

## Chapter 15

# *Moropus merriami* in the Early Barstovian Lower Snake Creek Fauna of Nebraska, with Comments on Biogeography of North American Chalicotheres

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### ABSTRACT

*Moropus merriami* Holland and Peterson (1914), an early Barstovian schizotheriine chalicothere from North America, is rediagnosed and redescribed on the basis of additional material. While originally recognized from the Virgin Valley and High Rock Canyon local faunas of northwest Nevada, *M. merriami* can also be identified from the Lower Snake Creek fauna preserved in the Olcott Formation of northwest Nebraska. It represents a derived species of *Moropus* in which the astragalus and metatarsals have become relatively broad and short. The large claw associated with digit II of the manus is laterally compressed, and proximal and middle phalanges of digit II of the pes are uniformly fused. In northwest Nebraska, *M. merriami* is the early Barstovian faunal replacement for the dome-skulled chalicothere *Tylocephalonyx skinneri*, which is found in the Sheep Creek Formation. The early Barstovian appearance on the Great Plains of a species best known from the Great Basin and Columbia Plateau is a significant event at a time when specific-level faunal differences between these regions were pronounced.

### INTRODUCTION

Although chalicotheres are among the most fascinating of extinct mammals, their preserved remains are rare. It took over 50 years after the first remains were discovered in Europe (Cuvier, 1825; Kaup, 1833) for their herbivorous dentitions to be correctly associated with clawed foot elements coming from the same deposits (Filhol, 1890). Even today, our fragmentary knowledge of many chalicothere taxa makes it difficult to complete systematic and biogeographic studies.

In North America, a few species of chalicothere are known from nearly complete remains. The most notable of these is *Moropus elatus* (Marsh, 1877; Holland and Peterson, 1914; Coombs, 1978), known from complete skeletal material from the late Arikarean fauna of the Agate Springs Quarries of northwestern Nebraska and from similar-aged deposits in adjacent areas of Nebraska and Wyoming. To date, the positively documented

distribution of *M. elatus* is still restricted to this small region of the North American central Great Plains, as is that of its close relative *M. hollandi*. *Tylocephalonyx skinneri* was described by Coombs (1979) on the basis of relatively complete material of late Hemingfordian age from the Sheep Creek Formation in northwestern Nebraska. The known distribution of this dome-skulled chalicothere species extends from Nebraska to central Wyoming. More fragmentary specimens of *Tylocephalonyx* from Idaho, Montana, and coastal Oregon attest to the wider geographic distribution of the genus, but cannot be attributed with certainty to *T. skinneri*.

The problems posed by trying to ally scattered and fragmentary remains in a single species are illustrated by the case of *Moropus oregonensis* (see Coombs et al., 2001). Although all specimens referable to this species are small representatives of *Moropus* of very early Miocene age, few of the remains recovered from different locations are corre-

sponding elements. Despite the difficulties, allying the small early Miocene chalicotheres from Oregon, Gulf Coast Texas, and Florida provides substantial insights into our understanding of the biogeography of *Moropus*, especially in view of the presence of a larger-sized contemporary, *M. elatus*, in the Great Plains.

Another opportunity to improve our understanding of North American chalicotheres distributions is presented by the middle Miocene species *Moropus merriami*. In 1911, Merriam described and figured material of a chalicotheres, identified as *Moropus* (?) sp., from the High Rock Canyon (Washoe County) and Virgin Valley (Humboldt County) areas of northwestern Nevada. Faunal and geologic associations suggested a younger age for these specimens than for North American chalicotheres described from Oregon and Nebraska by Marsh (1877). Shortly afterward, Holland and Peterson (1914) designated the Nevada material as a new species, *Moropus merriami*, in honor of Merriam, in their important monograph on North American chalicotheres. The Virgin Valley and High Rock Canyon local faunas are currently thought to be of early Barstovian age (Tedford et al., 1987; Janis et al., 1998), with the Virgin Valley local fauna slightly the earlier of the two (Tedford et al., in press).

In the time since 1914, the chalicotheres material from Virgin Valley and High Rock Canyon has been the subject of only brief published comment (Matthew, 1929; von Koenigswald, 1932; Stirton, 1939; Skinner, 1968; Coombs, 1979, 1998). Matthew (1929) suggested that this species should be critically compared with members of the Old World chalicotheriid subfamily Chalicotheriinae and referred to it as *?Macrotherium merriami*, terminology later followed in spirit by von Koenigswald (1932) and Stirton (1939). This idea is readily invalidated, however, because both dental and postcranial evidence place all known North American Neogene chalicotheriids in the subfamily Schizotheriinae.

Despite the shortage of published treatment, new material referable to *Moropus merriami* has been gradually accumulating. As would be expected, much of this material comes from early Barstovian faunas of Ne-

vada, most notably from the Esmeralda Formation and the Monarch Mill Formation (Stirton, 1939; Coombs, 1998). Further description of Nevada material will shed more light on the morphology of this chalicotheres, but is beyond the scope of the present paper. Identification of *M. merriami* in the Lower Snake Creek fauna of northwestern Nebraska has been more surprising and considerably expands the known geographic range of this species. The present paper aims to describe the Nebraska material sufficiently to confirm its identification as *M. merriami* and to comment on the biogeographic context of its appearance.

#### INSTITUTIONAL ABBREVIATIONS

AMNH	Division of Paleontology, American Museum of Natural History, New York
F:AM	Frick American Mammals, Division of Paleontology, American Museum of Natural History, New York
FMNH	Field Museum of Natural History, Chicago
LSUMG	Louisiana State University Museum of Geoscience, Baton Rouge
UCMP	University of California Museum of Paleontology, Berkeley
UF	Collection of Fossil Vertebrates, Florida State Museum, University of Florida, Gainesville

#### ANATOMICAL ABBREVIATIONS

Mc	metacarpal
Mt	metatarsal

### SYSTEMATICS

#### CLASS MAMMALIA

#### ORDER PERISSODACTYLA

#### SUPERFAMILY CHALICOTHERIOIDEA GILL, 1872

#### FAMILY CHALICOTHERIIDAE GILL, 1872

#### SUBFAMILY SCHIZOTHERIINAE HOLLAND AND PETERSON, 1914

#### Genus *Moropus* Marsh, 1877

#### *Moropus merriami* Holland and Peterson, 1914

*Moropus* (?) sp.: Merriam, 1911: 267.

*Moropus merriami*: Holland and Peterson, 1914.

*Macrotherium merriami*: Matthew, 1929: 519.

“*Chalicotherium merriami*”: von Koenigswald, 1932: 22.

*Moropus merriami*: Colbert, 1935: 13.

? *Macrotherium merriami*: Stirton, 1939: 629.

*Moropus merriami*: Coombs, 1978: 11; 1998: 564.

SYNTYPES: UCMP 12596, P4; UCMP 19404, astragalus; UCMP 19406, fused proximal and middle phalanges (duplex bone) of digit II of the manus; UCMP 10723, ungual phalanx; UCMP 12595, m2; UCMP 19405, calcaneum; UCMP 19407, large ungual phalanx. The first four specimens are from the Virgin Valley local fauna, Humboldt County, Nevada (UCMP Locality 1065), and the last three specimens are from the High Rock Canyon local fauna (UCMP Localities 1106 and 1107). All specimens were figured by Merriam (1911: figs. 39–45).

