded lingual lobes of the upper and lower premolars in this species slope lingually away from one another and hence, could not have met in occlusion. On that account, he suggested that the primary function of these lobes was to protect the gums from injury during the crushing of hard, resistant foodstuffs. As already shown (Fox and Naylor 1986; this paper), the premolars of *Didelphodon coyi*, like those of *D. vorax*, are greatly expanded lingually, but the better preservation of the available specimens of *D. coyi* that are now available suggests an alternative explanation of premolar function in *Didelphodon*.

If TMP 94.125.125, the right maxilla of *D. coyi* described above, is held in an in-life position, with the external wall of the maxilla above the molars oriented vertically as in *Didelphis virginiana*, the wear surface on P3 is in a nearly horizon-

tal plane, having a slope that is no more than one or two degrees more dorsal lingually than labially. If TMP 91.166.1, the right dentary of *D. coyi* described above, is held in a position so that the premolars and the dentary beneath are also in a vertical plane, the wear surfaces on the premolars face dorsomedially, i.e., the worn crowns of these teeth are higher labially than lingually. Consequently, the occlusal surfaces on the upper and lower premolars meet only at their labial margins, and slope away from one another more lingually, just as Clemens (1968) thought was the case in *D. vorax*. But if that were so, how could the upper and lower premolars have occluded to function as a crushing mechanism?

As described above, the intermandibular symphyseal surface is well preserved in TMP 91.166.1 and its orientation relative to that of the main body of the dentary gives an important clue to premolar function in *Didelphodon*. In life, when the two dentaries were in articulation at the symphysis, the symphyseal surface was oriented in the vertical plane. The relatively smooth topography of this surface suggests that the symphysis was a syndesmotic joint and mobile, as in *Didelphis virginiana* (Crompton and Hiiemae 1970). As noted above, if TMP 91.166.1 is held so that the symphyseal surface is vertically oriented, the anterior part of the dentary and the premolars that it supports lean strongly labially (Fig. 2A$_2$). This orientation of the crowns brings the lingually expanded wear facets of the lower premolars into a nearly horizontal plane, subparallel with the plane of the uppers. Slight rotation around the long axis of the dentary coincident with elevation of the lower jaw would bring the biting surfaces of the lower premolars into full occlusion with those of the uppers, allowing their entire areal extent of the upper and lower premolar biting surfaces to meet. Hence, the lingual lobes seem to have been directly engaged in the crushing function—as already suggested by their remarkably massive development in *Didelphodon*—and not merely passive protectors of the gums.

Were stagodontids aquatic?—Szalay (1994) and Longrich (2004) have speculated that stagodontid marsupials were aquatic, with Szalay (1994) citing the morphology of isolated tarsal bones and Longrich (2004) the morphology of isolated caudal vertebral centra as well as the taphonomy of stagodontid fossils to arrive at this conclusion. We find their arguments to be unconvincing, and we explain why as follows:

(1) From 1884 (the year of Marsh's description of the first known stagodontid, *Didelphodon vorax*) to the present, the taxonomy of stagodontids has been based solely on characters of the dentition. At no locality of Late Cretaceous age, in Alberta or elsewhere, have teeth of a stagodontid and postcranial remains recognizable as belonging to the same individual ever been found. Instead, Szalay's (1994) and Longrich's (2004) identifications of isolated postcranial bones as stagodontid have depended primarily on the relatively large size of the bones concerned, with these authors evidently assuming that stagodontids are the only "large" mammals occurring in the North American Late Cretaceous. They are not:

among therians, large "pediomyids", alphadontids, cimolestans, condylarths, and taeniodonts, each known from species having molar dimensions that overlap with those of stagodontids, occur in the same beds as stagodontids, as do cimolodontid and cimolomyid multituberculates, large multituberculates of less certain affinities (such as *Essonodon* Simpson, 1927a), and therians of presently unknown affinities (e.g., Fox 1989). Whereas the astragali and calcanea of Late Cretaceous therians can be readily distinguished from those of multituberculates, differences in these bones between Late Cretaceous marsupials and placentals are less certain (cf. Szalay 1994; Luo et al. 2003), and we know of no basis whatever for distinguishing the caudal vertebral centra of stagodontids from those of other therians or even of multituberculates, as Longrich's (2004) conclusions require.

