

Phylogeny and evolutionary history of the Aplodontoidea (Mammalia: Rodentia)

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Although over a hundred species of fossil aplodontoids have been described since the extant species, *Aplodontia rufa* (the mountain beaver), was first described by Rafinesque in 1817, a thorough survey of the relationships among all the species in this clade has not been undertaken since McGrew's study in 1941. Here, a complete phylogenetic analysis of all published species of aplodontoids is used to reconstruct the evolutionary relationships within the clade, and to present an updated classification of the Aplodontoidea. Several of the traditionally recognized subfamilies are found to be paraphyletic, namely the Prosciurinae, the Allomyinae, and the Meniscomyinae. Others, however, including the Aplodontinae and the Mylagaulidae, appear to be monophyletic. These latter two taxa, which include all of the hypsodont members of the aplodontoid clade, seem to be sister taxa. The history of the aplodontoid clade shows several episodes of rapid diversification in the Early Oligocene, the Late Oligocene, and the Early to Middle Miocene. The Ansomyinae and Aplodontinae show comparatively low speciation rates. The patterns of change in morphology and evolutionary rates suggest a need for a more detailed study of the causes of diversification, extinction, and ecological change in this lineage. © 2008 The Linnean Society of London, *Zoological Journal of the Linnean Society*, 2008, 153, 769–838.

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INTRODUCTION

Aplodontoids are a diverse group of rodents represented among modern mammals by only a single living species: the sewellel or mountain beaver, *Aplodontia rufa* (Rafinesque, 1817). Fossil aplodontoids have a Holarctic distribution. Most species are known from North America, but several species have been found in Europe and Asia. Although the extant species is very limited in distribution and abundance, aplodontoids were a common and diverse element in North American Oligocene and Miocene faunas (McGrew, 1941; Shotwell, 1958; Rensberger, 1983; Korth, 2000b).

Aplodontoids are diverse, abundant, and their morphology changes greatly through the history of the

lineage, making them well suited for phylogenetic analysis, despite the fact that the aplodontoid fossil record is composed mostly of teeth. Studying the phylogeny of this group is important for several reasons, among them understanding the evolution of hypsodony (high-crowned teeth). The evolution of hypsodony, although extensively studied in groups such as horses, is relatively poorly understood in other mammal taxa, especially in small mammals such as rodents, in which it evolved independently in many clades. Aplodontoids evolved hypsodony during the Late Oligocene and Early Miocene, and there is even some evidence to indicate that hypsodony may have evolved more than once in this clade (Rensberger, 1981, 1983; Korth, 1994b).

A comprehensive knowledge of the phylogeny of aplodontoids will also facilitate the understanding of the evolution of their morphology and ecology. Aplodontoids appear as small, generalized, squirrel-like rodents, little different from their paramyid ancestors. These evolve into distinct ecomorphological

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groups, including apparent arboreal frugivores (allomyines, which resemble flying squirrels in their dental and cranial morphology), small burrowing forms (meniscomyines), and two different groups of larger fossorial rodents, one of which occurs in open environments throughout western North America (mylagaulids), and one of which (aplodontines) remains limited to apparently more closed habitats in the northern Great Basin and northern Rocky Mountains. A well-resolved phylogeny will provide an evolutionary context for the study of these dramatic ecological changes.

Until now, most studies of aplodontoid systematics have been limited in scope, and have focused on describing one or more species from temporally and geographically restricted areas. The last study to survey all aplodontoids, rather than individual smaller clades or species, was that by McGrew (1941). The only attempt to apply modern phylogenetic methods to the problem of aplodontoid systematics (Hopkins, 2004) involved only a limited subset of aplodontid species. Thus, a major benefit of a comprehensive revision of the Aplodontoidea will be to simplify studies of individual new species, by bringing together in a consistent framework all of the species currently known. In analyzing all the known species of aplodontids, I can generate an evolutionary basis for studying all of the problems discussed above.

Historically, the superfamily Aplodontoidea has been subdivided into two families: the Aplodontidae and the Mylagaulidae (McGrew, 1941). The family Aplodontidae (known from Late Eocene to recent times) incorporates a huge range of morphological diversity. Early members of the family are similar in morphology to basal rodents, particularly to members of the Paramyidae: they have low-crowned teeth with bunodont (low, rounded) cusps, resembling those of modern squirrels. At least four other discrete morphological groups occur within the Aplodontidae in the Oligocene and in the Miocene: the Ansomyinae are all extremely small, brachydont, and relatively lophodont (Qiu, 1987); the Allomyinae are somewhat larger, brachydont, and characterized by complex, interlocking internal cusp morphology (Rensberger, 1983); the Meniscomyinae are mesodont and have a relatively simple lophodont tooth morphology (Rensberger, 1981, 1983); and the Aplodontinae range from very hypsodont to hypselodont (Shotwell, 1958). The family Mylagaulidae, on the other hand, includes a much more limited range of morphologies. Mylagaulids first appear in the Late Oligocene, but rapidly diversify to become extremely common and abundant in Middle and Late Miocene faunas all over North America. Mylagaulids have frequently been hypothesized to be derived from within aplodontids (McGrew, 1941; Rensberger, 1980; Korth, 1994b), although there is no clear

consensus on the specific ancestral group. Meniscomyines are the likely candidates, but have a stratigraphic range almost perfectly concurrent with the earliest mylagaulids, rather than preceding them as would be expected from the ancestral clade.

The last study to survey all aplodontoids, rather than individual smaller clades or species, was that by McGrew (1941). The only attempt to apply modern phylogenetic methods to the problem of aplodontoid systematics (Hopkins, 2004) was limited in scope, and made substantial assumptions about the species belonging in the ingroup. The analysis presented here is comprehensive, including all published species of aplodontids and mylagaulids, as well as some previously unpublished material. This comprehensive analysis makes it possible to determine the relationships among the putative subfamilies of aplodontids and mylagaulids, as well as the connections between the two families of aplodontoids.

The classification used throughout this paper is based on the phylogeny produced by this analysis. To reduce confusion, I have used this classification scheme (shown in Table 1) throughout the paper. However, for the sake of clarity, the systematic discussion is presented at the end of the paper, after the discussion of the phylogenetic analysis. The classification is shown here without justification; for an explanation of the reasons for taxonomic changes, see the systematic paleontology section, after the Discussion.

PHYLOGENETIC ANALYSIS

PHYLOGENETIC METHODS

All 98 published species of aplodontid rodents were included in the analysis. In addition, seven unpublished species of aplodontids have been included, although they will be described systematically elsewhere. A complete list of the included species treated as operational taxonomic units (OTUs) can be found in Table 1. Three additional taxa, *Ischyromys typus* Leidy, 1856, *Paramys delicatus* Leidy, 1871, and *Reithroparamys delicatissimus* Leidy, 1871, were used as outgroups to root the tree.

Most characters were obtained from two primary sources. Numerous characters were obtained from a thorough survey of all available published taxonomic literature, taking note of all characters used in the description of aplodontid species and higher taxa (see Table 1 for references used). New characters were also recognized in the course of comparing specimens and published images. The initial list included more than 500 characters. The resulting character list was pared down by removing all redundant characters, i.e. those that described the same feature in different terms or on different teeth, which do not vary

Table 1. List of included species with references used for taxonomy and morphology

INGROUP TAXA	References	Specimens (S) or literature only (L)?
<i>Pelycomys brulanus</i>	Korth 1986	L
<i>Pelycomys placidus</i>	Galbreath 1953	L
<i>Pelycomys rugosus</i>	Galbreath 1953	L
<i>Prosciurus vetustus</i>	Matthew 1903	S
<i>Prosciurus lohicolus</i>	Matthew and Granger 1923	S
	Kowalski 1974	
<i>Epeiromys spanius</i>	Korth 1989	L
<i>Ephemeromys hospes</i>	Wang and Heissig 1984	L
Aplodontidae		
<i>Campestrallomys annectens</i>	Korth 1989	L
<i>Campestrallomys dawsonae</i>	Macdonald 1963	S
	Korth 1989	
	Macdonald 1970	
<i>Campestrallomys siouxensis</i>	Korth 1989	L
<i>Leptoromys wilsoni</i>	Tedrow and Korth 1997	L
<i>Oropyctis pediasus</i>	Korth 1989	L
<i>Plesispermophilus atavus</i>	Schmidt-Kittler and Vianey-Liaud 1979	L
<i>Prosciurus albiclivus</i>	Korth 1994b	L
<i>Prosciurus daxnerae</i> *	Lopatin 2000	L
<i>Prosciurus magnus</i> *	Korth 1989	L
<i>Prosciurus ordosicus</i> *	Wang 1987	S
<i>Prosciurus parvus</i>	Korth 1989	L
<i>Prosciurus relictus</i>	Cope 1873	S
	Korth 1989	
<i>Haplomys arboraptus</i>	Shevyreva 1971	S
	Kowalski 1974	
	Wang 1987	
<i>Haplomys galbreathi</i>	Tedrow and Korth 1997	L
<i>Haplomys liolophus</i>	Cope 1884	S
	Rensberger 1975	
<i>Dakotallomys pelycomyoides</i>	Tedrow and Korth 1997	S
<i>Dakotallomys lillegraveni</i>	Tedrow and Korth 1997	L
Ansomyinae		
<i>'Allomys' storeri</i>	Tedrow and Korth 1997	S
<i>Ansomys crucifer</i> *	Lopatin 1997	L
<i>Ansomys descendens</i>	Dehm 1950	L
	Schmidt-Kittler and Vianey-Liaud 1979	
<i>Ansomys hepburnensis</i>	Hopkins 2004	S
<i>Ansomys nexodens</i>	Korth 1992a	S
<i>Ansomys orientalis</i>	Qiu 1987	L
<i>Ansomys shantungensis</i> *	Rensberger and Li 1986	L
<i>Ansomys shanwangensis</i>	Qiu and Sun 1988	L
<i>Plesispermophilus angustidens</i>	Filhol 1883	S
	Schmidt-Kittler and Vianey-Liaud 1979	
<i>Downsimus chadwicki</i>	Macdonald 1970	S
	Storer 2002	
Montana <i>Downsimus</i>	Rasmussen 1977	S
<i>Downsimus sharpi</i>	Macdonald 1970	S
Allomyinae		
<i>'Parallomys' cavatus</i>	Cope 1881b	S
	McGrew 1941	
	Rensberger 1983	
<i>'Parallomys' americanus</i>	Korth 1992b	S

Table 1. Continued

INGROUP TAXA	References	Specimens (S) or literature only (L)?
<i>'Parallomys' argoviensis*</i>	Stehlin and Schaub 1951	L
	Schmidt-Kittler and Vianey-Liaud 1979	
<i>'Parallomys' ernii</i>	Stehlin and Schaub 1951	S
	Schmidt-Kittler and Vianey-Liaud 1979	
	Rensberger 1983	
<i>'Parallomys' macrodon</i>	Schmidt-Kittler and Vianey-Liaud 1979	L
<i>'Parallomys' stirtoni</i>	Klingener 1968	S
<i>Allomys harkseni</i> (= <i>Alwoodia harkseni</i>)	Macdonald 1963	S
	Korth 1992b	
Cabbage Patch allomyine	Rasmussen 1977	S
<i>Allomys magnus</i> (= <i>Alwoodia magna</i>)	Rensberger 1983	S
	Rensberger 1983	
<i>Allomys cristabrevis*</i>	Barnosky 1986	S
<i>Allomys nitens</i>	Marsh 1877	S
	Rensberger 1983	
<i>Allomys reticulatus</i>	Rensberger 1983	S
<i>Allomys simplicidens</i>	Rensberger 1983	S
<i>Allomys tessellatus</i>	Rensberger 1983	S
<i>Sciurodon cadurcensis</i>	Schlosser 1884	S
	Schmidt-Kittler and Vianey-Liaud 1979	
Meniscomyinae		
<i>Ameniscomys selenoides</i>	Dehm 1950	L
<i>Promeniscomys sinensis</i>	Wang 1987	S
<i>Sewelleladon predontia</i>	Shotwell 1958	S
<i>Crucimys milleri</i>	Macdonald 1970	L
	Rensberger 1980	
	Storer 2002	
Drummond, MT meniscomyine	Rasmussen 1977	S
<i>Niglarodon blacki</i>	Rensberger 1981	S
<i>Niglarodon koernerii</i>	Black 1961	S
	Macdonald 1970	
	Rensberger 1981	
<i>Niglarodon loneyi</i>	Rensberger 1981	S
Lemhi Valley <i>Niglarodon</i> sp.	Nichols 1976	L
<i>Niglarodon progressus</i>	Rensberger 1981	L
<i>Niglarodon yeariani</i>	Nichols 1976	L
Cabbage Patch <i>Niglarodon</i>	Rasmussen 1977	S
<i>Niglarodon petersonensis</i>	Nichols 1976	L
	Nichols 1979	
<i>Meniscomys editus</i>	Rensberger 1983	S
<i>Meniscomys hippodus</i>	Cope 1879	S
	McGrew 1941	
	Rensberger 1983	
<i>Meniscomys uhtoffi</i>	Rensberger 1983	S
Homalodontia		
<i>Sinomylagaulus halamagaiensis*</i>	Wu 1988	L
<i>Tschalimys chhikvadzei*</i>	Shevyreva 1971	L
Aplodontinae		
<i>Rudiomys mcgrewi</i>	Rensberger 1983	S
<i>Liodontia alexandrae</i>	Furlong 1910	S
	McGrew 1941	
	Shotwell 1958	
Massacre Lake <i>Liodontia</i>	Morea 1981	S

Table 1. Continued

INGROUP TAXA	References	Specimens (S) or literature only (L)?
<i>Liodontia furlongi</i>	Gazin 1932	S
	Shotwell 1958	
<i>Aplodontia rufa</i>	Trouessart 1897	S
	Shotwell 1958	
	Carraway and Verts 1993	
<i>Pseudaplodon asiatica*</i>	Schlosser 1924	L
<i>Tardontia nevadans</i>	Shotwell 1958	S
<i>Tardontia occidentale</i>	Macdonald 1956	S
	Shotwell 1958	
Mylagaulidae		
<i>Promylagaulus riggsi</i>	McGrew 1941	L
	Macdonald 1963	
	Macdonald 1970	
	Rensberger 1979	
<i>Trilaccogaulus lemhiensis</i>	Nichols 1976	L
<i>Trilaccogaulus montanensis</i>	Rensberger 1979	S
<i>Trilaccogaulus ovatus</i>	Rensberger 1979	L
	Storer 2002	
Mesogaulinae		
<i>Galbreathia bettae</i>	Sutton and Korth 1995	L
	Korth 1999a	
<i>Galbreathia novellus</i>	Matthew 1924	S
	Munthe 1988	
	Korth 1999a	
<i>Mesogaulus ballensis</i>	Riggs 1899	L
	Korth 2000a	
<i>Mesogaulus paniensis</i>	Matthew 1902	S
	Cook and Gregory 1941	
	Galbreath 1984	
	Korth 2000a	
<i>Mylagaulodon angulatus</i>	Sinclair 1903	S
Mylagaulinae		
<i>Alphagaulus douglassi</i>	McKenna 1955	S
<i>Alphagaulus pristinus</i>	Douglass 1903	S
	Korth 2000a	
<i>Alphagaulus tedfordi</i>	Korth 2000a	S
<i>Alphagaulus vetus</i>	Matthew 1924	S
	Munthe 1988	
	Korth 2000a	
Deep River <i>Alphagaulus</i>	unpublished specimens from the Early Miocene Deep River formation, loc. UWA5867: UWBM #59077, 59088, 71132, 52897; loc. C0269: UWBM #71150, 53219, 53220	S
<i>Ceratogaulus anecdotus</i>	Korth 2000a	S
<i>Ceratogaulus hatcheri</i>	Gidley 1907	L
	Korth 2000a	
<i>Ceratogaulus minor</i>	Hibbard and Phillis 1945	L
<i>Ceratogaulus rhinocerus</i>	Matthew 1902	S
	Korth 2000a	

Table 1. Continued

INGROUP TAXA	References	Specimens (S) or literature only (L)?
<i>Hesperogaulus gazini</i>	Korth 1999b Shotwell 1958	S
<i>Hesperogaulus wilsoni</i>	Korth 1999b Shotwell 1958	S
<i>Mylagaulus kinseyi</i>	Webb 1966	S
<i>Mylagaulus ellassos</i>	Baskin 1980	S
<i>Mylagaulus sesquipedalis</i>	Cope 1878	S
<i>Pterogaulus barbarellae</i>	Korth 2000a	S
<i>Pterogaulus cambridgensis</i>	Korth 2000b	S
<i>Pterogaulus laevis</i>	Matthew 1902 Fagan 1960 Korth 2000a	S
<i>Umbogaulus galushai</i>	Korth 2000a	S
<i>Umbogaulus monodon</i>	Cope 1881a Korth 2000a	S
OUTGROUP TAXA:		
<i>Ischyromys typus</i>	Leidy 1856	S
<i>Paramys delicatus</i>	Leidy 1871	S
<i>Reithroparamys delicatissimus</i>	Leidy 1871	L

Species are listed within the taxonomic framework proposed here. The third column indicates whether species were coded for this analysis only from images in the literature (L), or from actual specimens or casts of specimens (S).

*Poorly known taxa not included in the primary phylogenetic analysis.

independently. It was also necessary to remove all characters that were fundamentally continuous and could not be converted to discrete states, as it is not possible to recognize the difference between homology and convergence in such characters. Characters were also discarded that were ambiguous, or did not clearly describe an observable character. This left a starting character set of 316 characters.

Additional characters were removed during the coding process, as the patterns of variation and distributions of character states became apparent. Characters were discarded if they did not vary within the ingroup (and hence did not provide any evolutionary information) or if they varied excessively within OTUs (and hence could not be reasonably coded or expected to represent homology). See Appendix 1 for the lists of characters that were discarded as a result of inadequate or excessive variation. Dental and orientation terminology (see Fig. 1) was standardized to generate a final list of 250 characters (Appendix 1) that meet the standards of phylogenetic analysis, i.e. they are variable within the ingroup (but not within OTUs), they appear to be heritable, they are discrete, and, to the degree that it is possible to determine, they are uncorrelated (Wiley, 1981; Neff, 1986). This last stipulation is difficult to determine in a group of almost exclusively

fossil organisms. There are two possible types of correlation: the sort that arises from constraints on pathways of development and evolution ('bad' correlation), and the sort that arises as a result of shared evolutionary history. These two can be very difficult to tease apart for complex morphological characters, even in modern animals, and can be impossible to distinguish in some cases in fossil organisms. For this analysis, obvious cases of correlation (such as cases of serial homology) were eliminated. Also, cases where there is an obvious mechanism of functional constraint (such as a posteriorly enlarged metaconule and a connection between the metaconule and the posterior cingulum), and in which there is an apparent pattern of strong correlation, are used to discard additional duplicate characters. Otherwise, all characters are included. This approach achieved a consistent standard by which to include adequate data for phylogenetic analysis, but possibly (and if so unavoidably) includes some correlated characters. The final character matrix used for phylogenetic analysis is shown in Appendix 2.

The final set of characters included in the analysis includes exclusively dental and cranial characters. A few postcranial characters were included in the initial list, but were eliminated because they were funda-

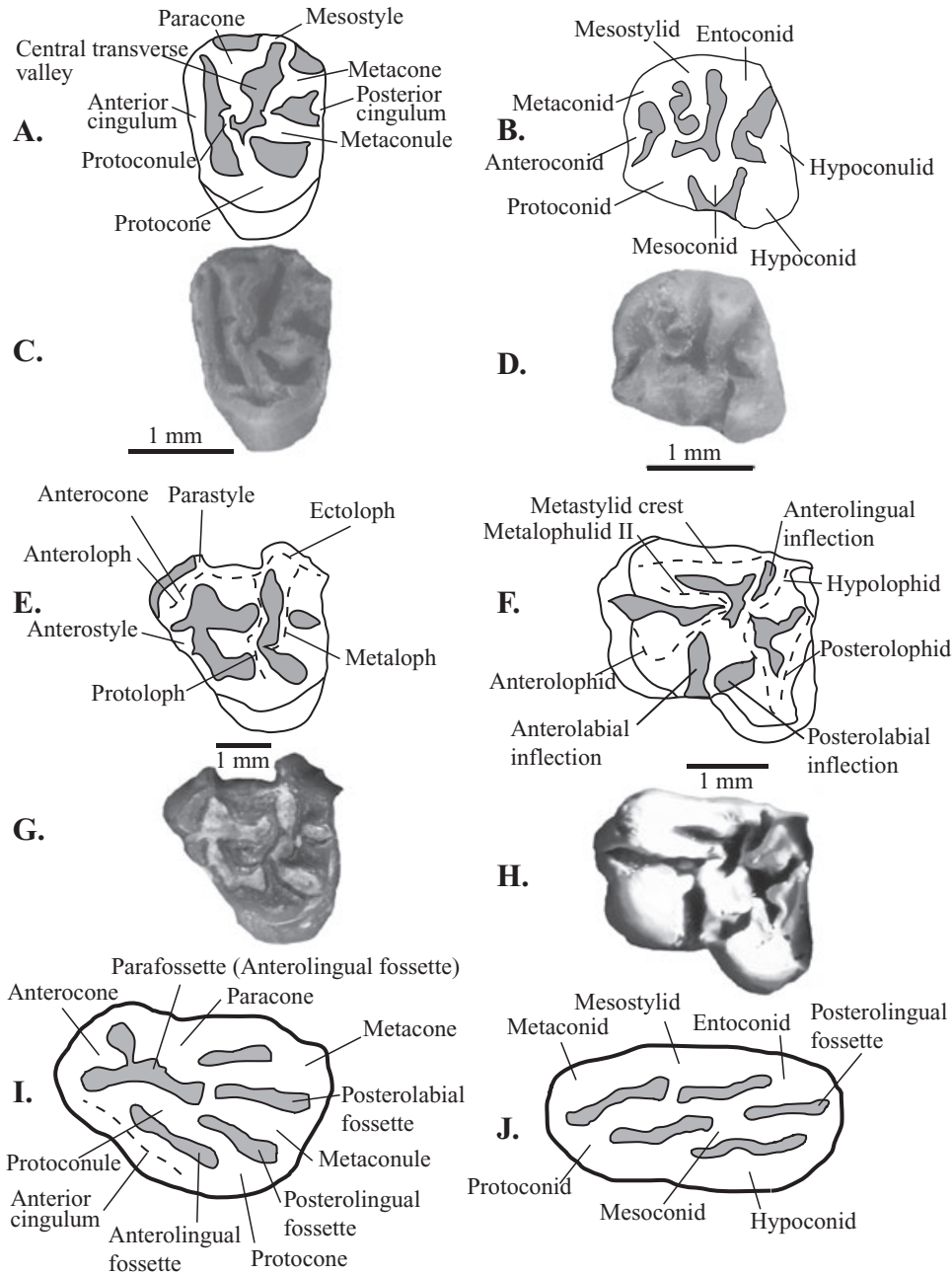


Figure 1. Dental terminology used throughout this paper, illustrated on a range of aplodontid morphotypes. Anterior is to the left, labial is up for upper teeth (A, C, E, G, and I) and down for lower teeth (B, D, F, H, and J) A, upper molar of a basal aplodontid (*Ansomys hepburnensis*) showing major cusps and cingula. B, lower molar of a basal aplodontid (*Ansomys hepburnensis*) showing major cusps. C, same as (A), photographic image. D, same as (B), photographic image. E, P^4 of a meniscomyine (*Meniscomys uhtoffi*) showing lophs and anterior cusps. F, P_4 of an allomyine (*Allomys magnus*) showing lophs of the lower teeth. G, same as (E), photographic image. H, same as (F), photographic image. I, P^4 of a mylagaulid (*Alphagaulus vetus*) illustrating cusp homologies with other aplodontids. J, P_4 of a mylagaulid (*Alphagaulus vetus*) illustrating cusp homologies with other aplodontids.

mentally continuous. Less than 5% of aplodontid taxa preserve associated postcrania. A few isolated humeri have been assigned to mylagaulids, as their high degree of fossoriality makes for highly modified post-

crania. However, the only taxa for which postcrania have been illustrated and formally referred are *Ansomys shanwangensis* Qiu & Sun, 1988, *Ceratogaulus minor* Hibbard & Phillis, 1945, *Ceratogaulus*

hatcheri Gidley, 1907, and *Pterogaulus laevis* Matthew, 1902. With so few available postcrania, postcranial characters are not useful in resolving aplodontid relationships. The included cranial characters can only be coded for a small minority of the ingroup taxa, but this group is large enough for these characters to be taxonomically useful. Using such a large number of dental characters does have the problem of potential correlation. Although research is beginning to uncover the genetic mechanisms underlying tooth development (Kangas *et al.*, 2004), we cannot say how the characters used here may be correlated developmentally and genetically. Here, I use them as if they were uncorrelated, using only patterns of character distribution to eliminate perfectly correlated characteristics. When more information is available on how characteristics of the dentition are developmentally related, the character set can be pared down in future analyses.

The phylogeny was reconstructed using the maximum parsimony algorithm in PAUP 4.0b10 for UNIX (Swofford, 2002). To facilitate the repeatability of the analysis, for each analysis that was run, the PAUP command block is provided in Appendix 3. Because neither exhaustive nor branch-and-bound searches were practical for such a large matrix, heuristic searches with a random taxon addition sequence and 1000 repetitions, using tree bisection and reconnection for branch swapping, were used in every analysis. The method of simple addition of taxa was also explored (note: results included in Results section).

The analysis was run with three different character configurations to determine the effect of character ordering on the resultant topology. Because little information is available on the mechanisms by which evolutionary transformations take place in complex morphological characters, it was necessary to examine multiple possible models of character evolution by different configurations of ordered and unordered characters. The first configuration has all characters unordered, implying that transitions between states in multistate characters are all equally likely. The second has treated as ordered the set of characters that are expected to be ordered, assuming that character evolution takes place by continuous morphological change (such as a given cusp being absent, small, or large). This group of characters is the narrowest group of characters that would be treated as ordered, assuming that any characters should be ordered. These characters are indicated in Appendix 1 as 'Ordered in semi-ordered and ordered analyses'. A third configuration treats all characters that could plausibly be construed to be ordered as ordered. This includes questionable ordered characters, such as character 231, 'Fossettes/fossettids: (0) with no consistent orientation, (1) ori-

ented consistently obliquely across the tooth, or (2) more a–p aligned on P4'. It may or may not be necessary for the fossettids to all come into alignment before achieving an anteroposterior orientation. The alignment of the fossettids in state 2 may have been achieved independently of those in state 1, or they may have been aligned as in state 1, and then rotated into an anteroposterior alignment. These characters are indicated in Appendix 1 as 'Ordered in fully ordered analyses'. Note that this still leaves some multistate characters unordered, such as the multistate character coding for the various orientations of accessory crests in the lower teeth, character 243. There is no a priori reason to expect that such characters should be ordered.

Using ordered characters creates another potential problem in the analysis. Because each state change in a multistate ordered character adds a step to the score of the tree, an ordered character is functionally up-weighted in proportion to the number of possible states. That is, if there are four possible states for a character (0, 1, 2, and 3), a change in that character may be worth as much as three steps for a single character state change, rather than one step as in the case of an unordered character. This assumes that each state transition represents the same level of evolutionary change. It could, instead, be argued that each character represents the same amount of evolutionary change, and that the character state changes should be weighted so as to make each character worth the same total level of evolutionary change. Thus, the analyses with some and with all ordered characters were rerun with those characters down-weighted in proportion to the number of character states for the character, such that the weight of the character is set to be $1/n - 1$, where n is the number of character states for a given ordered character.

In order to mitigate the effects of the large number of taxa, and the incompleteness of the matrix on the resolution of the tree, some taxa had to be removed from the primary phylogenetic analysis. Most aplodontid taxa are known from very small samples and incompletely preserved specimens. Consequently, despite the fact that more than 80% of the characters are derived from the dentition alone, an average species was only coded for 64% of the characters. When all taxa for which less than 50% of the characters could be coded were removed, the topology recovered was not well resolved. Better resolved trees were attained when a cut-off of 33% of characters coded was imposed. All taxa withheld using this less stringent cut-off are known from a single specimen (typically a single tooth, or a partial jaw or skull with worn teeth) and hence provide little information for phylogenetic analysis. One such taxon, *Parallomys argoviensis* (Stehlin & Schaub, 1951), was uninten-

tionally left in the matrix for the main analyses; it adds useful information on aplodontoid relationships, and it does not have an adverse effect on the resolution, so the analyses were not rerun. It did have a notable effect on the run-time of the analysis: it is likely that adding more such taxa would cause the analysis to slow down much more severely. The two down-weighted analyses ran relatively rapidly, which probably resulted from the decrease in the breadth of the most parsimonious treespace, a result of the larger universe of possible treescores arising from the down-weighting of many characters. The remaining three analyses could not be run in a reasonable period of time without constraints, and were run with two alternative methodologies. First, a broad survey of treespace was performed by limiting the analysis to 100 000 trees swapped per repetition, but with 1 000 000 random repetitions. This enabled the analysis to survey a larger range of tree space within a reasonable period of time, although it does not explore each tree island as completely. Second, a more in-depth analysis performed the same 1000-repetition run from the down-weighted analysis, with the single limitation that swapping on a single repetition was limited to a specific time period (one hour). This limit rarely cut off minimal analyses (i.e. analyses that found most parsimonious trees), but effectively avoided time-consuming nonminimal repetitions. The strict consensus presented in the results summarizes all of the trees found in both types of analyses.

Once tree topologies were determined, the poorly known taxa were fitted in by adding them to the analysis one at a time, in order to evaluate how each one affected the topology of the tree. Taking note of the results of these analyses, the analysis was run once more with all taxa included, and with the preferred tree input as a constraint tree. All of these taxon additions were performed using the partially ordered character set, and without down-weighting ordered characters.

RESULTS

PATTERNS IN PHYLOGENETIC ANALYSIS

The strict consensus trees resulting from each of the five character configurations (Table 2) are shown in Figures 2–6. Running the phylogenetic analysis in these different configurations yielded important information about the influence of character states and taxa on the phylogeny recovered. The simple addition of taxa in a heuristic search gave completely erroneous results (a common problem with large datasets), as revealed by a comparison of these results with the results produced by the more exhaustive searching of the random addition sequence. However, relatively

Table 2. Tree statistics for the five phylogenetic analyses (including both fast and slow runs of the unweighted analyses)

Char. status	1 (slow)		2 (slow)		3 (slow)		4		5		1 (fast)		2 (fast)		3 (fast)	
	Unordered	Semi-ordered	Semi-ordered	Ordered	Ordered	Semi-ordered, down-weighted	Semi-ordered, down-weighted	Ordered, down-weighted	Ordered, down-weighted	Unordered	Semi-ordered	Unordered	Semi-ordered	Unordered	Semi-ordered	Ordered
CI	0.236	0.229	0.229	0.223	0.223	0.226	0.226	0.219	0.236	0.236	0.229	0.236	0.229	0.236	0.229	0.223
RI	0.742	0.755	0.755	0.759	0.759	0.748	0.748	0.753	0.742	0.742	0.755	0.742	0.755	0.742	0.755	0.759
RC	0.175	0.173	0.173	0.169	0.169	0.169	0.165	0.165	0.175	0.175	0.173	0.175	0.173	0.175	0.169	0.169
HI	0.764	0.771	0.771	0.777	0.777	0.774	0.781	0.781	0.764	0.764	0.771	0.764	0.771	0.764	0.777	0.777
Tree length	1459	1504	1504	1552	1552	1363.94	1234.36	1234.36	1459	1459	1504	1504	1504	1504	1552	1552
# MP trees	4694	260	260	4940	4940	200	131	131	1523	1523	200	200	200	322	322	322
# reps	1000	1000	1000	1000	1000	1000	1000	1000	1 × 10 ⁶	1 × 10 ⁶	1 × 10 ⁶	1 × 10 ⁶	1 × 10 ⁶	1 × 10 ⁶	1 × 10 ⁶	1 × 10 ⁶
Rep for 1st MP tree	16	2	2	39	39	440	116	116	253	253	9222	9222	9222	47 930	47 930	47 930

See Material and methods for an explanation of fast and slow analyses. Abbreviations: CI, consistency index; RI, retention index; RC, rescaled consistency index; HI, homoplasy index; MP, most parsimonious; # reps, number of repetitions.

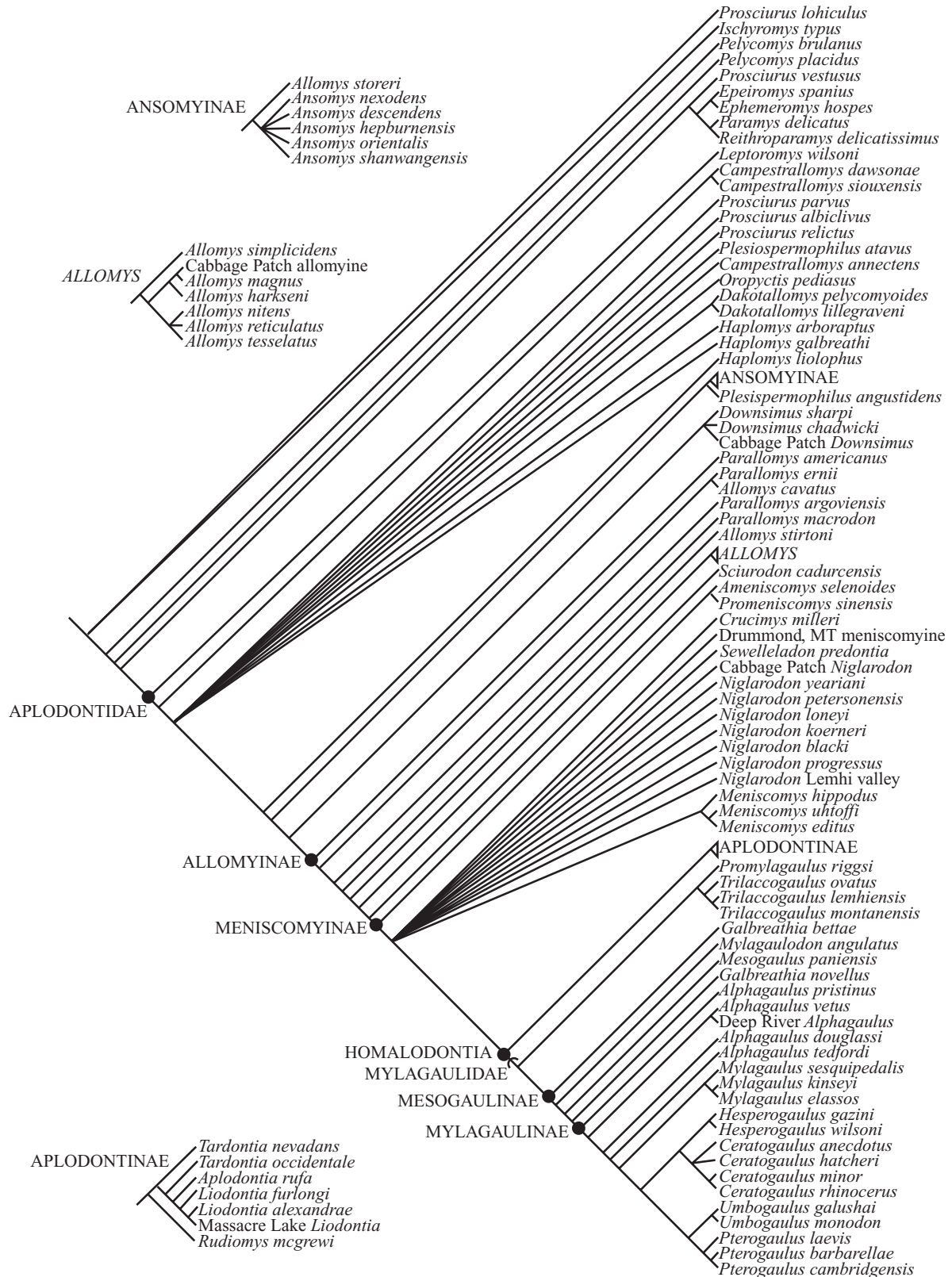
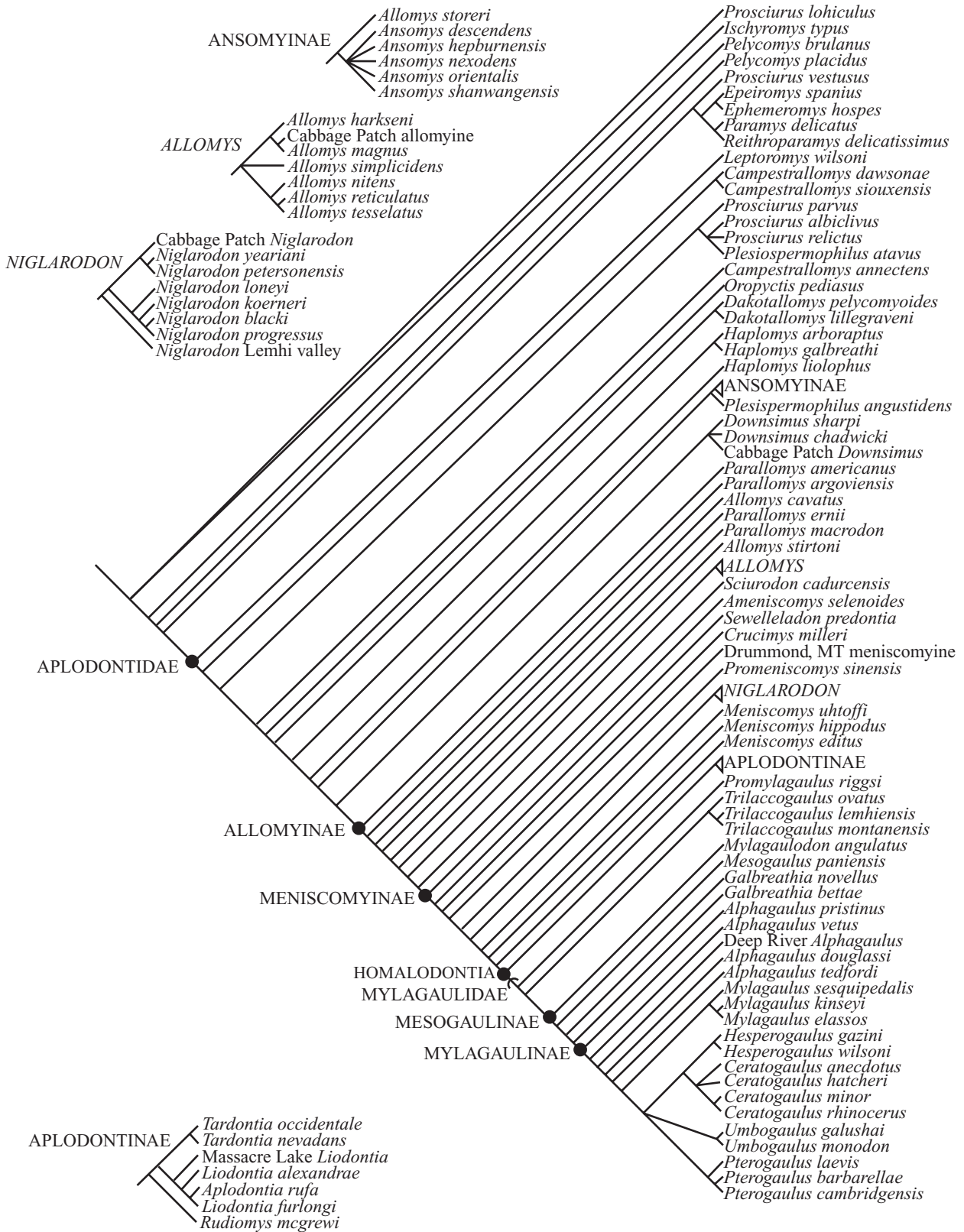
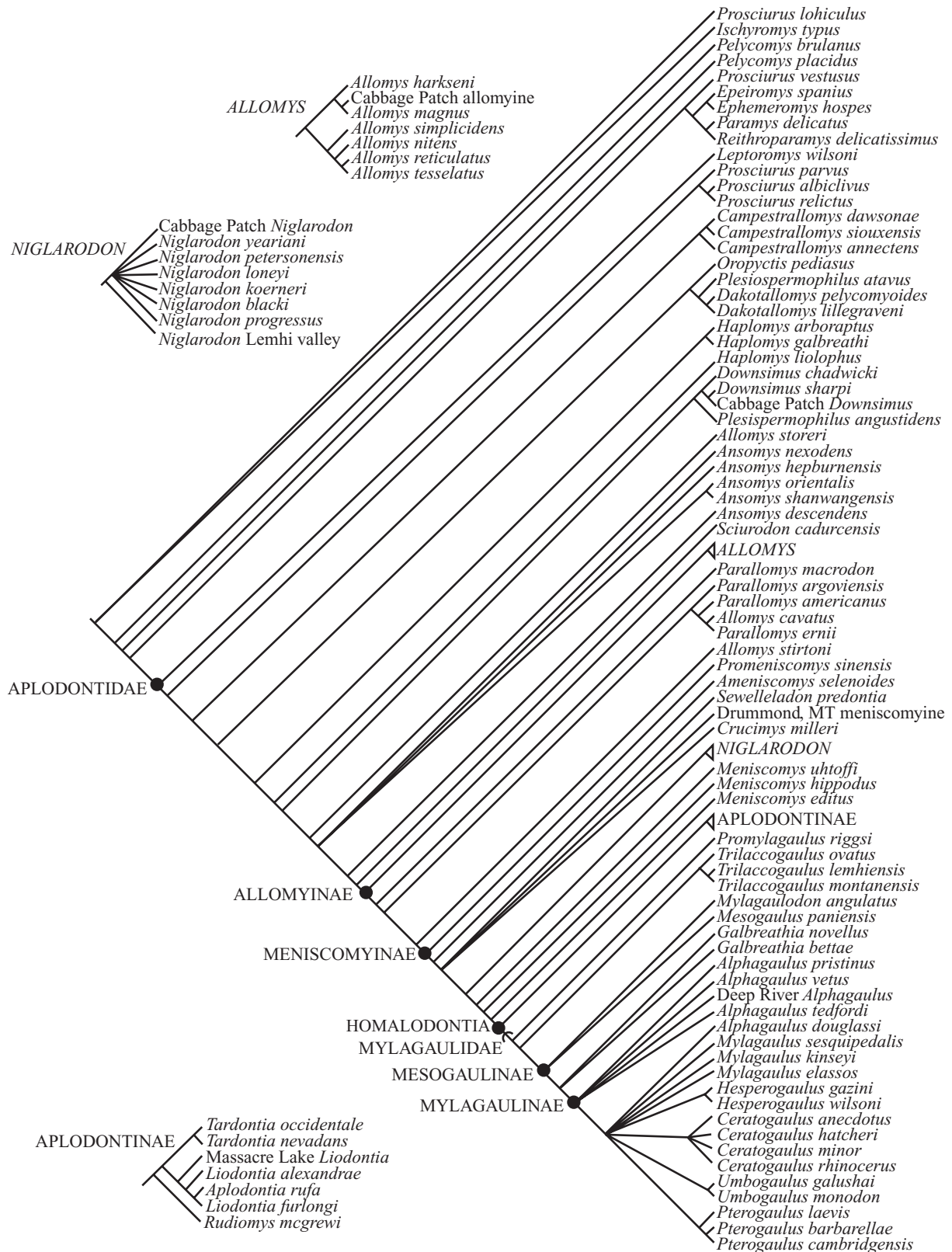


Figure 2. Phylogeny of apodontoids using all unordered characters. Tree scores are listed in Table 2.