COMMENT: In naming the species *Moropus merriami*, Holland and Peterson (1914) designated as types all of the remains “which have been well described and figured by Professor Merriam” (1911). Because these remains come from several localities in two different counties, they are clearly not a single individual. The International Code of Zoological Nomenclature, article 74 (International Commission on Zoological Nomenclature, 1999), allows a reviser to designate a single lectotype from a type series. I have given careful consideration to this issue and have evaluated each of the syntypes in terms of its possible sufficiency to be lectotype. At this time, I conclude that the complete type series gives the best sense of the species and therefore neither designate a lectotype nor eliminate any of the syntypes from the type series.

HYPODIGM: Additional material from the Virgin Valley local fauna, including UCMP 11605, astragalus; UCMP 11625, calcaneum; UCMP 11746, proximal end of radius; UCMP 11842, several phalanges, partial metapodials, and a broken astragalus; UCMP 78727, cuboid; UCMP 31417, Mt III, unciform, and magnum; UCMP 11858, Mt II and duplex of digit II of the manus; UCMP 41031, scaphoid; UCMP 136621, large duplex of digit II of the manus; UCMP 136616, large ungual phalanx; UCMP 136623, duplex of the pes. Additional material from the High Rock Canyon local fauna in the Washoe For-

mation, including UCMP 24303, two duplexes of the pes; UCMP 35582, distal end of tibia, partial M3 and small Mt III; UCMP 136618, distal end very large Mc III. The hypodigm specimens noted here are among those most useful for the comparisons in the present paper. Undescribed chalicothere material from several additional Nevada faunas of late Hemingfordian and early Barstovian age can also be included in *M. merriami* (Coombs, 1998: 564).

Chalicothere specimens from the Lower Snake Creek fauna of the Olcott Formation, Sioux County, Nebraska, are also referable to *M. merriami*. From Echo Quarry (or Campsite Echo Quarry): F:AM 54164, a right ramus with p4–m3, roots of p2–3, and part of coronoid process; F:AM 54898, ramus with p2–m1; F:AM 54899, juvenile ramus with dp2–dp4; F:AM 54187, right dp3; F:AM 54165, upper molar; F:AM 54166, upper molar; F:AM 54167, upper molar; F:AM 54168, P4 in maxilla with M1 roots; F:AM 104897, maxilla fragment with very worn M1, M2; F:AM 54181, proximal end ulna; F:AM 54171, distal end radius-ulna; F:AM 140018, scaphoid; F:AM 54180, Mc IV; F:AM 54178, Mc IV proximal end; F:AM 54177, tibia; F:AM 54174, calcaneum; F:AM 54175, calcaneum; F:AM 140020, small abraded astragalus; F:AM 54176, Mt III; F:AM 54172, Mt IV; F:AM 54169, duplex of pes; F:AM 54170, duplex of pes; F:AM 54173, duplex of pes; F:AM 54179, duplex of pes. From *Prosynthetoceras* Quarry: F:AM 54183, P4 in maxilla; F:AM 54182, ramus with worn p3–m2. From Humbug Quarry: F:AM 140019, proximal end juvenile Mt II.

REVISED DIAGNOSIS: A species of *Moropus* in which (1) wear on P4 quickly incorporates the protocone, (2) the metacone is well separated from the mesostyle in unworn upper molars, and no crista is present, (3) the lower jaw diastema is shorter than the premolar row and the symphysis ends well anterior to p2, (4) the ungual phalanx of digit II of the manus is tall and transversely compressed, (5) the astragalus is relatively broad and low with a reduced distal neck, (6) the ectal facet on the calcaneum is wide and does not extend far onto the calcaneal tuber, (7) metatarsals (especially Mt II and Mt III) are wider

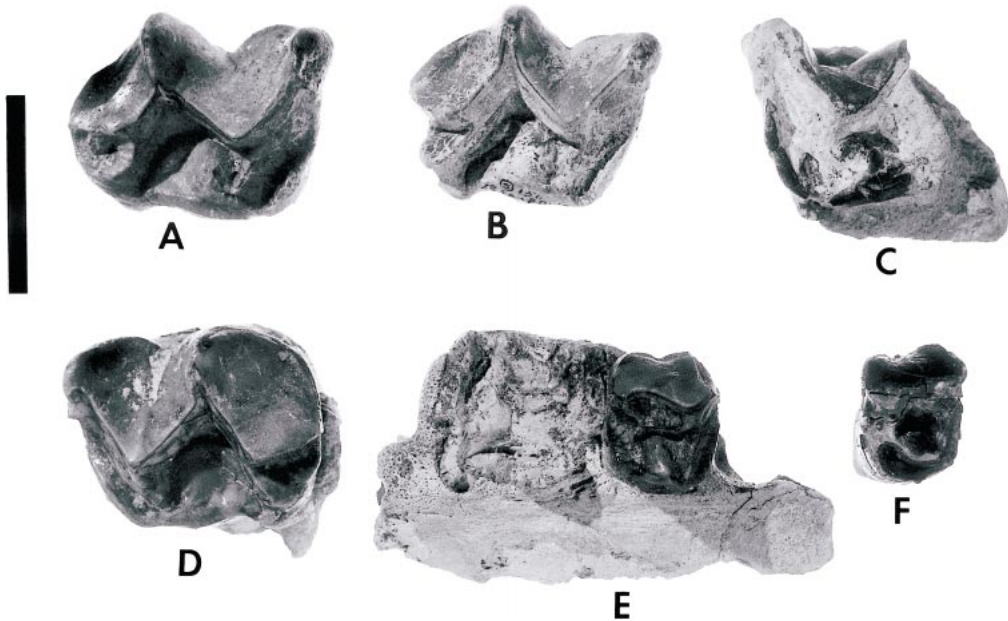


Fig. 15.1. Upper teeth of *Moropus merriami*. **A**, F:AM 54167, right M3(?); **B**, F:AM 54166, right M3(?); **C**, UCMP 35582, left M3; **D**, F:AM 54165, left M3(?); **E**, F:AM 54168, right maxilla fragment with P4 and roots of M1; **F**, UCMP 12596, right P4, one of the species syntypes. A, B, D, and E from Echo Quarry, Olcott Formation, Sioux County, Nebraska; C from High Rock Canyon local fauna, Washoe County, Nevada; F from Virgin Valley local fauna, Humboldt County, Nevada. Scale bar = 4 cm.

and deeper relative to length than in other North American chalicotheres, (8) dorsal and plantar facets between Mt III and Mt IV are strongly confluent, and (9) proximal and middle phalanges of digit II of the pes are fused.

**DESCRIPTION AND COMPARISON:** The following description, rather than detailing all known elements of *Moropus merriami*, emphasizes major aspects of skeletal morphology and characters that are important for placing specimens from the Olcott Formation of Nebraska in this species.

Like other chalicotheres, *M. merriami* shows substantial size variation consistent with sexual dimorphism (Coombs, 1975). Average size for this species is fairly close to that of *T. skinneri*, much larger than *M. oregonensis*, and slightly smaller than *M. elatus*. A few specimens collected from Virgin Valley and High Rock Canyon (for example, UCMP 136621, a duplex, and UCMP 136618, the distal end of Mc III) are much larger than the average, and a few (for ex-

ample, the Mt III included in UCMP 35582) are smaller, despite strong similarity in general morphology. The largest specimens are among the biggest chalicotheres known from North America. Most of the known specimens from Nebraska are close to the average size for the species.

