# PHYLETIC DIVERSIFICATION OF THE *CORMOHIPPARION OCCIDENTALE* COMPLEX (MAMMALIA; PERISSODACTYLA, EQUIDAE), LATE MIOCENE, NORTH AMERICA, AND THE ORIGIN OF THE OLD WORLD *HIPPOTHERIUM* DATUM

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# ABSTRACT

Study of the materials in the American Museum of Natural History that pertain to the taxon *Cormohipparion occidentale* Skinner and MacFadden (1977) reveals that at least six species are represented. This is based on data from the cranium, upper dentition, lower dentition, and mandible. The taxa embrace a period of time from about 12.5 Ma to 10 Ma. Major sites or faunas include the Dove Spring Formation (medial Clarendonian, California; Burge Local Fauna (early Clarendonian, Nebraska); Minnechaduza Fauna, Nebraska; MacAdams Quarry, Texas (early medial Clarendonian); Gidley Horse Quarry (late medial Clarendonian, Texas); XMas-Kat, Hans Johnson, and Machaerodus quarries (late medial Clarendonian, Nebraska); and Ash Hollow Formation (late medial Clarendonian, South Dakota). The name *Cormohipparion occidentale* is restricted to the larger of two species that occur contemporaneously in medial Clarendonian sites in Nebraska and, alone, at the Ed Ross Ranch Quarry, South Dakota. The second species in the XMas-Kat and related quarries is assigned to *Cormohipparion matthewi*, n.sp. A taxon from the Burge Local Fauna is assigned to *Cormohipparion merriami*, n.sp. Another taxon from the Burge Local Fauna is assigned to *Cormohipparion johnsoni*, n.sp. Materials from the Texas sites are allocated as *Cormohipparion fricki*, n.sp., and *Cormohipparion skinneri*, n.sp., from the MacAdams Quarry and Gidley Horse Quarry, respectively. *Cormohipparion fricki*, n.sp., also is represented in the Minnechaduza Fauna, Nebraska. *Cormohipparion* is restricted geographically to North America.

Based on this review, *Cormohipparion johnsoni*, n.sp., is the most plesiomorphic species of the *C. occidentale* group of taxa. *Cormohipparion quinni* is a plausible ancestor (sister-taxon) for the *C. occidentale* group, but also persisted with it until about 12 Ma. During their radiation, elements of the *C. occidentale* group demonstrate an increase in upper cheek tooth crown height and complexity of the enamel pattern, as well as an increase in overall cranial size, with each species showing its own mosaic of parameters. The interval of 12.5–10 m.y. witnessed the initiation of a period of climatic cooling and an eventual expansion of vegetation communities toward more open associations, in part showing an increase in grassy areas. Apparently, the *C. occidentale* group developed and maintained a mixed-feeding adaptation to these conditions, even though it had evolved very hypsodont cheek teeth by about 10 Ma (*C. occidentale*, *s.s.*; *C. skinneri*, n.sp.).

*Cormohipparion johnsoni*, n.sp., and *C. merriami*, n.sp., are followed by *C. fricki*, n.sp., at about 12–11.5 Ma, which demonstrates an increased crown height and complexity of the upper cheek teeth along with the persistence of a functional dP1 into the adult condition. At least in *C. fricki*, n.sp., and likely also *C. merriami*, n.sp., the pre- and postfossettes of P2 commonly were confluent. All of these features are to be found in early Pannonian C members of *Hippotherium* of the Old World, and it is likely that a taxon such as *C. fricki*, n.sp., was associated with the Old World dispersal event that resulted in the presence of *H. primigenium*. A specimen of *Cormohipparion* sp. from deposits about 12 Ma old in California shows the proper morphology (enhanced by a significant increase in fossette complexity) to be a possible member of the dispersal population prior to its exit to the Old World at about 11 Ma.

Subsequent North American species of the *Cormohipparion occidentale* group lived from about 11 Ma to 10 Ma and convergently approach (but do not equal) the enamel pattern complexity found in *Hippotherium primigenium* but surpass it in upper cheek tooth crown height, in the almost complete loss of dP1, and in a diminished frequency of confluence of the pre- and postfossetttes in P2. Two of these species, *C. occidentale*, *s.s.*, and *C. skinneri*, n.sp., apparently populated a more northern (Great Plains) versus a southern (Texan) district, with *C. occidentale*, *s.s.*, being sympatric with the (?secondarily) smaller *C. matthewi*, n.sp. The sample of *C. occidentale*, *s.s.*, from the XMas-Kat quarries of Nebraska differs somewhat in a few cranial and dental parameters from samples from the Machaerodus and Hans Johnson quarries. Whereas the material from the XMas-Kat and Machaerodus quarries seems contemporaneous on geological grounds, the age of the sample from the Hans Johnson Quarry is not as securely dated. It is possible that the cranial differences (mainly the size of the preorbital fossa) and dental parameters (the persistence of a small and apparently functionally insignificant dP1 in adult female, but not male, crania) are variations in a contemporaneous but somewhat polymorphic population. Alternatively, it is possible that the Hans Johnson sample, at least, may be chronologically somewhat older than that from the XMas-Kat quarries and that the morphological differences represent in part a more plesiomorphic condition for its specimens.

## INTRODUCTION

The rich collection of Neogene Equidae in the collections of the American Museum of Natural History has long contributed to the understanding of the evolution of the group. The purpose of the present study is to consider the taxonomy of samples from a number of sites in North America that yield material referred by MacFadden (1984) to *Cormohipparion occidentale*. At least six species are considered here to be contained within the extended sample. The material ranges temporally and geographically from the early Clarendonian of California and Nebraska to the medial Clarendonian of Nebraska, South Dakota, Texas, and California. All but the California material is composed of associated crania, upper dentitions, and, sometimes, lower mandibles and dentitions, and virtually all of the Texas and Nebraska and South Dakota specimens are contained in the Frick: American Mammals collection of the American Museum of Natural History.

An early Clarendonian form from the Burge Local Fauna (figs. 1–2) is assigned to *Cormohipparion johnsoni*, n.sp., and is considered the most plesiomorphic species of the *C. occidentale* group. A contemporaneous sample from the early Clarendonian Burge Local Fauna, Nebraska, is assigned to *Cormohipparion merriami*, n.sp. Specimens from the early medial Clarendonian MacAdams Quarry of Texas are assigned to *Cormohipparion fricki*, n.sp. The name *Cormohipparion skinneri*, n.sp., is proposed for the medial Clarendonian sample from the Gidley Horse Quarry, Texas. *Cormohipparion occidentale* is reserved for the larger of two species from the medial Clarendonian XMas-Kat and contemporaneous quarries of Nebraska and South Dakota, whereas the smaller species from the Nebraskan sites is nominated as *Cormohipparion matthewi*, n.sp.

All species of *Cormohipparion* treated here can be distinguished on a combination of cranial and dental criteria. However, both *C. occidentale*, *s.s.*, and *C. matthewi*, n.sp., show different morphologic subsets of each species' morphology, especially when dental material from the XMas-Kat quarries is compared with that from Hans Johnson and Machaerodus quarries. Whereas this compounds difficulties in species definition, it also suggests that these effectively contemporaneous medial Clarendonian quarries are sampling different parts of the overall population morphology of two equid species.

It is well known (e.g., Woodburne and Swisher, 1995: 349) that a member of *Cormohipparion s.l.* dispersed to the Old World about 11 Ma and formed there the basis for the radiation of hipparionine equids. This prochoresis event is termed the "*Hipparion*" or *Hippotherium* Datum. Evidence reviewed here suggests that *C. fricki*, n.sp., may be the most likely North American source for that dispersal event. Strict application of cladistic principles could require that a monophyletic taxon known as *Cormohipparion* include *Hippotherium* in order not to be paraphyletic. Were that done, *Hippotherium* Meyer 1829 is the senior synonym in comparison to *Cormohipparion* Skinner and MacFadden 1977. The present author refrains from pursuing that step until the phyletic relationships between *Hippotherium* and other Old World hipparionine taxa, such as *Sivalhippus*; *Hipparion*, *s.s.*; *Cremohipparion*; and so on, are clarified. In addition, it appears from the present study that the type material of *Hippotherium primigenium* from Eppelsheim, Germany, may pertain to a different species from the geologically oldest members of this genus, preserved in sites of Pannonian C age, in Austria. This aspect of the taxonomy of *Hippotherium* also requires resolution.

## ABBREVIATIONS AND DEFINITIONS

### Institutional Abbreviations

| | |
|---|---|
| AMNH | Department of Vertebrate Paleontology, American Museum of Natural History, New York. |
| ANSP | Academy of Natural Sciences, Philadelphia. |
| CIT | California Institute of Technology, Pasadena. |
| F:AM | Frick: American Mammals in the AMNH collections. |

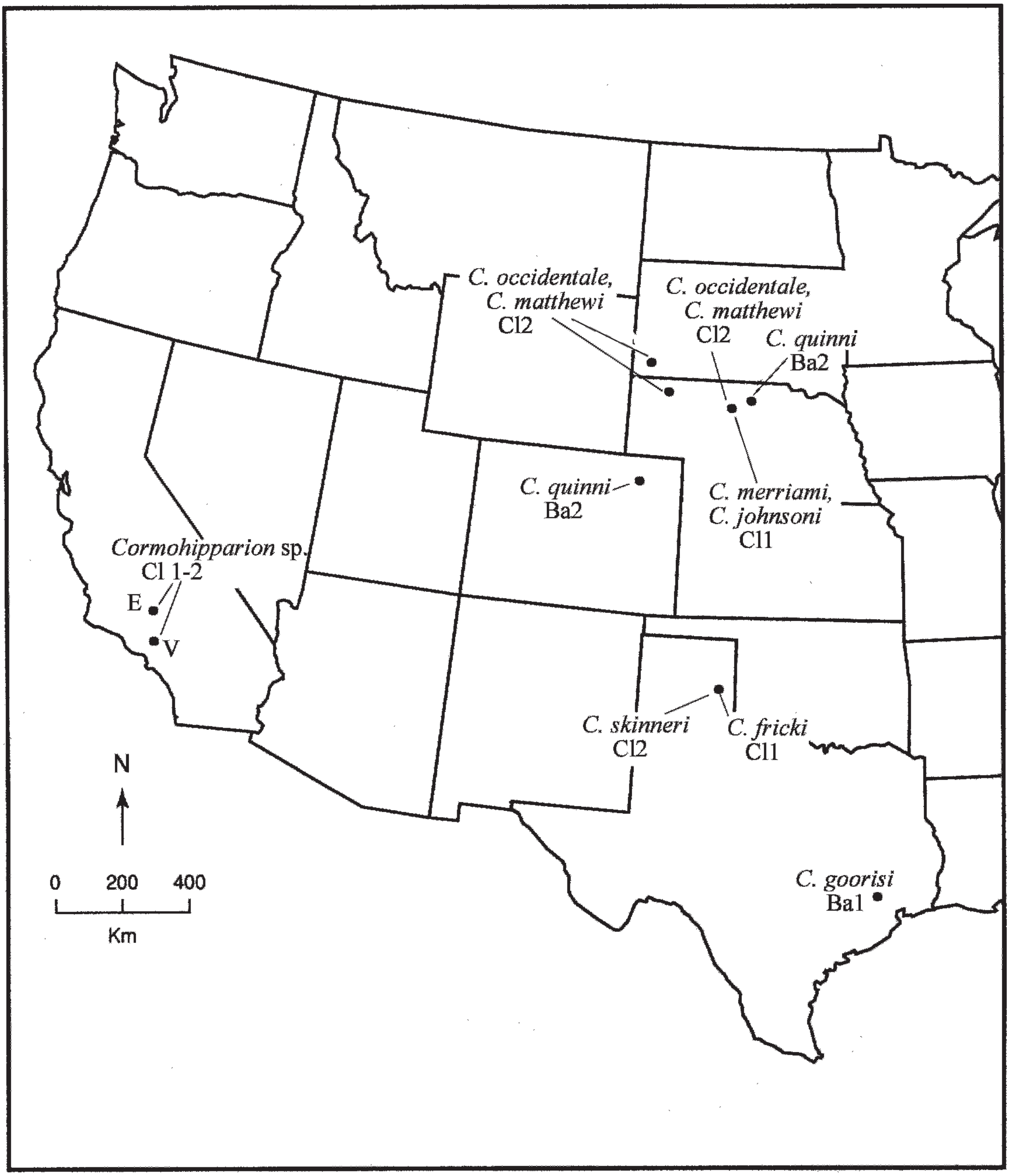


Fig. 1. Selected North American sites (and age) yielding species of *Cormohipparion*. In California, E = El Paso Basin; V = Valyermo, Devil's Punchbowl.