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Figure 3. Phylogeny of aplodontoids using some ordered characters, with ordered characters not down-weighted. Tree scores are listed in Table 2.



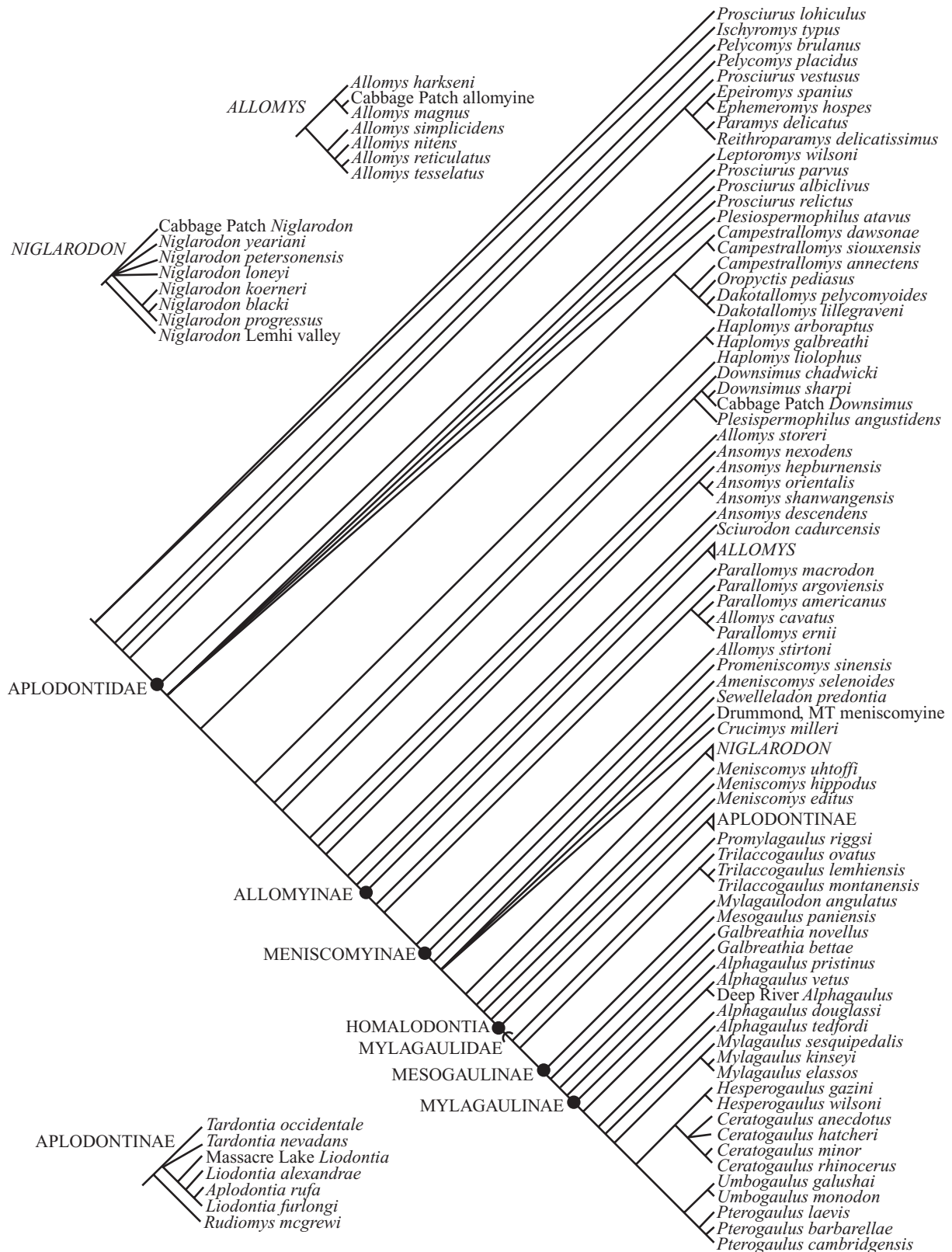
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Figure 4. Phylogeny of aplodontoids using all ordered characters, with ordered characters not down-weighted. Tree scores are listed in Table 2.



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Figure 5. Phylogeny of aplodontoids using some ordered characters, with ordered characters down-weighted. Tree scores are listed in Table 2.



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Figure 6. Phylogeny of apodontoids using all ordered characters, with ordered characters down-weighted. Tree scores are listed in Table 2.

few repetitions of the random addition algorithm were necessary to obtain minimal trees (Table 2), although additional minimal tree islands were encountered throughout the runs in many cases. In the analyses with down-weighted characters, it was possible to obtain non-integer tree scores. As a result, a greater array of potential tree scores and a smaller numbers of trees within the minimal tree island existed, so it took more repetitions to find the minimal tree score. However, even in these cases, the minimal tree island (in all four of these cases there was only one) was found within the first 300 repetitions (all of these analyses were run for 1000 repetitions). Some case could be made for the possibility of encountering additional most parsimonious trees in the first three analyses, as some additional tree islands were found within the last 100 repetitions, but these were small, containing generally no more than one or two trees. Additionally, these islands generally did not have an influence on the strict consensus tree, because they were composed of different combinations of previously discovered topologies in the subclades.

The analyses that included only taxa with at least 50% of the characters coded ran much faster than those that had all taxa with at least 33% of the characters coded. However, the less inclusive analyses (those with a 50% completeness cut-off) were plagued with large unresolved nodes, and there was more consistency across different character configurations in the more inclusive analysis. Thus, the results of the more inclusive analysis are more robust. In fact, some aspects of the tree were more clearly resolved with the inclusion of more taxa, vindicating the claim of numerous authors (Huelsenbeck, 1991; Wiens, 1998) that including more taxa can improve the resolution, even when those taxa are incompletely coded.

Measures of data fitted to trees vary relatively little between the different analyses. The homoplasy index (HI) is relatively high throughout (0.764–0.781), as is expected from an analysis with such a large number of taxa and characters (Naylor & Kraus, 1995). The retention index (RI) is also very high (0.742–0.759), and although it may be somewhat inflated by the presence of so many multistate characters, it does seem to indicate that the data fitted the tree reasonably well. The RI scores increase and the HI scores decrease with the number of ordered characters, suggesting that the ordered character trees fitted the data better, but these differences are very small, changing the scores by less than 0.02 in each case.

Tree support indices cannot be computed for these analyses, as the time required to run them would be prohibitive. Given the run-time of the analysis itself, running a bootstrap for a single one of these consensus trees would take more than a year of continuous

computing, an unreasonable time investment for the information gained. Rather than examining decay indices or bootstrap analyses, I use the agreement between different analyses and the stability of clades with the insertion and removal of taxa to assess the support for branches of the tree.

COMMON FACTORS AMONG ANALYSES WITH DIFFERENT CHARACTER CONFIGURATIONS

Throughout this section, analyses will be referred to by the numbers used in Table 2.

All five analyses: In all five main analyses, *Prosciurus lohicolus* Matthew & Granger, 1923 is consistently grouped with *I. typus*, and is not included in the Aplodontidae, indicating that this species is a member of a different clade of rodents. Several other species are similarly placed outside the Aplodontidae, namely the two species of *Pelycomys* (*Pelycomys brulanus* Korth, 1986 and *Pelycomys rugosus* Galbreath, 1953), *Epeiromys spanius* Korth, 1989, *Ephemeromys hospes* Wang & Heissig, 1984, and *Prosciurus vetustus* Matthew, 1903. Their phylogenetic position with the outgroups suggests that they should be more likely to be placed in the Ischyromyidae. *Leptoromys wilsoni* Tedrow & Korth, 1997, from the Lower Oligocene of South Dakota, is the first species to be consistently placed inside the aplodontid clade. A number of other taxa traditionally included in the subfamily 'Prosciurinae' are also placed at the base of the aplodontid clade. Relatively little consensus can be found for this group, as it is almost entirely unresolved in analysis 5. However, there are several species groups within the 'Prosciurinae' that are recovered repeatedly. Two species of *Campestrallomys*, *Campestrallomys dawsonae* Macdonald, 1963 (the type species of the genus) and *Campestrallomys siouxensis* Korth, 1989, are consistently recovered as sister species. All analyses using equally-weighted characters group *Prosciurus albiclivus* Korth, 1994b with the congeneric species *Prosciurus relictus* Cope, 1873 and *Prosciurus parvus* Korth, 1989. Furthermore, all analyses group *Haplomys galbreathi* Tedrow & Korth, 1997 and *Haplomys arboraptus* Shevyreva, 1971 as sister species, and result in a monophyletic genus *Dakotallomys* (containing *Dakotallomys pelycomyoides* Tedrow & Korth, 1997 and *Dakotallomys lillegraveni* Tedrow & Korth, 1997). All of the species mentioned above fall outside the clade formed by the Ansomyinae and the Allomyinae.

Two fundamentally different phylogenetic positions are reconstructed for the Ansomyinae (*sensu* Hopkins, 2004). Analyses 1, 2, and 4 result in a monophyletic Ansomyinae, diverging just after *Haplomys liolophus* Cope, 1884. Analyses 3 and 5 find a paraphyletic Ansomyinae, just outside the Allomyinae. This option

is less probable, because it reconstructs a very unlikely evolutionary relationship between *Allomys* and *Parallomys*, with *Allomys* diverging earlier, and hypothesizes the sequential loss of most of the characters that were originally used to diagnose *Allomys*. The poor fossil record of several species of *Parallomys* (two are known only from isolated teeth), the dramatic morphological differences between these rodents and the next clade to diverge (the Meniscomyinae), and the similar morphological trends in evolutionary history of the ansomyines may be responsible for the presence of this resolution in the ordered analyses. The most basal species among the ansomyines is '*Allomys*' *storeri* Tedrow & Korth, 1997.

Downsimus is monophyletic in all the analyses, and is placed either just before or just after the divergence of *Ansomys*. The species of '*Parallomys*' diverge sequentially from the main branch of the aplodontid tree, although the order in which they diverge differs between the ordered analyses (3, 5) and all other analyses (1, 2, 4). All analyses also show a monophyletic *Allomys* (composed of *Allomys simplicidens* Rensberger, 1983, *Allomys tessellatus* Rensberger, 1983, *Allomys reticulatus* Rensberger, 1983, *Allomys magnus* Rensberger, 1983, *Allomys harkseni* Macdonald, 1963, the Cabbage Patch allomyine, and *Allomys nitens* Marsh, 1877). *Allomys reticulatus* and *A. tessellatus* are sister species, and *A. nitens* is consistently placed outside this pair. *Allomys magnus* is consistently placed as sister species to the Cabbage Patch allomyine, with *A. harkseni* falling immediately outside. The relative position of these two species trios and *A. simplicidens* varies among the analyses.

Sciurodon cadurcensis Schlosser, 1884, *Promeniscomys sinensis* Wang, 1987, *Ameniscomys selenoides* Dehm, 1950, and then *Sewelleladon predontia* Shotwell, 1958, *Crucimys milleri* Rensberger, 1980, and the Drummond (MT) meniscomyine all diverge at the base of the meniscomyines. The most basal meniscomyine species is either *A. selenoides* or *P. sinensis*, depending on which analysis is considered. The next group to diverge is *Niglarodon*, which is monophyletic in all but analysis 1. Resolution within this genus is extremely poor, which could result from potential synonymy as some species are known from upper dentitions only, some from lower dentitions only, and many from worn teeth only. Further examination of meniscomyine systematics will be pursued elsewhere.

All analyses except for analysis 1 have resolved *Meniscomys* as a paraphyletic group at the base of the hypsodont aplodontid clade, with the species *Meniscomys uhtoffi* Rensberger, 1983, *Meniscomys hippodus* Cope, 1879, and then *Meniscomys editus* Rensberger, 1983 diverging in stratigraphic order. The sequence of divergence and the relatively small differences among species suggests a possible ancestor–

descendent relationship among these species, as suggested by Rensberger (1983), although the presence of autapomorphies in *M. uhtoffi* and *M. hippodus* suggests that they are independent lineages.

The Homalodontia are consistently present as a group, uniting the Aplodontinae and their sister group the Mylagaulidae. *Rudiomys mcgrewi* Rensberger, 1983 is found to be the most basal aplodontine, although it has been regarded as more primitive than *Meniscomys* (Rensberger, 1983). The relationships within the Aplodontinae are not well resolved, although there are similarities between the different analyses. First, a monophyletic group is formed by the union of *A. rufa* with the three species of *Liodontia*. The unordered analysis places these four species diverging in reverse stratigraphic order, which suggests a rooting problem; it would be more likely, given the more than 17 million years spanned by these four species, that they should diverge in stratigraphic order, as they do in all but the unordered analysis. It is likely that the long branches in this clade are causing incorrect rooting of the characters that differentiate this group relative to other aplodontines, as the topology is otherwise identical in all analyses. The two species of *Tardontia* are placed in a basal position with regard to the *Liodontia*–*Aplodontia* clade, but monophyly of *Tardontia* is not certain. The Mylagaulidae show some significant phylogenetic resolution. Consistently, *Promylagaulus riggsi* McGrew, 1941 is the most basal mylagaulid. The monophyletic *Trilaccogaulus* is the next to diverge, except in analysis 1, where it forms a monophyletic *Promylagaulinae* with *P. riggsi*. *Mylagaulodon angulatus* Sinclair, 1903 is the next diverging taxon in all analyses, except analysis 1, at the base of the Mesogaulinae. It is followed by the divergence of the two species of *Galbreathia* and *Mesogaulus panienensis* Matthew, 1902. *Alphagaulus pristinus* (Douglass, 1903) is the next to diverge in all but analysis 3, in which its position is unresolved. However, the majority of the trees in analysis 3 find *A. pristinus* to be the first to diverge as well: there are a small number of conflicting trees that destroy the resolution in the strict consensus. The next to diverge are a series of *Alphagaulus* species, with the order varying from one analysis to the next. Among the derived mylagaulids, *Hesperogaulus*, *Ceratogaulus*, *Umbogaulus*, and *Pterogaulus* appear to be monophyletic. *Ceratogaulus hatcheri* and *Ceratogaulus rhinocerus* Matthew, 1902 are sister species, and *Umbogaulus* and *Pterogaulus* are sister clades. Within *Pterogaulus*, *P. laevis* diverges first, just before *Pterogaulus cambridgensis* Korth, 2000a and *Pterogaulus barbarellae* Korth, 2000b.

All ordered analyses (2–5): The lack of resolution in the base of the tree in analysis 4 means that there are essentially no clades at the base of the aplodontid tree

that are recovered for all of the ordered analyses. All ordered analyses do recover a monophyletic *Niglarodon*, as well as a paraphyletic *Meniscomys* and 'Promylagaulinae'. Within the Aplodontinae, there is some degree of consistency; all ordered analyses recover the *Liodontia*–*Aplodontia* clade with the Massacre Lake *Liodontia* as the first to diverge, followed by *Liodontia alexandrae* Furlong, 1910, then *Liodontia furlongi* Gazin, 1932 and *Aplodontia*. This resolution is concordant with stratigraphy, and is entirely recorded in the sediments of the Northern Great Basin. Within the Mylagaulidae, there is very little in common across all ordered analyses, as analysis 3 has the Mylagaulidae largely unresolved, other than the major nodes recovered in all five analyses.

All semi-ordered analyses (2 and 4): These analyses share a great deal of resolution high in the tree, but basal resolution is so poor in analysis 4 that the two have little in common in the resolution of earlier taxa. Both recover the clade uniting the sister species pairs of *C. dawsonae* + *C. siouxensis* as being the first to diverge after *L. wilsoni*. Both also find *Downsimus* diverging above the monophyletic Ansomyinae. '*Parallomys*' *americanus* Korth, 1992b is the first '*Parallomys*' to diverge in both analyses, and '*Parallomys*' *macrodon* (Schmidt-Kittler & Vianey-Liaud, 1979) and '*Parallomys*' *stirtoni* (Klingener, 1968) are the last two; the order among '*Parallomys*' *ernii* (Stehlin & Schaub, 1951), '*Parallomys*' *argoviensis*, and '*Parallomys*' *cavatus* (Cope, 1881b) varies. Both analyses also find *S. cadurcensis* to be the first to diverge after *Allomys*, and find *A. selenoides* to be the first meniscomyine. The resolution among the remaining meniscomyines is also consistent; the order of divergence (from the base of the clade upwards) is *A. selenoides*, *S. predontia*, *C. milleri*, the Drummond, MT meniscomyine, *P. sinensis*, *Niglarodon*, *M. uhtoffi*, *M. hippodus*, *M. editus*, and Homalodontia. There is a consistent topology in the clade of *Niglarodon* species, with the Lemhi Valley *Niglarodon* sp. at the base, and then followed by two clades of *Niglarodon*. The four species from the Deep River beds form a clade: *Niglarodon loneyi* Rensberger, 1981 diverging first, followed by *Niglarodon koeneri* Black, 1961, and then a sister species pair of *Niglarodon blacki* Rensberger, 1981 and *Niglarodon progressus* Rensberger, 1981. The two named species from Lemhi Valley, *Niglarodon petersonensis* (Nichols, 1976) and *Niglarodon yeariani* (Nichols, 1976), form a sister species pair, with the Cabbage Patch *Niglarodon* just outside these two. The semi-ordered analyses both recovered an identical resolution of all the species in the Homalodontia.

All fully ordered analyses (3 and 5): There are a number of commonalities between the two fully

ordered analyses, particularly in the resolution of the base of the tree. Both find *Campestrallomys* to be more derived than *Prosciurus*, unlike the other three analyses. Both also find a clade uniting *Oropyctis pediasus* Korth, 1989 with the sister species pair of *Dakotalomys*. Both these analyses find the paraphyletic Ansomyinae, as well as the inverted order (relative to other analyses) among allomyines, with *Allomys* diverging first, before *Parallomys*. Both also have *A. simplicidens* placed just outside the *A. nitens* + *A. reticulatus* + *A. tessellatus* clade. Finally, both have the same topology within the Aplodontinae, with *Rudiomys* being the first to diverge, followed by a monophyletic Tardontia, then by the *Liodontia*–*Aplodontia* clade, in the order common to analyses 2–5.

All ordered, not down-weighted, analyses (2 and 3): Both these analyses recover a monophyletic *Prosciurus* composed of *P. albiclivus*, *P. relictus*, and *P. parvus*. These two analyses also share a common topology for the aplodontine clade, the same as is found in the two semi-ordered analyses. No other features are shared between these two clades, which are not shared with other analyses, as the differences resulting from the additional ordered characters are too great in their influence on the tree topology.

All down-weighted analyses (4 and 5): The only commonality between these two analyses not shared with other analyses is the topology among the Mylagaulidae. *Promylagaulus riggsi* diverges first, followed by a monophyletic *Trilaccogaulus*. The first mesogauline is *M. angulatus*, after which *M. paniensis*, *Galbreathia novellus* (Matthew, 1924), and *Galbreathia bettae* (Sutton & Korth, 1995) diverge sequentially. *Alphagaulus pristinus* is the most basal species of the mylagauline clade. The remaining species of *Alphagaulus* diverge in the following order: *A. vetus*, then the Deep River *Alphagaulus*, then *Alphagaulus douglassi* McKenna, 1955, and finally *Alphagaulus tedfordi* Korth, 2000b, just outside the clade of derived mylagaulids. A monophyletic *Mylagaulus* is first to diverge, followed by the *Ceratogaulus*/*Hesperogaulus* clade. The position of *Umbogaulus*, with *Ceratogaulus*/*Hesperogaulus* or with *Pterogaulus*, is uncertain: it differs between the two analyses.

Comparison of analyses, tree selection: The choice of unordered, semi-ordered, or fully ordered characters has a substantial effect on the outcome of the phylogenetic analysis. The most stratigraphically and geographically concordant result is produced by the semi-ordered character configuration. The results of this analysis are also more consistent with traditional, nonphylogenetic systematics. Down-weighting ordered characters does not seem to have a very large effect,

other than sometimes producing slightly more resolution, as a larger number of possible parsimony scores are possible if the characters are not all equally weighted. The effect for which this character weighting was intended to compensate, that of ordered characters having disproportionate influence on the topology of the tree, is not evident in the results, as the down-weighted analyses correspond better to the unweighted analyses with the same set of ordered characters. As a result, the preferred result is the phylogeny shown in Figure 3, which is the result of analysis 2.

DISCUSSION

PHYLOGENETIC ANALYSIS

Rodents, especially fossil rodents, have not been widely studied using morphological phylogenetics largely because rodents are highly speciose, and morphological diversity within families is generally low. This large number of morphologically similar species is very difficult to resolve phylogenetically, as there are relatively few homologous morphological features evident that diagnose clades, and many clades have convergently evolved similar morphologies. Moreover, fossil rodents are mostly known from isolated teeth. Although these teeth are frequently easily identifiable to the family, genus and even species level, it is often assumed that they provide few characters suitable for phylogenetic analysis. Cusp morphology may be obscured by wear, and may be merged into simple crests (Wood, 1947; Wood, 1955). In addition homoplasy is a problem as diverse species respond to similar selective pressures using a limited number of solutions (Ben-Moshe, Dayan & Simberloff, 2001; Renaud & Michaux, 2004). Posterania rarely add much to the analysis, as their morphology is generally both highly conservative and subject to a high degree of convergence.

Despite this bleak picture, however, the phylogenetic analysis presented here demonstrates that, at least in aplodontoids, phylogenetic analysis is possible and can produce meaningful resolution. Although previous, less complete versions of this analysis (Hopkins, 2001a, b; Hopkins, 2003) produced very different results, which were less concordant with geography, stratigraphy, and traditional systematics, the more comprehensive and complete analysis presented here demonstrates that morphological phylogenetics can be informative, even in clades with numerous poorly known taxa.

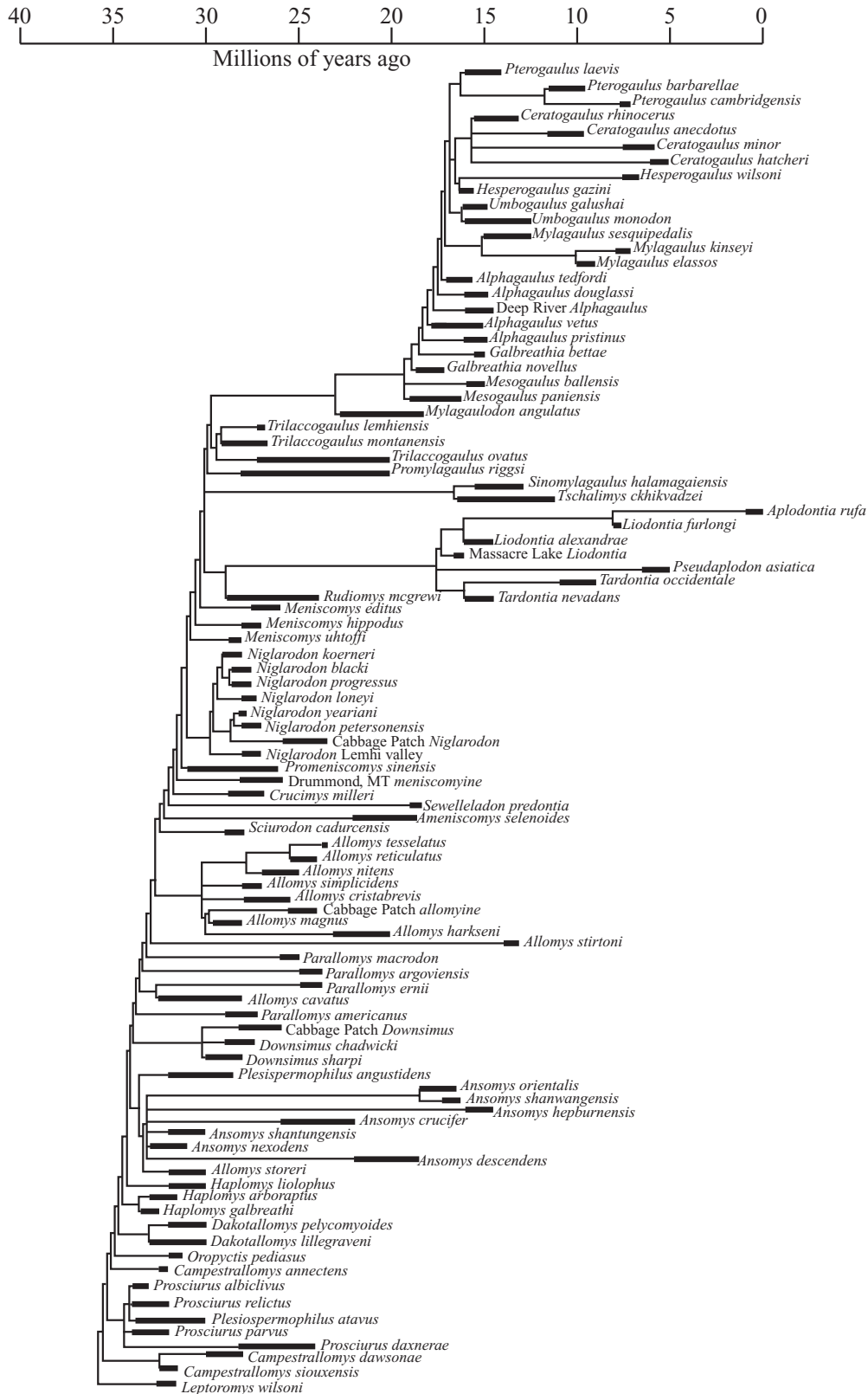
The less well-resolved results from previous, less comprehensive versions of this analysis highlight the importance of the inclusion of all available taxa. Including even a few poorly known taxa can provide a significant level of stability and resolution of the

resulting phylogeny. This conclusion is supported by the discovery that the topology was changed substantially, and became much more stable, after adding taxa that were coded for between 33 and 50% of the characters to the analysis. Even taxa for which only a third of the characters were coded were important to the stability and consistency of the phylogenetic analysis of their group. This finding emphasizes the importance of a complete survey of known species in understanding the phylogenetic position of new taxa. The analysis presented here provides such a survey for the published record of aplodontids, and constitutes a framework for future studies of new aplodontid taxa.

APLODONTID EVOLUTION

A composite phylogeny reflecting the topologies on which all or most of the analyses presented previously agree is illustrated in Figure 7. This topology is mainly the result of the semi-ordered analysis (number 2), and takes into account the consistencies between the earlier analyses, as well as stratigraphy and geography. The same topology is also depicted in Appendix 4, which plots all character changes (using delayed transformation or DELTRAN assumptions for ambiguous branches) on the tree without stratigraphic information. Figure 8 shows the approximate positions of poorly known taxa. It is apparent that evolution in aplodontids shows a pattern consistent with Eldredge & Gould's (1972) punctuated equilibria. There are episodes of rapid diversification in the 'prosciurines' during the Early Oligocene, in the allomyines and the meniscomyines during the Late Oligocene, and in the mylagaulids during the Early Miocene. The aplodontines and ansomyines appear to be exceptions to this pattern of 'bang-and-bust', and persist with relatively little morphological change or species diversity for millions of years. Neither of these two taxa are particularly speciose or widespread, but both can be quite locally abundant, suggesting the possibility of habitat specialization limiting diversification. This notion would be consistent with the known ecology for the modern aplodontine, *A. rufa*, which is a specialist in terms of its habitat and ecosystem role (Carraway & Verts, 1993). This interpretation of the ecological drivers for the diversification pattern of aplodontines suggests that the other taxa, which went through more rapid radiations, are likely to have been generalists taking advantage of available niche space during the time period in which they diversified. This idea will require testing.

Resolution among the 'prosciurines' is uncertain, which is not surprising given the fact that most fossils consist of isolated teeth and jaws, and few skulls have been described. Specimens of many of these taxa were not available for this study, and their characters had



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Figure 7. Preferred phylogeny of aplodontid rodents. Solid lines represent the known stratigraphic range of taxa; thinner lines represent inferred ranges. Where the temporal ranges of taxa are poorly constrained, the entire possible range is included as the known stratigraphic range.



Figure 8. Phylogenetic position of poorly known taxa. The most likely points of insertion of poorly known taxa are indicated with circles. Multiple lines for a single taxon indicate multiple equally likely positions. Dashed lines that fork indicate that the two taxa are placed as sister taxa in the analysis. The poorly known species are as follows: 1, *Prosciurus ordosicus* Wang, 1987; 2, *Prosciurus magnus* Korth, 1989; 3, *Prosciurus daxnerae* Lopatin, 2000; 4, *Ansomys crucifer* Lopatin, 1997; 5, *Ansomys shantungensis* Rensberger & Li, 1986; 6, *Parallomys argoviensis*; 7, *Allomys cristabrevis* Barnosky, 1986; 8, *Pseudaplodon asiatica* Schlosser, 1924; 9, *Sinomylagaulus halamagaiensis* Wu, 1988; 10, *Tschalimys chkhivadzei* Shevyreva, 1971.

to be coded exclusively from published images, which limited the number of characters coded for them. Even so, several putative aplodontid species can now be excluded from the Aplodontidae, including *P. lohicolus*, *Pelycomys*, *P. vetustus*, *E. spanius*, and *E. hospes*. The genus *Prosciurus* is polyphyletic, as previously defined, although it could be redefined so as to be monophyletic. *Campestrallomys* may be paraphyletic, although the evidence for this is slightly less clear. Both of these genera are relatively basal, along with *Oropyctis* and *Dakotallomys*. *Haplomys* appears to be a paraphyletic group of species, and was the last to diverge within the 'prosciurines'. The Ansomyinae appear to be monophyletic (although the ordered analysis casts some doubt on this), as is the genus *Downsimus*, including the undescribed species from the Cabbage Patch formation.

The Allomyinae as traditionally defined prove to be a paraphyletic group, because the support for and consistency of the paraphyly of 'Parallomys' is very strong. Several species previously placed in *Allomys* fall within this group. The species previously attributed to *Alwoodia* (Rensberger, 1983) appear to belong at the base of the derived *Allomys* clade: the available evidence seems to suggest that the grouping is based on plesiomorphies. The Cabbage Patch allomyine seems to ally strongly with *A. magnus*, and may even be the same species. *Allomys* is a strong monophyletic group mostly limited to the John Day basin, except for the Montana species *Allomys cristabrevis* Barnosky, 1986.

The Meniscomyinae also appear to be paraphyletic, as traditionally defined (Rensberger, 1983). A paraphyletic series of early meniscomyine species diverges before the two major diverse meniscomyine genera *Niglarodon* and *Meniscomys*. *Niglarodon* seems to be a monophyletic genus. This genus is difficult to resolve phylogenetically because few species of *Niglarodon* are known from unworn dentitions, and almost no skull material is preserved, and therefore coding is inevitably incomplete. It is hoped that future collecting efforts will produce additional material from these taxa that will clarify the relationships between species of *Niglarodon*. *Meniscomys* seems to be a paraphyletic group at the base of the hypsodont clade, and may represent a simple anagenetic series, in which case the designation of multiple species within the genus may not be merited. *Rudiomys mcgrewi*, traditionally placed in the Meniscomyinae, seems to be the earliest member of the aplodontine lineage. Given the small geographic and temporal range of meniscomyine species not belonging to the Homalodontia, anagenesis may explain some of the uncertainty in relationships between species in this group.

The Aplodontinae show a consistent phylogenetic grouping, with a sister-group relationship between the

two fossil genera *Liodontia* and *Tardontia*. The modern *A. rufa* also seems to be the most derived member of the *Liodontia* clade. The addition of more, as yet undiscovered basal aplodontine taxa may be important to polarize character states, to root the aplodontine tree, and to understand the path of aplodontine evolution from a *Rudiomys*-like ancestor. The poor support for relationships in this clade results from the fact that aplodontines lose most of their dental characters by wear early in life, as they are all quite hypsodont. Because skulls and jaws are also quite rare, there are few observable characters available that are not subject to confounding variation.

Mylagaulid relationships are variably resolved here. Whereas some relationships are quite clear, others remain unresolved. There is some evidence to suggest that *Ceratogaulus* and *Hesperogaulus* form a clade, and that *Pterogaulus* and *Umbogaulus* are closely related. However, these relationships are not robust. Evidence also suggests that *Mylagaulus* may be an isolated lineage, but, so little is known of this genus relative to other mylagaulids that it is difficult to say this with certainty. The recovery of a single skull of *Mylagaulus* could drastically change its phylogenetic position. The consistent monophyly of mylagaulid genera and the differentiation of some of the basal species suggest that the morphology has the potential to resolve the relationships. Given that many taxa from the Hemingfordian through Hemphillian of New Mexico, Texas, Oregon, and Nevada are still undescribed, or are in need of revision, it is not surprising that the inferred radiation of derived mylagaulines is poorly resolved.

SYSTEMATIC PALEONTOLOGY

The systematics presented here are based on the preceding phylogenetic analysis. The format for the phylogenetic definition of taxa largely follows that of Joyce, Parham & Gauthier (2004), although the use of 'Pan-' to denote stem groups is not followed here in order to retain the relative stability of the traditional clade names. The dental terminology is shown in Figure 1. The taxa for which specimens were examined first hand and for which data were extracted from the literature are indicated in Table 1. A list of the abbreviated names of the institutions that hold material is given in Appendix 5. A table of key synapomorphies is provided (Table 3) to facilitate the systematic placement of new taxa.