Virtually nothing of the skull and only isolated parts of the upper dentition are known. P4 is the only known upper premolar (fig. 15.1E, F), with UCMP 12596 included among the species syntypes. The ectoloph of UCMP 12596 is both worn and damaged. Wear continues about equally along the protocone and metaloph to and around the tip of the protocone. F:AM 54168 and F:AM 54183 from Nebraska are less worn examples of P4. On F:AM 54183 the protocone and transverse lophs are virtually unworn, whereas on F:AM 54168 slight wear encroaches on the protocone both anteriorly and from along the posterior surface of the metaloph. All three specimens of P4 preserve a small paraconule and fuse the lingual cin-

gulum to the base of the protocone. F:AM 54168 and F:AM 54183 have greater development of anterolingual and posterolingual cingula than does UCMP 12596 and thus are slightly more squared in occlusal outline. However, none of the P4 specimens of *M. merriami* is squared to the degree seen in *Tylocephalonix skinneri*, and the parastyle is also less developed. The wear pattern is also more similar to that of *Moropus oregonensis* or *Moropus elatus*, rather than to *Tylocephalonix skinneri*, in which the transverse lophids are strongly worn before significant wear encroaches on the protocone.

UCMP 35582 includes the only upper molar yet known of a Nevada chalicothere. Although only the anterior two-thirds of this tooth is preserved, its posterior narrowing suggests identification as M3 (fig. 15.1C). Three isolated upper molars from Echo Quarry (fig. 15.1A, B, D) show no wear on the segment of the ectoloph posterior to the metacone and thus may also represent M3; alternatively some of these teeth could represent M2 of young individuals in which m3 had not yet erupted. All are less worn than UCMP 35582, though F:AM 54166 is closest in morphology and degree of wear. UCMP 35582, F:AM 54166, F:AM 54165, and F:AM 54167 resemble one another in having weak development of the cingulum lingual to the protocone and some degree of enamel folding on the posterolabial base of the protocone in the central valley. The three Nebraska specimens share the following additional features not seen in UCMP 35582 because of breakage or wear: labial metaloph origin more separated from the mesostyle than in *M. oregonensis* and *M. elatus*, even when the tooth is little worn; protocone more pointed than in *T. skinneri*; cingulum posterior to postfossette higher than in *M. oregonensis* and *M. elatus*, but lower than in *T. skinneri*; no crista or crochet; and a variable (weak or absent) ectoloph rib at the paracone.

UCMP 12595 (fig. 15.2B) is one of the species syntypes and the only lower tooth among the Nevada material that can be compared with better specimens from Nebraska (fig. 15.2A, C, D). This m2 has relatively straight lophids and weak cingula. F:AM 54164 and F:AM 54898 also have straight

rather than curved lophids on the lower molars, but the cingula are stronger and there is a distinct low lingual cingulum along the opening of the talonid basin. The strong metastylid resembles that of *M. elatus* more than the weaker metastylid of *T. skinneri*. Premolar/molar row length proportions are close to those of *M. elatus* and higher (0.51 in F:AM 54164) than the average in *T. skinneri* (see table 3 in Coombs, 1979). The p2 of F:AM 54898 has a smaller, blunter paracoid and talonid than counterparts in *M. elatus*, but the talonid is less reduced and compressed against p3 than in *T. skinneri*. Well-preserved dp2–dp4 in F:AM 54899 are comparable to permanent lower molars of F:AM 54164 in having straight lophids, a strong metastylid, and a lingual cingulum at the opening of the talonid basin on dp3 and dp4. Like p2, dp2 is less shortened than dp2 in *T. skinneri*.

F:AM 54164 preserves the diastema and much of the lower jaw symphysis (fig. 15.2A, C). No incisors are preserved, but two small alveoli lie above the much larger mental foramen, which is thus near the anterior end of the diastema rather than partway along it as in *M. cf. oregonensis*, *M. elatus*, and *T. skinneri*. The diastema is relatively short, only about two-thirds the length of the premolar row. Among North American chalicotheres that retain this part of the jaw, only *M. cf. oregonensis* has a shorter relative diastema (about half the length of the premolar row), whereas that in *M. elatus* and *T. skinneri* equals or exceeds the premolar length (Coombs et al., 2001). The jaw symphysis also is short, ending well anterior to p2.

Known parts of the forelimb include fragments of the radius and ulna, individual carpals and metacarpals, and some phalanges. Except for an unusual enlargement on the radial side of the olecranon process of the ulna on F:AM 54181, the long bones show no notable differences compared to species (*M. elatus*, *M. hollandi*, *T. skinneri*) in which these bones are better known. The anconeal process on the ulna is strongly developed, comparable to that in *T. skinneri*. As in other chalicotheres, the radius and ulna are strongly fused at their distal ends (F:AM 54171).

The scaphoids of UCMP 41031 and F:AM 140018 (fig. 15.3D, E) are quite similar, al-