| | |
|---|---|
| HLMD | Hessisches Landesmuseum, Darmstadt, Germany. |
| LACM | Natural History Museum, Los Angeles County. CIT materials are now housed in this institution. |
| PIUW | Paläontologisches Institut Universität Wien, Vienna, Austria. |
| SENK | Senckenberg Museum, Frankfurt, Germany. |
| UCMP | University of California Museum of Paleontology, Berkeley. |

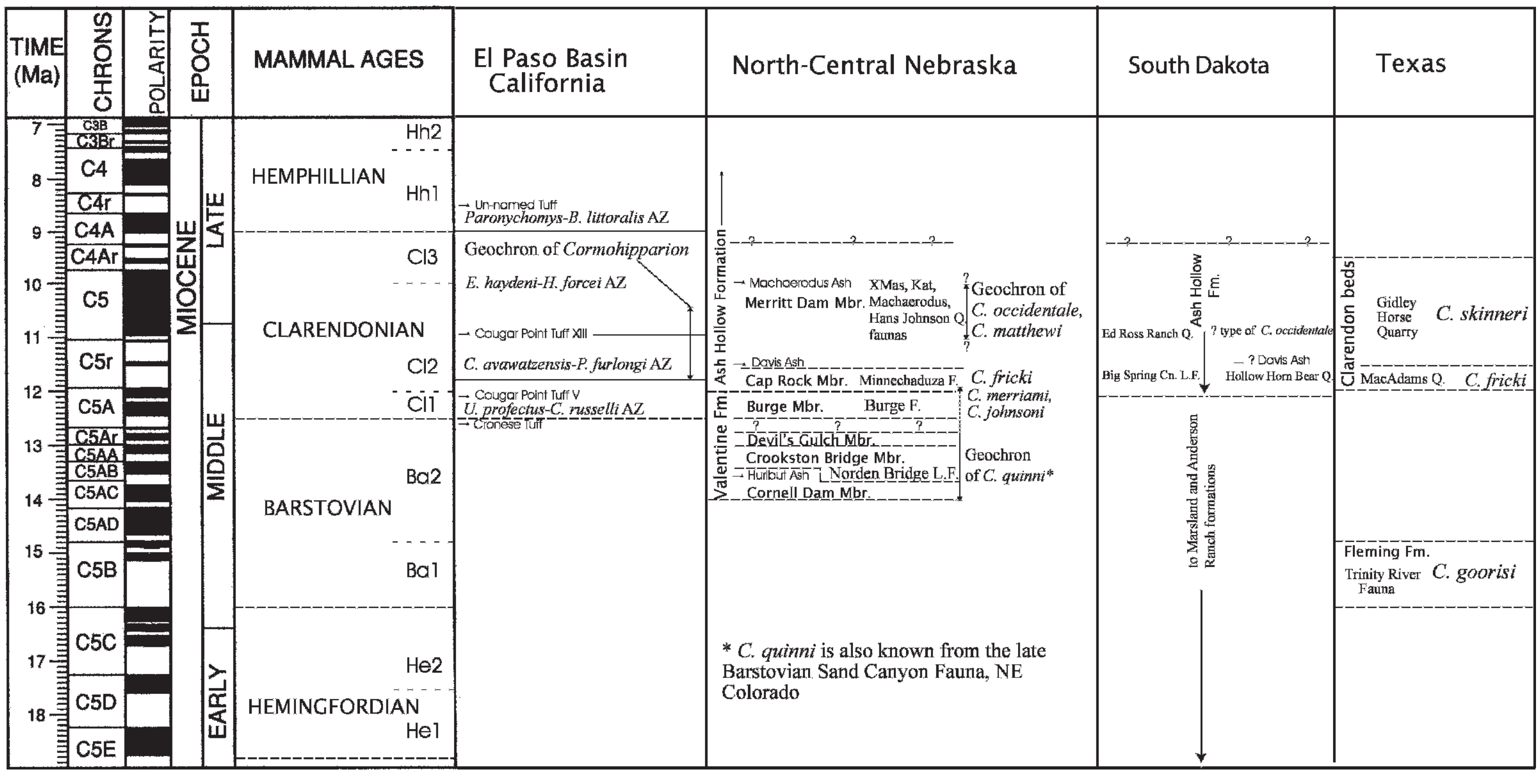


Fig. 2. Stratigraphic distribution of species of *Cormohipparion* in North America. Paleogmagnetic scale after Berggren et al. (1995). Mammal ages after Woodburne (2004b). Calibrations of specific mammal-bearing units are discussed in the text.

UF — University of Florida Museum of Natural History, Gainesville.

UNSM — University of Nebraska State Museum, Lincoln.

## Morphological Conventions

DPOF — Dorsal preorbital fossa is a general term for either the lacrimal or nasomaxillary fossa, or both, on the side of the face anterior to the orbit. It does not distinguish explicitly between LAF and NMF (see below); after MacFadden, 1984.

IOF — Infraorbital foramen.

LAF — Lacrimal fossa. The posterior portion of the DPOF when two fossae can be distinguished (fig. 5C). Occurs primarily on the lacrimal but may be expressed partially on the adjacent nasal and maxillary bones.

MSTHT — Mesostyle height of upper cheek teeth (after MacFadden, 1984; fig. 5C). For example, M1MSTHT = mesostyle height of M1.

NMF — Nasomaxillary preorbital fossa. The portion of the DPOF anterior to the lacrimal bone (fig. 5C). This is the DPOF of most taxa.

POB — Preorbital bar, or the space on the face between the orbit and the DPOF.

Protostylid. Angulate pattern formed at the anterior margin of the protolophid as a consequence of the anterior cingulum rising labially to reach the occlusal surface (= parastylid or ectoparastylid of authors). In the derived condition, a blade-like structure may be developed from the anterior cingulum which, when worn, forms a linear, labially directed spur at the anterolabial corner of the lower cheek tooth. In derived taxa, the structure may appear in the form of an isolated enamel lake.

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

p, m — Lower premolars and molars.

P, M — Upper premolars and molars.

Sex determination. MacFadden (1984: 39, fig. 11) indicates that female hipparionine equids possess significantly smaller C1s than do males of the same species, and this observation appears to be valid for the specimens analyzed in the present report. Reference to sex in these specimens (text and tables) follows this methodology.

## Chronological and Operational Terms

*C. occidentale* group. A general term for specimens referred to as *Cormohipparion occidentale* in previous literature and to taxa with the morphology collectively seen in samples herein referred to as *C. occidentale*, *C. matthewi*, n.sp., *C. merriami*, n.sp., *C. johnsoni*, n.sp., *C. fricki*, n.sp., and *C. skinneri*, n.sp.

FAD — First Appearance Datum. This is a change "… in the fossil record with extraordinary geographical limits" (Berggren and Van Couvering, 1974: IX). As a chronostratigraphic concept, a FAD expresses an interpretation that the first stratigraphic appearance of a taxon is likely to have been synchronous over a specified geographic region (e.g., Woodburne, 1996a). The origin for a FAD (= appearance) was not constrained by Berggren and Van Couvering (1974, 1978), except that the dispersing taxon would have been "newly evolved". For the paleobiotic event to be of "extraordinary geographical limits", dispersal of an organism at a major scale clearly is the primary consideration, presumably from an indigenous source at some location; see also Woodburne (2004a).

Fauna An assemblage of fossil vertebrates of specific taxonomic composition obtained from a small number of geographically diverse sites considered to have a limited temporal range (Tedford, 1970; Woodburne, 1987: xiv; Woodburne 2004a: xii).

*Hippotherium.* This generic-rank taxon is based on the genotypic species *Hippotherium primigenium* Meyer 1829, from the (Vallesian) Dinotherium Sands at Eppelsheim, Germany.

*Hippotherium* Datum. This refers to the medial Miocene dispersal event wherein hypsodont equids abruptly appear in the Old World and, at least conceptually, spread rapidly and widely throughout that region. Phylogenetic studies have shown that this equid should be known as *Hippotherium* rather than as *Hipparion*, as formerly utilized. Species of *Hipparion* are not closely related to those that make up *Hippotherium* and did not participate in the dispersal under discussion. It is appropriate that this dispersal event be known as the *Hippotherium* Datum (e.g., Berggren et al., 1985; Woodburne, 1989, 1996a; Woodburne et al., 1996a).

Local Fauna. An assemblage of fossil vertebrates of specific taxonomic composition recovered from one site or a few sites that are closely spaced stratigraphically and geographically (Tedford, 1970; Woodburne, 1987).

Ma Megannum in the radioisotopic time scale (e.g., Berggren et al., 1995).

Mammal age. A biochronologic unit by which a given interval of geologic time is based on the evolution of fossil mammals (e.g., Wood et al., 1941; Woodburne, 2004a). Criteria for recognition and span of time encompassed by the Arikareean, Hemingfordian, Barstovian, Clarendonian, and Hemphillian mammal ages follows Tedford et al. (2004).

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.

OTU Operational taxonomic unit, in this case considered to be a fossil species.

## Nomenclature for Dental Position and Crown Morphology

This follows standard format. The 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. If additional plications occur on the pli protoconule, these also are recorded. In a simple case, the figure 1.1.1.1 would signify that there was only one pli on the entire anterior (including anteromedial) border of the prefossette; one pli on the entire posterior (including posteromedial) border of the prefossette (meaning the pli protoconule was neither formed nor isolated); one pli on the entire anterior (including anteromedial) border of the postfossette; and one pli on the entire posterior (including posteromedial) border of the postfossette. Regarding the pli caballin, all branches are counted, including the bifurcations of individual plis. The shape of the protocone is considered oval if its lingual border is distinctly convex; it is considered slightly oval if the lingual-most point of that border is convex by at least one enamel thickness. The lingual border of the protocone is considered to be flat if neither of the preceding two conditions obtain. It is considered concave if the lingual border is indented by at least one enamel thickness.

## Mammal Age Terms

Calibration and correlation of the Hemingfordian, Barstovian, and Clarendonian intervals (figs. 1–2) of the North American land mammal age sequence follow Tedford et al. (2004) and Woodburne (2004a). Late Hemingfordian is equivalent to He2; early Barstovian to Ba1 and late Barstovian to Ba2; early Clarendonian to Cl1, medial Clarendonian to Cl2, and late Clarendonian to Cl3; early Hemphillian to Hh1, medial Hemphillian to Hh2, late Hemphillian to Hh3, and latest Hemphillian to Hh4 in Tedford et al. (2004). Informal notation for this report employs early medial Clarendonian (Cl2.1) for the time represented by the faunas from the Minnechaduza, Big Spring Canyon, Hollow Horn Bear Quarry, and MacAdams Quarry (ca. 12 Ma; fig. 2); late medial Clarendonian (Cl2.2) includes the time represented by the faunas from the Xmas-Kat, Machaerodus, and Hans Johnson quarries, the Ed Ross Ranch Quarry, and the Gidley Horse Quarry (ca. 10–11 Ma; fig. 2).

### Quarry Terms

Burge Quarry in Burge Member, Valentine Formation, Nebraska. See Skinner and Johnson (1984: 286, fig. 3).

Hans Johnson Quarry in Merritt Dam Member, Ash Hollow Formation, Nebraska. See Skinner and Johnson (1984: 316). About equivalent to Machaerodus and XMas-Kat quarries.

June Quarry in Burge Member, Valentine Formation, Nebraska. See Skinner and Johnson (1984: 288, fig. 3). Equivalent to Burge Quarry.

Midway Quarry in Burge Member, Valentine Formation, Nebraska. See Skinner and Johnson (1984: 289, fig. 3). Equivalent to Burge Quarry.

Machaerodus Quarry in Merritt Dam Member, Ash Hollow Formation, Nebraska. See Skinner and Johnson (1984: 315, fig. 3). The Machaerodus Ash, which overlies the fossil-bearing strata, has been dated (fission-track) at 9.95 ± 0.8 Ma (Skinner and Johnson, 1984: 315).

XMas-Kat quarries in Merritt Dam Member, Ash Hollow Formation, Nebraska. Skinner and Johnson (1984: 315; figs. 3, 16–17) indicate that these, and the Machaerodus, Leptarctus, Connection Kat, W. Line Kat, Line Kat, E. Kat, and XMas quarries, all derive from channels of the Merritt Dam Member, cut down into the Cap Rock Member of the Ash Hollow Formation, and that the fossil-producing units are also overlaid by the Machaerodus Ash. The quarries are considered to be virtually synchronous in depositional age.

