SYSTEMATICS OF THE DROMOMERYCINES AND ALETOMERYCINES (ARTIODACTYLA: PALAEOMERYCIDAE) FROM THE MIOCENE AND PLIOCENE OF NORTH AMERICA

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Abstract—The subfamilies Dromomerycinae and Aletomerycinae were part of an endemic radiation of North American Miocene and Pliocene cervid ruminant artiodactyls characterized by a variety of bony horns. Their species-level systematics has not been reviewed since Frick (1937), and the groups were oversplit with many redundant subgenera and 49 named species, most of which were *nomina nuda* (no diagnosis provided) and have not been analyzed since 1937. We use modern biological species concepts and statistical methods to greatly reduce the number of valid taxa in the subfamily. Among the Aletomerycinae, the late Arikareean immigrant *Aletomeryx* contains three species, *A. gracilis* (with three junior synonyms), *A. marslandensis*, and *A. occidentalis*. The peculiar, curve-horned *Sinclairomeryx* is monotypic; two other species are junior synonyms of *S. riparius*. Among the Dromomerycinae, *Drepanomeryx* (*Mathomeryx*) *matthewi* is a junior synonym of *D. falciformis*. The bow-horned *Rakomeryx* *sinclairi* is also monotypic, with five junior synonyms. Straight-horned *Dromomeryx borealis* is also monotypic (with three synonyms), as is *Subdromomeryx antilopinus* (raised to generic rank), which has four junior synonyms. As part of the simultaneous immigration event of the Cranioceratini in the late Arikareean, there is only one valid species, *Barbouromeryx trigonocorneus*, with two additional invalid subgenera and three invalid species. The common genus *Bouromeryx*, which had been split into eight species, contains only two: the smaller late Hemingfordian *B. submilleri*, and the Barstovian *B. americanus*. The monotypic three-horned *Procranioceras skineri* remains valid, but is elevated to generic rank. *Cranioceras*, which has two straight supraorbital horns and its posteriorly-oriented occipital horn, once contained seven species, but now consists of the larger *C. unicorns* and the smaller *C. teres*. The Hemphillian cranioceratins *Yumaceras* (elevated to generic rank) still has three valid species, and *Pediomeryx hemphillensis* (with two synonyms) of the late Hemphillian is the last member of the lineage. Thus, 49 previously recognized species has been reduced to just 18 species in 12 genera (most of which are now monotypic) with no subgenera. This clarification of the taxonomic confusion of such an important group greatly enhances their usefulness in biostratigraphy and paleoecology.

INTRODUCTION

The dromomerycines and aletomerycines were deer-like groups of ruminant artiodactyls found in North America during the Miocene and earliest Pliocene (Fig. 1). Most had brachyodont to mesodont dentitions and (based on the antorbital fenestrae in the skull) apparently had deer-like antorbital glands for scent marking. Dromomerycines and aletomerycines were distinguished by a great variety of bony horns with expanded terminal bulbs and no evidence for deciduous tips (unlike the partially deciduous horns in antilocaprids, or the completely deciduous antlers in cervids). Unfortunately, Frick (1937) illustrated these appendages with deciduous tips like those of pronghorns, and this practice was followed by later illustrators (e.g., Scheele, 1955). (In this paper, we will follow the common usage of “horn” instead of the more cumbersome but neutral “cranial appendage,” recognizing that palaeomercine “horns” were probably not covered by a keratin sheath as in the true horns of bovids). Nearly all skulls of presumed males have unbranched paired supraorbital horns, and the presumed males of the tribe Cranioceratini have a occipital horns as well. According to Janis and Manning (1998) and Semprebon et al. (2004), dromomercines and aletomercines were mostly browsers living in subtropical to temperate habitats from moderately open bushland/grassland ecotone to dense woodlands and thickets. They are apparently related to the European genus *Palaeomeryx* (family Palaeomerycidae), but dromomercines and aletomercines developed at least two endemic evolutionary radiations in North America after their first arrival in the late Arikareean around 19 Ma. They quickly diversified in the Hemingfordian, and (like many other mammalian groups, such as pronghorns and horses) reached peak diversity in the early Barstovian, after which they underwent both diversity decline and an increase in body size during the Clarendonian and Hemphillian (Webb, 1983; Janis and Manning, 1998). According to Janis and Manning (1998), both of these changes were due to the increased aridity and more open habitat, and the decline of their preferred subtropical/temperate brushy/woodland habitat. The last known dromomercine, *Pediomeryx hemphillensis*, is found alongside the first true cervid to immigrate to North America in the latest Hemphillian (earliest Pliocene, *fide* Tedford et al., 2004). Presumably the cervids took over this woodland browser habitat from the declining dromomercines, or possibly cervids outcompeted the dromomercines (Voorhies, 1990; Webb, 1998), although Janis and Manning (1998) and Janis (2000) relate their extinction to climatic events, not to competition from immigrant cervids. As Janis and Manning (1988, p. 488-489) noted, dromomercines follow the trend seen in many other groups in that the late Hemphillian taxa were smaller than early and middle Hemphillian forms.

Cope described the first known dromomercine, *“Cosoryx” teres* (Cope, 1874) from the Clarendonian Chamita Formation of New Mexico, and *“Blasteromyx” borealis* (Cope, 1878), based on a partial skull from the Barstovian Deep River beds of Montana. At that time, Cope used the genus *Blastomeryx* as a wastebasket for a variety of ruminants, including several antilocaprids and dromomercines, as well as blastomercines. Scott (1895) first noted that *“Blasteromyx” borealis* resembled the European genus *Palaeomeryx*. Douglass (1899, 1903) described additional material, and both Douglass (1903) and Matthew (1904, 1909) referred this material to *Palaeomeryx borealis*. In 1909, Earl Douglass recovered nearly complete skeletal material of *“Blasteromyx” borealis* from the Deep River beds, and renamed it *Dromomeryx borealis*. In the ensuing years, several more taxa were discovered, but were not considered related to *“Blasteromyx” borealis*. Sinclair (1915) described *Drepanomeryx* as an antelope; Matthew (1918) described *Cranioceras* and also thought it was an antelope. Lull (1920) described *Aletomeryx*, but thought that it
Aletomeryx gracilis (after Lull, 1920).

Frick’s (1945, p. 267, note 1) noted that, “Frick’s taxonomic system is not, and authors, or treated as genera (e.g., Janis and Manning, 1998). Simpson (1937) did not indicate to which subgenera his genera were attached, and most of these subgenera are so poorly defined, cumbersome, or redundant that they have been ignored by later authors, or treated as genera (e.g., Janis and Manning, 1998). Simpson (1945, p. 267, note 1) noted that, “Frick’s taxonomic system is not, and was not intended to be, comparable with that of anyone else. Frick’s genera were attached, and most of these subgenera are so poorly defined, cumbersome, or redundant that they have been ignored by later authors, or treated as genera (e.g., Janis and Manning, 1998). Simpson (1937) did not indicate to which subgenera his genera were attached, and most of these subgenera are so poorly defined, cumbersome, or redundant that they have been ignored by later authors, or treated as genera (e.g., Janis and Manning, 1998).

Figurably in the case of the Cranioceratinae, may be assigned to the wrong subfamilies on subgenera, without any included genus.” A much more serious problem is the fact that most of his new taxa were inadequately diagnosed, so it is not possible for later workers to tell how Frick (1937) distinguished them. The requirement that all valid species have a diagnosis was introduced to zoology during the International Zoological Congress in Monaco in 1913, and came into effect on January 1, 1931, after the International Zoological Congress in Padua in 1930. According to Article 13.1.1 of the current International Code of Zoological Nomenclature (1999), all names published after 1930 require a diagnosis. If they do not have one, they are nomina nuda. It is unclear why Frick did not follow the requirements of the codes of zoological nomenclature, but they were in force by 1930, and therefore binding on Frick’s (1937) taxonomy. Nearly all of Frick’s (1937) taxa are nomina nuda by this criterion. The current Code recommends that these names should not be used, but later authors (e.g., Janis and Manning, 1998) have validated many of the generic (but not trivial) names despite their inadequate diagnoses.

In most cases, it is impossible to see how anyone can distinguish most of the named species, since Frick performed no statistical comparisons. He typically measured a only few specimens and then grouped them into rough size classes labeled by Roman numerals, but never used the statistical techniques that were coming into biology at the time, nor did he ever plot data from the specimens in a useful fashion. It is clear from a close examination of Frick’s specimens and his published work that his thinking was strictly nineteenth-century typology, where nearly every locality produced a different taxon if the fossils looked even slightly different. Frick (1937, p. 20, footnote 2; p. 322) was explicit in stating that many of his “species” were simply convenient labels for specimens from different localities. Apparently, he was unfamiliar with or unaware of the statistical and populational thinking about species that was developing in biology and even in paleontology (e.g., Simpson, 1937) at the same time. To his credit, Frick’s (1937) monograph is beautifully illustrated and comprehensive, and describes an enormous amount of important new material that he paid his collectors to find. Frick was one of the first to conceive of the dromomerycines and aletomerycines as a group, and to recognize most of the valid genera within the group. This was no mean feat since most of the work was done at the height of the Great Depression.

Janis and Manning (1998, p. 481) noted that “the family is badly in need of revision at the subgeneric and specific levels. Many of these genera are greatly oversplit (most notably Aletomeryx, Rakomeryx, Cranioceras, and particularly Bouromeryx), and some species, especially in the case of the Cranioceratinae, may be assigned to the wrong genus.”

Since 1937, no one has attempted a complete revision of the group. A few additional specimens (with two new taxa) were described by Stirton (1936, 1944), Webb (1983), and Whistler (1984). Webb (1969) and Voorhies (1990) discussed the validity of some of Frick’s (1937) taxa. Webb (1983) reviewed the status of Pediomeryx and Yumaceras, the last and most advanced of the cranioceratins, placing the latter taxon as a subgenus of the former. Janis and Manning (1998) provided the first general overview of the group since Frick (1937), but retained most of Frick’s genera, and did not attempt a revision of the species. In this paper, we follow the cladistic relationships and generic diagnoses presented by Janis and Manning (1998, fig. 32.3—Figure 2 in this paper), which was based on a 1980 cladogram by Earl Manning. We focus instead on revising the species within the relatively distinct and clearly monophyletic genera.

The familial relationships of the dromomerycines and aletomerycines are also controversial. As noted above, the first known specimens were confused with a variety of ruminants, including bovids, cervids, moschids, and antilocaprids. Most early authors (e.g., Cope,
considered dromomerycines and aletomerycines to be cervids or cervoids. However, Stirton (1944) reclassified them as a subfamily of the European family Palaeomerycidae, which he allied with the Giraffoidea. That assignment has been followed by some authors (Crusafont, 1961; Viret, 1961; Hamilton, 1978), while others (e.g., Romer, 1966; Leinders, 1983) placed dromomercinec and aletomerycines with the cervids. Janis and Scott (1987) convincingly showed that dromomercinec and aletomerycines were cervids, a sister-taxa to cervids, and that the similarities to giraffids were plesiomorphic or convergent. Duranthon et al. (1995) described new palaeomercid material from Spain and France, and argued that the horns of palaeomercids and dromomercines were non-homologous, and therefore the two groups were not closely related. However, Janis (2000) showed that the overwhelming majority of the characters in dromomercids support their alliance with palaeomercids, and therefore these differences in horns are probably not significant.

Dromomerycines and aletomerycines have been raised to the family-rank name Dromomerycidae by many recent authors (Hamilton, 1978; Janis, 1982; Leinders, 1983; Webb, 1983; Stucky and McKenna, 1993; Janis and Manning, 1998), but Janis and Scott (1987) recommended that they be referred to the European family Palaeomerycidae, since Palaeomeryx is clearly the sister-taxa of the dromomerycines and aletomerycines; this was also followed by McKenna and Bell (1997). Even though the family rank name of Dromomerycidae is widely used in the current literature, we agree with Janis and Scott (1987) and McKenna and Bell (1997) that the more natural group should include the North American dromomercinecs and aletomercinecs with their Eurasian sister-taxa in a single monophyletic family.

