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Reappraisal of the *Cormohipparion* from the Valentine Formation, Nebraska

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ABSTRACT

The name *Cormohipparion sphenodus,* from deposits of late Barstovian age in North America, is modified because the species holotype is here referred to *Merychippus* s.s. A new name is given to this *Cormohipparion* and its cranial and dental morphology is thoroughly described on the basis of material from the Valentine Formation, Nebraska. The Valentine species is contrasted with *Cormohipparion goorisi* and certain material of *C. occidentale,* as well as with elements pertaining to *Merychippus sphenodus.* The geochron of the *Cormohipparion occidentale* group is revised, trends within the genus are noted, and the North American origin of the Old World taxon, *Hippotherium primigenium,* is inspected.

INTRODUCTION

Woodburne et al. (1981) referred specimens discussed here, along with certain others, to *Cormohipparion sphenodus,* basing the name on the holotype of *Merychippus sphenodus.* Subsequent study (presented here) indicates that the holotype of *M. sphenodus* pertains to that genus, and that a new name, *C. quinni,* n. sp., is required for other material formerly allocated to *C. sphenodus.* In developing the hypodigm for the new species, it appears to be mostly restricted to specimens from the Crookston Bridge and Devil's Gulch members of the Valentine Formation, Nebraska (figs. 1, 2). The genus, and perhaps this species, is represented from the subjacent Cornell Dam Member of the Valentine Formation. One specimen from Sand Canyon (Ogallala Group) of northeast Colorado is also referred to *C. quinni,* n. sp.

In the process of performing these analyses, new information on the morphology of the upper and lower dentition of *C. quinni,* n. sp., is presented and illustrated. A full documentation of its cranial and mandibular pa-

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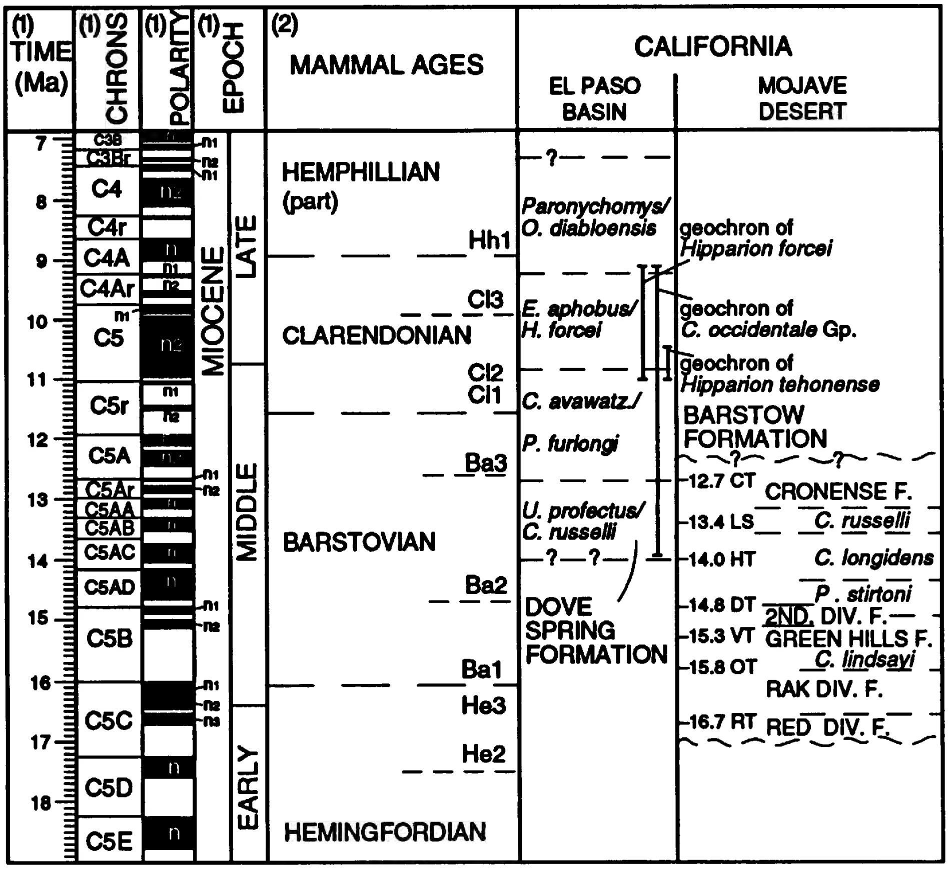

Fig. 1. Geochronology of rock and faunal units discussed herein. **(1)** after Berggren et al. (1995). Mammal ages discussed in text **(2)** modified from Tedford et al. (1987), based on Woodburne et al. (1990), Whistler and Burbank (1992), and Woodburne and Swisher (1995). Sea level **(3)** after Woodburne and Swisher (1995).

Abbreviations and conventions. **California.** Dove Spring Formation: Faunal units are assemblage-zones; correlation to time-scale based largely on paleomagnetic data (Whistler and Burbank, 1992). *C. avawatz* = *C. avawatzensis.* Barstow Formation: Faunal units after Lindsay (1972), Woodburne et al. (1990), MacFadden et al. (1990), and Woodburne (1991). Radioisotopically dated units: CT = Cronese Tuff; LS = Lapilli Sandstone; HT = Hemicyon Tuff; DT = Dated Tuff; VT = Valley View Tuff; OT = Oreodont Tuff; RT = Rak Tuff. Base of Barstow Formation, not shown, ca. 19.3 m.y. old (Red Tuff). **Northeast Colorado.** Faunal units in Ogallala Group correlated paleontologically; Pawnee Creek Fauna based on paleontological and radioisotopic data. 14.4 and 14.8 are unnamed tuffs. See text and Tedford et al. (1987). **North-central Nebraska.** Correlation of faunal units in Ash Hollow Formation based on paleontological and radioisotopic data. DA = Davis Ash; SWA = Swallow Ash. Faunal units of Valentine Formation arranged and correlated on lithostratigraphy, biostratigraphy, and limited radioisotopic data. HBA = Hurlbut Ash; SCA = Sheep Creek Ash. See text and Tedford et al. (1987). **Texas.** Faunal units in Clarendon beds not in superposition; correlation based on paleontology. Burkeville Fm. (part) correlated on regional stratigraphy. See text and Tedford et al. (1987). **Geochron of *Cormohipparion***; only those species shown; see text. **Dispersal.** See text.

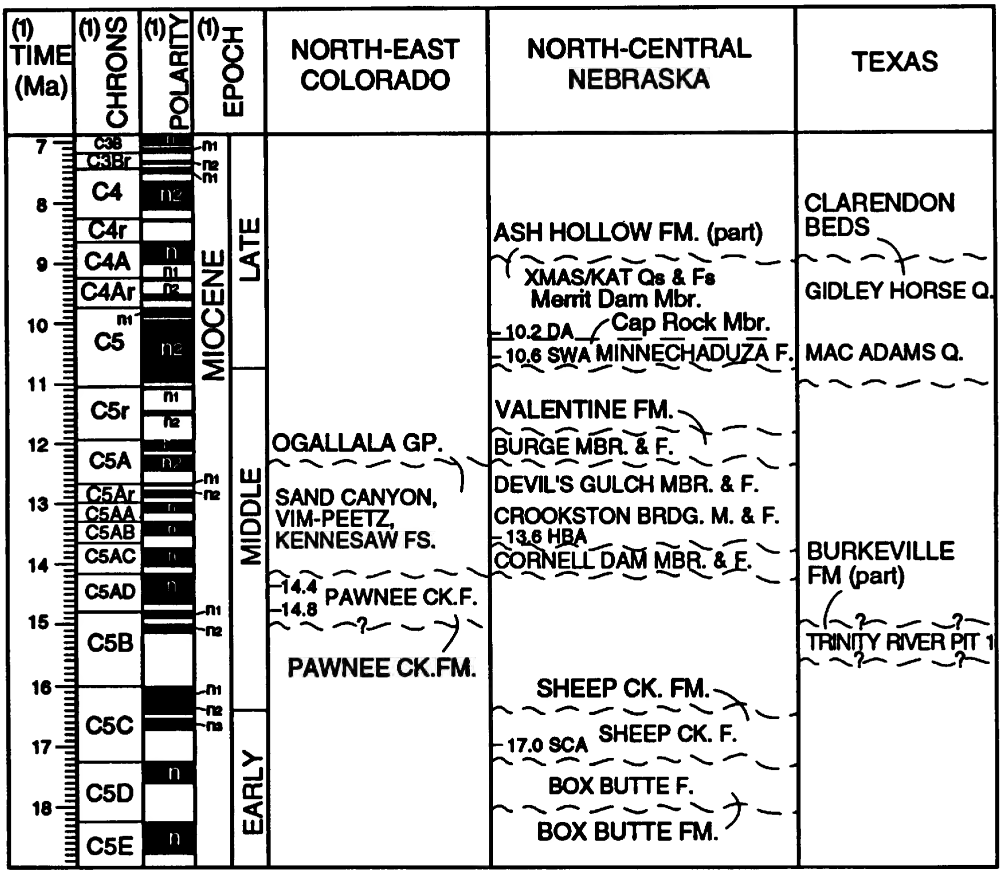

Fig. 1. Continued.

rameters as recommended by members of the 1980 *Hipparion* Conference, held at the American Museum of Natural History (Eisenmann et al., 1988), is also presented.

The results indicate that *C. quinni* is the likely sister taxon of a congregation of specimens here identified as the *Cormohipparion occidentale* group, and that these together are a sister taxon of *C. goorisi.*

This work is part of an ongoing study to reevaluate the morphology, and revise the taxonomy, of Barstovian to Clarendonian species of *Cormohipparion,* including their role in forming the beginning of the Old World "*Hipparion*" Datum (see Bernor et al., 1989; Swisher, 1996; Woodburne et al., 1996) and the beginning of the Vallesian mammal age, as represented in Europe by *Hippotherium primigenium* (Woodburne, 1989).

The new species is contrasted with an expanded development of the morphology of the antecedent, *C. goorisi,* and that of a restricted example of the subsequent species, *C. occidentale.* The report concludes with an appraisal of the type species of *Merychippus sphenodus* and the rationale for restricting that nomen to the type, as well as to a small number of specimens from the Pawnee Buttes district of Colorado.

METHODOLOGY

This report is designed to review and stabilize the morphology and phyletic relationships of a late Barstovian species of *Cormohipparion.* In doing this it is necessary to define the genus, *Cormohipparion,* as well as species precedent and subsequent to *C. quinni,* n. sp., the main focus of this investigation.

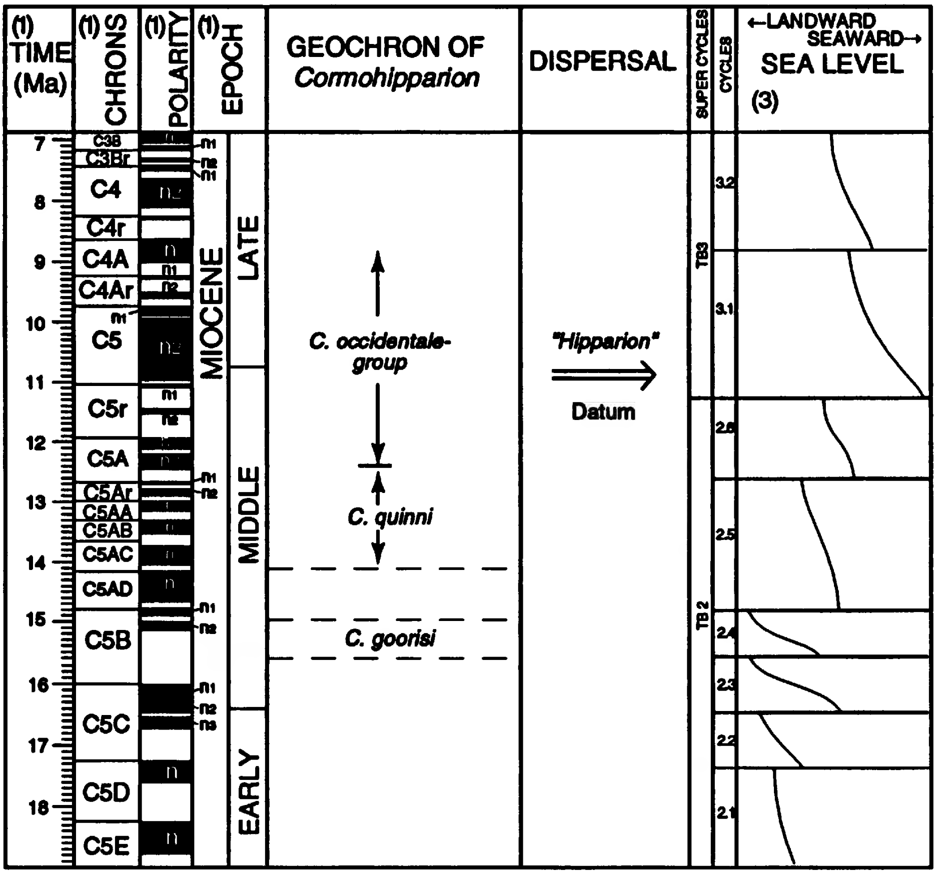

Fig. 1. Continued.

This is also the first report concerned with North American equid taxa to extensively utilize the parametric protocols established at the time of the 1980 *Hipparion* Conference (Eisenmann et al., 1988). Thus, figures 3–6 duplicate some illustrations found in Eisenmann et al. (1988). The intent is not only to promote clarity in exposition of methodology but also to increase the dissemination of these illustrations in the scientific literature, so as to further the aims of the *Hipparion* Conference in standardizing the acquisition of the data upon which *hipparion* phyletic analyses are based.

DEFINITIONS AND ABBREVIATIONS

Morphological Conventions

DPOF Dorsal preorbital fossa, or nasolacrimal fossa (after MacFadden, 1984).

IOF Infraorbital foramen.

MSTH Mesostyle height of upper cheek teeth (after MacFadden, 1984). M1MSTH refers only to M1.

OTU Operational taxonomic unit.

POB Preorbital bar, or distance between anterior edge of orbit and rear of DPOF (after MacFadden, 1984).

TRL Tooth-row length (after MacFadden, 1984).

Lower case p and m signify lower premolars and molars, respectively.

Upper case P and M signify upper premolars and molars, respectively.

Measurements

Cranial and mandibular parameters follow Eisenmann et al. (1988), as shown in figures 3–6. Dental parameters are standard. An important dimension for this study is the actual or estimated MSTH of a given tooth versus its unworn condition. The intent here is to make statements as to crown height that are

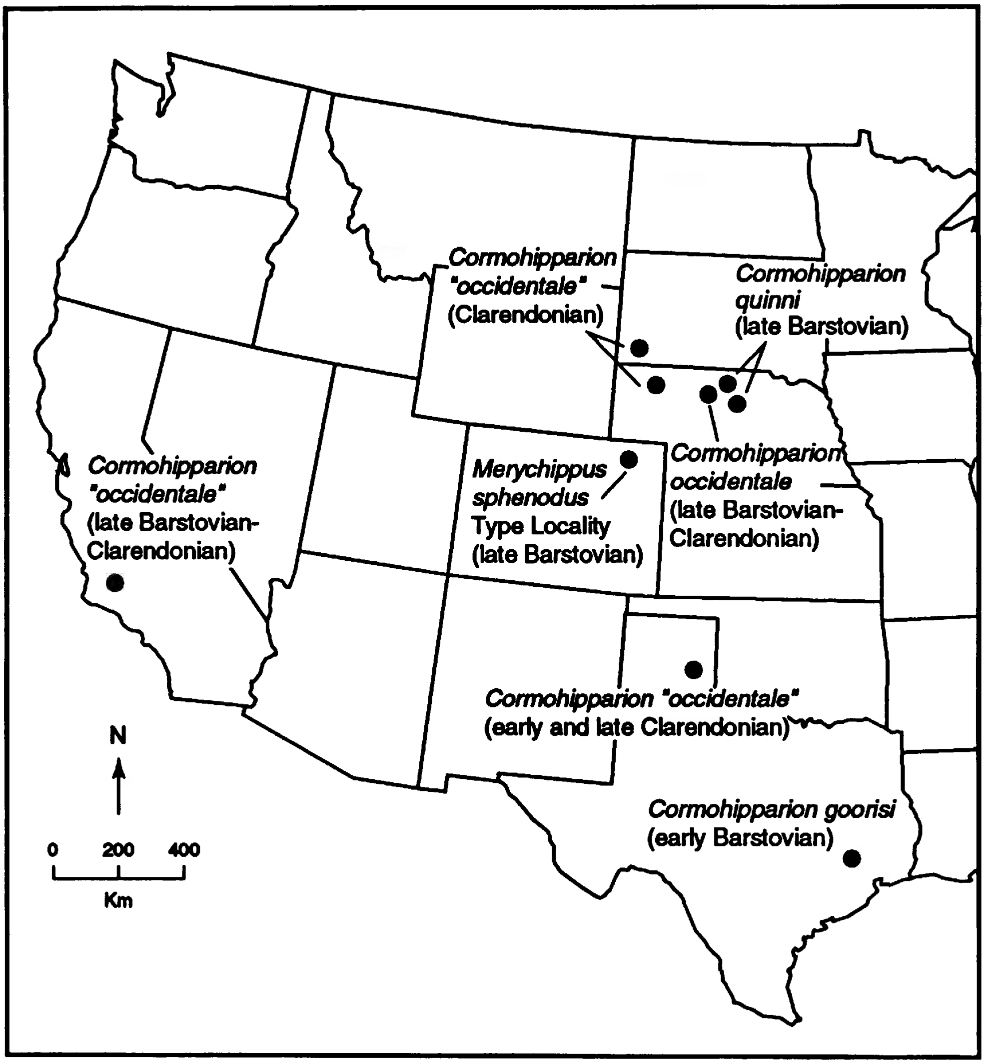

Fig. 2. Map showing localities discussed in the text.

as precise as possible, and to express this dimension as a percentage of the likely unworn MSTH for that tooth position. In almost all cases it is possible to obtain accurate measurements for the unworn MSTH for each tooth position based on isolated or otherwise measurable teeth (maxillary bone broken away), or to estimated MSTH to within narrow limits based on the associated outswelling of the lateral surface of the maxilla. In other instances, if one knows the unworn MSTH for P2, for example, it can be estimated that M1 and M2 have a crown height about 5 mm taller in *C. quinni*. Tables 6–15 present statistical data for individual tooth positions from samples in the Valentine Formation. Where possible, the order in which the specimens are listed is ontogenetically youngest to oldest progressively downward on the table. The actual or estimated MSTH of the specimens is given, and a percent wear determined from that number relative to the known or estimated unworn MSTH for the tooth position. This ensures that the teeth of various samples are evaluated at closely comparable wear stages to the extent possible. Estimated MSTH figures are considered reliable within ± 3 mm.

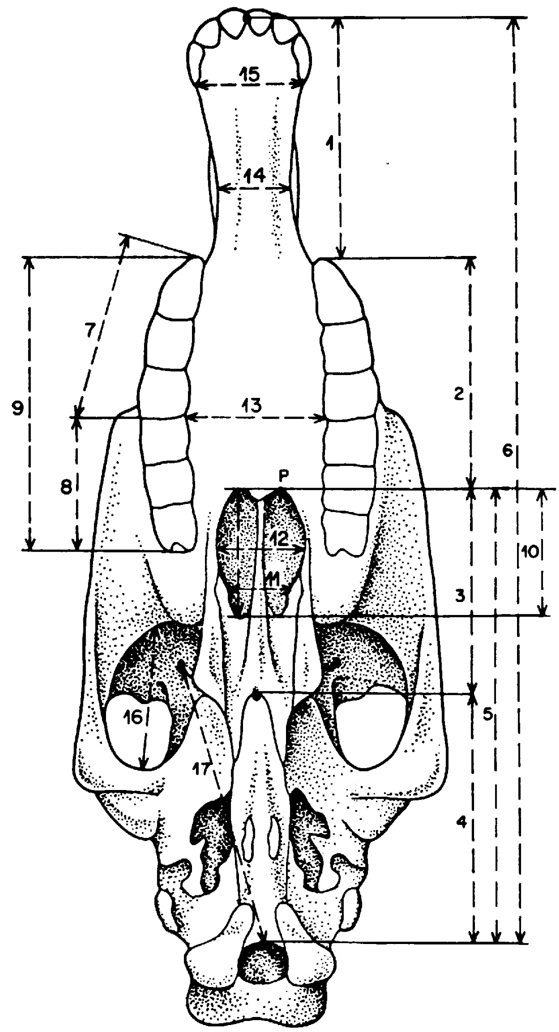

Fig. 3. Diagram showing location of cranial measurements. After Eisenmann et al. (1988). Ventral view.

Nomenclature for Dental Position and Crown Morphology

This follows standard format. See figure 6C, D. Fossette plication count procedure follows Eisenmann et al. (1988). This is somewhat subjective, but results are repeatable. A plication is counted only if it is deeper than the thickness of the enamel band of which it is formed. For this study, the frequent occurrence of an isolated pli protoconule required that a count of 2 plis be recorded as though it were connected. Thus the figure 1.1.1.1 would signify that there was only one single pli on the entire anterior and anteromedial face of the prefossette; only one single pli on the entire posteromedial and posterior faces of the prefossette, one single pli on the entire anterior and anteromedial faces of the postfossette, and one single pli on the entire posterior and posteromedial face of the postfossette.

Institutional Affiliations

AMNH American Museum of Natural History, New York
ANSP Academy of Natural Sciences, Philadelphia
F:AM Frick: American Mammals, in the collections of the AMNH
DVP Department of Vertebrate Paleontology at the AMNH
UNSM University of Nebraska State Museum, Lincoln, Nebraska
USNM U.S. National Museum, Smithsonian Institution, Washington, D.C.

Other Abbreviations

DGHQ Devil's Gulch Horse Quarry, Crooskton Bridge Member, Valentine Formation, Nebraska
RRQA Railway Quarry A, Crookston Bridge Member, Valentine Formation, Nebraska

Chronological Terms

Calibration Situation in which fossil-bearing strata are directly associated with materials yielding radioisotopic dates
Correlation A statement about the temporal relationship between data. Association of faunal and magnetostratigraphic data may carry an implication of age in the Ma scale, but this is not a calibration
FAD First appearance datum, a regionally significant change in the fossil record (e.g., Berggren and Van Couvering [1974])
Fauna and Local Fauna follow Tedford et al. (1987: 155)
HSD Highest stratigraphic datum, a local stratigraphic last appearance (e.g., Lindsay et al. [1984])
LF Local fauna(s)
LSD Lowest stratigraphic datum, a local stratigraphic first appearance (e.g., Lindsay et al. [1984])

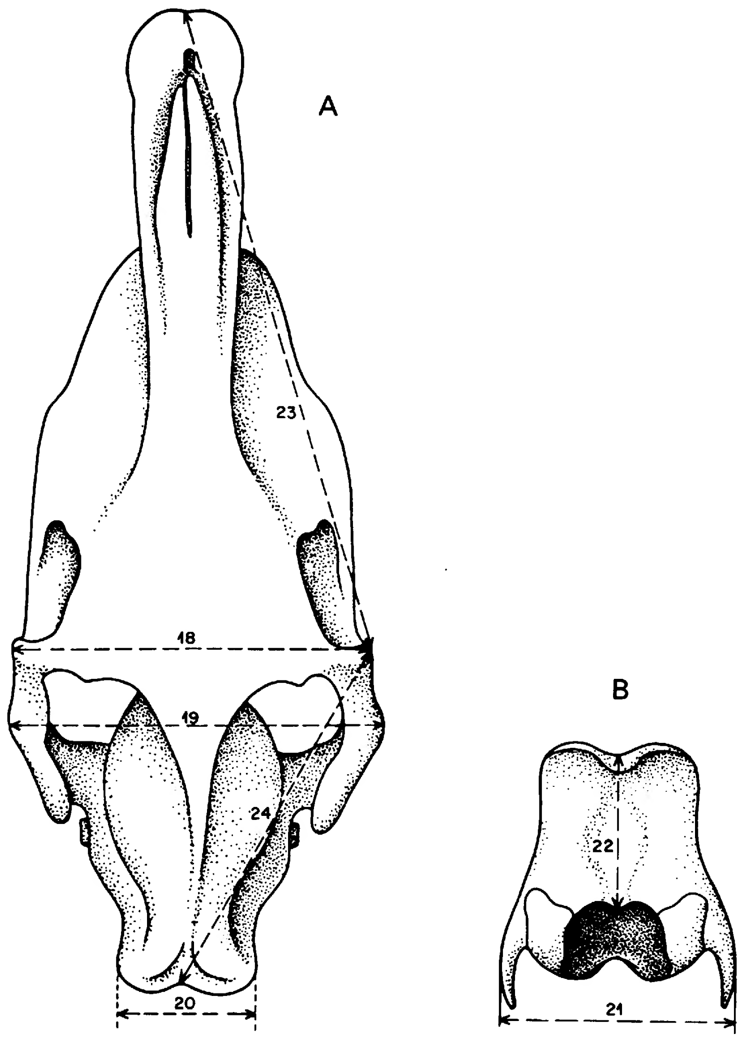

Fig. 4. Diagram showing location of cranial measurements. After Eisenmann et al. (1988). **(A)** Dorsal view. **(B)** Posterior view.