Additional abbreviations are either conventional or are explained in the text.

## METHODOLOGY

General: All OTUs discussed here are compared by means of the cranial and mandibular parameters (figs. 3–6) advocated by participants of the 1981 *Hipparion* Conference held at the American Museum of Natural History, New York (Eisenmann et al., 1988). Features of the cranial morphology also are discussed. Characters of dental morphology focus on the height of crown at which they are developed, guided in part by the methodology explained in Woodburne (2003), which also allocated lower dentitions to crania of *Merychippus insignis*, otherwise not previously published.

In addition to pertinent literature, evaluations of the morphology of the OTUs discussed here are based on specimens housed in the F:AM collections of the AMNH, with the hypodigm and geologic occurrence being specified for each.

Character States: Those used herein are comparable to, but in some cases different from, those presented by Bernor et al. (1988) and Hulbert and MacFadden (1991); they are also fewer in number. In those previous studies, as well as in this one and in Woodburne (2003), the morphology displayed by *Parahippus leonensis* is considered to be the plesiomorphic condition. Taxa utilized for this analysis, relevant localities (fig. 1), and stratigraphic settings (fig. 2) are indicated below and in table 2.

Cranial and Dental Parameters: See tables 1 and 2.

### Measurements

Cranial and mandibular parameters follow Eisenmann et al. (1988), as shown in figures 3–6. Plication counts of the upper cheek

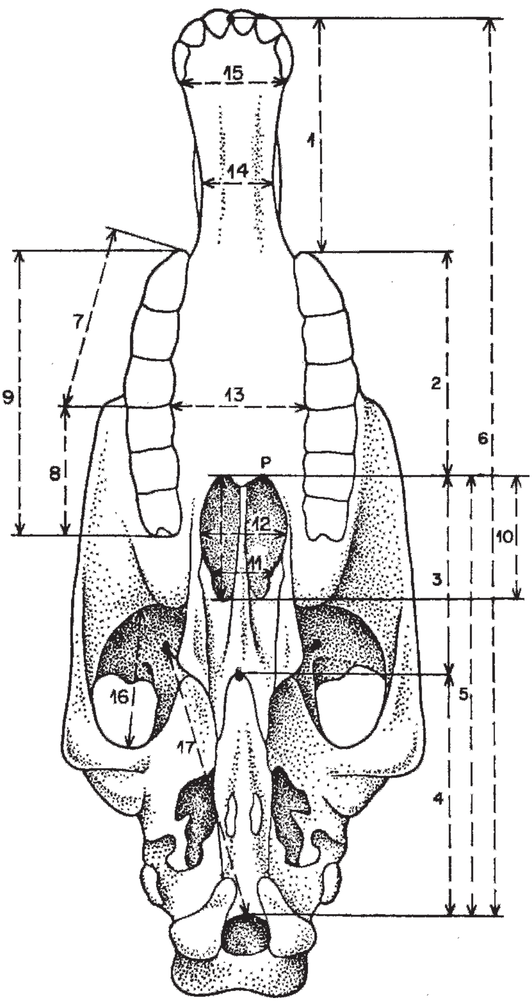


Fig. 3. Diagram showing location of cranial measurements. After Eisenmann et al. (1988). Ventral view.

tooth enamel pattern also follow Eisenmann et al. (1988). Length and width are taken at the tooth crown (contrary to taking those measurements 1 cm above the base of the tooth, as recommended by Eisenmann et al. [1988]), with the width including the edge of the crown lingual to the protocone (fig. 4C). An important dimension for this study is the actual or estimated MSTHT of a given tooth versus its unworn condition. The intent is to make statements as to crown height (MacFadden, 1984; fig. 5C) that are as precise as possible and to express this dimension as a percentage of the likely unworn MSTHT for that tooth position. In almost all cases, it is possible to obtain accurate measurements for the unworn MSTHT for each tooth position based on isolated or otherwise measurable teeth (maxillary bone broken away) or to estimate MSTHT to within narrow limits based on the associated swelling of the lateral surface of the maxilla. In other instances, if the unworn MSTHT for P2, for example, is known, it can be estimated that M1 and M2 likely have a crown height about 5 mm taller. For samples in which teeth are not directly associated with one another in the maxilla, the unworn MSTHT of a given tooth position can be estimated from teeth in adjacent tooth positions in the same species sample or in comparison with teeth of that tooth position in closely related species. Tables 4, 7–8, 10, 12–13, 15, 17–19, and 22–23 present statistical data for individual tooth positions from the various samples. Where possible, the order in which the specimens are listed is ontogenetically youngest to oldest progressively downward on the table. The actual or estimated MSTHT of the specimens is given, and a percent of wear is determined from that number relative to the known or estimated unworn MSTHT for the tooth position. This ensures that the teeth of various samples are evaluated at closely comparable wear stages, to the extent possible.

## Character Analysis

A character matrix developed for this project is shown in tables 1 and 2. The matrix was subjected to a parsimony analysis using PAUP 4.0b10 (Swofford, 2001). As indicated in the character state analysis, multistate characters are ordered and unordered. Heuristic searches employed 1,000 random input orders and equal weights for all characters. Bootstrap analyses included 500 replications and 10 random input orders per replicate. In all cases, *Parahippus leonensis* is taken as the out-group. Changes in character states for each node in a cladogram were developed via MacClade 4.08 (Maddison and Maddison, 2000).

## Statistical Computations

Where appropriate, statistical summaries of numerical data in the tables include Mean,

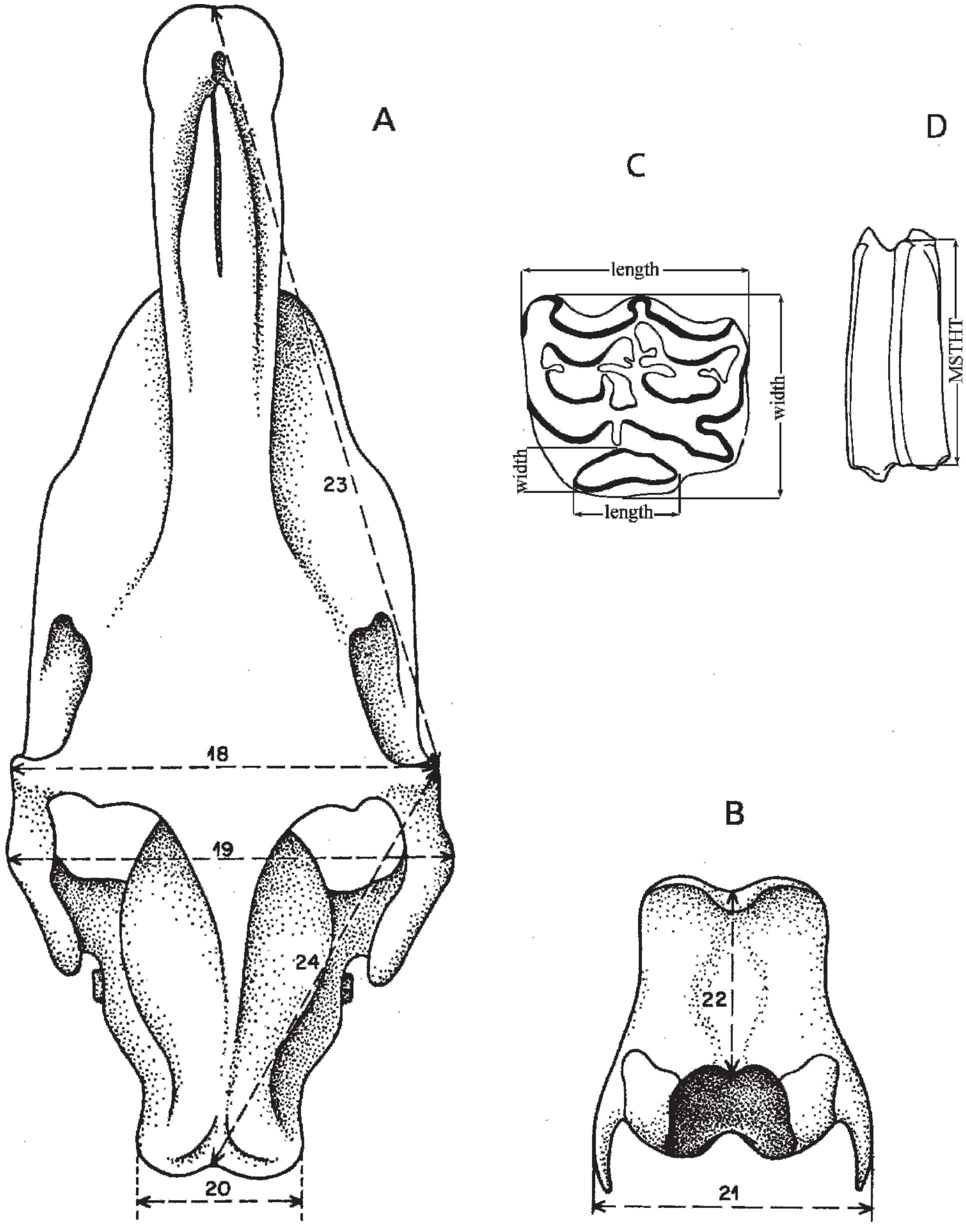


Fig. 4. Diagram showing location of cranial measurements and cheek tooth measurement methodology. **A,** dorsal view. **B,** posterior view. **A** and **B** after Eisenmann et al. (1988). **C,** measurement of length and width of upper cheek teeth and length and width of protocone. **D,** measurement of MSTHT from base to tip of mesostyle at labial surface of cheek tooth.

Standard Deviation, and Coefficient of Variation. These were calculated using the following functions in Quattro Pro 8.0: @AVG (Mean) or @PUREAVG (Mean, ignoring labels or gaps), @STDS (Sample Standard Deviation) or @PURESTDS (Sample Standard Deviation ignoring labels or gaps), and Coefficient of Variation using the formula: s100/0. The results were checked using data and examples in Simpson et al. (1960: 86, 90–91) and found to be identical.