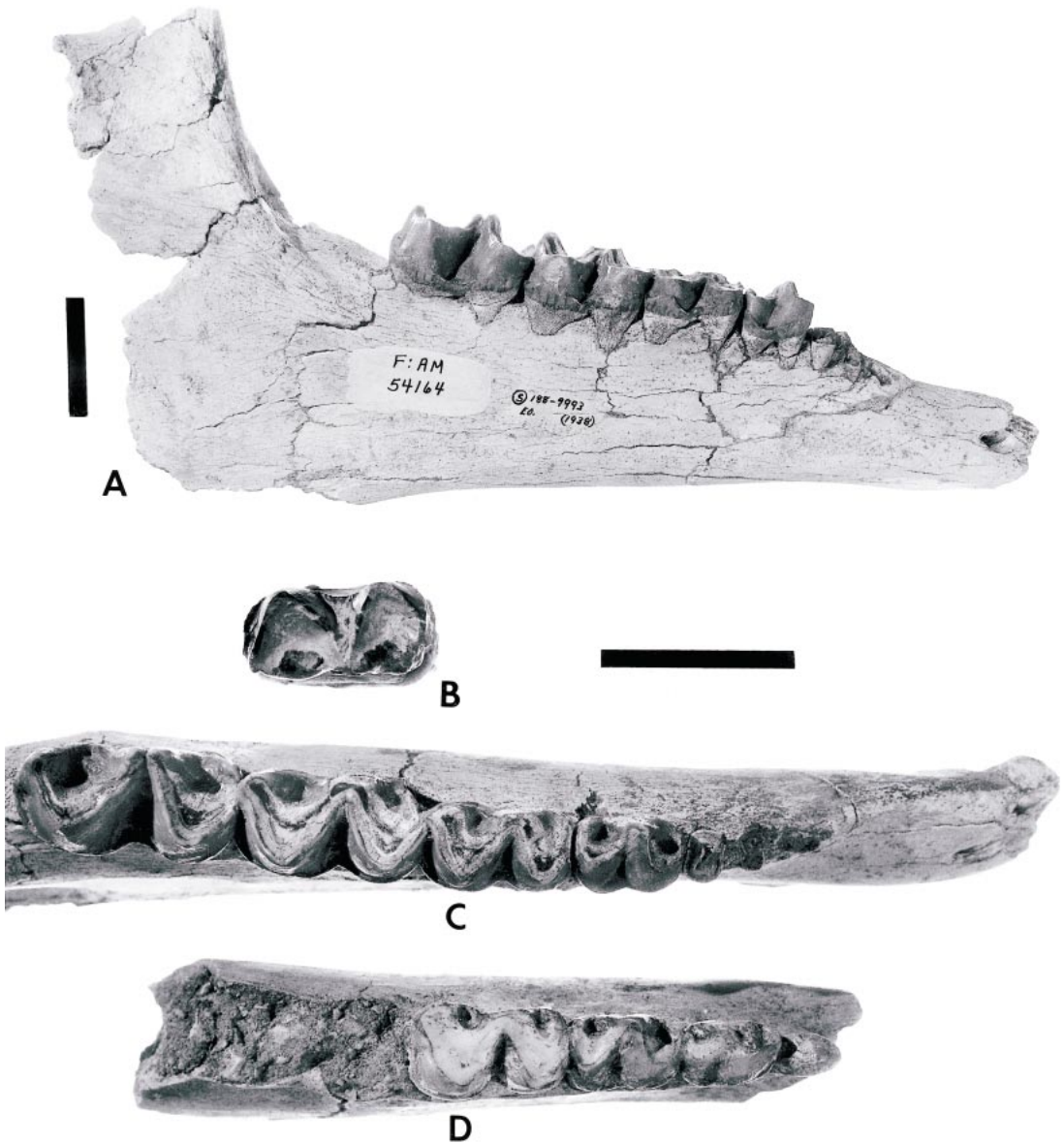


Fig. 15.2. Labial (A) and occlusal views (B–D) of lower teeth of *Moropus merriami*. A, C, F:AM 54165, a right mandibular ramus with p4–m3 and roots of p2–p3; B, UCMP 12595, left m2, one of the species syntypes; D, F:AM 54898, partial right ramus with p2–m1. A, C and D from Echo Quarry, Olcott Formation, Sioux County, Nebraska. B from High Rock Canyon local fauna, Washoe County, Nevada. Scale bar = 4 cm.

though articular facets in UCMP 41031 are much less well preserved. Both scaphoids show clear presence of a trapezium facet, thus confirming the presence of this bone, in contrast to its loss in *M. hollandi*. The distal process is less developed and less squared

than its counterpart in *M. elatus* or *M. hollandi*, resulting in a more oblique facet for the magnum on the ulnar surface of its distal end. This facet is only weakly visible on the abraded scaphoid of UCMP 41031, but the presence of an oblique contact between the

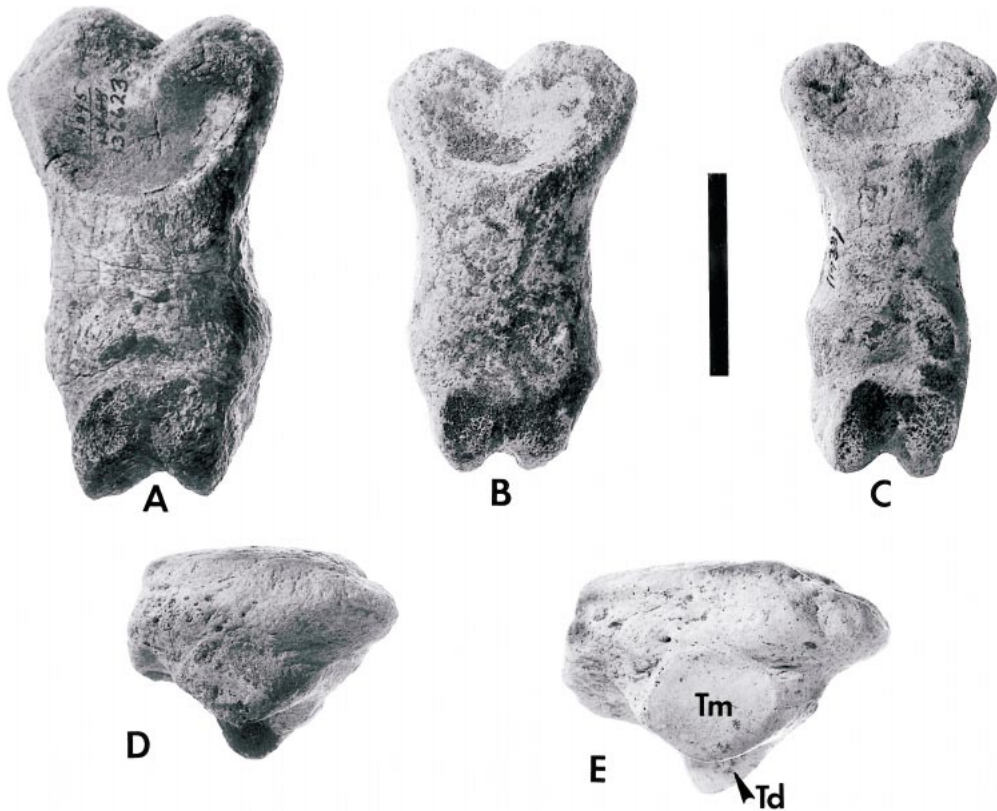


Fig. 15.3. A–C, fused proximal and middle phalanges (duplex bones) of the pes in dorsal view; D–E, radioplantar views of scaphoid bones. A, UCMP 136623; B, F:AM 54179; C, F:AM 54169; D, UCMP 41031; E, F:AM 140018. A and D from Virgin Valley local fauna, Humboldt County, Nevada; B, C and E from Echo Quarry, Olcott Formation, Sioux County, Nebraska. Abbreviations: Tm = trapezium facet; Td = part of trapezoid facet on distal process. Scale bar = 4 cm.

scaphoid and magnum is confirmed by the scaphoid facet on UCMP 31417, a magnum also from Virgin Valley. *T. skinneri* also reduces the distal process somewhat and has an oblique facet between the scaphoid and magnum.

F:AM 54178 (fig. 15.4A) and F:AM 54180 are the only metacarpals referable to *M. merriami* that preserve the proximal articulations. While F:AM 54180 preserves the entire bone, its articular surfaces are damaged by abrasion. Both specimens have a notch in the ulnoplantar surface near the proximal end, suggesting the retained presence of a vestigial Mc V; however, no well defined facet for this bone exists. Mc IV of *M. merriami* resembles those of *M. elatus* and *M. hollandi* in having the facet for Mc III on the radial surface of the proximal end

extend all the way from the dorsal to the plantar edge. In contrast, only the dorsal part of the Mc III facet occurs in *T. skinneri*. The dorsal part of the facet for Mc III is much larger than the plantar part and has an extensive distally directed tongue at the dorsoradial angle of the bone. The smaller, more plantar part of the Mc III facet has an entirely radial orientation. The two parts of the Mc III facet are continuous but delineated by a ridge. Another ridge delineates the Mc III facet from the radial margin of the unciform facet, which occupies the proximal surface of Mc IV.