METHODS

In this study, all of the dromomercine specimens in the AMNH were examined, and most were measured with digital calipers. Specimens were photographed with a Nikon 5700 digital camera. In addition, important material from the YPM, YPM(PU), LACM and UNSM collections were also examined and measured. Although skulls and upper dentitions were examined when available, most of the statistics were performed on lower dentitions, since these were the only elements that provided a sufficient sample size. Statistical analyses were performed using Excel and Systat software. Modern statistical and populational concepts of species were applied to Frick’s (1937) taxonomy, and coefficients of variation (CV) used to decide whether a size cluster is too large to contain only a single species. Coefficients of variation of most mammal species tend to be less than 10, except for sexually dimorphic features (Kurtén, 1953; Simpson et al., 1960; Yablokov, 1974). Student’s t-tests were used to determine whether two populations were statistically distinct, and Kolmogorov-Smirnov tests were used to determine if the populations followed a normal distribution.

The first question that arises when dealing with taxa that are largely based on slight size differences is whether some of that size disparity could be due to sexual dimorphism. Nearly all authors have presumed that skulls with larger horns are from males, analogous to the situation in the Cervidae and Bovidae. In some cases (such as the Aletomeryx Quarry sample, or the Sheep Creek Formation sample of Sinclairomeryx), there are multiple skulls of both presumed male and female individuals. The large samples from Aletomeryx Quarry show that both presumed males and females apparently had horns, while the Sinclairomeryx sample seems to show that only presumed males had horns. Apparently, in some groups (such as Aletomeryx), both males and females had large saber-like canines (usually found only in male hornless ruminants). However, the majority of dromomercine taxa lacked large upper canines in either males or females. In all these population samples where sex can be determined, there are no differences in size or characters...
of the skeleton other than horns (Lull, 1920; Janis, 2000). Thus, we can rule out sexual dimorphism as the cause of the majority of the size differences of dromomerycine taxa.

Once sexual dimorphism has been ruled out, samples that were from the same locality were compared to determine the typical range of variation. These were then amplified by samples from the same age and region, and finally samples from all regions of the same age. Finally, in taxa that span a significant temporal interval, samples from each subdivision of a land mammal age were compared to determine if there were long-term temporal trends.

The biostratigraphic assignment of specimens described in this report follows Tedford et al. (1987, 2004), Skinner et al. (1977), and Skinner and Johnson (1984).

**Institutional abbreviations:** AMNH, American Museum of Natural History, New York, NY; CMNH, Carnegie Museum of Natural History, Pittsburgh, PA; F:AM, Frick Collection, AMNH; DMNH, Denver Museum of Nature and Science, Denver, CO; MCZ, Museum of Comparative Zoology, Harvard University, Cambridge, MA; TAM, Texas A&M University collection, now at the Texas Memorial Museum, University of Texas, Austin, TX; UCMP, University of California Museum of Paleontology, Berkeley, CA; UCR, University of California, Riverside, collections (now housed at UCMP); UF, Florida Museum of Natural History, Gainesville, FL; SDSM, South Dakota School of Mines Museum, Rapid City, SD; UNSM, University of Nebraska State Museum, Lincoln, NE; USNM, National Museum of Natural History, Smithsonian Institution, Washington, DC; YPM, Yale Peabody Museum, New Haven, CT; YPM(PU), Princeton University collections, now housed at YPM.

**Other abbreviations:** CV = coefficient of variation; l.f. = local fauna.

**SYSTEMATIC PALEONTOLOGY**

**Class Mammalia Linnaeus, 1758**

**Order Artiodactyla Owen, 1848**

**Family Palaeomerycidae Lydekker, 1883**

**Subfamily Aletomerycinae Frick, 1937**

**Diagnosis**—Mesodont molars, with cingulae and *Palaeomeryx* fold (a ridge on the labial side of the protoconid that extends posteroomedially) reduced or lost, upper canine reduced, upper premolar protocone reduced, orbit moved posteriorly (anterior rim over M3), older females with small supraorbital horns, ramus deeper, premolars reduced, antorbital vacuity present, metapodials lengthened (after Janis and Manning, 1998, p. 480).

**Aletomeryx Lull, 1920**

**Type species**—*Aletomeryx gracilis* Lull, 1920

**Included species**—*A. marslandensis* Frick, 1937; *A. occidentalis* Whistler, 1984

**Distribution**—Latest Arikareean, Nebraska; early Hemingfordian, Colorado and California; early to late Arikareean, Nebraska;

**Diagnosis**—Short horns (no more than one-third skull length) that are fairly upright; posteriormedial corner of horn has a narrow vane, separating it from the posteroinfrontal border of the orbit. Smaller horns in females. Short nasals. Longest and most slender metapodials of all dromomyrcids. Small body size (modified from Janis and Manning, p. 482).

**Discussion**—Nearly all known specimens of *Aletomeryx* are from the early Hemingfordian of Nebraska, and a few are from the early Hemingfordian Martin Canyon Formation of Colorado. In addition, there is *A. occidentalis* from the early Hemingfordian of California. Janis and Manning (1998, p. 482) note there is a possible late Hemingfordian specimen from the Sheep Creek Formation of Nebraska, although they point out that it could also be referred to other dromomerycids from this locality, so this range extension is questionable. In addition, Lull (1920) and Frick (1937, p. 159-160) say that the material of *A. marshi* is from the “Harrison Formation of Nebraska.” However, it is likely that it is really from the overlying Runningwater beds in the same area, or possibly from the latest Arikareean Anderson Ranch Formation of Hunt (2002) (formerly the “upper Harrison beds” of Peterson, 1909).

*Aletomeryx gracilis* Lull, 1920

**Figures 1C, 3, 4; Table 1**

*Blastomeryx marshi* Lull, 1920

*Blastomeryx (Dysemeryx) marshi* Matthew, 1924

*Blastomeryx (Dysemeryx) scotti* Matthew, 1924

*Aletomeryx marshi* Frick, 1937

*Aletomeryx scotti* Frick, 1937

*Aletomeryx lugnii* Frick, 1937

**Type specimen**—YPM 10732, skull, jaws, and skeleton, from “Harrison beds” (Runningwater Formation, early Hemingfordian, fide Tedford et al., 1987, p. 167), Nebraska.

**Referred material**—Hundreds of specimens from *Aletomeryx* Quarry, Frick Dunlop Camel Quarry, and many other Runningwater quarries in the YPM, F:AM, AMNH, and UNSM collections (many listed by Frick, 1937, pp. 157-159).

**Distribution**—From the early Hemingfordian “Marsland” Formation (probably Runningwater Formation) and possibly the latest Arikareean Harrison or “upper Harrison” (Anderson Ranch Formation of Hunt, 2002), western Nebraska; early Hemingfordian Martin Canyon Formation of Colorado.

**Diagnosis**—Medium- to small-sized species of *Aletomeryx* (see Table 1).

**Description**—The large samples from *Aletomeryx* Quarry and other Runningwater localities were fully described by Lull (1920) and Frick (1937).

**Discussion**—*Aletomeryx gracilis* was described by Lull (1920) based on hundreds of excellent specimens from *Aletomeryx* Quarry in the “Harrison beds” (early Hemingfordian Runningwater Formation, fide Tedford et al., 1987, p. 167), Cherry County, Nebraska. Lull (1920) thoroughly described both male and female specimens of this species, and numerous other excellent male and female skulls, jaws, and postcranials were described by Frick (1937). Compared to other dromomerycids, *Aletomeryx gracilis* is one of the best-known species, with hundreds of specimens in many different collections, and mounted specimens on display at the YPM, at the Trailside Museum in Fort Robinson, Nebraska, and elsewhere.

Lull (1920, p. 125) described another specimen (YPM 10756, from the “Harrison beds,” Nebraska, probably early Hemingfordian) consisting of a skull and jaws and partial skeleton, which he named *Blastomeryx marshi*. The skull had no horn bases, but large canine tusks, giving Lull the impression that it belonged to *Blastomeryx*. However, he noted (p. 125) that it was also the size and morphology of some of his female specimens of *Aletomeryx gracilis*. Matthew (1924) referred this material to *Blastomeryx (Dysemeryx) marshi*. Frick (1937, p. 159) compared this specimen to the many female skulls of *A. gracilis* in his collection, and correctly concluded that “Blastomeryx marshi was a female specimen of *A. gracilis*.”

*Blastomeryx (Dysemeryx) scotti* was named by Matthew (1924, p. 193) based on MCZ 17743, a fragment of frontal horn, from the “Loup Fork” of Nebraska (probably early Hemingfordian Runningwater Formation, fide Tedford et al., 1987). This specimen was first mentioned by Scott (1890, p. 76) in his discussion of Cope’s genus *Blastomyx*. Frick (1937, p. 152) noticed that it bore a resemblance to the horn cores in his *Aletomeryx* collection, but that it was from an individual slightly larger than typical *A. gracilis*. No other material was referred to this species by Frick (1937, p. 161), although in the AMNH and other collec-
m1-3 length of 40 mm is within the range of variation of \textit{A. gracilis} (Fig. 4). Thus, since the type material is undiagnostic and its size is within the range of \textit{A. gracilis}, we regard it as a junior synonym of that taxon.

\textit{Aletomeryx marslandensis} Frick, 1937

Figures 3, 4; Table 1

\textbf{Type specimen}—UNSM 50-28-8-34, top of cranium, from the early Hemingfordian “Marsland” Formation (probably Runningwater Formation), Nebraska.

\textbf{Referred specimens}—UNSM 1-11-8-36, skull, mandible, and skeleton (“?\textit{Aletomeryx marslandensis} Var.” of Frick, 1937, p. 163); UNSM 1-13-6-35, female skull and mandible; numerous other UNSM specimens listed by Frick (1937, pp. 162-163).

\textbf{Diagnosis}—“Larger than \textit{A. gracilis} and smaller than \textit{S. riparius}” (Frick, 1937, p. 162). Horns taller than those of \textit{A. gracilis}. The \textit{p4} tends to be large relative to the much reduced \textit{p2-3}.

\textbf{Distribution}—From the early Hemingfordian “Marsland” Formation (probably Runningwater Formation), Box Butte and Dawes counties, Nebraska.

\textbf{Description}—No new material has been found since the descriptions of Frick (1937, p. 162).

\textbf{Discussion}—Frick (1937) based the species \textit{Aletomeryx marslandensis} on UNSM 50-28-8-34, a cranial fragment from the “Marsland” Formation of Box Butte County, Nebraska (early Hemingfordian). He referred numerous other specimens in the UNSM collections to that species. His diagnosis was based largely on size, and on horns that tended to be taller than \textit{A. gracilis}. The \textit{p4} tends to be large relative to the much reduced \textit{p2-3}.

Our data (Fig. 4) show that the specimens referred to \textit{A. marslandensis} do tend to be among the largest in the sample, with some of the most reduced premolar rows (relative to size) of all known \textit{Aletomeryx}. Although the separation between the \textit{A. marslandensis} specimens and the \textit{A. gracilis/scotti} cluster is slight, they are discrete enough to retain as a distinct species.

\textit{Aletomeryx occidentalis} Whistler, 1984

Figures 4, 5; Table 1

\textbf{Type specimen}—UCR 10335, right ramus with \textit{p2-m3}, from the early Hemingfordian Boron I.F., Kern County, California.

\textbf{Referred specimens}—Material listed by Whistler (1984, p. 25).
TABLE 1. Measurements of various dromomerycine and aletomerycine taxa (in mm). Number in parentheses = sample size.