TAXONOMIC PHILOSOPHY

The primary purpose of this study is to present the results of a phylogenetic analysis of the Aplodontidae. As the analysis does not present a single

Table 3. Key synapomorphies for the identification of the aplodontid taxa defined here

Taxon	Size range	Key synapomorphies
Ansomyinae	Very small aplodontids; P4 < 2.5 mm in length	<ol style="list-style-type: none"> 1. Doubled mesostyle on upper molars, creating top-hat shaped ectoloph. 2. Teeth with prominent crests, especially entoconid, mesostylid. 3. Metaconid low, reduced on molars. 4. Anterostyle of P⁴ without interior process. 5. Accessory cusps or cuspules in tooth basins.
<i>Ansomys</i>	Very small aplodontids; P4 < 2.5 mm in length	<ol style="list-style-type: none"> 1. Lophodont: teeth dominated by long, mostly straight crests. 2. Compressed, blade-like mesostylid, generally similar in size to entoconid. 3. Anteroposteriorly compressed hypoconulid. 4. Central basin of cheek teeth filled by crests.
Allomyinae	Small to large aplodontids; P4 from about 2 to 12 mm in length	<ol style="list-style-type: none"> 1. Lophodont, all cusps strongly crested. 2. Anteroposteriorly elongated hypoconid. 3. P4 slightly enlarged relative to molars. 4. Ectoloph very well formed, crests nearly as thick as cusps. 5. Anterior basin of P₄ narrow between close-set metaconid and protoconid.
<i>Allomys</i>	Small aplodontids; P4 from 2.5 to 4 mm in length	<ol style="list-style-type: none"> 1. Brachydont, but with complex occlusal morphology and extensive development of accessory crests. 2. Interpremaxillary foramen only a pit: does not penetrate the premaxillary bone. 3. Entoconid of M₁ anterior to posterolingual corner of tooth. 4. Anteroconid present anterior to protoconid on P₄. 5. Protoconule connected by crest to anterostyle on P⁴. 6. Second metaconule present, roughly equal in size to first metaconule on molars.
Meniscomyinae	Small to large aplodontids; P4 from about 2 to 15 mm in length	<ol style="list-style-type: none"> 1. Mesodont to hypsodont. 2. Thick, bulbous cusps and crests. 3. P4 distinctly enlarged (>1.5 times size of molars). 4. Central fossettid very deep, persistent with wear, with simple convex shape. 5. Prominent crest connecting mesostylid to mesoconid. 6. Hypoconulid anteroposteriorly compressed. 7. Inflection between hypoconulid and entoconid closed completely by crest. 8. Hypoconulid posterior to hypoconid on M₃. 9. Enamel in basins of cheek teeth smooth.
Homalodontia	Small to large aplodontids; P4 from about 3 to 15 mm in length	<ol style="list-style-type: none"> 1. Teeth subhypsodont to hypsodont or even hypselodont. 2. Skull broad and flat, occipital region widened. 3. External auditory meatus elongated into a tube. 4. Bulla reduced in size, not ventrally prominent. 5. Mastoid process enlarged, separated from bulla. 6. Upper molars have reduced roots and are rectangular or oval in occlusal outline. 7. Posterolabial crest of the anterocone meets the anterior crest of the paracone exactly, leaving no groove down the anterolabial face of the paracone. 8. Posterolabial fossettid of P₄ is large, elongate, and oval, extending posteriorly to be closed by posterior cingulum.
Aplodontinae	Small to medium aplodontids; P4 from about 3 to 5 mm in length	<ol style="list-style-type: none"> 1. Upper molars shield-shaped, lower molars crescentic or B-shaped, tending to lose enamel basins with wear. 2. Lower incisor anteriorly convex. 3. Mental foramen posteriorly positioned, just anterior to P₄. 4. Zygomatic arches lightly built, skull very shallow dorsoventrally. 5. Cheek teeth becoming more transversely compressed from M₁ to M₃. 6. Ectoloph on anterocone of P⁴ relatively short. 7. Metaconid of molars labiolingually compressed.

Table 3. *Continued*

Taxon	Size range	Key synapomorphies
Mylagaulidae	Medium to large aplodontids; P4 from about 3.5 to 15 mm in length	<ol style="list-style-type: none"> 1. Hypsodont. 2. Premolars enlarged even further, > 2 times size of molars. 3. Molars, especially M1, reduced in size. 4. Infraorbital foramen oval, not round. 5. Skull broad between orbits, not constricted. 6. Numerous enamel lakes on cheek teeth, more than three in all cases. 7. Central transverse valley of upper molars lost with central union of metaloph and protoloph. 8. Mesostyle round when unworn. 9. Precise occlusion of cusps lost, as teeth wear flat. 10. Posterolophid anterolabially directed, not labiolingually.
Mesogaulinae	Large aplodontids; P4 from about 5 to 15 mm in length	<ol style="list-style-type: none"> 1. Skull heavily built and broad, with especially thick zygomatic arches. 2. P4 enlarged, drives out M1 as it erupts. 3. Anterolabial fossette of P4 branching anteriorly; these branches often separate with wear. 4. Mesoconid on molars less prominent than on premolars. 5. Mesoconid strongly connected to hypoconid by crest on both molars and premolars. 6. Hypoconid and hypoconulid of M₃ aligned labiolingually. 7. Enamel lakes of cheek teeth all similar in depth, with no one lake remaining much longer than the others. 8. Palate deeply grooved. 9. Labial inflection of the P₄ is narrow and deeply incised closed fairly early in wear by a crest from the protoconid.
Mylagaulinae	Large mylagaulids, cheek teeth from 9 to 15 mm in length	<ol style="list-style-type: none"> 1. Oval premolars. 2. Reduced roots on premolars which close only after the premolar has been in wear for some time. 3. Ectoloph is distinctly convex around its entire circumference, with no concave indentations in the outline in mid-wear specimens. 4. Sagittal crest of skull doubled, forming two parasagittal crests, which become more posteriorly divergent with time. 5. Tall, thick anterior zygomatic plate is present, oriented perpendicular to the plane of the palate. 6. Zygomatic arch widely expanded laterally 7. Posterior end of zygomatic arch meeting the laterally extended external auditory meatus. 8. Premolar fossettids elongate and become more so through time.

answer for the phylogenetic history of aplodontoids, it would be premature to present a complete revision of aplodontoid systematics. However, there are some extremely well-supported results that are unlikely to change in future analyses. These results are applied to a revision of the broad-scale taxonomy of aplodontoids. Further fine-scale revision must await better knowledge of many taxa, and the examination of additional specimens.

Wherever possible, only monophyletic groups are defined, using the syntax of Joyce, Parham & Gauthier (2004). Where the paraphyly of a group is uncertain, or where the definition of monophyletic groups would require an excessive proliferation of

taxonomic terminology (such as the description of a half dozen monotypic genera), the taxonomy is left unaltered. Because diversification is extremely asymmetrical in the Aplodontoidea, it is difficult to make Linnean binomials that both reflect the evolutionary history and have a useful, nested, hierarchical relationship between the genus and species. Paraphyletic 'comb.' genera are left unrevised, but are placed in quotation marks to indicate their failure to meet the requirement of monophyly. As no formal publication has been made of the standards of the PhyloCode (still in draft form, <http://www.ohiou.edu/phylocode>), which addresses this problem of binomial nomenclature, there is no solution allowing for phylogenetically

correct taxonomy and binomials for species in these paraphyletic grades without creating many redundant taxonomic names (monotypic genera). To avoid this problem, I will refrain from these small-scale revisions until a phylogenetic solution to the taxonomic problem is available.

Monophyletic groups are defined in such a way as to minimize changes from existing terminology. Whenever possible, these are defined as node groups (groups defined by the union of a pair of taxa and all descendants of their most recent common ancestor), using taxa from within the traditional membership of the group as previously defined. In a few cases (e.g. the Aplodontinae and Mylagaulidae), stem groups (groups defined as one of the two lineages comprising a particular node group) are used for lineages where a substantial number of taxa are inferred to be missing, and where a node group defined using the taxa currently known would be likely to exclude morphologically similar species.

RODENTIA BOWDITCH, 1821

APLODONTOIDEA TROUESSART, 1897

APLODONTIDAE TROUESSART, 1897

Referred taxa: see Table 1.

Geographic and stratigraphic range: From the Early Oligocene to recent times in North America and Asia, and in the Oligocene of Europe.

Discussion: The Aplodontoidea is the superfamily that unites the Aplodontidae and the Mylagaulidae in traditional aplodontoid systematics. The phylogenetic result presented here shows that the Mylagaulidae are nested well within the group conventionally regarded as the Aplodontidae; so, in order to define the Aplodontoidea and the Aplodontidae as monophyletic entities, they must be synonymous. Throughout the rest of this paper, mylagaulids are included in any reference to the Aplodontidae. No formal definition is attempted here, because there is very weak support for the basal node of the tree. A stem definition would be best, especially as several of the taxa traditionally included in the Aplodontidae cannot be confidently placed within or outside the clade. A stem definition would make it possible to include these taxa, if they do actually belong to the line leading to aplodontids. Unfortunately, a stem-group definition would require knowledge of the sister clade, either an extant lineage or a relatively diverse fossil clade. Too little is known of the phylogenetic relationships among basal rodents for this to be possible. Thus, until the basal resolution

can be well supported, or until the sister group is determined, no formal phylogenetic definition can be given for this clade.

'PROSCIURINAE' WILSON, 1949

Discussion: The Prosciurinae have previously been defined as the species at the base of the aplodontid radiation (Rensberger, 1975; Korth, 1994a). It is clear from this analysis that this group is paraphyletic and that the only way to define it as a monophyletic group would be to synonymize it with the Aplodontidae as a whole. Because the Prosciurinae are necessarily a paraphyletic group, it is not given a phylogenetic definition here.

ANSOMYINAE QIU, 1987

Definition: The node group arising from the last common ancestor of *Allomys storeri* Tedrow & Korth, 1997 and *Ansomys orientalis* Qiu, 1987.

Revised diagnosis: Small brachyodont aplodontids characterized by a double mesostyle on the upper molars, a protoloph that connects to the protocone by a diagonally oriented crest, and an anterostyle of P⁴ without an interior process. The cusps are strongly crested, with several crests crossing the central valley of the tooth, and there are incipient cuspsules or accessory cusps in the tooth basins. The labial faces of the paracone and metacone are concavo-convex in most members of the clade, with the cusps bulging labially within concave faces of the ectoloph. In the primitive condition, the mesostylid is connected to the mesoconid, although this connection becomes interrupted by internal crests in more derived members of the clade. The metastylid crest extends posteriorly in most members of the clade. In the primitive condition, a cingulum is present at the base of the labial surface of the paracone, although this feature is lost in one species.

Referred taxa: See Table 1.

Geographic and stratigraphic range: From the Late Oligocene to the Middle Miocene of Montana and China, in the Late Oligocene of South Dakota and Germany, and in the Middle Miocene of Kazakhstan.

Discussion: Using the phylogenetic resolution preferred here, the Ansomyinae appear to be monophyletic, not containing the Allomyinae; however, it is possible that this group, as previously considered (Qiu, 1987; Qiu & Sun, 1988; Hopkins, 2004), would have to be defined as containing the Allomyinae in order to be monophyletic. This resolution is consid-

ered unlikely, so this clade is considered here to contain only species that this author would refer to the genus *Ansomys*, plus a single species (*A. storeri*) previously referred to *Allomys* by Tedrow & Korth (1997). This single species is distinct enough from the species previously placed in *Ansomys* by Hopkins (2004) to merit a genus of its own. The redescription and revision of '*Allomys storeri*' will be addressed in a separate publication. It is likely that additional taxa will be added to this group in the near future, as new *Ansomys* continue to be discovered in the fossil record of Asia and North America (Ye, Meng & Wu, 2003; Kelly & Korth, 2005).

ANSOMYS QIU, 1987

Definition: The node group arising from the last common ancestor of *Ansomys descendens* (Dehm, 1950) and *A. orientalis*.

Revised diagnosis: Ansomyines with relatively lophodont dentition, a compressed, blade-like mesostylid, an elongated entoconid, which is widest at the posterolingual end, an anteroposteriorly compressed hypoconulid on the molars, and lacking a large open central basin. Fossettids are well defined, and the enamel of the basins of the lower cheek teeth is slightly rugose in all but *Ansomys hepburnensis* Hopkins, 2004.

Referred taxa: See Table 1.

Geographic and stratigraphic range: From the Late Oligocene to the Middle Miocene of Montana and China, in the Late Oligocene of Germany, and in the Middle Miocene of Kazakhstan.

Discussion: The treatment here follows the revision of *Ansomys* in Hopkins (2004), and is consistent with most of the results of the phylogenetic analysis presented here; if *Ansomys* proves to be a paraphyletic group as suggested by analysis 5, redefinition of the genus will be necessary.

ALLOMYINAE MARSH, 1877

Definition: The node group arising from the last common ancestor of *Parallomys americanus* Korth, 1992b and *A. nitens*.

Revised diagnosis: Small to large, brachyodont to hypsodont aplodontids, with relatively lophodont dentition. Accessory crests incipient in most basal members of the clade, becoming more prominent and numerous in the nonmeniscomyine members of the lineage, especially among members of the genus *Allomys*. Lower

molars essentially the same size from M_1 to M_3 , but P^4 is slightly enlarged relative to the molars. Entoconid double crested, with one crest directed labially and one directed anterolabially into the centre of the tooth. The basin between the closely positioned metaconid and protoconid of P_4 is narrow and anteroposteriorly elongated, with sharp styles extending down the anterior faces of both metaconid and protoconid. The metaconid of the lower molars is labiolingually compressed, and the hypoconid is anteroposteriorly elongated. A second metaconule is present labially to the one present in all other aplodontoids. This metaconule is small early in the history of the clade, but becomes large later in time. The ectoloph is dominated by crests, not cusps, and is continuous between the paracone and metacone, and closes the central transverse valley. The paracone is positioned more lingually than the metacone. The labial face of M^3 is concave, with a well-formed ectoloph. The mesostyle of P^4 is positioned at the anterior end of the central transverse valley, and is anterolabially directed in the early members of the clade, but is positioned and directed more posteriorly in a few derived *Allomys*. Although all of these characters diagnose the base of the clade, a few of them, especially the second metaconule and the accessory crests, are lost again among the meniscomyines. Both these features have evolved several times among rodents, and are only useful on a relatively small taxonomic scale.

Referred taxa: See Table 1.

Geographic and stratigraphic range: From the Late Oligocene to recent times of North America, from the Late Oligocene to the Early Miocene of Europe, and from the Early to Late Miocene of Asia.

Stratigraphic range: From the Late Oligocene to the Middle Miocene.

Discussion: This definition roughly follows that of Rensberger (1983), but refers to a monophyletic group. The analysis presented here strongly supports the paraphyly of the traditional allomyine grouping, and of the allomyine genus *Parallomys* in particular. Thus, all more derived aplodontids are also nested within a monophyletic Allomyinae.

'PARALLOMYS' RENSBERGER, 1983

Referred taxa: See Table 1.

Geographic and stratigraphic range: In the Late Oligocene of South Dakota, Nebraska, Oregon, France, Germany, and Switzerland, and in the Middle Miocene of Nebraska.

Discussion: This purported genus is a paraphyletic group along the main 'backbone' of the aplodontoid lineage leading up to the divergence of *Allomys*. The arrangement of the species in this group is consistent across all the different combinations of taxa and configurations of characters. Although the genus is paraphyletic, the only way to give each species a binomial name (still required in the absence of a final version of the PhyloCode) would be to name a new genus for each of the species. For the time being, the genus is left as a paraphyletic entity, although it remains a poor systematic term.

'*PARALLOMYS*' *CAVATUS* (COPE, 1881)

COMB. NOV.

Allomys cavatus Cope, 1881b.

Material examined: Holotype & AMNH (6988) skull missing part of anterodorsal skull roof, with left P⁴-M³, right M³.

Geographic and stratigraphic range: In the Late Oligocene (Late Whitneyan or Early Arikareean NALMA) of Oregon.

Discussion: As this species also belongs to the paraphyletic region of the tree with all the other species previously referred to '*Parallomys*', it is also referred to this genus.

'*PARALLOMYS*' *STIRTONI* (KLINGENER, 1968)

COMB. NOV.

Allomys stirtoni Klingener, 1968.

Material examined: UNSM (85548), loc. Bw-106, UNSM 83000, loc. Bw-110, specimens referred by Voorhies (1990).

Geographic and stratigraphic range: In the mid-Miocene, Late Barstovian NALMA, Norden Bridge Quarry and Achilles Quarry, Brown County, NE, USA.

Discussion: This species also falls out in the paraphyletic region of the tree with all the other species previously referred to '*Parallomys*', so it is also referred to this genus.

ALLOMYS MARSH, 1877

Definition: The node group arising from the last common ancestor of *Alwoodia magna* Rensberger, 1983 and *A. nitens* Marsh, 1877.

Revised diagnosis: Brachyodont allomyines with numerous prominent accessory crests connecting cusps of cheek teeth and crenulate enamel in the basins of the lower teeth. The interpremaxillary foramen is only a pit. The hypolophulid is present, although it is weak in some taxa. The hypoconulid has a distinct crest, which in many *Allomys* is connected to the hypolophulid. The valley dividing the labial crest of the hypoconulid from the entoconid is at least partially closed, and is completely closed in some *Allomys*. The entoconid is shifted anteriorly on M₁, and an anteroconid is present anterior to the protoconid on P₄. The labial end of the protoconule joins the anterostyle and crosses the anterior basin of P⁴. The protoconule has two parallel anterior crests on M¹⁻².

Discussion: The only monophyletic group recovered within the traditional 'Allomyinae' was a grouping of *Allomys* and *Alwoodia* species. Although the species previously placed in the genus *Alwoodia* do seem to form a distinct clade, several of the phylogenetic analyses nest it within the clade formed by previously described *Allomys* species. The major feature distinguishing *Alwoodia* from *Allomys* is the presence or absence of accessory crests; however, specimens of *Alwoodia* can be found with a small number of accessory crests, particularly *Alwoodia harkseni* Korth, 1992a. Given the high morphological similarity between the two genera, and the fact that genera cannot be nested under a system of binomial nomenclature, the two species previously placed in *Alwoodia* are now assigned to *Allomys*. As *Alwoodia* is a monophyletic group, it is retained as a subgenus of *Allomys*. *Allomys cristabrevis* also seems to fall within this group, although more complete material would be necessary to be certain of its position. As *A. cristabrevis* is only known from a single isolated m1 or m2, determining its systematic affinities with certainty is currently difficult.

Referred taxa: See Table 1.

Geographic and stratigraphic range: From the Late Oligocene to the Early Miocene of Oregon, Montana, Wyoming, and South Dakota.

ALWOODIA RENSBERGER, 1983

Type species: *Alwoodia magna* Rensberger, 1983.

Included species: *Allomys harkseni* Macdonald, 1963, *Allomys magnus* Rensberger, 1983.

Discussion: See explanation in *Allomys*, above.

ALLOMYS HARKSENI MACDONALD, 1963

Allomys harkseni Macdonald, 1963.

Alwoodia harkseni Korth, 1992b.

Material examined: Holotype & SDSM (59155), and paratype SDSM 59156, both isolated upper molars from SDSM V592, SDSM 6273, a left dentary with P₄-M₃, from loc V627, as well as additional undescribed specimens from the same localities.

Geographic and stratigraphic range: From the Early Miocene (Late Arikareean NALMA) of South Dakota and Nebraska.

Discussion: Macdonald (1963) originally described this taxon as a species of *Allomys* from the Wounded Knee faunas of South Dakota. It was later recognized (Rensberger, 1983) that the type locality for this species included two distinct species of allomyines, both of which were lumped together in Macdonald's (1970) treatment of additional material from *A. harkseni*. Korth (1992a) described this second species as '*Parallomys*' *americanus*, but referred *A. harkseni* to the genus *Alwoodia*. Here, I return the species to its original placement in the genus *Allomys*.

ALLOMYS MAGNUS (RENSBERGER, 1983)

COMB. NOV.

Alwoodia magna Rensberger, 1983.

Material examined: Holotype & UCMP (76941), from UCMP Loc. V66116, and additional referred specimens UCMP 76938, 76946, 76945, 105022, 76933, and 105023 from UCMP Loc. V66111, as well as UCMP 76995 and 105021 from UCMP Loc. V6581.

Geographic and stratigraphic range: From the Late Oligocene (Early Arikareean NALMA) of Oregon.

Discussion: This species was described as the type of the genus *Alwoodia* by Rensberger (1983). For the reasons discussed above, it is now placed as the type of the subgenus *Alwoodia* in the genus *Allomys*. The change in generic assignment requires alteration of the specific epithet to match the gender of the genus to which it is now assigned.

MENISCOMYINAE RENSBERGER, 1981

Definition: The node group arising from the last common ancestor of *Ameniscomys selenoides* Dehm, 1950 and *Meniscomys hippodus* Cope, 1879.

Revised diagnosis: Mesodont to hypsodont apodontids with relatively simple cusp morphology, thick, bulbous cusps and crests, and distinctly enlarged premolars (relative to the size of the molars). The mesostyle of P⁴ is situated in the centre of the labial end of the central valley. The paracone is level with the metacone on the labial side of the tooth, not displaced lingually; this represents a reversal from the state in nonmeniscomyine allomyines. The anterolabial spur of the protocone, present basally in apodontids, is lost in this clade. There is no lingual ridge on the anterior end of the protocone. The central fossettid is extremely deep and persists with wear, and has a simple, convex shape, and is round or transversely elongated, in all meniscomyines. The crest from the entoconid to the mesoconid is a large, prominent feature, and is always directed obliquely, anterolabially in meniscomyines. The mesostylid is strongly connected to the mesoconid by a crest, and the entoconid crest of M₂ is bent anteriorly. The posterior inflection between the entoconid and hypoconulid is closed all the way to the top of the crown, and the hypoconulid is posterior to the hypoconid on M₃. The hypoconulid is anteroposteriorly compressed and linear on all the cheek teeth. The mesoconid of P₄ is reduced relative to that in the molars, but the mesostylid has a distinct lingual prominence on P₄. The crenulate enamel found in the basins of the upper cheek teeth of derived nonmeniscomyine allomyines is lost in meniscomyines.

Referred taxa: See Table 1.

Geographic and stratigraphic range: From the Late Oligocene to recent times in North America, from the Late Oligocene to the Late Miocene of Asia, and in the Early Miocene of Europe.

Discussion: This taxon is defined in such a way as to include most of the taxa traditionally assigned to the Meniscomyinae. The immediate outgroups to the Meniscomyinae, *P. sinensis* and *S. cadurcensis*, are left out of the group in order to use the most stable definition. *Sciurodon* lacks the crown height and wear pattern generally associated with meniscomyines, and *Promeniscomys* is not entirely stable in its placement. Similar to the Allomyinae, the monophyletic Meniscomyinae includes a number of derived taxa that nest within this group, which have not traditionally been included. The transition from earlier allomyines to meniscomyines is characterized by the simplification of cusp morphology and an increase in crown height.

HOMALODONTIA NEW TAXON

Definition: The node group arising from the last common ancestor of *Aplodontia rufa* Rafinesque, 1817 and *Alphagaulus vetus* Matthew, 1924.

Etymology: ‘Homalo-’ from the Greek word meaning ‘flat’ and ‘-odontia’ from the Greek word meaning ‘tooth’, referring to the flat chewing surfaces of the teeth in these rodents.

Diagnosis: Derived aplodontids with subhypsodont to hypsodont, lophodont teeth and broad, flat skulls. The occipital region of the skull is widened, and is often the widest part of the skull. The external auditory meatus is elongated into a tube, which is at least as long as the mediolateral width of the bulla itself. This elongated external auditory meatus extends the ear opening laterally to a point directly anterior to the lateral edge of the widened occipital plate. The bulla is somewhat reduced in relative size, and is not ventrally prominent on the skull. The mastoid process of the skull is enlarged and separated from the bulla, and the anterior edge of the basioccipital is expanded ventrolaterally around the outer surface of the bulla. The protoconule of P⁴ is expanded anteroposteriorly and connected to the anteroloph, which is composed of a single cusp, the anterocone. The posterolabial crest of the anterocone meets the anterior crest of the paracone, without leaving a groove down the anterolabial face of the paracone, and the posterolabial fossette on P⁴ remains closed throughout wear. The upper molars have reduced roots and are rectangular or oval in occlusal outline. The posterolabial and posterolingual inflections on M³ are closed by the posterior cingulum, and the mesostylid does not protrude lingually on M₃. Both represent reversals from the condition derived within the nonhomalodontian meniscomyine line. The posterolabial fossettid of P₄ is large, elongated, and oval, and extends posteriorly to be closed by the posterior cingulum.

Referred taxa: See Table 1.

Geographic and stratigraphic range: From the Late Oligocene to recent times in North America, and from the Middle to Late Miocene in Asia.

Discussion: The grouping of mylagaulids with aplodontines is one of the strongest associations found in phylogenetic analyses of aplodontids (Hopkins, 2001a; Hopkins, 2001b; Hopkins, 2003). This taxon is composed of all the fully hypsodont (having cheek tooth

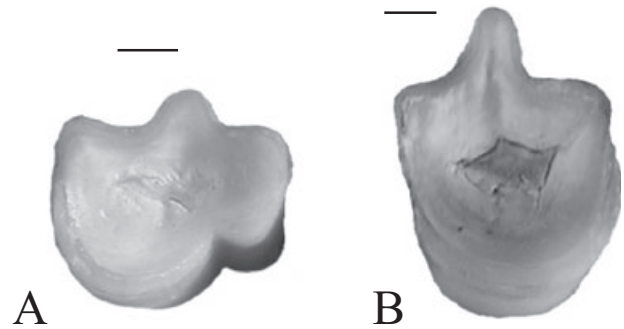


Figure 9. Aplodontine (*Aplodontia rufa*) molars, occlusal view. A, right lower molar (labial is down), showing B-shaped outline. B, left upper molar (lingual is down), showing shield-shaped outline.

crown height greater than crown length) aplodontids, as well as the mesodont aplodontine precursor *R. mcgrewi*.

APLODONTINAE TROUESSART, 1897

Definition: The stem group composed of all homalodontians more closely related to *Aplodontia rufa* Rafinesque, 1817 than to *Alphagaulus vetus* Matthew, 1924.

Revised diagnosis: Homalodontians with subhypsodont to hypselodont cheek teeth that lose the cusps early in wear, leaving shield-shaped upper molars and crescent- or B-shaped lower molars (Fig. 9). Both upper and lower molars are often a simple enamel band surrounding a dentine peg. The lower incisor is convex anteriorly, and the mental foramen is positioned relatively posteriorly, just anterior to P₄. The zygomatic arches are relatively lightly built, and the skull is low and flat. The paracone of the M³ has a concave labial face. The cheek teeth become more transversely compressed from M¹ to M³. The ectoloph on the anterocone of P⁴ is relatively short. The metaconids of M₁₋₃ are compressed labiolingually. The entoconid is anterolabially elongated and roughly rectangular. The inflection posterior to the mesostylid is very broad.

Referred taxa: See Table 1.

Geographic and stratigraphic range: From the Late Oligocene to recent times in Oregon, Nevada, and Montana.

Discussion: Like *Ansomys*, the Aplodontinae are easily diagnosed by a consistent morphology. All have hypsodont premolars and molars, and tend to wear the cusps away completely. The taxon is defined as a stem

group and is sister to the Mylagaulidae. There is a substantial interval between the divergence of aplodontines and mylagaulids and the first fossil record of aplodontines, and therefore it may be expected that more basal members of this clade will be found. The two Asian species, *Pseudaplodon asiatica* Schlosser, 1924 and *Tschalimys chhikvadzei* Shevyreva, 1971 are included, as they are morphologically similar to the other species in the clade. Unfortunately, their fossil remains are too fragmentary to include them in the phylogenetic analysis, because both are known from single specimens that are significantly worn. The current analysis indicates that *Sinomylagaulus halamagaiensis* Wu, 1988 may also be an aplodontine, but it is also known from a single specimen, and the published images leave some ambiguity about its affinities.

MYLAGAULIDAE COPE, 1881

Definition: The stem group composed of all homalodontians more closely related to *Alphagaulus vetus* Matthew, 1924 than to *Aplodontia rufa* Trouessart, 1897.

Revised diagnosis: Medium to large aplodontids with greatly enlarged premolars and a thick, heavily built skull. The zygomatic arch is thickened in the area where the jugal and squamosal overlap, making a distinct knot on the posterior end of the zygomatic arch. The infraorbital foramen is oval, and the skull is broad between the orbits. There more than three closed fossettes on the cheek teeth. The central valley of the upper molars is lost, as the metaloph and protoloph are joined in the centre of the tooth, emphasizing the anteroposteriorly elongated enamel lakes instead. The mesostyle is round, as in early aplodontids, and the ectoloph is convex on the metacone and sometimes on the paracone as well. The anteroloph of P⁴ is broad. The mesostylid is bulbous, with its greatest anteroposterior thickness near its labial end, and does not protrude lingually on P₄. The precise occlusion of cusps is lost, as the wear surfaces are all flat, rather than angled, as in all other aplodontoids. The posterolophid is anterolabially directed, not labiolingually as in other aplodontids. The entoconid is reduced in M₃ relative to other molars in early mylagaulids, as well as the derived forms; some mylagaulids from the Middle Miocene reverse this condition. The hypoconulid is triangular, not anteroposteriorly compressed as in meniscomyines. All mylagaulids have premolars that are more than twice the size of any of the molars.

Referred taxa: See Table 1.

Geographic and stratigraphic range: From the Late Oligocene to the Late Miocene in North America.

Discussion: Mylagaulids are defined as the stem group that is the sister group of the aplodontines. This leads to the inclusion of the ‘promylagaulines’ (see below), as well as the larger and more hypsodont species that are more typical of the Mylagaulidae. It is defined as a stem group because the apparent paraphyly of the promylagaulines suggests a high probability of discovering additional taxa that will be morphologically very similar to known species, but will fall outside the node group defined by all known mylagaulids. Promylagaulines are relatively poorly known, mostly from isolated teeth. Because only a limited number of partial skulls and jaws of these early mylagaulids are known, it is difficult to describe the characteristic morphology with any precision.

‘PROMYLAGAULINAE’ RENSBERGER, 1980

Discussion: This clade, much like the ‘Prosciurinae’, described the taxa at the base of the mylagaulid divergence. Only one of the phylogenetic analyses resolves this group as monophyletic. Furthermore, any other nonmesogauline mylagaulids are likely to fall into the same morphological grouping, as the features that diagnose the ‘Promylagaulinae’ are plesiomorphic features of the Mylagaulidae. Hence, this group is regarded as paraphyletic.

MESOGAULINAE KORTH, 2000

Definition: The node group arising from the last common ancestor of *Mylagaulodon angulatus* Sinclair, 1903 and *Mesogaulus paniensis* Matthew, 1902.

Revised diagnosis: Larger mylagaulids with a heavily built skull, reduced first molars, and increasingly enlarged premolars. The zygomatic arch is thick and robust. The premolar is enlarged and broadens towards the roots in such a way as to drive out the M¹ as it continues to erupt. Molars increase in size anteriorly (although M₁, when present in early-wear specimens, is often worn to a smaller size than M₂). Specimens in late wear frequently have lost the first molar. The skull is shorter and broader (the L/W ratio ranges from 1.25 to less than 1.0) than in nonmesogauline mylagaulids. The anterolabial fossette (parafossette) of P⁴ is branched anteriorly around the anterocone, with the branches frequently separating with wear. The crest on P⁴ connecting the protoloph to the protocone is anterolingually oriented. The mesoconid on the molars is not as prominent as on the premolars, and is strongly connected to the hypoconid by a labial crest on both the molars and the premo-

lars. The hypoconid and hypoconulid of M_3 are aligned labiolingually, and form the posterior margin of the tooth. The enamel lakes of the teeth are similar in depth. Enamel lakes on the premolars are much more persistent with wear than in other aplodontid taxa. The thickness of the enamel is relatively uniform around the circumference of the tooth, and is not thickened on the lingual surface of the protocone, as in aplodontines and some nonhomalodontian meniscomyines. The palate is deeply grooved. The labial inflection of the P_4 is narrow and deeply incised, and in the molars it remains equally deep with wear, and does not become increasingly open, as in some other aplodontids. The anterolabial inflection is closed in mid-wear by a crest from the protoconid in the molars. The anterior fossettid is narrow.

Referred taxa: See Table 1.

Geographic and stratigraphic range: From the Early to Late Miocene in North America.

Discussion: Korth (2000) first defined the Mesogauiinae as a distinct subfamily of mylagaulids. It appears that this group is a paraphyletic series of taxa, arranged along the stem leading to the Middle Miocene mylagaulids that Korth refers to as the Mylagaulinae. Thus, the Mesogauiinae are the group of mylagaulids that do not include the 'promylagaulines'. The most basal member of the clade is clearly *M. angulatus*. Resolution within the clade is otherwise lacking.

MYLAGAULINAE COPE, 1881

Definition: The node group arising from the last common ancestor of *Alphagaulus pristinus* Douglass, 1903, *Alphagaulus douglassi* McKenna, 1955, and *Umbogaulus monodon* Cope, 1881b.

Revised diagnosis: The largest of the mylagaulids, with hypsodont, oval premolars with highly reduced roots that close only after the premolar has been in wear for some time. The posterior pair of roots on the P^4 is fused, so that there are only two roots in line anteroposteriorly. The ectoloph is distinctly convex around its entire circumference, with no concave indentations in the outline in mid-wear specimens. The sagittal crest is doubled, forming two parasagittal crests, which become more divergent with time. A tall thick anterior zygomatic plate is present, oriented perpendicular to the plane of the palate; this zygomatic arch curves widely laterally past the orbits, and then medially and posteriorly to meet the laterally

extended external auditory meatus. The premolar fossettids are elongate, and become more so through time.

Referred taxa: See Table 1.

Geographic and stratigraphic range: From the Middle to Late Miocene (from Late Hemingfordian to Late Hemphillian NALMAs) of North America.

Discussion: More than two species are used to define this taxon, as it is unclear which species of *Alphagaulus* is most basal within this clade, and a stem definition is rendered impossible by the lack of positive resolution at the top of the nonmylagauline mesogauiines. The Mylagaulinae include all of the Middle and Late Miocene mylagaulids. The clade is quite diverse, and there are a number of as yet undescribed species from New Mexico, Texas, Nevada, and Oregon. Most of the described genera appear to be monophyletic, as does the clade of hornless mylagaulids from the Great Plains, formed by *Pterogaulus* and *Umbogaulus*. The monophyly of *Alphagaulus* and *Ceratogaulus* is questionable. *Alphagaulus* is probably just a plesiomorphic 'garbage bin' taxon, because none of the phylogenetic resolutions presented here have a monophyletic *Alphagaulus*. *Ceratogaulus* is monophyletic except when *C. anecdotus* is included. The poor preservation of this single species makes it difficult to place it confidently, and the type (at least when examined by this author) does not preserve nasal bones, so the presence or absence of the horns used to diagnose this genus cannot be determined.

CONCLUSIONS

Phylogenetic analysis of aplodontoids provides considerable resolution, despite the relatively fragmentary preservation of most aplodontoid taxa. Although a number of previously defined clades within the Aplodontidae are herein shown to be monophyletic, many others would be paraphyletic if pre-existing taxonomies were followed. Several genera, notably *Allomys* and *Prosciurus* seem to have been used as 'trash bins', including a number of poorly known species that are only very generally similar in morphology. Others (such as '*Parallomys*') are diagnosed based on symplesiomorphies, and hence form paraphyletic taxa. Still other groups (such as *Niglarodon*), which appear from traditional systematics to be good clades sharing a general morphological 'type', could not be consistently recovered with the characters and specimens available for phylogenetic analysis, either because the specimens are too worn or fragmentary, or because they are actually paraphyletic.

There is a clear need to revise the systematics of aplodontids at taxonomic levels that are more refined than those analyzed here. This analysis provides the first step in such a revision, uniting the broad spectrum of aplodontid diversity. Although the position of individual species is generally not consistently resolved here, the larger framework is relatively stable. This provides a context for ecological and diversity studies, and allows the placement of new species within this bigger framework. The character matrix provided here will hopefully also facilitate phylogenetic analysis of future aplodontid finds.

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APPENDIX 1

List of included taxonomic characters.