Like other species of *Moropus*, *M. merriami* enlarged the phalanges of digit II of the manus into a prominent clawed hook. The syntypes of *M. merriami* include proximal and medial phalanges of digit II that have



Fig. 15.4. A, F:AM 54178, proximal end of Mc IV in radial view, showing facet for Mc III. B, F:AM 54172, Mt IV, tibial view. Both specimens from Echo Quarry, Olcott Formation, Sioux County, Nebraska. Scale bar = 4 cm.

fused to form a duplex (UCMP 19406; Merriam, 1911: fig. 43). This duplex is more robust for its length and more asymmetrical in its fusion and development of the facet for Mc II than counterparts in *M. elatus* and *M. hollandi*; it resembles *T. skinneri* in these respects. The syntypes of *M. merriami* also include two ungual phalanges, UCMP 19407 (Merriam, 1911: fig. 45) and UCMP 10723 (Merriam, 1911: fig. 44). UCMP 19407 and UCMP 136616 represent enlarged claws of digit II of the manus of big individuals. They are unusually compressed transversely, with a prominent subungual process and a relatively short but thick dorsal process. Transverse compression is much greater than that seen in *M. elatus*, *M. hollandi*, and *T. skinneri* (Coombs, 1979: table 12) but is similar to that of AMNH 9076, part of the type of *Moropus matthewi* Holland and Peterson (1914). The nearly right angle bend in the claw articulation for the duplex suggests very little movement between these phalanges. UCMP 10723 is a smaller (but still good-sized), less compressed ungual; the digit to which it belongs is unclear. Unfortunately, no phalanges clearly attributable to the manus and no unguals have been recov-

ered among the specimens of *M. merriami* from Nebraska.

Hindlimbs of *M. merriami* are represented by some long bone material and a number of tarsals, metatarsals, and phalanges. UCMP 35582 includes the distal end of the tibia and F:AM 54177, a complete tibia of a subadult individual. Proportions of these bones are, in general, comparable to counterparts in *M. elatus*, *M. hollandi*, and *T. skinneri*.

The syntypes of *M. merriami* include both an astragalus (UCMP 19404, Merriam, 1911: fig. 42) and a calcaneum (UCMP 19405, Merriam, 1911: fig. 41). Additional specimens of both bones are found among the UCMP collections from northwest Nevada. Collections from the Olcott Formation include a small abraded astragalus (F:AM 140020) and two calcanea (F:AM 54174, F:AM 54175). The astragalus of *M. merriami* resembles that of *M. elatus* and *M. hollandi* in being less symmetrical than that of *T. skinneri*, with the fibular side of the trochlea broader and more gradually slanted than the tibial side. On the other hand, it differs from the earlier Miocene species *M. elatus* and *M. hollandi*, and resembles *T. skinneri*, in its reduced distal neck. Reduction of the distal neck and trochlear height compared to width seems to occur gradually over time in schizotheriine chalicotheres (see Coombs, 1978: table 4); reduction of the height of the astragalus never, however, reaches proportions observed in chalicotheriine chalicotheres such as *Chalicotherium*. As in other species of *Moropus*, the distal surface of the astragalus articulates only with the navicular, with no trace of a facet for the cuboid.

Figure 15.5 shows the similarities in proportions and facet shapes between calcanea from Nevada and Nebraska. The ectal facet is transversely broad but does not extend far onto the calcaneal tuber, a similarity with *T. skinneri*. In contrast, the ectal facet in *M. elatus* and *M. hollandi* is narrower but extends more substantially onto the tuber. In UCMP 19405 the ectal facet extends far enough in the tibial direction to contact the sustentacular facet, though the two facets are still delineated by a distinct ridge. In F:AM 54174 and F:AM 54175 the ectal and sustentacular facets remain separated by a groove; this condition is probably the more common one





Fig. 15.5. Right calcaneus of *M. merriami*. **A**, UCMP 19405, one of the species syntypes; **B**, F:AM 54175; **C**, F:AM 54174. **A** from High Rock Canyon local fauna, Washoe County, Nevada; **B** and **C** from Echo Quarry, Olcott Formation, Sioux County, Nebraska. Facet abbreviations for astragalus: **C** = calcaneal, **E** = ectal, **S** = sustentacular. Scale bar = 4 cm.

in *M. merriami* overall, as suggested by additional calcaneus and astragali from the Virgin Valley collections. The part of the ectal facet on the tuber is raised on a platform, which, when the astragalus and calcaneus are articulated, can form a contact with the tibia in continuation with the astragalar trochlea. This platform and its articular surfaces are best seen in UCMP 19405 (fig. 15.5A).

Metatarsals of *M. merriami* are reasonably well known and very useful taxonomically. Table 15.1 gives length:width proportions for metatarsals of a number of North American chalicotheres. *Moropus merriami* has proportionately the shortest and broadest Mt II of any North American chalicotheres, and Mt III and Mt IV among the shortest and broadest. Mt III is the only metatarsal for which complete elements from both northwest Nevada and Nebraska are available, and these bones are very similar in proportions, thus helping to confirm the species identity of the Nebraska material. Coombs (1979: table 9) also reported length:maximum distal depth and length:minimum shaft depth proportions for Mt III of North American chalicotheres. UCMP 35582 and UCMP 31417 have the lowest length:distal depth (2.3 and 2.4) and lowest length:shaft depth (4.2 and 4.1) of any

of the specimens listed; F:AM 54176 has similarly low ratios, with length:distal depth = 2.4 and length:shaft depth = 4.3. Both the width and depth of Mt III compared to length can be observed in figure 15.6. Another important issue concerns the relative lengths of Mt III and Mt IV in *M. merriami*. As has been noted elsewhere (Coombs, 1978, 1979), Mt IV is slightly longer than or subequal in length to Mt III in *Moropus*, whereas Mt III is longest in *Tylocephalonyx* and other schizotheriine chalicotheres such as *Ancylotherium*. Although F:AM 54176 (Mt III) and F:AM 54172 (Mt IV) from Echo Quarry are not associated, they appear to belong to a similar-sized animal and articulate well with each other. Of these specimens Mt IV is longer (135.5 mm, versus 128.3 mm for Mt III), suggesting the length proportions typical of *Moropus*.

UCMP 11858 is the best-preserved specimen of Mt II. Although proportionately shorter and more robust, it resembles Mt II of *T. skinneri* and *M. matthewi* in having its proximal articulation for the mesocuneiform in the form of an equilateral triangle with its apex midway on the tibial side (in *M. elatus* the triangular facet is not equilateral and its apex is at the plantar extremity of the tibial side). Another similarity to *T. skinneri* and

TABLE 15.1  
**Metatarsal Proportions in North American Schizotheriine Chalicotheres**  
 Includes data from Coombs (1978, 1979) and Albright (1999).

Taxon (specimen)	Max. length : max. distal width	Max. length : min. shaft width
<b>Mt II</b>		
<i>M. elatus</i>	3.2–3.7 (N = 8)	5.0–6.2 (N = 8)
<i>T. skinneri</i>	2.4–2.6 (N = 4)	3.3–3.7 (N = 3)
<i>M. matthewi</i> (AMNH 9368)	2.6	4.0
<i>M. merriami</i> (UCMP 11858)	2.0	2.9
<b>Mt III</b>		
<i>M. elatus</i>	3.2–3.5 (N = 4)	5.2–5.6 (N = 4)
<i>M. hollandi</i> (FMNH P13000)	3.3	4.6
<i>M. cf. hollandi</i> (F:AM 54903)	2.7	3.8
<i>T. skinneri</i>	2.5–2.8 (N = 3)	3.5–4.1 (N = 3)
<i>M. matthewi</i>	2.6–2.8 (N = 2)	3.6–3.7 (N = 2)
<i>M. merriami</i> (UCMP 35582)	2.4	3.5
<i>M. merriami</i> (UCMP 31417)	2.4	3.6
<i>M. merriami</i> (F:AM 54176)	2.5	3.6
<b>Mt IV</b>		
<i>M. elatus</i>	3.2–3.8 (N = 8)	4.8–5.5 (N = 8)
<i>M. cf. oregonensis</i> (LSUMG V-2260)	3.5	5.0
<i>M. cf. oregonensis</i> (UF 24129)	3.6	5.2
<i>M. cf. hollandi</i> (F:AM 54903)	3.4	4.7 (approx.)
<i>T. skinneri</i>	2.4–2.9 (N = 4)	3.0–3.3 (N = 5)
<i>M. merriami</i> (F:AM 54172)	2.9	3.6