(2) Szalay (1994) considered that certain surfaces of articulation borne by the tarsals that he referred to "*Eodelphis browni*", "*Eodelphis* sp.", and "stagodontid, cf. *Didelphodus*" [sic] implied a flexible pes and, hence, aquatic habits. Primary among these surfaces is a nearly circular calcaneocuboid facet, indicating "the rotational ability of the foot of an aquatic animal" (p. 144). We note, however, that the calcaneocuboid facet in the arboreal tree-shrew *Ptilocercus lowii* Gray, 1848 is also circular (Szalay and Drawhorn 1980: fig. 9) as is that in the gliding dermopteran *Cynocephalus volans* (Linnaeus, 1758) (Szalay and Drawhorn 1980: fig. 11E), while the facet in the didelphid *Chironectes minimus* (Zimmermann, 1780), a specialized swimmer having webbed hind feet (Macdonald 1984: 831), is clearly crescentic (Szalay 1994: fig. 7.12E) and, hence, not circular at all. In regards the purported astragalus of stagodontids, Szalay (1994: 149) wrote that the "reduced [astragalonavicular] and the large, wedge-shaped and highly convex [astragalocuboid] facet [...] suggest extensive mobility between the cuboid and the astragalus. Perhaps this also reflects habitual use of the foot in water." By contrast, in *Chironectes minimus*, the astragalonavicular facet is extensive and there is no well-developed, separate astragalocuboid facet (Szalay 1994: fig. 7.12). Indeed, in the absence of observations to the contrary, an expanded contact between the astragalus and the cuboid, as in the "stagodontid" astragalus, could be evidence of a *bracing* between these bones and hence, *increased* rigidity of the foot (see, e.g., Hildebrand 1974: 535), not an increase in its flexibility: such a contact, for example, is seen in the echidna *Tachyglossus aculeatus* (Shaw and Nodder, 1792) (Szalay 1994: figs. 5.1, 5.3), having limbs and feet highly specialized for digging and hence resistant to mechanical stress.

(3) Longrich (2004) cited an "unusual abundance in fluvial deposits" of stagodontids in support of his conclusions that these marsupials were aquatic mammals. At no horizon in the North American Late Cretaceous, however, are stagodontids "unusually abundant", being neither the most abundant mammals nor even the most abundant therians at any locality of which we are aware, and at some localities that are especially rich in mammalian remains (e.g., KUA-1, Scollard Formation,

Alberta), stagodontids are actually relatively rare (e.g., Lillegraven 1969). Moreover, all mammalian specimens from North American Upper Cretaceous rocks known to us have been collected from fluvial deposits, not just the fossils of stagodontids; hence, by Longrich's reasoning, all of these mammals must have been aquatic, along with dinosaurs and all other tetrapods having remains preserved in the same beds—a conclusion that we find thoroughly implausible.

Acknowledgements

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Appendix 1

Here we present for purposes of completeness the correct descriptions of morphological characters of *Didelphodon* that were erroneously presented for this genus in the recent analysis of marsupial relationships by Luo et al. (2003); these corrections are documented directly from specimens in the UALVP and TMP collections or are taken from primary literature sources, including those evidently overlooked by Luo et al. (2003) (e.g., Clemens 1968; Fox and Naylor 1986; Lofgren 1992); we have added further remarks to our entries as necessary. Although we have not reviewed character states for all taxa in Luo et al.'s analysis, we have found that other significant errors are included in it: for example, for none of the species of the North American Late Cretaceous marsupials traditionally referred to the genus *Pediomys* are the ankle bones (calcaneum, astragalus) known—contrary to fig. 3 of Luo et al.—nor is *Pediomys* itself a monophyletic taxon (Fox 1987a, b; Davis 2003, 2004; Kielan-Jaworowska et al. 2004); other errors are noted below, as appropriate. The original numbers {#} of the characters as given by Luo et al. (2003: Supplementary Information) are retained here. Whereas the revised description of the characters below undoubtedly would affect Luo et al.'s (2003) computer-assisted analysis of early marsupial relationships, that subject is beyond the scope of this paper.