<table>
<thead>
<tr>
<th>TAXON</th>
<th>m1-3</th>
<th>p2-4</th>
<th>m1 length</th>
<th>m1 width</th>
<th>Diastema</th>
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<tr>
<td><em>Aletomeryx gracilis</em> (38)</td>
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<td>20.8</td>
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<td>7.7</td>
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<td>11.0</td>
<td>7.0</td>
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<tr>
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<td>CV</td>
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<td>10.3</td>
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</tr>
<tr>
<td>All <em>Aletomeryx</em> (41)</td>
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<td>7.0</td>
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<td>15.5</td>
<td>6.9</td>
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<td>5.3</td>
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<td>36.3</td>
<td>15.5</td>
<td>12.0</td>
<td>68.1</td>
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<tr>
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<td>15.5</td>
<td>12.0</td>
<td>68.1</td>
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</tr>
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<td>6.9</td>
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<td>5.3</td>
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<td>36.1</td>
<td>15.8</td>
<td>11.3</td>
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</tr>
<tr>
<td>Mean</td>
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<td>36.1</td>
<td>15.8</td>
<td>11.3</td>
<td>—</td>
</tr>
<tr>
<td>SD</td>
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<td>2.2</td>
<td>1.2</td>
<td>0.8</td>
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</tr>
<tr>
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<td>0.8</td>
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<tr>
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<tr>
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<tr>
<td><em>Bouromeryx submilleri</em> (9)</td>
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<td>12.4</td>
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</tr>
<tr>
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<td>6.8</td>
<td>5.8</td>
<td>7.0</td>
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</table>
**Diagnosis**—Larger than *A. marslandensis*, but smaller than all *Sinclairomeryx*, with large p2; unreduced lower premolars, with more complicated crown pattern than found in other species of *Aletomeryx*, and with relatively expanded metaconid; hypostylid of p3-4 expanded into a distinct cusp that connects to the hypoconid with a short crest; well-developed metaconid on p4; anteriolabial buttress and anterior cingulum on m2; hypoconulid crescent on m3; and many other characters cited in Whistler (1984, p. 25).

**Distribution**—Known only from the type locality.

**Description**—No additional material has been reported since the descriptions of Whistler (1984).

**Discussion**—Whistler (1984) described the species *A. occidentalis* based on fragmentary specimens from the early Hemingfordian Boron l.f., Kern County, California. Although the material consisted mostly of jaw fragments, there was a broken horn base in the collection (Fig. 5C) that demonstrated clearly the *Aletomeryx* affinities of the material. As Whistler (1984) noted, this taxon is larger than *A. marslandensis*, but smaller than the much larger taxon *Sinclairomeryx*. In our data set, the specimens clearly plot on the large end of the size distribution, and seem disjunctly larger, without the premolar reduction seen in *M. marslandensis* (Fig. 4). This size distinction, in addition to the more subtle dental characters listed by Whistler (1984), plus its geographic isolation from the Great Plains species of *Aletomeryx*, seem to justify retention of this species.

*Sinclairomeryx* Frick, 1937

*Blastomeryx* Matthew, 1924 (in part)

*Sinclairomeryx* Frick, 1937

**Type and only species**—*Sinclairomeryx riparius* (Matthew, 1924)


**Distribution**—Late Hemingfordian-early Barstovian, Nebraska and Saskatchewan.

**Discussion**—Stirton (1944, p. 640) suggested that *Sinclairomeryx* Frick, 1937 was a junior synonym of Matthew’s (1924) subgenus *Dyseomeryx*. However, Matthew (1924) referred several different taxa to *Dyseomeryx*, including *Blastomeryx* (*Dyseomeryx*) marshi and *Blastomeryx* (*Dyseomeryx*) scotti, both of which are here referred to *Aletomeryx gracilis*, and *Blastomeryx* (*Dyseomeryx*) sinclairi, which is referable to *Rakomeryx*, not *Sinclairomeryx*. In addition, most of Matthew’s type specimens were undiagnostic fragmentary dental remains that are only doubtfully referable to *Sinclairomeryx*. Thus, the name *Sinclairomeryx* is the first available generic name that can be applied to the material discussed below.

*Sinclairomeryx riparius* (Matthew, 1924)

**Figure 6**

*Blastomeryx* (*Dyseomeryx*) riparius Matthew, 1924

*Sinclairomeryx* riparius Frick, 1937

*Sinclairomeryx sinclairi* Frick, 1937

*Sinclairomeryx tedi* Frick, 1937

**Type specimen**—AMNH 18956, left maxilla with P2-M3 (Fig. 6A), from Thomson Quarry, Stonehouse Draw, late Hemingfordian Sheep Creek Formation, Sioux County, Nebraska.

**Referred material**—Numerous specimens listed by Frick (1937, p. 164-168), all from the late Hemingfordian Sheep Creek Formation, Nebraska.

**Diagnosis**—Same as for genus.
could only compare it with the better known genus Formation (Fig. 6A). Based on such limited material, Matthew (1924, p. 197), based on AMNH 18956, a left maxilla with right ramus in labial and occlusal view. (after Whistler, 1984, figs. 51, 52, 57, p. 28).

Discussion—Most of the referred material is from the middle-late Hemingfordian Box Butte and Sheep Creek formations and equivalents, western Nebraska. According to Janis and Manning (1998, p. 482), there may also be specimens from the early Barstovian Olcott Formation of Nebraska, the late Hemingfordian Topham l.f. of the Cypress Hills, Saskatchewan, and the early Barstovian Wood Canyon Formation, Saskatchewan (Storer, 1975).

Distribution—Blastomeryx (Dyseomeryx) riparius was described by Matthew (1924, p. 197), based on AMNH 18956, a left maxilla with P2-M3, from Stonehouse Draw in the late Hemingfordian Sheep Creek Formation (Fig. 6A). Based on such limited material, Matthew (1924) could only compare it with the better known genus Blastomeryx, but it was clearly larger than any other Blastomeryx species then known. Frick (1937, p. 165) referred this specimen to his large sample of Sinclairomeryx specimens from the same quarry in Stonehouse Draw. He noted only that S. riparius was slightly smaller than the type skull of S. sinclairi, but were otherwise very similar.

Frick (1937, p. 165) named another species, Sinclairomeryx sinclairi, based on F:AM 33791 (Fig. 6B), a complete male skull with the distinctive, forwardly-curved horns with terminal knobs from Thomson Quarry in the late Hemingfordian Sheep Creek Formation, Nebraska. He referred additional material to this species, but did not provide a diagnosis or any way of distinguishing it from S. riparius. In fact, the specimens referred to S. sinclairi completely encompass the variation seen in S. riparius, so there is no valid size distinction between the two taxa. Since the type of S. riparius is so poor, we cannot see any basis for maintaining two species based on the referred material.

Sinclairomeryx tedi was named by Frick (1937, p. 168) based on a right ramus (Fig. 6E-F) with p2-M3 (F:AM 32875) from Ginn Quarry in the Sheep Creek Formation, Dawes County, Nebraska. Frick (1937, p. 168) compared it to Barbouroamerica trinogonorensis and Aletomeryx and Bouromeryx, but not to any Sinclairomeryx species, yet placed it in that genus. The type material consists mostly of rami and a few maxillae, and differs from typical S. riparius only in that it is slightly smaller. However, it is entirely within the range of size of specimens referred to S. sinclairi, so we regard it as a junior synonym of S. riparius.

Subfamily Dromomerycinae Frick, 1937

Tribe Dromomerycini Frick, 1937

Discussion—Janis and Manning (1998, p. 482) provide a thorough discussion and diagnosis of the subfamily Dromomerycinae, and the tribe Dromomerycini, so it will not be necessary to repeat that information here.

Drepanomeryx Sinclair, 1915

Figures 7-8; Table 1

Type and only species—Drepanomeryx falciformis Sinclair, 1915

Diagnosis—Supraorbital horns elongated and posteriorly directed, with small basal flanges; shafts widely bowed inwardly, moderately twisted with bulbous tips, flattened anteroposteriorly. Dentition similar to Dromomeryx, but open anterior fossette on p4. Limbs moderately heavily proportioned. Females may have also had horns (modified from Janis and Manning, 1998, p. 482).

Distribution—Early Barstovian, Nebraska and Texas.

Drepanomeryx falciformis Sinclair, 1915

Drepanomeryx (Drepanomeryx) falciformis Frick, 1937

Drepanomeryx (Matthomeryx) matthewi Frick, 1937

Type specimen—YPM(PU) 12072, left horn (Fig. 7A), from “Snake Creek” beds (West Sinclair Draw, early Barstovian Olcott Formation, fide Skinner et al., 1977, p. 349), Nebraska.

Referred material—Numerous specimens listed by Frick (1937, p. 140-141). All are from the early Barstovian Olcott Formation of Nebraska (mostly Mill Quarry in Sioux County) or early Barstovian Sand Canyon Formation in Dawes County (mostly Observation Quarry), or the early Barstovian Fleming Formation (Trinity River Pit 1) of Texas.

Diagnosis—Same as for genus.

Distribution—Same as for genus.

Discussion—Sinclair (1915) named Drepanomeryx falciformis based on a broken left horn (Fig. 7A) from the “Snake Creek” beds (actually early Barstovian Olcott Formation, fide Skinner et al., 1977, p. 349) with a distinctive distally widened tips, flattened ovoid profile and anterodorsal curvature. Frick (1937, p. 140) erected a separate subgenus, Drepanomeryx (Drepanomeryx) falciformis, for this specimen, and described additional material, including partial skulls, jaws, and skeletal elements. Frick gave no diagnosis for the subgenus, and it is unclear why a subgenus was necessary, since it is monotypic. It seems likely that Frick’s reason for the subgenus might have been the morphological differences between the two species, but these reasons are no longer applicable in modern systematics.

Frick (1937, p. 141) named another new subgenus and species, Drepanomeryx (Matthomeryx) matthewi, based on F:AM 33740, a cranial fragment with spectacular curved horns (Fig. 7B) from Observation Quarry in the early Barstovian Sand Canyon Formation. Once again, Frick (1937) created a monotypic subgenus, so it is not clear why it was necessary to erect subgenera to distinguish the two recognized species of Drepanomeryx. Frick’s (1937, p. 138) discussion separated Drepanomeryx (Matthomeryx) matthewi based on the fact that the horns narrow distally, rather than expand distally. Janis and Manning (1998, p. 483) followed this diagnosis, but argued that D. (M.) matthewi “differs in possession of cranial appendages that are narrowed distally, rather than expanded. Premolars more reduced and diastemata longer than in D. (D.) falciformis.”

We examined the specimens referred to both of these subgenera and species, and we are not convinced that they are truly distinct. Although their horns vary in shape and in the taper from proximal to distal ends, the available sample shows considerable variation in the shape of the horns (in addition to differences caused by postmortem deformation). We are not convinced that such variation is not within that found in normal populations. Given that cervoid antlers, antilocaprid horn cores, and bovid horns are notoriously variable due to aberrations in growth, we think that the single odd-shaped distally expanded horn of the type specimen of D. falciformis might simply be due to deformed growth of that individual. Many years of collecting in these beds has not produced another specimen like the type of D. falciformis, but the Frick Collection has a number of specimens like those referred to D. (M.) matthewi.

Janis and Manning (1998, p. 483) also distinguished the taxa by characters in their lower jaws (reduction in premolars and diastema). We measured all the available specimens, and the single lower jaw referred to D. (D.) falciformis falls within the small end of the size range (Fig. 8) of D. (M.) matthewi. The coefficient of variation (Table 1) of the total sample is within 4 to 6 on all dental variables, so it is consistent with the
hypothesis that it is from a single species. The symphysis and diastema referred to D. (D.) falciformis is indeed short, but there are specimens of D. (M.) matthewi that are shorter. In short, we see no basis for two separate species or subgenera of Drepanomeryx. We refer all specimens of this genus to a single species, D. falciformis.