Ma	Megannum in the radioisotopic time scale
MPTS	Magnetic polarity time-scale; specifically that of Berggren et al. (1995)
m.y.	Million years in duration or interval not tied directly to the radioisotopic time scale

Mammal Age Terms (figs. 1, 2)

Calibration and correlation of the Hemingfordian, Barstovian, and Clarendonian intervals (fig. 1) of the North American land mammal age sequence follows Tedford et al. (1987; their figs. 6.2, 6.3) and Woodburne and Swisher (1995), with some details discussed below. Also see Lindsay (1995).

The late Hemingfordian is based largely on the Sheep Creek Fauna as well as that from the older Box Butte Formation (Tedford et al., 1987: 186–187, and Appendix A; a fission-track average age of 17.0 ± 0.6 Ma recorded from a tuff just above the Sheep Creek Fauna). MacFadden et al. (1990) report an age of 16.3–16.5 ± 0.3 Ma for the clearly reworked and somewhat altered Rak Tuff that occurs near the base of a normal magnetozone in the lower part of the Barstow Formation, California. This magnetozone is plausibly correlated to Chron C5Cn.3 in the MPTS (implied but not stated in those terms in MacFadden et al., 1990: 490). According

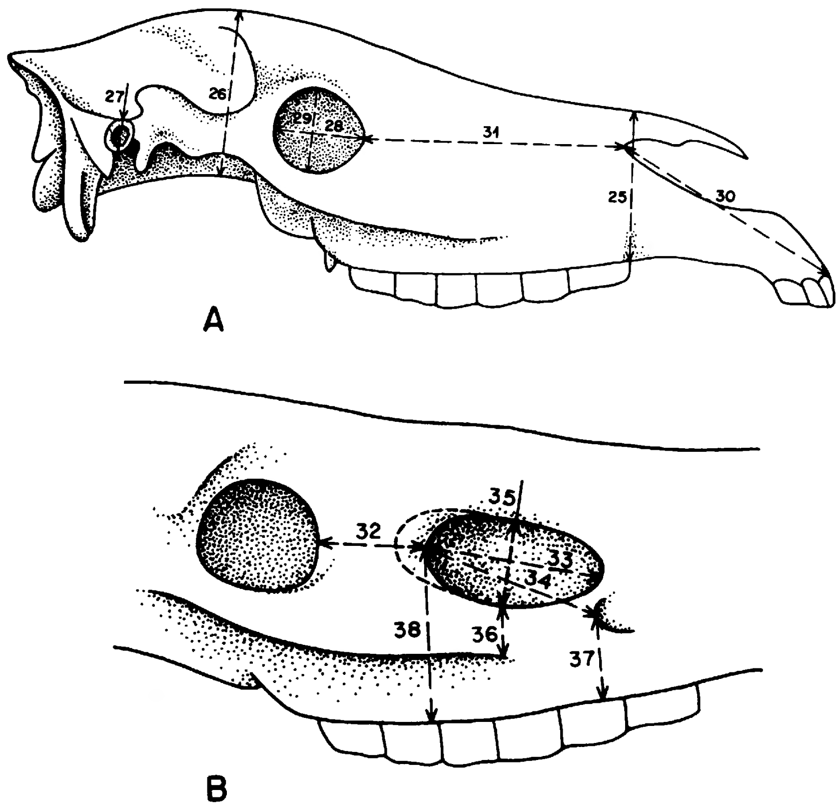

Fig. 5. Diagram showing location of cranial measurements. After Eisenmann et al. (1988). **(A)** Lateral view. **(B)** Close-up of facial region, lateral view.

to Berggren et al. (1995), Chron C5Cn.3 is about 16.5–16.7 m.y. old, so the actual age of the Rak Tuff is likely to be about 16.5–16.7 m.y. The Rak Tuff caps the interval from which the Red Division Fauna was recovered and which is considered to be of late (but not latest) Hemingfordian age (Woodburne et al., 1990). A tuff that separates early and late Hemingfordian mammal sites in California has been dated at about 17.9 Ma (Miller, 1980; Woodburne et al., 1982; Woodburne, 1991). This is consistent with the ca. 17.5 m.y. age for the beginning of late Hemingfordian discussed in Woodburne and Swisher (1995) and adopted herein (fig. 1).

The Hemingfordian-Barstovian boundary is taken at about 15.9 Ma, following Woodburne et al. (1990), but it is recognized that work by Lindsay (1991) may require that this age be revised downward somewhat if reliance is still placed at the LSD of the FAD of *Copemys* in North America. Lindsay (1995) shows that a *Copemys* LSD is correlated to about Chron C5Cr.2 (or between C5Cn.2 and C5Cn.3), considered by Berggren et al. (1995) as about 16.5 m.y. old (revised from 16.8 m.y. in Lindsay [1995]). Whereas this proposal has many interesting ramifications to be taken up elsewhere, none are critical to the present discussions.

Barstovian. The geochronological extent of the Barstovian in its type area follows Woodburne et al. (1990). Thus the boundary between early and late Barstovian utilized in Tedford et al. (1987) on the faunal bases discussed therein, is calibrated as about 14.8 Ma in age, based on the succession in the Mud Hills, perhaps likely the same age as the LSD of Proboscidea in the Pawnee Buttes section (calibrated provisionally at about 14.4 Ma [see below]).

The later part of the late Barstovian (correlated at 12.5 Ma in Tedford et al., 1987: fig. 6.3), is defined on the LSD of the gelocid,

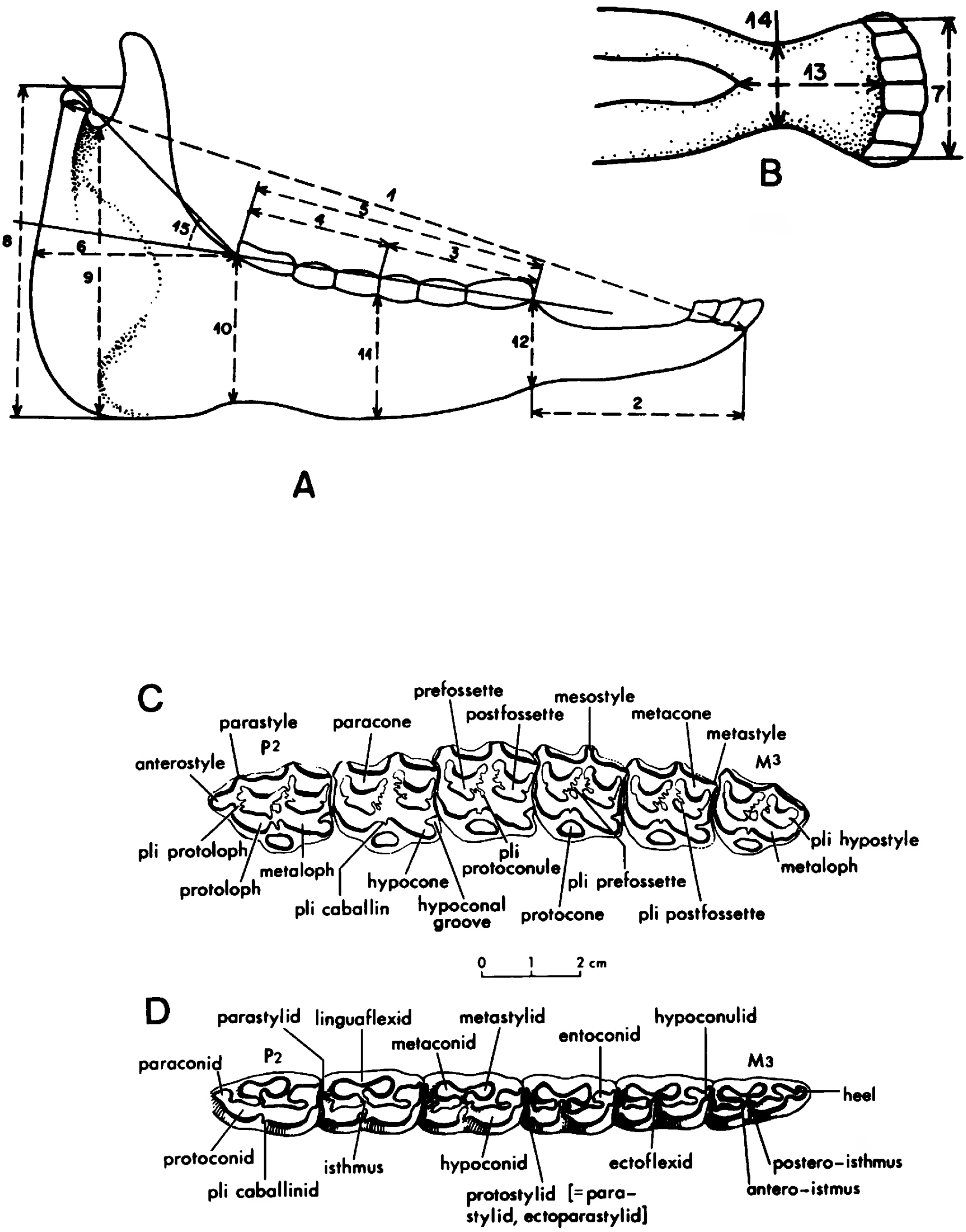

Fig. 6. Diagram of measurements and terminology. (A) Measurements of mandible. (B) Symphysis of mandible. (C) upper cheek teeth, and (D) lower cheek teeth dental terminology. A, B after Eisenmann et al (1988). C, D after MacFadden (1984).

Pseudoceras. This taxon has its LSD in the Burge Member of the Valentine Formation, Nebraska (Tedford et al., 1987: 169). The isotopic age of these rocks is unknown, but if the fauna from Burge Member of the Valentine Formation can be correlated as about 12.7 m.y. old based on a LSD of the *Cormohipparion occidentale* group in comparison to the LSD of that species in the Dove Spring Formation, California (Whistler and

Burbank, 1992), then the beginning of the late interval of late Barstovian can be considered to have begun about that time. This is comparable to the ca. 12.5 m.y. age ascribed to the beginning of the late late Barstovian in Tedford et al. (1987: fig. 6.3), but about 1 m.y. older than that shown in figure 6.2 of the same work. A Barstovian age for the Burge Member of the Valentine Formation has ramifications for the age of older members of the unit, as discussed below (see Stratigraphic Framework).

Clarendonian. Tedford et al. (1987: fig. 6.3) define the Clarendonian as beginning at the immigrant first occurrence of the nimravid carnivore *Barbourofelis,* present in Great Plains faunas equivalent to the Minnechaduza Fauna from the base of the Ash Hollow Formation, Nebraska (fig. 2). On the other hand, Whistler and Burbank (1992) suggest that at least in the Dove Spring Formation, the Clarendonian mammal age began about 12.7 Ma based, in part, on the LSD of the *Cormohipparion occidentale* group and that this and other taxa indicate that the correlative Burge Fauna is of early Clarendonian age (Whistler and Burbank, 1992: fig. 8).

For this report, however, the early Clarendonian in the Great Plains begins with the Minnechaduza Fauna (on the basis defined by Tedford et al. [1987]). The Minnechaduza Fauna apparently correlates with the upper third of the *Cupidinimus avawatzensis/Paracosoryx furlongi* Assemblage Zone in the Dove Spring Formation. This is consistent (fig. 1) with a correlation of about 11.5 Ma in the Berggren et al. (1995) time-scale, and with the Clarendonian beginning at about that time, as portrayed also by Tedford et al. (1987).

STRATIGRAPHIC AND CHRONOLOGIC FRAMEWORK (Fig. 1)

Nebraska. *C. quinni,* n. sp., is mostly represented in members of the Valentine Formation, Nebraska. From oldest to youngest these are: Cornell Dam Member, Crookston Bridge Member, Devil's Gulch Member, and Burge Member (e.g., Skinner and Johnson, 1984; Voorhies, 1990). Traditionally, *C. occidentale* first appears in the Burge Member (e.g., Woodburne et al., 1981), and nothing in the present report suggests otherwise. The Sand Canyon locality (Ogallala Group), northeast Colorado, also has produced a specimen of *C. quinni,* n. sp., and elements of the stratigraphy of that unit, as well as of the Pawnee Creek Formation that yielded the holotype and other material of *Merychippus sphenodus* also are discussed here.

As reviewed and elaborately illustrated in Skinner and Johnson (1984: 243–294), the Valentine Formation is the lower unit of the Ogallala Group in north-central Nebraska, and consists of "friable, cross-bedded channel sand, semiconsolidated argillaceous sandstone, occasional beds containing silicified casts of fossil roots and *Stipidium* . . . and massive sand and gravel" (p. 249). The formation reaches a thickness of about 100 m and has been separated into four members on lithologic grounds.

The lowest unit of the Valentine Formation, the Cornell Dam Member, is about 12.5 m thick, but commonly is thinner owing to erosion and deposition of younger strata. The Norden Bridge (Voorhies, 1990) and Egelhoff (Skinner and Johnson, 1984) quarries are the main fossil-bearing concentrations in the units near the base of the member. The Hurlbut Ash occurs near its top (Skinner and Johnson, 1984: fig. 4, p. 246), and has been dated (fission-track; glass) at 11.6 ± 1.1 Ma (Skinner and Johnson [1984: 252], revised from 13.6 ± 1.3 Ma [Boellstorf and Skinner, 1977]; see also Woodburne et al. [1981], and Tedford et al. [1987]). The revised age appears incompatible with other data discussed herein which suggest that the Valentine Formation likely ranges in age from about 14 to 12.5 m.y., and that the geochron of *C. quinni,* n. sp., extends from about 14 to 13 m.y.

There is a hiatus between the Cornell Dam (=unnamed member in Woodburne et al., 1981) and Crookston Bridge members, and between the Devil's Gulch and Burge members. The Crookston Bridge Member is about 45 m thick, contains the Railway Quarry A (near its base) and other important sites bearing remains of *C. quinni* (Skinner and Johnson, 1984: 246), and is gradationally overlain by the Devil's Gulch Member.

The Devil's Gulch Member of the Valentine Formation is about 13 m thick, and contains the Devil's Gulch Horse Quarry near its middle (Skinner and Johnson, 1984: 246). The Burge Member (with its Burge Quarry and associated sites) unconformably overlies the Devil's Gulch, and typically contains a LSD of the *Cormohipparion occidentale* group. Based on the correlation between the Burge Fauna and those of the Dove Spring Formation, California, the underlying members of the Valentine Formation are older than 12.7 Ma (e.g., Whistler and Burbank, 1992). Consideration of the Pawnee Buttes section (below) suggests that the geochron of *C. quinni,* n. sp., is younger than 14.4 Ma. On this basis, the basal age of the Cornell Dam Member of the Valentine Formation in Nebraska is about 14.0 Ma (fig. 1).

Colorado. The Pawnee Buttes area of northeastern Colorado (figs. 1, 2) contains the Pawnee Creek Formation, overlain unconformably by the Ogallala Group. The following discussion is directed at identifying the stratigraphic provenance of the type of *Merychippus sphenodus* and PU 12291, herein referred to *Cormohipparion quinni,* n. sp., but formerly (Osborn, 1918) allocated as a "neotype" of *M. sphenodus.* In figure 7A, the Pawnee Creek Formation is restricted to include only the F:AM-AMNH Pawnee Quarry and the Eubanks Local Fauna of Galbreath (1953). Overlying deposits designated as Ogallala Group contain taxa of the Kennesaw, Vim-Peetz and Sand Canyon local faunas formerly considered (Galbreath, 1953) to derive generally from the Pawnee Creek beds (e.g., Tedford et al., 1987). Figure 7A shows the present interpretation in which the Ogallala Group incises the Pawnee Creek Formation.

There is no doubt that the type of *Merychippus sphenodus* was obtained from near the vicinity of Pawnee Buttes. Osborn (1918) was the first to allocate *Hippotherium sphenodus* Cope 1889 as *Merychippus sphenodus.* Osborn's map (1918: 19) shows the Pawnee Buttes as a distinct outlier south and west of Pawnee Creek. Cope (1889: 449) certified the locality in stating that the type of *Hippotherium sphenodus* "was collected in the same locality as that furnishing the *H. paniense,* and at the same time. Several years later I obtained two other molars from the same place, viz., the Pawnee Buttes of N.E. Colorado." Figure 7B shows that Pawnee Quarry is located at least 18 miles southwest of Sand Canyon, the source of PU 12291, as discussed below.

Thus, the type of *M. sphenodus* was collected from the Pawnee Buttes region, but the stratigraphic level is somewhat less certain. Galbreath's measured section 1 of the Pawnee Creek beds (Galbreath, 1953: 20, 23) is at the "Eubanks Ranch House," Pawnee Buttes, NE¼ sect 1., T. 10 N., R. 59 W., Weld County, Colorado (fig. 7B). Unit 3 of that section contains the "Pawnee Buttes" volcanic ash, with "numerous bones and teeth, especially of *Merychippus paniensis,* and is the basis of the Eubanks Local Fauna of Galbreath (1953: 32). This ash includes the F:AM Pawnee Quarry which, noted below, includes specimens considered herein to be close to the type of *M. sphenodus.*

It is now known that other, stratigraphically higher, units at Pawnee Buttes are fossiliferous, but Tedford (personal commun., 1990) suggests that until the Frick Laboratory materials from Horse and Mastodon Quarry became known, fossils from this part of the Pawnee Creek beds mostly represented what is designated as the Eubanks Local Fauna. The Eubanks Local Fauna is now known to have come largely from F:AM Pawnee Quarry. Fossils from the level of Horse and Mastodon Quarry were rare, and whereas Cope's type of *M. sphenodus* could have come from that level, it more likely came from the beds at or near Pawnee Quarry which apparently was the best known fossiliferous unit in the buttes at that time.

Significantly, specimens of *M. sphenodus* morphology appear to be best matched (discussed below) in material from Pawnee Quarry, West Quarry, and 3 Points, E. Valley #1, W. Side of High Pit. The stratigraphic position of these quarries is shown in figure 7. A small number of specimens in F:AM collections from Horse and Mastodon Quarry (fig. 7A) are also similar to the type of *M. sphenodus.* Tedford (personal commun., 1992) believed that the paleochannel in which Pawnee Quarry is developed was the unit most likely prospected by the early Frick parties, and that the style of preservation seen in Pawnee Quarry materials, as well as in Cope's type materials, would best match that typical of specimens from Pawnee Quarry rather than

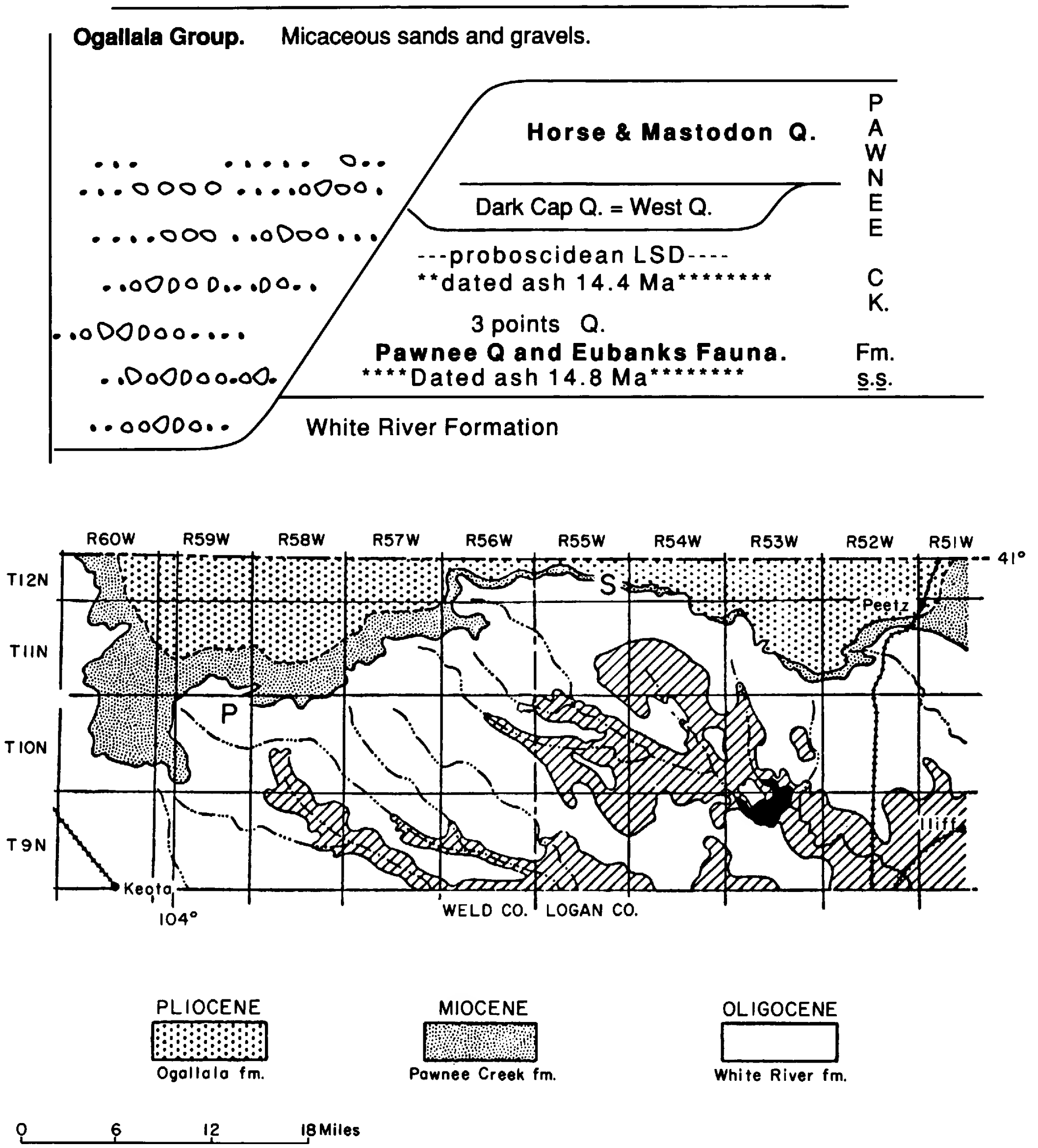

Fig. 7. Stratigraphy of the Pawnee Creek area, northeast Colorado. Top (**A**), Section at Pawnee Creek according to R. H. Tedford (personal commun., 1990). Bottom (**B**), Map of northeast Colorado, showing separation of sites that produced the type of *M. sphenodus* (P, Weld County) versus PU 12291 (S, Logan County). After Galbreath (1953).

Horse and Mastodon Quarry, for example. It appears most likely that the type of *M. sphenodus* did not derive from levels now recognized as producing faunas from the Horse and Mastodon Quarry. Thus, for the purposes of this report, the type of *Merychippus sphenodus* is considered as having been obtained from beds at, or equivalent to, Pawnee Quarry.

Some potential confusion as to the geologic occurrence of *M. sphenodus* may be a result of Galbreath (1953: 105) having referred a number of specimens from his Kennesaw Local Fauna to that species, and (p. 35), characterized this fauna on the presence of that taxon. The equid cranium, PU 12291, was identified by Osborn (1918) as a "neotype" of *M. sphenodus,* and Galbreath (1953: 105) explicitly focused on the "neotype" specimen when discussing the occurrence of *M. sphenodus* in the deposits along Pawnee Creek. The Princeton specimen (Osborn, 1918: pl. 12) was recovered from deposits in Logan County about one mile west of Sand Canyon, whereas the F:AM material resembling the type of *M. sphenodus* is from Weld County. A locality one mile west of Sand Canyon would be at least 18 miles northeast of Galbreath's localities in Pawnee Buttes (Weld County), the geographic source of the type and referred material of *M. sphenodus* (e.g., fig. 7B).

The Logan County deposits under discussion pertain to a portion of the Ogallala Group as designated by Tedford et al. (1987), although formerly included by Galbreath (1953) in the Pawnee Creek beds. These Logan County deposits also yielded the fossils that Galbreath (1953) referred to his Kennesaw, Vim-Peetz, and Sand Canyon local faunas. Note that the Sand Canyon LF of Galbreath (1953) is different from the early Barstovian faunas from the Sand Canyon beds of northwestern Nebraska. On both faunal and stratigraphic grounds, Tedford et al. (1987: 172–173) distinguish the Kennesaw, Vim-Peetz and Sand Canyon local faunas from those of the Pawnee Creek Formation s.s. and include the Horse and Mastodon Quarry in an upper part of the restricted Pawnee Creek Formation. The Kennesaw, Vim-Peetz, and Sand Canyon faunas from the post-Pawnee Creek Formation deposits are considered to have faunal affinities with taxa of the Crooskton Bridge and Devil's Gulch members of the Valentine Formation.

Preliminary radioisotopic data (figs. 1, 7) suggest that the deposits in northeast Colorado are younger than about 14.8 Ma, and are consistent with the late Barstovian age of the taxa contained therein. If recovered from strata that now produce the Eubanks Local Fauna, the type of *Merychippus sphenodus* would be between 14.4–14.8 m.y. old.