12. Location of the mandibular foramen (posterior opening of the mandibular canal): Scored as "(1) In the pterygoid fossa and offset from Meckel's sulcus (the intersection of Meckel's sulcus at the pterygoid margin is ventral and posterior to the foramen)." However, there is no evidence of Meckel's sulcus retained in the dentary of *Didelphodon* (or that of *Eodelphis*), so the most nearly correct alternative is "(3) In the pterygoid fossa but not associated with Meckel's sulcus."

22. Labial mandibular foramen inside masseteric fossa. Scored as: "(1) Present", which is incorrect; it is absent in *Didelphodon*. See, e.g., TMP 84.64.1, holotype of *Didelphodon coyi* (Fox and Naylor 1986: fig. 3).

23. Posterior vertical shelf of the masseteric fossa connected to the dentary condyle: (0) Absent; (1) Present as a thin crest along the angular margin of the mandible; (2) Present as a thick, vertical crest. Scored as "absent", which is incorrect; the crest is present in *Didelphodon coyi*, and is best characterized by alternative (2) (see Fox and Naylor 1986: fig. 1; TMP 90.12.29, described above). Unaccountably, Luo et al. have also scored this crest as absent in *Didelphis*, but in reality, it is hyperdeveloped in that taxon relative to its size in *Didelphodon* (see, e.g., Fox and Naylor 1986: fig. 5).

27. Orientation of the dentary peduncle (condylar process) and condyle. Scored as: "(1) Dentary condyle continuous with the semicircular posterior margin of the dentary; the condyle is facing up due to the upturning of the posterior-most part of the dentary", which is incorrect. The correct alternative is: "(0) Dentary peduncle more posteriorly directed" (see TMP 84.64.1, holotype of *D. coyi*; TMP 90.12.29, *D. coyi*, this paper); in *D. coyi*, the condyle is even more posteriorly directed than in *Didelphis*, which Luo et al. scored as "(0)".

30. Tilting of the coronoid process of the dentary (measured as the angle between the anterior border of the coronoid process and the horizontal alveolar line of all molars). Scored as unknown, which is incorrect. In TMP 84.64.1, the holotype of *Didelphodon coyi*, the coronoid process is extensively preserved (see Fox and Naylor 1986: fig. 3) and it "tilts" at about 104°, which is closest to alternative (3): "Coronoid process near vertical (95° to 105°)".

31. Alignment of ultimate molar (or posteriormost postcanine) to the anterior margin of the dentary coronoid process (and near the coronoid scar if present). Scored as "(1) Ultimate molar aligned with the coronoid process." In respect to *Didelphodon*, that is incorrect; the correct alternative is: "(0) Ultimate molar medial to the coronoid process." Both TMP 91.166.1 and 90.12.29, referred above to *D. coyi*, show that an extension of the molar row posteriorly would pass medial to the coronoid process, as was clear from already published illustrations of TMP 84.64.1, the holotype of this species (Fox and Naylor 1986: fig. 3). Moreover, this pattern had previously been documented in *D. vorax*: Clemens' (1966: fig. 37) illustration of an edentulous dentary of *D. vorax* (UCMP 54462) shows that the alveoli for m3–4 are medial to the base of the coronoid process, which extends further anteriorly than in *D. coyi*, and m2 and m1 are in successively more labial positions (and see Clemens 1968: figs. 1, 2). In another, more mature specimen of *D. vorax*, UALVP 1985, an incomplete right dentary from the Scollard Formation (Lillegraven 1969), m4 is well medial to the broken base of the coronoid process. Additionally, Luo at al. (2003) stated that in *Didelphis* m4 and coronoid process are in line. That is only partly correct, at least as seen in *Didelphis virginiana*: in young animals, in which dp3 is still in place, p3 just beginning to erupt, and m4 not completely erupted, the axis of the molar row passes medially to the coronoid process; only in older individuals, in which p3 and m4 are fully erupted, is the axis of the lower molar row brought in line with the long axis of the coronoid process (personal observation). Hence, relative to the condition in dentally mature *D. virginiana*, *Didelphodon* appears to be paedomorphic. The same relationship between the lower molars and the coronoid process in *Didelphodon* occurs in *Eodelphis* (Fox 1981: figs. 1, 2).