*M. matthewi* is the more proximal orientation of the plantar half of the ectocuneiform facet (in *M. elatus* the ectocuneiform facet has a more strictly fibular orientation). Facets for the ectocuneiform and Mt III are confluent on the fibular surface. UCMP 11858 has a lengthy rugose area in the location of the oblique ridge observed in *M. elatus* (Coombs, 1978: fig. 18). F:AM 140019, from Humbug Quarry, shares characters of the proximal facets with UCMP 11858 but, being immature with a missing distal epiphysis, has a slenderer shaft with no rugosities.

The Mt IIIs of UCMP 31417 and F:AM 54176 are extremely similar in proportions and morphology (fig. 15.6). A sharp ridge separates the ectocuneiform facet on the dorsal surface and the adjacent Mt IV facet on the fibular surface. The dorsal and plantar parts of the Mt IV facet are broadly confluent, a character unique to *M. merriami*. In *M. elatus*, *M. cf. hollandi*, and *T. skinneri*, there are distinctive dorsal and plantar parts to the Mt IV facet. The long, undivided facet probably allowed some abduction of Mt IV, a dis-

tinct difference from *T. skinneri*, in which Mt III and IV appear to have interlocked tightly. *Tylocephalonyx skinneri* also lacks the sharp ridge between the ectocuneiform and Mt IV facets, but there is sometimes a short gap between the facets instead. On the tibial surface of Mt III, the articular facet for Mt II forms a continuous dorsal to plantar band with small tongue-like distal expansions at both ends. Unlike *T. skinneri*, the shaft of Mt III is deep rather than compressed in depth and the phalangeal articulation is convex in all directions rather than flat or transversely concave.

F:AM 54172 (fig. 15.4B), a Mt IV, can be referred to *M. merriami* on the basis of confluent dorsal and plantar parts of the facet for Mt III. The more proximal part of this large facet merges into a more proximally oriented contact with the ectocuneiform. Although no ectocuneiform is available from these collections, it is clear when F:AM 54172 and F:AM 54176 (Mt III) are articulated that Mt IV would articulate with the ectocuneiform. A Mt IV to ectocuneiform contact is char-



acteristic of *Moropus* and does not occur in *Tylocephalonyx*.

Coombs and Rothschild (1999) reviewed phalangeal fusion in schizotheriine chalicotheres. Whereas the proximal and middle phalanges of digit II of the manus are known to fuse to form a duplex in *Moropus*, *Tylocephalonyx*, *Phyllotillon*, and *Ancylotherium*, fusion of other phalanges is more restricted. Fusion of proximal and middle phalanges of digit II of the pes occurs in approximately 11% of known specimens of *M. elatus* and 60% of known specimens of *T. skinneri* (Coombs and Rothschild, 1999: table 1). Synonymy of *M. distans* with *M. oregonensis* (Coombs et al., 2001) means that a duplex occurs in the only specimen of *M. oregonensis* for which these phalanges are known. Duplex phalanges of the pes are smaller than those of digit II of the manus and lack the distinctive facet enlargements and asymmetries (Coombs, 1978: figs. 19, 20; 1979: fig. 25; Coombs and Rothschild, 1999). Among specimens of *M. merriami* from Nevada, there are six duplexes that do not belong to digit II of the manus; four duplexes from Echo Quarry also do not belong to digit II of the manus. Because the only other digit for which duplex fusion is known is digit II of the pes, it is logical to assume that all ten of these duplexes should be attributable to this digit. No unfused proximal and medial phalanges of digit II of the pes are known, so fusion appears to be 100%. Figure 15.3A–C gives dorsal views of three of the ten duplexes: UCMP 136623, F:AM 54179, and F:AM 54169. All three of these duplexes are relatively large. UCMP 136623 and F:AM 54179 are robust bones, which are wide for their length. F:AM 54169 is much more slender than the other two duplexes figured, as is F:AM 54170. While some size variation is expected, the degree of difference in size and shape is surprising for the phalanges of a sin-

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Fig. 15.6. Dorsal (A), fibular (B), and tibial (C) views of Mt III of *M. merriami*. On left, UCMP 31417, a right Mt III from Virgin Valley local fauna, Humboldt County, Nevada. On right, F:AM 54176, a left Mt III from Echo Quarry, Sioux County, Nebraska. Scale bar = 4 cm.

gle digit. While some (and perhaps all) of these duplexes probably belong to digit II of the pes, it is possible that fusion of phalanges of other digits has occurred. More associated material is needed to help resolve this issue.

TAXONOMIC DISCUSSION: *Moropus merriami* is clearly a derived schizotheriine chalicotheriid, and its reference to *Moropus* is confirmed by the subequal lengths of Mt III and Mt IV and by articulation between Mt IV and the ectocuneiform. It further differs from *T. skinneri* in having earlier wear of the P4 protocone, a weaker cingulum immediately posterolingual to the protocone on upper molars, straighter (less curved) lower molar lophids and larger metastylids, a less reduced premolar row, a shorter diastema and jaw symphysis, a plantar component on the articulation between Mc IV and Mc III, a taller, more transversely compressed ungual phalanx of digit II of the manus, a more asymmetrical astragalus, wider and deeper Mt II and Mt III relative to length, more moveable articulation between Mt III and Mt IV with confluent dorsal and plantar facets, and fusion of all known proximal and middle phalanges of digit II of the pes. *Moropus merriami* does resemble *T. skinneri* in some regards, such as reduced lower incisors, robust duplex of digit II of the manus, shortened astragalus with reduced distal neck, shape of ectal facet on the calcaneum, shape of proximal facets on Mt II, and some degree of metatarsal shortening and broadening (especially Mt IV).

*Moropus merriami* differs from *M. elatus* in having smaller lower incisors, a shorter diastema and lower jaw symphysis, somewhat lower crowned and less elongated molar teeth, a less squared distal process on the scaphoid and a more oblique facet for the magnum, a more robust duplex of digit II of the manus, a taller and more laterally compressed ungual phalanx of digit II of the manus, a broader shorter astragalus with reduced distal neck, a wider ectal facet on the calcaneum which extends less onto the calcaneal tuber, much wider and shorter metatarsals, Mt II with the mesocuneiform facet forming more of an equilateral triangle and with a more proximal orientation of the plantar part of the ectocuneiform facet, strong confluence of the dorsal and plantar facets

between Mt III and Mt IV, and fusion of all known proximal and middle phalanges of digit II of the pes. These differences also apply in general to *M. hollandi*, though *M. hollandi* also differs in losing the trapezium.

*Moropus merriami* is much larger than *M. oregonensis* and is more derived in losing the crista and having a larger distance between the mesostyle and metacone on unworn upper molars. Metatarsals and an astragalus that have been referred to *M. cf. oregonensis* also lack the derived broadening and shortening that occurs in *M. merriami*. However, there are resemblances between *M. oregonensis* and *M. merriami* in the wear pattern on P4, general molar shape and cusp morphology, short diastema (see *M. cf. oregonensis* in Coombs et al., 2001), and fusion of known proximal and middle phalanges of digit II of the pes.