1. *Mesostyle*: (0) with no labial prominence; (1) moderate labial prominence; or (2) large labial prominence. Ordered in semi-ordered and ordered analyses. The degree of displacement of the mesostyle from the line formed by the paracone and the metacone has essentially three possible states. For state 0, no labial prominence, the mesostyle lies directly in line between the paracone and the metacone. State 1, moderate labial prominence, indicates that the mesostyle is positioned just labial to the line connecting the paracone and the metacone. In this case it forms a distinct knob or point on the labial side of the tooth, which is easily apparent and interrupts the outline of the tooth, but is not large relative to the size of the tooth. State 2, large labial prominence, is characterized by a mesostyle that is substantially labial to the line connecting the paracone and metacone. The interruption in the labial outline of the tooth is very large, with the distance from the labial end of the mesostyle to the line between the metacone and paracone equal to at least a third of the distance from the paracone to the protocone.
 2. *P⁴ mesostyle situated*: (0) slightly anterior to the labial end of the central transverse valley or (1) in the centre of the labial end of the central transverse valley. The mesostyle in *P⁴* closes the labial end of the central transverse valley, and can be aligned either at the anterior end of the central transverse valley (state 0) or at its centre, labial to the groove at the base of the valley (state 1).
 3. *M¹ or ² mesostyle*: (0) anteriorly directed or (1) pointing directly labially. For state 0, the line from the centre of the base of the mesostyle to the tip of the mesostyle is directed more anteriorly than the long axis of the central transverse valley. For state 1, the line from the centre of the base to the tip of the mesostyle is aligned with the long axis of the central transverse valley.
 4. *P⁴ mesostyle*: (0) straight, labially directed; (1) posteriorly directed; or (2) anteriorly directed.
- This character is coded as in character 3, above, using the angle between the long axis of the central transverse valley and the axis of the mesostyle. State 0 corresponds to state 1 in character 3, state 2 corresponds to state 0 in character 3, and state 1 occurs when the line from the centre of the base of the mesostyle to its labial tip is directed more posteriorly than the long axis of the central transverse valley.
5. *Ectoloph*: (0) divided by groove between paracone and metacone or (1) closing labial entrance to transverse valley. The ectoloph can either be one continuous crest across the labial side of the tooth crown (state 1) or be discontinuous across the central transverse valley, divided by the labial end of the groove that is the central transverse valley (state 0).
 6. *Ectoloph*: (0) convex on paracone and metacone; (1) with convex metacone and concave paracone; (2) paracone and metacone concavo-convex, with paracone and metacone expanded within ectoloph, creating complex outline; (3) with curved, concave labial faces; or (4) with deeply concave, V-shaped faces on paracone especially and metacone. Ordered in fully ordered analyses. The shape of the labial surface of the ectoloph varies widely between aplodontid taxa. State 0 occurs in taxa that have a convex labial outline. State 1 includes species with the labial face of the paracone concave labially, but with a labially convex metacone. State 2 has the cusps of the paracone and metacone inset from the labial border of the tooth, but the cusps have convex labial faces. State 3 includes taxa with shallowly concave labial faces on both the paracone and the metacone. State 4 is similar to state 3, but the labial faces of the paracone and the metacone are so deeply concave as to be V-shaped, rather than being essentially arcuate as in state 3.
 7. *Ectoloph*: dominated by (0) cusps or (1) crests. The ectoloph can be composed primarily of the distinct cusps of the paracone, the metacone, and the anterocone (in *P⁴*), or those cusps can be elongated and flattened into crests, to the degree where the ectoloph is composed essentially of the crests of those teeth.
 8. *Labial faces of paracone and metacone*: (0) bulbous, (1) sloped, or (2) almost vertical. Ordered in semi-ordered and ordered analyses. State 0 occurs when the labial surface of the tooth is bulbous, rounded, and slopes labially (outward) at the top of the crown, but curves smoothly down the face to the base of the crown, where it slopes lingually (inwards). Sloped faces of the paracone and metacone (state 1) are labially (outward) sloping all the way to just above

- the base of the crown, where they often curve back inwards toward the roots. State 2 is characterized by the labial faces of the paracone and metacone being essentially flat, and not sloping outwards or inwards.
9. *Cingulum at base of labial surface of anterior ectoloph and anterior invagination of mesostyle: (0) absent or (1) present.* A small lip or cingulum is present at the base of the labial face of the paracone, just above the base of the crown, in some aplodontids.
 10. *M³ mesostyle: (0) connected to or (1) separate from metacone.* The mesostyle can be either connected to the metacone by the ectoloph crest (state 0) or separate, lacking the connection of the crest (state 1).
 11. *M¹ or ² mesostyle: (0) single or (1) doubled.* The mesostyle on M¹ or ² is a single cusp (state 0) on many aplodontids; on some taxa it is divided into two small cusps, one anterior and one posterior, usually strongly connected by a crest (state 1).
 12. *M³ with single (0) or double (1) mesostyle.* The M³ sometimes has a doubled mesostyle as well, with one anterior and one posterior cusp; this occurs in some taxa that lack the doubled mesostyle on M¹ or ², and the cusps are more labiolingually elongate than those characterizing the doubled M¹ or ² mesostyle in character 11, and the cusps are rarely connected by a crest.
 13. *Mesostyle of upper cheek teeth: compressed a–p (1) or relatively round (0).* The mesostyle can be either a round, conical cusp (state 0) or a thin, blade-like cusp that is much longer labiolingually than anteroposteriorly (state 1).
 14. *Parastyle: (2) more prominent than mesostyle; (1) parastyle and mesostyle equally prominent; or (0) mesostyle more prominent than parastyle on P⁴.* Ordered in fully ordered analyses. The two styles commonly present on the P⁴ vary in their relative position. For state 0, the mesostyle is more labial in position than is the parastyle. In state 1, the two styles are aligned anteroposteriorly, being equally labial in position. In state 2, the parastyle is shifted more labially than is the mesostyle.
 15. *Ectoloph of P⁴ anterior to mesostyle: (0) displaced lingually or (1) level with ectoloph posterior to mesostyle.* In some taxa, the labial surface of the paracone is more lingually positioned than is the labial surface of the metacone (state 0). In others, the labial faces of the paracone and metacone are equally lingual in position. Generally, the labial surface of the anterocone anterior to the parastyle is aligned with the labial surface of the metacone, which is why the character is described as lingual displacement of the ectoloph.
 16. *Length of ectoloph on anterocone of P⁴: (0) short or (1) long.* The anterior portion of the ectoloph is considered long (state 1) when it is similar in length to or longer than the length of the ectoloph posterior to the mesostyle, which is the part of the ectoloph comprised by the metacone. It is short (state 0) when it is significantly shorter than the posterior portion of the ectoloph.
 17. *Ectoloph: (1) present or (0) absent.* This character codes the presence or absence of enlarged crests on the labial side of the tooth, creating a labial shear surface. This feature need not necessarily be a continuous crest or a complete loph; it simply requires the elongation of crests on the paracone and metacone to create a labial shearing blade.
 18. *Ectoloph: (0) continuous or (1) not continuous with metacone on upper molars.* This character codes for the presence (state 1) or absence (state 0) of an interruption or gap in the ectoloph between the metacone and the mesostyle.
 19. *P⁴ paracone: (0) larger than metacone or (1) same size as metacone.* The paracone is coded as larger than the metacone if larger in circumference, occlusal area, and overall volume.
 20. *M¹ or ² paracone: (0) level with or (1) more lingual than metacone.* The paracone and metacone can be either equally lingual (state 0) or offset, with the paracone being more lingual and the metacone being more labial (state 1).
 21. *M³ paracone with convex (0) or concave (1) labial face.* The occlusal outline of the paracone of M³ is often labially convex, even in some taxa that have concave labial faces on the paracone of M¹ and ².
 22. *Erupting premolar: (1) wearing away paracone of M², with paracone wearing off M³ or (0) teeth abutting neatly.* This character is found, thus far, only in mylagaulids, in which the premolar, as it erupts, drives out the first molar. The condition could theoretically occur in any of the aplodontid taxa; it is a result of crowding of the toothrow such that as the teeth erupt, the corners of the teeth overlap and wear into one another. State 0 occurs when the teeth abut one another evenly so that the anterior corners are not worn away.
 23. *Metacone: (1) lower than paracone or (0) similar in height to paracone.* This can only be coded in unworn teeth or teeth with little enough wear to infer the original height of the paracone and the metacone. In some taxa, these cusps are symmetrical and similar in labial aspect (state 0); in others, the paracone is significantly higher than the metacone (state 1).
 24. *Metacone (1) small or (0) large in M³.* A small metacone is one reduced to a size smaller than that of the conules. The metacone is large if it is roughly equal in size to the paracone or larger.

25. M^1 and M^2 second metaconule: (0) absent, (1) small, or (2) large. Ordered in semi-ordered and ordered analyses. The metaconule is doubled in some apodontids, primarily in allomyines. This feature has appeared at least one other time in rodents, in some *Reithroparamys* species. The second metaconule appears labial to the first metaconule, on the crest that joins the metaconule to the metacone. It is coded as small if it is distinctly smaller than the first, lingual metaconule. It is large if roughly equal in size to the first metaconule. This character appears in some species that do not have a second metaconule in P^4 (character 26).
26. P^4 second metaconule: (0) absent or (1) present. As with the previous character, this codes for the presence or absence of a second, labial metaconule. There does not appear to be a consistent phylogenetic signal in the size (large or small) of this metaconule; it is fairly consistently smaller than the lingual metaconule, and the size of the labial metaconule is variable between individuals of a single species.
27. P^4 metaloph: (0) not joining either the protoloph or protocone, or (1) joining protoloph or protocone. The metaloph, formed by the crests connecting the protocone, metaconule, and metacone, can either terminate by joining the protoloph or the protocone (1), or simply end in the central valley of the tooth without joining the protocone or protoloph. There is no consistency within a species in whether it joins the protocone directly or the protoloph between the protoconule and the protocone, but within a given species, the metaloph either does or does not connect to the protocone or protoloph.
28. P^4 protoloph connecting to protocone with (0) labiolingually or (1) diagonally oriented crest. The crest between the protocone and the protoconule can be directed either directly labiolingually and parallel to the crest from the protoconule to the paracone (state 0) or anterolabially from the protocone to the protoconule, forming an obtuse angle with the crest from the protoconule to the paracone (state 1).
29. Protoconule: (0) with no anterior crest or one anterior crest, (1) with two anterior crests on M^1 , or (2) with two anterior crests on M^1 and M^2 . Ordered in fully ordered analyses. The protoconule can have either a single crest or a pair of crests, associated with more of a square shape to the conule. If the protoconule has no crests, then it is coded as state 0, as this state is never associated with the change to the square conule.
30. Anterolingual fossette: (0) bounded on posterior end by central crest of protocone or (1) curving posterolingual in front of protocone. The anterolingual fossette is either terminated by the connection of the protoloph to the protocone (state 0) or continues lingual to the conules and labial to the protocone (state 1). This character could also be described as the presence or absence of the protoloph connection to the protocone.
31. M^1 and M^2 lingual metaconule with (0) one or (1) two posterior crests. This character is very similar in coding to character 29, but with the posteriorly directed crests of the metaconule instead of the anteriorly directed crests of the protoconule. The two characteristics vary completely independently; many taxa that have two crests on the protoconule have only one on the metaconule, and vice versa.
32. M^1 or M^2 protoconule and lingual metaconule: (0) both round, (1) metaconule elongate with round protoconule, or (2) both elongate. Ordered in fully ordered analyses. The conules in apodontids are either round or conical, or are lengthened anteroposteriorly, more than twice as long (anteroposteriorly) as they are wide (transversely). Although there are some taxa with an elongate metaconule and a round protoconule, elongate protoconules occur only on those taxa that have elongate metaconules. The lingual metaconule is used, as the labial metaconule is variably present, and is invariably round when small and has the same shape as the lingual metaconule when large.
33. M^3 metaconule: (1) anteroposteriorly elongated or (0) not elongated. The elongation of the M^3 metaconule occurs in some cases independently of the metaconules on M^1 and M^2 .
34. Anterolabial crest of lingual metaconule: (1) connected to or (0) disconnected from metacone on molars. The metaloph is sometimes discontinuous with the metacone between the metacone and the metaconule. The various gaps in the metaloph and protoloph do not covary.
35. Protoconule on molars: (0) minute or absent, (1) small, indistinct, or (2) distinct. Ordered in semi-ordered and ordered analyses. State 0 codes for a protoconule that is either absent or indistinguishable on the protoloph. State 1 occurs when the protoconule is very small, consisting of a small round cusp. The protoconule in state 1 is much smaller than the three main cusps (paracone, metacone, and protocone). State 2 indicates that the protoconule is large, and more than half the size of the paracone or metacone, and is clearly distinct from the rest of the protoloph.
36. Protoconule: (0) separated from or (1) joined to anterior cingulum on molars. The anterior crest of the protoconule either ends before reaching the

anterior cingulum (state 0) or is continuous with the anterior cingulum.

37. *Lingual part of central valley*: (0) joined to labial part, (1) isolated by central union of metaloph and protoloph, or (2) obliterated by union of protoloph and metaloph. Ordered in semi-ordered and ordered analyses. The central transverse valley of the upper cheek teeth is primitively continuous, at least to a point lingual to the conules (state 0), at which point it may or may not be closed by the union of the metaloph and protoloph. State 1 occurs when the protoloph and metaloph are joined a second time, labial to the conules, separating a labial and a lingual portion of the central transverse valley. State 2 occurs when the metaloph and protoloph are joined along essentially their entire length, so that the central transverse valley is lost entirely.
38. *Labial margin of protoconule on P⁴*: (1) joined to anterostyle, making protoconule extremely long anteroposteriorly, or (0) not joined to anterostyle. State 1 occurs when the anterior crest of the protoconule from the labial side is continuous with the posterior crest from the anterostyle. If these two crests are not continuous, state 0 is coded.
39. *Hypocone*: (3) similar in size to protocone, (2) strong, (1) weak, or (0) absent in posterolingual corner of posterior cingulum on M¹ and 2. Ordered in semi-ordered and ordered analyses. The presence of a hypocone is highly variable among taxa of mammals, and of rodents in particular. It can be formed in several ways, two of the most common being by a posterolingual shift of the metaconule or by the formation of an entirely new cusp on the posterior cingulum. In most apodontids, the hypocone appears to be formed in the latter manner, as a distinct metaconule is present in almost all forms with a hypocone. In some taxa, the metaconule is shifted posterolingually; this is not considered a hypocone for the purposes of this analysis, as it is not homologous to the feature described here. State 3 occurs when the hypocone and the protocone are essentially the same size. In state 2, the hypocone is a distinct cusp on the posterior cingulum, similar in size to the conules, but smaller than the protocone. State 1 has a very small hypocone, which is distinct as a cusp, but which is much smaller than the conules. For state 0, there is no indication of a hypocone on the posterior cingulum, and no thickening or elevation of a cusp in the posterolingual corner of the tooth, although there may still be a right-angle bend in the cingulum at this position.

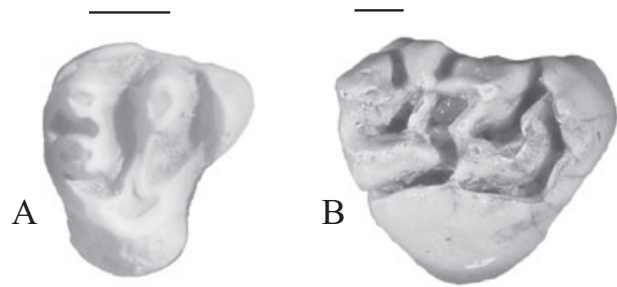


Figure 10. Apodontid P⁴s showing anteroposterior widening of the protocone. A, *Prosciurus* left P⁴ with unexpanded protocone. B, indeterminate mylagaulid right P⁴, with expanded protocone.

40. *Hypocone*: (1) with or (0) without very short lingual spur. This character codes for the presence or absence of a shallow-sloping cingulum or spur extending lingually a short distance from the hypocone, on the posterolingual face of the protocone. This character is coded as a question mark if the hypocone is absent.
41. *Hypocone*: (1) reduced in M³ relative to other molars, or (0) not reduced in M³. Coding of this character is only possible in the taxa that possess a hypocone. State 1 is coded if the hypocone of M³ would be coded as a different, smaller character state for character 39. State 0 is coded for taxa that have equivalently sized hypocones on all molars.
42. *Enamel*: (1) thickened on lingual surface of protocone or (0) same thickness as anterior enamel on upper molars. This character can only be coded for taxa for which worn teeth are available, and which expose the dentine on the occlusal surface. State 1 is coded for those taxa in which the enamel on the lingual surface of the protocone is at least 50% thicker than the enamel on the anterior surface. If the enamel is less than 50% thicker on the lingual surface of the protocone, state 0 is coded.
43. *Protocone of P⁴*: (1) expanded anteroposteriorly or (0) shorter anteroposteriorly. This character codes whether or not the protocone cusp is lengthened anteroposteriorly (Fig. 10). This is apparent when the lingual surface of the tooth becomes elongated into a half oval, rather than being essentially a semicircle centred at or just labial to the protocone. State 1 occurs in taxa for which the radius of curvature of the lingual outline of the tooth is much larger, i.e. greater than or equal to half the transverse width of the tooth, with the curve centred labial to the conules. State 0 occurs when the radius of curvature of the tooth is less than half the width of the tooth, and the protocone is at or very close to the centre of the curve.

44. *Protocone of M^{1-3} : (1) with or (0) without anterolingual spur.* This character codes for the presence or absence of a short cingulum or spur on the anterior margin of the protocone, leaving a groove just posterior to the spur. This character is very similar in appearance to character 40, but varies independently; taxa without an anterolingual spur sometimes have the lingual extension of the hypocone, and vice versa.
45. *Anterior crest of protocone on P^4 : (0) joining anteroloph, or (1) not joining anteroloph.* The anterior cingulum from the protocone in P^4 can either be continuous with the lingual cingulum of the anteroloph (state 0) or pass just anterior to the lingual cingulum of the anteroloph, ending lingual to the anterostyle (state 1).
46. *Protocone of upper cheek teeth: (1) with or (0) without anterolabial spur.* The anterolabial spur is a short crest extending from the protocone between the anterior cingulum and the protoloph, terminating without connection to other crests or cusps.
47. *Lingual surface of protocone on upper molars: (0) smooth or (1) rugose.* The lingual surface of the protocone is coded as rugose (state 1) only when the enamel has large, distinct vertical ridges. The enamel is often faintly crenulate, but rugosity must be clearly distinguishable from taphonomic wear, with deep ridges and grooves.
48. *Posterolingual surface of protocone on P^4 : (0) sloping more strongly transversely or (1) more vertical.* The lingual surface of the protocone can be either straight and vertical (state 1) or sloping ventrolabially (state 0) from the base to the top of the crown.
49. *Cheek teeth: (1) becoming more transversely compressed from M^1 to M^3 , or (0) maintaining a fairly constant relative width from M^1 to M^3 .* More transversely compressed cheek teeth have a higher ratio of anteroposterior length to transverse width; this is not simply a decrease in the transverse width dimension of the teeth, but is rather a change in the proportions of the tooth outline. This character codes for a change in the way these proportions vary through the toothrow. State 1 indicates that, from M^1 to M^3 in the toothrow, the proportions of the teeth do not remain constant, but rather the anteroposterior length to transverse width ratio increases significantly posteriorly. For state 0, the ratio is essentially the same for all three molars, although the M^3 is occasionally slightly longer than the anterior molars.
50. *P^4 : (0) similar in size to M^1 , (1) slightly larger (perhaps 1.5 times the size of M^1), or (2) much larger (two or more times the size of M^1).* Ordered in semi-ordered and ordered analyses. There are three distinct states in the enlargement of the P^4 in aplodontids. Rodents primitively have a fourth premolar, which is similar in size to the M^1 (state 0), although it often has at least a small anterocone on the labial end of the anterior cingulum. Many aplodontids have an enlarged premolar, 1.25–1.5 times the size of the first molar (state 1), mainly through the enlargement of the anterocone and the addition of an anterostyle, but also through an increase in the size of the tooth as a whole, both anteroposteriorly and, to a slighter degree, transversely. In some mylagaulids this character is extreme, with a premolar that is essentially the major chewing surface, and the total area of the molars adding up to only slightly more or, in some cases, less than that of the premolar alone (state 2).
51. *P^4 crown: (0) rectangular, (1) triangular, or (2) oval in outline.* Ordered in fully ordered analyses. This character codes the shape of the overall outline of the base of the crown of P^4 . The state is determined by which of the three shapes best approximates the cross section of the crown.
52. *(1) Right-angle bend or (0) smooth curve in the occlusal outline of P^4 present lingual to anterocone.* A right-angle bend in the occlusal outline occurs when the lingual crest of the anterocone extends directly posteriorly, meeting a labially directed anterior crest from the protocone at a ninety degree angle (state 1). Otherwise, the intersection of these two crests is more smoothly curved or is even simply a straight line (state 0).
53. *P^4 posterolabial crest of anterocone meeting anterolabial crest of paracone: (0) exactly or (1) curving just labial and posterior to it, creating a small groove down the anterior edge of the labial face of the paracone.* The posterolabial crest of the anterocone in some taxa does not form a completely continuous ectoloph, but passes just labial to the anterolabial crest from the paracone, and curves posterolingually beyond it. This is not the same as the cingulum present in some taxa labial to the paracone; the feature described in character 53 forms a vertical groove down the posterior face of the parastyle, not a horizontal groove parallel to the occlusal surface, as in the labial cingulum of the paracone.
54. *P^4 anteroloph: (1) with small or (2) with large anterolingual cusp, subequal in size to anterocone, or (0) without anterolingual cusp.* Ordered in semi-ordered and ordered analyses. This character codes for the presence of an anterostyle, or second cusp, on the anteroloph lingual to the anterocone. In state 1, it is present, but is less than half the size of the anterocone. In state 2,

- the anterostyle is present and is essentially the same size as the anterocone.
55. *P⁴ anteroloph*: (1) thin or (0) broad. This character codes the anteroposterior breadth of the anteroloph. A broad anteroloph (state 0) has a thick base and forms a large part of the anteroposterior length of P⁴. A thin anteroloph is blade-like and thin all the way to the base. The anteroloph itself is not, in this case, a large part of the anteroposterior length of the P⁴.
 56. *Anterior cingulum*: (0) absent or (1) complete from protocone to anterocone on P⁴. The anterior cingulum is present and complete from the protocone to the anterocone (state 1) if it is raised significantly, and is recognizably above the anterior basin of P⁴. If absent (state 0), the anterior basin of P⁴ is open anterolingually.
 57. *P⁴ with (1) large or (0) small anterocone*. The anterocone is large (state 1) if it is similar in size to the protocone, paracone, and metacone. It is considered small (state 0) if it is significantly smaller than the protocone, paracone, and metacone.
 58. *Occlusal surface of anterocone on P⁴*: (0) nearly horizontal in mature stages of wear, (1) with slight inclination posteriorly, or (2) with pronounced inclination posteriorly. Ordered in fully ordered analyses. This character codes for how the occlusion of the anterior loph of P⁴ with the anterior end of P₄ wears the tooth. The wear surface is considered strongly posteriorly inclined (state 2) when inclined at an angle of more than 30°. State 1 is generally characterized by an inclination between 10° and 30°. State 0 occurs when this wear surface is horizontal, i.e. parallel to the occlusal plane.
 59. *Anterostyle of P⁴*: (1) with or (0) without interior process. The anterostyle of P⁴ in some taxa has a posteriorly directed crest extending into the anterior basin. This crest may or may not connect to other crests or cusps in the basin.
 60. *Anterior dentine tract*: (0) absent or (1) present in angle of anterolingual inflection of P⁴. This character codes for the presence or absence of a gap in the deposition of enamel lingual to the anteroloph and anterior to the protocone, in the bend on the anterolingual side of the tooth. This is a discontinuity in the enamel band that otherwise surrounds the tooth.
 61. *Anterolingual inflection*: (2) absent or (1) present, but disappearing with moderate wear, or (0) persistent with wear on P⁴. Ordered in semi-ordered and ordered analyses. This character codes for the presence or absence of a concave inflection in the anterolingual quadrant of the occlusal outline of P⁴. When present, it may be either persistent throughout wear (state 0), or it may slope out towards the base of the crown, and be lost with wear.
 62. *Anterolingual fossette*: (1) anteroposteriorly elongated, more than three times as long as wide on P⁴, or (0) small and circular or oval. This character describes the shape of the basin or fossette formed between the protocone, paracone, and anterocone. This basin can be short and rounded (state 0) or extremely elongated (state 1).
 63. *Anterolabial fossette of P⁴*: (1) expanded lingually or (0) not expanded lingually. The fossette formed by the anterocone, protocone, and paracone can either be roughly round or anteroposteriorly elongate, or it can become more lingually elongate with the labial extension of the parastyle, and the broadening of the basin between the anterior and posterior crests of the parastyle.
 64. *Posterolingual fossette of P⁴*: (1) expanded anteriorly or (0) shorter anteroposteriorly. The posterolingual fossette in some taxa extends anteriorly and labially towards the centre of the tooth (state 1). In most, however, it ends more posteriorly at the lingual crest of the metaloph. This character does not code for the presence or absence of a crest connecting the metaloph to the protoloph; it is possible for the posterolingual fossette to extend anteriorly in a taxon that retains a connection between the protoloph and the metaloph.
 65. *Posterolabial fossette of P⁴*: (0) a single convex fossette, (1) C-shaped or wrench-shaped, divided posteriorly by an anterior crest from the posterior cingulum, or (2) dividing into two fossettes early in wear, separated by anteroposterior crest from posterior cingulum to anterior crest of metaconule (metaloph). Ordered in fully ordered analyses. This character is described in terms of fossettes, as the only occurrences of states 1 and 2 are in mylagaulids. The crest that gives rise to the shape of the posterolabial fossette is directed anteriorly from the posterior cingulum, just lingual to the metacone. When this crest is present, but unconnected to the metaloph, state 1 occurs. When the crest is present and connects to the metaloph just labial to the metaconule, state 2 occurs.
 66. *Posterolingual fossette on P⁴ aligned*: (0) more nearly anteroposteriorly or (1) more obliquely. The basin between the metaconule, protocone, and metaloph forms the posterolingual fossette; this basin can be oriented directly anteroposteriorly on P⁴ (state 0), or it can be turned anterolabially by the posterolingual slant of the metaconule (state 1).
 67. *Posterolabial fossette of P⁴*: (1) small and round/oval or (0) large and elongate. State 1 indicates a

- fossette or basin that is round or ovate, but that is less than twice as long as it is wide, whereas state 0 indicates an elongated fossette, i.e. long and oval or almost linear, and is more than twice as long as it is wide. This character is independent of both characters 70 and 71, which may seem similar. This fossette is sometimes elongated independently of the others, and the encroachment into the central basin is not necessarily associated with the elongation.
68. *Posterolabial fossette of P⁴*: (0) approximately as deep as anterolingual fossette, (1) much shallower than anterolingual fossette, or (2) much deeper than anterolingual fossette. The differences in the depth of fossettes generally do not arise in brachydont taxa; however, in mesodont and early hypsodont aplodontids, the posterolabial fossette varies significantly in its depth and persistence with wear. The anterolingual fossette is used as a baseline for comparison with the knowledge that if it undergoes changes in depth independently, it may appear that a change has occurred in the depth of the posterolabial fossette. Unfortunately, it is difficult to find an absolute standard for the depth of a basin in hypsodont teeth, so the character is coded in a way that is, admittedly, flawed; it would be difficult to find a better way without sectioning teeth of all taxa studied, and even then, with the differences in crown height and overall size, all standards are, in the end, relative.
69. *P⁴ with posterolabial fossette*: (1) open posterolabially in early wear or (0) closed throughout wear. In some taxa, a gap is present in the posterior cingulum, labial to the metaconule and lingual to the posterior crest of the metacone. This leaves the posterolabial fossette open near the top of the crown (state 1). Otherwise, the posterior cingulum is complete and continuous with the ectoloph on P⁴, in which case the posterolabial fossette is closed throughout wear (state 0). This character is not coded for taxa lacking specimens with relatively early wear stages.
70. *P⁴ with two labial fossettes*: (1) elongated, almost meeting near the centre of the tooth, or (0) short, well separated by the central valley. The labial fossettes closely approach one another when the labial end of the central transverse valley is extremely narrowed. In this case, they are elongated towards the centre of the tooth. This elongation is independent of character 71; it is not related to the overall elongation of the fossettes.
71. *Fossettes on P⁴*: (1) long or (0) short. The fossettes on P⁴ can be short, i.e. less than three times as long as they are wide (state 0), or long, on average much more than three times as long as they are wide (state 1). The tooth can be elongated and lack elongate fossettes, which is sometimes characterized by a series of small round fossettes.
72. *Anterolabial fossette on P⁴*: (1) branching anteriorly or (0) unbranched. The branches are formed between the labial end of the anteroloph, the protoconule, the protoloph, and the paracone. The anterior branches result from a crest from the anterocone extending posteriorly into this basin, thereby dividing the anterior portion of the basin. This crest is never as high as the protoloph and metaloph, or the major crests of the tooth, so that early in wear, the basin is never completely divided. However, in many mylagaulids, the crest joins either the protoloph or the protoconule with wear, dividing the anterior part of the basin.
73. *Branches of anterolabial fossette of P⁴*: (0) remain joined until very late stages of wear, or (1) labial branch separates first, (2) lingual branch separates first, or (3) both branches separate with wear. This character is only coded for specimens that have a branched anterolabial fossette (character 72). There are some specimens where the position at which the posterior crest of the anterocone joins the protoloph or protoconule is variable, leading to the presence of both states 1 and 2 in a single population. Many other taxa, however, do not vary, and are completely consistent with one character state or another. Taxa in which both character states are present are composite coded: 1/2.
74. *Overall size*: (1) large or (0) small. Although size, as a continuous character, is often a dubious homology for phylogenetic reconstruction, in aplodontids it appears to fall into two very discrete categories. Those taxa with skulls less than 5 cm in length (or with tooth dimensions indicative of such a size) are small (state 0), and those with skulls greater than 5 cm in length (or with tooth dimensions indicative of such a size) are large (state 1). There are simply two size groups present in aplodontids, and the significant gap between them suggests that size may actually be meaningful within this taxon, perhaps as a result of the strong tie between body size on this broad scale and ecological role. A large difference in size requires a significant difference in energetics, and hence would be unlikely to be highly variable in the history of a lineage.
75. *Cheek teeth*: (0) bunodont or (1) lophodont. Although this character is likely to be related to a number of other characters in the analysis, lophodonty is achieved in the same way in all lophodont aplodontids, by the elongation of many of the same cusps and crests. As all of those changes are not individually coded in this analy-

sis, it does not seem redundant to code lophodonty as one of the characters included in the analysis.

76. *Cheek teeth: (3) hypselodont; (2) hypsodont, with fused, drastically reduced roots and closed pulp cavity; (1) rooted, but hypsodont (taller than wide); or (0) rooted and brachydont.* Ordered in semi-ordered and ordered analyses. The crown height of aplodontid teeth changes greatly through their evolutionary history. Whereas most early forms retain roots and are low crowned (state 0), crown height increases dramatically in some lineages around the Oligo–Miocene boundary. Taxa are considered hypsodont when the crown height from the enamel–dentine junction to the apex of the highest cusps exceeds the transverse width. State 1 indicates the presence of large, distinct roots, similar to those present in brachydont taxa. State 2 indicates that the roots are highly reduced, short, thick, and stubby, and are often fused. The pulp cavity closes in mid-to-late wear in these taxa and roots are still present at the base of the tooth, so that the teeth are not truly ever-growing. One major difference between states 1 and 2 is that the roots are the major anchor for the tooth in taxa with state 1, whereas the roots are too reduced to be a major anchor in taxa with state 2, and the base of the crown extends well into the alveolus and serves as the main anchoring mechanism. State 3 occurs in very few aplodontids, and is characterized by ever-growing cheek teeth. The roots never form, and the pulp cavity remains open throughout life.
77. *P⁴–M² with (1) dorsolaterally curved or (0) straight crowns.* In some hypsodont aplodontids, the upper cheek teeth, especially the premolar teeth, have curved crowns, with the roots extending laterally into the orbit. This characteristic is not correlated with the degree of hypsodonty, or with other characters used here; it is one of several ways of accommodating tall crowns in the upper teeth.
78. *Roots of M¹ and 2: (0) two or three, or (1) one.* The upper molars generally have three roots, although some taxa have the two labial roots fused into a single root: both these morphologies are coded as state 0. It may be possible to separate the two, but it would result in a number of taxa being equivocally coded, as they are known from incomplete specimens. Unless the preservation of isolated molars for a taxon is exceptional, the two states can be quite difficult to distinguish. State 1, on the other hand, is very easy to recognize, because the roots of the molars are completely fused. Partial fusion is not apparent in any of the taxa known: the fusion of the labial and lingual roots is not as gradual a process as is the fusion of the labial roots, it seems. Thus, these two states are fairly easily distinguished, even with the fragmentary preservation common in fossil aplodontid species.
79. *Erupting P₄ driving out (0) no molars, (1) first molar, (2) first and second molars, or (3) all molars in old individuals.* Ordered in semi-ordered and ordered analyses. The P₄ of mylagaulids is enlarged and much higher crowned relative to the molars. It is also longer antero-posteriorly at the base of the crown than at the top of the crown, so that as it erupts, it squeezes out the molars from M₁, posteriorly. This character codes for the number of molars pushed out by the premolar through the life of an individual. This is most apparent in specimens in mid-to-late wear, as the maximum premolar length is erupted by mid-wear. This is also apparent when the roots of the teeth are exposed, as any molars with roots ending directly above (in the lower jaw), or below (in the upper jaw), the premolar are eventually driven out by the eruption of the premolar. Finally, isolated molars can give evidence of this feature, as the erupting premolar wears the base of the roots of the molar as it is pushed out, although this evidence has not been solely relied on to determine the character state for any of the included taxa.
80. *Bases of anterolingual (central) and posterolingual inflections on P₄ on (0) same or (1) different levels.* This character is coded in a similar manner to character 68, and with the same caveats about the relativity involved in determining the character state.
81. *Lower molars: (1) with or (0) without significant vertical continuation of anterolingual inflection downwards, beneath closure of anterior inflection, or (2) inflection continues to base of enamel crown.* Ordered in semi-ordered and ordered analyses. This character refers to a groove down the lingual face of the metastylid crest, between the metaconid and the mesostylid. The groove may be completely absent (state 0), may continue partway down the face of the tooth (state 1), or may continue all the way to the base of the crown, shaping the base of the enamel at the point where it joins to the roots of the tooth (state 2).
82. *Layer of cementum overlapping enamel of cheek teeth: (0) absent, (1) present and thin, or (2) present and thick.* Ordered in fully ordered analyses. Cementum is present in some taxa surrounding the occlusal outline of the premolar, in particular. This layer can be thick, subequal to

- the thickness of the enamel band (state 2), or thin, much less than the thickness of the enamel. The cementum layer is particularly apparent in later wear: in those taxa for which inadequate specimens are available to judge whether or not this layer might be present, the character is not coded.
83. *P⁴ root shape*: (0) three discrete roots, two labial and one lingual; (1) three roots, but posterior pair fusing, posterolabial root evident on labial side of posterolingual root; (2) two roots, the posterior one larger and wider than the anterior one; (3) two discrete roots aligned anteroposteriorly, roughly equal in size; (4) one root, forming very late in wear; or (5) no roots, hypselodont. Ordered in semi-ordered and ordered analyses. The roots of the *P⁴* differ greatly across aplodontid lineages. State 0 indicates the presence of the primitive root configuration, with three roots separate all the way to the crown. In state 1, the two posterior roots are fused for most of their length, but the tips are separate, with the tip of the posterolabial root just ventral to the tip of the lingual root on the labial side of the tooth root. In state 2, the two posterior roots are completely fused, and no second root tip is apparent on the labial side of the posterior root, but the posterior root is still roughly 50% larger than the anterior root. In state 3 there are only two roots, and the anterior and posterior roots are essentially equal in size. In state 4, there is only a single root, which is apparent in specimens in mid-to-late wear. For state 5, the roots are never formed, so it is not completely analogous to any of the other character states.
84. *P³*: (1) curving anterolingually or (0) entirely convex. The occlusal outline of *P³* can either be completely convex and ovate or round (state 0), or be crescentic, with the concave side directed posterolingually (state 1). This character, like all the other characters of *P³* except character 90, is not coded for those taxa that lack *P³*.
85. *P³*: (3) strongly compressed transversely, (2) weakly compressed transversely, (1) with flattened labial surface, or (0) roughly conical. Ordered in fully ordered analyses. The occlusal outline of *P³* may be round (state 0), may have a single flat surface directed labially (state 1), or may be transversely compressed. There are two states for transversely compressed or ovate *P³*. If only anteroposteriorly elongate, it is coded as state 2; if very thin and blade-like, coming to a point at the anterior and posterior ends, it is coded as state 3.
86. *P³*: (0) expanded or (1) not expanded at base. This character codes for the presence or absence of a bulbous broadening at the base of the *P³* crown.
87. *Prominent grooves*: (1) present or (0) absent on posterior surface of *P³*. The grooves addressed by this character are deep, and occur as one each on the labial and lingual sides of the posterior side of the *P³*.
88. *Long axis of P³ oriented*: (1) anteroposteriorly, (0) posterolabially, or (2) posterolingually. This character cannot be coded in taxa with a round occlusal outline; in all others, this codes the orientation of the long axis of the oval occlusal outline.
89. *P³*: (1) with or (0) without faint cingulum on posterior edge. The *P³* may have a cingulum or ridge at the base of the posterior face of the tooth, curving around the back of the tooth, and parallel to the occlusal surface.
90. *P³*: (0) retained, or (1) lost or pushed out by eruption of *P⁴*. This character codes for the presence or absence of the *P³* in adult specimens. In mylagaulids, it is sometimes present in juveniles, but is pushed out as the premolar erupts, or is simply not replaced with a permanent tooth.
91. *Crown height of P³*: (0) low or (1) high. The crown height of the *P³* is somewhat independent of the crown height of the other teeth; in a number of hypselodont taxa that retain *P³*, the *P³* is much lower crowned than the other teeth, and wears very little because it does not occlude strongly with *P₄*, and most of the chewing is performed on the larger cheek teeth posterior to *P³*.
92. *M^{1 and 2}*: (0) triangular, (1) rectangular, or (2) oval in occlusal outline. Ordered in fully ordered analyses. This character describes the occlusal shape of the molars. This varies independently of the occlusal outline of the premolars (character 51) because there is no anterocone in the molars, which is largely responsible for the difference between rectangular and triangular crowns in the premolars. In the molars, the shape is more a result of the shape of the anterior and posterior cingula on either side of the protocone. As with character 51, this shape is not an exact description of the occlusal outline, but is simply a 'best-fit' shape.
93. *Central transverse valley of upper cheek teeth*: (0) broad and U-shaped or (1) narrow and V-shaped. The central transverse valley is shaped primarily by the shape of the paracone and the metacone, and of the protoloph and metaloph. A narrow, V-shaped central valley (state 1) has a distinct groove or crease down the centre, where the posterior face of the paracone and the anterior face of the metacone meet at the base of the valley. The two cusps tightly constrain the valley