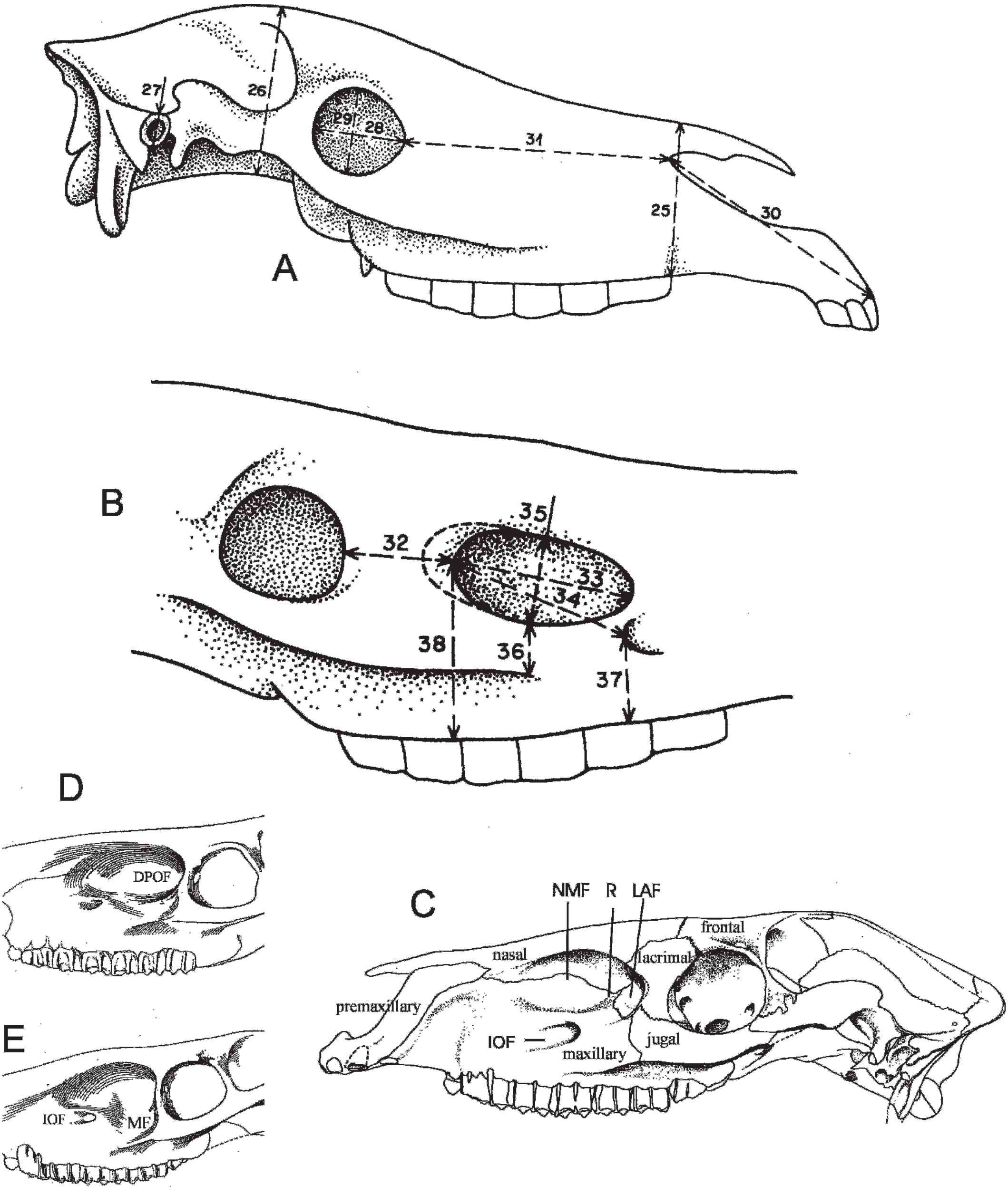


Fig. 5. Diagram showing location of cranial measurements and features cited in Table 2. **A,** lateral view. **B,** close up of facial region, lateral view. **A** and **B** after Eisenmann et al. (1988). **C,** lateral view of *Merychippus insignis*, F:AM 87001, Echo Quarry (early Barstovian), Nebraska. NMF = nasomaxillary fossa. LAF = lacrimal fossa. R = ridge that separates the NMF from the LAF. IOF = infraorbital foramen. After Woodburne (2003: fig. 16.7). **D,** malar fossa developed below the DPOF but not bounded by definite posterior and ventral rims. **E,** malar fossa developed below the DPOF, bounded by definite posterior and ventral rims. **D** and **E,** *Acritohippus isonesus* (Kelly, 1995), after Osborn (1918: plate 10, figs. 3, 4; *Merychippus isonesus*).

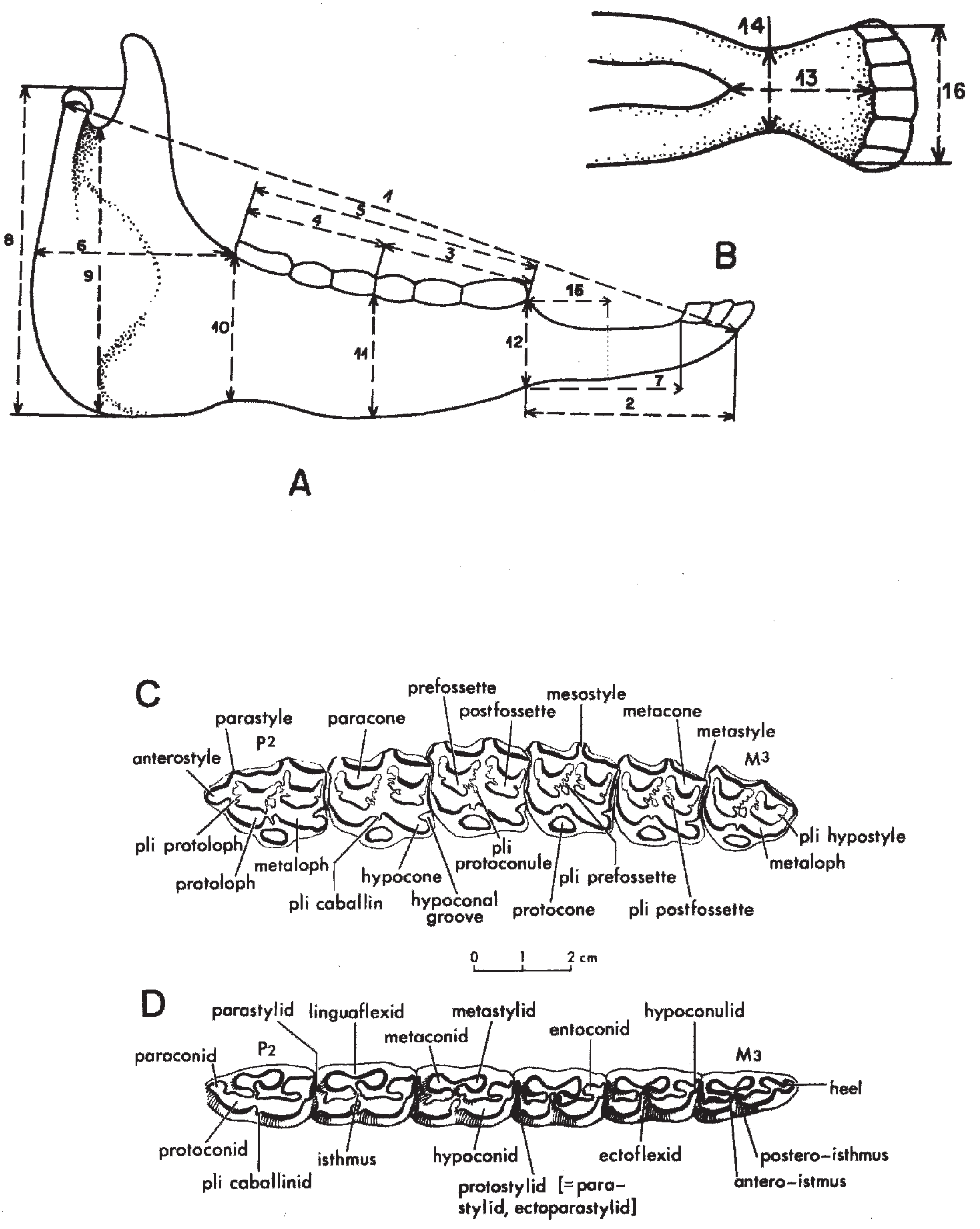


Fig. 6. Diagram of measurements and terminology. **A,** measurements of mandible. **B,** symphysis of mandible. **C** and **D,** dental terminology. **C,** upper cheek teeth. **D,** lower cheek teeth. **A** and **B** after Eisenmann et al. (1988). **C** and **D** after MacFadden (1984).

TABLE 1
**Character States and Polarity, Phyletic Analysis of Mesodont to Hypsodont Equids**

Many of the characters discussed below are continuous variables rather than present or absent states, and discrete intervals along a continuum are recognized. In all pertinent character states the indicated metric pertains to the mean for the species indicated. If the listed taxon is represented by a single specimen, its dimensions are presumed to be the mean. For species of *Cormohipparion* and *Hippotherium*, the information is contained in the present report and Woodburne (1996b, 2003). For other taxa, the data are based on unpublished files, available from the author on request.

1. Lacrimal fossa. The dorsal preorbital fossa extends onto the lacrimal bone as the lacrimal fossa (LAF, fig. 5C). The fossa commonly is separated from the nasomaxillary portion of the DPOF by a slight ridge (R, fig. 5C). In other cases (fig. 12A) there is no ridge, but the DPOF extends onto the lacrimal bone nevertheless. That portion is the lacrimal fossa. It is either present (0) or absent (1).
2. Nasomaxillary fossa. This portion of the DPOF is located anterior to the lacrimal bone and to the ridge that separates the two features (NMF, fig. 5C). In some cases the ridge is not present, but the DPOF extends anterior to the lacrimal bone (fig. 12A). It is either present (0) or absent (1).
3. Lacrimal fossa length. This is the anteroposterior length of the fossa as described in character no. 1. This is calculated from the mean lacrimal-fossa length, divided by the mean nasomaxillary-fossa length. In (0) the lacrimal fossa is about 50% as long as the nasomaxillary fossa. In (1) the ratio is 25–30%. In (2) the ratio of 15–20%. In (3) the fossa is absent.
4. The anterior end of the nasomaxillary fossa is located (0) very near the anterior tip of the IOF (e.g., fig. 10A). In (1) it is farther posteriorly (fig. 12). In (2) it is absent.
5. Nasomaxillary fossa orientation. In (0) a line drawn between the posterior mid-height of the fossa and its anterior margin projects anteroventrally, to the diastemal region of the snout, usually in the vicinity of C1 (fig. 10A). In (1) the line projects anteriorly, to the anterior edge of the snout, near its mid-height (fig. 5C).
6. The pocketing of the DPOF is indicated in various figures by heavy dashed lines. In (0) the depth, as measured from the rear margin of the DPOF to the posterior limit of the pocket interior to the POB is 5 mm or less. In (1) the dimension is between 5 mm and 10 mm (fig. 10B). In (2) the dimension is greater than 10 mm. In (3) the pocket is internal to the anterior edge of the orbit, and in (4) the pocket ends distinctly posterior to the anterior edge of the orbit.
7. DPOF depth. This is the medial depth of the DPOF relative to the lateral surface of the adjacent POB. In (0) the depth is 5 mm or less. In (1) the depth is 5–10 mm. In (2) the depth is greater than 10 mm.
8. DPOF anterior rim. The DPOF either has no anterior rim (0; fig. 12A, C); an anterior boundary of the DPOF can be slightly developed and not formed into a definite edge (1), but still is palpably recognized (fig. 5C), or is developed (2) into a distinct edge (fig. 10A, B).
9. Malar fossa. When present, the malar fossa is located on the maxillary and jugal bones below the DPOF (usually the LAF) and posterior to the IOF. In (0) there is no malar fossa (fig. 5C). In (1) a distinct fossa is present just dorsal to the anterior edge of the facial crest but is not bounded by a distinct rim, either ventrally or posteriorly (fig. 5D). In (2) such rims are distinct (fig. 5E).
10. IOF location. In (0) it is anterior in position, above the P2–P3 boundary (fig. 5B). In (1), it is more posterior, above P3 mesostyle or P3–P4 boundary (fig. 10A). In (2), the IOF is located above the P4 mesostyle or P4–M1 boundary (fig. 12C).
11. IOF alignment. In (0), the IOF is aligned with the lower margin of the orbit, using the alveolar border as "horizontal" (fig. 5C). In (1), the IOF is higher on the face and aligned within the lower one-third of the orbit (fig. 10A). In (2), the IOF is still higher on the face and aligned at or near the vertical midpoint of the orbit.
12. DPOF development on the lacrimal bone. In (0), the lacrimal fossa is present (fig. 5C). In (1), the lacrimal fossa is absent, but the DPOF (nasomaxillary fossa) may still be present on the POB, at the anterior edge of, or slightly anterior to, the lacrimal, either as a shallow depression or as a sharply defined feature developed distinctly medial to the lateral surface of the POB. In (2), the DPOF is well anterior to the lacrimal, either as a shallow depression or as a sharply defined feature (fig. 10A).
13. Lacrimal shape. In (0) this is subrectangular, where the dorsal and ventral borders of the bone are approximately parallel rather than approaching each other anteriorly, and the anterior border is approximately vertical (fig. 5C). In (1) the dorsal and ventral borders of the lacrimal approach each other anteriorly, so the bone is narrower anteriorly than at the orbit (fig. 10A, B). In (2) the lacrimal tapers to, or nearly to, a point anteriorly and extends anterior to the maxillo-jugal suture (fig. 19A).