As shown in figure 7A, strata that contain faunas from and equivalent to Horse and Mastodon Quarry are younger than ca. 14.4 Ma, and it is useful to recall that Tedford et al. (1987: 173) considered the taxa from those levels to be "intermediate" between those of the Olcott and Valentine formations in Nebraska. In terms of the data shown in figure 7A, this would be consistent with a post-14.4 Ma age for the Valentine Formation (fig. 1), and also consistent with the older ages for the Hurlbut Ash in the Cornell Dam Member, as discussed above. An approximately 14 m.y. age for the base of the geochron of *C. quinni* appears reasonable.

Strata that unconformably overlie the restricted Pawnee Creek Formation include the Sand Canyon LF (Ogallala Gp., figs. 1, 7). Taxa from these strata (also including the Kennesaw and Vim-Peetz faunas) are regarded (Tedford et al., 1987: 173) as being comparable to those of the Crookston Bridge and Devil's Gulch members of the Valentine Formation. As assessed herein, the stage of dental evolution of PU 12291 is best reflected in samples of *C. quinni* from the Devil's Gulch Horse Quarry (and Member) of the Valentine Formation. The Devil's Gulch Member predates the Burge Member (and Fauna), correlated as being about 12.7 m.y. old. Combining all of the available stratigraphic and radioisotopic data, the geochron of *Cormohipparion quinni* appears to be contained within an interval from about 14 to 12.5 m.y. (fig. 1).

Voorhies (1990: 82) concurred in this assessment in allocating the taxa (Norden Bridge and Egelhoff quarries) from the basal Valentine Formation to the "medial Barstovian," correlated at ca. 13–14.5 Ma. "Medial Barstovian" is not utilized here.

SYSTEMATIC PALEONTOLOGY

THE *CORMOHIPPARION* COMPLEX

According to Skinner and MacFadden (1977), Woodburne et al. (1981), and Bernor et al. (1989, 1995), certain hipparionine horses from Eurasia (chiefly of Vallesian age, ca. 10.8–9 m.y.) might prove referable to *Cormohipparion,* or some species of *Cormohipparion* in North America might prove referable to *Hippotherium* von Meyer 1829. In the present report, only North American species are considered. The group ranges in age from about early Barstovian to late Hemphillian (or roughly 16 to 5 m.y.), and most likely contains the species that gave rise to the Old World "*Hipparion* Datum," (*Hippotherium* Datum) now considered to be about 10.5–10.9 m.y. old (Woodburne et al., 1996). Throughout the geochronologic range of the genus *Cormohipparion,* its species display increased size, hypsodonty, and dental complexity, although not in a linear fashion (e.g., MacFadden, 1984; Hulbert, 1988). The DPOF is well developed in Barstovian and Clarendonian taxa, but is effectively lost by the late Hemphillian, comparable to the situation in a number of other hipparionine lineages (e.g., MacFadden, 1984; Woodburne, 1989). In fact, as discussed below, the reduction in pocketing of the DPOF prefaces the reduction of the fossa itself, which is underway by the late Barstovian (e.g., *C. quinni* n. sp., contra *C. goorisi*–earlier Barstovian; fig. 1). Furthermore, the depth of pocketing of the DPOF in *C. goorisi* is greater than that of any other species of *Cormohipparion* (see below), contrary to the interpretation of Evander (1985) *in* Hulbert (1988: 295).

Below, the named species are briefly cited along with provenance and age. Note that Hulbert (1988, 1989), Hulbert and MacFadden (1991), and Hulbert (1993) advocated removing *C. goorisi* from *Cormohipparion.* That suggestion is not followed here for the following reasons:

Cormohipparion goorisi as a Species of that Genus

Hulbert (1988) and Hulbert and MacFadden (1991) considered *Cormohipparion goorisi* as a species of "*Merychippus*" based largely on the configuration of the lacrimal and adjacent parts of the cranium. Hulbert and MacFadden (1991, their fig. 10) interpret "*M.*" *goorisi* as possessing the autapomorphies of a deep DPOF, and a large posterior pocket; a distinct anterior rim; lacrimal bone that is not involved with the DPOF; protocone-protoloph connection not present until very late wear stage; complex internal fossette plications; persistently open hypoconal grooves that do not form lakes, and well developed protostylids on p3–m3.

A deep DPOF (Hulbert and MacFadden, 1991: 17) is considered as being 10–15 mm. As shown in table 9 (character 2) of Hulbert (1988), this is a synapomorphy for all species of *Cormohipparion* except *C. emsliei* which has secondarily lost the DPOF. It also occurs in an unnamed species attributed to *Nannippus* in an as-yet unpublished manuscript. Until that manuscript is published this specimen shall not be considered further.

Hulbert and MacFadden (1991) considered a deep posterior pocket of DPOF as being greater than 5 mm. This trait is shared among all *Cormohipparion* species in which the feature is preserved (Hulbert, 1988: table 9 column 3). Furthermore, the extremely deep penetration of the DPOF relative to other species of the genus is herein considered to be one of the greatest synapomorphies of *C. goorisi.*

In regard to the district anterior rim of the DPOF, Hulbert (1988: table 9 column 4) showed that this is a synapomorphy for all species of *Cormohipparion* in which the DPOF is preserved.

Lacrimal bone not involved with DPOF. Based on a reconsideration of all pertinent material, this is shown to be wrong. Like other species of *Cormohipparion, C. goorisi* has a lacrimal that is subtriangular in shape and sufficiently long so as to reach, and be partly eroded by, the posterior border of the DPOF (fig. 8). In fact, the character-state interpreted by Hulbert and MacFadden (1991) is not even scored for other taxa. Hulbert (1988: table 9 column 10) correctly scores *C. sphenodus* (here = *C. quinni*) as having a lacrimal that reaches the DPOF, but also shows that this is the plesiomorphic condition.

Protocone-protoloph connection scored as being in late wear stage. Hulbert (1988: 27, 28) shows that this character-state (level 5) is a synapomorphy for all species of *Cormohipparion.*

Complex internal fossette plications. This is well-recognized (and herein demonstrated) to be a common attribute to species of *Cormohipparion.* Hulbert (1988: table 9 column 33) shows that *C. goorisi* is more complex than all other hipparionine horses except other species of *Cormohipparion* and *Hippotherium primigenium* (Old World). This conclusion was reached by Woodburne et al. (1981) and is also reached in the present study as far as species of *Cormohipparion* are concerned.

Persistently open hypoconal grooves. Whereas this character is distinctive of *C. goorisi* in Hulbert and MacFadden (1991: table 1), it also is common to all species of *Cormohipparion.* Hulbert (1988: table 9 col-

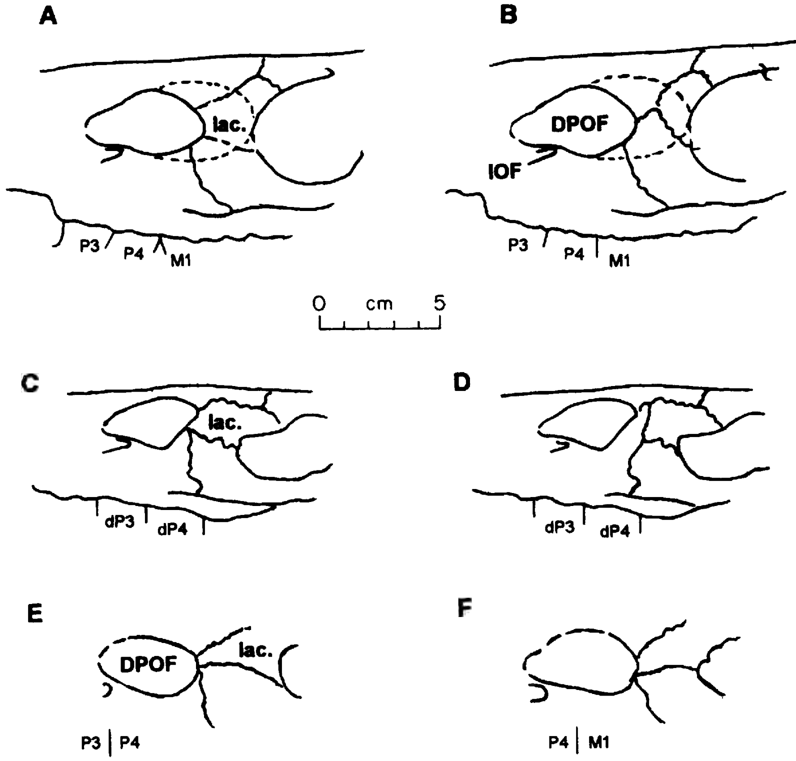

Fig. 8. Configuration of the lacrimal in *Cormohipparion goorisi*, Trinity River Pit 1, Fleming Formation, early Barstovian, Texas (A–E), and (F) *Cormohipparion* near *C. goorisi*. (See location of infraorbital foramen [IOF] and boundary between upper cheek teeth for reference.) **(A)** holotype cranium, F:AM 73940, as interpreted herein, with lacrimal extending to within rear of DPOF. **(B)** F:AM 73940 as interpreted by MacFadden and Skinner (1981). **(C)** Juvenile cranium, F:AM 73941, as interpreted herein and **(D)** F:AM 73941 as interpreted by MacFadden and Skinner (1981). **(E)** F:AM 73942, somewhat distorted cranium still showing penetration of lacrimal to rear of DPOF. **(F)** F:AM 99387, McMurry Pit 1, Fleming Formation, San Jacinto County, Texas, showing lacrimal penetrating to within rear of DPOF.

umns 38, 39) shows that this plesiomorphic character is shared among all species of *Cormohipparion*, as well as with *Hipparion forcei*, *H. tehonense* and species of *Neohipparion*.

Hypoconal grooves do not form lakes. This is fundamentally plesiomorphic or homoplasious (e.g., Hulbert and MacFadden, 1991; table 1). Hulbert (1988: table 9 column 40) shows that this character has the same distribution as the persistently open hypoconal groove.

Well developed protostylids on p3–m3. Although scored autapomorphously for *C. goorisi* in Hulbert and MacFadden (1991), this is shown to occur as well in all species of *Cormohipparion*, *Hippotherium primigenium*, and in species of *Neohipparion* and *Pseudhipparion* (Hulbert, 1988: table 9 column 52).

If Hulbert (1988: table 9) is consulted, and if a taxon listed as *Nannippus* is excluded as not yet published, then a clade that embraces all species of *Cormohipparion* including *C. goorisi* can be defined on the following synapomorphies: deep DPOF (slightly less in *C. ingenuum* and much less in *C. emsliei* where the fossa is greatly reduced); strong posterior pocket of DPOF; strong anterior margin of DPOF (except *C. emsliei*); protocone connects to protoloph in late wear stage (only *Neohipparion* is later); complex internal fossette plications in upper cheek-teeth; and lower cheek tooth protostylids very well developed (also only in *Neohipparion* and *Pseudhipparion*). This clade would also include *Hippotherium primigenium,* generally considered to be related to the *C. occidentale* group (e.g., Woodburne et al., 1981; Bernor et al., 1989).

Cormohipparion Skinner and MacFadden, 1977

TYPE SPECIES: *Hipparion occidentale* Leidy, 1856.

TYPE SPECIMEN: ANSP 11287, four left and one right upper cheek teeth (MacFadden, 1984: 162).

INCLUDED SPECIES: *Cormohipparion goorisi* MacFadden and Skinner 1981 (about early Barstovian, Texas); *C. quinni,* n. sp., (late but not latest Barstovian, Nebraska and Colorado); *C.* subgenus *Notiocradohipparion* Hulbert 1988. Species of the subgenus, *Notiocradohipparion*: *C.* (*N.*) *plicatile* (MacFadden, 1984; Hulbert, 1988), late Clarendonian, Texas; *C.* (*N.*) *ingenuum* (MacFadden, 1984; Hulbert, 1988), late Clarendonian, Texas; *C.* (*N.*) *emsliei* (Hulbert, 1987), late Hemphillan to Blancan, Florida, have been briefly mentioned above. They are not considered further in as much as they are distinctly derived over either *C. quinni* or *C. occidentale* (e.g., Hulbert, 1988).

TYPE LOCALITY: Little White River, South Dakota (Skinner and Taylor, 1967).

AGE: Minnechaduza Fauna, late Clarendonian (e.g., Webb, 1969; Tedford et al., 1987).

DEFINITION OF *CORMOHIPPARION*: Note that this definition does not depend on a reappraisal as to the number of OTUs present in *C. quinni* or *C.* "*occidentale.*" The definition is taken from MacFadden (1984: 146) with **boldface changes** added, based on the present author's observations on *C. occidentale* specimens. For the purposes of this report, *C. occidentale* is considered to be defined on the basis of the major cranial morphology (herein designated as Type 1) from the XMas-Kat Quarries of western Nebraska. This is discussed further below.

> Medium to large **size,** and mesodont to hypsodont hipparion. Mean TRL ranges from 116.83 to 138.00 mm. Unworn or little worn M1MSTH ca. **34-60** mm. Prominent DPOF with a relatively well-developed and usually continuous anterior rim **with IOF located above P3 and consistently very close to the anteroventral tip of the DPOF**. Posteriorly this fossa also has a well-developed and pocketed rim. In general outline this fossa is oval or teardrop in shape and situated far forward on cheek resulting in a very wide POB. Anterior margin of the lacrimal bone **enters into the rear of the DPOF (primitive species) or does not reach the rear of the fossa (advanced species; fossa may be lost or severely reduced in advanced species).** Protocones rounded with anterior spur, oval, or elongate (with angular margins). Fossette borders moderately to very plicated. Protostylids usually present and moderately developed. **Premolar ectoflexids do not penetrate isthmuses except in late wear**. Pli caballinids moderate to absent.

Hulbert (1987) also presented a revised diagnosis of *Cormohipparion* that agrees with the above. In addition, Hulbert (1987: 453–454) added:

> P2 anterostyle well developed and P2 much longer than other cheek teeth. In advanced species (excluding *C. goorisi*), pli caballin prominent, usually bifurcated, fossettes moderately to very complicated, with persistent plis protoloph and hypostyle, and well developed prefossette loop [fig. 9]; styles strong, parastyle frequently grooved. Lower cheekteeth have large, well separated, oval or angular metaconids and metastylids; usually well developed protostylids and plicated isthmuses; plis caballinids variably developed, become more prominent and persistent in younger species. Paraconid of p2 relatively expanded. Ectostylids prominent on dp2–dp4.

Note that the definition utilized in this report includes *C. goorisi.* Note also that the dimensions of the lacrimal shown in MacFadden and Skinner (1981) and subsequently interpreted by MacFadden (1984) and Hulbert (1988: 295) appear to be wrong. The frontal "shingles over" the lacrimal in the type (F:AM 73940; MacFadden and Skinner, 1981: fig. 2B = fig. 8B of the present report). Figure 8A shows this author's interpretation of the actual condition. The lacrimal has been similarly distorted in the juvenile cranium, F:AM 73941 (MacFadden and Skinner, 1981: fig. 2D = fig. 8D of the present report). Figure 8C shows this author's interpretation of the lacrimal in F:AM 73941. The unfortunately

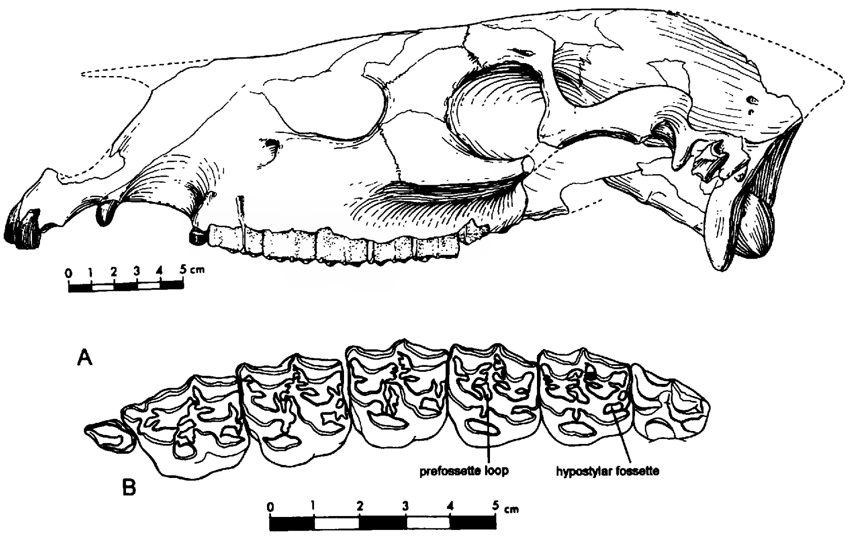

Fig. 9. *Cormohipparion quinni,* new species, F:AM 71888, **(A)** holotype male cranium; and **(B)** upper cheek tooth dentition, left side, from Devil's Gulch Horse Quarry, Devil's Gulch Member of the Valentine Formation, late Barstovian, Brown County, north-central Nebraska.

multi-cracked skull F:AM 73942 (fig. 8E) is consistent with the species having had a normal lacrimal morphology. Another factor in the new interpretation of the shape and extent of the lacrimal in this species is aided by F:AM 99387 (fig. 8F). This specimen is considered to be close to *Cormohipparion goorisi.* It consists of a partial cranium with right and left M1–M3 in late occlusal wear, from F:AM locality McMurry Pit 1, two miles north of Cold Springs and ½ mile northeast of Maxie Hill, east side of wash, San Jacinto County, Texas. This specimen shows a "normal" lacrimal penetrating the rear of the DPOF with the naso-lacrimal suture lying about 7 mm dorsal to the maxillo-lacrimal as they enter the DPOF. The anterior tip of the lacrimal is eroded by the rear of the DPOF such that about 3–5 mm of its normally pointed tip is obliterated. This morphology results in the lacrimal having an elongate, subtriangular shape. The fronto-lacrimal suture is about 30 mm long; the lacrimal is about 7 mm high anteriorly (at the DPOF), and about 25 mm tall posteriorly (at the orbit; somewhat crushed). For comparison, the basicranium (fig. 3, dimension #4) is about 72 mm long, virtually the same as the holotype skull of *C. goorisi* (table 5). Thus, the lacrimal configuration of *C. goorisi* is taken to be consistent with *C. quinni,* n. sp., and not radically different from that of *C. occidentale,* contrary to Hulbert and MacFadden (1991: fig. 10, Node 23). In fact, the present interpretation argues in favor of *C. goorisi* having had a relatively normal arrangement of bones in the preorbital bar region, and a relatively normal POB (e.g., figs. 8A, C, E–F). The new interpretation obviates the main reasons that Hulbert (1988: 295) separated *C. goorisi* from other species of *Cormohipparion,* as discussed above. Other comments in the text otherwise uncited regarding *Cormohipparion goorisi* and *Merychippus insignis* are based on data developed for the present report.

Cormohipparion quinni, new species
Figures 9-15, 17; Tables 1-17

Cormohipparion sphenodus Woodburne, MacFadden, and Skinner 1981 (in part): 503.
Merychippus sphenodus Osborn 1918 (in part): 112.

Type Specimen: F:AM 71888, associated male cranium and mandibles (figs. 9, 10). Cranium is slightly crushed laterally, and is missing most of the left and right nasal bones, facial part of the left maxillary, left zygomatic arcade and post-orbital cranium, elements of the pterygoid bones. Dentition is nearly com-

TABLE 1
Cranial Measurements, *Cormohipparion quinni*, n. sp., Valentine Formation, Nebraska, and Pawnee Creek Formation, Colorado

Measurements follow Eisenmann et al. (1988). Numbers **39** and **40** are new. **39** = length, rear DPOF to anterior tip of lacrimal. Negative value indicates estimation of amount of lacrimal eroded by rear of DPOF; **40** = medial depth of DPOF. a = approximate; y = young individual.

	Characters[a]						
Specimen	1	2	3	4	5	6	7
Valentine Fm., NE, Railway Quarry A; Cornell Dam Mbr.							
AMNH 105229♂[b]	75.5	92.9	78.8	73.4	147.5	315.8	66.7
F:AM 71896	–	–	–	–	–	–	67.4
Range	–	–	–	–	–	–	67.4–66.7
Mean	75.5	92.9	78.8	73.4	147.5	315.8	67.1
S	–	–	–	–	–	–	0.50
CV	–	–	–	–	–	–	0.74
N	1	1	1	1	1	I	2
Pawnee Creek Fm., CO							
PU 12291 ♂	–	70.3	–	69.0	–	–	68.3
Valentine Fm., NE, Devil's Gulch Horse Quarry, Devil's Gulch Mbr.							
F:AM 71888♂	82.3	93.0	79.3	73.2a	–	–	74.0
F:AM 71890♀	–	–	–	72.1	–	–	74.5
F:AM 108729	–	–	–	–	–	–	–
F:AM 108230	–	–	–	–	–	–	76.0
F:AM 108231♂	87.7	–	–	76.4	–	–	61.4
Range	82.3–87.7	–	–	72.1–76.4	–	–	61.4–76.0
Mean	85.0	93.0	79.3	73.9	–	–	71.5
S	3.8	–	–	2.2	–	–	6.8
CV	4.5	–	–	3.0	–	–	9.6
N	2	1	1	3	0	0	4
Sawyer Quarry, Devil's Gulch Mb.							
F:AM 71892♂	82.7	–	–	–	–	–	73.1

[a] See figures 3–5 for parameters.
[b] Plaster cast of original specimen.
[c] Dimension taken from Woodburne et al. (1981) as more reliable.
[d] After Van Valen, 1964.

TABLE 2
Mandible Measurements (mm), *Cormohipparion quinni*, Devil's Gulch Horse Quarry, Devil's Gulch Member, Valentine Formation, Late Barstovian, Nebraska

	Characters																
Specimen	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	p2 to mandibular foramen	Wear stage
F:AM 71888	–	72.0	69.0	64.0	133.0	–	43.0	–	–	68.0	48.0	35.0	56.0	26.0	22.0	21.0	I

Note: Protostylid present on p3, m1–2.

TABLE 1
(*Extended*)

Characters[a]											
8	9	10	11	12	13	14	15	16	17	18	19
69.3	123.1	—	—	32.3	53.3	26.7	41.0	—	—	96.0	112.0
58.8	125.1	—	—	—	55.3	—	—	—	—	—	—
69.3–58.8	125.1–123.1	—	—	—	55.3	—	—	—	—	—	—
64.1	124.1	—	—	32.3	55.3	26.7	41.0	—	—	96.0	112.0
7.4	1.4	—	—	—	1.4	—	—	—	—	—	—
11.6	1.1	—	—	—	2.6	—	—	—	—	—	—
2	2	0	0	1	2	1	1	0	0	1	1
55.5	124.2	—	—	29.9	58.1	—	—	—	—	110.2	123.0
61.0a	132.5a	—	—	—	—	—	41.6	—	—	—	—
60.3	132.3	—	—	32.0	49.0	—	—	—	—	—	—
—	—	—	—	—	—	—	—	—	—	—	—
63.2a	134.8	—	—	—	—	—	—	—	—	—	—
60.4	119.5	—	—	—	—	—	—	—	—	—	—
60.3–63.2	119.5–134.8	—	—	—	—	—	—	—	—	—	—
61.2	129.8	—	—	32.0	49.0	—	41.6	—	—	—	—
1.4	6.9	—	—	—	—	—	—	—	—	—	—
2.3	5.3	—	—	—	—	—	—	—	—	—	—
4	4	0	0	1	1	0	1	0	0	0	0
61.5	134.0	—	—	—	—	—	—	—	—	—	—

plete, with right and left I1–2, left canine, right and left dP1, P2–M3; M3s are barely erupted. The mandible lacks the condyles and ascending rami. The lower dentition includes right and left i1–2, canines and p2–m3. P3s are barely erupted.

TYPE LOCALITY: Devil's Gulch Horse Quarry (figs. 1 and 2), Devil's Gulch Member of the Valentine Formation, south side of Devil's Gulch, SW ¼ sect. 28, T. 32 N., R. 21 W., Brown County, Nebraska. See Skinner and Johnson (1984: 282–283).

AGE: Late (but not latest) Barstovian, likely correlative to an interval from about 13–14 Ma (fig. 1). The type section of the Devil's Gulch Member is defined at the Devil's Gulch Horse Quarry, and the fauna from the Devil's Gulch Horse Quarry is the type fauna for the Devil's Gulch Member of the Valentine Formation (Skinner and Johnson, 1984: 283).

DISTRIBUTION: Late Barstovian of Nebraska and Colorado.

ETYMOLOGY: Named in honor of J. H. Quinn in recognition of the precocious aspects of his 1955 publication on Texas Miocene equids. His text and phylogram clearly show Quinn's intent to describe generic level clades that contained lineages of species, and his methodology was comparable to modern phylogenetic treatment in that he described and presented a polarized character state analysis (Quinn, 1955: 66–68, fig. 4).