- in this case, and the valley is generally taller than it is wide. A broad, U-shaped valley (state 0) is rounded and lacks a crease or groove. The boundaries of the valley are generally not as strongly defined, and the width is similar to or greater than the depth of the valley.
94. (2) *Anterolingual fossette* or (1) *anterolabial fossette lost earlier with wear in M^{1-3} , or (0) both equally deep*. Ordered in fully ordered analyses. This and the following two characters code for the differences in the depth of the basins of the molars. This character discriminates between the depth of the fossettes labial and lingual to the protoconule. In those taxa that do not lose the fossettes or basins with wear, or for which late-wear specimens were not available, this character is coded using the relative depth of the basins.
95. *Posterolabial fossette of M^1 : (0) more or (1) less persistent with wear*. The posterolabial fossette is the basin labial to the metaconule. It is coded as more persistent (state 0) if still present in late-wear specimens, and as less persistent if absent in late wear or if absent earlier than the other three primary fossettes on the molar (state 1).
96. *Posterolingual fossette: (1) persistent long after others have worn away or (0) similar in persistence to others in $M^{1 \text{ and } 2}$* . The posterolingual fossette is the basin lingual to the metaconule. State 1 is coded for those taxa in which the posterolingual fossette is present and well defined in specimens that have lost the other three primary fossettes, as well as in the case of taxa in which the posterolingual fossette is perceptibly deeper than the other three fossettes. State 0 is coded for those taxa in which the posterolingual fossette is similar in depth to the other three basins, or for which it is not present alone after the other three fossettes have worn away.
97. *Anterior dentine tract: (1) present or (0) absent on $M^{1 \text{ and } 2}$ at mid-crown height*. The anterior dentine tract is a gap in the enamel band along the anterior face of the molars, which exposes the dentine in a band between the paracone and the protocone. This character and character 98 are only coded for taxa in which mid-wear specimens are available, or for which the entire crown can be examined.
98. *Posterior dentine tract: (1) present or (0) absent on $M^{1 \text{ and } 2}$ at mid-crown height*. The posterior dentine tract is a gap in the enamel band along the posterior face of the molars, which exposes the dentine in a band between the metacone and the protocone.
99. *Sides of posterior dentinal tract of $M^{1 \text{ and } 2}$: (1) less vertical or (0) more vertical*. The sides of the dentine tract are considered essentially vertical (state 0) if the dentine tract on the posterior side of the tooth is flanked by parallel or nearly parallel anterior and posterior contacts with the enamel. This would result in the width of the gap in the enamel band remaining roughly constant throughout wear. They are less vertical (state 1) if the enamel–dentine contacts anterior and posterior to the dentine tract diverge from the top of the crown towards the base, with the result that the gap in the enamel band becomes notably wider with wear. This character is not coded for any taxa that lack a posterior dentine tract.
100. *Anterior cingulum: (0) well developed or (1) poorly developed on M^{1-3}* . The anterior cingulum is well developed (state 0) if it is distinctly higher than the depth of the basins, and closes the anterolingual and anterolabial basins. In this case, it is generally at least half the height of the protoloph and metaloph, or higher. It is poorly developed (state 1) if it does not close the anterior basins, or if it is much lower than the protoloph and metaloph.
101. *Posterior cingulum: (0) much weaker than the anterior one or (1) equal in strength to anterior cingulum on M^{1-3}* . The strength of the cingulum is its height above the central basin of the tooth. The posterior cingulum is coded as much weaker if it is notably lower relative to the central basin than is the anterior one.
102. *Anteroposterior length of M^3 : (0) similar to or greater than $M^{1 \text{ and } 2}$ or (1) smaller*. This character codes for the reduction of the third molar; generally those taxa that have M^3 reduced also have M^2 smaller than M^1 .
103. *Transverse width of central fossette on M^3 : (1) great or (0) small*. The central fossette is the basin between the protoloph and the metaloph. The width is coded as great (state 1) if it is at least half the transverse width of the tooth, and small (state 0) if it is less than half the transverse width of the tooth.
104. *Posterolabial and posterolingual inflections of M^3 : (1) closing to form fossettes only in the late stage of wear or (0) closed early in wear*. The posterior cingulum on some aplodontids is much lower on the M^3 than the other molars, leaving the posterior inflections open until very late in wear (state 1). In most cases, however, the M^3 posterior cingulum is the same as the cingulum on the other molars (state 0).
105. *Metaconid of M_{1-3} : (1) compressed labiolingually or (0) not compressed labiolingually*. The metaconid may be either a flattened, blade-like cusp,

- compressed labiolingually (state 1), or a conical or triangular cusp (state 0), not transversely compressed.
106. *Metaconid*: (0) short, crest-like, or (1) tall, distinct cusp. The metaconid may be reduced to a cingulum around the anterolingual margin of the tooth (state 1), or it may remain a large cusp of similar magnitude to the protoconid (state 0).
107. *Metaconid of M₁*: (0) at anterolingual corner, making right or acute angle, or (1) shifted labially, making obtuse angle between anterior cingulum, metaconid, and mesostylid. The metaconid on M₁ may be shifted labially inwards, which changes the anterolabial corner of the tooth from a right-angle to a wider obtuse angle, when the positions of the protoconid and entoconid remain relatively constant.
108. *Metalophulid II of M₁₋₂*: (0) absent, not connecting protoconid and metaconid, (1) present as crest on posterolabial face of metaconid, unconnected to protoconid, or (2) present and connecting to protoconid. Ordered in fully ordered analyses. The metalophulid II is a crest running down the posterointernal faces of the protoconid and metaconid, and connecting posterior to the anterior cingulum in the central basin of the lower molars. It may be a continuous crest, connecting the two cusps (state 2), a discontinuous crest, present only on the internal face of the metaconid without a connection to the protoconid (state 1), or completely absent on both cusps (state 0).
109. *Interior space of trigonid*: (1) filled by large, closely set protoconid, metaconid, and mesostylid crest, or (0) trigonid fairly open. State 1 codes for a tooth in which the protoconid, metaconid, and mesostylid are all large and inflated, and fill in the centre of the trigonid. This leaves no flat, dorsally oriented surface at the bottom of the basin. State 0 codes for a trigonid basin that is less dominated by the cusps, and that contains a significant flat surface in the bottom of the basin.
110. *P₄ protoconid and metaconid divided by* (1) steep-sided, deep basin or by (0) shallow, low-sloping basin. The protoconid and the metaconid may be close set, forming a very narrow basin or fossette, with the bases of the two cusps meeting at the bottom of the basin (state 1), or they may be farther apart, leaving a shallower, broader basin, with a smooth curve from one side to the other (state 0).
111. *Sharp styles*: (0) absent or (1) present extending down anterior faces of protoconid and metaconid on P₄. Narrow, blade-like crests may be present or absent on the anterior faces of the metaconid and protoconid of the premolars. These crests, when present, are a substantial anterior extension of these cusps, often as long as or longer than the rest of the cusp.
112. *M₁₋₂*: (1) with or (0) without interior crest of mesostylid connecting to posterior end of anteroconid crest or centre of metalophulid II. This character codes for the presence or absence of an anterolabially directed crest from the mesostylid, which connects to the crests in the trigonid basin. Depending on the presence or absence of the anteroconid crest and metalophulid II, this crest of the mesostylid may connect with either one; however, the character codes for a long anterolabial crest from the mesostylid.
113. *Metaconid*: (0) anterior to or (1) level with protoconid on lower molars. The metaconid and protoconid may be directly in line with one another on the labial and lingual sides of the trigonid basin (state 1), or the metaconid may be slightly more anterior than the protoconid.
114. *Mesostylid*: (0) straight or (1) angled/bent. The mesostylid may be directed straight labially across the tooth, or it may be angled or bent anteriorly. This is unrelated to character 113, which has to do with the anterior extent of the labial crest; the crest may be bent without extending far enough forwards to connect to the internal crests of the trigonid. Angled and bent are coded as the same character, as the place in the crest where it is bent varies, so angled crests are assumed to be, essentially, bent right at the lingual edge of the tooth.
115. *Re-entrant posterior to mesostylid*: (0) directed almost transversely across P₄ or (1) obliquely directed. This character codes the orientation of the re-entrant posterior to the mesostylid and anterior to the entoconid. The orientation of the re-entrant is shaped by the size, orientation, and relative position of both mesostylid and entoconid; it is not the same as character 118.
116. *Mesostylid on M₁ and 2*: (3) connecting only to mesoconid; (2) a large, distinct cusp with long crest into central fossettid; (1) small, significantly smaller than entoconid; or (0) tiny, hardly distinguishable, without crest extending into central basin. Ordered in semi-ordered and ordered analyses. The mesostylid is highly variable in the aplodontid lineage. At its largest, it extends all the way across the central basin to connect with the mesoconid (state 3). If it is slightly smaller and less labiolingually elongate, but still large and with a strong internal crest, state 2 is coded. State 1 indicates a small cusp, not of the same size as the other main cusps of the tooth, and of secondary prominence, much smaller than the entoconid. If

the mesostylid is either completely absent or reduced so much as to be hardly distinguishable as a cusp, it is coded as state 0.

117. *Mesostylid*: (1) *lingually prominent* or (0) *not protruding lingually on M₃*. This character codes for whether or not the mesostylid protrudes lingually beyond the entoconid and metaconid. It is coded as lingually prominent (state 1) if it is more lingually placed than both the metaconid and entoconid.
118. *Metastylid crest extending* (0) *posterolingual* or (1) *posteriad on molars*. The metastylid crest is the crest connecting the metaconid to the mesostylid, whether or not the mesostylid is a distinct crest. This character codes its orientation.
119. *P₄*: (0) *retains indication (outline) of mesostylid* or (1) *mesostylid not lingually prominent on P₄*. The lingual prominence of the mesostylid on M₃ (character 117) varies independently from the mesostylid on P₄. This character is coded in the same way as character 117.
120. *Mesostylid of molars*: (0) *more bulbous* or (1) *more compressed and blade-like*. The mesostylid of the molars may either be bulbous and conical (state 0) or be elliptical and more anteroposteriorly compressed into a rectangular or blade-like cusp (state 1).
121. *Posterolingual inflection (posterior to mesostylid) of molars*: (0) *extending labially to ectolophid*, (1) *cut off short by small crests or accessory cusps in central basin from mesostylid and/or entoconid*. The posterolingual inflection is the inflection posterior to the mesostylid and anterior to the entoconid. State 1 is generally coded for taxa that have this inflection closed by an accessory crest connecting the mesostylid and the entoconid; as the location of this crest varies, it is difficult to determine the exact homology of the connection. It must simply be assumed, and if it is incorrect, this should be revealed by the balance of evidence.
122. *Mesostylid crest of M₁ and 2*: (0) *with greatest anteroposterior thickness near lingual end*, (1) *near labial end*, (2) *near transverse midpoint*, or *with* (3) *relatively uniform thickness throughout*. The shape of the mesostylid is coded here; because it is generally labiolingually elongated to a greater or lesser degree, the shape is phrased in terms of the position of greatest anteroposterior thickness.
123. (0) *Single mesostylid on M₃*, (1) *two mesostylids on M₃*, (2) *more than two mesostylids on M₃*, (3) *more than two mesostylids on all lower molars*. Ordered in fully ordered analyses. The entoconid and primary mesostylid are distinct in that they are always the most anterior and posterior cusps, respectively, on the lingual margin of the tooth. This character codes for the addition of cusps between them, treated here as additional mesostylids. There are no cases where cusps have been added to the tooth posterior to the entoconid or anterior to the mesostylid (which would be a nonhomologous state yielding similar cusp counts), because the entoconid and metaconid remain among the largest cusps on the tooth. For all characters that refer to the shape of the mesostylid, the largest of these cusps is used to determine the character state.
124. *Posterolingual inflection (posterior to mesostylid)* (0) *narrow* or (1) *broad*. The re-entrant is narrow (state 0) if it is narrower than the mesostylid itself; it is broad (state 1) if it is wider than the mesostylid.
125. *Posterolingual inflection (posterior to mesostylid)*: (1) *broader on M₃* or (0) *similar on M₃ to other molars*. The re-entrant is coded as broader on M₃ (state 1) if it is noticeably and consistently broader than that of M₁ or M₂. Otherwise, it is coded as similar (state 0).
126. *Anterolingual fossettid*: (0) *present* or (1) *absent on P₄ early in wear*. The anterolingual fossettid is the enamel lake or basin formed between the metalophulid II, the metastylid crest, and the mesostylid. This character codes for whether it is present in early-wear specimens; even when present it is frequently lost in later wear.
127. *Crest on posterior margin of mesostylid partially closing posterolingual inflection to form fossettid*: (1) *present* or (0) *absent*. This codes for a crest on the lingual margin of the cheek teeth extending posteriorly from the mesostylid towards the entoconid, and at least partially closing the inflection between these two cusps.
128. *P₄ with anterolabial inflection*: (2) *closed by process from protoconid to form fossettid*; (1) *with posterolabial crest extending from protoconid, not connected to mesoconid or hypoconid*; or (0) *without posterolabial crest, inflection open*. Ordered in semi-ordered and ordered analyses. The anterolabial inflection is the one between the protoconid and the mesoconid. This character codes for the presence and length of a crest between the labial margins of the protoconid and the mesoconid. State 2 has a complete crest connecting the two cusps. State 1 is coded for taxa with a crest extending from the protoconid part-way across the re-entrant. State 0 is coded for those taxa with no crest at all extending across the labial margin of this basin.
129. *Facet on anterior face of protoconid of P₄ for occlusion with anterocone of P¹*: (1) *nearly horizontal with wear* or (0) *remaining semivertical*.

The wear facet from occlusion with the anterocone of P^4 forms on the anterior face of the protoconid of P_4 . This facet varies depending on how the two occlude: it is horizontal in those for which there is lots of sliding of the teeth against one another in the occlusal plane; in those taxa that chew with a motion more perpendicular to the occlusal plane, the facet is more vertical. This facet forms one of the most easily seen indicators of this difference in the plane of jaw motion.

130. *Labial border of trigonid of molars: (1) angular/sharp or (0) rounded in early wear, particularly on M_1 .* The labial border of the trigonid (also called the anterior moiety) of the molars may be relatively round (state 0), as it is in most aplodontid taxa, or it may be sharply angular, making an acute bend at the labial extremity of the protoconid (state 1). In this case, the anterior and posterior faces of the protoconid are quite flat.
131. *Minute cingulum present at base of protoconid: (1) present or (0) absent on molars.* This character codes for a tiny cingulum on the anterolabial face of the protoconid, just above the base of the crown. This cingulum is neither continuous with any of the other crests on the tooth nor is it connected to any of the cusps. It curves around the anterolabial surface of the tooth parallel to the occlusal surface, and is generally fairly short and tightly pressed against the posterolabial margin of the tooth anterior to it.
132. *Mesoconid on molars: (0) large, (1) small, or (2) reduced to a crest on ectolophid connecting protoconid, hypoconid, and entoconid.* Ordered in fully ordered analyses. The mesoconid is always smaller than the other major cusps on the teeth; this character codes its overall shape and size. It is coded as small (state 1) if it is of the size of a cuspule or accessory cusp, which is an order of magnitude smaller than the main cusps. It is coded as large (state 0) if it is larger than the cuspules and distinctly triangular or conical, generally from half to quarter of the size of the other major cusps on the tooth. State 2 is coded for the taxa that have reduced the size of the mesoconid relative to the crests connecting to it so that it cannot be distinguished from those crests. In this case, it can only be located by finding the junction of the crests leading out from it, and is not a distinct cusp at all.
133. *Crest on lower cheek teeth connecting labial margins of hypoconid and mesoconid, and closing the posterolabial fossettid: (0) absent; (1) present on molars alone, but weak; (2) present on molars alone, strong; or (3) present on premolars and molars.* Ordered in fully ordered analyses. The crest connecting the hypoconid and mesoconid appears relatively early in the aplodontid lineage, and persists through the derived clades of the lineage, giving the extant members of the lineage their distinctive B-shaped lower molars. The crest, when present on the molars, is coded as weak (state 1) when it is much lower than the interior crest connecting these two cusps. It is coded as strong (state 2) when it is of similar height to the interior (lingual) crest between the mesoconid and hypoconid. State 3 occurs when the premolars also have the connection between the mesoconid and hypoconid, a state that only occurs when the crest connecting the labial margins of the hypoconid and mesoconid is well developed in the molars.
134. *Mesoconid of P_4 : (1) less labially prominent than on the molars or (0) same as on the molars.* State 1 indicates that the mesoconid is closer to the labial margin of the tooth on P_4 than it is on the molars. State 0 indicates that the position of the mesoconid relative to the other cusps on the labial side of the tooth is similar between molars and premolars.
135. *Mesoconid on molars with anterolingual spur: (1) present or (0) absent.* The anterolingual spur of the mesoconid is a crest extending anteriorly from the mesoconid into the central basin. It does not join any other cusps or crests, just leaving an isolated spur into the basin, lingual to the crest connecting the lingual margins of the protoconid and mesoconid.
136. *Mesoconid: (0) circular, (1) triangular, or (2) roughly linear.* The mesoconid may be circular or conical (state 0), triangular, with a distinct crest or edge down the labial side of the cusp (state 1), or linear and anteroposteriorly compressed, without a broad lingual base (state 2).
137. *Trigonid: (0) present, distinct on lower molars; (1) reduced, less than a third of the anteroposterior length of talonid; or (2) lost on lower molars, leaving crescentic, not B-shaped, occlusal outline.* Ordered in semi-ordered and ordered analyses. This character codes for the reduction of the trigonid basin, or, in taxa for which unworn teeth are unavailable, for the expression of the trigonid basin in the outline of the teeth. The anterolabial inflection, between the protoconid and the mesoconid, generally gives the tooth a B-shaped occlusal outline; the position of that inflection is used to find the posterior limit of the trigonid basin in worn teeth. In taxa where the position of this inflection shifts anteriorly or posteriorly during life as the tooth wears, the maximum size of the trigonid is used to determine the coding for this character.

138. *Anterior inflection / fossettid of P_4 : (0) short or (1) long anteroposteriorly.* The anterior fossettid or inflection of P_4 is the one formed between the protoconid and the metaconid. It is considered long (state 1) when it occupies roughly half of the anteroposterior length of the tooth, and is the dominant feature of the occlusal surface. It is short (state 0) when it is less than a third of the total anteroposterior length of the tooth, and does not dominate the occlusal surface.
139. *Anterior fossettid of P_4 : (0) wide transversely or (1) narrow.* The anterior fossettid of P_4 may be either wide, and two or fewer times as long as it is wide (state 0) or narrow and more than twice as long as it is wide (state 1).
140. *Anterolophid of P_4 : (2) high, continuous, closing trigonid in unworn specimens; (1) closing trigonid in mid-to-late wear; or (0) incomplete or absent, not closing trigonid in any wear stage.* Ordered in semi-ordered and ordered analyses. The anterolophid is the crest or loph on the anterior margin of the tooth connecting the anterior edges of the protoconid and metaconid, and enclosing the tooth anteriorly. This character codes for the prominence of this lophid. State 2 is the highest prominence of the anterolophid, in which case it encloses the anterior fossettid in unworn teeth. In some taxa, it is lower, but the anterior fossettid is still closed by middle or late wear (state 1). State 0 codes for the taxa that have no continuous anterolophid at all and an open anterior fossettid at any wear stage.
141. *Large anterior basin: (0) present or (1) absent in centre of trigonid.* This character codes the presence or absence of a substantial basin or fossettid in the anterior moiety of the tooth, anterior to the inflection between the protoconid and mesoconid.
142. *Anteroconid crest on cheek teeth: (1) present or (0) absent.* The anteroconid is a small cuspule on the anterior cingulum of the cheek teeth. The anteroconid crest is a crest extending posteriorly from the anteroconid, between the protoconid and the metaconid.
143. *P_4 with anteroconid: (2) closing anterior end of valley between metaconid and protoconid, (1) anterior to protoconid, or (0) absent.* Ordered in fully ordered analyses. The presence of the anteroconid on P_4 varies independently of that on the molars. It can be positioned directly anterior to the protoconid (state 1) or anterolingual to the protoconid, closing the anterior fossettid (state 2), or it may be entirely absent (state 0).
144. *Anteriorly directed crest of P_4 from protoconid: (1) present or (0) absent.* The anterior crest of P_4 may be present or absent, and is unrelated to the presence or absence of an anteroconid. This character also varies independently of character 112, in that the protoconid crest may be present, but curves anteriorly, or maybe present and continuous with an anterolophid, or may be present in the absence of a style down the front of the metaconid, all of which lead to a lack of congruence between these two characters.
145. *M_3 : (0) subtriangular in occlusal outline or (1) rectangular / trapezoidal in outline because of the lingual placement of entoconid.* Because the entoconid is at the posterolingual corner of the lower molars, shifts in its relative position can affect the overall occlusal outline. In some taxa, it is almost in line between the large hypoconid and metaconid, leading to a roughly triangular occlusal outline (state 0). In others, the entoconid is distinctly lingual to the line connecting the posterior edge of the hypoconid and the posterior end of the metastylid; in that case the occlusal outline is more rectangular or trapezoidal (state 1), with a distinct angle at the posterolingual corner.
146. *M_1 entoconid: well forward of posterolingual corner of molars (1) or at posterolingual corner (0).* The entoconid of M_1 may be relatively posterior in position, and hence aligned with the hypoconulid (state 0), or it may be forward of that position, with the lingual crest of the hypoconulid extending to a point almost directly posteriorly to the entoconid (state 1).
147. *M_2 separation of lingual end of posterior cingulum from the entoconid: (1) greater than in M_1 or (0) equal to M_1 .* This character can only be coded for taxa that are known from a jaw with M_1 and M_2 associated. In that case, the width of the re-entrant between the posterior cingulum, that is the lingual crest of the hypoconulid, and the entoconid is either the same in M_1 and M_2 (state 0) or greater in M_2 than in M_1 (state 1).
148. *M_1 mesostylid: (0) separated from entoconid by deep inflection or (1) mesostylid and entoconid not separated by notch, lingual cingulum relatively complete from entoconid to metaconid.* The mesostylid may be closely connected to the entoconid, with a continuous crest between them (state 1), or the two may be separated by a valley on the lingual margin of the tooth, leaving an interruption in the lingual cingulum (state 0).
149. *M_1 entoconid oriented primarily (0) anterolabially or (1) labiolingually.* The entoconid on the first molar may proceed labially from the lingual margin of the tooth (state 1) or it may be oriented more anteriorly, crossing the central basin of the tooth at a diagonal (state 0).
150. *M_3 entoconid: (1) reduced relative to other molars or (0) large.* This character codes for whether the

- entoconid is roughly the same size in all the molars (state 0) or is much smaller half the size or less) in M_3 than in M_1 and M_2 (state 1).
151. *Entoconid*: (0) with no crests, conical; (1) with one labially or posterolabially directed crest; or (2) with two crests, one directed one labially or posterolabially, and the other running anteriorly and slightly labial. Ordered in fully ordered analyses. This character codes for the number of crests on the entoconid; the orientations are specified to verify the homology of the crests under consideration.
152. M_3 posterolingual inflection/fossettoid (valley behind entoconid and anterior to hypoconulid crest): (2) closed, (1) open only in early-wear specimens, or (0) open even in later wear. Ordered in semi-ordered and ordered analyses. The valley between the entoconid and the lingual crest of the hypoconulid may be completely closed by the lingual cingulum (state 2), or it may be closed by a low crest, leading to the closure of the valley in mid-to-late wear (state 1), or it may be entirely open, and not closed by a crest between the hypoconulid and entoconid (state 0).
153. *Entoconid crest of M_2* : (0) straight, (1) bent anteriorly, or (2) bent posteriorly. The entoconid crest is generally directed labially or anterolabially; once it reaches the central basin it may continue in the same direction, yielding a straight crest (state 0), or it may turn anteriorly (state 1) or posteriorly (state 2).
154. *Entoconid*: (1) elongate, but rounded and widening posterolingual to connection with hypoconid; (2) anterolabially elongate, and roughly rectangular; or (0) roughly conical in mid wear. The entoconid may be a simple, conical cusp (state 0), or, if elongate, it may be rectangular, with the internal crest retaining the same thickness as the cusp itself (state 2), or it may have the internal crest narrowing labially, so that the cusp itself is the widest part (state 1).
155. *Posterior inflection between entoconid and hypoconulid on P_4 - M_2* : (0) open for some vertical extent, (1) closed most of the vertical height of the crown, or (2) closed all the way to the top of the crown. Ordered in semi-ordered and ordered analyses. This character is much like character 152, but is for the anterior cheek teeth. The two characters seem to vary independently, as the M_3 may have the metafossettoid (inflection between entoconid and hypoconulid) open when it is closed in all the other cheek teeth.
156. *Inflection posterior to entoconid directed*: (1) anterolabially or (0) transversely. The inflection posterior to the entoconid is between the entoconid and the lingual crest of the hypoconulid.
- This character varies independently from the orientation of the inflection anterior to the entoconid (character 116), as it is also affected by the crests from the hypoconulid, and by the fact that the entoconid may have both anterior and posterior crests with differing orientations.
157. *Posterior fossettes of P^4 - M^3* : (1) more compressed and elongate or (0) more ovate and broad. The posterior fossettes are the valleys of the upper cheek teeth on the labial and lingual sides of the metaconule, posterior to the central transverse valley. Compressed and elongate (state 1) implies the state in derived mylagaulids, in which the labial and lingual sides of the basins are parallel, and the length of the fossette is many times its width. More ovate and broad (state 0) fossettes are more rounded and are generally no more than two or three times as long as they are wide.
158. P_4 posterior inflection/fossettoid: (1) becoming two separate fossettoids with wear in lower molars or (0) single late in wear. This character is illustrated by Rensberger (1983): fig. 2). The posterior inflection is the valley between the entoconid and the lingual cingulum of the hypoconulid; it is closed labially to form the posterior fossettoid by the anterior crest of the hypoconulid, and lingually by the lingual cingulum of the tooth. It may become two separate fossettoids with wear if there is a secondary crest between the posterior cingulum and the internal crest of the entoconid.
159. M_1 and 2 hypoconid: (0) transversely elongated or (1) anteroposteriorly elongated. The hypoconid is rarely a simple, conical cusp; it is generally longer in one dimension than the other, as a result of the presence of prominent crests. It is anteroposteriorly elongated (state 1) when the anterior and posterior crests are large and prominent, and when the talonid is long. It is transversely elongated (state 2) when the anterior crest is weak, and the connection with the hypoconulid is strong; in this case the cusp itself is also ovate, with the long axis labiolingually oriented.
160. *Posterolophid*: (1) anterolabially or (0) labiolingually directed. The posterolophid is formed by the union of the hypoconid and the hypoconulid; this lophid forms the posterior edge of the tooth. In most taxa, this lophid is directed labiolingually, directly across the tooth (state 0); however, in some cases the lophid runs posteriorly from the hypoconid towards the hypoconulid (state 1), and the lingual crest of the hypoconulid is often also shifted posteriorly to remain parallel to the rest of the posterolophid.

161. *Lower molars: (0) trapezoidal because of the protrusion of the hypoconid; (1) nearly rectangular, without protruding hypoconid; or (2) with hypoconid shifting posteriorly from P₄ to M₂.* This character is coded using the position of the hypoconid relative to the hypoconulid. State 0 codes for the hypoconid to be at the posterior-most extent of the tooth. State 1 codes for the hypoconid and the hypoconulid to be roughly aligned labiolingually, or for the hypoconid to be more anterior. State 2 codes for a special case in which the hypoconid is more posterior on each tooth from P₄ to M₂.
162. *Posterolabial fossettid or re-entrant of P₄: (0) small, roughly circular, and closed posteriorly by a lingual crest of the hypoconid, or the hypoconid itself significantly anterior to the posterior cingulum; or (1) large, oval to linear, extending posteriorly to posterior margin of tooth, and closed posteriorly by the posterior cingulum.* The posterolabial fossettid is the one formed between the hypoconid and the mesoconid; in cases where this fossettid is not closed labially, it can still be coded based on which crests close the re-entrant posteriorly. The fossettid may remain small, and be closed by the hypoconid or its anterolingual crest well anterior to the posterior cingulum (state 0), or it may be elongated posteriorly, so that it extends all the way to the posterior cingulum.
163. *Hypoconulid: (0) single or (1) doubled on molars.* The presence of a second cusp lingual to the hypoconid on the posterior cingulum is considered a doubled hypoconulid; any characters coded for the hypoconulid are coded for the largest of these, generally the labial one.
164. *Hypoconulid: (0) lacking distinct anterior crest, (1) with anterior crest not joining any other crests, (2) with anterior crest joining entoconid labial crest on molars only, (3) with anterior crest joining entoconid crest on all cheek teeth, or (4) with crest joining entoconid crest only on P₄.* The hypoconulid crest varies in length, and, if present, may simply end in the posterior valley of the tooth without connecting to any other crests (state 1), or it may extend anteriorly as far as the labial crest of the entoconid. Some taxa have this junction only on P₄, some only on the molars, and some on both. Ambiguous coding means the states cannot be distinguished because of the state of preservation: this might occur if molars and premolars are not both preserved for a given taxon. This character can be a bit confusing in mylagaulids: the lingual connection between the mesoconid and hypoconid is often shifted lingually relative to its position in less derived mylagaulids, and so may look like a hypoconulid crest; however, in mylagaulids the hypoconulid frequently lacks an anterior crest.
165. *Hypoconulid: (2) anteroposteriorly compressed and linear on all teeth, (1) triangular on P₄ only, or (0) triangular on all cheek teeth.* Ordered in fully ordered analyses. All taxa that have the triangular hypoconulid on the molars also have it on P₄; the opposite is not necessarily the case. When the hypoconulid is anteroposteriorly compressed it is difficult to distinguish from the rest of the posterolophid. Composite coding of this character implies that the two states cannot be distinguished with the available material, i.e. that the specimens available do not preserve both premolars and molars.
166. *Posterolophid: (0) terminating abruptly at hypoconulid or (1) extending lingually past hypoconulid.* The hypoconulid is the widening in the posterolophid lingual to the hypoconid; any crest extending lingually from this cusp is considered an extension of the posterolophid past the hypoconulid (state 1).
167. *M₃ hypoconid: (0) posterior to hypoconulid, (1) level with hypoconulid, or (2) anterior to hypoconulid.* Ordered in fully ordered analyses. The position of the hypoconid relative to the hypoconulid on M₃ varies independently of that in all other cheek teeth; the posterior portion of M₃ is often expanded in a variety of ways, by shifting the hypoconid, the hypoconulid, or both posteriorly.
168. *Lower molars with central fossettid (basin between mesostylid and entoconid): (1) much deeper and more persistent with wear than other fossettids or (0) similar in depth to anterior and posterior fossettids.* The central fossettid is the basin in the centre of the tooth, between the labial ends of the internal crests of the mesostylid and the entoconid, often bounded labially by the mesoconid. This character is coded to emphasize differences between the depth of the basin and the others on the tooth. State 1 is coded for the taxa with a substantial difference in the depth of the basins between the central fossettid and all others, such that a mid- or late-wear specimen will have the central fossettid still present and clearly defined, whereas the others will all be worn away.
169. *Central fossettid on M₁₋₃: (0) open, (1) closed and persistent, or (2) absent mid wear.* Ordered in fully ordered analyses. This character refers to the same fossettid as character 169. The central fossettid is open (state 0) if it is not clearly bounded on all sides, particularly on the labial

- side. State 1 codes for a closed central fossettid present in mid wear, whereas in state 2 it is not deep enough or well-defined enough to be present in mid wear.
170. *Central fossettid of molars (the one formed posterior to mesostylid) generally: (0) simple, round; (1) with complex, nonconvex form; (2) triangularly shaped; or (3) transversely elongate and oval.* This character codes for the shape of the central fossettid as formed by the surrounding crests and cusps. State 1 is formed by assorted intruding crests, and often includes accessory cuspules. State 3 is elongated labiolingually across the tooth and is roughly ovate.
171. *Central fossettid of P_4 : (1) becoming two separate fossettids or (0) remaining a single fossettid with wear.* The central fossettid may become two separate fossettids with wear if crossed by a crest of significant height.
172. *Molars increasing in size: (0) posteriorly, (1) roughly the same from M_1 – M_3 , or (2) anteriorly.* State 0 is coded where the size of the teeth increases perceptibly and consistently from M_1 to M_2 , and from M_2 to M_3 . Similarly, state 2 codes for a taxon in which the size increases from M_3 to M_2 , and from M_2 to M_1 . State 1 is coded where there are no substantial differences in the sizes of the teeth.
173. *P_4 : (1) oval or (0) rectangular/trapezoidal.* This character codes for the occlusal shape of the premolar. Often an oval premolar is associated with round or oval molars, especially on the upper teeth. The difference is fairly discrete: the P_4 generally has either four distinct corners formed by the hypoconid, entoconid, metaconid, and protoconid, or the outline has no distinct projections and is smoothly oval.
174. *P_4^4 anteroposteriorly: (0) subequal to or smaller than first molar, (1) somewhat larger than first molar, or (2) more than twice as large as first molar.* Ordered in semi-ordered and ordered analyses. The enlargement of the premolar proceeds independently of the differences in sizes of molars from M_1^1 to M_3^3 . State 0 codes for premolars that are not substantially and consistently larger than M_1^1 . State 1 is coded when P_4^4 is notably bigger than M_1^1 , but is less than twice as large as M_1^1 . State 2 is coded when the P_4^4 is a great deal larger than M_1^1 , more than twice as large, a state found only in derived mylagaulids. This change occurs in parallel between the upper and lower cheek teeth, and is an obvious result of the constraints of occlusion.
175. *Lower incisor: (1) flat anteriorly or (0) convex.* The anterior face of the incisor, that is, the labial side, may be rounded and convex, or it may form a wide, flat surface, with a distinct edge on the distal (lateral) side. The lower incisor always has a distinct edge on the mesial (medial) side.
176. *Upper incisor: (0) with smooth anterior enamel surface; (1) with broad, shallow groove along medial border of anterior surface; or (2) with narrow, sharply incised groove along centre of anterior face.* Ordered in fully ordered analyses. The upper incisor may have a flat anterior (labial) face (state 0), or may be grooved in one of two ways. The groove may be broad and shallow, on the mesial (medial) edge, and is generally perceptible only by touch, or by the reflection of light from the enamel surface (state 1). Alternatively, there may be a narrow and sharply incised groove, more like that present on the modern *Reithrodontomys*, down the middle of the anterior face of the incisor (state 2).
177. *Lower incisor root: (1) ascends into coronoid process or (0) root is not in coronoid process.* The incisor may be rooted low in the jaw, ventral or posterior to M_3 (state 0), or it may extend further into the jaw. When the jaw is shortened, the incisor root extends further dorsally into the jaw and into the tip of the coronoid process, forming a distinct thickening or bump at the dorsal end of this thin process. There is an intermediate state in which the incisor root is at the back of the jaw between the mandibular condyle and the coronoid process; this state is coded as state 0.
178. *Coronoid process ascends: (0) on a low angle or (1) vertically.* In early aplodontids, the anterior edge of the coronoid process slants dorsally and posteriorly, and the entire process is directed posterodorsally (state 0). In some derived aplodontids the coronoid process is directed completely dorsally, and the anterior edge is oriented dorsoventrally (state 1).
179. *Coronoid process ascends: (0) with anterior margin at middle of M_3 , (1) with anterior margin at anterior edge of M_3 , (2) with anterior margin at middle of M_2 , or (3) with anterior margin at anterior edge of M_2 .* Ordered in fully ordered analyses. The position of the anterior edge of the coronoid process varies in how far forward it is positioned relative to the tooththrow; this character is coded by how many molars are obscured by the coronoid process in lateral view.
180. *Anterior margin of masseteric fossa: (0) below posterior end of M_2 , (1) below anterior end of M_2 , (2) below posterior end of M_1 , or (3) below anterior end of M_1 (or of P_4 in mid-wear mylagaulids).* Ordered in fully ordered analyses. The anterior extent of the masseteric fossa is determined from the anterior end of the depression that forms the masseteric fossa, not the ridge that sometimes

curves anterodorsally from the anterior edge of the fossa. The position of the anterior end of this fossa relative to the molars is used to code this character. In mylagaulids the fourth premolar pushes out the molars early in ontogeny: if the molar is missing, the position of M_1 is estimated using the positions of M_2 and M_3 , and is used to estimate the character state.