Rakomeryx Frick, 1937
Figures 9-10; Table 1

Type and only species—Rakomeryx sinclairi (Matthew, 1918)
Distribution—Late Hemingfordian of Florida, Montana, California, and Nebraska; early Barstovian, Nebraska and California; late Barstovian of Oregon and Montana (see Janis and Manning, 1998, p. 483, for localities).

Diagnosis—Horns with less pronounced basal flange, anteriorly directed, with bases strongly flattened anteroposteriorly, attenuated at tips; shafts strongly bowed laterally, forming concave half-moon shape when viewed from front. Orbits shifted posteriorly over anterior M3. Premolars more reduced than in Dromomeryx, but p4 may lack closure of anterior fossette. Metastylids on upper molars, and large metacone on P4. Limb proportions like that of Drepanomeryx (after Janis and Manning, 1998, p. 483).

Rakomeryx sinclairi (Matthew, 1918)
Cervatus sinclairi Matthew, 1918
Blastomeryx (Dyseomeryx) sinclairi Matthew, 1924
Dromomeryx near borealis Gazin, 1932 (in part)
Rakomeryx raki Frick, 1937
Rakomeryx jorakius Frick, 1937
Rakomeryx yermonensis Frick, 1937
Craniceras unicorns Frick, 1937 (in part)
Rakomeryx gazini Frick, 1937
Rakomeryx sinclairi Skinner et al, 1977
Rakomeryx sinclairi Janis and Manning, 1998

Type specimen—AMNH 18879, a partial skull (Fig. 9A) from the early Barstovian Olcott Formation (Skinner et al., 1977), Nebraska.


Diagnosis—Same as for genus.
Distribution—Same as for genus.
found in the early Barstovian of the Mojave Desert. Rakomeryx jorakius was named by Frick (1937, p. 105), based on F:AM 31332, a crushed posterior cranium and associated dentition, from the early Barstovian Green Hills Division in the Barstow Formation (Fig. 9C). Frick (1937) assigned no other material to this species nor did he provide a diagnosis of this species. Examining the type material, it is based on a very large individual of Rakomeryx with heavier horns than the type specimen of R. raki, but there is no basis for making it a distinct species. Thus, we synonymize it with Rakomeryx sinclairi.

Rakomeryx yermoensis was named by Frick (1937, p. 105) based on F:AM 31800, a mandible (Fig. 9D), from a quarry 5 miles east of Yermo, California. Additional material from this quarry was also referred to this species. Frick (1937, p. 100) provided no diagnosis for the species, except to state that “the premolars are slender and somewhat different, particularly as seen in the p3” from the Barstow sample. Examining the type specimen (Fig. 9D), we find no features to distinguish it from typical R. sinclairi other than its small size (Fig. 10). However, this size is within the small end of the size range of typical R. sinclairi, and the coefficient of variation of the R. sinclairi samples is between 5 and 7 for all dental measurements (Table 1), so there is no justification for retaining R. yermoensis. The alleged slenderness of the premolars is also within the normal range of variation of R. sinclairi, and the vague reference to the p3 being “somewhat different” is useless in diagnosing a taxon.

Rakomeryx gazini was erected by Frick (1937, p. 106) based on LACM (CIT) 351, partial left horn core, from the early Barstovian Skull Spring l.f., southeast Oregon. It was originally described and figured by Gazin (1932, p. 82), but Gazin referred it to Dromomeryx near borealis, even though he commented that the horn was more robust and curved than in typical Montana Dromomeryx borealis. Frick (1937, p. 107) transferred this specimen (and the remaining referred material described by Gazin, 1932) to Rakomeryx, and erected the new taxon, R. gazini, without any diagnosis, other than reference to Gazin’s (1932) comments. Shotwell (1968) placed this taxon in Dromomeryx borealis. We have examined this material, and find no obvious differences from the material now referred to R. sinclairi. Thus, R. gazini is here considered a junior synonym of R. sinclairi.

**Dromomeryx Douglass, 1909**

Figures 1A-B, 10-11; Table 1

**Type and only species—**Dromomeryx borealis (Cope, 1878)

**Diagnosis—**Horns large and broad, forwardly directed (forming an angle of 60 degrees with the nasals) and somewhat laterally bowed; prominent lateral basal flange, and deeply grooved on the anterolateral face. Orbit moved posteriorly (anterior rim over posterior M3). Shallow
lacral fossa. Lower p4 with anterior fossette closed by anterior extension of metaconid (modified from Janis and Manning, 1998).

Distribution—Compared to most other dromomerycines, D. borealis was very widespread in North America through much of the Miocene. Its distribution includes the late Hemingfordian of Nebraska, early Barstovian of Montana, Oregon, Nevada, and New Mexico; late Barstovian of Nebraska, Colorado, Wyoming, Nevada, and California; and early Clarendonian of South Dakota and California (see Janis and Manning, 1998, p. 484).

Discussion—Dromomeryx is a very abundant and well-known Barstovian taxon, based on numerous complete and partial skeletons and excellent skulls and jaws from both Montana and the Great Plains. It was the first genus to be distinguished from the wastebasket usage of late nineteenth-century taxa such as Cosoryx, Blastomeryx and Palaeomeryx, based on Douglass' (1909) description of much more complete material than was available to Cope, Matthew, Cook, and Douglass before 1909. Frick (1937) split off the subgenera D. (Dromomeryx) and D. (Subdromomeryx) based on the larger and smaller size clusters of Dromomeryx. He also oversplit Dromomeryx into numerous species based on inadequate comparisons with no diagnoses.

We find that there is a clearly defined larger size group, D. borealis, and a smaller species, Subdromomeryx scotti with a possible second Subdromomeryx species, S. antilopinus (Fig. 10). There is no evidence for any other valid species among all the many named dromomercines. Nor is there any justification for two separate subgenera for essentially two monotypic genera. Thus, we reject the unnecessary subgenera D. (Dromomeryx) and D. (Subdromomeryx) in favor of two genera, Dromomeryx and Subdromomeryx (the latter elevated to generic rank).

**Dromomeryx borealis** (Cope, 1878)

Blastomeryx borealis Cope, 1878
Palaeomeryx borealis Douglass, 1903
Palaeomeryx borealis Matthew, 1904
Blastomeryx borealis Matthew, 1908
Palaeomeryx borealis Matthew and Cook, 1909
Palaeomeryx borealis Matthew, 1909
Dromomeryx borealis Douglass, 1909
Dromomeryx whitfordi Sinclair, 1915
Dromomeryx pawniensis Frick, 1937

**Type specimen**—AMNH 8132, cranium with left horn and cheek teeth, from the early Barstovian Deep River beds, Montana

**Referenced specimens**—Most of the known material was listed by Frick (1937, p. 114-122).

**Diagnosis**—Same as for genus.

**Distribution**—Late Hemingfordian: Box Butte and Sheep Creek Formations, Nebraska; Early Barstovian: Fort Logan Formation, Deep River beds, Montana; Sixmile Creek Formation, Montana; Flint Creek beds, Montana; Barnes Creek beds, Montana; Chalk Cliffs l.f., Hepburn Mesa Formation, Montana; Mescal Formation, Oregon; Beatty Buttes Beds, Oregon; Cloud Springs fauna, Oregon; Sucker Creek Fauna, Oregon; Quartz Basin fauna, Oregon; Olocott Formation and Sand Canyon beds, Nebraska; Virgin Valley Formation, Washoe Formation, Nevada; Skull Ridge Member, Tesuque Formation, New Mexico; Lower Pawnee Creek fauna, Colorado; Late Barstovian: Cornell Dam Member, Valentine Formation, Nebraska; Upper Pawnee Creek Fauna, Colorado; Gravel Quarry, Goshen Hole, Wyoming; Stewart Spring/Tonopah l.f., Nevada; Burstow Forma-
show that D. pawniensis is within the same size range as the type of D. borealis, so there is no clear basis for defining the species other than D. pawniensis comes from the Pawnee Creek Formation of Colorado, and D. borealis is primarily from Montana. Since their geographic differences are not distinguished by any obvious morphological or size differences, we synonymize D. pawniensis with D. borealis.

Sinclair (1915, p. 94) named Dromomeryx whitfordi, based on YPM(PU) 12054, partial left and right horns (Fig. 11C), from West Sinclair Draw in the early Barstovian Olcott Formation, Sioux County, Nebraska (Skinner et al., 1977). He distinguished this species from D. borealis by having “horn bases about one third wider than D. borealis, with the posterior upper corner of the wing-like expansion at the base of the horn sharply angular instead of a flowing curve as in D. borealis” (Sinclair, 1915, p. 94-95). Matthew (1924, p. 72) referred this material to D. borealis. Frick (1937, p. 117) restored the taxon D. whitfordi, and referred much additional material from his collection from the Olcott Formation to this taxon. However, he provided no additional diagnosis, and the only obvious distinction is that D. whitfordi is from Nebraska, while his D. pawniensis is from Colorado and D. borealis from Montana. We measured a large number of referred specimens from the Frick Collection (Fig. 10) and found that they are in the same size range as D. borealis or D. pawniensis, nor is there any other morphological feature which distinguishes these samples. In addition, Sinclair’s (1915) supposed differences in the type horn core of D. whitfordi from D. borealis are now completely subsumed within the range of variation of horn cores now in the collections. Thus, we place D. whitfordi in synonymy with D. borealis.

Subdromomeryx (Frick, 1937), new rank

Blastomeryx Scott, 1893 (in part)
Dromomeryx Scott, 1913 (in part)
Dromomeryx (Subdromomeryx) Frick, 1937
Cranioceras Frick, 1937 (in part)
Rakomeryx Tedford et al., 1987 (in part)
Rakomeryx Janis and Manning, 1998 (in part)
Dromomeryx (Subdromomeryx) Janis and Manning, 1998

Type species—S. scotti (Frick, 1937).

Included species—S. antilopinus (Scott, 1893).

Diagnosis—Similar to Dromomeryx, but much smaller size (Table 1; Fig. 10), molars more mesodont; premolar row shorter, and Palaeomeryx fold usually lost. Supraorbital horns relatively smaller, with basal flange less pronounced, and limbs relatively longer and more slender than those of Dromomeryx (after Janis and Manning, 1998, p. 483).

Distribution—Late Hemingfordian of Nebraska and Nevada; early Barstovian of Texas.

Discussion—As discussed above, the smaller materials referred to Dromomeryx (Subdromomeryx) by Frick (1937) are distinct in size and morphology from Dromomeryx (Dromomeryx), and there seems to be no justification for subgenera when there are so few species in each genus and subgenus. Instead, we elevate Subdromomeryx from subgeneric to generic rank, in parallel with Dromomeryx, its sister taxon (Fig. 2).

Subdromomeryx antilopinus (Scott, 1893)

Figures 10, 12; Table 1

Blastomeryx antilopinus Scott, 1893
Dromomeryx antilopinus Scott, 1913
Dromomeryx (Subdromomeryx) scotti Frick, 1937
Dromomeryx wilsoni Frick, 1937
Cranioceras kinseyi Frick, 1937
Rakomeryx kinseyi Tedford et al., 1987
Rakomeryx kinseyi Janis and Manning, 1998

Type specimen—YPM(PU) 10401, partial skull and skeleton, from the Deep River beds, Montana.
Diagnosis—Same as for genus.
Distribution—Same as for genus.
Description—All known material of *S. antilopinus* was described by Frick (1937).