TABLE 1
(*Continued*)

14. The maxillolacrimal and nasolacrimal sutures meet at an obtuse angle (figs. 5C, 10A) in (0). In (1), the sutures meet at a right angle. In (2) the sutures meet at an acute angle (fig. 23A). In (3), the anterior tip of the lacrimal is pointed (figs. 16B, 19A).
15. The maxillolacrimal and lacrimojugal sutures meet at a right angle (fig. 10B) in (0). In (1) the sutures meet at an obtuse angle (fig. 10A). In (2), the sutures meet at an acute angle. In (3), the sutures are aligned (180°) or nearly aligned (fig. 19A).
16. The preorbital bar width (no. 32, fig. 5) is is divided into these intervals. In (0) it is 5 mm wide or less. In (1) the width is 7–10 mm. In (2) the width is 12–17 mm. In (3) the width is 20–30 mm. In (4) the width is 32–40 mm. In (5) the width is 42–50 mm.
17. The length of dP1/P2 ± 3% is divided into these intervals. (0) = 60%. (1) = 50%. (2) = 40%. (3) = 30%. In (4), dP1 is mostly absent in the sample under consideration.
18. Unworn upper P4 or M1 mesostyle height is divided into these intervals. (0) = 18–20 mm or less. (1) = 21–27 mm. (2) = 28–35 mm. (3) = 36–42 mm. (4) = 43–39 mm. (5) = 50–57 mm. (6) = 60–66 mm.
19. The crochet of P2 connects the protoloph and metaloph in these intervals, expressed as a percentage of the unworn MSTHT. (0) = 0–10% (early wear). (1) = 20–30%. (2) = 30–40%. (3) = 40–50%. (4) = 50–60%. (5) = virtually never connects.
20. The protocone of P2 connects to the protoloph in these intervals, expressed as a percentage of the unworn MSTHT. (0) = 0–10%. (1) = 20–30%. (2) = 30–40%. (3) = 40–50%. (4) = 50–60%. (5) = more than 60%.
21. The number of plis on the anterior border of the premolar prefossette is divided into these intervals. (0) = 0 or 1. (1) = 2 or 3. (2) = 4 or 5. (3) = 6 or 7. (4) = 8 or 9. (5) = 10 or more.
22. The number of plis on the anterior border of the molar prefossette is divided into these intervals. (0) = 0 or 1. (1) = 2 or 3. (2) = 4 or 5. (3) = 6 or 7. (4) = 8 or 9. (5) = 10 or more.
23. The number of plis on the posterior border of the premolar prefossette is divided into these intervals. (0) = 0 or 1. (1) = 2 or 3. (2) = 4 or 5. (3) = 6 or 7. (4) = 8 or 9. (5) = 10 or more.
24. The number of plis on the posterior border of the molar prefossette is divided into these intervals. (0) = 0 or 1. (1) = 2 or 3. (2) = 4 or 5. (3) = 6 or 7. (4) = 8 or 9. (5) = 10 or more.
25. The number of plis on the anterior border of the premolar postfossette is divided into these intervals. (0) = 0 or 1. (1) = 2 or 3. (2) = 4 or 5. (3) = 6 or 7. (4) = 8 or 9. (5) = 10 or more.
26. The number of plis on the anterior border of the molar postfossette is divided into these intervals. (0) = 0 or 1. (1) = 2 or 3. (2) = 4 or 5. (3) = 6 or 7. (4) = 8 or 9. (5) = 10 or more.
27. The number of plis on the posterior border of the premolar postfossette is divided into these intervals. (0) = 0 or 1. (1) = 2 or 3. (2) = 4 or 5. (3) = 6 or 7. (4) = 8 or 9. (5) = 10 or more.
28. The number of plis on the posterior border of the molar postfossette is divided into these intervals. (0) = 0 or 1. (1) = 2 or 3. (2) = 4 or 5. (3) = 6 or 7. (4) = 8 or 9. (5) = 10 or more.
29. The number of plis caballin in the premolars is divided into these intervals. (0) = usually absent (mean count). (1) = usually single. (2) = usually double. (3) = usually triple. (4) = usually four.
30. The mean number of molar plis caballin is divided into these intervals. (1) = usually single. (2) = usually double. (3) = usually triple.
31. The configuration of the premolar ectoflexid is shown as (0) penetrating the metconid-metastylid isthmus. In (1) this does not occur except in early wear and soon retracts to its usual labial position. In (2) the ectoflexid is broad lingually, and the bases of the metaconid and metastylid are extensively developed so that a definite X (P3, P4) or H (M1, M2) pattern results.
32. The development of a metaconid-metastylid isthmus in lower premolars is shown as (0) not being developed. In (1) the isthmus is developed in later wear. In (2) it is developed in early wear.
33. The development of the hypoconal groove in upper-cheek teeth is smooth (fig. 6C) in (0). In (1) the groove develops one or two plis (M3, fig. 9C). In (2) it shows 3 or more plis. In (3) it develops a hypoconal fossette (M2 in fig. 9B).
34. The protocone of the upper cheek teeth is scored as connected to the protoloph (P2, M1, fig. 12D) in (0). In (1) it is isolated from the protoloph (P3, P4, M2, M3, fig. 12D).

TABLE 1
(*Continued*)

35. The protocone of the upper-cheek teeth has a spur on its anterolabial end that persists into at least medial wear (0; M1 of *Cormohipparion goorisi*, fig. 9A). In (1) the protocone lacks a spur (fig. 9C, D).
36. The IOF is aligned with respect to the upper cheek teeth. In (0) the IOF is situated above P3 (fig. 10A). In (1) the IOF is situated above P2. In (2) the IOF is sited above P4. In (3) the IOF is situated above M1 or more posteriorly (fig. 12C).
37. The IOF is aligned with respect to the DPOF. In (0), the IOF is aligned below the DPOF midpoint (fig. 5C). In (1), the IOF is located near, but below, the anterior end of the DPOF (fig. 8A). In (2), the IOF is located within the DPOF just above its ventral margin.
38. The location of the orbit relative to the upper-cheek teeth. In (0), the orbit is located above M2/M3 boundary. In (1), the orbit is located above M3 (fig. 5C). In (2) it is located posterior to M3 (fig. 12C).

Log-ratio diagrams were constructed by means of Corel Quattro Pro 8.0, including calculation of log 10 sample mean, observed range, and standard deviation. The incremental scale on the Y axis was produced by the graphing methodology inherent to the application and considered sufficient for the present purpose. The standard of comparison is the sample of *C. occidentale* from the XMas Kat Quarry. In figure 13, as an example, the method portrayed the log 10 mean and standard deviation of that sample versus the means for the various parameters of, for instance, the samples for *C. occidentale* from Machaerodus and Hans Johnson quarries. To this I manually added the Quattro Pro-calculated log 10 ranges of the standard deviation for the Machaerodus and Hans Johnson quarry samples. A similar approach was taken with respect to the other log-ratio diagrams. The intent is to be able to compare the log 10 cranial parameter means and standard deviations between the indicated species samples and to diminish the effect of absolute size when making comparisons between them (Simpson, 1941).

TABLE 2
**Character States for Species of *Cormohipparion* and Other Taxa Subjected to Phyletic Analysis in Text**

| Taxon | Character[a]<br>         11111111112222222222333333333<br>12345678901234567890123456789012345678 |
|---|---|
| *Parahippus leonensis* | 00010000010000110040000000000000000000 |
| *Merychippus primus* | 00010000011000002110001100001000000000 |
| *Merychippus insignis* | 00111111021002121144001111001100110001 |
| *Cormohipparion goorisi* | 10321422011111??3222300221100101101001 1 |
| *C. quinni* | 1032122201111?03241400222200211211101 1 |
| *C. fricki* | 103212210112 1??54505113322002110011112 |
| *C. skinneri* | 1032122201121215 4??510332300212001111 1 |
| *C. johnsoni* | 10321222012213143405002323002 1??011012 |
| *C. merriami* | 10321222011222153505303322003 1??011011 |
| *C. matthewi* | 10321222011210154305104333002 1??011011 |
| *C. occidentale* | 10321222011210154605324433112210011012 |
| LACM 150080 | ?????????1???????5021055231142??011011 |
| *H. primigenium* | 10321222000211251505234534113210011011 |

[a]Characters and character states are described in detail in table 1.

## STRATIGRAPHIC AND CHRONOLOGICAL FRAMEWORK
figures 2, 7

NEBRASKA: *Cormohipparion merriami*, n.sp., is represented in the Burge Fauna, of Nebraska, in the Burge Member of the Valentine Formation. Stratigraphically, this is the highest member in that formation. The lower three members (Cornell Dam, Crookston Bridge, and Devil's Gulch) contain specimens referred to *C. quinni*, with the Hurlbut Ash near the top of the Cornell Dam Member having been dated at about 11.6 ± 1.1 Ma (Skinner and Johnson, 1984: 252; revised from 13.6 ± 1.3 Ma in Boellstorff and Skinner, 1977). Woodburne (1996b) argued in favor of the older of these fission-track ages being more accurate. Perkins and Nash (2002) indicated an interpolated age for the Hurlbut Ash as 13.6 ± 0.1 Ma, which is consistent with the proposals of Woodburne (1996b). Swisher (1992) confirmed this age as 13.6 ± 0.21 Ma by $^{40}$K-$^{40}$Ar dating of glass shards.

According to Skinner and Johnson (1984: 285), the Burge Member unconformably overlies the Devil's Gulch Member (fig. 7) and is composed of cross-bedded friable quartz sand with greenish-gray to olive-green clasts of clay. Tedford et al. (1987) considered the Burge Fauna to be of late Barstovian age, and this was followed by Woodburne (1996b). Whistler and Burbank (1992) correlated the Burge Fauna with that of the *Cupidinimus avawatzensis/Paracosoryx furlongi* Assemblage Zone of the Dove Spring Formation, California, the base of which is correlated to Chron C5A or about 12.5 Ma in the Berggren et al. (1995) time scale (fig. 2). Tedford et al. (2004) assigned the faunas formerly allocated to the latest Barstovian interval (Ba3; Tedford et al., 1987) to early Clarendonian (Cl1), as followed here and as correlated by Whistler and Burbank (1992).

The Valentine Formation is unconformably overlaid by the Ash Hollow Formation (Skinner and Johnson, 1984: 298), which contains faunas that range in age from early Clarendonian to late Hemphillian (Tedford et al., 1987: 169–170, fig. 6.2). The Ash Hollow Formation reaches a thickness of at least 80 m (Skinner and Johnson, 1984: 295) and is composed of a succession of massive, friable sandstone and interbedded arenaceous siltstone. Species of *Cormohipparion* occur in the lower two members of the Ash Hollow Formation, the Cap Rock Member and overlying Merritt Dam Member.

The Cap Rock Member contains the Minnechaduza Fauna of early Clarendonian age, with a species formerly assigned to *Cormohipparion occidentale* (described as *Neohipparion occidentale* by Webb [1969]). This material has been examined for the present report and determined to be comparable to *Cormohipparion fricki*, n.sp., from Texas (figs. 2, 7). The Cap Rock Member contains the Swallow Ash, near its base. Swisher (1992) reported a $^{40}$Ar/$^{39}$Ar total fusion age of 12.18 ± 0.1 Ma for the Swallow Ash, herein considered more accurate than the fission-track age of 10.6 ± 0.2 Ma provided by Skinner and Johnson (1984: 296). Whistler and Burbank (1992: fig. 8) indicate that the Minnechaduza Fauna of Nebraska correlates with the lower part of the *Epicyon haydeni/Hipparion forcei* Assemblage Zone in California or within Chron C5N in the Berggren et al. (1995) time scale. This suggests that the Minnechaduza Fauna is contained within an interval of about 10.0–11.0 m.y., but this is surely too young. Based on the underlying Swallow Ash dated at 12.18 Ma, and the 11.5 Ma Davis Ash (see below) that overlies the Cap Rock Member, the Minnechaduza Fauna is estimated to be about 12 m.y. old.

The Merritt Dam Member of the Ash Hollow Formation contains the XMas-Kat, Machaerodus, and Hans Johnson quarries. Faunas from these quarries are of medial Clarendonian (Cl2) age (Tedford et al., 2004: fig. 6.2). The Davis Ash occurs stratigraphically below these fossil quarries, in the lower part of the Merritt Dam Member. The Davis Ash is thus both superpositionally above the Minnechaduza Fauna sites in the Cap Rock Member of the Ash Hollow Formation and below those of the XMas-Kat, etc., quarries. Swisher (1992) indicated a $^{40}$Ar/$^{39}$Ar total fusion age of 11.5 ± 0.1 Ma for the Davis Ash. This age is followed here and replaces fission-track ages of 9.7 ± 1.2 Ma (on zircons) and 7.5 ± 2.2 Ma (glass shards)