181. *Anterior angle of masseteric fossa: (1) curving dorsally or (0) not.* The masseteric fossa is surrounded anteriorly by a ridge. At the anterior-most extent, which generally occurs about halfway between the base of the tooth crowns and the ventral edge of the jaw, there is sometimes a curved anterodorsal extension of this ridge. When present, it generally has a small groove or indentation posterodorsal to the ridge.
182. *Masseteric fossa: (0) broadly rounded or (1) pointed, V-shaped.* The masseteric fossa may come to a point anteriorly (state 1), or it may be a continuous, rounded arc, without an abrupt change in angle.
183. *Mental foramen: (0) near midpoint of diastema or (1) more posterior, just anterior to anterior root of P_4 .* The mental foramen may occur around the midpoint of the diastema, below the lowest point in the dorsal edge of the diastema (state 0), or it may be positioned more posteriorly, just dorsal to and in front of the anterior root of P_4 .
184. *Masseteric fossa: (1) strongly sculpted by masseter attachments or (0) relatively smooth.* This character is difficult to code, and may vary through the ontogeny of an individual; however, samples are inadequate to test this possibility at this time. It is included because it seems to be variable, and because it is generally better to include all potentially informative characters in a phylogenetic analysis. State 1 is coded for taxa in which there are distinct ridges crossing the masseteric fossa dividing the attachments of different layers of the masseter. State 0 is coded for taxa that do not have these distinct sculptures or ridges.
185. *Mental foramen: (0) single or (1) double.* This character codes for the number of distinct foramina in the position of the mental foramen, on the lateral side of the jaw near the middle of the diastema.
186. *Mastoid process: (0) small, appressed to posterior surface of bulla or (1) large and wing-like.* The mastoid process is flat on the surface of the bulla in many taxa; however, in some it is enlarged and flattened anteroposteriorly into a wing-like process projecting anterolaterally behind the bulla.
187. *Basioccipital: (1) wrapping ventrolaterally around middle of auditory bulla or (0) flat between bullae, abutting along a straight edge.* The basioccipital extends anteriorly between the auditory bullae on the ventral side of the skull to where it meets the basisphenoid. In some taxa, the anterior edge of the basioccipital is extended ventrolaterally around the ventral surface of the auditory bulla, as a small process extending from the basioccipital just posterior to its fusion with the basisphenoid.
188. *Lateral surface of periotic anterior to external auditory meatus: (1) restricted in area, not depressed, or (0) depressed.* The ventrolateral surface of the periotic is sometimes depressed, often in association with a large depression in this entire area of the skull, posterior to the masseteric fossa. This may be related to accommodation of the anteroposterior motion of the lower jaw.
189. *Upper edge of masseteric fossa: (0) a raised ridge, (1) a shallow groove, or (2) a deeply incised groove.* Ordered in fully ordered analyses. The dorsal edge of the masseteric fossa running from the coronoid process to the anterior point of the fossa may be a ridge (state 0), a shallow, parallel-sided groove flanked by slightly raised ridges on either side (state 1), or a deep groove, often with sloping sides and more deeply incised posteriorly, towards the base of the coronoid process.
190. *Periotic septae: (0) few, (1) more numerous and enclosing parallel transverse chambers, or (2) reticulate, forming small cells over most of interior of bulla wall and mastoid.* Ordered in semi-ordered and ordered analyses. This character can only be coded in taxa with thin-walled bullae that show the outline of the interior septae on the outer surface, or in those specimens in which the outer wall of the bulla has been broken away. Periotic septa are few (state 0) if less than five are present. Parallel transverse chambers (state 1) cross the bulla from the lateral to the medial side of the bulla, roughly parallel to the external auditory meatus. Reticulate septae enclose numerous little cells, which are generally round, rather than elongate, in their expression on the surface of the bulla.
191. *Bulla: (0) relatively large and inflated; (1) smaller relative to skull size, not prominent ventral to the occipital plate; or (2) reduced, only slightly larger than diameter of external auditory meatus.* Ordered in fully ordered analyses. The bulla may be large and inflated (state 0), protruding substantially ventral to

- the occiput and notably prominent in lateral view. They may also be slightly smaller, but still visible in lateral view (state 1), or they may be reduced to a size not much larger than the diameter of the external auditory meatus, yielding a bulla that is essentially a mediolaterally oriented tube (state 2).
192. *Conical anterodorsal expansion of auditory bulla, separated from remainder of bulla by single septum: (1) present or (0) absent.* A small conical tip may be present or absent on the anteromedial end of the ventral side of the bulla, making a right angle in the ventral outline of the bulla where the bulla meets the basisphenoid.
193. *External auditory meatus: (0) a triangular lip or (1) an elongate tube, longer than the bulla is wide.* The external auditory meatus may be a small lip, much shorter than the bulla is wide, or it may be elongated into a tube, longer than the width of the bulla, extending the ear opening lateral to the margin of the occipital plate.
194. *Boss: (1) present or (0) absent on anterior zygomatic arch, dorsal and slightly lateral to infraorbital foramen, and anteromedial to orbit, creating a small notch just anterior to the orbit.* The frontal extends laterally a short way above the anterior end of the zygomatic arch. In some taxa, a small rugose boss is present just dorsal and lateral to the infraorbital foramen on the dorsal edge of the zygomatic arch. This process often extends slightly posteriorly and creates a notch medial to it between the medial part of the frontal and the process.
195. *Occipital plate: (2) slanted strongly anteriorly, (1) slanted at a lower angle, or (0) vertical.* Ordered in semi-ordered and ordered analyses. The occipital bone forms a flat plate dorsal and lateral to the foramen magnum in aplodontids. This plate may be flat, and perpendicular to the occlusal plane (state 0), or it may be tilted slightly anteriorly, less than 10° (state 1), or it may be tilted strongly anteriorly, more than 10° (state 2).
196. *Nuchal crest in dorsal view: (0) straight, transversely directed, or (1) deflected anteriorly, forming a curve.* The nuchal crest is the crest along the top of the occipital bone, on the intersection between the parietal or interparietal and occipital bones. It marks the boundary between the dorsal and posterior surfaces of the skull. This crest may curve anteriorly (state 1) or may be straight and transverse (state 0)
197. *Sagittal crest on skull: (0) single; (1) double, converging posteriorly; or (2) double, widely divergent.* Ordered in semi-ordered and ordered analyses. The sagittal crests extend from above the posterior edge of the orbit, just posterior to the postorbital processes of the frontals (if present) posteriorly to the occipital crest. These crests may meet the nuchal crest as a single, joined crest, as is common in many other mammals (state 0), or they may remain separate to the occipital crest, forming lyrate crests. In this case, they may be converging and fairly close set, much closer than they are above the orbits (state 1), or they may be widely divergent, roughly as far apart posteriorly as they are anteriorly (state 2).
198. *Zygomatic arch: (1) deepened dorsoventrally above jugal-squamosal joint, making a raised surface on the squamosal above the joint; or (0) uniform in thickness across jugal-squamosal joint.* The jugal meets the squamosal slightly posterior to the midpoint of the zygomatic arch. This suture crosses the zygomatic arch at an angle, with the jugal diving posteroventrally below the anterior arm of the squamosal. The depth at the joint may be similar to that of the rest of the zygomatic arch (state 0), or the zygoma may be deepened at this point by a dorsal projection of the squamosal (state 1).
199. *Zygomatic arch: (0) gracile or (1) robust.* The zygomatic arch may be relatively lightly built and thin (state 0), or it may be thick and heavily built, especially in the anterior half (state 1).
200. *Zygomatic arch: (2) curving posteriorly from glenoid fossa to meet external auditory meatus; (1) extended posteriorly, but not meeting meatus; or (0) zygoma not posteriorly expanded.* Ordered in semi-ordered and ordered analyses. The squamosal portion of the zygomatic arch is, in some taxa, curved posteriorly lateral to the glenoid fossa, meeting the tubular extension of the external auditory meatus near the opening (state 1). In earlier aplodontids, the zygomatic arch is more D-shaped in dorsal aspect, with a smooth convex-curved shape, with no posterior extension (state 0).
201. *Attachment fossa for masseter: (0) continued to ventral surface of squamosal or (1) positioned on ventrolateral surface of squamosal.* The smooth surface where the masseter attaches in these protrogomorphous rodents to the zygomatic arch is, in most taxa, slightly laterally oriented, especially on the posterior, squamosal part of the zygoma (state 1); however, some have the attachment fossa facing directly ventrally.
202. *Zygomatic arch: (1) inflated and D-shaped, dorsal surface inclined medially; or (0) mediolaterally compressed.* The zygomatic arch is mediolaterally compressed (state 0) in most taxa,

although it varies in size and robustness. In a few mylagaulids, however, the middle of the zygomatic arch is rounded on the lateral side, with a roughly D-shaped cross section (state 1). The dorsal surface there is inclined medially in these taxa, creating a slightly concave medial side to the zygomatic arch.

203. *Skull: (0) not broadened posteriorly (only half as wide as long) or (1) broad across occipital plate and zygomatic arches.* The skull in early aplodontids is similar in proportion to squirrels and early rodents, in which the widest point is across the middle of the skull, at the middle of the zygomatic arches. In this case, the skull is also generally much longer than it is wide. In some derived aplodontids, the skull has been broadened posteriorly and shortened anteroposteriorly, leading to a skull that has a breadth across the occiput as great or almost as great as that across the zygomatic arches, and is very short relative to its width. One extreme case is actually wider transversely than it is long anteroposteriorly.
204. *Skull: (1) constricted or (0) not constricted between orbits.* This character codes for whether or not the skull is narrowed between the posterior borders of the orbits, at the middle of the region enclosed by the zygomatic arches. This is coded without considering the width of the postorbital processes.
205. *Postorbital process: (0) absent, (1) present on frontals but small, or (2) present and large.* Ordered in semi-ordered and ordered analyses. The postorbital processes are the lateral extensions of the frontals just behind the orbits, which in some mammals may meet with the postorbital processes of the jugals to form a postorbital bar. No postorbital bar is formed in any aplodontid, but the postorbital process may be completely absent (state 0) on the frontals, it may be small, only defined as a small knob or flange (state 1), or, in a few cases, it may be large, extending for more than half of the lateral distance to the jugal (state 2).
206. *Postorbital process of frontals: (1) thickened, raised above medial frontal suture; or (0) not thickened, roughly flat across skull.* The postorbital processes, when present, are usually quite thin and roughly flat with the dorsal surface of the frontals (state 0). In some few cases, however, they are thickened dorsally, so that the medial surface of the frontals between the postorbital processes is notably lower than the dorsal surface of the postorbital process (state 1). The process is often textured in such a way as to suggest increased vascularization.
207. *Postorbital process: (1) present or (0) absent on jugal.* The postorbital process of the jugal is either present or absent; it is rarely large, and is never thickened like the process on the frontal.
208. *Nasal bones: (0) narrow or (1) broad.* The nasal bones may be very long and thin, much narrower than the dorsoventral depth of the rostrum (state 0), or they may be wide, part of a broad rostrum, and much broader in proportion to their length, and closer to half as wide as the rostrum is deep.
209. *Tips of nasal bones: (2) widen anteriorly, (1) pinch in anteriorly, or (0) are straight anteroposteriorly.* This character is coded based on the relative widths of the anterior and posterior ends of the nasal bones. State 1 codes for nasal bones that are wider on the posterior end than on the anterior end. State 0 is coded for taxa that have nasal bones with roughly the same width at the anterior and posterior ends. State 2 is coded for nasal bones that are wider at the anterior end than at the posterior end.
210. *Nasal bones: (1) extend more posteriorly, level with centre of orbit; or (0) are not elongated posteriorly, level with anterior margin of orbit or anterior divergence of zygomatic arch.* The nasal bones in some taxa are extended further posteriorly, with the frontals proportionately shortened. The nasals are considered elongated (state 1) when the nasal–frontal suture is positioned medial to the centre of the orbit, halfway between the posterior edge of the anterior wall of the zygomatic arch and the postorbital process of the frontal. The nasals are not elongated if, like most aplodontids, they extend posteriorly to a position medial to the posterior face of the anterior wall of the zygomatic arch (state 0); some do not extend even this far posteriorly, and are still coded as state 0.
211. *Horns on nasals: (3) very tall, (2) short, (1) bosses or thickened ends present, or (0) nasals unmodified.* Ordered in fully ordered analyses. Tall horns are similar in height to the length of the skull. Short horns are roughly as tall as the rostrum is long. Bosses are thickened, rugose regions on the nasal bones, thicker than the more posterior portions of the nasal bones. Unmodified nasals may be thick bone, but are relatively uniform in thickness along the length of the bone.
212. *Horn: (0) circular or (1) flat-sided, triangular, trapezoidal, or square in cross section.* This character can only be coded for taxa that have nasal horns. The shape of the horn may be either conical, with a round cross section (state 0), or the horns may have a flat medial face (state 1). The shapes of the posterior, lateral, and anterior faces vary, even within a putative species, but the

- dichotomy between the flat and rounded medial faces seems consistent. The flat face is very distinct, with sharp, right-angle edges bounding it anteriorly and posteriorly.
213. *Interpremaxillary foramen*: (0) absent, (1) a pit, (2) a small foramen, or (3) large. Ordered in fully ordered analyses. The interpremaxillary foramen is a small, unpaired foramen positioned between the premaxillae, just anterior to the incisive foramina. If present, it may be simply a depression, not penetrating the bone (state 1), it may be very small, smaller than the other foramina, such as the posterior palatine foramina (state 2), or large, similar in size to the other arterial and nerve foramina (state 3).
214. *Incisive foramina*: (1) bordered on posterior end by maxillary-premaxillary suture or (0) entirely within premaxilla. The incisive foramina are large, anteroposteriorly elongate foramina in the premaxillae, sometimes also extending into the maxillae. In aplodontids, they may be bounded by the maxillae only posteriorly, at the intersection with the maxillary-premaxillary suture (state 1), or they may extend some distance into the maxillae, with part of the lateral and medial borders formed by the maxillae on the posterior ends of the foramina (state 0).
215. *Grooves in palate anterior to posterior palatine foramina*: (0) absent; (1) present, shallow; or (2) present, deep. Ordered in semi-ordered and ordered analyses. This character codes for the presence of grooves or shallow fossae proceeding posteriorly down the maxillary portion of the palate, from a point medial to the premolars to their end at the posterior palatine foramina. These grooves may be completely absent, with a flat palatal surface (state 0). Alternatively, palatal grooves may be present and are either shallow, with low-angled sides (state 1), or deep, with steeply sloping sides (state 2).
216. *Major pair of posterior palatine foramina medial to (0) second molars or (1) third molars*. This character is coded for the largest pair of posterior palatine foramina, if more than one pair is present. If the molars are absent, the character is coded using the alveoli.
217. *Posterior palatine foramina*: (0) one pair, (1) two pairs, or (2) three pairs. Ordered in fully ordered analyses. The posterior palatine foramina occur in the posterior part of the palate, medial to the posterior molars in the middle of the maxillo-palatine suture. If additional foramina are present, they are directly posterior to the main pair, entirely in the palatine bone, and are significantly smaller than the primary posterior palatine foramina.
218. *Infraorbital foramen*: (1) large or (0) small. The infraorbital foramen passes through the anterior wall of the zygomatic arch, just lateral to the rostrum. This foramen is much larger in most nonprotrogomorphous rodents than in aplodontids; however, there are differences within the lineage in the size of this foramen. Some have a very small foramen, no more than two or three times the size of most of the small foramina that transmit individual nerves and blood vessels (state 0); however, others have a much larger infraorbital canal, which is larger than the other foramina in the skull and occupies a significant part of the anterior face of the zygomatic arch (state 1).
219. *Infraorbital foramen*: (0) round or (1) oval. The infraorbital canal may be roughly circular in shape (state 0), or it may be significantly elongated, generally with the long axis oriented dorso-laterally, as in *Aplodontia* (state 1).
220. *Infraorbital foramen*: (1) relatively dorsal or (0) relatively ventral. The infraorbital foramen may be positioned at the extreme ventral edge of the zygomatic arch (state 0), or it may be more dorsally positioned, near the centre of the anterior face of the zygomatic arch (state 1).
221. *Nasolacrimal foramen (immediately above the posterior opening of the infraorbital foramen)*: (1) large or (0) small. The nasolacrimal foramen is positioned just behind the anterior face of the zygomatic arch, just dorsal to the infraorbital canal, and may be small and similar in size to the other small nerve or blood-vessel foramina (state 0), or may be larger, more open, and anteroposteriorly elongate, similar in size to the incisive foramina (state 1).
222. *Sphenopalatine foramen*: (0) more anterior, above P^4 , or (1) posterior, above M^2 . The position of the sphenopalatine foramen varies within the aplodontid lineage. For a more complete discussion of the changes in this feature, see Wahlert (1974).
223. (0) Zero, (1) one, or (2) two small foramina anterior to sphenopalatine foramen. Ordered in fully ordered analyses. This character codes for the presence or absence of additional very small foramina directly anterior to the sphenopalatine foramen.
224. *Development of anterior branch of labial inflection*: (0) poor or (1) extensive in P_4 . The anterior branch of the labial inflection is the inflection or re-entrant between the mesoconid and the protoconid. This re-entrant may be deep, similar in lingual extent to the re-entrant or fossettoid between the mesoconid and the hypoconulid (state 1), or it may be much shallower and shorter labiolingually (state 0).

225. *Entrance to labial inflection on P₄: (1) narrow, deeply incised; or (0) broad, shallow.* The labial inflection referred to here is the inflection between the mesoconid and the protoconid. The entrance to the labial inflection is considered narrow (state 1) if the sides of the re-entrant are essentially parallel for most of its length. The entrance is shallow if the re-entrant is much wider labially than lingually, and the sides of the re-entrant are not parallel (state 0).
226. *Labial inflection of lower molars: (1) shallowing significantly with wear or (0) remaining equally deep throughout wear.* This character addresses the same labial inflection as character 225. The base of the inflection may slope labially, in which case wearing of the tooth results in a much shallower inflection than was present in an unworn tooth (state 1). On the other hand, the labial inflection base may be flat, with the lingual wall essentially vertical (dorsoventrally oriented), in which case the depth of the inflection does not change as the tooth wears (state 0).
227. *Labial inflection on M_{1 and 2}: (1) closed or (0) open in late wear.* The labial inflection (the same one addressed in the previous two characters) may be closed in late wear on M_{1 and 2} by a low ridge connecting the bases of the mesoconid and the protoconid: this character is coded without regard to whether or not the taxon in question actually has the tendency to wear its teeth down to that level, so as to be independent of wear pattern.
228. *Labial inflection of M₃: (1) relatively broader than or (0) roughly equal to that in M_{1 and 2}.* The anteroposterior width of the labial inflection (the same one addressed in the previous three characters) may be the same throughout all the molars (state 0), or may be wider and more open in the third molar than in the two anterior molars (state 1).
229. *Fossettes/fossettids on premolars: (1) more elongated, or (0) more ovate or circular.* The fossettes and fossettids on the premolars are formed by wear of the cusps and crests, leaving lakes of enamel where the valleys in the tooth used to be. This character is coded, regardless of whether the cusps are worn, in such a way as to make fossettes of the valleys. The fossettes are considered elongate if they are generally parallel sided and much longer than wide, on average (state 1); they are considered ovate or circular if all are not more than three times as long as wide, and are with curved, not straight sides.
230. *Number of fossettids on M₁: (0) three or fewer, or (1) more than three.* Fossettids are considered closed if bounded at some wear stage on all sides by enamel. The break in the character is placed at this position, as no aplodontid taxa have four fossettids on M₁, and most have either three or fewer, or six or more; a few have only five. Hence, this appears to be a natural break in the character between those with many fossettids and those with few; the character does not vary continuously.
231. *Fossettes/fossettids: (0) with no consistent orientation, (1) oriented consistently obliquely across the tooth, or (2) more a-p aligned on P₄.* Ordered in fully ordered analyses. The fossettes and fossettids may be simply oriented randomly as crests join (state 0), or they may be oriented consistently, with the worn enamel edges forming a series of shearing blades for processing tough food. In that case, the shearing blades may be oriented obliquely (state 1), which corresponds to the approximate orientation of the major fossettes in many early aplodontids, as the crests tend to trend labiolingually or anterolingually across the teeth. In some taxa, the fossettids are oriented along the anteroposterior axis of the tooth, creating shearing blades for the labiolingual motion of the jaw (state 2).
232. *Posterior fossettoid of P₄: (0) present or (1) absent in moderately advanced wear.* The posterior fossettoid referred to in this case is the one that is present posteriorly in many aplodontines and meniscomyines, and is formed between the posterior cingulum (or posterolophid) and the labiolingual crest that connects the mesoconid crest, or between the hypoconid and the entoconid (the hypolophulid), which is labial to the hypoconulid. The wear stage referred to as moderately advanced here is slightly past mid wear (the average wear stage in representatives of a taxon, indicating an adult individual), but not worn down to the base of the crown, as in an old individual.
233. *Posterior fossettoid trending: (0) anterolabially or (1) anteroposterior on M_{1 and 2}.* The position of the posterior fossettoid is the same as the one referred to in character 232. The posterior fossettoid is not usually completely round, but is generally at least slightly ovate. This character codes for the orientation of the long axis of this fossettoid.
234. *Hypolophulid (crest from entoconid to mesoconid) on M_{1 and 2}: (0) present, strong; (1) present, weak; or (2) absent.* Ordered in semi-ordered and ordered analyses. The hypolophulid is the transverse crest connecting the entoconid to the posterior crest of the mesoconid or the anterior crest of the hypoconid. This crest, when present,

- may be broad, thick, and high, extending across the tooth (state 0), or it may be thin or low, and not a dominant crest on the occlusal surface of the tooth (state 1).
235. *Hypolophulid (crest from entoconid to mesoconid) of lower molars: (1) diagonal and oblique or (0) directed transversely.* The hypolophulid (the same one described in character 235) may be oriented labiolingually (state 0), or it may be oriented somewhat anterior to the labiolingual axis, trending anterolabially (state 1).
236. *Posterolophid on M_1 and 2 joining hypoconid: (0) lingually, leaving posterior groove on hypoconid; or (1) posteriorly.* The posterolophid may intersect the hypoconid in the middle of its lingual side, with a small part of the hypoconid extending posteriorly on the labial side of the posterolophid, producing a small groove down the posterior face of the hypoconid (state 0). Alternatively, the posterolophid may join the hypoconid at its posterolingual corner, leaving the posterior face of the tooth flat or smoothly curving.
237. *M_1 anterior cingulum: (0) S-shaped; or (1) straight or simply convex.* The anterior cingulum of the first molar may be straight or curved, with a convex shape, joining the metaconid at its anterolabial corner (state 1). In some taxa, however, the anterior cingulum joins the metaconid more posteriorly, in the middle of the labial side of the cusp, creating a broad groove down the anterior face of the tooth, and making the anterior cingulum more S-shaped.
238. *Cheek teeth: (1) forming nearly flat occlusal surface after little wear or (0) retaining relief on wear surfaces relatively late in wear.* The wear pattern of the cheek teeth varies a great deal in aplodontids, and is one of the reasons it is difficult to code the complete character set for many taxa. Early aplodontids have a wear pattern more like a squirrel or a primate, in which the wear facets are all at a high angle to the occlusal plane, on the sides of the cusps, and where even late-wear specimens retain relief in the tooth surface (state 0). Some derived aplodontids have a wear pattern more like castorids or heteromyids, in which the tooth surface wears flat across, with the wear facets essentially parallel to the occlusal surface. In this case, the surface of a worn tooth has little relief, and the dominant features of a mid-wear tooth are enamel lakes or fossettids, rather than crests or cusps (state 1). It should be pointed out that this character is not necessarily the same as hypsodonty, although it is more common to have low-relief wear in hypsodont teeth, as meniscomyines, which are not hypsodont, have this flat, low-relief wear pattern.
239. *(0) Most fossettids poorly defined after wear, with gently sloping walls, or (1) fossettids pronounced throughout wear.* This character codes for the overall appearance of the fossettids or valleys of the tooth. State 1 codes for deep, steep-sided, often narrow fossettes and fossettids, whereas state 0 codes for low-sloping fossettes and fossettids, not bounded by thin, high crests, and ridges, and which are usually relatively open.
240. *Crests of cheek teeth: (0) low or (1) high.* This character codes for the relative height of the crests connecting the cusps of the cheek teeth. The crests are high if similar in height to the cusps of the tooth, whereas they are low if much lower than the height of the cusps.
241. *Internal crests of primary cusps on lower teeth: (0) low or absent, never reaching centre of diagonal valley; (1) only entoconid crest (hypolophulid) crossing central valley; or (2) several high crests, crossing central valley.* Ordered in semi-ordered and ordered analyses. The internal crests of the teeth are those that extend into the central valley, rather than parallel to the boundaries of the tooth. This character codes for the degree to which these crests invade the central valley. State 0 indicates that no internal crests reach the centre of the central valley, and it remains fairly open. State 1 indicates that the only major internal crest is the hypolophulid, or the internal crest of the entoconid. This state is common in taxa that have no other crests whatsoever, and occurs in some Eocene rodents; this character appears to be independent of the development of the other internal crests. State 2 codes for a tooth where the central valley is crossed by several of the internal crests of the major cusps.
242. *Accessory crests of lower cheek teeth: (0) radially oriented from central basin, (1) orthogonally arranged, (2) all anteroposterior, or (3) without consistent orientation.* This character codes for the orientation of the accessory crests that occur in the central basins of the lower cheek teeth. These are crests that arise between the internal crests of major cusps, and often connect crests, rather than cusps. State 0 codes for a radial orientation, where all the crests seem to be directed from a point just anterior to the centre of the tooth and radiate outwards. State 1 codes for all these accessory crests oriented either anteroposteriorly or labiolingually. State 2 codes for all these crests oriented anteroposteriorly, and state 3 codes for random orientation of the accessory crests.
243. *Accessory crests: (0) simple, (1) branched, or (2) interconnected.* Accessory crests may be simple: i.e. connecting only between other internal crests

of cusps, or to those crests on only one end (state 0). In some taxa, the accessory crests may branch or fork, connecting to one another on one end, but with the other end free (state 1). Finally, some taxa have the accessory crests connecting to one another and to the crests of cusps, yielding a complexly interconnected occlusal configuration (state 2).

244. *Accessory crests: (0) absent; (1) incipient, only tiny bumps and cuspules in tooth basins; (2) present, but few; or (3) present and numerous.* Ordered in fully ordered analyses. The accessory crests (the same ones addressed by the previous two characters) may be completely absent (state 0) or present. In those taxa in which the accessory crests are present, there are a variety of degrees of development. The accessory crests may be 'incipient' or formed only as tiny bumps, and often not connecting to anything else (state 1). If present and clearly developed, they may be very few (state 2) or more numerous, as abundant as the internal crests of the major cusps (state 3).
245. *Lower cheek teeth dominated: (0) by shallow basin or (1) by crests and cusps.* The major feature of the lower cheek teeth may be the open central basin (state 0), or it may be the complex arrangement of crests and cusps crossing the basin (state 1).
246. *Marginal cusps of lower cheek teeth: (0) peg-like or bulbous; or (1) strongly crested.* The marginal cusps may be simple and conical or rounded (state 0), or they may have strong crests, giving them a more angular shape (state 1). This character is not the same as character 242, which addresses the degree to which crests cross the central basin. Crests can be strongly developed, but can also be short and not crossing the central basin.
247. *Walls of valleys of upper cheek teeth: (1) faintly crenulated or (0) smooth.* The walls of the basins on the upper cheek teeth may have smooth, flat enamel (state 0), or may have a faint rugosity or crenulation (state 1).
248. *Enamel in talonid basin of cheek teeth: (0) smooth or (1) crenulated/rugose.* This is similar to the coding for character 247, but seems to vary independently; some taxa that have rugose enamel in the lower molars have smooth enamel in the upper molars.
249. *Fossettes/fossettids: (0) more open or (1) more closed, narrow, sides closely appressed.* State 0 indicates that the enamel in the centre of the fossettes and fossettids may be visible, but that they are relatively open, even when elongate. State 1, on the other hand, has the enamel bands on either side of the fossettes and fossettids

closely pressed together, not exposing the inside of the enamel lake.

250. *Enamel of fossettes/fossettids: (1) thinner than enamel on outer edge or (0) similar in thickness to enamel of tooth margin.* The enamel of the internal enamel lakes in some derived mylagaulids is noticeably thinner than the enamel around the outside occlusal outline of the tooth. The appearance of this feature is sometimes accompanied by the presence of cementum around the outside of the tooth, but the enamel itself is thinner in the enamel lakes. This character cannot be coded for taxa with no specimens worn enough to expose the outside and inside enamel thickness.

Excluded characters:

Characters discarded for excessive within-taxon variation

- *Lower edge of masseteric fossa strongly defined or weakly defined.* This character seems to change through ontogeny.
- *Anterior portion of lower edge of masseteric fossa enlarged or similar in size to rest of edge.* This character also seems to change during ontogeny.
- *Horns on nasals positioned more anteriorly or on posterior ends of nasals.* This character clearly changes through ontogeny as the horns grow, which became apparent by examining multiple individuals from populations of individual taxa.

Characters discarded for inadequate within-ingroup variation

- Protoloph incomplete on P⁴, complete on molars, or complete on both P⁴ and molars.
- Parafossette of P⁴ disappearing fairly early in wear or remaining more persistent.
- Mesostylid widely separated from or close to metaconid.
- Posterolingually and anterolingually directed crests from mesoconid absent or present on M₁₋₃.
- Labial inflection ends internally at flat surface of mesoconid of P₄.
- Mesoconid flattened labially in mature wear on P₄.
- M₁ anteroconid vertical or posteriorly inclined.
- Entoconid large or small.
- Posterolingual fossette frequently closing appreciably later with wear than anterolingual inflection, or anterolingual and posterolingual fossettes dominating equally in length and persistence with wear.
- Posterior surface of hypoconid flattened or not flattened.
- Posterolabial fossettoid absent on all molars, absent on M₃, or present on all molars.

- Posterolabial apex of hypoconulid extends into posterior cingulum, joining posterior base of hypoconid or not joining hypoconid.
- P₄ with central basin strongly or weakly enclosed anteriorly and posteriorly.
- Central fossettid with internally convex or concave labial border.
- Tympanic bulla thin walled or thick walled.
- Labial re-entrant closing with wear prior to its division into two lakes or open after division, or undivided.
- Posterolophid posteriorly convex or posteriorly flat on M₁ and 2.
- Anterior cingulum on trigonid of molars absent or present.

APPENDIX 2

Character matrix used in phylogenetic analyses. Species names are abbreviated as follows: Alcav, *Allomys cavatus*; Alcri, *Allomys cristabrevis*; Aldin, Cabbage Patch allomyine; Alnit, *Allomys nitens*; Alret, *Allomys reticulatus*; Alsim, *Allomys simplicidens*; Alsti, *Parallomys stirtoni*; Alsto, *Allomys storeri*; Altes, *Allomys tessellatus*; Apdou, *Alphagaulus douglassi*; Appri, *Alphagaulus pristinus*; Apted, *Alphagaulus tedfordi*; Apvet, *Alphagaulus vetus*; ApDR, Deep River *Alphagaulus*; Awhar, *Allomys harkseni*; Awmag, *Allomys magnus*; Amsel, *Ameniscomys selenoides*; Ancru, *Ansomys crucifer*; Andes, *Ansomys descendens*; Anhep, *Ansomys hepburnensis*; Annex, *Ansomys nexodens*; Anori, *Ansomys orientalis*; Ansht, *Ansomys shantungensis*; Anshw, *Ansomys shanwangensis*; Adruf, *Aplodontia rufa*; Caann, *Campestralomys annectens*; Cadaw, *Campestralomys dawsonae*; Casio, *Campestralomys siouxensis*; Ceane, *Ceratogaulus anecdotus*; Cehat, *Ceratogaulus hatcheri*; Cemin, *Ceratogaulus minor*; Cerhi, *Ceratogaulus rhinocerus*; Crmil, *Crucimys milleri*; Dkpel, *Dakotalomys pelycomyoides*; Dklil, *Dakotalomys lillegraveni*; Docha, *Downsimus chadwicki*; Domon,

Montana *Downsimus*; Dosha, *Downsimus sharpi*; Epspa, *Epeiromys spanius*; Ehhos, *Ephemeromys hospes*; Fodru, Drummond; MT meniscomyine; Gabet, *Galbreathia bettae*; Ganov, *Galbreathia novellus*; Haarb, *Haplomys arboraptus*; Hagal, *Haplomys galbreathi*; Halio, *Haplomys liolophus*; Hegaz, *Hesperogaulus gazini*; Hewil, *Hesperogaulus wilsoni*; Lewil, *Leptoromys wilsoni*; Liale, *Liodontia alexandrae*; Lidai, Massacre Lake *Liodontia*; Lifur, *Liodontia furlongi*; Meedi, *Meniscomys editus*; Mehip, *Meniscomys hippodus*; Meuht, *Meniscomys uhtoffi*; Msbal, *Mesogaulus ballensis*; Mspan, *Mesogaulus paniensis*; Mdang, *Mylagaulodon angulatus*; Mykin, *Mylagaulus kinseyi*; Myela, *Mylagaulus ellassos*; Mysese, *Mylagaulus sesquipedalis*; Nibla, *Niglarodon blacki*; Nikoe, *Niglarodon koernerii*; Nilon, *Niglarodon loneyi*; Nimcg, Cabbage Patch *Niglarodon*; Nipet, *Niglarodon petersonensis*; Nilem, *Niglarodon lemhiensis*; Nipro, *Niglarodon progressus*; Niyea, *Niglarodon yeariani*; Orped, *Oropyctis pediasus*; Paame, *Parallomys americanus*; Paarg, *Parallomys argoviensis*; Paern, *Parallomys ernii*; Pamac, *Parallomys macodon*; Pebru, *Pelycomys brulanus*; Pepla, *Pelycomys placidus*; Perug, *Pelycomys rugosus*; Plang, *Plesispermophilus angustidens*; Plata, *Plesispermophilus atavus*; Pmsin, *Promeniscomys sinensis*; Pyrig, *Promylagaulus riggsi*; Prpar, *Prosciurus parvus*; Pralb, *Prosciurus albiclivus*; Prloh, *Prosciurus lohculus*; Prvet, *Prosciurus vetustus*; Prmag, *Prosciurus magnus*; Prord, *Prosciurus ordosicus*; Prrel, *Prosciurus relictus*; Psasi, *Pseudaplodon asiatica*; Ptbar, *Pterogaulus barbarella*; Ptcam, *Pterogaulus cambridgensis*; Ptlae, *Pterogaulus laevis*; Rumcg, *Rudimomys mcgrewi*; Sccad, *Sciurodon cadurensis*; Sepre, *Sewelleladon predontia*; Siham, *Sinomylagaulus halamagaiensis*; Tanev, *Tardontia nevadans*; Taocc, *Tardontia occidentale*; Trlem, *Trilaccogaulus lemhiensis*; Trmon, *Trilaccogaulus montanus*; Trova, *Trilaccogaulus ovatus*; Tsckh, *Tschalimys chikhvadzei*; Umgal, *Umbogaulus galushai*; Ummon, *Umbogaulus monodon*; IstypO, *Ischyromys typus* (outgroup); PdeliO, *Paramys delicatus* (outgroup); RedelO, *Reithroparamys delicatissimus* (outgroup).

	#1–20	#21–40	#41–60	#61–80
Alcav	11021311110100111011	00111101000111200011	00011101001000101200	00010110100000000001
Alcri	????????????????????	????????????????????	????????????????????	??????????????010?0?
Aldin	11?013121?0?10011?1?	?01?0/111?0????2?11?1	?0?01100?1011111210	20000010100000100001
Alnit	11001312100100111011	10002101201111200111	1?01110011001111210	00000110100000100001
Alret	110013121?0?00111011	?00?21002012?1210121	?01010001101111210	00000010100000100001
Alsim	20121412110110111011	10002100201111200111	1?010110011001111210	20000110100100100001
Alsti	100?13121?0?1???10?1	??1?2???0002?1200?10	??01?00????????????	?????????????0000001
Alsto	1?1?0/12011?1?00111000	001000010000/111200120	0?001100001011011210	2000001010010000000?
Altes	????????????????????	????????????????????	????????????????????	??????????????010?0?
Apdou	01?01012000?11110?0	00?0001000021121210?	?010000102200?0110?0	2101211000012112111?