Discussion—Scott (1893, 1895) described *Blastomeryx antilopinus* based on YPM(PU) 10401, partial skull and skeleton, from the late Hemingfordian Deep River beds, Montana. Scott’s (1893, p. 662) original description gave no figures or type specimen, and the diagnosis consisted only of “size decidedly smaller than that of *B. borealis* Cope, and ribs of external crescents on upper molars less prominent.” Fortunately, Scott (1895) provided good figures and a much more detailed description and diagnosis, so this potential *nomen nudum* was validated. In 1913, Scott transferred this species to *Dromomeryx*. Frick (1937) recognized this species, but did not provide any diagnosis, nor any criteria to distinguish it from *S. scotti*. The known measurements of the specimen (m1-3 length = 44 mm) do not distinguish it from *S. scotti* as currently defined, and it lies completely within the size distribution of *S. scotti* (Fig. 10). Nor can we find any consistent morphological difference between the material of *S. antilopinus* and of *S. scotti*, given the intrapopulational variability typical of dromomercines. Thus, we consider *S. antilopinus* to be the senior synonym of all the *Subdromomeryx* species.

Frick (1937, p. 123) described *S. scotti*, based on F:AM 33758, a nearly complete skull (Fig. 12B-E). He provided no diagnosis of this taxon, but based on the referred material, it was largely diagnosed on size. Numerous excellent skulls and jaws and partial skeletons were listed by Frick (1937, p. 123-126), nearly all from the Frick Greenside and Thomson Quarries in the Sheep Creek Formation, Sioux County, Nebraska.
Frick (1937, p. 126) erected another species, *S. wilsoni* (Fig. 12F), based on a posterior portion of a skull (F:AM 33800) with both horns from the Thomson Quarry in the Sheep Creek Formation, Sioux County, Nebraska (Fig. 12C). The taxon was distinguished from *S. scotti* (which also occurs in Thomson Quarry) only by its smaller size and slender horns. As Skinner et al. (1977, p. 344-345) pointed out, these differences might just be due to the fact that the type specimen of *S. wilsoni* is a smaller and possibly less mature individual, and falls within the range of variation of *S. scotti*. Our own measurements (Fig. 10) place the type specimen of *S. wilsoni* at the small end of the range of *S. scotti*, but the coefficients of variation (Table 1) are within the range for a single species, so we follow Skinner et al. (1977) in regarding *S. wilsoni* as a junior synonym of *S. antilopinus*.

_Cranioceros kinseyi*_ was named by Frick (1937, p. 91), based on a fragmentary right ramus with p2-m3 from the Kinsey Collection (number 3-6-1927), obtained from the early Barstovian lower Madison Valley beds in Montana. Frick (1937, p. 91) referred additional material from the Deep River beds and from the north end of north Boulder Creek. Although the type specimen is no longer available for study, a cast is present in the AMNH collections. It was referred to *Rakomeryx kinseyi* by Tedford et al. (1987), and this was followed by Janis and Manning (1998). However, close examination of the cast of the type specimen shows that it is much smaller than any known specimen of *Rakomeryx* (Fig. 10), and in size and morphology it is a much better match to *S. antilopinus*. We are not sure why Tedford et al. (1987) placed it in *Rakomeryx*, but since there is no diagnostic skull material known to be associated with the type, we feel that it is a much better assigned to *Subdromeryx antilopinus*. The skull material mentioned by Frick is not clearly associated with the type specimen, but comes from a different locality, so we cannot use this as evidence for its affinities with *Rakomeryx*.

**Tribe Cranioceratini Frick, 1937**

**Characteristics**—Males with supraorbital horns that are shifted anteriorly (nearly vertical), short to tall, triangular to rounded in cross section, and lacking a basal flange. Posterior occipital region elongated, with pronounced posterior dorsal projection of the occiput, producing a mediocostal occipital horn of varying lengths. Lower rim of orbit expanded laterally. Absence of lacrimal vacuity but presence of a narrow, slit-like antorbital vacuity paralleling the anterior wing of the frontal. Upper canines present in *Barbouromeryx* only. Diastema moderate to long. Premolars variably reduced; posterior premolars uninalarized to submolariform; anterior fossite (trigonid) on p4 may be open or closed; dp1 lost in more derived taxa. Molars brachyodont to mesodont; *Palaeomeryx* fold present in lower molars of early taxa, but absent in later ones. Limbs generally shorter and more heavily proportioned than in the Dromomerycini; lateral digits may be present (after Janis and Manning, 1998, p. 484).

**Barbouromeryx Frick, 1937**

_Blastomeryx* Cook, 1934 (in part)

_Barbouromeryx* (Barbouromeryx) Frick, 1937

_Barbouromeryx* (Probarbouromeryx) Frick, 1937

_Barbouromeryx* (Prootobarbouromeryx) Frick, 1937

_Blastomeryx* (Parablastomeryx) Frick, 1937 (in part)

**Type and only species**—_B. trigonocorneus_ (Barbour and Schultz, 1934)


**Distribution**—Latest Arikareean Anderson Ranch Formation (= “upper Harrison” of Peterson, 1909), Nebraska; early Hemingfordian Runningwater (“Marsland”) Formation, Nebraska, Batesland Formation, South Dakota, Martin Canyon Formation (Clay Quarry), Colorado, and Oakville Formation, Texas; middle Hemingfordian Box Butte Formation, Nebraska, and Split Rock Formation, Wyoming.

**Barbouromeryx trigonocorneus** (Barbour and Schultz, 1934)

_Blastomeryx trigonocorneus_ Barbour and Schultz, 1934

_Barbouromeryx* (Barbouromeryx) *trigonocorneus* Frick, 1937

_Barbouromeryx* (Probarbouromeryx) *sweeti* Frick, 1937

_Barbouromeryx* (Prootobarbouromeryx) *marslandensis* Frick, 1937

_Blastomeryx* (Parablastomeryx) *galushi* Frick, 1937

**Type specimen**—UNSM 3-27-11-35, partial skull and rami (Fig. 13A-E) with skeletal elements, “from 3.5 miles south, 9.5 miles west of Hay Springs, Antelope Creek” (early Hemingfordian Runningwater Formation, Nebraska).

**Referred specimens**—Nearly all the known material was listed by Frick (1937, p. 134-136).

_Diagnosis_—Same as for genus.

**Description**—Nearly all known material was described by Frick (1937).

**Distribution**—Same as for genus.

**Discussion**—Barbour and Schultz (1934, p. 2, 4) described a broken skull and rami (UNSM 3-27-11-33) as *Dromomeryx trigonocorneus*, recognizing that it had the general appearance of *Dromomeryx*, but that it was distinct (Fig. 13A) in having two short horns over the orbits and a pronounced occipital knob (a precursor of the much longer occipital horn in later taxa). In addition to the distinctive horns, a large canine tusk was found with the skull (although the nasal and premaxillary regions are missing from the type).

Frick (1937, p. 134) made this specimen (and additional referred material) the basis for his new genus and subgenus, *Barbouromeryx* (Barbouromeryx). All of the material came from the early Hemingfordian Runningwater Formation of Nebraska, primarily from the Antelope Creek area in Dawes County (Janis and Manning, 1998, p. 484). Frick (1937) provided no diagnosis of his new genus *Barbouromeryx* or the species *trigonocorneus*, even though a much larger number of specimens was available to him.

Frick (1937, p. 135) named another new subgenus and species, *Barbouromeryx* (Probarbouromeryx) *sweeti*, based on UNSM 53-25-6-35, a partial skull from Quarry 1 in the early Hemingfordian Runningwater Formation, near Bridgeport, Morrill County, Nebraska. His only diagnosis claimed that the molars were smaller than *B. (B.) trigonocorneus*, but larger than those of the blastomerycine *Parablastomeryx gregorii*. Finally, Frick (1937, p. 136) erected the new subgenus and species *Barbouromeryx* (Prootobarbouromeryx) *marslandensis*, based on UNSM 3-24-7-34, a left ramus with p2 alveolus and p3-m3, from the Box Butte Formation “11 miles southwest of Marsland,” Dawes County, Nebraska. His only diagnosis for this new subgenus and species was that the premolars were smaller proportioned, but that the molars approached the size of *B. (P.) sweeti*.

Thus, Frick (1937) created three monotypic subgenera of *Barbouromeryx*, but the only apparent distinction between the taxa was size and relatively smaller premolars. Janis and Manning (1998, p. 484) noted that they in fact all appear to be about the same size, and that “the distinctness of the species may also be in question,” and this is borne out by our measurements (Fig. 14). Even though the sample is small, the size range of *trigonocorneus*, *sweeti*, and *marslandensis* completely overlap, and the coefficients of variation of this sample (Table 1) are consistent with the hypothesis that this is a single species. Contrary to Frick (1937), the specimens assigned to *marslandensis* range from shorter to longer premolar rows. It is a mystery why Frick did not measure more of the specimens available to him, nor do any kind of simple plot to check...
whether his subjective impressions of size were in fact supported by the data, but it is clear that there is no basis for distinguishing these three taxa. It seems likely that Frick was splitting them based on locality, even though they are all from the same formation in a relatively small area of western Nebraska. Thus, they are all here considered synonyms, and *trigonocorneus* is the senior trivial name. In agreement with Janis and Manning (1998, p. 484), we also regard the subgenera as useless, since they were never properly diagnosed, have no basis in fact, and are superfluous when each is monotypic. Thus, the only valid arrangement is a single genus and species, *Barbouromeryx trigonocorneus* (Barbour and Schultz, 1934).

Frick (1937, p. 244) erected the species *Blastomeryx* (*Parablastomeryx*) *galushi* based on a crushed skull (F:AM 33775) from the “Upper Marsland” Formation in the Hay Springs area, Dawes County, Nebraska. He compared it only to the blastomerycine specimens in his collection, but it is clearly too large for any blastomerycine. Instead, it an excellent match for the type skull of *Barbouromeryx trigonocorneus* (Fig. 15A), as noted by Beryl Taylor when he curated the collection (notes found in specimen drawer). Thus, we synonymize *Blastomeryx* (*Parablastomeryx*) *galushi* with *Barbouromeryx trigonocorneus* (Barbour and Schultz, 1934).

**Specimens possibly referable to Barbouromeryx trigonocorneus**—Cook (1934, p. 158) named the new species *Blastomeryx cursor*, based on a fragmentary ramus (Fig. 15B) with p2-m3 (Harold Cook collection 142, now AMNH 81086) from the “upper Harrison” beds (now Anderson Ranch Formation of Hunt, 2002) four miles northeast of Agate, Nebraska. The fragmentary material was difficult to assess at the time, although Cook (1934) compared it to *Leptomeryx* and “*Blastomeryx riparius*” (now *Sinclairomeryx riparius*) and the living brocket deer *Mazama*. Frick (1937) made no mention of this species, even though he had large collections from the same area. During curation of the Frick Collection, Beryl Taylor observed that the m3 of the type of *Blastomeryx cursor* is a good match for *Barbouromeryx trigonocorneus*. This synonymy was suggested by Janis and Manning (1998, p. 484), based on Taylor’s observations, although they did not formalize it. Nor do we formalize that synonymy here, because the type material of *Blastomeryx*...
Blastomeryx cursor is so poor and non-diagnostic. Blastomeryx cursor is best regarded as a nomen dubium.

Blastomeryx vigoratus was named by Hay (1924) based on an isolated m2-3 (TAM 2378) and paratypes (under the same number) consisting of a right M3 and left m1 (Fig. 15C). These isolated teeth were discovered in the early Hemingfordian Garvin Gully F., Oakville Formation, Grimes County, Texas. Frick (1937) referred the material questionably to Longirostromeryx. Patton (1969) considered the type specimens to be too fragmentary to assign to any known taxon, so it would be a nomen dubium. Webb (1998, p. 472) considered it to be referable to Blastomeryx, since other Garvin Gully material lacks the long diastema of Longirostromeryx. We agree with Patton (1969) that the specimens are too poor to be diagnostic. However, Beryl Taylor (notes in AMNH collection, 1974) made detailed comparisons, and thought that the type material could be assigned to Barbouromeryx trigonocorneus, although again it is best to regard the name as a nomen dubium.