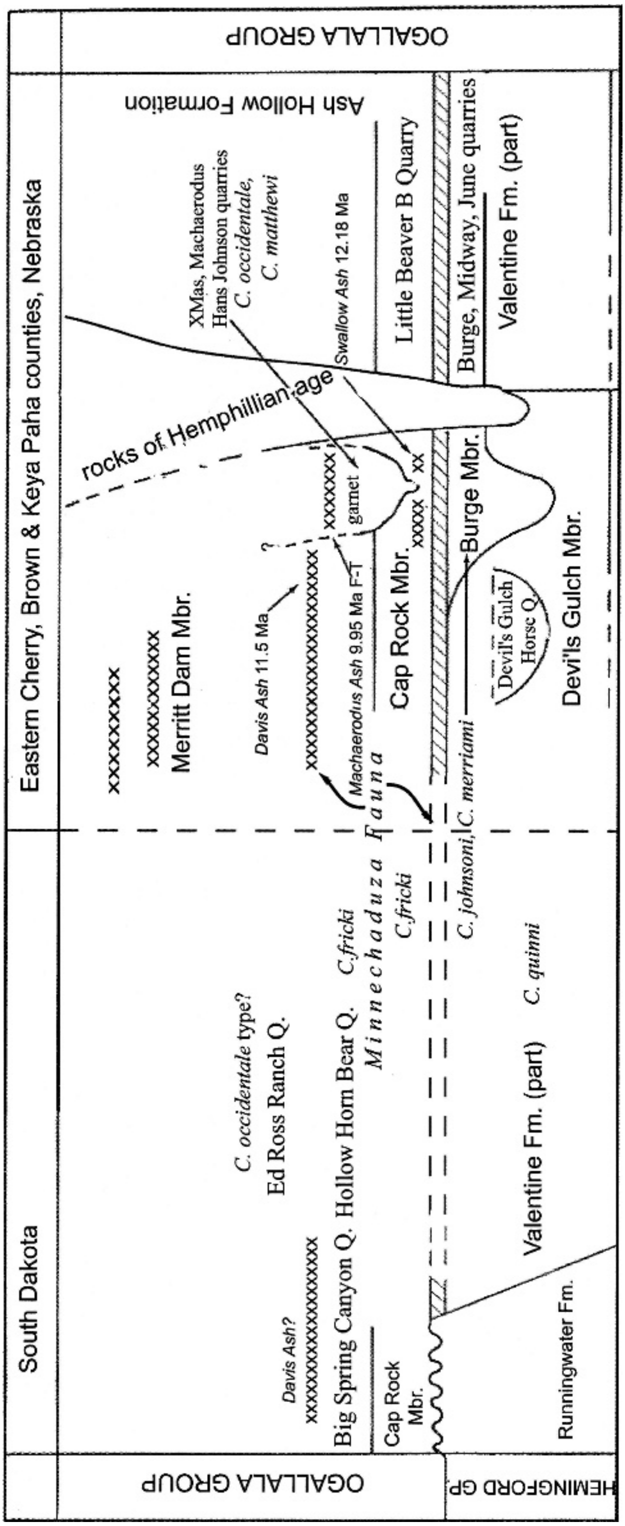


Fig. 7. Correlation of rock and faunal units of the Valentine and Ash Hollow formations, Nebraska and South Dakota, modified after Skinner and Johnson (1984: fig. 3).

obtained by Izett (1975) and another glass shard fission-track age of 10.2 ± 0.7 Ma cited by Skinner and Johnson (1984: 297) from the same split sample of Davis Ash. Another ash, the Machaerodus Ash, occurs stratigraphically above the quarries of the extended XMas-Kat and Machaerodus channels. Skinner and Johnson (1984: 307) report a fission-track (glass shard) age of 9.95 ± 0.8 Ma for the Machaerodus Ash. Based on the above comparisons between $^{40}Ar/^{39}Ar$ total fusion ages and the fission-track results, it is likely that the Machaerodus Ash is about 10 Ma old.

The Hans Johnson Quarry is also considered equivalent to the XMas-Kat and Machaerodus quarries, even though the Machaerodus Ash is not recorded at the Hans Johnson Quarry (Skinner and Johnson, 1984: 297, 306–316, figs. 3, 16–17). On radioisotopic grounds, the XMas-Kat and Machaerodus (and Hans Johnson by correlation) sites are about 10 Ma old. Whistler and Burbank (1992: fig. 8) suggested that the XMas-Kat quarry faunas are about equivalent to the upper part of the *Epicyon haydeni/Hipparion forcei* Assemblage Zone in California, which is correlated to an interval in about the upper half of Chron C5N to Chron C4Ar in the Berggren et al. (1995) time scale. This suggests that the XMas-Kat and correlative sites in Nebraska are contained within an interval of about 11–9 m.y. In that faunas of early Hemphillian age appear to be as old as about 9 Ma (Woodburne and Swisher, 1995; Tedford et al., 2004), an age of about 10 Ma for the XMas-Kat and correlative sites seems plausible.

*Cormohipparion occidentale* (as here restricted) occurs in the medial Clarendonian faunas from the Xmas-Kat, Machaerodus, and Hans Johnson quarries in Nebraska. *Cormohipparion matthewi*, n.sp., also is represented in these sites.

SOUTH DAKOTA: Skinner and Johnson (1984) discussed the Big Spring Canyon and Hollow Horn Bear Quarry local faunas and indicate the Big Springs Canyon Local Fauna as being part of the Minnechaduza Fauna (see also Webb, 1969: 19). Hollow Horn Bear Quarry occurs on the north side of the Little White River drainage, in Todd County, South Dakota (Skinner and Johnson, 1984: fig. 2A, loc. 96), in the lower part of the undifferentiated Ash Hollow Formation (Skinner and Johnson, 1984: fig. 3, table 1). Locality information indicates that a thick white ash occurs stratigraphically above the Hollow Horn Bear Quarry, which is most likely the areally extensive Davis Ash (R. H. Tedford, personal commun., 2002), dated at 11.5 ± 0.1 Ma (Swisher, 1992).

If the Hollow Horn Bear Quarry is overlaid by the Davis Ash (figs. 2, 7), then the fossils from that site are somewhat older than those of the XMas-Kat quarries in Nebraska, in contrast to the correlation shown in Skinner and Johnson (1984: fig. 3). In that report, the Big Springs Canyon, the Hollow Horn Bear Quarry, and sites from the Thin Elk Formation of Harksen and Macdonald (1961) were all aligned with the present position of the Ed Ross Ranch Quarry (figs. 2, 7). The material from Hollow Horn Bear Quarry (F:AM 71880; fig. 8A) has a plesiomorphously much shorter lacrimal relative to the length of the POB (ca. 50%; table 3A), with the anterior tip of the lacrimal terminating about 5 mm posterior to the maxillo-jugal suture instead of reaching it (as seen in figs. 10A–B); it shows a somewhat more ovate protocone than in the type of *C. occidentale* (fig. 9D) and likely is lower crowned (unworn M1 MSTHT likely 55 mm; table 4B) versus a likely unworn MSTHT of 50–65 mm in the type (table 4A). This dental and cranial morphology is more compatible with that found in *Cormohipparion fricki*, n.sp. (see below).

Specimens possibly from the Thin Elk Formation, F:AM 71872 (fig. 11) and AMNH 10869, show a more derived dental morphology (higher crowned [ca. 60 mm unworn MSTHT; table 4C), and have more elongate protocones (table 4C) than F:AM 71880 (table 4B) and are considered more plausibly allied with *C. occidentale*. If the phyletic correlation also is a temporal one, then it suggests that these materials are likely to be younger than those from the Hollow Horn Bear Quarry and elicits the proposal that the type material of *C. occidentale* is of about this age rather than as old as taxa from the Minnechaduza-equivalent interval (see Webb, 1969). The presence of abundant garnet crystals in both the Thin Elk Forma-

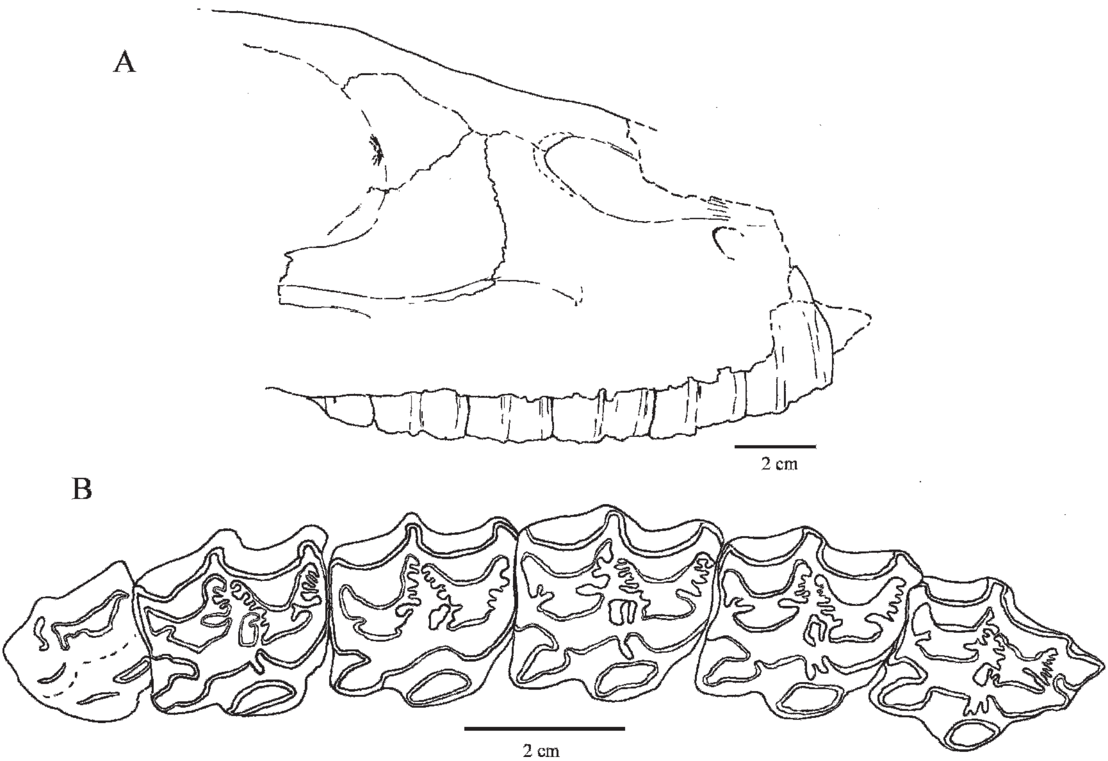


Fig. 8. *Cormohipparion fricki*, referred. F:AM 71880, Hollow Horn Bear Quarry, Ash Hollow Formation, Little White River, South Dakota; early Clarendonian. **A,** lateral view of facial region of cranium. **B,** occlusal view of cheek tooth dentition, LP2–M3.

TABLE 3

**Lacrimal Length versus POB Length, Unworn Crown Heights, and Protocone Dimensions, Species of *Cormohipparion***

**A. Lacrimal length versus POB length**

| Taxon | Quarry | Biochronology | Length 1 Lacrimal-rear DPOF/length POB (#39/#32) | Length 2 Lacrimal/length POB [(#39–#32)/#32] |
|---|---|---|---|---|
| *C. occidentale* | XMas-Kat | Cl 2.2 | 0.38 | 0.62 |
| | Machaerodus | Cl 2.2 | 0.37 | 0.63 |
| | Hans Johnson | Cl 2.2 | 0.38 | 0.62 |
| cf. *C. occidentale* | Ed Ross Ranch | ?Cl 2.2 | 0.25[a] | 0.75[a] |
| *C. matthewi* | XMas-Kat | Cl 2.2 | 0.39 | 0.61 |
| *C. skinneri*[b] | Gidley Horse | Cl 2.2 | 0.38 | 0.62 |
| *C. fricki* | Mac Adams | Cl 2.1 | 0.52 | 0.48 |
| *C. fricki* | Hollow Horn Bear | Cl 2.1 | 0.51 | 0.49 |
| *C. merriami*[c] | June | Cl 1 | 0.42 | 0.59 |
| *C. johnsoni* | Burge | Cl 1 | 0.20 | 0.80 |

Notes: Cl 1 = early Clarendonian; see text: Mammal Age Terms. Cl 2.1 = early medial Clarendonian. Cl 2.2 = late medial Clarendonian.

[a]Dimensions approximate.

[b]Similar to *C. occidentale.*

[c]Dimensions are comparable to Cl 2.1 taxa.

TABLE 3 (*Continued*)

**B. Unworn MSTHT heights[a] (mm) for P3–M3 in *Cormohipparion* species**

| Taxon | Quarry | P2–M3 | P4–M1 |
|---|---|---|---|
| *C. occidentale* | XMas-Kat | 50–66 | 62–66 |
| | Hans Johnson | 50–66 | 62–66 |
| | Machaerodus | 50–66 | 62–66 |
| *C. matthewi* | XMas-Kat | 40–45 | 52–55 |
| *C. skinneri* | Gidley Horse | ?60 | ?60 |
| *C. fricki* | Mac Adams | 50–55 | 52–55 |
| *Cormohipparion* sp. | Punchbowl Fm. | ?45–50 | ?45–50 |
| *C. merriami* | June & Midway | 45–55 | 52–55 |
| *C. johnsoni* | Burge | 40–50 | 45–50 |
| *C. quinni*[b] | Valentine Fm. (Ba 2) | 40–45 | 42–45 |
| *C. goorisi*[c] | Fleming Fm. (Ba 1) | 26–34 | 30–34 |

Notes: Ba 1 = early Barstovian, Ba 2 = late Barstovian.