APPENDIX 2 *Continued*

	#1-20	#21-40	#41-60	#61-80
Appri	11?010120?0???111???	?1???01?????2?121?0?	??1?0001??200?0110?0	?00??110010111120111
Apted	11?012120?????11110??	?0???011?0?2?121210?	??1?0001?2200?0110?0	2101011001012112?11?
Apvet	01101012000001111010	0100001000021121210?	?0100001022000011000	21012110010111121111
ApDR	011010120000?1111010	0000001000020121210?	?010000102200?011000	21010010011111121111
Awhar	10101312110100111011	100020/101100210201110/1	1?010110011001111210	0000010100000100001
Awmag	11101312100000011011	101020/111100211201121	1?010110011011111210	20000010100000100001
Amsel	211013121?0?11011010	?0??00100?02?0212?0?	?0001000010000101200	0?0?0?00/11000010000?
Ancru	?????????????????????	?????????????????????	?????????????????????	????????????????010?01
Andes	1?1?12011?1?0??10?0	?0??0??0?01?1210?0?	??01110??0??0??0???	????????????????0100001
Anhep	11100/120011110111000	0010001120011120010?	??00000001012011210	20000010100000100001
Annex	?????????????????????	?????????????????????	?????????????????????	????????????????010?0?
Anori	11100/1100111100111000	10?0001110011121000?	??000000?1012011210	00000010100000100001
Ansh	?????????????????????	?????????????????????	?????????????????????	????????????????010?0?
Anshw	1?1?010011110?0?10?0	10?00??1?0111210?0?	?00?00000??0??0???	????????????????0100001
Adruf	21101212000010001010	1000000/10000211?1110?	?1100001111100111101	001000012000001130101
Caann	011000001?0?00100110	?0??0000000?1200011	??0111000010?0100200	2000001010000000000?
Cadaw	0?0?00001?0?0??00?0	?0??0??0?00?1100?10	???0?10?0?0?0??0???	?????????01????0000001
Casio	01100000110002100010	10?1000000000110000?	??011100000010100200	20000010100000000001
Ceane	0???01020??1111?1?	?????011?0??1?210?	??1?00?1?200?0110?0	21012110011121121110
Cehat	0???01020??1111?1?	?????011?0??1?210?	??1?00?102200?0110?0	2101211001112112111?
Cemin	0???01020?0?1111010	00??00110002?121210?	?010000102200?0110?0	2101111?01112112111?
Cerhi	0???01020?0?1111010	00?0001100021121210?	?010000102200?0110?0	21002110011121121110
Crmil	?????????????????????	?????????????????????	?????????????????????	????????????????010?0?
Dkpel	?????????????????????	?????????????????????	?????????????????????	????????????????0000?01
Dklil	?????????????????????	?????????????????????	?????????????????????	????????????????0000?01
Docha	1?1?03011?0?0??1010	?0??0??0?00?1200?11	?0?1?00??0??0??0???	?????????01??0000000?
Domon	1?1?03011?0?0??10?0	?01?0??0000?1200?10	?0?1?10??0??0??0???	????????????00000000?
Dosha	?????????????????????	?????????????????????	?????????????????????	????????????????0000?01
Epspa	?????????????????????	?????????????????????	?????????????????????	????????????????0000?0?
Ehhos	01100000010000100100	00?010/10001000/1120000/10	1?001001000000100200	2000001010000000000?
Fodru	11121212000010101010	000?0010000111201000	?0000001011001111210	0000010/1000/10000100001
Gabet	1???11120?0?0111???	?????011?00?1?1?21??	?01?0001??1/20000110?0	2001001001012011??11
Ganov	111010/112000001111010	01000011000201212100	?0100001021/2000011010	10000110010120110111
Haarb	11110100111001101000	1010000000000120000?	?00100000000?100200	20000010100000000001
Hagal	?????????????????????	?????????????????????	?????????????????????	????????????????0000?0?
Halio	11110100110000111010	0010001000000120000?	?000/1110000/11010001200	00000010100000000000
Hegaz	0?1?01020?0??1111010	00?0001100121121210?	?010000102200?0110?0	2001001001113112111?
Hewil	0???01020?0?111101?	?0??0011?0??12?2100	?01?000102200?0110?0	2101001001113112112?
Lewil	?????????????????????	?????????????????????	?????????????????????	????????????????0000?0?
Liale	21101212000011001010	10000010000210211100	?1101001111100110201	00100112000000120101
Lidai	21101212000011101011	10100010000211211100	?1100001111100110101	00000110000000120101
Lifur	211012120?0010001010	101??010?1???12?1100	?1101001111100110111	00100012000000130101
Meedi	11101212000010111010	000?001000021121100?	?1100011011012111100	20000111100000100001
Mehip	11101212000011111010	00100010000211210/100?	?1000001011012111100	2000010100000100001
Meuht	11121212000110111010	00000000000211210/100?	?1000001011012111110	00000111100000100001
Msbal	?????????????????????	?????????????????????	?????????????????????	????????????????111?1?1
Mspan	111011120?0?00111010	0110001100021121210?	?0100001021/2001011000	10000110010111110111
Mdang	111010/1120/1?0??11010	?????00110002?1212100	?01000010210?0110?0	10000110010100110011
Mykin	0???01020????111?1?	?????010?0??0?2?2100	??1?0001??200?0110?0	20011110010101121???
Myela	0???01020????111?1?	?0??010?0??0?12?2100	??1?0001??200?0110?0	200111100101011211?1
Myses	0???01020????1111?1?	?????011?0??0?2?2100	??1?0001??200?0110?0	20011110010101121???
Nibla	11101212000011111010	0000001000/1021021210?	?1000001011112111110	00000102010000100001
Nikoe	11121212000010111010	000?00100002?021210?	?1000001011012111110	20000101110000110001
Nilon	11121212000011111010	00000010000211021200?	?1000001011012111110	00000102110000100001
Nimeg	11101212000011111010	1000000100021121210?	?1001001011012101110	0000010110000010000?
Nipet	?????????????????????	?????????????????????	?????????????????????	????????????????011??0?
Nilem	11121212000011111010	00?0001000021121?10?	?1001001011011101110	00000111?0000010/1000?
Nipro	?????????????????????	?????????????????????	?????????????????????	????????????????011?0?1
Niyea	111012120?0?11111010	?0??00000002?121?10?	?1000001011011110110	00000101000001?000?
Orped	?????????????????????	?????????????????????	?????????????????????	????????????????0000?01
Paame	10121311110001111011	10101000100111200111	1?010100011000111210	0000010100000000001

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APPENDIX 2 *Continued*

	#1–20	#21–40	#41–60	#61–80
Paarg	????????????????	????????????????	????????????????	?????????????010?0?
Paern	2002141110011111011	10001101000001200011	10011111011001101200	0000001010000000001
Pamac	10001312110100111011	10?01011?00011200011	1?01111011000101200	0000001010000110000?
Peburu	0?1?000001000??01?0	00100/1???000001100?20	10?1?10?0???????????	?????????????0000001
Pepla	????????????????	????????????????	????????????????	?????????????0000?01
Perug	????????????????	????????????????	????????????????	?????????????0000?0?
Plang	01110201111100101111	00100000000111200010/1	1001010000/1100/12011200	00100010100100000001
Plata	?????0?0?1?0?????1??	00?0?????????11000???	???1?1???????????????	?????????????0000001
Pmsin	111212121?0?11111000	?00?00010001?120000?	?1001001011010001200	2000010010000010000?
Pyrig	1110/210/112000?1111010	00?00010?00?121210?	?1100001021000011100	100/100000000?0110?0?
Pralb	01100000010101100110	00?00011000011200020/1	0?0111000010?01012?0	0000001010000000000?
Prdax	????????????????	????????????????	????????????????	?????????????0000?0?
Prloh	0??00000?????100110	?00?001000011110000?	?01000010000?01112?0	2000001000000010000?
Prmag	????????????????	????????????????	????????????????	?????????????000?0?
Prord	0??000000?????01?0	??0?0??0000?1000?10	??01?10?????????????	?????????????00000??
Prpar	01100000010001100100	00?000110000010/100020/1	1?0100000010?0110200	2000001010000000001
Prrel	01100000010001110110	?0??00110000?1100021	??0110/10000/110?0001200	20000010100000000001
Prvet	01100000010001100110	00101110000001000020	100101000000?01012?0	20000010100000000001
Psasi	????????????????	????????????????	????????????????	?????????????011?0?
Ptbar	0??10120????1111010	000?00110002?0212100	?010000102200?0110?0	2101?011011111121121
Ptcam	0??10120????111?1?	?????011?0???2?2100	?01?00?1??200?0110?0	2101?01101111112112?
Ptlae	01??10120000?1111010	000000110002?1212100	?010000102200?0110?0	2101?110111?112111?
Rumcg	????????????????	????????????????	????????????????	?????????????011?0?
Secad	10101311110010111011	10?00010000111200020	11010110011011011210	00000110100000100001
Sepre	????????????????	????????????????	????????????????	?????????????010?0?
Siham	11?012120????11101?1?	?????010?0???1??0???	??1?00?1??100?111100	20000110000000110???
Tanev	11101212000011101011	10000010000211211100	?1100001111000111210	0000001200000011000?
Taocc	21?012120??010101?1?	?00?01??????12??100	?11?00?1??1101111211	00000??2?000000110?0?
Trlem	01?010/11200??0111010	?0?0001??10?11?1210?	?1100001021/200?011000	20110011?100?011?0?
Trmon	????????????????	????????????????	????????????????	?????????????011?0?
Trova	001010/1120?0?00/1111010	??0000100102?121210?	??100001?21/2000011000	2011000011100?0110?01
Tsckh	11?012120??010001?1?	?????010?0???1??01??	??1?00?1??100?111?00	2000011?000000110???
Umgal	0??10120??01111?1?	?????011?0???12?210?	??1?00?1??200?0110?0	2101?11000010112111?
Ummon	0??101200??01111010	0000001100020121210?	?010000102200?0110?0	2101?11000111/2112111?
IstypO	00100000010001110110	00000010000001000030	0100000000000001100	20000010000000100000
PdeliO	01110000010100100110	00000110000011100030	1?01000000000000200	20000010100000000000
RedelO	01000000010000100100	00?01110000001100030	1?010000000000100?00	20000010000000000000
	#81–100	#101–120	#121–140	#141–160
Alcav	000?????0?1100000?0	001011001?000?100?0	00000?0?0012?110???	1??1100002100100?101
Alcri	?0????????????????	???11101?0000?0?0?1	0000?0?0002?110???	1??0?00?2??2100?101
Aldin	0/100?????0?1???????	???1101111100130011	10000110?000?11011?	1?110000021020000101
Alnit	000010010011100000?0	10101100111101130011	10000110000020110110	11111001022020000101
Alret	000030120011100000?0	1??1100111100130111	10100110000120120110	111110110220210000101
Alsim	0000000?0011100000?0	1010110?11110011?011	1000?110?000201?0110	11111001022020000?01
Alsti	00????????1100000?0	1??11101??100?1?0?1	1000??10?0012?120???	1??0?00?2??0000?101
Alsto	?00?????0?1100000?0	0010010000001103?110	1000?100?000?1010000	001?0?01?1?00000002
Altes	00????????????????	???11001?101?301?1	101?0?1?0002?110???	1??11011022202000101
Apdou	?13?????1?21??000?0	1100????????????????	????????????????	????????????????
Appri	0?2?????1?1?1???????	???01?0110?1?130111	000?01121?232?20112	02010?00012012100111
Apted	?1??????1?1?1???????	?????1?01100111?11?	?00?1121?0?3?020112	020?????1??12100?1?
Apvet	022?????1?11?0000?0	11000100110010130111	1000?112100232020112	02010000012012101111
ApDR	021/2?????1?1111000?0	11000101110010130111	100001121?0232020112	0201????112012101111
Awhar	0/100?????0?1100000?0	10101100111100110111	10000110000020110110	11110000021020000101
Awmag	0/10002002?011100000?0	10101101111100110111	10000110000020110111	12110000021020000101
Amsel	?0??????0?0120000?0	1?01110111000131001	10011110?00221020110	00110010010122100101
Ancru	?0????????????????	?????1?000?00?00?1?	?300?1000?01?0?0000	01?????1?1?1200000?
Andes	00????????1100000?0	1??10101000/10113?111	100?01100?030020000	001?1001?1?110100002
Anhep	000?????0?1100000?0	001010101010/101020011	0/1310010000000010002	00110001010010000002
Annex	00????????????????	???00100??0/101?2/300?1	10201?0??0101?110???	1??1000101021000?002

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APPENDIX 2 *Continued*

	#81-100	#101-120	#121-140	#141-160
Anori	00??????0?1100000?0	0??11010100001020111	1310010100001100/10000	00100001010010000002
Anshnt	00???????????????????	????00?00?000?2?0?1	1000??0??0000?010???	0??1?1?1?1?01000?00?
Anshw	?0?020010001100000?0	00111010100001020111	10100100?00001000000	00010001010010000002
Adruf	205000010010121010/100	10001001111000111101	11010110010130?21000	00010010012122000101
Caann	?0?0000?0001000000?0	0???010000000000?10	00000100?00000000000	01110001010010000001
Cadaw	00?????????1000000?0	1???010000000000010	000001000001000000000	00110001001?00000002
Casio	000?????????1000000?0	001?010200000000?010	0020?100000100000000	000?1001?00?0000002
Ceane	023??????1?1?1?1?1?1?1?	?????1?1?110?00?2?1?1?	1000?0121?2?3?2?2?112	120?????1?1?12111?11
Cehat	?23??????1?1?1?1?1?1?1?	?????1?1?110?0?0?1?1?	?0?0?0121?2?3?2?2?112	120?????1?1?12111?11
Cemin	02??????1?21?0000?0	110?1?1?110?0?1030?11	?000?0121?0?3?2?2?112	1201?????1?1?12111?11
Cerhi	002??????1?21?0000?0	1100?1?1?110?0?10?1?11	??0?0121?2?3?2?2?112	120?????1?1?12111?11
Crnil	?0???????????????????	??0?0100111010130101	0/10000100?00121020010	00110000010012100111
Dkpel	00???????????????????	??0?0112000000010100	0?000100001010000000	00011001110010000001
Dklil	?0???????????????????	??0?011200000001?110	?000?100001001010000	011?0001?1?010000001
Docha	00?????????1100000??	0??0?011?0?0000?100?0	00000?0??0101?000???	00?10001000010000000
Domon	00?????????1100000?0	1???01100/10?000?100?0	00000100?0102?010???	0??10001000010100001
Dosha	00???????????????????	??0?010/100/100000010100	00000110001120010010	00110001102010100101
Epspa	00???????????????????	??0?01000?000?001?0	00000?0??0000?000???	?0?10001002?01000000
Ehhos	00?????????0000000?1	0?100110000000000010	000001000000000000000	0000001002?01000000
Fodru	000??????0?1100000?0	10010100111011130101	02000100000221020010	00010000010112100101
Gabet	00?????????1?1?1?1?1?1?	??0?0?0/2110?003?2?11	1?0?1?1?1?232?2?102	020?0?00?1?012100111
Ganov	010001020102100000?0	10000100/21100/110030111	100?0112100232020112	02010000012112100111
Haarb	000000021001100000?0	00100110000000000010	03000100000001000000	00?10001010010000002
Hagal	00???????????????????	??0?0110/2000000010010	00000100?0000/11000000	00011001010010000002
Halio	000??????0?1100000?0	001001100?0000020010	0000010000001001001?	00011001010010000001
Hegaz	?23??????1?21?0000?0	1100?1?1?110?00?0?1?1	?200?012100?32?2?112	000?????1?1?12110?1?
Hewil	02??????1?21?0000?0	?10001?1?110?10030111	1200?012?00?32?20112	120?????1?1?12110?11
Lewil	00???????????????????	??0?0100000010/100/10110	00101100?0010100/10000	000100010102100?0002
Liale	004001010001121010/100	1000010?111?10030111	1?010110010130021001	00010?10011?22100101
Lidai	00001100001112101100	10001100111011?30111	130?0?110010130021001	00010010011122100101
Lifur	0150010200011?101100	?0?0?00?110?100?0111	1?0101100/110?3?22001/2	00010?????2?22100101
Meedi	100031020000111100?0	11010100111001131101	13000100010121010002	02010000012112100101
Mehip	000010010010111100?0	10010100111010131101	10000100000021010000	00110000012112100101
Meuht	00003011000011?100?0	10110100111000131101	03000100000021010002	00/2010000010112100101
Msbal	01???????????????????	??0?011?110?01?0?1?1?	??0?0112?0?3?2?2?112	0?1?1?1?1?12?2?100?11
Mspan	00002102000211110000	10?0?0100110?00130111	100001121?0232020112	00110??012112100111
Mdang	0000010200111000???	1???01?0110010030111	?0000112100232020112	0011?????112012100111
Mykin	?1???????????????????	??0?01?1?110?01?1?1?	?0?0?0121?0?3?2?2?112	120?????1?1?12110?11
Myela	013??????1?1?1?000???	??0?01?1?110?01?1?1?	?0?0?01210023?020112	120?????1?012110111
Myses	?22??????1?1?1?000???	??0?01?1?110?01?1?1?	?000?0121?2?3?2?2?112	120?????1?1?12110?11
Nibla	200031010010120011?0	10010100111010131101	0/13010100000121020000	00010000010112100101
Nikoe	200031110000120011?0	10010100111010131101	02010100010121020110	00010000010112100101
Nilon	200001100010120000?0	1001010011101113?0?01	1201?1000?0121020010	000100000101?2100101
Nimcg	10003111001012010/10?0	10010100111010131101	11011100?00121020000	00010000010112100101
Nipet	?0???????????????????	??0?0100111010031101	0/11010100?001210?0110	00010000010112100101
Nilem	?0?03101001012000/10?0	1001???????????????????	???????????????????????	???????????????????????
Nipro	20???????????????????	??0?0100111011131101	10010100000121020000	00010000010112100101
Niyea	?0?0210100101201000?0	1??0?1?1?11?0?0?0?01	?10?0?100?0?0?0?0?010	000?????1?1?12100101
Orped	?0???????????????????	??0?0110000000000010	00000100?0020?000010	00010001110010000000
Paame	000??????0?1100000?0	10101110001000000011	00000100000020010110	01111001020000000101
Paarg	?0???????????????????	??0?011100?0/100?0?01?	1000?0?0?0012?120???	?1?1?01?2?0?0000?101
Paern	000?20010011100000?0	1010111000100010001?	00000111000120110100	10111101020000000101
Pamac	?0?021020011100000?0	101011011?000?1?010	0000?1?0?002?120???	1??1?01?2??0000?101
Pebru	00?????????1000000?0	0010010200001001?110	0000?100?00100000001	000?1001?1?010000001
Pepla	00???????????????????	??0?01020?01?000100	0?00?10?00101000???	0?01000111?0100?0001
Perug	00???????????????????	??0?01020?01?00001?0	?000010?00010?000???	0?100010120100?0001
Plang	00000002?001100000?0	10100110/2000001000110	00000100000000000000	0111110101000/10000002
Plata	?0?????????1?1?1?0?0	??100112000000020011	10000100?00000000000	00011?01?10010000002
Pmsin	?000100100101000000?0	0???????????????????	???????????????????????	???????????????????????
Pyrig	?0?030020001111110/1??	?1000100/21100/111030111	10000110?00220020001	00010000112112100111
Pralb	?00??????0?1000000?0	0010???????????????????	??0???????????????????	???????????????????????
Prdax	00???????????????????	??0?01100?000101?011	0000?0?0?0000?000???	0??0?01?1?1?1100?00?

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APPENDIX 2 *Continued*

	#81–100	#101–120	#121–140	#141–160
Prloh	000000020001000000?0	1???01?201010102?111	0300?000?00200000000	000?1?01?1??210?0002
Prmag	00???????????????????	????01?00??0000?0?10	0000??0??0000?000???	0???0?01?1?00000?002
Prord	?0?????????1000000?0	0???????????????????	???????????????????????	???????????????????????
Prpar	00?????????1000000?0	00100100000000010?11	00000101?00000000000	000101010100100000002
Prrel	000000021001000000?0	0???0100010000010010	000001000000000000000	000/1111010100100000002
Prvet	00000000?0001000000?0	001001100??01001???0	0000??0??0020?010???	1???0?0??0??0??000001
Psasi	00???????????????????	?????10?111??1?011?	1??10110010?3??1000	00010??0?0?0?2100101
Ptbar	012??????1?210?000?0	1100010011001113?111	1?00?0121?0232020112	120??????1?1?12110111
Ptcam	?13??????1?1?1???	?????1?110?11?1???	??0?0121??3??2?112	120??????1?1?12110?11
Rumcg	20???????????????????	?????11001?011?3?001	0/13010?0??1002?010???	0??1?0001?122100101
Sccad	0000000?0011100000?0	00101110000000110011	00000111000130020002	00111001010021100102
Sepre	00???????????????????	???0100111011130101	10001100010021020000	00110000010112100101
Siham	?02?????????1?1???	???????????????????????	???????????????????????	???????????????????????
Tanev	000??????0?111100110	?00011001??010?301?1	1?010?10010131021000	00010010010122100101
Taocc	000??????0?1?1???	?????110?111?0?030101	1?010110010?31021000	00010??0?010?22100101
Trlem	0000310200001?0110/1??	???0102111111130111	12000110/1?001/220020102	00110000112112100111
Trmon	00???????????????????	???0102111111130111	12000110?00121020112	00010000?12112100111
Trova	00?????????0?112?1???0	1??010211111113?111	10000110/1100121020002	00110000?1?112100111
Tsckh	?02?????????1?1???	???????????????????????	???????????????????????	???????????????????????
Umgal	003??????1?21?1???	???0100110011130111	10000012100232020112	120100?0112212110111
Ummon	011??????1?2100000?0	110001?0110011130111	100000121?0232020112	12010??012012110111
IstypO	000000111001000000?1	1010110210001?000?1?	0??10100?0020?0?0010	000110010100100000001
PdeliO	000000??001000000?1	0010010010001?00011?	0??10100000100000010	00010101002?02000001
RedelO	000000021001000000?1	0010010010001?00010?	0??10100?00100000010	00010001012000000001
	#161–180	#181–200	#201–220	#221–240
Alcav	00?010001?1000?00121	1?0?00110000?????01	?00110?????????100010	?10??001000?02011000
Alcrl	?0?1?0?1???????????	???????????????????????	???????????????????????	?????00?00?00011011
Aldin	002?11001010?000033?	1?0????100000?????0?	?0?1?0?0200?????001	??10001010000010011
Alnit	01311101101000000/1220	1100??0010000??0/1?0?	?00110?0?0???1000010	?1?10000010000010011
Alret	01311101101000000120	1?0????1?????????????	???11??0?????11000010	?1?10000010000010011
Alsim	01101?00100000?00121	1000??1???????????????	??????????????1?0?????	??1000?000000011011
Alsti	?00??001?????????????	???????????????????????	???????????????????????	?????00?00?02?11010
Alsto	00321?00?00000???????	???????????????????????	???????????????????????	??1000?00000100/11000
Altes	?1??10011?1?0?00220	1?0????1???????????????	???????????????????????	??1?000?10?01?10011
Apdou	?????????????2?0?????	??????????????????1?1?	?1020?1201?11?0/10111	012?????0?0??????111
Appri	100012013?1121?1132?	0001111?1111012?12	101010?????0??100101	00?11010110/1000111111
Apted	?0001?0101?121101230	0000??11?1?11011112	10102011200?112?001	??1101?1?00?0????111
Apvet	1000110100212111320	010011122111101112	10101011200?11200111	0011010111000111111
ApDR	100?1101302121001230	000001112111?00?112	10101011200?11100011	??1101011001011?111
Awhar	00211101101000?00221	1?00??1???????????????	???????????????????????	??10001010001010011
Awmag	00211101101000000131	1000??1???????????????	?0?110?0200?21101001	?1210001010000010011
Amsel	0002120130100/11?00101	1100???????????????????	???????????????????????	??10000010001111011
Ancru	0??1?????1?0?????????	???????????????????????	???????????????????????	??10?0?0?00?????010
Andes	00?11?00011100?0?????	??0???????????????????	???????????????????????	??1100?000001?01011
Anhep	0002110011100?00121	1?0????1???????????????	???????????????????????	??1000000000010010
Annex	?01211001?1????00101	1?0????1???????????????	???????????????????????	?????000?0?00001010
Anori	0032110010100?0?????	???????????????????????	???????????????????????	??100000?000000/10010
Ansh	?0??1?00???????????????	???????????????????????	???????????????????????	?????00?0?00000010
Anshw	0041100010100?0?????	???????????????????????	???????????????????????	??1000100000000/11010
Adruf	?0121202101010001230	0100110122011012002	10110001200?31011010	10010000011101010111
Caann	00021100?0000?0?????	???????????????????????	???????????????????????	??10001000002?0/11000
Cadaw	00021000?00000?0?????	??00???????????????????	???????????????????????	??10000000002?01000
Casio	00021?00?0000?0?????	??00??0?010?00?????	?0?0????????????010???	?101000?000002?01000
Ceane	1?001?????0?1?????????	?????????????????21211?	101?1?1??2/31?????????	??11??1?10??1?111
Cehat	1?001?????12121?113?0	0????111??11212112	10100/101113021200101	??11??1?10????1111
Cemin	1?001??1012121?11320	0110??1?1??11102?1?	10101011??2?????????1	??1101?1?10????1111
Cerhi	1?001?????1212111320	0000?1?1?11102111	101010111211110/10011	0??11??1?10??1?111
Crnil	0002121100201?????????	???????????????????????	???????????????????????	??10101000100111111
Dkpel	00021100?01000?00120	1100??0?0?????????????	???????????????????????	??10001000000001000
Dklil	00021?00?01000?00120	1100??0?0?????????????	???????????????????????	??1000?000001001000

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APPENDIX 2 *Continued*

	#161–180	#181–200	#201–220	#221–240
Docha	?0000100?00??0?00131	1?0????1???????????	?????????????????????	?????101000002?11000
Domon	?0100100?00??0?00130	1000??1?????????????	?????????????????????	?????101000002?11000
Dosha	00100100?00000?00221	1?0????1?????????????	?????????????????????	?????10101000002?11000
Epspa	?0021100?00?????0000	1?00??0?????????????	?????????????????????	?????000000002?01000
Ehhos	00021000?0100?????????	?????????????????????	?????????????????????	?????10001000002?01000
Fodru	00020200301010?00120	1100??1?????????????	?????????????????01???	???10100000010111111
Gabet	10001?0100?01?????????	?????????????????????	?????????????????????	???01?1?011010111111
Ganov	10001?01002121111321	01100?1221?11010101	10111010200?21210011	?1?01010011010111111
Haarb	0002110010100??0231	1100??1?????????????	?????????????????0???	???1000000001001000
Hagal	0002110010100?????????	?????????????????????	?????????????????????	???1000000001001000
Halio	00021100100000?00021	0/1?0?00?0100/100000000	0000100??0??001011	?101000000000001000
Hegaz	1?001??100/12121?1???	??00?????1111212112	10101011201??200001	???11??1?20?????111
Hewil	1?001?0101212?111320	00111?11?1?11202112	101010112?1??2?011	???1101?1?201011?111
Lewil	0002110010100?????????	?????????????????????	?????????????????????	???10000000?2001000
Liale	10021212001010?0??30	??0??122?1?????0?	?0?100?0??0??1100???	???10000?01??111111
Lidai	10021212001010001230	00101101?101?0?0001	10111010200??120001	10010000001?0011111
Lifur	10021?02?0101?201230	0?0/10??1???????????	?????10?0200??103001	???10000001??111111
Meedi	00021211001011001231	1010??1120100??0001	10011000200??1100001	?0/1010100001?0111111
Mehip	00021211001011001231	10000?11201000??0?	00100?0200?21101011	1121010000010111111
Meuht	00021211001011001131	1000001120100011?0?	10011000?00?21101001	10/1210?00000010111111
Msbal	1?001?0??02121?01330	0?0????1?????????????	?????????????????????	???1?1?1?0?20?0??111
Mspan	10001101002121001330	00001111?1111010?011	10111011200?21200111	11?1101001201011?111
Mdang	1?0011?130201100?23?	?0?0?????1???????????	??0?10?0?00?0??0?111	???110100?000011?111
Mykin	10001?0??1?12?????????	?????????????????????	?????????????????????	???110??1?10?????111
Myela	10001?0101?121?112?0	0110??1?????????????	?????????????????????	???1101?1?1010111111
Myses	1?001??0?0?1?1?????????	?????????????????????	?????????????????????	???11??1?00?????111
Nibla	00021200/130101?0?121	0?0????1?????????0?	?0?????????????10?001	?1?10100000011111111
Nikoe	00021200301010?01121	0000??1?????????????	??????????????1??001	???10100000010111111
Nilon	0002121100101?0???????	?????????????0?????0?	?0?110?0200?01101001	01?101010001??111111
Nimcg	00021201301010?00131	100????1?????????????	?????????????????101???	???10100000110111111
Nipet	00021?1100101?????????	?????????????????????	?????????????????????	???10101000111111111
Nilem	????????????????0???????	?????????????????????	?????????????????????	?????????0??????111
Nipro	000212?1301011?????21	?0?0??1?????????????	?????????????????????	???10100000011111111
Niyea	0?021??0?0?0?????????	?????????????????????	?????????????????????	???10??0?01?????111
Orped	?0021100?0000??0?120	1100??0?????????????	?????????????????????	???0001000002?11000
Paame	0010100010100?????????	?????????????????????	?????????????????????	???1000000002?10010
Paarg	?0??1?0?1?????????????	?????????????????????	?????????????????????	?????00?00002?11000
Paern	00001000101000?00111	1100??1?????????????	?????????????????100???	???1000000002?10000
Pamac	?1??1?0?1?????????????	?????????????????????	?????????????????????	?????00?000002?11000
Pebru	00021?00100000??0?010	1100??0?????????????	?????????????????????	???1000?0000?1001000
Pepla	00021200100000??020	1100??0?????????????	?????????????????????	???100010000?2001000
Perug	000?1100100?????0???	1?0????0?????????????	?????????????????????	???1?001?00??2001000
Plang	00101000100000?00101	1000??1?????????????	?????????????????????	???1000000002?01000
Plata	00021?0010?00?????????	?????????????????????	?????????????????????	???1000?000002?00000
Pmsin	???????????????????????	???????????????????????	?????????????????0?????	?????????0?0?????110
Pyrig	1000121120101?????????	?????????????0???????	???0?0?12?0?0?110011	?1210100010110111111
Pralb	?????????????0???????	?????????????0???????	???100?020?0?00001010	?10?????0?0?????000
Prdax	?0021?00???????????????	???????????????????????	???????????????????????	?????00?00?00001000
Prlloh	10021?0020?00?????????	???????????????????????	?????????????????0?0?1	???0000?0?0000011111
Prmag	?0021?00???????????????	???????????????????????	???????????????????????	?????00?????02?0?000
Prord	???????????????????????	???????????????????????	???????????????????????	?????????????????0000
Prpar	00021100?0000?????????	???????????????????????	???????????????????????	???1000000002?01000
Prrel	00021100?00000000100	11000?00?00000??000	?00?0000?00?00001111	?101000000000001000
Prvet	00021?00???????????????	???????????????????????	?????????????????000001	?????00?000??2?00000
Psasi	???121100101?0?021	0?0????1?????????????	???????????????????????	???100010?01??111111
Ptbar	10001?01002121111320	010/10/101?12111112112	11102111200?11200101	0101101?11201011?111
Ptcam	1?001????0?1?111320	000/11??220???????????	???????????????????????	???11??1?20?????111
Rumcg	?0021?00/10?1?0?0?221	1100?????1010???????	???????????????????????	???110??0??11111111
Secad	004010001?100??020?	1100??1?????????????	???????????????????????	???10000010002?10011
Sepre	00020211001010?0?121	0110??2?????????????	???????????????????????	???10000010010111111
Siham	???????????????????????	???????????????????????	???????????????????????	?????????0?0?????111

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APPENDIX 2 *Continued*

	#161–180	#181–200	#201–220	#221–240		#241–250	#241–250	#241–250
Tanev	100212120010???01230	111????1???????????	?????????????????????	???10000010110111111				
Taocc	10021202001010???230	1100???1???????????	?????????????????????	???100000?1?01111111				
Trlem	0000121120101?0?2??	??????????????????10?	1?????1??0?????????	???001000?0010111111				
Trmon	0000121120101???????	?0?0???????????????	?????????????????????	???0010?010000111111				
Trova	00001??120101????2??	?????????????????????	?????????????????????	???0010?010010111111				
Tsckh	?????????????????????	?????????????????????	?????????????????????	?????????0?0?????111				
Umgal	10001101312121111330	0000?1?1??111?2?12	10102011211?11200???	???11010112010111111				
Ummon	10001101312121111320	001001?0/1?1?1112112	10102011211?21200001	?1?1101011201011?111				
IstypO	00021200001000000210	1100000010000000000	?0010000000?11000101	10010000000010001100				
PdeliO	00021100000000000000	01000000?1?00000000	10010000010?01001101	?10100000000?2001000				
RedelO	00021100101000?00000	11000000?0100011000	10010000000?01000?10	???100000000?2001000				
Alcav	0301000100	Hegaz	2??0110010	Ptlae	2??0110011			
Alcri	230211?000	Hewil	2??0110010	Rumcg	2??011?000			
Aldin	23021111100	Lewil	0??000?00?	Sccad	20021111100			
Alnit	20131111100	Liale	2??0110000	Sepre	2??011?000			
Alret	21231111100	Lidai	2??0110000	Siham	???0??0?00			
Alsim	20031111100	Lifur	2??0110?00	Tanev	2??0110000			
Alsti	20011111000	Meedi	2??0110000	Taocc	2??0110?00			
Alsto	2301001000	Mehip	2??0110000	Trlem	2??0110000			
Altes	202311?000	Meuht	2??0110000	Trmon	2??011?000			
Apdou	2??0110?00	Msbal	2??011?0?0	Trova	2??0110000			
Appri	2??011?010	Mspan	2??0110000	Tsckh	???0??0?00			
Apted	2??0110000	Mdang	2??0110000	Umgal	2??0110010			
Apvet	2??0110010	Mykin	2??0110000	Ummon	2??0110010			
ApDR	2??0110010	Myela	2??0110000	IstypO	1??0010000			
Awhar	23021111100	Myses	2??0110000	PdeliO	0??0000100			
Awmag	23011111100	Nibla	2??0110000	RedelO	0??0000000			
Amsel	2??0110000	Nikoe	2??0110000					
Aneru	2??011?00?	Nilon	2??0110000					
Andes	220111010?	Nimcg	2??0110000					
Anhep	2201110000	Nipet	2??011?000					
Annex	230?11?10?	Nilem	???0??0?00					
Anori	230111110?	Nipro	2??011?000					
Ansht	2??011?00?	Niyea	2??0110?00					
Anshw	230111010?	Orped	0??000?00?					
Adruf	2??0111100	Paame	0301110000					
Caann	0/1??000000?	Paarg	030111?00?					
Cadaw	0??000000?	Paern	0??000000					
Casio	0??000000?	Pamac	001211110?					
Ceane	2??0110000	Pebru	0/1??000000?					
Cehat	2??0110000	Pepla	0??000?00?					
Cemin	2??0110000	Perug	0/1??000?00?					
Cerhi	2??0110000	Plang	0??000000					
Crmil	2??011?000	Plata	0??000000?					
Dkpel	1??000?00?	Pmsin	???0??0?00					
Dklil	1??000?00?	Pyrig	2??0110000					
Docha	0??000?00?	Pralb	0??0??0?0?					
Domon	0??000010?	Prdax	1??000?00?					
Dosha	0??000?00?	Prloh	1??0?10000					
Epspa	0??000?00?	Prmag	0??000?00?					
Ehhos	0??000000?	Prord	???0??0?0?					
Fodru	2??0110000	Prpar	0??000000?					
Gabet	2??0110010	Prrel	1??0000000					
Ganov	2??0110010	Prvet	0??0000100					
Haarb	1??0000000	Psasi	2??011?000					
Hagal	0/1??000?000	Ptbar	2??0110011					
Halio	1??0000000	Ptcam	2??0110011					

APPENDIX 3

PAUP blocks for all analyses. Abbreviated taxon names are the same as those used in Appendix 2.

Analysis 1: Unordered

```
Begin PAUP;
outgroup IstypO PdeliO RedelO;
delete Alcri Ancru Ansht Msbal Perug Prdax Prmag
Prord Psasi Siham Tsckh;
log file=012205unord_slow_display.txt;
hsearch nreps=1000 addseq=random timelimit=3600
limitperrep=yes;
savetrees file=012205unord_slow.tre;
contree /strict = yes majrule=yes
treefile=012205unord_slow_cons.tre;
pscores 1 /ci=yes ri=yes rc=yes hi=yes
scorefile=012205unord_slow_scores.txt;
End;
```

Analysis 2: Semi-ordered, not down-weighted

```
Begin PAUP;
outgroup IstypO PdeliO RedelO;
delete Alcri Ancru Ansht Msbal Perug Prdax Prmag
Prord Psasi Siham Tsckh;
ctype ord:1 8 25 35 37 39 50 54 61 76 79 81 83 116 128
137 140 152 155 174 190 195 197 200 205 215 234
241;
log file=012205semiord_slow_display.txt;
hsearch nreps=1000 addseq=random timelimit=3600
limitperrep=yes;
savetrees file=012205semiord_slow.tre;
contree /strict = yes majrule=yes
treefile=012205semiord_slow_cons.tre;
pscores 1 /ci=yes ri=yes rc=yes hi=yes
scorefile=012205semiord_slow_scores.txt;
End;
```

Analysis 3: Ordered, not down-weighted

```
Begin PAUP;
outgroup IstypO PdeliO RedelO;
delete Alcri Ancru Ansht Msbal Perug Prdax Prmag
Prord Psasi Siham Tsckh;
ctype ord:1 6 8 14 25 29 32 35 37 39 50 51 54 58 61
65 76 79 81 82 83 85 92 94 108 116 123 128 132 133
137 140 143 151 152 155 165 167 169 174 176 179 180
189 190 191 195 197 200 205 211 213 215 217 223 231
234 241 244;
log file=012205ord_slow_display.txt;
hsearch nreps=1000 addseq=random timelimit=3600
limitperrep=yes;
savetrees file=012205ord_slow.tre;
contree /strict = yes majrule=yes
treefile=012205ord_slow_cons.tre;
pscores 1 /ci=yes ri=yes rc=yes hi=yes
scorefile=012205ord_slow_scores.txt;
End;
```

Analysis 4: Semi-ordered, down-weighted

```
Begin PAUP;
outgroup IstypO PdeliO RedelO;
delete Alcri Ancru Ansht Msbal Perug Prdax Prmag
Prord Psasi Siham Tsckh;
ctype ord:1 8 25 35 37 39 50 54 61 76 79 81 83 116 128
137 140 152 155 174 190 195 197 200 205 215 234
241;
wts 0.5:1 8 25 35 37 50 54 61 81 128 137 140 152 155
174 190 195 197 200 205 215 234, 0.33:39 76 79 116
244, 0.2:83;
log file=012205semiord_down_display.txt;
hsearch nreps=1000 addseq=random;
savetrees file=012205semiord_down_big.tre;
contree /strict = yes majrule=yes
treefile=012205semiord_down_cons.tre;
pscores 1 /ci=yes ri=yes rc=yes hi=yes
scorefile=012205semiord_down_scores.txt;
End;
```

Analysis 5: Ordered, down-weighted

```
Begin PAUP;
outgroup IstypO PdeliO RedelO;
delete Alcri Ancru Ansht Msbal Perug Prdax Prmag
Prord Psasi Siham Tsckh;
wts 0.5:1 8 14 25 29 32 35 37 50 51 54 58 61 65 81 82
92 94 108 128 132 137 140 143 151 152 155 165 167
169 174 176 189 190 191 195 197 200 205 215 217 223
231 234 241, 0.33:39 76 79 85 116 123 133 179 180
211 213 244,0.25:6, 0.2:83;
ctype ord:1 6 8 14 25 29 32 35 37 39 50 51 54 58 61
65 76 79 81 82 83 85 92 94 108 116 123 128 132 133
137 140 143 151 152 155 165 167 169 174 176 179 180
189 190 191 195 197 200 205 211 213 215 217 223 231
234 241 244;
log file=012205ord_down_big_displaybuffer.txt;
hsearch nreps=1000 addseq=random;
savetrees file=012205ord_down.tre;
contree /strict = yes majrule=yes
treefile=012205ord_down_cons.tre;
pscores 1 /ci=yes ri=yes rc=yes hi=yes
scorefile=012205ord_down_scores.txt;
End;
```

Secondary analysis, checking 1, 2, and 3 by running with more repetitions and fewer trees per repetition. Identical, but the following is substituted for the search command:

```
hsearch nreps=1000000 addseq=random rear-
rlimit=10000 limitperrep=yes;
```

Addition of poorly known taxa:

```
Begin PAUP;
outgroup IstypO PdeliO RedelO;
```

```
delete Apdou Apted Ceane Cehat Cemin Cerhi Hegaz
Hewil Ptbar Ptcam Ptlae Umgal Ummon Mykin
Myela Myses Apvet ApDR Appri Gabet Ganov Mspan
Mdang Pyrig Trlem Trmon Trova Adruf Lifur Liale
Lidai Taocc Tanev Crmil Nibla Nikoe Nipro Rumcg
Nilon Nimcg Nipet Niyea Nilem Meedi Meuht Mehup
Fodru Sepre Amsel Pmsin;
delete Ancru Ansht Msbal Perug Prdax Prmag Prord
Psasi Siham Tsckh;
```

```
ctype ord:1 8 25 35 37 39 50 54 58 61 65 76 79 81 82
83 118 130 134 140 142 153 154 157 174 176 181 182
191 193 197 199 202 207 213 217 219 225 236 246
247;
```

```
log file=041905other_taxa_displaybuffer.txt;
hsearch nreps=1000000 rearrlimit=10000
limitperrep=yes addseq=random;
savetrees file=041905other_taxa.tre;
contree /strict = yes majrule=yes
treefile=041905other_taxa_cons.tre;
pscores 1 /ci=yes ri=yes rc=yes hi=yes
scorefile=041905other_taxa_scores.txt;
```

Restore Ancru Ansht;

```
delete Alcri Msbal Paarg Perug Prdax Prmag Prord
Psasi Siham Tsckh;
```

```
log file=041905other_taxa_2_displaybuffer.txt;
hsearch nreps=1000000 rearrlimit=10000
limitperrep=yes addseq=random;
savetrees file=041905other_taxa_2.tre;
contree /strict = yes majrule=yes
treefile=041905other_taxa_2_cons.tre;
pscores 1 /ci=yes ri=yes rc=yes hi=yes
scorefile=041905other_taxa_2_scores.txt;
```

Restore Perug Prdax Prmag Prord;

```
delete Alcri Ancru Ansht Msbal Paarg Psasi Siham
Tsckh;
```

```
log file=041905other_taxa_3_displaybuffer.txt;
hsearch nreps=1000000 rearrlimit=10000
limitperrep=yes addseq=random;
savetrees file=041905other_taxa_3.tre;
contree /strict = yes majrule=yes
treefile=041905other_taxa_3_cons.tre;
pscores 1 /ci=yes ri=yes rc=yes hi=yes
scorefile=041905other_taxa_3_scores.txt;
```

delete 1-108;

```
restore Apdou Apted Ceane Cehat Cemin Cerhi Hegaz
Hewil Ptbar Ptcam Ptlae Umgal Ummon Mykin
Myela Myses Apvet ApDR Appri Gabet Ganov Mspan
Mdang Pyrig Trlem Trmon Trova Adruf Lifur Liale
Lidai Taocc Tanev Crmil Nibla Nikoe Nipro Rumcg
Nilon Nimcg Nipet Niyea Nilem Meedi Meuht Mehup
Fodru Sepre Amsel Pmsin;
```

Restore Msbal Psasi Siham Tsckh;

```
log file=041905other_taxa_4_displaybuffer.txt;
hsearch nreps=1000000 rearrlimit=10000
limitperrep=yes addseq=random;
savetrees file=041905other_taxa_4.tre;
contree /strict = yes majrule=yes
treefile=041905other_taxa_4_cons.tre;
pscores 1 /ci=yes ri=yes rc=yes hi=yes
scorefile=041905other_taxa_4_scores.txt;
End;
```

APPENDIX 4

The preferred topology (same as Fig. 7) showing all character changes. Character changes are reconstructed using DELTRAN assumptions for ambiguous branches. Character state changes at nodes are as follows.