Bouromeryx (Frick, 1937)

Palaeomeryx Douglass, 1899 (in part)
Dromomeryx Douglass, 1909 (in part)
Dromomeryx Cook, 1922 (in part)
Blastomeryx Cook, 1922 (in part)
Blastomeryx Cook, 1934 (in part)
Barbouromeryx (Bouromeryx) Frick, 1937
Rakomeryx Shotwell, 1968
Bouromeryx Webb, 1983
Bouromeryx Tedford et al., 1987
Bouromeryx Voorhies, 1990
Bouromeryx Janis and Manning, 1998

Type species—B. americanus (Douglass, 1909)
Included species—B. submilleri Frick, 1937


Distribution—Late Hemingfordian of Montana, Oregon, Nevada, California, Nebraska and Saskatchewan; early Barstovian of Montana, Nevada, Oregon, California, Colorado, Nebraska, Florida, and Texas; late Barstovian of Nebraska, Montana, and Texas.

Discussion—Material of a medium-sized late Hemingfordian-early Barstovian cranioceratin with medium-sized occipital and supraorbital horns was first described by Douglass (1899) as Palaeomeryx americanus, and then in 1909 as Dromomeryx americanus. Frick (1937, p. 131) had much more material available to him, and recognized that it
was not *Dromomeryx*, but related to *Barbouroumeryx* and *Cranioceras*, so he erected *Barbouroumeryx* as a subgenus without indicating to which genus it was referred. Most authors have interpreted Frick’s (1937) intent to place it as a subgenus of *Barbouroumeryx*. As Webb (1983), Tedford et al., (1987), Voorhies (1990, p. A221-A222) and Janis and Manning (1998, p. 485) pointed out, however, *Barbouroumeryx* is a distinctly larger and more derived taxon, and deserves its own genus, so they raised the subgenus to generic rank.

*Barbouroumeryx* is one of the most widespread dromomerycid genera, found in nearly every important late Hemingfordian and Barstovian locality. However, it is still poorly known. Nearly all the material consists of lower jaws and rami, with only a few poor skulls and maxillae recorded so far, and few postcranials.

*Bouromeryx americanus* (Douglass, 1899)

**Figures 14, 16; Table 1**

**Palaeomeryx americanus** Douglass, 1899
**Palaeomeryx madisonius** Douglass, 1899
**Dromomeryx americanus** Douglass, 1909
**Dromomeryx madisonius** Douglass, 1909
**Blastomeryx parvus** Cook, 1922
**Bouromeryx milleri** Frick, 1937
**Bouromeryx nebrascensis** Frick, 1937
**Bouromeryx supernebrascensis** Frick, 1937
**Bouromeryx pseudonebrascensis** Frick, 1937
**Bouromeryx pawniensis** Frick, 1937
**Dromomeryx americanus** McGrew, 1938
**Rakomeryx americanus** Shotwell, 1968

**Type specimen**—CMNH 705, left ramus p2-m3, from the Madison River beds, Montana (Fig. 16A).

**Referred specimens**—Nearly all the known specimens were listed by Frick (1937, p. 130-134).

**Diagnosis**—Larger species of *Bouromeryx* (Table 1).

**Distribution**—Late Hemingfordian: Box Butte and Sheep Creek formations, Nebraska; Massacre Lake f.f., Nevada; Topham f.f., Cypress Draw, respectively. Although they were not diagnosed, there is a clear size difference between them.

Cook (1922, p. 21) described a partial left ramus with p4-m3 (AMNH 81018) from the Olcott Formation as *Dromomeryx parvus* (Fig. 16H). Frick (1937, p. 131) transferred this taxon to *Bouromeryx* without justification or diagnosis. Skinner et al. (1977, p. 349) pointed out that *B. parvus* was indistinguishable from *B. nebrascensis* Frick, 1937, from the same area and the same beds, and so synonymized *B. nebrascensis* with *B. parvus*. Voorhies (1990, p. A224) noted that both *B. parvus* and *B. nebrascensis* were very similar to Douglass’ (1909) *B. americanus*, and suggested they were all synonyms of Douglass’ taxon. However, he did not deal with the rest of Frick’s (1937) oversplit and undiagnosed species of *Bouromeryx*.

Because nearly all of these late Hemingfordian-early Barstovian species of *Bouromeryx* were based on lower jaws, with no apparent distinctions other than size, we measured the entire Frick sample of these species (Fig. 14). All of the bivariate plots of different variables show only two distinct and diagnosable size clusters: a smaller one (for which the only available name is *B. submilleri* Frick, 1937) and a larger one (for which the first available name is *B. americanus* Douglass, 1909). These clusters are statistically distinct, with a t-test probability of p<0.5. Both samples have univariate binomial distributions (Kologorov-Smirnov test, p<0.05). Because Frick provided no diagnoses and there are no morphological features to distinguish them, most of his names are technically *nomina nuda*. However, it is simplest to regard *B. nebrascensis*, *B. pseudonebrascensis*, *B. supernebrascensis*, *B. milleri*, and *B. pawniensis* (all named by Frick, 1937) as well as the older taxa *B. madisonius* and *B. parvus* as junior synonyms of *Bouromeryx americanus* (Douglass, 1909).

Clustering of these taxa within *B. americanus* is biologically defensible, because the coefficients of variation of most dental variables (Table 1) are within the range for a biological species. Instead of nine species of *Bouromeryx* in the late Hemingfordian and early Barstovian of the Great Plains and Montana, we believe that there are only two valid species (the smaller *B. submilleri* and the larger *B. americanus*, formerly *B. milleri*) from the late Hemingfordian, and only one (*B. americanus*) out of the original eight named species from the early Barstovian.

*Bouromeryx submilleri* Frick, 1937

**Figures 14, 17; Table 1**

**Type specimen**—F:AM 33729, right ramus with p2-m3 (Fig. 17), from Greenside Quarry, Sheep Creek Formation, Nebraska.

**Referred specimens**—Frick (1937, p. 131) listed only the type specimen (F:AM 33729). In addition, the following specimens are among the referred material in the Frick Collection from the late Hemingfordian Sheep Creek Formation: F:AM 53040, 53037, 53038.

**Diagnosis**—Smaller species of *Bouromeryx* (Table 1).

**Distribution**—Late Hemingfordian Box Butte and Sheep Creek Formations, Nebraska; Ollsece Sand, California; Massacre Lake f.f., Nevada; Haystack Valley Member, John Day Formation, Oregon (*vide* Janis and Manning, 1998, p. 485).

**Description**—The known material of *B. submilleri* was described by Frick (1937, p. 131), and no new material has been reported since then.
Discussion—As noted above, of the nine species of *Bouromeryx* originally recognized by Frick (1937), only the late Hemingfordian species *B. submilleri* stands out as distinctly smaller and worthy of recognition (Fig. 14).

**Procranioceras Frick, 1937**

*Figure 18; Table 1*

**Type and only species**—*Procranioceras skinneri* (Frick, 1937)

**Diagnosis**—Differs from *Cranioceras* in having a shorter occipital horn, which is transversely flattened and anteriorly curved. Both the occipital and supraorbital horns are much longer than those of *Bouromeryx*. The premolars are larger than those in *Cranioceras*, but the anterior fossette on p4 tends to be open. Molars more brachyodont, usually with the *Palaeomeryx* fold (modified from Janis and Manning, 1998, p. 485).

**Distribution**—Late Barstovian, Crookston Bridge and Devil’s Gulch members, Valentine Formation, Nebraska; Wood Mountain Formation, Saskatchewan.

**Discussion**—Unlike nearly every other Frick dromomerycine taxon, *Procranioceras* was erected with only one species, *P. skinneri* (based on an outstanding skull that has been illustrated many times), so it is not oversplit. It is easily distinguished from *Bouromeryx* by its larger size and longer supraorbital and occipital horns, and from all species of *Cranioceras* by its shorter and more anteriorly curved occipital horn. Janis and Manning (1998, p. 485) point out that its first appearance in the late Barstovian is actually later than the first appearance of its descendant species, *Cranioceras*, in the early Barstovian. Thus, there is not a strict chronocline of taxa within the cranioceratins (contrary to Webb, 1983, fig. 1).

**Cranioceras Matthew, 1918**

**Cosoryx** Cope, 1874 (in part)

**Dicrocerus** Cope, 1875 (in part)

**Palaeomeryx** Gidley, 1907 (in part)

**Cranioceras** Matthew, 1918

**Cranioceras Frick, 1937**

**Type species**—*Cranioceras unicornis* Matthew, 1918

**Included species**—*Cranioceras teres* (Cope, 1874)

**Diagnosis**—Long, upright supraorbital horns, tapering distally and curved slightly inward; round in midshaft cross-section; long median occipital horn, round in cross-section and directed posteriorly. No upper canine. Short to moderate-length diastema. Premolar row shortened; anterior fossette on p4 open. Brachyodont to mesodont molars with *Palaeomeryx* fold usually lost (modified from Janis and Manning, 1998, p. 485).

**Distribution**—Early Barstovian, California, New Mexico, Nebraska; late Barstovian, Nebraska, New Mexico; early Clarendonian, California, New Mexico, Texas, South Dakota, Nebraska; late...
Clarendonian, California, Nebraska.

**Discussion**—Cope (1874) first recognized the existence of a taxon with unusual horns when he described a partial occipital horn he called *Cosorxy teres* from the early Clarendonian of the Chamita Formation of New Mexico. Originally assigning it to the pronghorn genus *Cosorxy*, in 1875 he transferred the material to the cervid genus *Diceros*. In 1907, Gidley transferred it to the genus *Palaeomeryx*; but little else was written about the specimen until Frick (1937) assigned it to *Cranioceras*, a genus based on another unusual horn described by Matthew in 1918.

Frick (1937) considerably expanded the scope of *Cranioceras* beyond Cope’s and Matthew’s original two species. He named *Cranioceras granti* and *Cranioceras mefferdi* from the early Clarendonian lower Ash Hollow Formation and late Barstovian Valentine Formation of Nebraska (respectively), *Cranioceras dakotensis* from the “vicinity of the Rosebud Agency, South Dakota.” *Cranioceras pavaniiensis* from the Clarendonian of the Pawnee Creek area, Colorado, and *Cranioceras clarendonensis* from the early Clarendonian MacAdams Quarry, near Clarendon, Texas. Most of these taxa were based on large samples of mandibles and rami, although some had associated skull material that showed the distinctive long vertical supraorbital horns and posteriorly-inclined occipital appendage. Thus, with his large sample Frick (1937) was able to reconstruct most of the cranial anatomy of the genus *Cranioceras*, but as usual, he oversplit it into numerous similar species without adequate diagnoses, largely based on their different provenance.


In examining Frick’s (1937) taxa and measuring the *Cranioceras* specimens in the Frick Collection, it became apparent that there are few differences in the various named species except size and provenance. Thus, we measured and plotted numerous variables of the lower dentition and diastema, and found only two clusters that are distinct (Fig. 19). There is a larger cluster that is assignable to *C. unicorns* Matthew, 1918, and includes *C. granti* Frick, 1937, and *C. mefferdi* Frick, 1937. There is also a smaller cluster whose senior name would be *C. teres* (Cope, 1874), and includes *C. clarendonensis* Frick, 1937, and *C. dakotensis* Frick, 1937. These two clusters are statistically distinct, with a student’s t-test probability of p<0.5, and both samples have univariate binomial distributions (Kologmorov-Smirnov test, p<0.05). In addition, the coefficients of variation of the two clusters (Table 1) are reasonable for a single species, but if the entire sample of *Cranioceras* is lumped together, the CV’s are greater than 10, too large for a single species. Thus, we recognize only two of Frick’s (1937) original seven species.