DESCRIPTION OF TYPE SPECIMEN: General cranial morphology (fig. 9) is comparable to

TABLE 1
(*Extended*)

Specimen	Characters[a] 20	21	22	23	24	25	26	27	28	29	30	31	32
Valentine Fm., NE, Railway Quarry A; Cornell Dam Mb.													
AMNH 105299	38.7	–	49.0	–	–	69.2	–	–	50.6	41.8	69.9	139.5	26.6
F:AM 71896	–	–	–	–	–	–	–	–	–	–	–	–	–
Range	–	–	–	–	–	–	–	–	–	–	–	–	–
Mean	38.7	–	49.0	–	–	69.2	–	–	50.6	41.8	69.9	139.5	26.6
S	–	–	–	–	–	–	–	–	–	–	–	–	–
CV	–	–	–	–	–	–	–	–	–	–	–	–	–
N	1	0	1	0	0	1	0	0	1	1	1	1	1
Pawnee Creek Fm., CO													
PU 12291	–	–	–	–	–	64.7	73.5	–	51.7	39.7	–	–	28.4[c]
F:AM 71888	–	–	–	–	–	–	–	–	48.3	44.7	–	–	27.3
F:AM 71890	–	–	–	–	–	–	–	–	–	–	–	–	30.8
F:AM 108729	–	–	–	–	–	–	–	–	–	–	–	–	31.3
F:AM 108230	–	–	–	–	–	–	–	–	–	–	–	–	–
F:AM 108231	–	–	–	–	–	–	–	–	–	–	–	–	30.9
Range	–	–	–	–	–	–	–	–	–	–	–	–	27.3–31.3
Mean	–	–	–	–	–	–	–	–	48.3	44.7	–	–	30.1
S	–	–	–	–	–	–	–	–	–	–	–	–	1.9
CV	–	–	–	–	–	–	–	–	–	–	–	–	6.3
N	0	0	0	0	0	0	0	0	1	1	0	0	4
Sawyer Quarry, Devil's Gulch Mb.													
F:AM 71892	–	–	–	–	–	–	–	–	–	–	–	–	–

that of many contemporaneous equids. The nasal notch appears to have been positioned dorsal to a point about midway between the canine and the cheektooth dentition; the orbit is comparatively large (tables 1, 16, 17), with its anterior margin located above the rear part of M2, at this ontogenetic stage. The postorbital bar is complete. The infraorbital foramen is located above the anterior part of P3 and, as typical of species of *Cormohipparion,* not far below the anterior tip of the DPOF, which is somewhat obscured in this specimen. As preserved, however, the DPOF is relatively large (fig. 5, **33**, **35**; tables 1, 16, 17) and its posterior margin has eroded the lacrimal such that the anterior end of this bone is not a sharp point as in *C. occidentale* (MacFadden, 1984: figs. 131–133); rather, it is blunt. The upper and lower sutures of this bone are well preserved on the left side. Preservation on the right side is permissive of the DPOF having had relatively well developed anterior and dorsal rims, in addition to the well defined ventral and posterior margins.

The upper incisors are ovate, with I2 tapering laterally. Both I1 and I2 have cement-filled infundibula (comparable to PU 12291, fig. 15). I1 is 13.0 mm long transversely, and 8.7 mm wide anteroposteriorly; comparable dimensions for I2 are 14.2 mm and 7.0 mm. Alveoli show that I3 was present. The canine is relatively large (7.6 mm × 6.3 mm; maximum crown dimensions). DP1 is relatively small (10.8 mm × 7.4 mm), especially in comparison to the length of P2 (27.4 mm), but still retains a definite morphology (anterior cusp and posterior basin, fig. 9B). The condition of dP1 in *Cormohipparion quinni* is thus more derived than seen in *C. goorisi* (where it is proportionately much larger) and

TABLE 1
(*Extended*)

Characters[a]							
33	34	35	36	37	38	39	40
49.2	45.5	27.0	25.6	31.3	56.0	−6	20.9
—	—	—	—	29.0	—	—	21.7
—	—	—	—	29.0–31.3	—	—	20.9–21.7
49.2	45.5	27.0	25.6	30.2	56.0	−6	21.3
—	—	—	—	1.6	—	—	0.6
—	—	—	—	5.3	—	—	2.8
1	1	1	1	2	1	1	2
58.8[c]	54.6	37.8	29.5	32.8	54.5a	0	20.0a
52.7a	50.4	34.8a	22.8	36.4	64.4	—	23.0a
62.2	57.9	38.8	30.0	37.5	61.0a	−3	17.0a
47.0y	—	37.0	—	—	—	—	10.0a
—	—	—	—	37.2	—	—	19.0a
56.3	49.5	36.0	25.2	35.0	61.5	1.2	20.0a
47.0–62.2	49.5–57.9	34.8–38.0	22.8–30.0	35.0–37.5	61.0–64.4	1.2–−3	10.0–23.0
54.6	52.6	36.7	26.0	36.5	62.3	−0.9	17.8
6.4	4.6	1.7	3.7	1.1	1.8	—	4.9
11.7	8.7	4.6	14.2	3.0	2.9	—	27.3
4	3	4	3	4	3	2	5
—	—	—	—	—	—	—	—

Specimen	Wear class[d]	Remarks
Valentine Fm., NE, Railway Quarry A; Cornell Dam Mbr.		
AMNH 105299	IV+; M3 well worn	Little distortion; old individual. Pocket ca. 15 mm deep.
F:AM 71896	IV+; M3 well worn	Little distortion. Pocketing not preserved.
Devil's Gulch Horse Quarry; Devil's Gulch Mbr.		
F:AM 71888	III; M3 erupting	Laterally crushed so **11** and **12** not taken. Pocketing not visible.
F:AM 71890	III; M3 in very early wear	Slightly dorsoventrally crushed and skewed, so **23** and **24** not taken. Pocket about 15 mm deep.
F:AM 108229	I; very young; DP 2–4 in	Skull highly fractured. Pocket about 15 mm deep.
F:AM 108230	III; M3 in early wear	Pocket is about 15 mm deep.
Sawyer Quarry; Devil's Gulch Mbr.		
F:AM 71892	II; very early wear	P2 MSTH 36.8; P3 MSTH 42.8 and in very early wear. Note: lacrimal tip end just reaches rear of DPOF. Pocket about 15 mm deep.
Pawnee Creek Fm., CO		
PU 12291	IV; M3 erupted; adult wear	Originally virtually perfect, the skull is now extensively fractured, although restored. Width measurements **18** and **19** twice hemi-width. Snout completely restored in plaster.

less derived than in *C. occidentale* (where dP1 usually is absent or, if present, merely a peg (e.g., MacFadden, 1984).

P2 (tables 3, 6) is in a relatively early stage of wear (fig. 9). The prefossette is not completely formed, the pli caballin is separated from the protoloph, and the pre- and postfossettes are linked near their labial margins. The protocone is isolated and ovate, but still shows a definite spur. The hypoconal groove is well developed, but nearly closed posteriorly. The mesostyle is 29.0 mm tall (table 6).

P3 and P4 are in relatively more advanced wear stages (fig. 9), although the pli caballin still is not confluent with the protoloph, and the pli protoconule not fully developed. Both have elongate isolated protocones with narrow anterior and posterior tips. Protocone width/length ratios are 0.30 and 0.43, respectively (tables 8, 10). The hypoconal groves are well developed, with relatively complex margins in P3; it is simpler but nearly closed posteriorly in P4. A hypostylar fossette is present in P3 (fig. 9). In P3 the plication count is 2.4.5.2; for P4 it is 1.6.4.1. The pli caballin appears to be single in P3, but double in P4. The mesostyle in P3 appears to have been about 30–32 mm tall at this ontogenetic stage. As shown in tables 8 and 10 these teeth are considered to have been about 20% (P3) to 30% (P4) worn.

M3 has just begun to erupt and is virtually unworn. Its mesostyle is about 35.2 mm tall. M1 and M2 show a fully developed wear pattern (fig. 9), and are considered to have been about 33 to 38 percent worn (tables 12, 14). The protocone is isolated in both, ovate and elongate in M1, subovate and elongate, with narrow, but not sharply pinched anterior and posterior ends in M2. Protocone width/length ratios are 0.58 and 0.43, respectively (tables 12, 14). Hypoconal grooves are well developed; the groove is closed posteriorly in M2. A hypostylar fossette is present in M2 (fig. 9). Plication count is 1.4.4.1 and 3.4.4.1, respectively, and plis caballins are single. The pli protoconule, which is nearly isolated in M2, extends posteriorly, but bends sharply lingually toward the pli caballin in both molars.

The mandible is relatively slender (table 2; fig. 10A), and deepens slightly posteriorly from below p2 to the anterior edge of m3. The symphysis extends posteriorly to a point about two-thirds of the diastema between the canines and p2. In contrast, the mandibular foramen lies almost midway along the diastema.

I1 and i2 have cement-filled infundibula, although the lateral margin of i2 is not yet closed by wear. I3s are not yet erupted. The first two incisors are 11.9 × 8.2 mm and 13.3 × 8.1 mm respectively, with i2 being wider medially than laterally. c1 is 7.3 × 6.2 mm (maximum crown dimensions).

P2 (fig. 10B) is notable in having a metastylid that is distinctly smaller than the metaconid. The metastylid is still much more distinct than in *C. goorisi,* but much less well developed than in *C. occidentale* (e.g., MacFadden, 1984: fig. 23). All lower premolars show a single pli caballinid, as present in *C. occidentale,* but absent in *C. goorisi.* The labial enamel band of the protoconid and hypoconid is relatively straight (also as in *C. occidentale*), rather than curved as in *C. goorisi.* In p3 and p4, metaconids and metastylids are well developed, subrounded, and separated by a shallow, but narrow and "V"-shaped linguaflexid. As is characteristic of *C. goorisi* and *C. occidentale,* these two premolars show the ontogenetically early development of isthmuses. A protostylid is present on p3, but not on p4.

M3 (fig. 10B) has barely erupted and is virtually unworn. Bone removed from the lateral surface of the right ramus reveals that the protoconid column is about 42 mm tall (table 4). M1 and m2 show a somewhat broader and more rounded linguaflexid and typically lack isthmuses, as compared to the premolars. Wear reveals that protostylids are present on these two molars; occlusal topography is much more uneven in these molars than in the premolars.

DIAGNOSIS: Based on the type and referred material, *Cormohipparion quinni* differs from *C. goorisi* in being larger; higher crowned; having a more complex upper cheek tooth enamel pattern; shorter dP1 as compared to P2; lower cheek teeth with stronger protostylids; longer isthmuses on p3–p4; straighter labial enamel band of proto- and hypoconid; better separated metaconid-metastylid on p2; cranium with DPOF only slightly (versus greatly) pocketed posteriorly. The tip of the

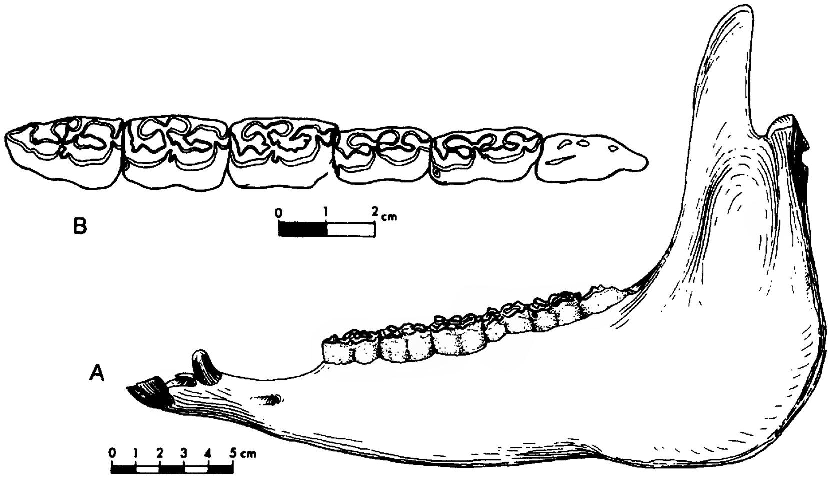

Fig. 10. *Cormohipparion quinni,* new species, F:AM 71888, from Devil's Gulch Horse Quarry, Devil's Gulch Member of the Valentine Formation, late Barstovian, Brown County, north-central Nebraska. **(A)** Holotype, mandible, left side. **(B)** Holotype lower dentition, left side, occlusal view.

lacrimal is similarly eroded by the rear of the DPOF in the two species. Whereas the basicranial dimension (fig. 3, **4**, a measure of general size; tables 5, 16) is comparable in the two species, the cranium of *C. quinni* differs from that of *C. goorisi* in being disproportionately larger in many features. As shown in tables 5, 16 and figures 3–5, 16 this is reflected in a longer skull (fig. 3, **6**), longer cheektooth dentition (**9**), longer (**2**, **31**, **32**) and higher facial dimensions (**32**, **36**, **38**); a generally more robust snout and palate (**12**, **13**, **14**, **15**, **25**); a wider frontal region (**18**) and trans-glenoid distance (**19**). Finally, the DPOF is pocketed only about 15 mm posteriorly in contrast to penetrating twice as far, and is thus medial to the anterior border of the orbit in *C. goorisi.*

Cormohipparion quinni differs from *C. occidentale* (as defined here for specimens from XMas Quarry, Nebraska; figs. 1–2) in being smaller; lower crowned; having a less complex upper cheek tooth enamel pattern (contra fig. 13A); dP1 present with a distinct morphology rather than being virtually absent or, if present, only peglike; lower cheek teeth with weaker protostylids; cranium with DPOF mainly an elongate oval rather than being commonly tear-drop shaped (dorsoventrally much higher posteriorly than anteriorly); lacrimal reaches rear of DPOF. As indicated in tables 5, 17 and figure 16, the basicranium (and hence general size) is larger in *C. occidentale,* despite which *C. occidentale* still has a longer skull overall (**6**), longer (**1**) and wider muzzle (**15**), a much longer DPOF (**33**) and POB (**32**) and other facial elements (**34**), and a generally wider (**18**, **19**, **20**) and higher (**35**, **36**, **37**) skull. At the same time, the length of the upper molar series (**7**) is relatively shorter, the palate relatively narrower (**12**, **13**). Finally, although larger, the DPOF is medially shallower (**40**) than in *C. quinni.*

REFERRED MATERIAL: *From the Devil's Gulch Member, Valentine Formation, Nebraska.* Taxa are of late Barstovian age.

Devil's Gulch Horse Quarry (DGHQ) — F:AM 71890, nearly complete cranium, right dP1, right and left P2–M3. Medial wear, except M3 which is in early wear (fig. 13D). F:AM 108228, partial cranium, right and left dP2–4, M1, right unerupted P2–4, early wear M1, unerupted M2. F:AM 125819, maxillary fragment with right P2–M3 (fig. 13F). F:AM 108227, maxillary fragment with left P4–M3 (fig. 13B). F:AM 108230, cranial fragment, with right and left P2–M3, right dP1 (fig. 13C). F:AM 108229, ventral part of cranium with right and left I1–2, right I3, C, dP1, P2–M3 in medial (P2) to early (M3) wear (fig. 13E).

TABLE 3
Measurements (mm) of Upper Cheek Tooth Dentition of *Cormohipparion quinni*, Nebraska and Colorado

H = mesostyle height; LO = length at occlusal surface; W = width at occlusal surface; L = protocone length; W = protocone width; a = approximate.

	P2					P3					P4		
				Protocone					Protocone				
	H	LO	W	L	W	H	LO	W	L	W	H	LO	W
Sand Canyon Beds, CO													
PU 12291♂	28.3	25.6	20.6	4.2	3.6	–	21.8	22.3	5.3	3.3	–	20.1	21.7
Crookston Bridge Mbr., Valentine Fm., NE, Railway Quarry A													
F:AM 71896	22.3	26.4	20.7	6.5	3.7	–	20.9	22.9	7.0	4.0	–	20.1	22.1
F:AM 107888	18.0	25.7	20.2	6.3	4.7	–	–	–	–	–	–	–	–
F:AM 108226	–	–	–	–	–	28.0	21.4	23.2	7.2	3.4	28.1	21.2	22.9
F:AM 105299	16.8	24.3	20.3	7.2	4.0	14.5	19.5	22.6	8.0	4.0	15.5	20.3	22.4
Devil's Jump Off Quarry													
F:AM 107886	24.3	23.2	18.9	4.8	3.1	24.3	19.6	21.3	5.9	3.5	26.0	18.6	21.1
Nenzel Quarry													
F:AM 108223	–	–	–	–	–	–	–	–	–	–	–	–	–
F:AM 108224 No pattern; all virtually unworn except M1.	–	–	–	–	–	40.0a	25.3	–	–	–	40.0	26.0	20.8
Schoettger Quarry													
F:AM 108225	–	–	–	–	–	41.1	29.1	24.3	6.9	3.5	42.5	25.2	22.5
Cormohipparion quinni from Devil's Gulch Mbr., Devil's Gulch Horse Quarry, Valentine Fm., NE; and type of *Merychippus sphenodus* from Pawnee Creek Fm., CO													
F:AM 71888♂ (holotype)	29.0	26.9	20.7	4.7	3.0	–	23.6	24.3	9.3	2.8	–	22.4	21.6
F:AM 71890	26.3	28.5	20.8	5.5	4.3	–	23.3	24.4	7.0	3.4	–	23.0	23.6
F:AM 108228	32+	(roots not formed)				33.5	(roots not formed)				44.0	22.8	20.6
F:AM 125819	24.0	22.8	17.7	5.8	3.8	26.5	19.2	21.3	7.6	3.5	28.2	19.8	22.3
F:AM 108227	–	–	–	–	–	–	–	–	–	–	–	23.4	23.2
F:AM 108230	31.6	28.1	21.3	5.3	2.8	33.0	24.2	25.1	8.5	3.3	–	22.4	23.5
F:AM 108229♂	26.5	25.7	19.8	6.5	3.3	30.1	21.5	22.8	6.4	3.8	–	22.8	21.8
F:AM 108231	–	–	–	–	–	–	–	–	–	–	7.2	–	–
F:AM 71892♂	36.8	25.0	21.3	6.2	4.0	42.8	22.1	24.4	7.0	3.2	–	23.1	23.1
Pawnee Creek Fm., CO													
Merychippus sphenodus (holotype)													
AMNH 8281	16.6	26.0	20.0	5.6	3.9	17.5a	21.3a	–	6.4	4.5	According to comparisons, these teeth are about 50% worn.		
Railway Quarry A													
OR		24.3–26.4	20.2–20.7	6.3–7.2	3.7–4.7		19.5–21.4	22.6–23.2	7.0–8.0	3.4–4.0		20.1–21.2	22.1–22.9
$\bar{x}$		25.5	20.4	6.4	4.1		19.0	22.9	7.4	3.8		20.5	22.5
S		1.1	0.3	0.5	0.5		2.9	0.3	0.5	0.3		0.6	0.4
CV		4.3	1.5	7.8	12.1		15.2	1.3	6.8	7.9		2.9	1.8
N		3	3	3	3		3	3	3	3		3	3

TABLE 3
(*Extended*)

P4		M1					M2					M3				
Protocone					Protocone					Protocone					Protocone	
L	W	H	LO	W	L	W	H	LO	W	L	W	H	LO	W	L	W
6.0	3.2	—	19.8	20.7	6.2	3.5	—	19.3	20.2	6.0	2.5	—	16.9	14.3	6.0	2.2
6.8	3.3	—	18.3	21.4	6.5	3.7	—	19.0	20.4	6.4	3.1	—	20.0	18.4	6.3	3.4
—	—															
6.8	3.7	25.2	19.8	21.8	6.7	3.0	27.7	19.8	20.5	7.2	3.0	—	—	—	—	—
8.0	3.8	12.0a	17.1	21.3	7.0	3.5	14.0	17.8	21.3	7.5	4.4	18.0a	20.6	19.8	7.8	4.2
6.0	3.2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
—	—	26.0a	21.7	22.1	7.8	4.0	29.0a	19.4	20.8	7.2	3.6	29.0	21.8	21.0	7.2	2.5
		43.5a	25.7	21.0	8.1	3.2	41.0a	23.6	19.5	—	—	—	—	—	—	—
7.6	3.4	39.2	21.2	22.7	7.8	3.8	45.2	22.6	22.5	8.0	3.8	38.2	20.4	very early wear		
8.8	3.8	—	20.3	22.6	7.2	3.8	—	21.0	20.4	8.0	3.4	35.1	—	—	—	—
6.8	3.4	—	28.7	22.2	7.1	3.9	—	21.0	21.8	6.8	3.6	very early wear			—	—
7.4	2.9	40.4	22.8	20.6	7.4	2.9	41.3	23.0	17.6	—	—	very early wear			—	—
7.8	3.6	—	18.2	20.5	7.3	3.1	—	19.4	19.6	7.7	3.1	32.5	—	very early wear		
7.1	3.8	—	22.2	23.7	7.3	4.3	—	19.2	21.0	7.1	3.3	31.0	20.9	21.3	—	—
8.2	3.4	—	21.1	22.4	3.0	3.6	—	22.5	20.0	—	—	erupting		—	—	—
6.8	4.1	—	20.1	20.5	5.7	3.0	28.0a	20.0	20.1	6.2	3.3	32.3	17.8	18.2	—	—
—	—	8.2	—	—	—	—	9.4	—	—	—	—	8.9	—	—	—	—
7.5	3.2	—	22.1	—	6.8	3.4	—	22.1	21.9	7.3	3.5	—	18.4	17.4	—	—
6.8–	3.3–		17.1–	21.3–	6.5–	3.0–		17.8–	20.4–	6.4–	3.0–		20.0–	18.4–	6.3	3.4
8.0	3.8		19.8	21.8	7.0	3.7		19.8	21.3	7.5	4.4		20.6	19.8	7.8	4.2
7.2	3.6		18.4	21.5	6.7	3.4		18.9	20.7	7.0	3.5		20.5	19.1	7.1	3.8
0.7	0.3		1.4	0.3	0.3	0.4		1.0	0.5	0.6	0.8		0.4	0.9	1.1	0.6
9.7	8.3		7.6	1.4	4.5	11.8		5.3	2.4	8.6	22.9		2.0	4.7	15.5	15.8
3	3		3	3	3	3		3	3	3	3		2	2	2	2

TABLE 3
(*Continued*)

	P2				P3				P4	
			Protocone				Protocone			
	LO	W	L	W	LO	W	L	W	LO	W
Devil's Gulch Horse Quarry										
OR	22.8–28.5	17.7–21.3	4.7–6.2	2.8–4.3	19.2–24.2	21.3–25.4	6.4–9.3	2.8–3.8	19.8–23.4	20.6–23.6
$\bar{x}$	26.2	20.3	5.7	3.5	22.3	23.7	7.6	3.3	22.5	22.5
S	2.1	1.4	0.6	0.6	1.8	1.4	1.1	0.3	1.1	1.1
CV	8.0	6.9	10.5	17.1	8.1	5.9	14.5	9.1	4.9	4.9
N	6	6	6	6	6	6	6	6	8	8

TABLE 4
Measurements (mm) on Lower Cheek Teeth of *Cormohipparion quinni*, Devil's Gulch Member, Valentine Formation, Late Barstovian, Nebraska

	P2			P3			P4			M1			M2			M3		
	H	L	W	H	L	W	H	L	W	H	L	W	H	L	W	H	L	W
F:AM 71888	–	24.5	12.5	–	22.9	14.3	–	21.6	13.3	–	20.5	11.3	–	24.4	11.2	42.0*	–	–

Notes: * height measured at metastylid. Protostylids present in p3, m1–2.

F:AM 108231, aged adult cranium, right I3, right and left C, left Dp1, P2–M3, right P2, P4, M1 in late wear.

Sawyer Quarry — F:AM 71892, partial cranium, with right P2–M3 (sawn to reveal pattern) and nearly unworn left P2–P3 (fig. 12).

From the Crookston Bridge Member, Valentine Formation, Nebraska. All of these sites contain taxa of late Barstovian age, but stratigraphically precede those listed above.

Railway Quarry A (RRQA) — F:AM 71896, cranial fragment preserving palate, part of facial region, right dP1, right and left P2-M3 in early third wear (fig. 11). F:AM 107888, left P2 in about medial wear (fig. 14A). F:AM 108226, left P3, M1–M2 in about early third of wear (fig. 14B). P4 of this specimen was sacrificed for geochemical analysis. AMNH 105229 (=cast of UNSM 1352), virtually complete cranium, right I3, dP1, P2–M3, left C, P2–M3 in about late third of wear (e.g., MacFadden, 1984: fig. 124).

Devil's Jump Off — F:AM 107886, maxillary fragment with left P2–P4 (fig. 14C).

Nenzel Quarry — F:AM 108223, maxillary fragment with left P4–M2. F:AM 108224, unworn left P3–M2 (fig. 14E).

Schoettger Quarry — F:AM 108225, associated left dP3–dP4, left P2–M3, in early wear (fig. 14D).

From Sand Canyon, northeast Colorado. PU 12291, nearly complete cranium (lacking rostrum) with cheek teeth in early third of wear (see Osborn, 1918: 112 and pl. 12 = neotype of *Merychippus sphenodus* [see fig. 15]).