Node 1 ch 13 (1→0), ch 58 (1→0), ch 70 (0→1), ch 95 (1→0), ch 129 (0→1), ch 140 (0→2), ch 141 (0→1), ch 144 (0→1), ch 198 (0→1), ch 207 (0→1), ch 232 (1→0)
Node 2 ch 28 (0→1), ch 42 (1→0), ch 61 (2→1), ch 72 (0→1), ch 79 (0→1), ch 85 (3→0), ch 111 (1→0), ch 114 (1→0), ch 128 (0→2), ch 132 (1→2), ch 133 (2→3), ch 134 (1→2), ch 138 (0→1), ch 139 (0→1), ch 167 (2→1), ch 172 (1→2), ch 218 (0→1), ch 225 (0→1), ch 226 (1→0), ch 227 (0→1)

Node 3 ch 22 (0→1), ch 78 (0→1), ch 150 (1→0), ch 168 (1→0), ch 173 (0→1), ch 174 (1→2), ch 179 (2→3), ch 181 (1→0), ch 182 (1→0), ch 194 (0→1), ch 215 (1→2), ch 231 (0→2)

Node 4 ch 90 (0→1), ch 96 (1→0), ch 143 (0→2), ch 144 (1→0), ch 177 (0→1), ch 180 (3→2), ch 231 (2→1), ch 249 (0→1)

Node 5 ch 61 (1→2), ch 64 (0→1), ch 153 (1→0)

Node 6 ch 6 (1→0), ch 51 (1→2), ch 73 (0→1), ch 74 (0→1), ch 76 (1→2), ch 83 (0→2), ch 199 (0→1), ch 200 (1→2), ch 204 (1→0), ch 221 (1→0), ch 229 (0→1)

Node 7 ch 1 (1→0), ch 28 (1→0), ch 62 (0→1), ch 77 (0→1), ch 82 (0→2), ch 102 (0→1), ch 197 (0→1), ch 208 (0→1), ch 213 (2→1)

Node 8 ch 22 (1→0), ch 150 (0→1), ch 179 (3→2), ch 186 (1→0), ch 231 (1→0)

Node 9 ch 73 (1→2), ch 82 (2→1) ch 83 (2→3), ch 92 (1→2), ch 171 (0→1), ch 205 (1→2), ch 249 (1→0)

Node 10 ch 28 (0→1), ch 176 (0→1), ch 218 (1→0), ch 219 (1→0)

Node 11 ch 126 (1→0), ch 142 (0→1), ch 157 (0→1)

Node 12 ch 71 (0→1), ch 94 (1→0), ch 114 (0→1), ch 179 (2→3), ch 195 (0→1), ch 197 (1→2), ch 231 (0→2), ch 249 (0→1)

Node 13 ch 68 (0→1), ch 171 (1→0), ch 202 (0→1), ch 206 (0→1), ch 218 (0→1), ch 250 (0→1)

Node 14 ch 66 (1→0), ch 73 (2→1), ch 79 (1→2)

Node 15 ch 82 (1→2), ch 115 (1→0), ch 205 (2→1)

- Node 16 ch 65 (0→2), ch 80 (1→0), ch 158 (0→1), ch 209 (2→1), ch 210 (0→1), ch 211 (0→2), ch 231 (2→1), ch 249 (1→0)
- Node 17 ch 66 (1→0), ch 73 (2→3), ch 114 (1→0), ch 122 (0→2), ch 195 (1→2), ch 211 (0→1)
- Node 18 ch 70 (1→0), ch 170 (0→3), ch 210 (0→1), ch 211 (0→1)
- Node 19 ch 62 (1→0), ch 65 (0→1), ch 73 (2→0)
- Node 20 ch 28 (1→0), ch 231 (0→1)
- Node 21 ch 1 (1→0), ch 30 (0→1), ch 63 (0→1), ch 64 (0→1), ch 66 (1→0), ch 68 (0→1), ch 108 (0→2), ch 112 (0→1), ch 162 (1→0), ch 170 (0→2), ch 224 (1→0)
- Node 22 ch 122 (0→2), ch 138 (0→1)
- Node 23 ch 83 (3→2), ch 180 (2→3), ch 213 (1→2), ch 219 (0→1), ch 231 (2→1)
- Node 24 ch 34 (1→0), ch 153 (0→1), ch 183 (0→1)
- Node 25 ch 83 (3→2), ch 185 (0→1), ch 189 (1→2)
- Node 26 ch 64 (1→0), ch 82 (2→0), ch 83 (3→2), ch 196 (1→0), ch 200 (2→1), ch 215 (2→1), ch 219 (0→1)
- Node 27 ch 68 (0→1), ch 114 (1→0), ch 171 (1→0), ch 195 (1→2)
- Node 28 ch 65 (2→1), ch 183 (0→1), ch 184 (0→1), ch 196 (1→0)
- Node 29 ch 195 (1→2), ch 211 (2→3), ch 212 (1→0), ch 213 (1→2), ch 218 (0→1)
- Node 30 ch 79 (1→2), ch 184 (0→1), ch 185 (0→1), ch 186 (0→1), ch 196 (1→0), ch 219 (0→1)
- Node 31 ch 31 (0→1), ch 62 (1→0), ch 142 (1→0), ch 143 (2→0)
- Node 32 ch 71 (0→1), ch 82 (1→0), ch 153 (0→2), ch 180 (2→3)
- Node 33 ch 33 (1→0), ch 83 (3→1), ch 150 (1→0), ch 184 (0→1), ch 213 (1→2)
- Node 34 ch 83 (3→2), ch 171 (1→0)
- Node 35
- Node 36 ch 183 (0→1), ch 184 (0→1)
- Node 37 ch 1 (0→1), ch 6 (0→2), ch 114 (0→1), ch 177 (1→0), ch 180 (2→3)
- Node 38 ch 65 (0→2), ch 70 (1→0), ch 211 (0→1), ch 223 (0→1), ch 229 (1→0)
- Node 39 ch 33 (1→0), ch 66 (1→0), ch 71 (0→1), ch 95 (0→1), ch 108 (0→1), ch 158 (0→1), ch 170 (0→3), ch 177 (1→0), ch 180 (2→3), ch 196 (1→0), ch 215 (2→1), ch 218 (1→0)
- Node 40 ch 65 (0→2), ch 158 (0→1), ch 176 (0→1), ch 183 (0→1), ch 189 (1→2), ch 195 (0→1), ch 196 (1→0), ch 233 (1→0)
- Node 41 ch 121 (1→0), ch 167 (1→2), ch 170 (0→3), ch 172 (2→1), ch 185 (0→1), ch 197 (0→2), ch 215 (2→1), ch 219 (1→0), ch 222 (1→0), ch 233 (1→0)
- Node 42 ch 14 (1→0), ch 66 (1→0), ch 73 (0→2), ch 115 (1→0), ch 139 (1→0), ch 141 (1→0), ch 173 (1→0), ch 174 (2→1), ch 224 (1→0)
- Node 43 ch 33 (1→0), ch 59 (0→1), ch 73 (0→2), ch 82 (0→1), ch 92 (1→2), ch 94 (1→0), ch 115 (1→0), ch 176 (0→1), ch 181 (0→1), ch 183 (0→1), ch 184 (0→1), ch 186 (1→0), ch 189 (1→2), ch 216 (0→1), ch 218 (1→0), ch 224 (1→0)
- Node 44 ch 74 (0→1), ch 82 (0→1)
- Node 45 ch 14 (1→0), ch 23 (0→1), ch 54 (0→1), ch 73 (0→1), ch 74 (0→1), ch 85 (0→2), ch 92 (1→2), ch 95 (0→1), ch 113 (1→0), ch 199 (0→1), ch 208 (0→1)
- Node 46 ch 91 (0→1), ch 94 (1→0), ch 96 (1→0), ch 115 (1→0), ch 153 (1→0), ch 170 (0→3), ch 204 (1→0), ch 233 (1→0)
- Node 47 ch 14 (1→0), ch 97 (0→1), ch 134 (1→0)
- Node 48 ch 139 (0→1), ch 144 (1→0), ch 233 (1→0)
- Node 49 ch 2 (1→0), ch 67 (1→0), ch 69 (0→1)
- Node 50 ch 61 (2→1), ch 66 (1→0), ch 67 (1→0), ch 97 (0→1), ch 102 (0→1), ch 111 (1→0), ch 115 (1→0), ch 132 (1→2), ch 134 (1→0), ch 140 (0→1), ch 170 (0→2), ch 204 (1→0), ch 208 (0→1), ch 213 (2→0), ch 216 (0→1), ch 223 (0→1)
- Node 51 ch 12 (1→0), ch 13 (0→1), ch 25 (2→0), ch 27 (0→1), ch 40 (1→0), ch 135 (1→0), ch 141 (1→0), ch 142 (1→0), ch 151 (2→1), ch 156 (0→1), ch 230 (0→1)
- Node 52 ch 2 (0→1), ch 20 (0→1), ch 39 (1→0), ch 44 (1→0), ch 46 (1→0), ch 110 (0→1), ch 116 (1→3), ch 119 (1→0), ch 134 (0→1), ch 149 (1→0), ch 153 (0→1), ch 155 (0→2), ch 165 (0→2), ch 167 (0→2), ch 169 (0→1), ch 235 (0→1), ch 244 (2→0), ch 247 (1→0)
- Node 53 ch 105 (1→0), ch 107 (1→0), ch 113 (0→1), ch 118 (0→1), ch 127 (1→0), ch 154 (2→1), ch 168 (0→1), ch 170 (1→0), ch 174 (0→1), ch 234 (2→0), ch 238 (0→1)
- Node 54 ch 226 (0→1), ch 230 (1→0)
- Node 55 ch 4 (0→2), ch 6 (3→2), ch 10 (1→0), ch 21 (1→0), ch 48 (0→1), ch 104 (0→1), ch 122 (0→2), ch 144 (1→0), ch 233 (0→1)
- Node 56 ch 14 (0→1), ch 42 (0→1), ch 53 (0→1), ch 88 (2→1), ch 92 (1→0)
- Node 57 ch 9 (1→0), ch 32 (1→2), ch 36 (0→1), ch 54 (0→1), ch 58 (2→1), ch 85 (0→3), ch 117 (0→1), ch 183 (1→0), ch 215 (0→1), ch 219 (1→0)
- Node 58 ch 54 (1→2), ch 94 (0→1), ch 96 (0→1), ch 122 (2→3), ch 136 (2→1), ch 139 (1→0), ch 175 (0→1), ch 178 (0→1), ch 180 (2→3), ch 188 (0→1), ch 190 (1→2), ch 192 (0→1), ch 196 (0→1), ch 201 (0→1), ch 213 (0→2)
- Node 59 ch 4 (2→0), ch 59 (1→0), ch 61 (0→2), ch 95 (0→1), ch 152 (0→2), ch 179 (1→2)
- Node 60 ch 43 (0→1), ch 86 (0→1), ch 91 (1→0), ch 114 (0→1), ch 217 (1→0), ch 223 (1→0), ch 232 (0→1)
- Node 61 ch 38 (0→1), ch 53 (1→0), ch 54 (2→0), ch 69 (1→0), ch 76 (0→1), ch 92 (0→1), ch 104 (1→0), ch 117 (0→1), ch 162 (0→1), ch 186 (0→1), ch 187 (0→1), ch 191 (0→1), ch 193 (0→1), ch 203 (0→1)
- Node 62 ch 16 (1→0), ch 83 (0→2)
- Node 63 ch 16 (1→0), ch 105 (0→1), ch 124 (0→1), ch 130 (0→1), ch 154 (1→2), ch 175 (1→0), ch 183 (0→1), ch 192 (1→0)

- Node 64 ch 21 (0→1), ch 37 (0→1), ch 49 (0→1), ch 61 (2→0), ch 96 (1→0), ch 98 (0→1), ch 127 (0→1), ch 133 (2→3), ch 136 (1→2), ch 137 (0→1), ch 148 (0→1), ch 226 (1→0)
- Node 65 ch 1 (1→2), ch 52 (0→1), ch 57 (1→0), ch 60 (0→1), ch 76 (1→2), ch 78 (0→1), ch 94 (1→2), ch 97 (0→1), ch 119 (0→1), ch 134 (1→0), ch 140 (0→1), ch 152 (2→1), ch 169 (1→2), ch 181 (1→0), ch 182 (1→0), ch 188 (1→0), ch 222 (1→0)
- Node 66 ch 15 (1→0), ch 63 (0→1), ch 68 (0→2), ch 85 (3→0), ch 114 (1→0), ch 191 (1→2)
- Node 67 ch 14 (1→0), ch 66 (1→0), ch 76 (2→3), ch 83 (0→5), ch 106 (1→0), ch 152 (1→2), ch 168 (1→0)
- Node 68 ch 58 (1→2), ch 59 (0→1), ch 68 (0→2), ch 152 (2→0), ch 169 (1→2), ch 181 (1→0)
- Node 69 ch 38 (0→1), ch 68 (0→1), ch 86 (0→1), ch 94 (0→2)
- Node 70 ch 37 (0→2), ch 67 (1→0), ch 124 (0→1)
- Node 71 ch 34 (1→0), ch 54 (1→2), ch 70 (0→1), ch 81 (0→2)
- Node 72 ch 97 (0→1), ch 98 (0→1), ch 168 (1→0), ch 170 (0→3), ch 182 (1→0)
- Node 73 ch 139 (1→0), ch 234 (0→1)
- Node 74 ch 4 (2→0), ch 27 (1→0), ch 96 (0→1), ch 122 (2→1), ch 232 (0→1)
- Node 75 ch 115 (1→0)
- Node 76 ch 26 (0→1), ch 29 (0→2), ch 38 (0→1), ch 47 (0→1), ch 54 (0→1), ch 107 (1→0), ch 110 (0→1), ch 112 (0→1), ch 132 (1→0), ch 136 (2→1), ch 143 (0→1), ch 152 (0→2), ch 167 (0→1), ch 213 (0→1), ch 234 (2→0), ch 248 (0→1)
- Node 77 ch 2 (0→1), ch 3 (1→0), ch 31 (0→1), ch 116 (1→3), ch 146 (0→1), ch 163 (0→1), ch 164 (0→3), ch 165 (0→1), ch 169 (0→1), ch 181 (1→0), ch 217 (1→0), ch 220 (1→0), ch 230 (0→1), ch 237 (1→0), ch 244 (2→3)
- Node 78 ch 118 (0→1), ch 123 (0→1), ch 148 (0→1), ch 243 (0→2)
- Node 79 ch 28 (0→1), ch 29 (2→1), ch 32 (1→2), ch 37 (0→1), ch 149 (1→0), ch 152 (2→1), ch 164 (0→2), ch 165 (0→1), ch 228 (0→1), ch 230 (0→1), ch 237 (1→0), ch 242 (0→3)
- Node 80 ch 2 (0→1), ch 15 (1→0), ch 23 (0→1), ch 27 (0→1), ch 53 (0→1), ch 61 (0→2), ch 66 (1→0), ch 108 (0→1), ch 180 (2→3), ch 219 (1→0)
- Node 81 ch 6 (2→1), ch 37 (0→2), ch 50 (1→2), ch 55 (1→0), ch 88 (1→2), ch 122 (3→0), ch 150 (0→1), ch 160 (0→1), ch 165 (2→0), ch 219 (0→1), ch 230 (0→1)
- Node 82 ch 38 (1→0)
- Node 83 ch 14 (1→0), ch 15 (1→0)
- Node 84 ch 57 (0→1), ch 74 (0→1), ch 81 (0→2), ch 91 (0→1), ch 92 (1→0), ch 108 (0→1), ch 113 (1→0), ch 116 (3→1), ch 117 (0→1), ch 119 (1→0), ch 122 (3→1), ch 140 (1→0), ch 156 (1→0), ch 164 (0→1), ch 170 (0→1), ch 194 (0→1), ch 197 (0→2), ch 200 (1→2), ch 205 (1→0), ch 208 (0→1), ch 213 (2→3), ch 215 (1→0), ch 216 (0→1), ch 217 (0→1), ch 219 (0→1), ch 220 (1→0), ch 230 (0→1), ch 231 (0→1), ch 233 (1→0), ch 234 (0→1), ch 235 (1→0), ch 237 (1→0), ch 247 (0→1), ch 248 (0→1)
- Node 85 ch 23 (0→1), ch 30 (0→1), ch 45 (0→1), ch 59 (0→1), ch 82 (0→1), ch 88 (1→2), ch 111 (1→0), ch 115 (1→0), ch 137 (1→2), ch 176 (0→2), ch 217 (0→3)
- Node 86 ch 34 (1→0), ch 45 (0→1), ch 58 (1→2), ch 83 (0→4), ch 105 (1→0), ch 115 (1→0), ch 205 (1→0)
- Node 87 ch 20 (0→1), ch 23 (0→1), ch 85 (3→1), ch 88 (1→0), ch 91 (0→1), ch 184 (0→1), ch 207 (0→1), ch 215 (1→2), ch 235 (1→0)
- Node 88 ch 119 (0→1), ch 152 (2→0), ch 179 (2→0), ch 180 (3→2), ch 182 (1→0), ch 228 (0→1)
- Node 89 ch 1 (1→2), ch 14 (1→0), ch 52 (0→1), ch 54 (0→1), ch 60 (0→1), ch 113 (1→0), ch 115 (1→0), ch 168 (1→0)
- Node 90 ch 20 (0→1), ch 66 (1→0), ch 99 (0→1), ch 114 (1→0), ch 184 (0→1), ch 230 (0→1)
- Node 91 ch 81 (0→2), ch 118 (1→0), ch 132 (1→0), ch 168 (1→0), ch 180 (3→2), ch 234 (0→1)
- Node 92 ch 14 (1→0), ch 37 (0→1), ch 47 (0→1), ch 68 (0→1), ch 88 (1→2), ch 102 (0→1), ch 113 (1→0), ch 130 (0→1), ch 140 (0→2), ch 143 (0→2), ch 184 (0→1)
- Node 93 ch 23 (0→1), ch 85 (3→1), ch 122 (3→0), ch 132 (1→0), ch 144 (0→1), ch 205 (1→0), ch 219 (0→1)
- Node 94 ch 12 (0→1), ch 14 (1→0), ch 27 (1→0), ch 68 (0→1), ch 87 (0→1), ch 91 (1→0), ch 103 (0→1), ch 113 (1→0), ch 121 (1→0), ch 132 (1→0), ch 140 (0→2), ch 197 (0→1)
- Node 95 ch 14 (1→0), ch 61 (0→2), ch 76 (0→1), ch 87 (0→1), ch 91 (1→0), ch 121 (1→0), ch 130 (0→1), ch 138 (0→1), ch 169 (1→0), ch 178 (0→1)
- Node 96 ch 4 (2→0), ch 52 (0→1), ch 68 (1→2), ch 69 (1→0), ch 122 (2→3)
- Node 97 ch 76 (0→1), ch 114 (0→1), ch 122 (2→0), ch 175 (0→1)
- Node 98 ch 38 (1→0), ch 68 (1→2), ch 85 (3→0), ch 87 (0→1), ch 88 (1→0), ch 114 (0→1), ch 221 (1→0), ch 228 (0→1), ch 232 (0→1)
- Node 99 ch 57 (1→0), ch 85 (3→2)
- Node 100 ch 138 (0→1), ch 228 (0→1), ch 234 (0→1)
- Node 101 ch 21 (0→1), ch 28 (0→1), ch 45 (0→1), ch 54 (1→2), ch 56 (1→0), ch 81 (0→1), ch 87 (0→1), ch 125 (0→1), ch 139 (1→0), ch 168 (1→0), ch 170 (0→3), ch 180 (2→3)
- Node 102 ch 45 (0→1), ch 56 (1→0)
- Node 103 ch 19 (1→0), ch 27 (1→0), ch 28 (0→1), ch 45 (0→1), ch 55 (1→0), ch 56 (1→0), ch 59 (1→0), ch 61 (0→2), ch 67 (1→0), ch 85 (0→1), ch 101 (1→0), ch 103 (1→0), ch 240 (1→0)
- Node 104 ch 9 (1→0), ch 16 (1→0), ch 37 (0→1), ch 54 (0→1), ch 69 (1→0), ch 114 (0→1), ch 121 (1→0), ch 132 (1→2), ch 166 (0→1), ch 168 (1→0), ch 169 (1→0), ch 170 (0→3), ch 181 (1→0)

- Node 105 ch 153 (1→0), ch 160 (0→1), ch 172 (1→2), ch 228 (0→1), ch 232 (0→1)
- Node 106 ch 114 (0→1), ch 125 (0→1), ch 130 (0→1), ch 132 (1→0), ch 139 (1→0), ch 166 (0→1), ch 182 (1→0), ch 184 (0→1), ch 189 (1→2), ch 233 (0→1)
- Node 107 ch 1 (1→2), ch 14 (0→1), ch 15 (1→0), ch 32 (1→2), ch 34 (1→0), ch 36 (0→1), ch 37 (0→2), ch 45 (0→1), ch 51 (1→0), ch 56 (1→0), ch 59 (1→0), ch 70 (0→1), ch 92 (1→0), ch 94 (0→2), ch 117 (0→1), ch 124 (0→1), ch 125 (0→1), ch 132 (1→2), ch 148 (0→1), ch 170 (1→3), ch 175 (0→1), ch 180 (2→0), ch 234 (2→1)
- Node 108 ch 8 (2→1), ch 39 (1→2), ch 42 (0→1), ch 47 (0→1), ch 53 (0→1), ch 54 (0→1), ch 55 (1→0), ch 101 (1→0), ch 109 (1→0), ch 111 (1→0), ch 121 (1→0), ch 128 (0→1), ch 133 (2→3), ch 138 (1→0), ch 139 (1→0), ch 140 (0→2), ch 146 (0→1), ch 155 (0→1), ch 161 (1→0), ch 164 (0→4), ch 179 (1→2), ch 180 (2→0), ch 237 (1→0), ch 248 (0→1)
- Node 109 ch 114 (0→1), ch 153 (0→2), ch 154 (2→0), ch 155 (0→2), ch 167 (1→0), ch 179 (1→2), ch 234 (0→1), ch 248 (1→0)
- Node 110 ch 32 (1→2), ch 36 (0→1), ch 39 (1→2), ch 47 (1→0), ch 53 (0→1), ch 66 (1→0), ch 85 (0→3), ch 87 (0→1), ch 132 (0→1), ch 136 (1→2), ch 155 (0→1), ch 242 (0→1)
- Node 111 ch 10 (1→0), ch 28 (0→1), ch 45 (0→1), ch 85 (0→1), ch 88 (2→1), ch 114 (0→1), ch 179 (1→2), ch 189 (1→0), ch 243 (0→1)
- Node 112 ch 1 (1→2), ch 4 (0→2), ch 6 (3→4), ch 13 (0→1), ch 31 (0→1), ch 61 (0→2), ch 72 (0→1), ch 146 (0→1), ch 163 (0→1), ch 164 (0→1), ch 183 (1→0), ch 244 (2→3)
- Node 113 ch 107 (0→1), ch 112 (1→0), ch 116 (1→0), ch 121 (1→0), ch 127 (1→0), ch 149 (1→0), ch 155 (0→1), ch 242 (0→3), ch 248 (1→0)
- Node 114 ch 13 (0→1), ch 116 (1→3), ch 179 (1→3), ch 190 (1→0)
- Node 115 ch 10 (1→0), ch 12 (1→0), ch 39 (1→2), ch 85 (0→2), ch 118 (0→1), ch 140 (0→1), ch 143 (1→2), ch 169 (0→1), ch 183 (1→0), ch 213 (1→2), ch 215 (0→1), ch 244 (2→1)
- Node 116 ch 34 (1→0), ch 118 (0→1), ch 169 (0→1), ch 179 (1→2), ch 234 (0→1)
- Node 117 ch 45 (0→1), ch 113 (1→0), ch 118 (1→0)
- Node 118 ch 40 (0→1), ch 51 (0→1), ch 132 (1→0), ch 192 (1→0), ch 217 (0→1)
- Node 119 ch 35 (1→2), ch 107 (0→1), ch 161 (2→1), ch 228 (0→1)
- Node 120 ch 180 (0→2)
- Node 121 ch 241 (0→1)
- Node 122 ch 1 (0→1), ch 4 (0→1), ch 6 (0→1), ch 17 (0→1), ch 93 (0→1), ch 181 (0→1), ch 228 (1→0)
- Node 123 ch 16 (0→1), ch 57 (0→1), ch 61 (2→0), ch 136 (0→1), ch 205 (0→1)
- Node 124 ch 8 (0→1), ch 33 (0→1), ch 89 (1→0), ch 144 (0→1), ch 164 (0→1), ch 189 (0→1), ch 241 (1→0)
- Node 125 ch 6 (1→3), ch 39 (3→1), ch 133 (0→2), ch 139 (0→1), ch 165 (2→0), ch 236 (0→1)
- Node 126 ch 2 (1→0), ch 4 (1→2), ch 5 (0→1), ch 7 (0→1), ch 20 (0→1), ch 21 (0→1), ch 25 (0→1), ch 50 (0→1), ch 53 (1→0), ch 105 (0→1), ch 111 (0→1), ch 138 (0→1), ch 146 (0→1), ch 151 (1→2), ch 154 (1→0), ch 159 (0→1), ch 167 (1→0), ch 172 (0→1), ch 244 (0→1)
- Node 127 ch 3 (1→0), ch 12 (0→1), ch 91 (0→1), ch 115 (0→1), ch 132 (0→1), ch 135 (0→1), ch 142 (0→1), ch 164 (1→0), ch 200 (0→1)
- Node 128 ch 75 (0→1), ch 136 (1→2), ch 245 (0→1), ch 246 (0→1)
- Node 129 ch 4 (2→0), ch 8 (1→2), ch 109 (0→1), ch 116 (0→1), ch 127 (0→1), ch 141 (0→1), ch 242 (3→0), ch 247 (0→1)
- Node 130 ch 25 (1→2), ch 120 (0→1), ch 121 (0→1), ch 146 (1→0), ch 239 (0→1), ch 241 (0→2)
- Node 131 ch 26 (0→1), ch 28 (0→1), ch 48 (0→1), ch 215 (0→1), ch 217 (1→0)
- Node 132 ch 116 (0→1), ch 131 (0→1), ch 151 (1→0), ch 166 (0→1), ch 226 (0→1), ch 228 (0→1)
- Node 133 ch 6 (1→2), ch 11 (0→1), ch 12 (0→1), ch 32 (0→1), ch 54 (0→2), ch 55 (1→0), ch 56 (0→1), ch 114 (0→1), ch 161 (1→2)
- Node 134 ch 19 (1→0), ch 28 (0→1), ch 44 (1→0), ch 59 (0→1), ch 121 (0→1), ch 239 (0→1), ch 241 (0→2), ch 244 (0→1)
- Node 135 ch 4 (1→0), ch 27 (0→1), ch 39 (3→0), ch 75 (0→1), ch 106 (1→0), ch 116 (0→2), ch 120 (0→1), ch 141 (0→1), ch 171 (0→1), ch 172 (0→1), ch 234 (2→0), ch 245 (0→1), ch 246 (0→1)
- Node 136 ch 6 (2→1), ch 8 (1→0), ch 21 (0→1), ch 29 (0→1), ch 36 (0→1), ch 46 (1→0), ch 104 (0→1), ch 105 (0→1), ch 109 (0→1), ch 118 (0→1), ch 123 (0→1), ch 134 (0→1), ch 171 (1→0), ch 248 (0→1)
- Node 137 ch 134 (0→1), ch 161 (1→2), ch 172 (0→1), ch 234 (2→1)
- Node 138 ch 108 (0→2), ch 116 (0→1), ch 118 (0→1), ch 131 (0→1), ch 172 (0→1)
- Node 139 ch 9 (1→0), ch 14 (0→1), ch 18 (0→1), ch 27 (0→1), ch 28 (0→1), ch 39 (3→2), ch 116 (0→1), ch 120 (0→1), ch 147 (0→1)
- Node 140 ch 33 (0→1), ch 57 (0→1), ch 146 (0→1), ch 214 (1→0)
- Node 141 ch 18 (1→0), ch 151 (1→0), ch 154 (1→0)
- Node 142 ch 3 (0→1), ch 23 (1→0), ch 32 (0→1), ch 45 (1→0), ch 56 (0→1), ch 59 (0→1), ch 66 (0→1), ch 154 (0→2), ch 223 (0→1), ch 240 (0→1), ch 244 (1→2)
- Node 143 ch 13 (0→1), ch 32 (0→2), ch 40 (1→0), ch 46 (1→0), ch 75 (1→0), ch 112 (0→1)
- Node 144 ch 27 (0→1), ch 28 (0→1), ch 47 (0→1), ch 48 (0→1), ch 74 (0→1), ch 85 (0→2), ch 86 (0→1), ch 107 (1→0), ch 108 (0→1), ch 132 (1→0), ch 163 (0→1), ch 243 (0→1), ch 244 (1→2), ch 248 (0→1)

Node 145 ch 121 (0→1)

Node 146 ch 1 (1→2), ch 6 (3→4), ch 10 (1→0), ch 13 (0→1), ch 14 (0→1), ch 23 (1→0), ch 33 (1→0), ch 47 (0→1), ch 54 (0→1), ch 85 (0→2), ch 88 (2→1), ch 127 (0→1), ch 128 (0→1), ch 139 (1→0), ch 147 (0→1), ch 180 (2→1), ch 237 (1→0), ch 244 (1→0)

Node 147 ch 2 (0→1), ch 21 (1→0), ch 24 (0→1), ch 32 (0→1), ch 41 (1→0), ch 50 (1→0), ch 64 (0→1), ch 66 (0→1), ch 101 (1→0), ch 107 (1→0), ch 109 (0→1), ch 116 (0→1), ch 149 (1→0), ch 152 (0→1), ch 155 (0→1), ch 188 (0→1), ch 190 (1→0), ch 220 (1→0), ch 228 (0→1), ch 248 (0→1)

Node 148 ch 14 (0→1), ch 29 (0→1), ch 32 (0→1), ch 38 (0→1), ch 45 (1→0), ch 56 (0→1), ch 59 (0→1), ch 66 (0→1), ch 120 (0→1), ch 143 (0→1), ch 237 (1→0), ch 239 (0→1), ch 245 (0→1), ch 246 (0→1)

Node 149 ch 40 (1→0), ch 101 (0→1), ch 156 (0→1), ch 180 (2→3), ch 181 (1→0), ch 183 (1→0), ch 248 (0→1)

Node 150 ch 46 (1→0), ch 133 (2→1), ch 136 (1→0), ch 161 (1→0), ch 164 (1→0), ch 180 (2→3)

Node 151 ch 118 (0→1), ch 119 (1→0), ch 127 (0→1), ch 132 (0→1), ch 150 (0→1), ch 152 (0→2), ch 156 (0→1), ch 159 (0→1), ch 179 (1→2)

Node 152 ch 1 (1→0), ch 16 (1→0), ch 18 (0→1), ch 20 (0→1), ch 39 (3→1), ch 45 (1→0), ch 63 (0→1), ch 72 (0→1), ch 101 (0→1), ch 118 (0→1), ch 136 (1→0), ch 143 (0→1), ch 146 (0→1), ch 147 (0→1), ch 165 (2→0), ch 167 (1→0), ch 180 (2→0), ch 183 (1→0)

Node 153 ch 45 (1→0), ch 122 (0→3), ch 128 (0→1), ch 133 (0→1), ch 145 (1→0), ch 164 (1→3), ch 237 (1→0), ch 247 (0→1)

Node 154 ch 85 (0→2), ch 88 (2→1), ch 136 (1→0), ch 144 (1→0), ch 164 (1→4), ch 165 (2→1), ch 167 (1→0), ch 228 (0→1)

Node 155 ch 8 (1→0), ch 14 (0→1), ch 29 (0→2), ch 38 (0→1), ch 45 (1→0), ch 46 (1→0), ch 61 (0→2), ch 105 (0→1), ch 109 (0→1), ch 111 (0→1), ch 122 (0→3), ch 123 (0→1), ch 140 (0→2), ch 164 (1→0), ch 236 (0→1), ch 237 (1→0), ch 242 (3→2)

Node 156 ch 106 (0→1), ch 114 (1→0), ch 122 (0→3), ch 133 (0→1), ch 136 (1→0), ch 244 (1→0)

Node 157 ch 114 (1→0), ch 146 (0→1), ch 237 (1→0), ch 244 (1→0)

Node 158 ch 123 (0→2), ch 125 (0→1), ch 131 (0→1), ch 133 (0→1), ch 135 (0→1), ch 142 (0→1), ch 153 (0→2), ch 180 (2→0), ch 248 (0→1)

Node 159 ch 5 (0→1), ch 36 (0→1), ch 44 (0→1), ch 101 (0→1), ch 105 (0→1), ch 109 (0→1), ch 115 (0→1), ch 116 (2→3), ch 118 (0→1), ch 126 (1→0), ch 127 (0→1), ch 128 (0→1), ch 133 (0→3), ch 136 (1→2), ch 146 (0→1), ch 153 (0→1), ch 156 (0→1), ch 165 (2→1), ch 225 (0→1), ch 234 (0→1), ch 240 (0→1), ch 242 (3→2), ch 248 (0→1)

Node 160 ch 38 (0→1), ch 39 (3→2), ch 40 (1→0), ch 41 (1→0), ch 54 (2→1), ch 61 (0→2), ch 72 (0→1), ch 107 (1→0), ch 113 (0→1), ch 116 (0→3), ch 118 (0→1),

ch 134 (0→1), ch 154 (1→0), ch 164 (1→3), ch 234 (2→1), ch 247 (0→1)

Node 161 ch 27 (0→1), ch 39 (3→0), ch 55 (1→0), ch 80 (1→0), ch 116 (0→2), ch 133 (0→1), ch 139 (0→1), ch 146 (0→1), ch 179 (1→0), ch 204 (1→0), ch 234 (2→0)

Node 162 ch 11 (0→1), ch 14 (0→1), ch 19 (1→0), ch 21 (0→1), ch 39 (3→0), ch 45 (1→0), ch 46 (1→0), ch 51 (1→0), ch 122 (0→3), ch 179 (1→2), ch 180 (2→3), ch 189 (0→1)

Node 163 ch 116 (0→2), ch 146 (0→1)

Node 164 ch 119 (1→0), ch 133 (0→1), ch 146 (0→1), ch 150 (0→1), ch 234 (2→0)

Node 165 ch 134 (0→1), ch 136 (0→1), ch 143 (0→1), ch 144 (0→1), ch 234 (2→1)

Node 166 ch 132 (0→2), ch 139 (0→1), ch 150 (0→1), ch 161 (1→0), ch 236 (0→1)

Node 167 ch 18 (0→1), ch 39 (3→1), ch 89 (1→0), ch 143 (0→1), ch 144 (0→1)

Node 168 ch 12 (0→1), ch 35 (1→2), ch 41 (1→0), ch 61 (2→0), ch 220 (1→0)

Node 169 ch 16 (0→1), ch 55 (1→0), ch 110 (0→1), ch 120 (1→0), ch 218 (0→1), ch 234 (2→0), ch 241 (0→1)

Node 170 ch 35 (1→0), ch 93 (0→1), ch 107 (0→1), ch 108 (0→2), ch 116 (1→2), ch 121 (0→1), ch 141 (0→1), ch 237 (1→0)

Node 171 ch 19 (1→0), ch 45 (1→0), ch 46 (1→0), ch 56 (0→1), ch 128 (0→1)

Node 172 ch 107 (0→1), ch 114 (0→1), ch 155 (0→1), ch 234 (2→0), ch 241 (0→1)

Node 173 ch 3 (1→0), ch 39 (3→1), ch 44 (1→0), ch 101 (0→1), ch 144 (0→1), ch 152 (0→1), ch 167 (1→0)

Node 174 ch 14 (0→2), ch 21 (0→1), ch 24 (0→1), ch 39 (3→0), ch 108 (0→2), ch 123 (0→2), ch 146 (0→1), ch 216 (0→1)

Node 175 ch 123 (0→1), ch 125 (0→1), ch 134 (0→1), ch 153 (0→2), ch 172 (0→1)

APPENDIX 5

Institute abbreviations: AMNH, American Museum of Natural History; JODA, John Day Fossil Beds National Monument; KUVF, University of Kansas Museum of Natural History; LACM, Los Angeles County Museum; MVZ, University of California Museum of Vertebrate Zoology; NALMA, North American Land Mammal Age; SDSM, South Dakota School of Mines and Technology; UCMP, University of California Museum of Paleontology; UNSM, University of Nebraska State Museum; UOMNH, University of Oregon Museum of Natural History; UWBM, University of Washington Burke Museum.