36. Ultimate upper premolar—protocone or protoconal swelling: "(0) Little or no lingual swelling; (1) Present." Scored as present in *Didelphodon* and homologous with the protocone on the ultimate upper premolar in eutherians (P5), which is plainly incorrect. In *D. vorax*, Clemens (1968) identified this structure simply as a "lingual lobe", and Lillegraven (1969) identified it as an "accessory lobe", as did Archibald (1982) and Lofgren (1992). Expressed differently, none of these major contributors to the modern, primary research literature concerning the anatomy and systematics of North American Late Cretaceous marsupials concluded that the lingual lobe on P3 in *D. vorax* is a protocone. Moreover, in *D. vorax* similarly swollen lobes are developed on the lingual side of P1 and P2 (Clemens 1966: figs. 48, 49; 1968; Lofgren 1992: fig. 1); if these lobes are serially homologous with the lingual lobe on P3 (as would appear to be the case) and the latter is a protocone or protoconal swelling, then *Didelphodon*, unlike other marsupials (see, e.g., Clemens 1979: 196), possesses semimolariform P1–3 (semimolariform upper premolars of tribosphenic therians are defined by their possession of a protocone and lack of a metacone: Scott et al. in press). We emphasize that these lingual structures in *Didelphodon* clearly lack the diagnostic features of protocones: they do not occlude within a basined talonid on the lower premolars nor are they modified from ancestral conditions displaying such a pattern (the lower premolars

of *Didelphodon*, the ancestral stagodontid *Eodelphis*, and all other marsupials lack a basined talonid). Instead, the lobe on the upper premolars met the lower premolar crowns in a mace-like fashion in which the occlusal surfaces were initially convex and became flat with wear. By contrast, the protocone and basined talonid of tribosphenic dentitions "were initially developed to supply additional *shearing* surfaces" (Crompton and Hiiemae 1970: 43 [emphasis added]), not for crushing or grinding. The molars of *Didelphodon* still retain these shearing surfaces, but there is no evidence of them on the premolars. Moreover, the lingual lobe on the upper premolars of *Didelphodon* is not supported by a separate lingual root (Lillegraven 1969; Clemens 1973; Lofgren 1992), as is the protocone in semimolariform premolars of eutherians. Plainly, the molar developmental field (Butler, 1939) in stagodontids or any other marsupials had not extended anteriorly to produce a molar-like morphology of the premolars. Consequently, to score the lingual lobe of the upper premolars in *Didelphodon* as a "protocone or protoconal swelling" as in eutherians is willfully to ignore an abundance of long-established evidence to the contrary and constitutes an hypothesis of homology between what are only superficially similar structures containing no evidence of community of descent.

37. Penultimate upper premolar—protocone or protoconal swelling: Scored as "unknown" in *Didelphodon*. However, Clemens (1966: fig. 49; 1968) and Lofgren (1992: fig. 1) showed that the penultimate upper premolar of *Didelphodon vorax* is swollen lingually, although this lingual lobe is not homologous to the protocone (see above).

38. Position of the tallest posterior upper premolar within the premolar series: scored as unknown. Clemens (1966) identified isolated teeth of *Didelphodon vorax* at the P1–3 loci, with their positions corroborated by Lofgren (1992) and, for P3, by the present paper; of the three upper premolars, P3 is clearly the tallest (Clemens 1966: figs. 48–50). Whereas it is true that P1–2 of *Didelphodon* have yet to be discovered articulated in a maxilla, there is far greater certainty as to the taxonomic identification and homologies of these as isolated teeth than there is concerning any of the isolated tarsal bones that Luo et al. have referred to *Didelphodon* and other North American Late Cretaceous marsupials as a crucial part of their analysis (see items 313–338 below).

39. Diastema posterior to the first upper premolar (applicable to taxa with premolar-molar differentiation): (0) Absent; (1) Present. Luo et al. scored this character as unknown in *Didelphodon*, although Lofgren (1992) had already shown that there is no diastema between P1 and P2 in this genus. Luo et al. (2003: 1934–1935) considered a diastema between P1 and P2 a derived feature uniting Late Cretaceous "metatherians" and Cenozoic "didelphid-like" marsupials (but see Discussion above and {142} below).