*Cranioceras pavaniiensis* Frick (1937, p. 93) was based on a fragmentary supraorbital horn (F:AM 31294) from the early Clarendonian of the Pawnee Buttes area, Colorado. There were no additional specimens referred to this species, so it is not possible to compare its dental dimensions to the other better-characterized taxa. Frick (1937, p. 93) compared it to a specimen of *Procranioceras skinneri* (F:AM 31264) from the Devil’s Gulch area of the Valentine Formation. However, it could also match some of the specimens referred to *Cranioceras*. As Frick (1937) noted, it is shorter and more attenuated than other known specimens of the supraorbital horn, but this may be because it represents a juvenile. Given the variability of horns in many groups of ruminants, and the fact that this specimen bears marks of juvenile, it is unlikely that the “diagnostic” features that Frick (1937) used to erect the species *C. pavaniiensis* can be justified. Instead, we consider the single type specimen inadequate to diagnose a species, and consider *C. pavaniiensis* a nomen dubium. If the specimen had come from the better-sampled localities in Nebraska, we suspect that Frick would not have given it a new name. Because it was the only cranioceratine from the Pawnee Creek beds of Colorado, it was designated a new taxon.

As noted by Janis and Manning (1998, p. 486), the supposed late Barstovian first occurrence of *Cranioceras* (Tedford et al., 1987) has now been questioned by the possibility of a new unnamed species of *Cranioceras* from the late Hemingfordian and early Barstovian of the Caliente Formation in California (Kelly and Lander, 1988), as well as possible early Barstovian records of *C. unicorns* in Nebraska (Survey Quarry, Sand Canyon beds) and early Barstovian records of *C. teres* in the Skull Ridge Member of the Tesuque Formation of New Mexico.

**Cranioceras unicornis** Matthew, 1918

**Figures 19-20; Table 1**

*Cranioeras unicornis* Matthew, 1918

*Cranioeras granti* Matthew, 1918

*Cranioeras mefferdi* Frick, 1937

**Type specimen**—AMNH 17343, fragmentary occipital horn, from the late Clarendonian Laucomer Member of the Snake Creek Formation, Sinclair Draw, Sioux County, Nebraska (Fig. 20A-B).

**Referred specimens**—Most of the known material was listed by Frick (1937, p. 82-97).

**Diagnosis**—Larger species of *Cranioceras* (Table 1).

**Distribution**—Early Barstovian Sand Canyon beds, Dawes County, Nebraska; late Barstovian Devil’s Gulch and Burge members, Valentine Formation, Nebraska; late Clarendonian Laucomer Member and early Hemphillian Johnson Member, Snake Creek Formation, Nebraska; early Clarendonian Cap Rock Member and late Clarendonian Merritt Dam Member, Ash Hollow Formation, Nebraska; late Clarendonian North Tejon Hills I,F, Chanac Formation, California.

**Description**—Almost all of the known material of *C. unicorns* was described by Frick (1937).

**Discussion**—Matthew (1918, p. 223) described a fragmentary horn (AMNH 17343) from the late Clarendonian Laucomer Member of the Snake Creek Formation (Skinner et al., 1977) of Nebraska (Fig. 20A-B) as *Cranioceras unicorns*. It seemed to suggest an animal with a single occipital horn, reminiscent of a unicorn. Matthew (1918) also referred a ramus (AMNH 17344) to this taxon, but Frick (1937, p. 82) argued that they do not belong together, and made the ramus the type specimen of

**FIGURE 19.** Bivariate plot of m1-3 length vs. p2-4 length of lower jaws of *Cranioceras*. Open circles = *C. granti*; solid circles = topotypic samples of *C. unicorns*; open squares = *C. dakotensis*; solid diamonds = *C. clarendonensis*; open triangles = topotypic material of *C. teres*. 

— Tedford et al. (1987) has}
the protoceratid *Prosynthetoceras siouensis*. Frick (1937, p. 83-84) referred additional specimens from the early Barstovian Olcott Formation to *C. unicornis*, and on this basis Webb (1969, p. 168) synonymized several of the species of *Cranioceras*. Skinner et al. (1977, p. 349) clarified the confused stratigraphy and locality information of the Sheep Creek-Olcott-Snake Creek beds. They checked the locality information carefully, and argued that there are no *Cranioceras* in the Olcott Formation, and that much of Frick’s (1937) alleged topotypic sample is actually *Rakomeryx*. Accordingly, the only material in Frick’s (1937) sample that actually comes from the same formation as the type (Laucomer Member of the Snake Creek Formation) are derived from just two Frick quarries, Olcott Quarry and “The Pits.” This considerably reduces the known topotypic sample of *Cranioceras unicornis*.

Frick (1937, p. 84) named another species, *C. granti*, based on F:AM 32064, a broken cranium that clearly shows the long supraorbital horns and posteriorly-inclined occipital horn (Fig. 20C). It differs little from the material referred to *C. unicornis*, except that the former comes from the early Clarendonian *Leptarctus* Quarry, in the Merritt Dam Member of the Ash Hollow Formation (Skinner and Johnson, 1984, p. 316), and the latter from the Snake Creek Formation. Frick (1937, p. 77) himself noted that *C. granti* does not differ in size or cranial characters from *C. unicornis*, and they are distinct only in their provenance, and on this basis Webb (1998, p. 169) synonymized the two. As can be seen from Figure 19, the type of *C. unicornis* falls with the large cluster of Valentine specimens referred to *C. granti*, so this synonymy is reasonable.

Frick (1937, p. 88) described *C. mefferdi* based on F:AM 32243, a fragmentary skull that shows the same *Cranioceras* condition of the horns (Fig. 20D). He provided no diagnosis for this species, and it differs from *C. unicornis* and *C. granti* only in that it is derived from near Nenzel Quarry in the late Barstovian Burge Member of the Valentine Formation (Skinner and Johnson, 1984, p. 293). Webb (1969, p. 169) noted that *C. mefferdi* is identical in size to *C. unicornis*, and differs only in that it comes from a different locality, and we support this synonymy.

**Cranioceras teres** (Cope, 1874)

*Cosoryx teres* Cope, 1874
*Dicrocerus teres* Cope, 1875
*Palaeomeryx teres* Gidley, 1907
*Cranioceras teres* Frick, 1937
*Cranioceras clarendonensis* Frick, 1937
*Cranioceras dakotensis* Frick, 1937

**Type specimen**—USNM 2044, fragment of cranium with broken horns (Fig. 21A), from the “Santa Fe marls” (early Clarendonian Chamita Formation of New Mexico, *fide* Galusha and Blick, 1975).

**Referred specimens**—Most of the known material was listed by Frick (1937, p. 82-97).

**Diagnosis**—Smaller species of *Cranioceras* (Table 1).

**Distribution**—Early Barstovian Skull Ridge Member and late Barstovian Chama-el-Rito Member, Tesuque Formation, New Mexico; early Clarendonian Chamita and Pojoaque formations, New Mexico; early Clarendonian Clarendon beds, Texas; early Clarendonian Lapara Creek Member, Goliad Formation, Texas; early Clarendonian Merritt Reservoir Member, Ash Hollow Formation, South Dakota; early Clarendonian South Tejon Hills l.f., California.

**Description**—Almost all of the known material was described by Frick (1937).

**Discussion**—As discussed above, Cope (1874, p. 150) first described the fragmentary cranium with a partial occipital horn (USNM 2044) as *Cosoryx teres* (as an antilocaprid), then in 1875 transferred it to the cervid *Dicrocerus*. Gidley (1907) referred it to the genus *Palaeomeryx*. Frick (1937, p. 92-93) transferred *P. teres* to Matthew’s (1918) genus *Cranioceras*, and referred a number of additional specimens from the

Chamita Formation to this taxon. These specimens (Fig. 19) plot in the smaller size cluster, so this makes *Cranioceras teres* the senior name for all the smaller species of *Cranioceras*.

Frick (1937, p. 94) described another new species, *C. clarendonensis*, based on a large sample from the early Clarendonian (primarily MacAdams Quarry) of Texas. He designated F:AM 32454, a right ramus with p2-m3 (Fig. 21B) as the type specimen, and referred and illustrated a few broken horns and dozens of rami to this taxon. However, he provided no adequate diagnosis to distinguish it from other smaller *Cranioceras*, and we can find no characteristics that distinguish it from the New Mexico sample of *C. teres*. Indeed, the entire sample (Fig. 19) encompasses the range of variation of *C. teres*, so there are good grounds for considering *C. clarendonensis* a junior synonym of *C. teres*.

Frick (1937, p. 90) named another new species, *C. dakotensis*, based on AMNH 10952, a right ramus with p2-m3 (Fig. 21C) “from the vicinity of the Rosebud Agency, South Dakota.” He suggested that it might be “Lower Miocene” (Arikareean) in age. Webb (1969, p. 169) cast doubt on this provenance, and Skinner and Johnson (1984, p. 320) showed that this specimen actually came from the early Clarendonian Ash Hollow Formation. Additional referred material included a number of AMNH specimens from the same locality, as well as partial skulls (Fig. 21D). Frick (1937, p. 90) provided no diagnosis of his species other than to note that it was smaller than *Procranioceras skinneri*, but had shorter premolars. He made no comparisons to the many other species of *Cranioceras*, however. Webb (1969) suggested that it was a junior synonym of *C. unicornis*, but provided no detailed analysis of the material. Measurements of the referred rami in the Frick Collection (Fig. 19) show that most of the specimens referred to *C. dakotensis* falls within the smaller size cluster, and is a junior synonym of *C. teres*, not *C. unicornis*.

**Yumaceras** (Frick, 1937)

*Yumaceras* Frick, 1937

*Pediomeryx* Savage, 1951

*Pediomeryx* (*Yumaceras*) Webb, 1983

*Pediomeryx* (*Yumaceras*) Janis and Manning, 1998

**Type species**—*Yumaceras figginsi* (Frick, 1937)

**Included species**—*Yumaceras hamiltoni* Webb, 1983; *Y. ruminalis* Stirton, 1936

**Diagnosis**—Long, nearly vertical supraorbital horns with retrocurved and anteriorly flattened tips, and round midshaft section. Occipital appendage longer than in *Cranioceras*, and rising more vertically, with more anteroposteriorly flattened tip. No upper canine. Diastema moderate. Mandible with nearly straight ventral border. Premolar row reduced, with p2 greatly reduced; p4 closed lingually by long metaconid. Mesodent molars without *Palaeomeryx* fold (modified from Janis...

**Distribution**—Latest Clarendonian Love Bone bed and early Hemphillian Mixson’s bone bed, Alachua Formation, Florida; early Hemphillian Norris Canyon l.f., Siesta Formation, California; middle Hemphillian Kern River Formation, California; late Clarendonian to middle Hemphillian, Ogallala Formation, Texas; middle Hemphillian Wray l.f., Ogallala Formation, Colorado; middle Hemphillian Johnson Member, Snake Creek Formation, Nebraska; early Hemphillian Ash Hollow Formation, Nebraska and Oklahoma; early Hemphillian Drewsey Formation, Oregon.

**Discussion**—*Yumaceras figginsi* was named by Frick (1937, 143) based on a skull (DMNH 314) from the middle Hemphillian Wray localities, Yuma County, Colorado. It was based on very incomplete material, with large cheek teeth showing highly reduced premolars, but little cranial material. Frick (1937) placed *Yumaceras* with the Aletomerycini because of its dental characteristics. Just months earlier, Stirton (1936) named *Pediomeryx hemphillensis*, based on material (UCMP 30703) from the late Hemphillian Coffee Ranch Quarry (= UCMP Miami Quarry) of Texas. Stirton (1944) suggested that the two genera might be synonyms. The confusion was not resolved until Webb (1983) described additional new material from Love Bone Bed in Florida that showed that *Yumaceras* and *Pediomeryx* had occipital horns that placed them with the Cranioceratini, not the Aletomerycini. Webb (1983) suggested that *Yumaceras* should be treated as a subgenus of *Pediomeryx*, and this was followed by Janis and Manning (1998, p. 486). However, these authors also pointed out that the two subgenera were quite distinct, and could easily be restored to generic rank. Given that most of the subgenera within the dromomerycines have proven superfluous, we agree that it is simpler to restore *Yumaceras* to generic rank, and clarify and simplify the taxonomy, especially since placing it within *Pediomeryx* makes that genus paraphyletic.