*Moropus matthewi* Holland and Peterson (1914) from northeastern Colorado has poor type locality information, which makes its (possibly early Barstovian) age assignment difficult to verify (see Skinner, 1968). The fragmentary material of this species shows some similarities to *M. merriami*, for example, the tall, transversely compressed large ungual phalanx of digit II of the manus. However, known Mt II specimens of *M. matthewi* show less shortening and broadening than occurs in Mt II of *M. merriami* (table 15.1).

Despite the substantial similarities between material of *M. merriami* from the Olcott Formation and Nevada specimens from Virgin Valley and High Rock Canyon, some minor differences do occur. Specimens from the Olcott Formation have better developed anterolingual and posterolingual cingula on P4 and more development of lingual cingula opposite the talonid basin on the lower molars. The Olcott collection of pedal duplexes includes some specimens that are proportionally more slender than any of the Nevada specimens. These differences can be considered within the range of a single species, especially in view of the geographic distance between the two populations.

The present paper omits detailed discussion of Frick chalicothere material collected from Observation Quarry in Dawes County, Nebraska. The fauna from Observation

Quarry has been considered to be roughly equivalent to the Lower Snake Creek fauna and thus early Barstovian in age (Tedford et al., 1987). Chalicotheres material from Observation Quarry includes a skull and jaws (F:AM 54889), a large humerus (F:AM 54891), and a large femur (F:AM 54890). The teeth of F:AM 54889 are extremely worn and are thus difficult to compare with those of other chalicotheres. The skull is clearly not domed and thus is unlikely to belong to *Tylocephalonyx*. The posterior part of the mandibular ramus is well preserved and displays a large angular process. The humerus and femur are more robust, especially in shaft width, than in any other known North American chalicotheres. In contrast, available limb bones of *M. merriami* (parts of radius and ulna, tibia) are not too different from material of *M. elatus*, *M. hollandi*, and *T. skinneri* and are inconsistent with the unusually robust proportions of the humerus and femur from Observation Quarry. It is possible that the Observation Quarry chalicotheres elements represent an individual variant, most likely a large, old male. While this chalicotheres needs to be kept in mind in any discussion of *M. merriami*, its taxonomic referral is still uncertain.

#### BIOGEOGRAPHIC COMMENTS

Chalicotheres faunas of northwestern Nebraska and nearby areas of the central Great Plains are the best known in North America and are critical to our understanding of changes in distributions of these animals (see fig. 15.7). Late Arikareean chalicotheriids in this region belong to *Moropus elatus*, a species best known from the Agate Springs Quarries and nearby Morava Ranch Quarry and Harper Quarry. Numerous remains of *M. elatus* are typically associated with rhinocerotids (*Menoceras*, *Diceratherium*), some equids (*Kalobatippus*, *Parahippus*), carnivores (especially canids and amphicyonids), entelodonts (*Dinohyus*) and occasional other artiodactyls in bone bed deposits formed in ephemeral waterholes (Hunt, 1990; Coombs and Coombs, 1997). As the animals most often entombed in the waterhole bonebeds, *Moropus* and *Menoceras* were probably highly water dependent and were thus drawn

under drought conditions to diminishing water supplies, where death, disarticulation, and burial sometimes ensued.

A closely related species, *M. hollandi*, succeeds *M. elatus* in the earliest Hemingfordian. Somewhat later, a different chalicotheres, attributed to *Moropus* sp. by Coombs (1998), is known in early Hemingfordian faunas from Runningwater equivalent beds in Nebraska, northeastern Colorado, and South Dakota. The fragmentary remains of these chalicotheres should help in our ultimate understanding of the group, but further analysis of the material is needed.

*Tylocephalonyx skinneri* is the only documented chalicotheres in late Hemingfordian faunas of the Sheep Creek Formation. It is replaced by *M. merriami* in the early Barstovian Lower Snake Creek fauna of the Olcott Formation. Because of complicated erosion and channel fill stratigraphy in the Sheep Creek Formation and Olcott Formation, Olcott localities such as Humbug Quarry and *Prosynthetoceras* Quarry, which produce *M. merriami*, and Sheep Creek localities such as Greenside Quarry, the primary source of *T. skinneri*, lie in very close proximity to one another (Skinner et al., 1977).

Outside the central Great Plains, *M. oregonensis*, a small contemporary of *M. elatus*, is represented by a number of fragmentary specimens from Oregon (Coombs et al., 2001). *Moropus* cf. *oregonensis* also occurs along the Gulf Coast in eastern Texas and Florida. Small chalicotheres are also present in Hemingfordian faunas of California (Coombs, 1998), but it is difficult to determine on the basis of present evidence how these chalicotheres are related to other species of *Moropus*. Late Hemingfordian to early Barstovian specimens of *M. merriami* from northwestern Nevada are the best material of any North American chalicotheres outside the Great Plains and provide an important link between the Great Plains Lower Snake Creek and Columbia Plateau Virgin Valley–High Rock Canyon faunas.

Early Barstovian faunas of the Great Basin and Columbia Plateau are in general less diverse than those of the Great Plains. Species occurring in Nevada at this time have strong affinities with contemporaries from nearby California and Oregon but are uncommon