42. Ultimate lower premolar—arrangement of principal cusp a, cusp b (if present), and cusp c (assuming the cusp to be c if there is only one cusp behind the main cusp a). *Didelphodon* is scored as alternative (0): "Aligned in a single straight line or at a slight angle." There are only two cusps on p3 of *Didelphodon*, the protoconid (cusp a) and a talonid cusp, located directly posterior to the protoconid (Clemens 1966, 1968; Fox and Naylor 1986; this paper), as in the less specialized p3 of *Eodelphis* (Fox 1981). We are puzzled as to why, however, one would "assume", as have Luo et al., that this second cusp on p3 of *Didelphodon* is a metaconid (cusp c of Luo et al.; see {59}). This "assumption" constitutes an a priori statement concerning the homology of the cusp in question (i.e., it is by no means a neutral assumption) and as such contradicts long-estab-

lished evidence to the contrary: the metaconid—which would be positioned posterolingual to the protoconid as a trigonid cusp, not on the talonid directly posterior to the protoconid—is not developed on the lower premolars of any Late Cretaceous marsupial, including *Didelphodon*.

53. Development of postvallum shear on the second upper molar. Scored as "(2) Metacingulum/metaconule present, in addition to postprotocrista, but the metacingulum crest does not extend beyond the base of the metacone." This is incorrect: M1–3 of *Didelphodon* possess a metaconule and postmetaconule crista but lack a metacingulum, i.e., no crest at all is developed that continues labially from the postmetaconule crista along the posterior side of the metacone at its base; hence, none of the alternatives by Luo et al. describe the actual disposition of these structures in *Didelphodon* (see, e.g., Clemens 1966: fig. 53b; Clemens 1973: fig. 32b; UALVP 1600, *Didelphodon vorax*); the same pattern is seen in *Eodelphis* (UALVP 43005; Fig. 3C).

70. Paraconid position relative to the other cusps of the trigonid on the lower molars (based on the second lower molar). Scored as "(1) Paraconid lingually positioned (within lingual 1/4 of the trigonid width)." This is correct but incomplete, and (2) is the better alternative: "Paraconid lingually positioned and appressed to the metaconid." Appression of the paraconid to the metaconid on m2–4 is a characteristic feature of the stagodontid lower molar dentition (see, e.g., Fox and Naylor 1986: fig. 9; Cifelli and Eaton 1987).

72. Angle of the paracristid and the protocristid on the trigonid: (0) >90°; (1) 90~50°; (2) <35°. This is scored as (1), but the trigonid angle is about 35°on m2 and less than 30°on m3–4 of *Didelphodon coyi* and *D. vorax*, with the paraconid increasingly appressed to the metaconid posteriorly along the molar row (see, e.g., Fox and Naylor 1986: fig. 9).

77. Morphology of the talonid (or the posterior heel [sic]) of the molar: Scored as (5), but no alternative "(5)" for this character is given. The correct alternative is: "(4) Present as a functional basin, rimmed with three functional cusps."

82. Last lower molar—hypoconulid—orientation and relative size. Scored as "unknown" for *Didelphodon*. In UALVP 43006, a left m4 of *D. vorax* from the Lance Formation, Wyoming, the hypoconulid is erect but lower than the hypoconid, thereby matching the first alternative in this character description: "(0) Short and erect" (and matching the proportions of these cusps in m4 of *D. vorax* as already illustrated by Clemens 1966: fig. 47).

86. The length vs. width ratio of the functional talonid basin of the lower molars (in occlusal view, measured at the cingulid level, and based on the second molar): scored as "(1) Length equals width". However, in *Didelphodon*, the talonid basin is wider than long on m2 (see Clemens 1966: fig. 45; TMP 91.161.1, *D. coyi*), as it is in *Didelphis virginiana* (*contra* Luo et al.).

101. Presence of the paraconule and metaconule on the upper molars: scored as "(0) Absent." This is incorrect; the conules are present and well developed in *Didelphodon vorax* (e.g., UALVP 1600, incomplete maxilla with M1–3, from the Lance Formation, Wyoming) and *D. coyi* (TMP 94.125.125, described above); they are also well developed in *Eodelphis* (Fox 1981).

102. Relative position of the paraconule and metaconule on the upper first and second molars. Scored as: " (1) Both positioned near the midpoint of the protocone-metacone." This is incorrect; the correct alternative is: "(2) Paraconule and metaconule labial to the mid-

point." The conules are positioned at the base of the paracone and metacone in stagodontids, including *Didelphodon*.