Description of Referred Material: In all cases the following descriptions first treat specimens from the Devil's Gulch Horse Quarry as being the nominal hypodigm of the species. This is followed by considering material from other quarries in the Devil's Gulch Member, followed by material from Railway Quarry A and other quarries in the underlying Crookston Bridge Member. A following section treats the much less abundant material from the Cornell Dam Member of the Valentine Formation. The goal here is to encourage evaluation of the presence of more

TABLE 3
(*Continued*)

P4		M1				M2				M3			
Protocone				Protocone				Protocone				Protocone	
L	W	LO	W	L	W	LO	W	L	W	LO	W	L	W
6.8–	2.9–	18.2–	20.5–	3.0	2.9–	19.2–	17.6–	6.2–	3.1–	17.8–	17.4–	–	–
8.8	4.1	28.7	23.7	7.4	4.3	23.0	21.9	8.0	3.6	20.9	21.3	–	–
7.6	3.5	21.9	21.8	7.0	3.5	21.0	20.3	7.2	3.4	19.0	19.0	–	–
0.7	0.4	3.1	1.3	0.5	0.5	1.4	1.4	0.6	0.2	1.6	2.1	–	–
9.2	11.4	14.2	6.0	7.1	14.3	6.4	6.9	8.3	5.9	8.4	11.1	–	–
8	8	8	7	8	8	8	8	6	6	3	3	0	0

than one species-level taxon of this kind of equid in these parts of the Valentine Formation. The conclusion is that specimens from the Devil's Gulch and Crooskton Bridge members constitute a single species; those from the Cornell Dam Member may constitute a different species.

In the Devil's Gulch Member, dP1 is relatively smaller than in *C. goorisi.* From Devil's Gulch Horse Quarry dP1 ranges in length from 10.2–10.8 mm (N = 3). P2 length for the same specimens ranges from 25.7–28.5, with the ratio of dP1/P2 length being 0.36–0.42 (mean is 0.39).

Comparable figures for the dP1 in Railway Quarry A sample are 10.0–17.4 mm (N = 3); P2 length ranges from 24.3–26.4 mm; ratio of dP1/P2 length is 0.30–0.41 (mean is 0.36).

If all specimens are analyzed together, the dP1/P2 length ratio mean (N = 6) is 0.38.

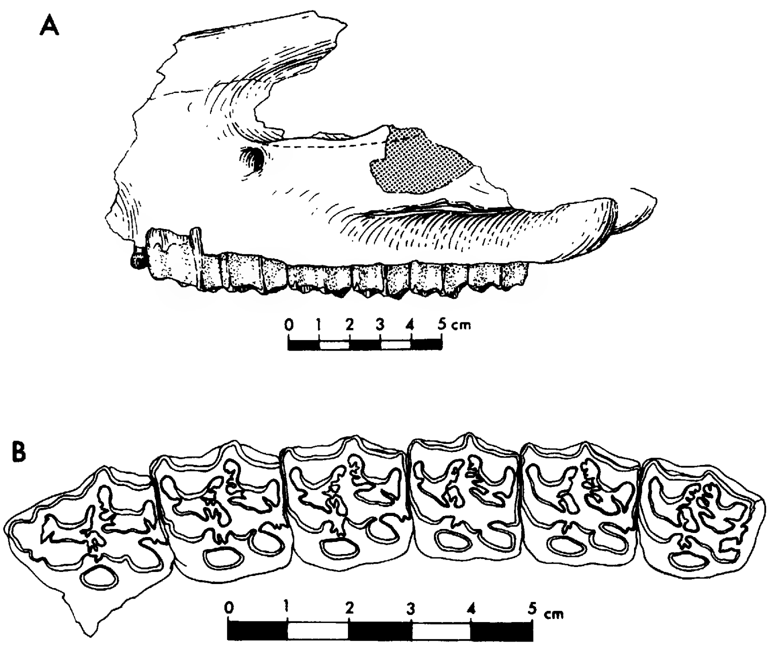

Fig. 11. *Cormohipparion quinni,* new species, F:AM 71896 from Railway Quarry A, Crookston Bridge Member, Valentine Formation, late Barstovian, Cherry County, north-central Nebraska. **(A)** Left lateral view of face. Dotted line represents lower internal margin of DPOF. **(B)** Left upper cheek tooth dentition, P2–M3.

TABLE 5

Comparison of Cranial Measurements, *Cormohipparion* Species, Fleming, Valentine, and Ash Hollow Formations, Texas and Nebraska

Measurements follow Eisenmann et al. (1988). Numbers **39** and **40** are new. **39** = length, rear DPOF to anterior tip of lacrimal. Negative value indicates estimation of amount of lacrimal eroded by rear of DPOF; **40** = medial depth of DPOF. Specimens from McMurry Pit 1 co-occur with type and referred material of *Hipparion shirleyi* MacFadden (1984: fig. 31) = *H. shirleyae* Hulbert and MacFadden (1991: 39). These specimens are herein removed from *H. shirleyae* and included within *Cormohipparion,* possibly close to *C. goorisi.* Note that as figured (MacFadden, 1984: fig. 31), F:AM 99386 shows a well developed DPOF, the anterior border of which is closely applied to the IOF, the latter being located above the anterior portion of P3, as in other species of *Cormohipparion.* The McMurry Pit 1 material differs from *C. goorisi,* possibly at the species level, as being smaller in most cranial parameters, medially shallower DPOF, and somewhat simpler upper cheek tooth pattern, albeit the specimen is at a relatively early stage of wear (M3 barely worn).

Characters													
1	2	3	4	5	6	7	8	9	10	11	12	13	14
Cormohipparion goorisi													
Trinity River Pit 1; Fleming Fm., TX N = 1–4 (mode 2; MOW unpubl. data)													
78.2	83.9	78.3	72.3	139.8	294.8	64.8	55.7	116.0	—	—	24.1	45.7	21.6
Cormohipparion cf. *goorisi*													
McMurry Pit 1; Fleming Fm., TX N = 2 (MOW unpubl. data)													
69.1	85.5	—	72.5	—	—	59.5	47.8	107.1	—	—	—	48.9	20.5a
Cormohipparion quinni													
Railway Quarry A; Cornell Dam Mbr., Valentine Fm., NE N = 1–2 (see table 1)													
75.5	92.9	78.8	73.4	147.5	315.8	67.1	64.1	124.1	—	—	32.3	54.3	26.7
Devil's Gulch Horse Quarry, Devil's Gulch Mbr., Valentine Fm., NE N = 1–4 (see table 1)													
85.0	93.0	79.3	73.9	—	—	71.5	61.2	129.8	—	—	32.0	49.0	—
Sawyer Quarry, Devil's Gulch Mbr., Valentine Fm., NE N = 1													
82.7	—	—	—	—	—	73.1	61.5	134.0	—	—	—	—	—
Cormohipparion occidentale													
XMas Quarry; Merritt Dam Mbr., Ash Hollow Fm., NE (N = 2–9; mode 4–5 (MOW unpubl. data)													
106.0	111.3	95.0	84.5	184.2	391.6	79.5	66.7	145.0	49.1	25.8	33.1	55.1	33.2

This compares with a mean of 0.45 for *C. goorisi* (N = 3). The relatively large dP1 in *C. goorisi* is a plesiomorphic state (e.g., Hulbert and MacFadden, 1991: 18; fig. 6, **45**). In 11 crania of *C. occidentale* from XMas Quarry where this state could be examined, dP1 had been evolutionarily lost in all cases.

Tables 6 and 7 show parameter statistics for *Cormohipparion quinni* P2 in the Devil's Gulch and Crookston Bridge Members of the Valentine Formation. In all such tables (6–15) specimens from each quarry sample are arranged in progressively decreasing crown height as actually measured, or carefully estimated.

An unworn P2 probably was about 40 mm tall in the equid from the Devil's Gulch Horse Quarry (table 6). The unworn M3 in F:AM 108230 is about 40 mm tall, and the unworn P2 is usually as tall as M3. The immature dental pattern of P2 in F:AM 71888 (fig. 9A) at about 27% wear (table 6) is shared with F:AM 108230 (table 6; fig. 13C) at 17% wear; with F:AM 108229 (table 6; fig. 13E) at 30% wear and with F:AM 71890 (table 6; fig. 13D), at 34% wear. Whereas the protocone always remains isolated even in very late wear (F: AM 108321; table 6), the remainder of the protoloph also tends to remain incompletely formed until about 40% wear, at which time the fossette border morphology is essentially complete (F:AM 125819; table 6, fig. 13F). Here, the plication count is only moderately complex (table 6), and although the crochet

TABLE 5
(*Extended*)

Characters														
15	16	17	18	19	20	21	22	23	24	25	26	27	28	29
35.9	–	–	70.3	101.4	–	64.0	47.4	225.0	124.6	38.0	–	–	47.8	45.6
35.4	–	–	–	–	–	60.0a	–	–	–	–	–	–	–	–
41.0	–	–	96.0	112.0	38.7	–	49.0	–	–	69.2	–	–	50.6	41.8
41.6	–	–	–	–	–	–	–	–	–	–	–	–	48.3	44.7
49.8	70.2	121.9	132.0	139.7	58.8	91.8	63.9	306.7	–	77.8	82.9	11.6	57.3	46.6

is still not fully formed (protoloph not yet connected to metaloph), the double pli caballin is typical of the premolar series, as is the relatively ovate protocone (width/length ratio is 0.66). There also tends to be a single plication in the hypoconal groove. A specimen from Sawyer Quarry (F:AM 71892) is in a very early stage of wear, and adds little to the morphology of P2, except to corroborate the interpretation that the tooth was about 40 mm tall in the unworn state (table 6; fig. 12). A hypoconal fossette is present here.

P2 is estimated as having an unworn MSTH of 35 mm in the Crookston Bridge Member. This is based on an unworn M1 from Nenzel Quarry (table 13; fig. 14E, F) being about 43.5 mm tall and in recognition of the fact that P2 is usually about 5 mm lower-crowned than M1. If this estimate is correct, F:AM 71896 from Railway Quarry A (table 7, fig. 11) indicates that a mature crown pattern was developed at about 36% wear (pre- and postfossettes fully formed; crochet through-going). On the other hand, F:AM 107888 from the same quarry is nearly 50% worn, but retains an immature pattern. The incompletely developed protoloph (no connection to the anterostyle) in F:AM 107886 (Devil's Jump Off Quarry; table 7; fig. 14C) is consistent with its relatively early wear stage.

At this point it could be suggested that the unworn P2 from the Cornell Dam Member is slightly lower-crowned than that from the

TABLE 5
(*Extended*)

Characters										
30	31	32	33	34	35	36	37	38	39	40
Cormohipparion goorisi										
Trinity River Pit 1; Fleming Fm., TX N = 1–4 (mode 2; MOW unpubl. data)										
65.0a	128.0a	24.0	48.3	38.7	28.8	21.5	32.6	48.2	0 to −3?	21a
Cormohipparion cf. *goorisi*										
McMurry Pit 1; Fleming Fm., TX N = 2 (MOW unpubl. data)										
—	—	24.6	46.8a	—	27.0a	17.2	26.5	—	0 to −5	10a
Cormohipparion quinni										
Railway Quarry A; Cornell Dam Mbr., Valentine Fm., NE N = 1–2 (see table 1)										
69.9	139.5	26.6	49.2	45.5	27.0	25.6	30.2	56.0	0 to −3	21.3
Devil's Gulch Horse Quarry, Devil's Gulch Mbr., Valentine Fm., NE N = 1–4 (see table 1)										
—	—	30.1	54.6	52.6	36.7	26.0	36.5	62.3	0 to −1.5	17.8
Cormohipparion occidentale										
XMas Quarry; Merritt Dam Mbr., Ash Hollow Fm., NE N = 2–9; mode 4–5 (MOW unpubl. data)										
116.7	157.9	45.1	70.4	60.4	33.5	31.9	41.4	58.0	17	18.0

Devil's Gulch, but otherwise the morphology of the two samples seems to be comparable. On the other hand, if the unworn P2 were equally tall in the two samples, then that from the Crookston Bridge Member might be characterized as delaying into somewhat later wear the development of a mature crown pattern.

Based on all these specimens, P2 in *Cormohipparion quinni* is about 35–40 mm tall in the unworn condition, the protocone is developed by at least 17% wear, at which time the hypocone still is nearly closed (but open by about 30% wear in all); the crochet is fully developed after about 30% wear; fossette count is 1.3.2.2 as late as about 40% wear, but diminishes to ca. 0.2.2.1 at about 52% wear. The mature protocone is subovate in shape, with a width/length ratio of 0.63. The protocone connects to the protoloph at about 52% wear (e.g., F:AM 105229, RRQA; table 7), but is still isolated at nearly 80% wear in F:AM 108231 (DGHQ: table 6).

By contrast, P2 in *C. goorisi* is about 30 mm tall; fossette count is somewhat higher, ca. 1.6.5.1 when expressed at a comparable wear stage; and the protocone connects to the protoloph only after about 30% wear. The crochet is developed later, after about 40% wear.

P3 in the DGHQ sample is taken to have been about 45 mm tall in the unworn state (based on F:AM 71892; table 8, fig. 12). P3 is at least 33.5 mm tall in the unworn F:AM 108228, but roots are not formed in this specimen. M2 of the same specimen is 41.3 mm tall, and in a very early stage of wear. It is likely that M2 was about 45.0 mm tall in the unworn condition. In comparison with M1 and M2, and allowing for the extremely unworn condition of P3, it is likely that the total unworn MSTH of this tooth was about 45 mm.

Of specimens from the DGHQ that show occlusal wear, F:AM 108230 is the least worn P3 (ca. 26%; table 8; fig. 13C). The protocone is lozenge-shaped, posterolingually oriented, and has a narrow anterior tip that is aligned parallel to the body of the cusp. It thus is drawn out anterolabially, but not sharply divergent from the cusp axis, and is not described as having a spur. The hypocone is still nearly isolated from the metaloph. The

TABLE 6
***Cormohipparion quinni*; Devil's Gulch Member, Valentine Formation, Nebraska, P2 Statistics**
MSTH = mesostyle height; % WR = percent wear; Fossettes = count; PRF = protocone yet formed (Y or N); CRD = ?crochet developed; # pli caballin; HGP = ? plis in hypoconal groove; HPC = hypocone Not, Open & Narrow, or Open & Widely connected; PRR = protocone W/L ratio.

Specimen No.	MSTH	% WR	Fossettes	PRF	CRD	HGP	HPC	PRR	Remarks
Devil's Gulch Horse Quarry									Unworn MSTH est. at 40 mm. Nearly unworn M3 at 40 mm. MSTH in F:AM 108230.
F:AM 108230	33.3	16.8	?.?.?.?	Y	N	1	O–N	0.53	Crochet not formed; still elongate, trapezoidal protocone
F:AM 71888 type	29.0	27.5	2.?.?.1	Y	N; 4	0	O–N	0.64	M3 unworn MSTH 35.2 mm. Pattern not stabilized; cf. F:AM 108225; Schoettger Q., Crookston Bridge Mbr.
F:AM 108229	28.0	30.0	1.1.2.1	Y	Y; 2	0	N	0.51	Crochet formed but pattern not stabilized. Nearly unworn M3 MSTH 35.2 mm.
F:AM 71890	26.3	34.3	?.?.?.1	Y	N; 0	1	O–N	0.78	Pattern not stabilized.
F:AM 125819	24.0	40.0	1.3.2.2	Y	N; 2	1	O	0.66	Pattern fully formed; cf. F:AM 18223; Nenzel Q., Crookston Bridge Mbr.
F:AM 108231	8.8	78.0	–.–.–.–	Y	Y; 0	?	?	–	Very late wear; protocone still isolated.
Sawyer Q.									Unworn MSTH est. at 40 mm based on this tooth.
F:AM 71982	36.8	0.80	?.?.?.?	Y	N	0	O–N	0.65	Very early wear; shows P2 very tall. Hypoconal fossette present.

protoloph connects to a double pli caballin; the hypoconal groove has a single pli. It is difficult to count plications on the prefossette in this condition, but the fossette count appears to be 4.5.6.1

P3 in F:AM 71888 (table 8; fig. 9B) was comparably worn (about 29%) and is slightly less complex than F:AM 108230. The specimen shows that the rear border of the prefossette and crochet are still incomplete, and that a hypoconal fossette was present. F:AM 108229 (33% worn) shows a persistently isolated pli protoconule, as well as hypoconal fossette. Also at about this wear stage, F:AM 71890 shows a very complex enamel pattern, and incompletely formed prefossette and crochet. A fully mature crown pattern is seen in F:AM 125819 (43% worn), still with a double pli caballin as typical of premolars in this species. At this level (also seen in F:AM 108227; 49% worn), the hypocone is fully open to the metaloph. A sole specimen from Sawyer Quarry (F:AM 71892; 5% worn) shows the pattern at very early wear; hypoconal fossette present and pre- and postfossettes still connected.

Based on all Devil's Gulch Member specimens, the crown pattern of P3 begins to form

TABLE 7

***Cormohipparion quinni*; Crookston Bridge Member, Valentine Formation, Nebraska, P2 Statistics**

Specimen No.	MSTH	% WR	Fossettes	PRF	CRD	HGP	HPC	PRR	Remarks
Railway Q. A									Est. unworn height P2 at 35 mm.
F:AM 71896	22.3	36.2	1.4.3.1	Y	Y; 1	1	O–N	0.60	Relatively mature pattern.
F:AM 107888	18.0	48.6	?.?.3.1	Y	Y; 2	1	O–N	0.75	Remnant hypoconal fossette; complex hypoconal groove plications.
F:AM 105299	16.8	52.0	0.2.2.1	Y	N; 0	0	O	0.56	Protocone connected to protoloph at about 50% wear. Protoloph disconnected to metaloph.
Nenzel Q.									Est. MSTH P2 at least 35 mm based on F:AM 108224.
F:AM 180224	???	0.0	0.0.0.0	N	N	?	N	?	Tooth is unworn; roots not formed.
Devil's Jump Off Q.									Est. unworn P2 MSTH 35 mm, follows Nenzel Q.
F:AM 107886	22.8	34.9	2.3.3.1	Y	Y; 1	0	O–N	0.65	Note isolated protocone.

Abbreviations; see table 6.

by at least 5% wear (F:AM 71892). The protocone is isolated from the protoloph at virtually all wear stages, and is subovate in most. A distinct spur is not developed although the anterior tip is pointed in early wear. In some specimens, the hypocone is fully open to the metaloph by about 33% wear, but in others not until after 43% wear. The crochet is de-

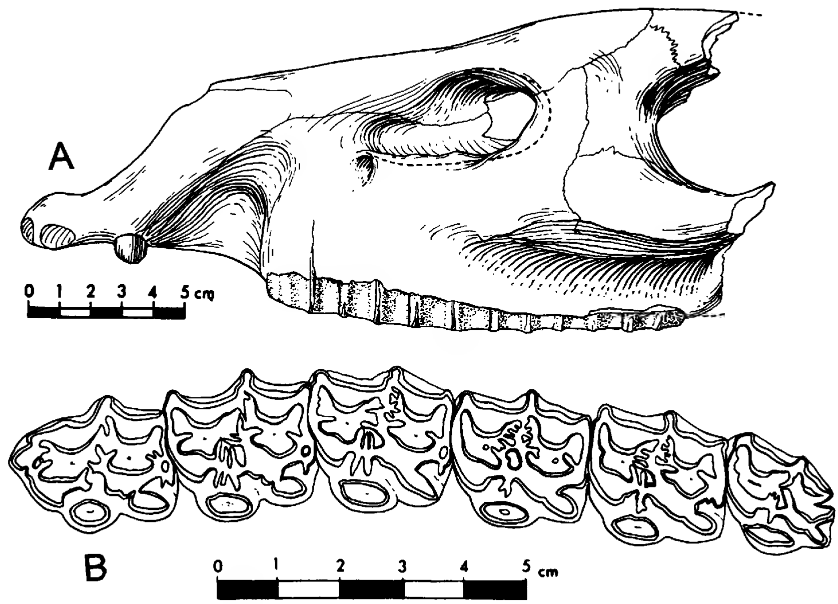

Fig. 12. *Cormohipparion quinni*, new species. F:AM 71892, from Sawyer Quarry Extension, Devil's Gulch Member of the Valentine Formation, late Barstovian, Brown County, north-central Nebraska. **(A)** Facial region, with muzzle. Dotted line indicates extent of DPOF. **(B)** Right P2–M3, sectioned to show pattern (reversed here).

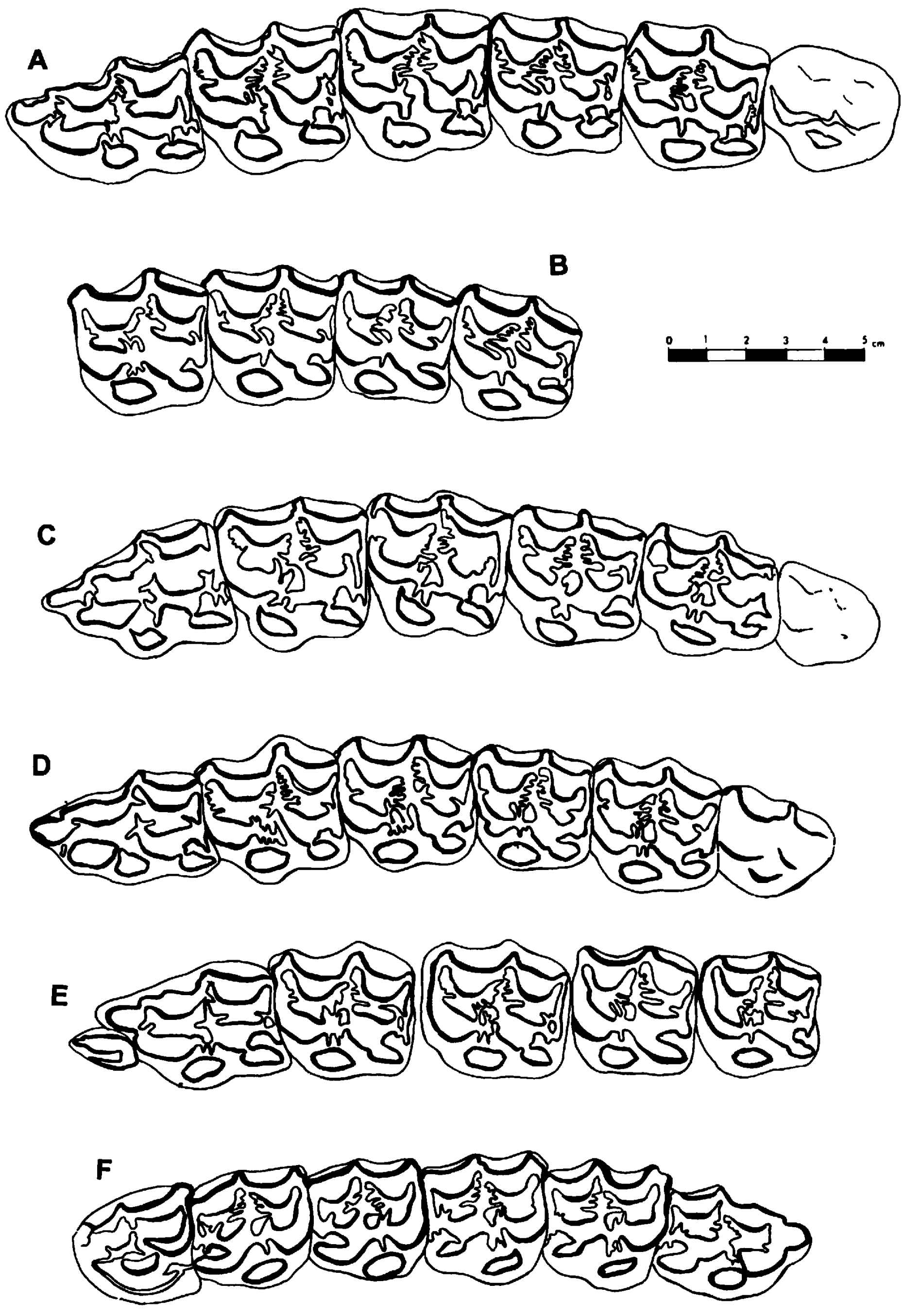

Fig. 13. **(A)** *Cormohipparion occidentale* group, F:AM 71889, Burge Member, Valentine Formation, early Clarendonian, Brown County, north-central Nebraska. **(B–F)** *Cormohipparion quinni*, new species, from Devil's Gulch Horse Quarry, Devil's Gulch Member of the Valentine Formation, late Barstovian, Brown County, north-central Nebraska. Upper cheek tooth dentition in approximately increasing stage of wear. **(A)** F:AM 71889, left P2–M3. **(B)** F:AM 108227, left P3–M2. **(C)** F:AM 108230, left P2–M3. **(D)** F:AM 71890, left P2–M3. **(E)** F:AM 108229, left dp1, P2–M2. **(F)** F:AM 125819, left P2–M3.

TABLE 8
***Cormohipparion quinni*; Devil's Gulch Member, Valentine Formation, Nebraska, P3 Statistics**

Specimen No.	MSTH	% WR	Fos-settes	PRF	CRD	HGP	HPC	PRR	Remarks
Devil's Gulch Horse Quarry									Unworn MSTH est. at 45 mm.
F:AM 108228	–	16.3	0.0.0.0	N	N; 0	0	N	–	Unerupted; roots unformed.
F:AM 108230	33e	26.7	4.5.6.1	Y	Y; 2	1	O–N	0.39	Still elongate and trapezoidal protocone.
F:AM 71888 type	32e	28.9	2.4.5.2	Y	N; 1+	1	O–N	0.30	Hypostylar fossette; crochet and pli caballins incompletely formed.
F:AM 108229	30.1	33.1	2.4.3.1	Y	Y; 2	1	O–N	0.59	Note isolated pli protoconule; hypoconal fossette.
F:AM 71890	30e	33e	5.5.7.1	Y	N; 4	1	O–N	0.49	4 plis caballin; no crochet.
F:AM 125819	25.6	43.0	0.4.3.2	Y	Y; 2	1	O–N	0.49	Pattern fully formed.
F:AM 108227	23e	49e	2.3.4.1	Y	Y; 3	0	O	0.54	Still relatively complex at ca. 50% wear.
Sawyer Q.									Unworn MSTH est. at 45 mm.
F:AM 71892	42.8	4.9	1.5.2.1	Y	Y; 3	0	O–N	0.46	Shows pattern at very early wear. Hypoconal fossette; pre- and postfossettes still connected.