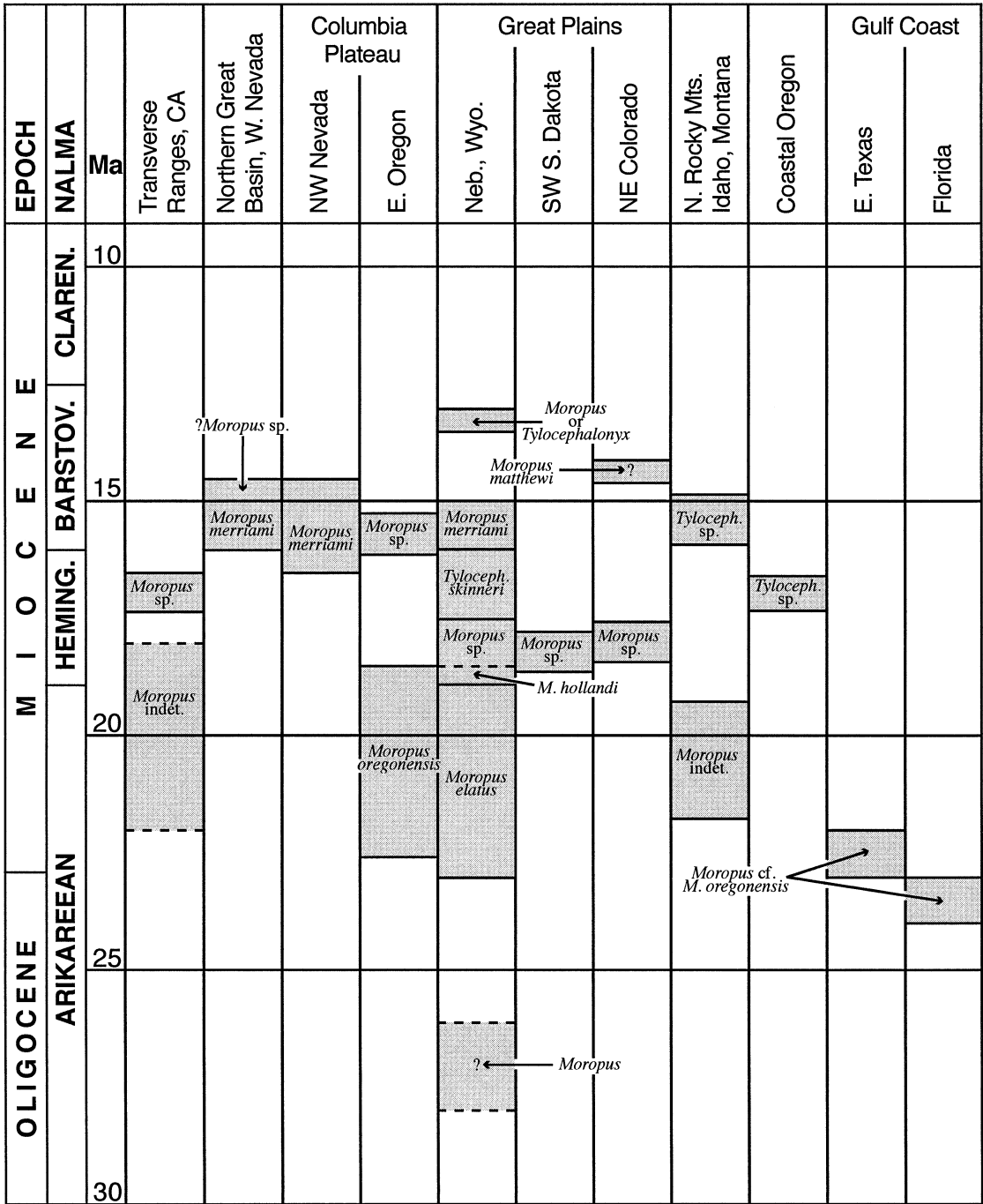


Fig. 15.7. Correlation chart showing relative ages of chalicothere fossil occurrences mentioned in the text. For more complete listings of occurrences (such as possible late Hemingfordian single occurrences of *Tylocephalonyx* in Utah and north-central Colorado) and discussions of localities see Coombs (1978, 1979, 1998) and Skinner (1968). The possible arrival in North America of *Moropus* in the late early Arikareean follows Coombs (1978, 1998) and Tedford et al (1987). Dating of deposits yielding chalicotheres follows Tedford et al (MS), Albright (1999), Prothero et al (2001), and Janis et al. (1998). *Tyloceph.* = *Tylocephalonyx*.

outside this region. The occurrence of *M. merriami* in early Barstovian faunas of both Nevada and Nebraska thus represents an unusual and unexpected Great Plains appearance of a species that is otherwise known only from the more limited Great Basin–Columbia Plateau region. Of course we cannot be absolutely certain that dispersal occurred at precisely this time or that it progressed from west to east. Possibly, environmental and depositional conditions in the Olcott Formation simply favored the preservation of a species that previously lived on the Great Plains in small numbers or under conditions not conducive to fossilization. There is some evidence of spread of other western taxa to the Great Plains, though mostly at a later date. Immigrant proboscideans, which first occur in the late Hemingfordian to early Barstovian of the Great Basin and Columbia Plateau, appear later in the Barstovian in the Great Plains (Woodburne and Swisher, 1995). Despite intensive large-scale collecting, no proboscideans have been found in the Olcott Formation (Tedford et al, 1987). The borophagine canid *Aelurodon asthenostylus*, a component of early Barstovian faunas of California and Nevada, shows up in the late early Barstovian fauna of the Pawnee Creek Formation in northeastern Colorado and by the late Barstovian in Nebraska (Wang et al, 1999); other western lineages of borophagines arrive in the Great Plains in the Clarendonian or Hemphillian.

Understanding the reasons for the chalicothere turnover between the deposition of the Sheep Creek Formation and Olcott is difficult because it is not altogether clear how *T. skinneri* and *M. merriami* differed in their adaptations and environmental tolerances. Various kinds of synthetic studies are needed that can bring together sedimentary, floral, and anatomical data to improve our knowledge of these faunas. Among promising studies that have potential to shed light on these issues is that by Semprebon (2002), who used dental microwear to analyze dromomerycid artiodactyls from the Sheep Creek Formation and Olcott Formation. She concluded that, although Sheep Creek dromomerycids include both browsers and mixed feeders, large pits and scratch textures in the teeth of all of them are consistent with sig-

nificant intake of grit coating the surface of food items. Sheep Creek dromomerycids appear to have occupied relatively open dusty country. Dromomerycids from the Olcott Formation have less enamel gouging and show wear patterns consistent with browsing in relatively closed habitats with little grit. Dental microwear analysis of the equid *Merychippus insignis* from the Olcott Formation also shows little suggestion of grit or C4 grass consumption, despite high-crowned teeth and probable mixed feeding, which included C3 grasses in closed habitats (Semprebon, 2002; Solounias and Semprebon, 2002). Although microwear results for other components of the two faunas are not yet available, it is tempting to hypothesize that *T. skinneri* from the Sheep Creek Formation and *M. merriami* from the Olcott Formation might show comparable microwear differences, which would shed more light on the conditions in which these chalicotheres lived. A currently ongoing study of dental microwear in North American chalicotheres by Semprebon, Coombs and Sise should help to elucidate any dietary changes in this primarily browsing group of perissodactyls.

Although *Tylocephalonyx* does not occur in the Olcott Formation and is unknown in Nebraska after the Hemingfordian, there is some evidence that it survived into the early Barstovian of Montana and Idaho (fig. 15.7). After the early Barstovian, few chalicotheres fossils are known from the Great Plains, the best known case being the late Barstovian Mc III described by Skinner (1968) from the Crookston Bridge Member of the Valentine Formation. This chalicotheres represents a survivor of a North American lineage and does not resemble its Eurasian contemporaries, but it is not clearly linked to either *T. skinneri* or *M. merriami*.

Much has been written about the gradual environmental drying, spread of C3 (and later C4) grassland and retreat of forests in the middle to late Miocene of the Great Plains (Webb, 1977; Janis, 1993; Retallack, 1997). Many groups that included browsers and mixed feeders, such as dromomerycids and equids, had their highest diversities in the late Hemingfordian and Barstovian (Janis and Manning, 1998; MacFadden, 1998). Later in the Miocene, dromomerycids and

browsing anchitheriine equids became rarer and eventually became extinct. North American chalicotheres, with their brachydont browsing teeth, tall forequarters, presumed ability to rear on their hindlimbs while feeding (Coombs, 1983), and probable water dependence, would have been increasingly challenged by the retreat of trees and water resources. Their rarity after the early Barstovian and final demise mirrors and to some extent precedes extinction events that also affected other browsing groups.

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In his acceptance speech on receiving the Society of Vertebrate Paleontology Romer-Simpson Medal in 2001, Malcolm McKenna mentioned several achievements that he personally valued most. Among these was his role in the incorporation of the Frick Collection into the American Museum of Natural History. Much of my work on chalicotheres has been made possible by access to the Frick Collection, and I am grateful for this opportunity. McKenna (1965) provided stimulus for the publication of further biostratigraphic work in the Hemingford Group of northwestern Nebraska and encouraged studies such as Skinner (1968) and Skinner et al. (1977), which provided a basis for my research.

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