103. Internal conular cristae. Scored as: "(0) Cristae indistinctive" [sic]. This is incorrect; the correct alternative is "(1) Cristae distinct and winglike" (see, e.g., UALVP 1600, *D. vorax*; TMP 94.125.125, *D. coyi*).

107. Stylar cuspule "B" (opposite the paracone): "(0)Vestigial to absent; (1) Small but distinctive [sic]; (2) Subequal to the parastyle; (3) Large (subequal to the parastyle), with an extra 'B-1' cuspule in addition to 'B'"; alternative "(3)" was scored for *Didelphodon*. Most students consider "stylar cuspule 'B'" to be homologous to the stylocone or primary cusp B of Crompton (1971) (see, e.g., Patterson 1956; Clemens 1966; Fox 1975; Bown and Kraus 1979; Kielan-Jaworowska et al. 2004), as do we. In *Didelphodon*, the stylocone is substantially larger than the parastyle (stylar cuspule "A" of Luo et al.) and is not usually accompanied by a "B-1" cusp (e.g., Clemens 1966; Hunter and Pearson 1996: fig. 2)—consequently, none of the alternatives presented by Luo et al. describe the condition in *Didelphodon*.

111. Position of the stylar cuspule "E" relative to "D" or "D-position": Scored as "(0) 'E' more lingual to 'D' or 'D-position'" in *Didelphodon*, which is incorrect; the correct alternative is "(1) 'E' distal to or at same level as 'D' or 'D-position'" (e.g., Clemens 1966: 71).

112. Upper molar interlock: scored as alternative (2) "Parastylar lobe of a succeeding molar lumbricated with metastylar region of a preceding molar." We do not know the intended relation characterized here because "lumbricated" is not a word in the English language.

118. Functional development of occlusal facets on individual molar cusps: (0) Absent; (1) Absent at eruption but developed later by crown wear; (2) Wear facets match upon tooth eruption (inferred from the contact surface upon eruption). For this character, Luo et al. have scored the taxa in their data matrix only for alternative "(0)" and "(1)"; peculiarly, no taxa in the matrix have been scored for alternative "(2)". Jenkins and Crompton (1979: 79) noted that in basal non-therian mammals, such as morganucodontids, intercusp wear facets develop only as a consequence of tooth-on-tooth contact during occlusion. By contrast, in early mammals having a reversed triangle dentition (Symmetrodonta and their derivatives), "the occluding crests....appear to have been under much more rigorous genetic control" (Cassiliano and Clemens 1979: 157), and opposing wear facets match at eruption, before use. Although these same differences are expressed in Luo et al.'s alternatives above, their distribution and scoring in the data matrix itself is obviously erroneous. *Didelphodon* should have been scored as exhibiting alternative "(2)", not "(1)".

119. Topographic relationships of wear facets to the main cusps: (0) Lower cusps a, c support two different wear facets (facets 1 and 4) that contact the upper primary cusp A; (1) Lower cusps a, c support a single wear facet (facet 4) that contacts the upper primary cusp B (this facet extends onto cusp A as wear continues, but 1 and 4 do not develop simultaneous [sic] in these taxa); (2) Multicuspate series, each cusp may support 2 wear facets. This character description is riddled with errors. According to homologies followed elsewhere in Luo et al.'s character descriptions, lower molar primary cusps a, b, and c are the protoconid, paraconid, and metaconid, respectively (see {57} and {58}); these homologies follow those of Crompton [1971; also followed by Crompton and Kielan-Jaworowska (1978), Bown and Kraus (1979), and Kielan-Jaworowska et al. (2004) and are otherwise widely accepted in the literature]. As for the upper molars, in Crompton's (1971) system primary cusp A is the para-