Abbreviations, see table 6; e = estimated.

veloped by about 30% wear. A fully mature pattern is developed by about 40% wear, with the plication count being 0.4.3.2, and the usual condition is for a single pli hypostyle to be present at least to this stage. In very early wear (e.g., F:AM 71890) there may be as many as four plis caballins, but usually there are three or, more commonly, two in other specimens from this member.

The protocone and hypocone are usually anteroposteriorly oriented, except in early wear and in F:AM 125819 (fig. 13F) where the protocone is posterolingually oriented at about 43% wear. The hypoconal groove is usually smooth, except in early wear (F:AM 71888) where it bears two plicae.

P3 in the sample from the Crookston Bridge Member is considered to have an unworn MSTH of 45 mm (table 9). The least worn P3 in the Railway Quarry A sample is about 38% worn (F:AM 108226; table 9; fig. 14B). The specimen still shows a complex crown pattern, an isolated pli protoconule, and four plis caballin. At slightly later wear, F:AM 71896 (table 9; fig. 11) shows a very complex but fully mature pattern. F:AM 105299 (table 9) is in late wear (68%) and is important in showing the beginning of the connection of the protocone to the protoloph.

F:AM 108224, from Nenzel Quarry is about 9% worn (table 9; fig. 14F), and shows a relatively simple enamel pattern with the metaloph connected to the prefossette, the crochet still unformed, and a hypoconal fossette present. The slight spur on the protocone and its elongate shape also indicate the wear stage. F:AM 107886 (table 9; fig. 14C) is about 38% worn, shows a very complex enamel pattern, and isolated (and complex) pli protoconule.

In summary, P3 from the Crookston Bridge Member of the Valentine Formation is likely about 45 mm tall in the unworn condition, the protocone is developed by at least 8% wear, but the hypocone is not fully open until much later. The crochet is fully developed by at least 37% wear, but was still unformed at about 10% wear; fossette count is 6.5.5.1 by as late as 30% wear, but more typically is 1.5.4.1 to 1.6.6.1 by 40–45% wear. At all wear stages recorded, the protocone is subovate in shape with a mean width/length ratio of 0.52 (N = 5). In F:AM 108225 (very

TABLE 9

***Cormohipparion quinni*; Crookston Bridge Member, Valentine Formation, Nebraska, P3 Statistics**

Specimen No.	MSTH	% WR	Fossettes	PRF	CRD	HGP	HPC	PRR	Remarks
Railway Q. A									Unworn P3 MSTH est. at 45 mm, based on F:AM 108225.
F:AM 108226	28.0	37.8	1.5.4.1	Y	Y; 4	1	O–N	0.47	Note isolated pli protoconule; complex enamel pattern and four plis caballin.
F:AM 71896	25e	44.4	1.6.6.1	Y	Y; 2	2	O–N	0.57	Est. actual MSTH based on the specimen.
F:AM 105299	14.5	67.8	0.4.0.1	Y	Y; 1	0	O	0.50	Note beginning of connection of protocone.
Nenzel Q.									Unworn MSTH est. 45, based on M1.
F:AM 108224	40e	0	0.0.0.0	N	N	N	N	N	Unworn pattern.
Schoettger Q.									Unworn MSTH est. at 45 mm based on this specimen.
F:AM 108225	41.1	8.7	1.2.4.1	Y	N; 0	1	O–N	0.51	Crochet not connected; slight spur on protocone; hypoconal lake in early wear.
Devil's Jump Off Q.									Unworn MSTH at 45 mm based on Schoettger Q.
F:AM 107866	25e	29e	6.5.5.1	Y	Y; 1	0	O–N	0.59	Note isolated and complex pli protoloph.

Abbreviations; see table 6.

early wear) the protocone retains a distinct spur (absent in all other specimens). The protocone connects to the protoloph at about 68% wear (e.g., F:AM 105229).

The protocone and hypocone are almost anteroposteriorly oriented, except in F:AM 180225, where the hypocone is posterolingually directed. Even in this earliest wear stage (9%) however, the hypocone is narrowly open to the metaloph. The hypoconal groove is usually marked by a single to triple pli on its labial border into medial wear (e.g., F:AM 71896), but this is lost subsequently. The pli caballin is usually double, but even in moderate wear (F:AM 108226) can be quadruple.

As indicated above, F:AM 108225 (about 9% worn) presents an unusually morphology in that the metaloph connects to the ectoloph and adjacent part of the prefossette, so that neither the pli protoconule loop nor the crochet are completely formed. This kind of morphology is also found in F:AM 71888 (fig. 10B; Devil's Gulch Horse Quarry; ca. 30% wear). Specimens in both samples show that the mature crown pattern is developed between about 30–40% wear.

The number of specimens from each unit of the Valentine Formation is limited. In possible contrast to P2, P3 in the Crookston Bridge Member appears to have been as tall as in the sample from the Devil's Gulch Member. At comparable stages of wear, the enamel complexity seems to be slightly greater in the Crookston Bridge versus the Devil's Gulch Member. One Crookston Bridge specimen (F:AM 108225) in very early wear (9%) shows a spurred protocone (fig. 14D). This is reminiscent of F:AM 108230 (DGHQ; 27% wear; fig. 13C). The pli protoconule loop may be more consistently isolated in the Crookston Bridge than in the Devil's Gulch sample. Other than these slight (and not provably significant) differences, there appears to be no reason to separate the remaining Valentine Formation specimens of *Cormohipparion* into more than a single species, at least as based on the morphology of P3.

P3 in *C. goorisi* is about 30 mm tall; fossette count is somewhat higher, ca. 1–2.4–6.2–3.1–2; and protocone connects to the protoloph earlier (at about 50% wear). P3 protocone is more prominently spurred in *C. goorisi.*

P4 in the Devil's Gulch Member is estimated to have had an unworn MSTH of 45 mm, based on the condition in M1–2 in F:AM 108228. F:AM 108229 (table 10; fig. 13E) is the least worn tooth showing occlusal wear in the DGHQ sample. The specimen is about 30% worn, shows relatively complex fossette borders, a double pli caballin, isolated pli protoconule, single pli in the hypoconal groove, and a hypoconal fossette. The protocone is completely formed, subovate, and the hypocone is partly open to the metaloph. F:AM 108230 (table 10; fig. 13C) is at a comparable wear stage, and shows a more immature crown pattern, with the prefossette incomplete, and many plications on the posterior border of the postfossette. F:AM 71888 (table 10; fig. 9B) is only slightly more worn and still shows an incomplete crown pattern, a very elongate protocone, and a barely opened hypocone. At a comparable wear stage (ca. 33%), F:AM 71890 shows a very complex enamel pattern that is additionally notable in the isolated pli protoconule. The occlusal pattern seems to be stabilized at about 40% wear, as represented by F:AM 125819 (table 10; fig. 13F), but the hypocone is not completely open to the metaloph until about 44% wear (F:AM 108227; table 10; fig. 13B). Note that the pli protoconule is still isolated in this specimen, however. The protocone remains isolated into very late wear as indicated in F:AM 108231 (table 10).

The unworn P4 in the Crookston Bridge Member of the Valentine Formation was about 45 mm tall, based on F:AM 108225. Here the specimen is about 6% worn (table 11), and shows (fig. 14D) that the protocone is well developed, with a spur. The immature crown pattern is demonstrated by the plication count being relatively low (1.3.4.1), with the hypocone still fundamentally closed; hypoconal groove simple; crochet unformed, and with metaloph enamel being continuous with the posterior part of the prefossette.

Specimens from RRQA are more mature with those at about 40% wear (table 11; fig. 11, 14B) having somewhat more complex fossette borders, a more complex pli caballin and hypoconal groove; the hypocone being more open to the metaloph. F:AM 107886 (Devil's Jump Off Quarry; table 11; fig. 14C) is slightly more worn (ca. 42%) but retains considerable pattern complexity as well as an isolated pli protoconule (the latter can also be seen in F:AM 108226).

According to the available data, the general condition for the Crookston Bridge sample is: protocone rounded oval, connects to protoloph only in basal third of crown; fossette complexity is about 1.6.4.1 (but sometimes greater in medial wear), the pli protoncule is well developed (commonly isolated), pli caballin at least double. The hypoconal groove retains a single pli into about medial wear. The morphology of P4 in the Valentine Formation samples seems comparable and seems to represent the morphology contained within a single species, especially when specimens are compared at about 40% wear. In both P3 and P4, F:AM 107886 from the Crookston Bridge Member shows a somewhat greater enamel complexity than any other specimen at this stage of wear (ca. 42%), but pending further evidence based on additional specimens this specimen is considered to pertain to *Cormohipparion quinni.*

M1 in the Devil's Gulch Member sample is considered to have been about 45 mm tall in the unworn condition. The MSTH is 40 mm in F:AM 108228, the only tooth for which a direct measurement is possible (table 12). The pattern is in very early wear (ca. 11%), with a lenticular protocone developed as an isolated structure and most of the rest of the pattern visible, but the hypocone is not fully formed.

By about 30% wear (F:AM 125819; fig. 13F, F:AM 108230; fig. 13C), the pattern is fully formed, but pli protoconule still isolated, and relatively complex fossette plications (table 12). In most specimens from DGHQ, the pli caballin is generally single (except F:AM 180230). At about 40% wear the hypocone is fully open to the metaloph (F:AM 108227, fig. 13B: F:AM 71890, fig. 13D). The hypoconal groove is usually smooth. As shown in F:AM 108231 (table 12), the protocone is still isolated in late wear.

M1 in Crookston Bridge Member specimens is considered to be about 45 mm tall

TABLE 10
***Cormohipparion quinni*; Devil's Gulch Member, Valentine Formation, Nebraska, P4 Statistics**

Specimen No.	MSTH	% WR	Fossettes	PRF	CRD	HGP	HPC	PRR	Remarks
Devil's Gulch Horse Q.									Unworn MSTH est. at 45 mm based on F:AM 108228, M1–2.
F:AM 108228	30.5	0	0.0.0.0	N	N; 0	N	N	–	Unerupted; roots not formed.
F:AM 108229	31.1	30.1	1.5.5.2	Y	Y; 2	0	O–N	0.60	Pli protoconule isolated and complex.
F:AM 108230	30e	33e	1.4.5.3	Y	Y; 2	1	N	0.41	Note elongate and trapezoidal protocone; pli protoconule isolated.
F:AM 71888 type	30e	33e	1.6.4.1	Y	N; 2	0	N	0.43	Note incomplete prefossette; connects to metaloph.
F:AM 71890	30e	33e	1.5.5.1	Y	Y; 5	0	O–N	0.50	5 plis caballin; pli protoconule isolated.
F:AM 125819	27.5	38.9	1.6.4.2	Y	Y; 2	1	N	0.46	Pli protoconule connected.
F:AM 108227	25e	44e	2.4.4.1	Y	Y; 1	1	O	0.54	Pli protoconule isolated; single pli caballin.
F:AM 108231	7.2	84.0	0.0.0.0	Y	Y; 0	0	O	–	Very late wear; protocone still isolated.
Sawyer Q. F:AM 71892	?	?	3.5.6.1	Y	Y; 2	0	O–N	0.43	Hypoconal fossette present. Pattern on sectioned tooth at ca. 30 mm, MSTH.

Abbreviations as in table 6.

in the unworn state. F:AM 108224 was about 43.5 mm tall before it was sectioned (table 13) and shows a very early wear pattern at the occlusal surface (fig. 14E). At about medial wear, specimens from RRQA (table 13; figs. 11, 14B) show a mature occlusal pattern with relatively complex fossette borders, two plis caballins, an effectively open hypocone, and smooth hypoconal groove. In late wear, F:AM 105229 (table 13) shows incipient connection of the protocone to the protoloph. The other specimens from the Cornell Dam Member are comparable to the above. F:AM 108225 (table 13: fig. 14D) shows a relatively unworn, open hypocone.

The general morphology for the Crookston Bridge M1 appears to be a plication count of about 1.5.4.1; pli caballin mostly single; pli hypostyle single or absent; protocone rounded oval. There appears to be no significant difference in M1 morphology between the Valentine Formation samples discussed here, especially in comparable stages of wear.

M2 in the Devil's Gulch sample is estimated to have an unworn MSTH of about 45 mm. F:AM 108228 is 41.3 mm tall, and in very early wear (table 14), with enamel showing wear, but not yet breached. Specimens at about 20% wear (table 14) show a relatively mature (F:AM 125819; fig. 13F) to still immature pattern (F:AM 108230; fig. 13C), with an isolated pli protoconule in the latter. Specimens in the 30% (F:AM 71888; table 14; fig. 9) to 40% wear range (F:AM 108229; fig. 13E, F:AM 108227; fig. 13B) show an effectively mature pattern, but still have a tendency for the hypoconal groove to be closed posteriorly. F:AM 71888 has a persistent hypoconal fossette; F:AM 108229 an isolated pli protoconule. F:AM 71890 (table 14; fig. 13D) is comparably complex at this wear stage. The protocone is still isolated in late wear (F:AM 108231; table 14).

The general M2 morphology for the Devil's Gulch sample appears to be 1.5.4.1, with one or two plis caballins and usually no pli hypostyle. The protocone is rounded oval.

The unworn crown height of M2 in the RRQA sample is considered to have been about 45 mm. F:AM 108224 is unworn, but

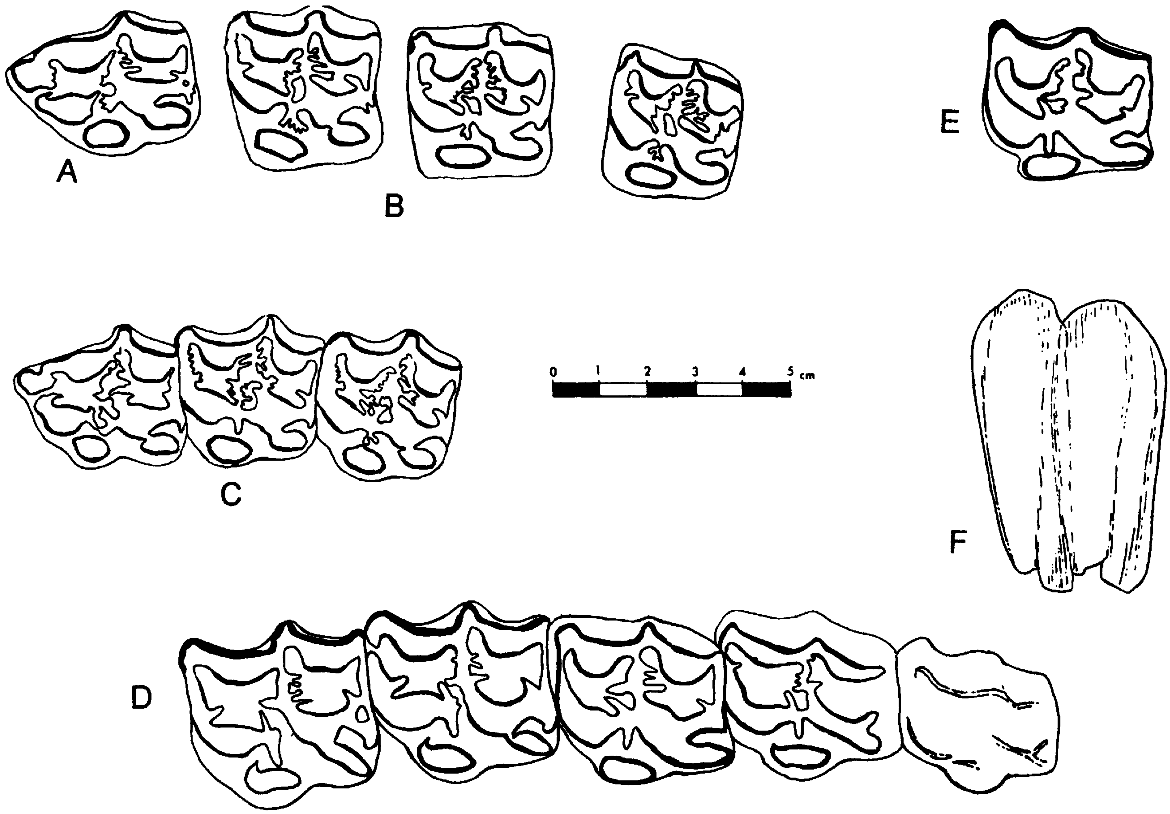

Fig. 14. *Cormohipparion quinni,* new species, A–B from Railway Quarry A, Crookston Bridge Member of the Valentine Formation, late Barstovian, Cherry County, north-central Nebraska. **(A)** F:AM 107888, left P2. **(B)** F:AM 108226, left P4–M2. **(C)** F:AM 107886, left P2–4, from Devil's Jump Off, Crookston Bridge Member of the Valentine Formation, late Barstovian, Cherry County, north-central Nebraska. **(D)** F:AM 108225, LP3-M3, from Schoettger Quarry, Crookston Bridge Member of the Valentine Formation, late Barstovian, Keya Paha County, north-central Nebraska. **E** and **F**. F:AM 108224, from Nenzel Quarry, Crookston Bridge Member of the Valentine Formation, late Barstovian, Cherry County, north-central Nebraska. **(E)** left M1, sectioned, **(F)** left P4, unworn, labial (?) view.

the base of the crown is not fully formed, so the preserved height (41 mm) is a minimum figure. In comparison with Devil's Gulch specimens of similar wear, those from RRQA are similar in morphology, as well. A chief difference in the RRQA sample is an apparently persistently complex pli caballin in F:AM 108226 (table 15; fig. 14B) and F:AM 71896 (fig. 11). F:AM 105299 (table 15) suggests that the protocone connects to the protoloph at about 70% wear, contrary to DGHQ F:AM 108231 in which it is still isolated at about 80% wear (table 14).

The overall condition for M2 in the Crookston Bridge sample appears as follows: plication count is 1.4.5.1, pli caballin sometimes triple, pli hypostyle usually absent, protocone is elongate oval, pli protoconule usually well expressed.

F:AM 108225, from Schoettger Quarry (table 15; fig. 14D) appears to have had an unworn MSTH about 5 mm taller than any other specimen from the these parts of the Valentine Formation. If the height of this tooth is indicative of a generally taller dentition for its associated elements, then some of the preceding estimates of character acquisition for these specimens need to be revised in favor of a later wear stage than that portrayed here (tables 7, 9, 11, 13, 15).

TABLE 11
***Cormohipparion quinni*; Crookston Bridge Member, Valentine Formation, Nebraska, P4 Statistics**

Specimen No.	MSTH	% WR	Fossettes	PRF	CRD	HGP	HPC	PRR	Remarks
Railway Q. A									Unworn P4 MSTH est. at 45 mm based on F:AM 108224 M1.
F:AM 108226	28.1	37.5	1.5.4.1	Y	Y; 4	1	O–N	0.53	Note isolated pli protoloph.
F:AM 71896	27e	40e	1.7.5.1	Y	Y; 3	1	N	0.48	Complex fossettes; 3 plis caballin.
F:AM 105299	15.5	65.5	1.4.0.0	Y	Y; 1	0	O	0.48	Note beginning connection of protocone; lack of plis on postfossette; openness of hypocone connection.
Nenzel Q.									Unworn P4 MSTH est. 45 mm based on M1.
F:AM 108224	40e	0	0.0.0.0	?	?	?	?	?	MSTH estimated; roots not formed.
F:AM 108223	31e	31e	1.4.4.1	Y	Y; 2	1	O–N	0.51	
Schoettger Q. F:AM 108225	42.5	5.6	1.3.4.1	Y	Y; 0	0	O–N	0.45	Note actual MSTH; crochet still unformed; minor spur on protocone.
Devil's Jump Off Q.									Estimated P4 MSTH based on F:AM 108224.
F:AM 107886	26.0	42.2	1.3.4.1	Y	Y; 2	0	O	0.53	Isolated pli protoconule; very complex fossette borders.

Abbreviations as in table 6.

TABLE 12
***Cormohipparion quinni*; Devil's Gulch Member, Valentine Formation, Nebraska, M1 Statistics**

Specimen No.	MSTH	% WR	Fossettes	PRF	CRD	HGP	HPC	PRR	Remarks
Devil's Gulch Horse Q.									Unworn MSTH est. at 45 mm, based on F:AM 108228.
F:AM 108228	40.0	11.1	0.0.0.0	Y	N	N	N	0.39	Barely worn.
F:AM 125819	31e	31e	0.6.3.1	Y	Y; 1	1	O–N	0.42	Pli protoconule separate.
F:AM 108230	31e	31e	2.5.4.1	Y	Y; 2	0	O–N	0.45	Early wear, still with elongate and trapezoidal protocones. Pli protoconule isolated.
F:AM 108229	30e	33e	0.4.4.1	Y	Y; 1	0	O	0.52	Pli protoconule isolated.
F:AM 71888, type	28e	38e	1.4.4.1	Y	Y; 1	0	O–N	0.58	Mature pattern but hypocone narrowly open; cf. F:AM 108225 (Schoettger Q.; Crookston Bridge Mbr; also F:AM 108224, sectioned tooth).
F:AM 108227	27e	40e	1.5.3.1	Y	Y; 1	0	O	0.58	Fully mature pattern.
F:AM 71890	28e	38e	1.6.5.1	Y	Y; 1	1	O	0.55	Isolated pli protoconule.
F:AM 108231	8.2	81.7	0.0.0.0	Y	Y; 0	0	O	—	Very late wear. Protocone still isolated.
Sawyer Q. F:AM 71892	?	?	1.6.5.1	Y	Y; 1	0	O	0.50	Pattern on sectioned tooth at est. MSTH 30 mm.

Abbreviations, see table 6.

TABLE 13
***Cormohipparion quinni*; Crookston Bridge Member, Valentine Formation, Nebraska, M1 Statistics**

Specimen No.	MSTH	% WR	Fossettes	PRF	CRD	HGP	HPC	PRR	Remarks
Railway Q. A									Est. MSTH M1 is 45 mm based on F:AM 108224.
F:AM 108226	25.2	44.0	1.6.5.1	Y	Y; 2	1	O	0.48	Complexity at midwear.
F:AM 71896	24e	47e	1.5.4.1	Y	Y; 2	0	O–N	0.57	Near connection of pli protoconule; still relatively complex opposing fossette borders.
F:AM 105229	12e	73.3	0.3.2.1	Y	Y; 1	0	O	0.50	Incipient connection of protocone at late ⅓ wear.
Nenzel Q.									Unworn MSTH est. at 45 mm based on F:AM 108224.
F:AM 108224	43.5	30.0	0.4.3.1	Y	Y; 1	1	O–N	0.40	Tall crown height; pattern shown at 31.5 mm = 30% wear. See figure 14 E, F.
F:AM 108223	24e	47e	0.4.3.1	Y	Y; 1	1	O	0.49	Relatively simple pattern at this stage of wear.
Schoettger Q.									Unworn MSTH est. at 45 mm, from F:AM 108224.
F:AM 108225	39.2	12.9	0.2.3.1	Y	Y; 1	0	O	0.49	See isolated protocone at this early stage of wear. Barely worn M3 MSTH 38.8 mm in this specimen.

Abbreviations as in table 6.

M3 is relatively poorly represented in these collections. It appears to have been about 40 mm tall in the unworn state (35.2 MSTH in barely worn F:AM 71888 [Devil's Gulch] and 39.0 MSTH in barely worn F:AM 108225 [Crookston Bridge]). In F:AM 108231, the tooth is about 9 mm tall and the protocone is slightly open to the protoloph, suggesting that this linkage occurs at about 75% wear.

REMARKS: In comparison with *Cormohipparion goorisi, C. quinni* is larger, higher crowned, and has a more complex dental configuration. Unworn upper cheek tooth heights range from 35–45 mm in *C. quinni,* versus 26–34 mm in *C. goorisi.* Upper cheek tooth protocones are more elongate and lose the anterior spur (if present) in very early wear. dP2 appears to be both relatively and actually reduced in the Valentine species.

In the cranium, the DPOF is pocketed only about 15 mm posteriorly, or about half the distance from the rear of the fossa and the anterior border of the orbit. This is in contrast to the condition in *C. goorisi* in which the pocket passes posteriorly well medial to the anterior edge of the orbit and is both actually and relatively deeper than in the Valentine form. In both species, the IOF is located dorsal to P3, and the anterior rim of the DPOF varies from relatively faint (Cornell Dam and Crookston Bridge members) to more sharply defined (Devil's Gulch Member). The POB is not as long anteroposteriorly as in *C. occidentale,* so that the lacrimal still touches (or enters into) the rear of the DPOF.