[a]Upper part of range seen in P4–M1.

[b]From Woodburne (1996b).

[c]From Woodburne (2003).

TABLE 3 (*Continued*)

**C. Protocone width/length ratio in *Cormohipparion* species**

| Taxon | Quarry | P2 | P3 | P4 | M1 | M2 | M3 |
|---|---|---|---|---|---|---|---|
| *C. occidentale* | Type specimen | 0.43 | 0.39 | 0.39 | | 0.43 | |
| | XMas-Kat | 0.52 | 0.45 | 0.45 | 0.51 | 0.44 | 0.31 |
| | Hans Johnson | 0.54 | 0.44 | 0.45 | 0.47 | 0.44 | 0.37 |
| | Machaerodus | 0.51 | 0.48 | 0.44 | 0.49 | 0.43 | 0.37 |
| *C. matthewi* | XMas-Kat | 0.49 | 0.44 | 0.45 | 0.53 | 0.47 | 0.42 |
| *C. skinneri* | Gidley Horse | 0.50 | 0.35 | 0.41 | 0.45 | 0.39 | 0.22 |
| *C. fricki* | Mac Adams | 0.50 | 0.43 | 0.43 | 0.48 | 0.43 | 0.39 |
| *C. merriami* | June & Midway | 0.67 | 0.50 | 0.47 | 0.51 | 0.53 | 0.46 |
| *C. johnsoni* | Burge | 0.76 | 0.53 | 0.57 | 0.50 | 0.50 | 0.46 |
| *C. quinni*[a] | Railway[b] | 0.63 | 0.52 | 0.50 | 0.51 | 0.50 | 0.53 |
| *C. quinni*[a] | Devil's Gulch Horse[b] | 0.61 | 0.43 | 0.49 | 0.50 | 0.47 | — |
| *C. goorisi*[c] | Trinity River Pit 1[d] | 0.91 | 0.71 | 0.70 | 0.67 | 0.62 | — |
| *Cormohipparion* sp.[e] | Punchbowl Fm., Calif. | 0.79 | 0.65 | 0.65 | 0.59 | 0.58 | — |

Notes: Except for the type specimen of *Cormohipparion occidentale* and LACM 150080,[e] all results are mean dimensions. See tables 7, 10, 12, 13, 15, 17. Protocone dimensions are more elongate in the type specimen than in all other species except for M2 in Machaerodus Quarry, *C. fricki*, and most teeth in *C. skinneri*. This is generally consistent with a late medial Clarendonian age for the type specimen of *C. occidentale.* Protocone dimensions in Burge Member species *C. merriami* and *C. johnsoni* are more ovate than in any other species, except for M1 in *C. occidentale* and *C. matthewi*, and are generally most comparable to those of *C. quinni* (see Woodburne, 1996b).

[a]Woodburne (1996b).

[b]Valentine Formation, Nebraska.

[c]Woodburne (2003).

[d]Fleming Formation, Texas.

[e]LACM 150080, Woodburne (2005). This specimen has more ovate protocones than any other species, except *C. goorisi*, and is comparable in that regard to *Hippotherium "primigenium"* (see text).

tion and from the Merritt Dam Member of the Ash Hollow Formation (there associated with the XMas-Kat and Machaerodus quarries) led Skinner and Johnson (1984) to propose a correlation based thereon, compatible with the stage of evolution of the *C. occidentale* specimens.

TEXAS: As indicated in Tedford et al. (1987), the main F:AM collections are derived from the MacAdams and Gidley Horse

TABLE 4
**Measurements (mm) of *Cormohipparion occidentale*, Type, and *Neohipparion affine***

**A. Measurements (mm) of upper dentition of *C. occidentale* (based on casts of AMNH 10794)**

| Specimen | Tooth | Height | Length | Width | Ratio W/L | Plication index | Protocone Length | Protocone Width | Protocone Ratio W/L | Pli caballin | Hypoconal groove |
|---|---|---|---|---|---|---|---|---|---|---|---|
| ANSP 11287 | RP2 | 30.1 | 33.1 | 24.1 | 0.73 | 3:4:3:1 | 7.9 | 3.4 | 0.43 | 3 | simple; open |
| (AMNH 10794) | RP3 | 38.2 | 30.1 | 27.4 | 0.91 | 3:6:3:1 | 9.9 | 3.9 | 0.39 | 2 | simple; open |
| | LP3 | 37.8 | 28.7 | 26.2 | 0.91 | 5:7:3:1 | 10.3 | 4.0 | 0.39 | 2 | simple; open |
| | RM2 | 40.9 | 24.0 | 23.7 | 0.99 | 3:6:5:1 | 8.3 | 3.6 | 0.43 | 1 | simple; open |

Remarks: About medial wear; relatively complex; protocones slender. Unworn MSTHT likely about 50–65 mm. Anterior and postfossettes linked labially still. Anterior enamel from hypocone connects to posterior border of prefossette. Pli protoconule loop strong. Tooth height is consistent with all specimens pertaining to a single individual, concurrent with Gidley (1909: 877) and Osborn (1918: 176). Pli protoconule not prominent except as isolated in M2.

**B. Measurements (mm) of upper dentition of *C. fricki* from Hollow Horn Bear Quarry, early medial Clarendonian; Ash Hollow Formation undifferentiated (Skinner and Johnson, 1984). Likely below Davis Ash dated at 11.5 ± 0.1 Ma.**

| Specimen | Tooth | Height | Length | Width | Ratio W/L | Plication index | Protocone Length | Protocone Width | Protocone Ratio W/L | Pli caballin | Hypoconal groove |
|---|---|---|---|---|---|---|---|---|---|---|---|
| F:AM 71876[a] | RM1 | 49.0 | 24.2 | 21.1 | 0.87 | 0:4:3:1 | 9.3 | 3.7 | 0.40 | 1 | simple; open |
| F:AM 71875[b] | LP2 | 18.3 | 27.8 | 20.2 | 0.73 | 1:4:1:0 | 8.0 | 3.6 | 0.45 | 2 | simple; open |
| | LP3 | 9.6 | 22.5 | 21.8 | 0.97 | 1:4:5:1 | 9.1 | 4.6 | 0.51 | 1 | simple; open |
| | LP4 | 11.6 | 21.7 | 22.5 | 1.04 | 1:7:5:1 | 9.5 | 4.0 | 0.42 | 2 | simple; open |
| | LM1 | — | 21.3 | — | — | 1:7:6:1 | — | — | — | — | simple; narrow |
| | LM2 | 30.0a | 23.1 | 22.3 | 0.97 | 1:6:4:1 | 9.9 | 4.2 | 0.42 | 1 | simple; narrow |
| | LM3 | 31.5 | 23.9 | 21.9 | 0.92 | data not recorded | | | | | |
| F:AM 71880[c] | RP2 | 30.6 | 29.7 | 22.9 | 0.77 | 6:7:4:1 | 7.0 | 3.1 | 0.44 | 3 | simple; narrow |
| | RP3 | 39.0a | 24.5 | 24.6 | 1.00 | 6:8:5:2 | 8.2 | 4.8 | 0.59 | 3 | simple; open |
| | RP4 | — | 24.7 | 24.3 | 0.98 | 6:6:3:2 | 8.5 | 3.8 | 0.45 | 1 | simple; open |
| | RM1 | — | 23.0 | 23.4 | 1.02 | 4:7:5:1 | 8.3 | 5.0 | 0.60 | 1 | simple; open |
| | RM2 | — | 23.2 | 22.3 | 0.96 | 3:5:5:1 | 8.2 | 3.7 | 0.45 | 1 | simple; open |
| | RM3 | 37.0a | | data not recorded | | | | | | | |

Remarks: Comparison is with type material of *Cormohipparion occidentale* in **A**.

[a]Specimen consists of LdP2–P4, M1–M2; M1 slightly worn; M2 unerupted. Unworn MSTHT of M1 likely was about 55 mm; MSTHT of unerupted M2 is about 50 mm.

[b]Specimen consists of LP2–M3 in late wear; somewhat more complex than in type; ?smaller premolars due to later wear. P2 still shows labially connected pre- and postfossettes; protocone is isolated. P3 and P4 protocones are shorter than in type specimen; are isolated. Pli protolophs are relatively strong, still relatively complex. M1 still has strong pli protoconule; still relatively complex. M2 is in medial wear; still with strong pli protoconule; still relatively complex. M3 in late wear still is relatively complex.

[c]Specimen is partial facial region and right and left P2–M3 in about medial wear, still shows relatively complex enamel pattern. P2 shows labially connected pre- and postfossettes on right side; protocone relatively ovate. P3 protocone tapers anteriorly more than in type specimen. Hypocone with normal connection to pli caballin, contra type specimen. M1 protocone tapers anteriorly more than in type specimen; strong pli protoconule as in type, with two plis anterior to pli protoloph. M2 protocone tapers posteriorly more than in type specimen; strong pli protocone as in type, but deflected; 2 plis on anterior side of prefossette. M3 is erupting. MSTHT not likely taller than 40 mm, suggesting that unworn MSTHT in P4 and M1 would have been no higher than 55 mm.

TABLE 4 (*Continued*)

**C. Measurements (mm) of upper dentition of *Cormohipparion* cf. *C. occidentale*, Ed Ross Ranch, South Dakota, ?late medial Clarendonian; ?Thin Elk Formation. Not Hollow Horn Bear Quarry; possibly correlative of Xmas Quarry, Nebraska.**

| Specimen | Tooth | Height | Length | Width | Ratio W/L | Plication index | Protocone Length | Protocone Width | Protocone Ratio W/L | Pli caballin | Hypoconal groove |
|---|---|---|---|---|---|---|---|---|---|---|---|
| F:AM 71872[a] | LP2 | 34.0 | 32.0 | 22.8 | 0.71 | 2:4:5:1 | 8.5 | 4.4 | 0.52 | 1 | simple; open |
| | LP3 | 38.5 | 25.7 | 24.6 | 0.96 | 2:4:4:1 | 9.3 | 3.7 | 0.40 | 1 | simple; open |
| | LP4 | 48.0 | 26.1 | 25.0 | 0.96 | 1:5:3:1 | 8.9 | 3.8 | 0.43 | 1 | simple; open |
| | LM1 | 41.3 | 21.9 | 22.0 | 1.00 | 1:6:3:1 | 8.2 | 3.3 | 0.40 | 1 | simple; open |
| | LM2 | 46.8 | 22.7 | 22.4 | 0.99 | 1:5:4:1 | 8.4 | 3.4 | 0.41 | 1 | simple; open |
| | LM3 | 46.0a | — | — | — | — | — | — | — | 1 | not developed |
| AMNH 108969[b] | RM1 | 60.3 | 27.4 | 24.3 | 0.89 | 0:4:4:1 | 9.2 | 4.0 | 0.44 | 1 | simple; open |

[a]Specimen is broken ♂ skull, with face, snout, right and left C1, P2–M3 in early medial wear. Unworn P4 MSTHT likely about 60 mm. Short Length Lacrimal/Length POB ratio indicates a later Clarendonian age. Differs from type of *C. occidentale* mainly in simpler anterior prefossette, "fatter" protocone. P2 and P3 with more ovate protocone than in type; fossettes separate labially; single pli caballin. P4 with strong pli protoconule loop, as in type. M1 with slight anterior slope of pli caballin, as in M2 of type. M2 with slightly lingually concave protocone, as in type. M3 pattern not yet developed.

[b]*Cormohipparion* sp., Little White River, S.D.; ?Thin Elk Fm., early wear, M1 unworn MSTHT about 65 mm. Tooth height is from unerupted tooth; morphology is based on sectioned tooth. Protocone is flattened oval, slightly convex lingually. Compares favorably in size with M2 of type specimen of *C. occidentale* in **A**, but not in anterior prefossette complexity. Almost unworn LM1 is 60.5 mm tall at mesostyle.