cone and cusp B is the stylocone (and see Patterson 1956; Clemens 1966; Jenkins and Crompton 1979), but in Luo et al.'s system, it is the paracone that has been dubbed cusp B (see {96}), an unfortunate and unnecessary source of confusion. Luo et al. did not explicitly state their opinion concerning the homology of their primary upper molar cusp A, but from their description of molar wear patterns (see {56-1}), this cusp appears to be located immediately anterior (mesial) to their cusp B; in Crompton's (1971; Jenkins and Crompton 1979) system, the primary cusp immediately anterior to the paracone in basal mammals is the stylocone (his cusp B). Hence, cusp A of Luo et al. is in the position of cusp B (stylocone) of Crompton (1971) but cusp B of Luo et al. is cusp A (paracone) of Crompton (1971). Luo et al. equated upper molar primary cusp C with the metacone ({96}), an homology that is disputable but of no relevance here. In Crompton's (1971) study of occlusal patterns in the evolution of the tribosphenic molar, wear facet 1 in the tribosphenic dentition was reconstructed as extending along the anterior or prevallum side of the upper molar and the posterior or postvallid side of the lower molar trigonid, i.e., along the anterior side of the paracone [cusp A of Crompton (1971), cusp B of Luo et al., and the preparacrista] and the posterior sides of the protoconid and metaconid (cusps a and c and the protocristid) on the occluding lower molar (see characters {121, 122}). In the tribosphenic dentition in Crompton's (1971) system, wear facet 4, however, is developed on the anterolingual side of the metacone and the posterolabial side of the lower molar talonid ({123}); hence, it is spatially separated (discontinuous) from wear facet 1 on both the upper and lower molars and does not appear in mammals more basal than *Peramus*, i.e., in mammals lacking a basined talonid (see Crompton, 1971: fig. 8). If primary upper molar cusp A is anterior to the paracone, as in Luo et al.'s terminology, alternative (0) in {119} "Lower cusps a, c support two different wear facets (facets 1 and 4) that contact upper primary cusp A" is physically impossible to achieve for occluding teeth at the same locus: by definition, the position of facet 4 on the lower molar is not on the metaconid but further posteriorly, on the posterolabial side of the talonid and well separated from the postvallid wall and facet 1. Similarly, alternative (1) is incorrect: cusp c (metaconid) is the posterolingual cusp of the trigonid; it is not a talonid cusp and is not implicated in the development of facet 4, which is generated on the posterolabial side of the talonid. Luo et al. scored *Didelphodon* (and most other mammals in their data matrix) as exhibiting alternative (2), but this alternative describes the pattern of molar wear in tritylodontids and multituberculates (see {56-4}), not tribosphenic therians, whereas tritylodontids and the two groups of multituberculates included in this analysis, "plagiaulacidans" and "cimolodontans", were scored for alternative "(3)", but there is no alternative "(3)" in this character description.

122. Upper molars—development of facet 1 and the preprotocrista (applicable to molars with reversed triangulation): (0) Facet 1 (prevallum crest) short, not extending to the stylocone area; (1) Facet 1 extending into the hook-like area near the stylocone; (2) Preprotocrista long, extending labially beyond the paracone. Luo et al. scored *Didelphodon* as exhibiting alternative (1). The descriptions and scoring for this character, however, include several errors. While the upper molars of *Didelphodon* do match alternative (1), they also match alternative (2), at least after the terminology of that alternative has been corrected: In no therians having fully tribosphenic molars known to us does the preprotocrista extend labially beyond the paracone; instead, it terminates more lingually, at the base of the paraconule (see, e.g., Bown and Kraus 1979: fig. 9-1). The preparaconule crista and paracingulum, not the preprotocrista,

are the second-rank prevallum crests that continue more labially to the parastylar area, as part of the basic design of these teeth (Fox 1975). Although not scored as such by Luo et al., this pattern is nonetheless matched by the upper molars of *Didelphodon* (e.g., Clemens 1966: figs. 52, 53). Luo et al.'s alternative "(2)", however, also includes reference to the "preprotocrista" as "long", claimed to be exhibited by, among others, the early insectivorans *Gypsonictops* and *Leptictis* (see Lillegraven 1969: figs. 27, 28), the Late Cretaceous/Paleocene archaic ungulate *Protungulatum* (see Crompton and Kielan-Jaworowska 1978: fig. 16; Kielan-Jaworowska et al. 1979: fig. 12-19A), and the extant lipotyphlan *Erinaceus* (Thenius 1989: fig. 126.). In fact, these eutherians exhibit a narrow stylar shelf and a correspondingly *shorter* "preprotocrista" than that in *Didelphodon* and several other similarly scored Late Cretaceous marsupials, such as *Albertatherium* (Fox 1971). Hence, not only is Luo et al.'s scoring of this character for *Didelphodon* mistaken but that for several other taxa as well.