Tables 5, 16 and figure 16 show a comparison of average cranial parameters between *C. goorisi, C. quinni,* and *C. occidentale* (in part; see below). These comparisons utilize dimension 4 (fig. 16, "basc" = basicranial length) as a base indicator of brain

TABLE 14
***Cormohipparion quinni*; Devil's Gulch Member, Valentine Formation, Nebraska, M2 Statistics**

Specimen No.	MSTH	% WR	Fossettes	PRF	CRD	HGP	HPC	PRR	Remarks
Devil's Gulch Horse Q.									Unworn MSTH est. at 45 mm, based on F:AM 108228.
F:AM 108228	41.3	8.2	0.0.0.0	N	N; 0	N	N	—	Shows M2 taller at same ontogenetic age than M1.
F:AM 125819	36.0	20.0	0.4.4.2	Y	Y; 1	1	O	0.40	Shows mature pattern at 20% wear.
F:AM 108230	35e	22e	1.5.4.1	Y	Y; 2	0	O–N	0.31	Immature pattern; elongate protocone; isolated pli protoconule.
F:AM 71888 type	30e	33e	3.4.4.1	Y	Y; 1	0	O–N	0.43	Hypoconal fossette; hypoconal groove closed. M3 unworn MSTH likely 40 mm.
F:AM 108229	28e	38e	1.4.4.1	Y	Y; 1	0	O	0.53	Isolated pli protoconule.
F:AM 108227	27.5	38.9	2.5.4.2	Y	Y; 1	0	O–N	0.40	Pattern fully formed, but hypoconal groove closed at ca. 40% wear.
F:AM 71890	28e	38e	2.6.4.1	Y	Y; 2	0	O–N	0.53	Strong fossette complexity; isolated pli protoconule.
F:AM 108231	8.9	80.0	0.0.0.0	Y	Y; 0	0	O–W	—	Protocone still isolated at very late wear.
Sawyer Q.									Unworn MSTH est. at 45 mm based on P3.
F:AM 71892	?	?	1.5.6.1	Y	Y; 1	1	O	0.50	Pattern on sectioned tooth at ca. 30 mm MSTH.

Abbreviations as in table 6.

and body size (e.g., Radinsky, 1984). In the following paragraphs character numbers in tables 5 and 16 are boldfaced; abbreviated names correspond to the notation in figure 16.

C. goorisi and *C. quinni* have a similar basioccipital dimension and thus would be expected to be of comparable size in other cranial dimensions (±5%). In fact, this is not the case. As shown in table 16 and figure 16, important divergences from the predicted condition include: **2** (lpal), a measure of facial length in which *C. quinni* is about 10% longer; **6** (tsl; total skull length), and **9** (tcl; total cheektooth length), in which *C. quinni* is about 6% longer; **12** (choa; choanal breadth), about 25% wider; **13** (pal; palatal width), about 16% wider; **14** (snt; minimum premaxillary width at diastema), about 19% wider; **15** (wmuz; muzzle width at rear of I3), about 12% wider; **18** (fwd; trans-frontal width), about 27% wider; **19** (trgl; transverse width at glenoid fossa), about 10% wider; **25** (snh; muzzle height) about 45% higher; **31** (fac; orbit to nasal notch), about 8% longer; **32** (pobl; POB length), about 10% longer; **34** (iof; rear DPOF to IOF), about 15% longer; **36** (fch; base of DPOF to facial crest), about 16% deeper; **38** (mpof; rear DPOF bisector to alveolar border), about 7% deeper.

On the other hand, **22** (in; occipital height), **28** (orl; orbital length), **29** (orw; orbital height), **33** (dpof; DPOF length), **35** (hdof; DPOF height), **37** (ioa; IOF bisector to alveolar border) dimensions are about the same in the two species. Also, the DPOF erodes the tip of the lacrimal to about the same extent in both species.

Finally, the DPOF pocket reaches only about 15 mm posteriorly (about ½ the length of the POB [32] in *C. quinni,* versus its being over twice as deep (beneath all of the POB

TABLE 15
***Cormohipparion quinni*; Crookston Bridge Member, Valentine Formation, Nebraska, M2 Statistics**

Specimen No.	MSTH	% WR	Fossettes	PRF	CRD	HGP	HPC	PRR	Remarks
Railway Q. A									Unworn M2 MSTH at 45 mm based on F:AM 108224, M1.
F:AM 108226	27.7	38.4	1.4.5.1	Y	Y; 2	0	O	0.41	Note pli protoloph still isolated.
F:AM 71896	22e	55.6	0.3.5.1	Y	Y; 1	1	O	0.48	Prominent pli protoconule.
F:AM 105299	14.0	68.9	0.4.4.0	Y	Y; 0	0	O	0.53	Note protocone small connection. In M3 at MSTH of about 18 mm, protocone still is isolated.
Nenzel Q.									Unworn M2 MSTH est. at 45 mm based on F:AM 108224, M1.
F:AM 198224	41.0	8.9	0.0.0.0	N	N	N	N	N	Unworn; roots not formed. MSTH minimum.
F:AM 108223	29e	35.6	0.4.3.1	Y	Y; 1	1	O	0.50	Actual MSTH est. based on M3 which is 29.0 and shows full pattern.
Schoettger Q.									Unworn MSTH est. at 50 mm based on this specimen.
F:AM 108225	45.2	9.6	0.3.4.1	Y	Y; 1	?	?	0.47	Protocone very elongate; slight anterior spur; hypocone not well developed at this wear stage. M3 in very early wear (no pattern) is 38.2 at MSTH.

Abbreviations; see table 6.

and continuing medial to the anterior border of the orbit) in *C. goorisi*. See below for a discussion of the cranial dimensions of *C. occidentale*.

Cormohipparion ?quinni

SPECIMENS FROM NORDEN BRIDGE QUARRY: *Cormohipparion quinni* is best represented by specimens from the Crookston and Devil's Gulch members of the Valentine Formation, with only a few specimens (dentition) possibly represented in AMNH collections of the Cornell Dam Member. Voorhies (1990: A185–A188) allocates a juvenile cranium from the Norden Bridge Quarry (USNM 352554) to *Neohipparion republicanus*. This skull, with right P1, dP2–4, M1, left P1, dP2, partial dP3, dP4, M1, has a well-developed DPOF (ca. 60 mm long, 36 mm high, 14 mm deep medially, and a pocket 15 mm deep). The DPOF has well-developed dorsal, posterior, and ventral rims, but a relatively faint anterior rim. The IOF is not preserved, but likely was above DP3 because it definitely is not present above dP2, dP4 or M1. The deciduous premolars are worn, and show relatively complex fossette enamel patterns, and isolated protocones (on dP3 and dP4). M1 is in early wear, with the enamel breached on the protocone, paracone, metacone, protoloph, and crochet. That of the right side is 40.9 mm tall at the mesostyle (Voorhies, 1990: A185), and in the unworn condition would have been at least 5 mm taller.

AMNH specimens from the Cornell Dam Member (below) are mostly worn, but even so virtually all are as tall as, or taller than, unworn teeth in the same position in the dentition as seen in *C. goorisi,* and have a dental morphology compatible with that of specimens in the Crookston Bridge and Devil's

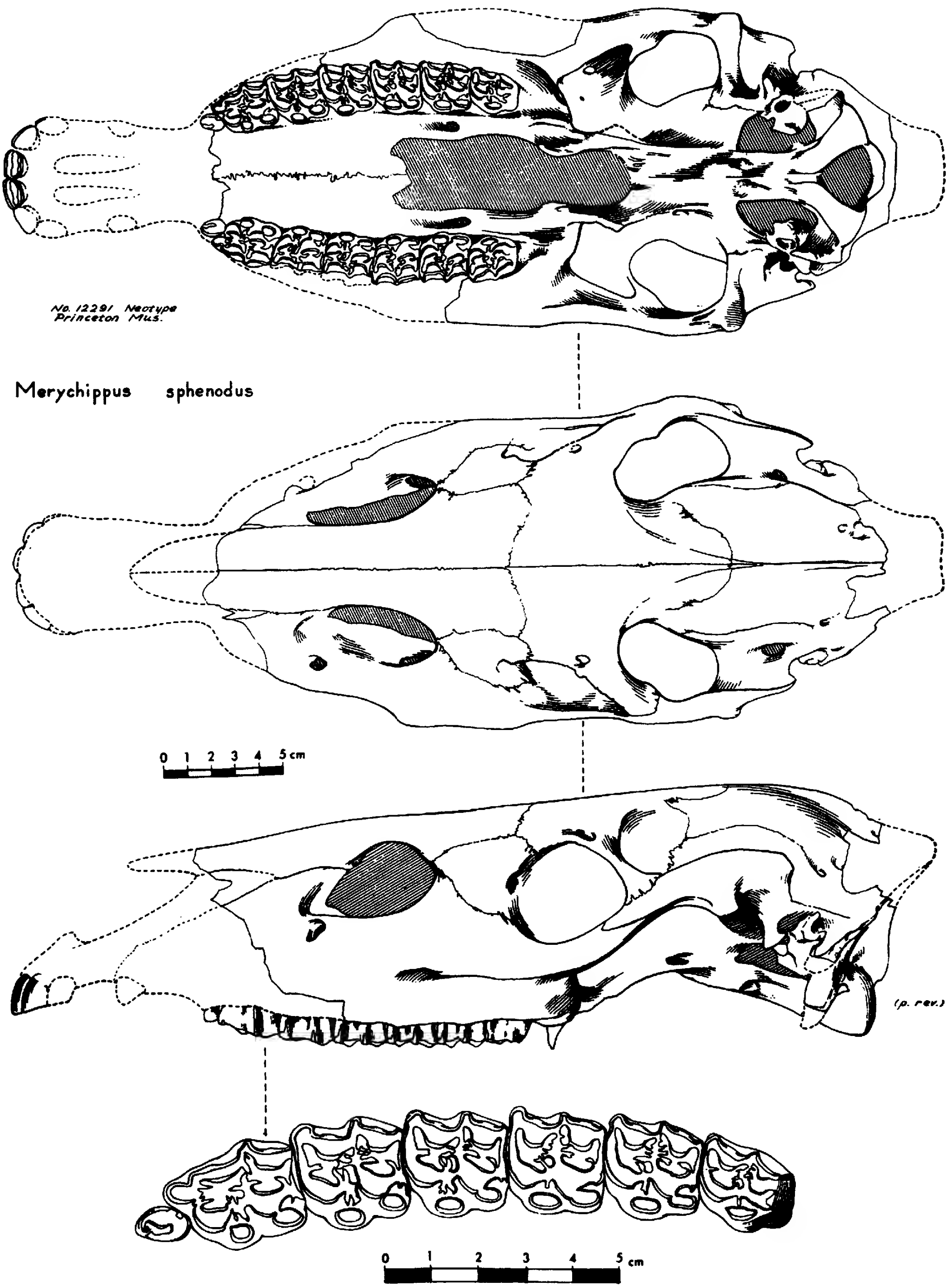

Fig. 15. *Cormohipparion quinni,* new species. PU 12291. Ventral, dorsal and lateral view of cranium, and occlusal view of left upper cheek teeth. After Osborn (1918: pl. 15). Sand Canyon Local Fauna, northeast Colorado. "Neotype" of *Merychippus sphenodus,* according to Osborn (1918: 112).

TABLE 16

Cranial Parameter Comparisons, *C. goorisi* vs. *C. quinni*

MN = measurement number; C. goor. = *C. goorisi*; C. quin. = *C. quinni*; % diff. = percent change [+ or −]; % adj. = percent change when adjusted for difference in braincase length. Data from average of samples shown in table 5.

MN	C. goor.	C. quin.	% diff.	% adj.	Remarks
1	78.2	75.5	−3.0	−3.0	Muzzle actually shorter in *C. quinni.*
2	83.9	92.9	+9.6	+9.6	Palate actually longer in *C. quinni.*
3	78.3	78.8	–	–	Postpalatal length similar in these species.
4	72.3	73.4	–	–	Basicranial length similar in these species.
5	139.8	147.5	+5.2	+5.2	Combined 3 + 4 longer in *C. quinni.*
6	294.8	315.8	+6.3	+6.3	Total cranial length greater in *C. quinni.*
7	64.8	67.1	+3.4	+3.4	Upper premolars longer in *C. quinni.*
8	55.7	64.1	+13.1	+13.1	Upper molars longer in *C. quinni.*
9	116.0	124.1	+6.5	+6.5	Upper cheek teeth longer in *C. quinni.*
10	–	–	–	–	No data.
11	–	–	–	–	No data.
12	24.1	32.3	+25.4	+25.4	Choanae wider in *C. quinni.*
13	45.7	54.3	+15.8	+15.8	Palate wider in *C. quinni.*
14	21.6	26.7	+19.1	+19.1	Snout wider at diastema in *C. quinni.*
15	35.9	41.0	+12.4	+12.4	Muzzle wider in *C. quinni.*
16	–	–	–	–	No data.
17	–	–	–	–	No data.
18	70.3	96.0	+26.7	+26.7	Frontal width greater in *C. quinni.*
19	101.4	112.0	+9.5	+9.5	Transglenoid width greater in *C. quinni.*
20	–	38.7	–	–	Incomplete data.
21	64.0	–	–	–	Incomplete data.
22	47.4	49.0	–	–	Similar inion height in both species.
23	225.0	–	–	–	Incomplete data.
24	124.6	–	–	–	Incomplete data.
25	38.0	69.2	+45.0	+45.0	Much taller snout in *C. quinni.*
26	–	–	–	–	No data.
27	–	–	–	–	No data.
28	47.8	50.6	+5.5	+5.5	Orbit slightly longer in *C. quinni.*
29	45.6	41.8	−8.3	−8.3	Orbit vertically shorter in *C. quinni.*
30	65.0	69.9	+7.0	+7.0	Nasal notch more incised in *C. quinni.*
31	128.0	139.5	+8.2	+8.2	Facial region longer in *C. quinni,* cf. **2.**
32	24.0	26.6	+9.7	+9.7	Longer POB in *C. quinni.*
33	48.3	49.2	–	–	DPOF length comparable.
34	38.7	45.5	+14.9	+14.9	IOF relatively more anterior in *C. quinni* or DPOF reaches farther posteriorly.
35	28.8	27.0	–	–	Height of DPOF comparable.
36	21.5	25.6	+16.0	+16.0	Facial crest farther below DPOF in *C. quinni.*
37	32.6	30.2	−7.3	−7.3	IOF nearer alveolus in *C. quinni.*
38	48.2	56.0	+7.3	+7.3	Mid-rear DPOF nearer alveolus in *C. goorisi.*
39	0/−	−3	–	–	Anterior tip of lacrimal at or slightly eroded by rear of DPOF in both.
40	23a	21.3	–	–	Medial depth DPOF comparable.

Gulch members. Thus, based both on dental and cranial morphology, the *Cormohipparion* seen in the Cornell Dam Member on one hand differs from *C. goorisi,* and on the other, is similar to *C. quinni* from the Crookston Bridge and Devil's Gulch members of the Valentine Formation.

Voorhies (1990) indicates that an adult cranium of *Neohipparion republicanus* (UNSM 84000) effectively duplicates the cranial and

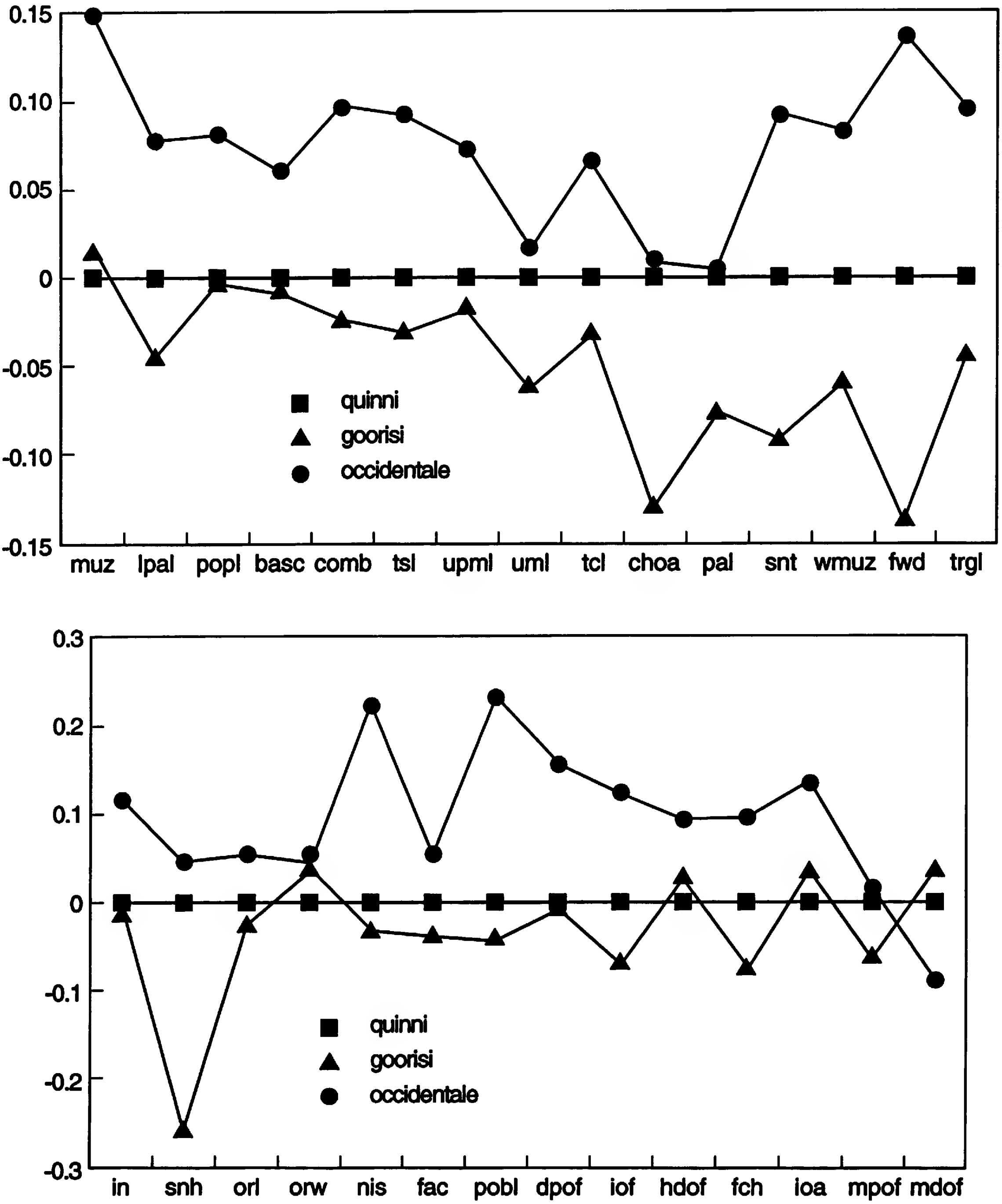

Fig. 16. Log-ratio diagrams of cranial dimensions of *Cormohipparion goorisi* and *C. occidentale* s.s. relative to *C. quinni.* Data based on tables 16 and 17. Note change in vertical scale between 16A and 16B.

dental morphologies shown by the type of *Merychippus republicanus* as described and figured by Osborn (1918: 125, fig. 99). As figured (Voorhies, 1990: fig. A-45), this specimen seems to have a better developed DPOF than in the type of *M. republicanus,* but that is attributed to crushing. Regardless of this, the IOF lies dorsal to P4 in both specimens which is one tooth position posterior to its location in all species of *Cormohipparion* (not preserved in *C. emsliei*; Hulbert, 1987), including USNM 352554. Voorhies (1990: A180) apparently is willing to utilize the presence or absence of the DPOF to aid in taxonomic segregation, but not variations in the morphology, degree of expression, and location of that feature, and bases his argument on partially described—but not illustrated—material from the Railway Quarry sample of the Valentine Formation. Pending further information, I rely on my own analysis of quarry-level samples of hipparionine horses to underwrite my assertion that the morphology and other attributes of the DPOF are stable and useful in taxonomic segregation (see also MacFadden, 1984, for other examples; but also Eisenmann et al., 1987, and MacFadden, 1987, for additional commentary).

In addition, a small number of isolated teeth have been allocated to this genus in AMNH collections from Norden Bridge Quarry in the Cornell Dam Member of the Valentine Formation. Brief comments on these specimens are made here.

P2 of F:AM 129211: The specimen is nearly 30 mm tall; protocone is barely separate from protoloph and would connect fully after about 7 mm additional wear, as shown by its broken anterior surface. The tooth likely would be about as tall as materials referred here to this species and taller than those referred to *C. goorisi.*

P3 of F:AM 108219: This is a worn specimen, about 28 mm tall, with a subovate, spurred protocone, plication count of 1.5.2.2, a bifid pli caballin and bifid pli hypostyle; pli protoconule well developed. The unworn height of this tooth would be much taller than predicted for *C. goorisi.*

M1 of F:AM 108219: This is a worn specimen, about 27 mm tall, with an ovate protocone, plication count of 1.2.2.1, single pli caballin, simple hypoconal groove, pli protoconule not markedly developed. The tooth seems to be simpler overall than is typical of teeth in this position in *Cormohipparion.*

M3 of F:AM 108221: The tooth is essentially unworn, 35 mm tall. It is consistent with referral to this species.

F:AM 108220 is a worn M3, 21 mm tall. It is possibly referable to this sample.

SUMMARY: The material from the Norden Bridge Quarry, Cornell Dam Member, of the Valentine Formation is here referred to the genus *Cormohipparion* and provisionally to the species *C. quinni.* USNM 84000 is here considered to pertain to *Cormohipparion ?quinni,* but other specimens assigned by Voorhies (1990) to *Neohipparion republicanus* are left allocated thereto.

Cormohipparion occidentale (Leidy, 1856)

This section briefly establishes a revised description of the morphology of *C. occidentale* to enable a comparison with *C. quinni* and other taxa.

TYPE SPECIMEN: ANSP 11287, four left upper cheek teeth and one right upper cheek tooth.

TYPE LOCALITY: Probably from along the Little White River, South Dakota.

AGE: Late Clarendonian.

DISTRIBUTION: From sites of late Barstovian to early Hemphillian age in California; early to late Clarendonian age in Texas, late Barstovian to possibly early Hemphillian in Nebraska, late Clarendonian in South Dakota and New Mexico (modified from MacFadden, 1984; see below).

DESCRIPTION OF TYPE SPECIMENS: As shown in Osborn (1918: fig. 140), the type of *C. occidentale* consists of five right upper cheek teeth, P2, P3, M2, another right upper molar (?M1) and left P3. Note that the four teeth from the right side are reversed as illustrated in Skinner and MacFadden (1977: fig. 4). Leidy (1869: 281, *in* Osborn, 1918: 176) notes that the teeth are "between a third and a half worn away." As taken from Osborn (1918: fig. 140), the right P2 is about 31 mm tall at the mesostyle; right P3 about 38 mm tall, and right M2 about 42 mm tall. Based on Leidy's (1869: 281) statement, these teeth would have been about 60 mm tall in the unworn condition, and this is borne out by study of other specimens of this species. The pattern in the type dentition is well developed, and shows that the protocone is an elongate oval, with a slightly convex lingual border in P2 and P3; the pli caballin is trifid (P2) to bifid (P3) and single in M2 and ?M1. The enamel pattern is complex, with plication formulae being 4.6.4.1 (right P2), 4.5.3.1 (right P3), 5.7.4.1 (left P3), and 4.6.5.1 (M2). Both M2 and ?M1 show an enlarged pli protoconule. The protocone width/length ratios are 0.43 (right P2); 0.31 (right P3); 0.29 (left P3); and 0.40 (right M2). The hypocone projects posteriorly in the premolars, more posterolingually in the molars.

Note that these specimens are in advanced stages of wear, but in actual mesostyle height are comparable to virtually unworn teeth at the same tooth position in *C. quinni.* Note also that the enamel complexity is significantly greater, and protocone width/length ratios significantly lower, than those aspects of the upper cheek tooth dental morphology of *C. quinni.* On the basis of these, and other specimens now under study by the author, a revised diagnosis for the species is presented below.

REVISED DIAGNOSIS: Entries in **boldface** show modifications from MacFadden (1984: 162). In comparison to *C. quinni*: "**Larger** and **more** hyposodont. Mean TRL 138.00 mm. Unworn or little worn M1MSTH ca. **60** mm (see also Hulbert, 1987: 462; 1988: 242). Protocones oval and **elongate**. Fossette borders more complex, **but not as complicated as in *C. emsliei***. DPOF with moderately developed (ca. 5 mm or less) posterior pocket. **Lacrimal well exposed but does not penetrate the rear of DPOF. POB wider.** In lower molars protostylids **better** developed, and sometimes isolated. Lower p2 metaconid and metastylid more strongly separated.

Comment on the allocation of the type material. An early result of the 1980 "*Hipparion* Conference" was the recognition that in the late Clarendonian sample from XMas Quarry, Nebraska, there were two morphotypes based on cranial parameters (Eisenmann et al., 1987; fig. 3) formerly attributed to *C. occidentale* (MacFadden, 1984). Parallel with those observations, I began compiling cranial and dental characteristics of quarry samples of late Barstovian and Clarendonian age from Texas to Nebraska, aided by R. L. Bernor, as well as volunteers in the AMNH. Some of the results of these studies were briefly summarized in Bernor et al. (1989). Others are added here (below). Fundamentally, the data suggest the presence of at least three morphologies subsumed within AMNH-F:AM specimens currently allocated as *C. occidentale* by MacFadden (1984). Finally, Whistler and Burbank (1992) have suggested that the North American regional FAD of the *C. occidentale* style of dental morphology is recorded in deposits that are calibrated (in California) and correlated (in Nebraska) to an age of about 12.7 Ma (using the Berggren et al., 1995, Magnetic Polarity Time Scale, revised from Cande and Kent, 1992). In correlated terms, then, the *C. occidentale* style of morphologies ranges in North America from about 12.7 to about 9 Ma (fig. 1).