Webb (1983) and Janis and Manning (1998) updated the species-level taxonomy of these genera, so there is no need to review the species here. *Yumaceras* was the common latest Clarendonian-early Hemphillian dromomercine, whose size increased gradually through this time until the peak size was reached in the middle Hemphillian (Wray sample) with the appearance of *Yumaceras figginsi*. In the late Hemphillian, *Pediomeryx* species were characterized by decreasing body size (Webb, 1983, fig. 7).

**Pediomeryx** Stirton, 1936

*Pediomeryx* Stirton, 1936

*Procoilus* Frick, 1937

*Yumaceras* Frick, 1937 (in part)

*Pediomeryx* (Pediomeryx) Webb, 1983

*Pediomeryx* (Pediomeryx) Janis and Manning, 1998

**Type and only species**—*P. hemphillensis* Stirton, 1936 (= *Procoilus edensis* Frick, 1937; = *Yumaceras falkenbachi* Frick, 1937).

**Diagnosis**—Similar to *Yumaceras* but with more hypsodont cheek teeth and smaller size (modified from Janis and Manning, 1998, p. 486).

**Distribution**—Middle Hemphillian, Alachua Formation, Florida; late Hemphillian Mixten Formation, California; latest Hemphillian Mt. Eden l.f., California; late Hemphillian Hemphill beds, Oklahoma and Texas; late Hemphillian Johnson Member, Snake Creek Formation, Nebraska; middle Hemphillian Cambridge l.f., Nebraska; latest Hemphillian Devill’s Nest Airstrip l.f., upper Ash Hollow Formation, Nebraska.

**Discussion**—As discussed above, *Pediomeryx* was named by Stirton in 1936, based on some of the same material that Frick (1937) assigned to *Yumaceras*. Stirton (1944) placed *Yumaceras* in synonymy with *Pediomeryx*, but Webb (1983) and Janis and Manning (1998) placed *Pediomeryx* in a separate subgenus, *Pediomeryx* (Pediomeryx), to accommodate the specimens that Stirton originally placed in that genus. As Janis and Manning (1998) point out, whether to place them in different subgenera of the same genus, or recognize two genera, is largely a matter of taste (and avoiding paraphyly). We have already discussed our reasons for rejecting subgenera in the dromomercines and aletomercines, so it makes more sense to keep *Yumaceras* and *Pediomeryx* as separate genera. Although they are similar in many ways, *Yumaceras* is part of the increasing size trend through the late Clarendonian to middle Hemphillian, while *Pediomeryx hemphillensis* is the late Hemphillian species that gradually reduced in size through time. There is no need to review the species-level taxonomy of *Pediomeryx hemphillensis*, because it was updated by Webb (1983) and by Janis and Manning (1998).

**TEMPORAL, DIVERSITY, AND BIOGEOGRAPHIC PATTERNS**

Once the confusion of Frick’s (1937) taxonomy is cleared away, an interesting pattern of temporal distribution of the 17 valid dromomercine species emerges (Figure 22). It differs markedly with the simplistic orthogenetic cranioceratin lineage shown by Webb (1983, fig. 1), or with the generic range distribution (they did not attempt to plot the many invalid species of Frick, 1937) shown by Janis and Manning (1998, fig. 32.4). In contrast to earlier interpretations that had at least three subgenera and five species in the late Arikareean, only one species, *Barbouroumeryx trigonocornes* (and possibly two, *Aletomeryx gracilis* is truly known from the late Arikareean) is known during that time. As mentioned by Janis and Manning (1998), the distribution of the aletomercin-dromomercin and cranioceratin lineages in time suggests that there were at least two different immigration events from Eurasia, one of which brought the cranioceratins about 20 Ma and the other of which brought the more primitive aletomercins and dromomercins about 18 Ma (or possibly earlier). When they first appear, dromomercines are widespread over the entire earliest Miocene outcrop in North America. *Barbouroumeryx trigonocornes* is known not only from the High Plains of Nebraska, South Dakota, and Colorado, but also from central Wyoming and the Texas Gulf Coastal Plain. *Aletomeryx* occurs in Nebraska and Colorado, but also in the Mojave Desert of California.

By the late Hemingfordian, *Aletomeryx* was gone, replaced by *Sinclairoumeryx riparius*, plus the ghost lineage of *Drepanomeryx falciformis*, and known occurrences of *Rakomeryx sinclairi*, *Dromomeryx borealis*, *Subdromomeryx antilopinus*, *Bouromeryx submilleri*, *Bouromeryx americanus*, and relict *Barbouroumeryx trigonocornes*. This late Hemingfordian increase of 6 genera and 7 species (plus one additional ghost lineage) represents a dramatic development of dromomercine diversity, as also shown by Janis (2000, fig. 3.5, based on older generic diversity data). At this point, the dromomercines were also biogeographically widespread. *Sinclairoumeryx riparius* is known from Nebraska and Saskatchewan; *Rakomeryx sinclairi* from Nebraska, Montana, California, and Florida; *Dromomeryx borealis* from Nebraska and Montana; *Subdromomeryx antilopinus* from Nebraska, Montana, and Nevada; *Barbouroumeryx trigonocornes* from Nebraska and Wyoming; *Bouromeryx submilleri* from Nebraska, California, Nevada, and Oregon; and *Bouromeryx americanus* from Nebraska, Nevada, and Saskatchewan.

In the early Barstovian, diversity was at its peak. *Sinclairoumeryx riparius*, *Drepanomeryx falciformis*, *Rakomeryx sinclairi*, *Dromomeryx borealis*, *Subdromomeryx antilopinus*, and *Bouromeryx americanus* persisted from the late Hemingfordian. *Barbouroumeryx trigonocornes* was gone, but *Cranio ceras unicornis* and *C. teres* (plus the ghost lineage of *Procranioceras skinneri*) are added. This diversity of 7 genera and 8 species (plus another ghost lineage) is the highest in the history of the group, and higher than that shown by Janis (2000, fig. 3.5). These species are known from practically every region that has a good early Barstovian record. *Sinclairoumeryx riparius* occurs in Nebraska and Saskatchewan; *Drepanomeryx falciformis* is known from Nebraska and Texas; *Rakomeryx sinclairi* occurs in Nebraska and California; *Dromomeryx borealis* in Nebraska, Montana, Oregon, Nevada, New Mexico, and Colorado; *Subdromomeryx antilopinus* is found in Texas;
only; *Bouromeryx americanus* from Nebraska, Montana, California, Florida, Colorado, and Texas; *Cranioceras unicornis* from Nebraska only; and *Cranioceras teres* from New Mexico (plus the unnamed new species from the Caliente Formation of California, *fide* Kelly and Lander, 1988).

In the late Barstovian, diversity was still very high. *Sinclairomeryx*, *Subdromomeryx*, and *Drepanomeryx* vanished, but *Rakomeryx sinclairi*, *Dromomeryx borealis*, *Bouromeryx americanus*, *Cranioceras unicornis*, and *C. teres* persisted, and the primitive *Procranioceras skinneri* appeared (much later than its presumed descendant, *Cranioceras*). This diversity of 5 genera and 6 species is much higher than the diversity values shown by Janis (2000, fig. 3.5). The geographic spread of these taxa is still high. *Sinclairomeryx*, *Subdromomeryx*, and *Drepanomeryx* vanished, but *Rakomeryx sinclairi*, *Dromomeryx borealis*, *Bouromeryx americanus*, *Cranioceras unicornis*, and *C. teres* persisted, and the primitive *Procranioceras skinneri* appeared (much later than its presumed descendant, *Cranioceras*). This diversity of 5 genera and 6 species is much higher than the diversity values shown by Janis (2000, fig. 3.5). The geographic spread of these taxa is still high, too. *Rakomeryx sinclairi* occurs in Oregon and Montana; *Dromomeryx borealis* is found in Nebraska, Colorado, Wyoming, Nevada, and California; *Bouromeryx americanus* is known from Nebraska, Texas, and Montana; *Procranioceras skinneri* occurs in Nebraska and Saskatchewan; *Cranioceras unicornis* was found in Nebraska only, and *C. teres* in New Mexico only.

By the early Clarendonian, diversity had dropped dramatically. Only *Dromomeryx borealis*, *Cranioceras unicornis*, and *C. teres* are known, but this is still a higher generic and specific diversity than shown by Janis (2000, fig. 3.5). The geographic spread of the group was also reduced. No dromomerycines are known from Montana, Saskatchewan, Oregon or Florida (although beds of this age are rare in these regions). *D. borealis* occurred in California and South Dakota; *Cranioceras unicornis* in Nebraska only, and *C. teres* is known from New Mexico, Texas, South Dakota, and California.

In the late Clarendonian and early Hemphillian, only *Cranioceras unicornis* plus the new taxon *Yumaceras* are known. *C. unicornis* is still found in Nebraska and California, while *Yumaceras figginsi* occurs in Colorado, Texas, and Nebraska, *Y. hamiltoni* in Florida, and *Y. ruminalis* in California. In the late Hemphillian, *Cranioceras* and *Yumaceras* vanished, and only a single species, *Pediomeryx hemphillensis*, survived. But it was very widespread, being known from late Hemphillian beds in Florida, California, Oklahoma, Texas, and Nebraska. This drop in diversity from the late Clarendonian through the Hemphillian is consistent with the data plotted by Janis (2000, fig. 3.5).

The great reduction in diversity of valid species also affects other studies that were based on the old, oversplit taxonomy of Frick (1937). More than half of the dromomerycine species cited in Alroy's North American mammalian database (http://www.nceas.ucsb.edu/~alroy/nafmsd.html) are invalid, casting doubt on the overall validity of such "taxon counting" studies which use outdated taxonomy to draw general conclusions about mammalian evolution. The problem is equally severe in the moschids (Prothero, this volume), and in the oreodonts, pronghorns, and camels, so a significant portion of such databases cannot be trusted because the taxonomy of North American fossil mammals is not sufficiently updated to make such surveys worthwhile. Although Alroy (2002, 2003) has begun to acknowledge the problem, it runs deeper than he realizes, and casts doubt on the whole process of taxon counting.

**CONCLUSIONS**

From 49 named species and over a dozen genera and subgenera recognized by Frick (1937) in the subfamily Dromomerycinæ and Aletomerycinæ, we recognize only 18 valid species in 12 genera. Most
of Frick’s (1937) taxa can be synonymized because he failed to account for populational variation, or failed to diagnose his taxa adequately. With an updated taxonomy of the Dromomerixinae, a much clearer understanding of their diversity and biogeographic distribution emerges. Instead of the orthogenetic sequence presented by Webb (1983, fig. 1), the group has a very bushy phylogeny, with multiple contemporaneous lineages, and several ghost lineages where more primitive taxa (e.g., Drepanomeryx, Procranioceras) appeared later than their supposed descendants. A minimum of two immigration events from Eurasia (bringing the aletomerycins and the cranioceratins in the latest Arikareean at 18-20 Ma) established the group in North America, after which they underwent rapid evolution to peaks of diversity in the late Hemphidian (6 genera, 7 species) and early Barstovian (7 genera, 8 species). During these times, they were also extremely widespread in North America, occurring in just about every region that has beds of that age. In the Clarendonian and Hemphillian, their diversity and geographic spread declined dramatically, so that by the late Hemphillian, only one species, *Pediomeryx hemphillensis*, is known, although it occurred in late Hemphillian beds in Florida, California, Oklahoma, Texas, and Nebraska.

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**REFERENCES**