132. Upper canine—presence vs. absence, and size. Luo et al. scored the upper canine of *Didelphodon* as "unknown", which is incorrect in terms of the alternatives cited here. Lofgren (1992) showed that this tooth in *Didelphodon* is large, as would be expected and as it is in *Eodelphis* (this paper).

142. Procumbency and diastema of first (functional) upper premolar or postcanine in relation to upper canine: (0) Not procumbent and without a diastema; (1) Procumbent and with a diastema. This character was scored as "?" for *Didelphodon*. Although it is still not known whether P1 of *Didelphodon* is procumbent, Lofgren (1992) showed that P1 in this stagodontid follows closely behind the canine, with no space intervening between the two teeth; this same pattern is now known in *Eodelphis*, as well (this paper). Luo et al. scored *Didelphis* as "1" for this character, but in fact there is no diastema between C and P1 in the Virginia opossum (personal observation). Moreover, neither of the character state alternatives in {142} express the purported synapomorphy that Luo et al. cited in their text as uniting Late Cretaceous "metatherians" and Cenozoic "didelphid-like" marsupials ["The first upper premolar (P1) is procumbent and close to the upper canine, followed by a large diastema behind" (Luo et al.: 1934–1935)], nor is the distribution of this purported synapomorphy included in the data matrix (see {39} above).

156. Enamel microstructure. Scored as alternative "(2)". Incorrect: Luo et al. present only alternatives "(0)" and "(1)" as states of this character.

213–238. In Luo et al.'s analysis, twenty-six characters describing aspects of the morphology of the proximal tarsals (astragalus, calcaneum) were scored for *Didelphodon*. The tarsals of stagodontids,

however, are unknown. Szalay (1994) referred an isolated calcaneum to "stagodontid, cf. *Didelphodus*", the latter presumably a lapsus for *Didelphodon* [*Didelphodus* is an Eocene cimolestid eutherian (McKenna and Bell 1997)]; however, the specimen in question, TMP 87.101.5, is from the Dinosaur Park Formation, southern Alberta, a Judithian horizon that in respect to stagodontids has yielded only fossils referrable to *Eodelphis* spp. Szalay (1994) identified the other purported stagodontid tarsals that he described as pertaining to *Eodelphis*, not *Didelphodon*, but, in fact, all of these specimens are isolated elements (collected by underwater screening) and none can be demonstrated to pertain to any stagodontid (see Introduction and Discussion above).

278. Rostral tympanic process of the petrosal: (0) Absent or low ridge; (1) Tall ridge, but restricted to the posterior half of the promontorium; (2) Well-developed ridge reaching the anterior pole of the promontorium. Luo et al. scored this character as "(1)" for *Didelphodon* and the extant marsupials included in their analysis; Wible (1990: table 1), however, had characterized the process in *Didelphodon* and Late Cretaceous marsupial petrosal types A–C as "low", contrasting them with a raised rostral tympanic process, which he believed "is a synapomorphy of Recent marsupials" (Wible 1990: 199).

279. Caudal tympanic process of the petrosal: Luo et al. scored this feature as "unknown" in *Didelphodon*; however, Wible (1990: table 1, p. 198) had scored it as present and extending "medially from paroccipital process and contact[ing] promontorium medial to fenestra cochleae."

302. Epitympanic recess lateral to crista parotica: Luo et al. scored this character as unknown in *Didelphodon.* However, Wible (1990: 200) had earlier characterized the epitympanic recess (the "medial chamber of the epitympanic sinus of Clemens 1966: fig. 56c) as "enlarged" in *Didelphodon* and in the position of the epitympanic recess in *Didelphis* and Late Cretaceous marsupial petrosal types A and B (Wible 1990: figs. 2B, 4A, 5A). Further confounding Luo et al.'s scoring for this character in *Didelphodon* is their scoring for character {264} Squamosal—epitympanic recess, alternative (2) "Large contribution [of the squamosal] to the lateral wall of the epitympanic recess." If the epitympanic recess of *Didelphodon* is not known, how could the composition of its lateral wall be determined?

306. Stapedial artery sulcus on the petrosal: (0) Absent; (1) Present. Luo et al. indicated that this character is unknown in *Didelphodon*; by contrast, Wible (1990: table 1) scored the intratympanic stapedial artery as absent in *Didelphodon* (no sulcus is present on the petrosal), a synapomorphy of marsupials (p. 201).