With regard to allocation of type material of *C. occidentale,* the work in progress shows that of the two morphologies found in Hans Johnson, XMas-Kat, and correlative quarries in Nebraska, a congregation designated here as Type 1 is the most common (about 90%), largest, and dentally most complex of the groups of specimens contained in those quarries. Accordingly, the morphology shown by the type upper cheek teeth of *C. occidentale* is here taken provisionally as contained within Type 1 and all remarks below are based on specimens considered herein to pertain to that morphology. The following crania from XMas Quarry are used in developing the following remarks: F:AM 71800, 71801, 71803, 71806–71810, 71813, 71814, 71968.

CRANIUM: Tables 5, 17, and fig. 16 show that *Cormohipparion occidentale* from the XMas-Kat quarry, Merritt Dam Member, Ash Hollow Formation, Nebraska, differs from *C. quinni* in the following ways, using the dimension of the basicranium (**4**: basc) as a standard of comparison. As shown in figure 16, parameter **4** (basc) is about 13% larger in *C. occidentale* than in *C. quinni.* Thus, all parameters showing an increase of about that difference would be considered to represent a regular allometric increase in size. These parameters include: **7** (upml: upper premolar series length), **9** (tcl: total tooth row length, +14%), **25** (snh: snout height), **28** (orl: orbital length), **29** (orw: orbital height), **31** (fac: orbit to nasal notch length).

On the other hand, a number of parameters increase to a lesser extent than predicted if all increases were allometric. These include: **8** (uml: molar length). This means that premolar length increase (7 = 16%) influences the result in the dimensions of **9** (see above). Also in this class of dimension is **12** (choa; choanal fossa width), **13** pal: transverse width of palate), and **38** (mpof: height, rear of DPOF to alveolar border).

In most other instances, the dimensions for *C. occidentale* were significantly larger than those in *C. quinni*: **1** (muz: muzzle length), **5** (comb: combination of **3** and **4**), **6** (tsl: total skull length), **14** (snt: muzzle width at diastema), **15** (wmuz: muzzle width), **18** (fwd: frontal width), **19** (trgl: transverse width at rear of glenoid fossa), **20** (width of lambdoidal crest: not shown in figure 16 because not measurable in *C. goorisi*), **22** (in: height of occipital region), **30** (nis: nasal notch incision), **32** (pobl: length of POB), **33** (dpof: length of DPOF), **34** (iof: rear of DPOF to rear IOF), **35** (hdof: dorsoventral height of DPOF), **36** (fch: height between ventral border of DPOF and malar crest), **37** (ioa: rear, IOF to alveolar border).

A major difference between *C. quinni* and *C. occidentale* also is seen in the medially much shallower DPOF (**40**: mdof).

Thus, in comparison to *C. quinni, C. occidentale* differs in being proportionately and actually larger in length of premolar series (7), skull length (**14** and **15**); skull width at rear of orbit (**18**) and at glenoid fossa (**19**); width (**20**) and height (**21**) of occiput; retraction of nasal notch to above the anterior edge of P2 (**30**); length of POB (**32**) and DPOF (**33**), height of DPOF (**35**); height of DPOF above malar crest (**36**), and height of IOF above alveolar border (**37**). At the same time, most other dimensions that can be compared have either remained proportionately the same, or are reduced relative to the condition seen in *C. quinni*. Finally, even though the length of the DPOF in *C. occidentale* is increased over that seen in *C. quinni*, the posterior depth of its pocket reduced from nearly 15 mm (or about half the length of the POB) to about 5 mm (or about $\frac{1}{14}$ the length of the POB).

DENTITION: Based on specimens in XMas Quarry that are associated with crania, and thus can be determined to belong to Type 1 in that sample (to which the type of *C. occidentale* is herein assigned), the upper cheek tooth dentition of this species group (partly represented in figure 13A, from the Burge Member of the Valentine Formation) is comparable to that of the holotype in which fossette borders are substantially more complex than seen in *C. quinni*. In addition to being larger, the protocone is more elongate, commonly lingually concave, and unworn cheek tooth crown heights (parastyle) are in the range of 50–60 mm. The lower dentition differs from that in *C. quinni* in having more prominent and persistent protostylids and a more strongly developed metaconid, as distinct from the metastylid in p2.

Geochron of *Cormohipparion occidentale* group in North America. Based on dental evidence, Whistler and Burbank (1992) report that the LSD of *C. occidentale* in the Dove Spring Formation is at the base of the *Cupidinimums avawatzensis/Paracosoryx furlongi* Assemblage Zone and that its HSD lies just above the base of the *Paronychomys/O. diabloensis* Assemblage Zone. Utilizing the time-scale of Berggren et al. (1995), this interval is correlated herein on the basis of magnetic polarity stratigraphy to mid C5Ar.1n (ca. 12.7 Ma) to C4Ar.1r (ca. 9.0 Ma). In terms of the correlations used in this report, this range extends from latest Barstovian to latest Clarendonian (note that Whistler and Burbank [1992] correlate this interval as early Clarendonian to early Hemphillian). As shown in figure 1, rock and faunal units in Nebraska and Texas that contain specimens of the *C. occidentale* group also display the time-range shown in the Dove Spring Formation. Thus, the *C. occidentale* group has a duration of about 3.7 m.y., in contrast to the sojourn of about 1 m.y. for *C. quinni*.

Trends in late Barstovian and Clarendonian samples of *Cormohipparion*. Most of the trends seen in the progression from *C. goorisi* to *C. occidentale* involve increase in the size of the cranium anterior to the braincase, along with some increase in occipital height and transfrontal width of the skull. A notable decrease, however, is in the degree of posterior pocketing of the DPOF, regardless of a general increase in length of the POB and DPOF, itself. Thus, the loss in pocketing of the DPOF can be viewed (as here) as part of the general trend for reduction of the DPOF seen in later species of the *Cormohipparion* complex, especially *C. ingenuum, C. plicatile* and *C. emsliei* of Hemphillian to Blancan age. At the same time, the cheek tooth dentition generally became increasingly complex in at least one of these species (e.g., Hulbert, 1987) such that *C. emsliei* came to resemble the geologically much older Old World taxon, *Hippotherium primigenium,* in complexity of fossette borders of the upper cheek teeth (*C. emsliei* is derived at least in having lost the DPOF).

Origin of the Old World Vallesian taxon *Hippotherium primigenium.* As summarized in Woodburne and Bernor (1980), Woodburne (1989), and Bernor et al. (1989), the early Vallesian immigrant, *Hippotherium primigenium,* typified by the sample at Höwenegg, southwestern Germany, can be characterized as a hipparionine equid with the following cranial and dental morphology: This is a large-size hipparionine horse; TRL is 154–170 mm (as compared to about 124 and 145 in *C. quinni* and *C. occidentale,* respectively). All of the "*Hipparion* Conference" parameters have not been published for the Höwenegg taxon, but the snout length (#1) is 112 versus 76 and 106; POB length is 44–51 versus 26 and 45; POF length is 84–88 versus 49 and 70; depth of posterior pocket of POF is ca. 5 versus 15 and 5; upper cheek tooth enamel is more complex than any North American hipparionine (approached only in the late Hemphillian to Blancan *C. emsliei*; Hulbert, 1987). At the same time unworn MSTH is 55–60 mm (Woodburne et al., 1981: 517), in comparison with ca. 45 and 55–60, respectively. In most parameters discussed here, *H. primigenium* appears to have been most like *C. occidentale* s.s., but at between 9–10 m.y. old (fig. 1 and Tedford et al., 1987) the XMas Quarry sample appears to be too young to have been directly involved with the ancestry of the Old World immigrant. Ongoing studies on geologically older samples of the *Cormohipparion occidentale* group will hopefully shed additional light on this topic.

Merychippus sphenodus (Cope, 1899)

Hippotherium sphenodus (Cope, 1889: 449, no figure.

Merychippus sphenodus (Cope) 1899; Osborn, 1918: 112 (in part).

Cormohipparion sphenodus Woodburne, MacFadden, and Skinner, 1981: 503 (in part).

TYPE SPECIMEN. Cope (1889) did not designate a type for this species. That was done by Osborn (1918: 112) who designated AMNH 8281, right P2, Pawnee Creek beds, Colorado, as the lectotype and AMNH 8281, left P3 as "co-type." Osborn also designated PU 12291, from the Pawnee Creek beds, as a "neotype." Woodburne et al. (1981) followed Osborn's lectotype designation, but not his co-type or neotype.

Both Osborn (1918) and Woodburne et al. (1981) variously allocated a number of specimens from Colorado, Nebraska, New Mexico, and California to *Cormohipparion sphenodus,* based on a combination of cranial and dental criteria. This is reviewed here, with the result that the nomen *sphenodus* is restricted to the type and some referred material from the Pawnee Creek beds of Colorado. The species *sphenodus* is provisionally retained in the genus *Merychippus.*

TYPE LOCALITY: Pawnee Buttes, northeastern Colorado, most likely from the Pawnee Quarry level (Eubanks Local Fauna), tentatively calibrated as between 14.8 and 14.4 Ma.

DISTRIBUTION: Early Barstovian of Colorado (Tedford et al., 1987: 200).

REVISED DESCRIPTION: The type and referred P3 show that this equine has relatively hypsodont dentition, likely 33–36 mm tall (based on specimens from Horse and Mastodon Quarry, F:AM 125920, 125931); protocone is subcircular and still isolated from the protoloph at about medial wear (ca. 17 mm in AMNH 8281); opposing borders of the pre- and postfossettes are moderately complexly crenulated. The plication count for P2 is ?.3.4.?; for P3 it is 1.5.5.2. The metaloph is relatively linear with the hypocone not sharply demarcated; the hypoconal groove thus is oriented posterolingually and (in P2) bears one plication; the hypoconal fossette is remnant in P2; the adjacent part of hypostyle projects lingually such that the hypoconal groove exits virtually on the lingual side of the tooth (both specimens); in P3 the protocone still shows a remnant spur. Both teeth have bifid plis caballins; the P3 both are directed posterolingually. P3 has a hypoconal spur.

Note that the line drawing of P2 in Osborn (1918: Pl. 15.2) is a little misleading in the degree to which the presence of a spur is suggested on the protocone, and the single, rather than double, pli caballin (see fig. 17 herein). The crochet does connect to the protoloph, as well as the prefossette, in contrast to the figure by S. Oka (Osborn, 1918: fig. 87). This is very different from the clear separation between the protoloph and metaloph in comparably worn P2s in, for example *M. insignis*. A new drawing made for this study (fig. 17) shows that the crochet was complete, the hypoconal groove had a spurred margin, and a hypoconal fossette was present. The anterior part of the prefossette is difficult to see.

As discussed above (Stratigraphic Framework) specimens from both Pawnee Quarry and Horse and Mastodon Quarry (fig. 7A) were compared with the type of *M. sphenodus*, with the best match both in morphology and in preservation being found in F:AM 129215 (right M1), and F:AM 129214 (right P4) from Pawnee Quarry; F:AM 129213 (right P2–M3) from West Quarry, and F:AM 129212 (right P2–M2) from 3 Points, E. Valley #1, W. Side of High Pit. The stratigraphic position of these quarries is shown in figure 7. No cranial elements were preserved in the material from known quarries, but an unallocated specimen from the Pawnee Creek Formation (F:AM 129216) preserved an IOF located above the P4/M1 boundary and a DPOF that was well developed above the IOF. The analysis was hampered by many specimens from Pawnee Fm. quarries being too strongly worn, or of obviously different morphology. Nevertheless a reasonable "match" with the type of *M. sphenodus* was achieved, and future work might identify a plausible hypodigm for this species in specimens from the lower part of the Pawnee Creek Fm.

A search was also made of the isolated teeth as well as crania from the Horse and Mastodon Quarry in the AMNH collections. Several teeth were found that resembled the above morphology, but no single tooth duplicated all aspects. Whereas many of the crania and cranial fragments in this suite of specimens differed dentally from the combination features cited above, two specimens (F:AM 125920 and 125921, both partial palates) have dentitions sufficiently close to the type and P3 to be potentially referable to *M. sphenodus*. In the comparison, emphasis was placed on the protocone being isolated and dental pattern still complex in late wear, the hypostylar area projecting lingually, and the hypoconal groove having a lingual exit, and a hypostylar plication present. At the same time, however, these Colorado specimens differed from the type of *M. sphenodus* in having less prominent plis caballins, and in having generally simpler fossettes. In F:AM 125921, the IOF is located above the M1/P4 boundary, and the ventral border of a DPOF can be seen above that; the DPOF extended from at least a position above about M1 to part of P2. This morphology is restricted to *Merychippus* s.s. as used herein. This comparison is taken as persuasive, but not conclusive, evidence that the type material of *M. sphenodus* is likely to be referable as a species of *Merychippus* s.s. Whereas cranial materials from Horse and Mastodon Quarry appear to represent merychippines, as well as other equines potentially, none was found that could be allocated to *Cormohipparion*.

Distinction between *Merychippus sphenodus* and *Cormohipparion*. Based on material studied for this report, *Merychippus sphenodus* s.s. differs from *Cormohipparion quinni* in having persistently spurred protocones in P3 as late as about 50% wear. Even at this stage of wear, a prominent pli protoconule is a hallmark of *Cormohipparion* species, not shown in *M. sphenodus*. Also, the teeth of *M. sphenodus* are more strongly curved as compared with *C. quinni* and are considered to have been 6–22% lower crowned in the unworn condition. Also, the teeth of *M. sphenodus* show the generally plesiomophic condition (not shown in *C. quinni*) in which the roots below the protocone and hypocone project strongly lingually. The association with dentitions of this kind of morphology with

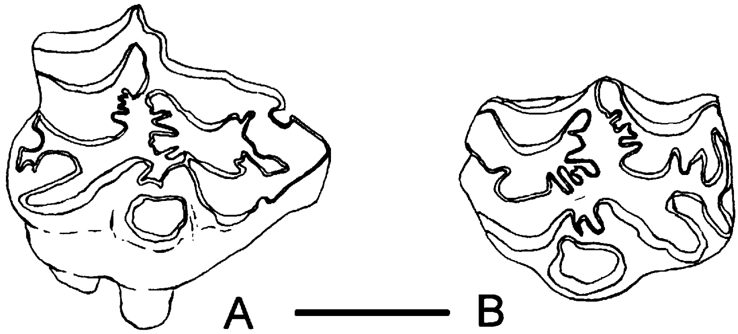

Fig. 17. *Merychippus sphenodus.* **(A)** Type, AMNH 8281, right P2. **(B)** Paratype, left P3. Camera lucida drawings from original specimens. Bar = one centimeter.

crania (above) that show the retraction of the IOF to above P4 or M1 is an important difference from species of *Cormohipparion.* There, the IOF retains its plesiomorphic location above P3. Further, the IOF is closely associated with the anterior tip of the DPOF in *Cormohipparion,* reflective of its considerable length, rather than projecting much less anteriorly in specimens assigned by this author to *Merychippus* s.s. Even if the dentition of *M. sphenodus* cannot be associated conclusively with specimens having the merychippine cranial morphology discussed above, Cope's type material is sufficiently different dentally as to preclude assignment to a species of *Cormohipparion.*

CONCLUSIONS

Cormohipparion goorisi, from the early Barstovian of the Gulf Coastal Plain, is the geologically oldest species of the genus, and appears to be morphologically the most plesiomorphic, especially as regards the evolutionary stage of its dentition. Salient features in this regard include the retention of a robust and relatively complex dP1, the retention of a relatively mesodont height of its cheek tooth dentition, and the incomplete separation of metaconid and metastylid on p2. As detailed below, *C. goorisi* is more derived from its nearest out-group taxon, *Merychippus insignis,* and appears to be the sister taxon of a clade composed of both *C. quinni* and *C. occidentale* s.s.

Woodburne (unpublished) developed an appraisal of *C. goorisi* and its nominal sister taxon, *Merychippus insignis.* Based on that review, as well as upon tables 5 and 16, and figure 16 of the present report, and upon MacFadden and Skinner (1981) and MacFadden (1984) *Cormohipparion goorisi* can be characterized on the basis of its hypodigm from Trinity River Pit 1 as being of relatively small size; having a short muzzle; nasal notch retracted to a position about midway between C1 and P2; relatively wide POB (e.g., 24 mm); DPOF distinctly expressed with strongly defined anterior, dorsal, posterior, and ventral borders; DPOF strongly pocketed posteriorly (virtually to a position opposite the anterior edge of the orbit), but its facial expression is relatively short (ca. 48 mm) in comparison to the cheek tooth row length (ca. 116 mm); IOF is located above the P3/P4 boundary, at or very close to the anteroventral rim of the DPOF; lacrimal is dorsoventrally narrow anteriorly and reaches the rear of the DPOF; dP1 is persistently large (ca. 10 mm long, but shorter than in *M. insignis*), two rooted, and present into old age; upper cheek teeth are hyposodont (taller than in *M. insignis,* ca. 26–34 mm tall at the mesostyle in the unworn condition versus 22–25 mm for *M. insignis*); protocone is isolated from the protoloph in P2 except in late wear, as in the other cheek teeth; fossette borders are relatively complex in the upper half of the cheek tooth crown, with as many as six (but usually four) plications on the opposing faces of the pre and post-fossettes; pli prefossette loop usually conspicuously large and bifid posterolingually; protocones virtually uniformly not spurred; those of P2 are nearly circular, whereas those of the other premolars and molars are more elongate; hypoconal groove

TABLE 17

Cranial Parameter Comparisons, *C. quinni* vs. *C. occidentale* (Merritt Dam Mbr.)

Abbreviations as in table 16. % adj. uses value for *C. occidentale* × .8686, which equalizes basicranial length (number **4**) in both samples. C. occ. = *C. occidentale.*

MN	C. quin.	C. occ.	% diff.	% adj.	Remarks
1	75.5	106.0	+28.7	+18.0	Muzzle actually and relatively longer.
2	92.9	111.3	+16.5	+3.4	Palate only slightly longer relatively.
3	78.8	95.0	+17.1	+4.4	Post-palatal length relatively slightly greater.
4	73.4	84.5	+13.1	—	Basicranium actually longer.
5	147.5	184.2	+19.9	+7.8	Combined 3 + 4 longer.
6	315.8	391.6	+19.4	+7.1	Longer total cranial length.
7	67.1	79.5	+15.6	+2.3	Relatively similar upper premolar length.
8	64.1	66.7	+3.8	−9.6	Relatively shorter upper molar series.
9	124.1	145.0	+14.4	+1.2	Relative upper cheek tooth series nearly comparable.
10	—	49.1	—	—	Incomplete data.
11	—	25.8	—	—	Incomplete data.
12	32.3	33.1	+2.4	−1.1	Relatively narrower choanae.
13	54.3	55.1	+1.5	−11.7	Relatively much narrower palate.
14	26.7	33.2	+19.6	+7.2	Snout wider at diastema.
15	41.0	49.8	+17.6	+5.3	Muzzle slightly wider relatively.
16	—	70.2	—	—	Incomplete data.
17	—	121.9	—	—	Incomplete data.
18	96.0	132.0	+27.3	+16.3	Greater frontal width.
19	112.0	139.7	+19.8	+7.7	Greater trans-glenoid width.
20	38.7	58.8	+34.2	+24.3	Greater occipital width.
21	—	91.8	—	—	Incomplete data.
22	49.0	63.9	+23.3	+11.7	Taller inion.
23	—	306.7	—	—	Incomplete data.
24	—	—	—	—	No data.
25	69.2	77.8	+11.1	−2.3	Snout relatively about same height.
26	—	82.9	—	—	Incomplete data.
27	—	11.6	—	—	Incomplete data.
28	50.6	57.3	+11.7	−1.6	Relatively same orbit length.
29	41.8	46.6	+10.3	−3.1	Relatively same orbit height.
30	69.9	116.7	+40.1	+31.1	Nasal notch more greatly incised.
31	139.5	157.9	+11.6	−1.6	Facial length relatively similar; cf. **2**.
32	26.6	45.1	+41.0	+32.1	POB distinctly longer.
33	49.2	70.4	+44.3	+19.5	DPOF distinctly longer.
34	45.5	60.4	+24.7	+13.3	IOF relatively more anterior, or rear of DPOF more posterior.
35	27.0	33.5	+25.4	+7.2	Slightly taller DPOF, relatively.
36	25.6	31.9	+19.7	+7.6	DPOF situated higher relative to alveolus.
37	30.2	41.4	+27.0	+16.1	IOF higher relative to alveolus.
38	56.0	58.0	+3.4	−10.5	Mid-rear DPOF nearer alveolus, relatively.
39	−3	17.0	+	+	Much longer POB; cf. **32**.
40	21.3	17.3	−18.7	−29.5	Much shallower DPOF.

commonly lacks plications; metaconids and metastylids are subequal in size and mostly have rounded outlines and are separated by shallow, U-shaped linguaflexids; premolar ectoflexids virtually never penetrate the metaconid/metastylid isthmuses and maintain a position at or labial to the pre- or postflexid throughout wear; protostylids are developed on p3–m1 in later wear and are usually little more than an angulate bend in the enamel at the pertinent part of the tooth; mandibular rami have short symphyses and become markedly shallower in depth from the anterior end of m3 to p2.

In comparison with its likely nearest outgroup taxon, *Merychippus insignis, Cormohipparion goorisi* appears to be more derived in all of the above-mentioned traits. Dp1 is not preserved in the lower cheek tooth dentition of *C. goorisi,* however.

Although a number of intervening steps are indicated by Hulbert and MacFadden (1991), the changes involved in comparing *M. insignis* to *C. goorisi* appear to involve modifications that result in a taxon with a somewhat shorter basicranium, narrower skull overall, shorter DPOF, as well as being proportionately larger in cheektooth length, having a longer preorbital region of face, longer muzzle, longer POB, and a more deeply pocketed DPOF. In addition, *C. goorisi* has a much more hypsodont and complex cheek tooth dentition, a lower jaw that is more attenuated anteriorly, and a lower cheek tooth dentition in which the premolar ectoflexids penetrate the metaconid/metastylid isthmus, and develop protostylids on p3–m3 only in later wear.

Based on the foregoing, *C. goorisi* is strongly different, both cranially as well as dentally, from *Merychippus insignis.* If each species can be said to stand at the base of their respective clades, then it seems clear that the generic-rank taxa which they each represent are phyletically separate, and that neither was the ancestor of the other.

C. goorisi, C. quinni and a restricted example of *C. occidentale* have been diagnosed above. Contrary to Woodburne et al. (1981) and MacFadden (1984), the lacrimal in *C. goorisi* resembles that of *C. quinni* in reaching, and being eroded by, the rear of the DPOF. The sutures of the jugal and lacrimal bones also are similarly configured in the two species (contra Hulbert, 1988).

C. goorisi appears to be the sister taxon of a clade that contains *C. quinni* and *C. occidentale.* The fundamental reason for this proposal is the hypertrophy of the DPOF and its posterior extension (pocket) to a point medial to the anterior edge of the orbit. In *C. quinni,* the posterior pocket of the DPOF extends to only about ½ the distance between the rear of the DPOF and the anterior edge of the orbit, and in *C. occidentale,* the pocket is even further reduced. At the same time both of these species are substantially larger, more hypsodont, have upper cheek teeth with considerably more complex enamel patterns, and p2 metaconids and metastylids much better developed than in *C. goorisi.* Not only within *Cormohipparion,* but also in comparison to all Barstovian equines, *C. goorisi* is unique in the degree to which the posterior pocket of the DPOF is developed.

In summary, *Cormohipparion* (exclusive of the subgenus, *Notiocradohipparion*) consists of three species, *C. goorisi* (early Barstovian, Texas), *C. quinni* (late Barstovian, Nebraska and Colorado), and *C. occidentale* (restricted, herein, to specimens from the late Clarenodian XMas-Kat quarry, Nebraska). Skinner and MacFadden (1977) refer other materials to *C. occidentale* s.l., and these are herein taken as representing the *C. occidentale* group. Eisenmann et al. (1987) suggests that late Clarendonian samples of *C. occidentale* s.l. contain two cranial morphologies. This report makes a similar conclusion, but includes F:AM 71800 and F:AM 71806 within the main group, rather than outside of it. Information recently presented by Whistler and Burbank (1992) shows that the *Cormohipparion occidentale* species group ranges in age from about 12.7 to 9 Ma. Although it is a likely source for the Old World "*Hipparion*" Datum, it appears that late Clarendonian *Cormohipparion occidentale* s.s. is differently derived and too late in time to have been that source, and other candidates must be sought in the North American record. Based on the definition of the genus presented here, *Cormohipparion goorisi* is retained as a member of this genus and is considered to be the sister taxon of a clade that includes *C. quinni* and *C. occidentale.*

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