**D. Measurements (mm) of upper dentition of *Neohipparion affine* from Hollow Horn Bear Quarry, South Dakota; medial Clarendonian; Ash Hollow Formation undifferentiated.**

| Specimen | Tooth | Height | Length | Width | Ratio W/L | Plication index | Protocone Length | Protocone Width | Protocone Ratio W/L | Pli caballin | Hypoconal groove |
|---|---|---|---|---|---|---|---|---|---|---|---|
| AMNH | RdP1 | | 8.2 | 5.5 | | | | | | | |
| 141218 | RP2 | 27.2a | 26.6 | 20.3 | 0.76 | 1:1:2:0 | 7.9 | 2.6 | 0.33 | 1 | oblique; narrow |
| | RP3 | 34.5a | 24.9 | 23.3 | 0.94 | 1:3:3:1 | 9.9 | 2.8 | 0.28 | 1 | oblique; narrow |
| | RP4 | — | 24.4 | 23.7 | 0.97 | 1:3:2:0 | 9.8 | 3.6 | 0.37 | 1 | oblique; nearly closed |
| | RM1 | 45.1 | 22.3 | 22.1 | 0.99 | 0:2:2:0 | 9.2 | 3.9 | 0.42 | 1 | linear; narrow |
| | RM2 | 49.5 | 21.9 | 21.1 | 0.96 | 1:2:2:1 | 8.4 | 2.9 | 0.35 | 1 | fossette; triangular |
| | RM3 | 44.5 | — | — | — | — | — | — | — | — | |

Remarks: Specimen consists of a palate with right and left P2–M3, RdP1; M3 erupting; partial face with shallow DPOF. LdP1/LP2 ratio is 0.31. Unworn MSTHT is about 45–55 mm, based on M2 and M3. P2–P3 heights are comparable to type of *Cormohipparion occidentale*, as preserved. P2 anterior and postfossettes are not linked labially. P2–M2 single pli caballin points slightly anteriorly; canted hypoconal groove; protocone more elongate; somewhat smaller size overall; comparable to type in lingually convex protocone. M2 in very early wear. Hollow Horn Bear Quarry appears to be older than the level that produced the type specimen of *C. occidentale*.

TABLE 4 (*Continued*)

**E. Measurements (mm) of upper dentition of *Neohipparion affine* from MacAdams Quarry, Texas; medial Clarendonian.**

| Specimen | Tooth | Height | Length | Width | Ratio W/L | Plication index | Protocone Length | Protocone Width | Protocone Ratio W/L | Pli caballin | Hypoconal groove |
|---|---|---|---|---|---|---|---|---|---|---|---|
| F:AM 123656[a] | RP2 | 36.4 | 29.1 | 23.0 | 0.79 | 1:1:1:0 | 7.4 | 3.1 | 0.42 | 1 | oblique; narrow |
| | RP3 | 38.4 | 26.1 | 25.9 | 0.99 | 1:2:2:1 | 9.2 | 3.8 | 0.41 | 1 | oblique; open |
| | RP4 | 39.8a | 25.6 | 26.0 | 1.02 | 1:2:1:0 | 9.1 | 3.7 | 0.41 | 1 | oblique; open |
| | RM1 | — | 23.7 | 24.0 | 1.01 | 0:4:2:0 | 10.2 | 3.7 | 0.36 | 1 | linear; narrow |
| | RM2 | — | 24.5 | 24.7 | 1.01 | 0:2:2:0 | 10.0 | 2.7 | 0.27 | | open |
| F:AM 132653[b] | LP2 | 32.7 | 29.9 | 20.7 | 0.69 | 2:3:1:0 | 8.4 | 3.9 | 0.46 | 1 | linear; open |
| | LP3 | 34.9a | 26.2 | 23.1 | 0.88 | 1:3:1:1 | 10.5 | 3.5 | 0.33 | 1 | linear; open |
| | LP4 | — | 25.8 | 21.9 | 0.85 | 1:3:2:1 | 10.0 | 3.0 | 0.35 | 1 | open |
| | LM1 | — | 24.2 | 22.9 | 0.95 | 1:2:3:0 | 9.9 | 3.6 | 0.35 | 1 | open; narrow |
| | LM2 | — | 25.5 | 21.4 | 0.84 | 1:2:3:0 | 10.4 | 3.2 | 0.35 | 1 | open; narrow |
| F:AM 132652[c] | LP2 | 16.0 | 30.9 | 23.1 | 0.75 | ?:?:1:1 | 8.5 | 4.5 | 0.35 | 1 | open; narrow |
| | LP3 | 15.2a | 24.6 | 25.6 | 1.04 | 0:1:1:0 | 10.7 | 4.2 | 0.35 | 1 | open |
| | LP4 | — | 23.7 | 25.1 | 1.06 | 0:1:1:0 | 10.7 | 4.3 | 0.35 | 1 | open |
| | LM1 | — | 21.0 | 22.4 | 1.07 | 0:2:1:0 | 8.9 | 4.0 | 0.35 | 1 | open; narrow |

[a]Specimen consists of laterally flattened skull with RP2–M3. Unworn MSTHT is estimated to be 45–55 mm based on P4. Relatively small pli protoconule in all cheek teeth. P2 with labially linked pre- and postfossettes; P2–P4 pattern simple; pli caballins single; hypoconal grooves canted; protocone lingually concave. Protocone short in P2. M1–M2 similar to premolars, flatter lingual protocone.

[b]Specimen is partial skull with right and left P2–M2, Loc 17, MacAdams Quarry 2. P2–M2 with simple pattern, anteriorly pointed single pli caballin, slightly lingually concave protocone.

[c]Specimen is partial skull with right and left P–M3, canine, LI1–3. Cheek teeth low, worn. P2 protocone nearly connects to protoloph. P3–M1 simple pattern, pli caballin points anteriorly, protocone slightly concave lingually.

Quarry sites in the Clarendon beds of the Texas Panhandle. Schultz (1977) provided the most recent summary of the geological setting of these sites. As shown in figure 2, the MacAdams Quarry is chronologically older than the Gidley Horse Quarry sample, although both are of medial Clarendonian age (Cl2; Tedford et al., 2004: fig. 6.2). According to the radioisotopic evidence cited above, the MacAdams Quarry is between 11.5 Ma and 12.0 Ma old, and the Gidley Horse Quarry is about 10 Ma old. These correlations are about 1 m.y. older in each case than suggested by Whistler and Burbank (1992: fig. 8). *Cormohipparion fricki*, n.sp., occurs in the MacAdams Quarry, and *C. skinneri*, n.sp., is represented in the Gidley Horse Quarry.

CALIFORNIA: Whistler and Burbank (1992) described the biochronology and the radioisotopic and magnetostratigraphic geochronology of the Dove Spring Formation in the El Paso Mountains of Southern California (E, fig. 1). The Dove Spring Formation is about 1,800 m thick and contains the classical "Ricardo Fauna" of Merriam (1919). Whistler and Burbank (1992: fig. 4) indicated that *C. occidentale*, *s.l.*, ranges through the *Cupidinimus avawatzensis/Paracosoryx furlongi* and *Epicyon haydeni/Hipparion forcei* assemblage zones, with *C. occidentale s.l.* correlated on the basis of the paleomagnetic data to an age of 12.6–8.8 m.y. in the Berggren et al. (1995) time scale. Whistler and Burbank (1992: fig. 8) indicate that the *Cupidinimus avawatzensis/Paracosoryx furlongi* Assemblage Zone correlates with the Burge Fauna of Nebraska, at its base, and about with (likely somewhat older than) the Minnechaduza Fauna, Nebraska, and the MacAdams Quarry fauna, Texas, at its top. In the present report, the Burge and Minnechaduza faunas are considered to be of early and medial Clarendonian age, respectively, following Tedford et al. (2004). In any case, the *Cupidinimus avawatzensis/Paracosoryx furlongi* Assemblage Zone is from about 11.8 to 11 m.y. old and, following Tedford et al. (2004), the *Epicyon haydeni/Hipparion forcei* Assemblage Zone ranges in age from about 11 Ma to 9 Ma. In the present report, the material from the Dove Spring Formation, which lacks crania, is referred to *Cormohipparion* sp. and has a range from about 11.8 m.y. to 10.4 m.y. (fig. 2).

Woodburne (2005) described an upper dentition referred to *Cormohipparion* sp. from the Devil's Punchbowl, Valyermo, California (V, fig. 1). This is considered to be of likely medial Clarendonian age.

## PREVIOUS INVESTIGATIONS

Skinner and MacFadden (1977) segregated *Cormohipparion* from other mesodont to hypsodont equids in the Neogene record of North America; demonstrated its hipparionine affinities; documented the stability of the DPOF as a feature important to systematic analysis for these and other contemporary horses; and stabilized the Clarendonian taxon, *Cormohipparion occidentale*, as the genotypic species. MacFadden and Skinner (1981) demonstrated that the genus was at least as old as early Barstovian, represented by *Cormohipparion goorisi* from Texas, and Woodburne et al. (1981) posited a later Barstovian taxon, *Cormohipparion sphenodus*, as a potential ancestor for the Old World *"Hipparion"* Datum, a remarkable event that resulted in a Eurasian population of hipparionine horses then considered to be about 12 Ma in age, and prior to the ca. 10 Ma time of origin of *Hipparion*, *s.s.* (MacFadden, 1980) in that theater, either by immigration from North America (e.g., Woodburne et al. 1981; Woodburne et al., 1996) or from an endemic source (Bernor et al., 1988). MacFadden (1980) proposed a definition for *Hipparion*, *s.s.*, as opposed to other hipparionine horses, followed by Bernor et al. (1980), Woodburne et al. (1981, who advocated distinguishing Vallesian-aged hipparions as a separate taxon, *"Hipparion"*), and by Woodburne (1996a; Woodburne et al. 1996a, who invoked the nomen, *Hippotherium*, for this taxon). Bernor et al. (1996, 1997) utilized *Hippotherium primigenium* for samples from Höwenegg, Germany, in recognition that the nomen *Hippotherium primigenium* Meyer 1829 is applicable to Vallesian-age hipparionine samples from Germany and elsewhere in Europe. In the present work, the dispersal event from North America that resulted in the Vallesian appearance of hipparionine horses is termed the *Hippotherium* Datum.

MacFadden (1984) produced a seminal review of North American hipparionine taxa, including the three species of *Cormohipparion* then known (*C. goorisi*, *C. sphenodus*, and *C. occidentale*). Woodburne (1996b) revised the late Barstovian material from the Valentine Formation, Nebraska, as *C. quinni* and restricted the nomen *Merychippus sphenodus* to its type material. Hulbert (1987) described a derived species, *Cormohipparion emsliei*, from the late Hemphillian to Blancan of Florida. Subsequently, Hulbert (1988) segregated *C. emsliei*, *C. plicatile*, and *C. ingenuum* as the subgenus *Notiocradohipparion* and included *Hippotherium* (as *"Hippotherium"*) *primigenium* in the new subgenus *Cormohipparion*. Woodburne (2003) further distinguished *C. goorisi* from the merychippine stem taxon *Merychippus insignis* and pursued the method of dental morphology appraisal used here. Studies undertaken since 1985 have led to the appreciation, alluded to by Woodburne (in Bernor et al., 1996), that samples allocated to *C. occidentale* contain more than one specific-rank taxon, and that one of these was the source of the *Hippotherium* dispersal event. Documentation of these proposals forms the corpus of this report.

## SYSTEMATIC PALEONTOLOGY

### *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). In Osborn (1918: fig. 140) and Skinner and MacFadden (1977), RP2, RP3, ?RM1, RM2, and LP3 are represented.

INCLUDED SPECIES: Species included in the subgenus *Cormohipparion*, revised from Hulbert (1988), are *C. goorisi* MacFadden and Skinner 1981 (early Barstovian, Texas); *C. quinni* Woodburne 1996b (late Barstovian, Nebraska and Colorado); *C. matthewi*, n.sp. (late medial Clarendonian, Nebraska); *C. merriami*, n.sp. (early Clarendonian, Nebraska); *C. johnsoni*, n.sp. (early Clarendonian, Nebraska); *C. fricki*, n.sp. (early medial Clarendonian, Texas and Nebraska); *C. skinneri*, n.sp. (late medial Clarendonian, Texas); and *C. occidentale* (late medial Clarendonian, Nebraska and South Dakota). Materials allocated here to *Cormohipparion* sp. occur in El Paso Basin faunas of medial Clarendonian age in California (fig. 2) and in the Devil's Punchbowl, Valyermo, California (fig. 1), also likely of medial Clarendonian age (Woodburne, 2005).

Species included in the subgenus *Notiocradohipparion* Hulbert 1988 are *C. (N.) plicatile* (MacFadden, 1984; Hulbert, 1988); medial Clarendonian through medial Hemphillian, Florida; *C. (N.) ingenuum* (MacFadden, 1984; Hulbert, 1988); medial Clarendonian through medial Hemphillian, Florida; medial Clarendonian, Texas; early or medial Hemphillian, Honduras; *C. (N.) emsliei* Hulbert, 1987; late Hemphillian to Blancan, Florida; late Hemphillian, Louisiana.

GEOGRAPHIC AND CHRONOLOGIC DISTRIBUTION: Early Barstovian of Texas; late Barstovian of Colorado and Nebraska; early Clarendonian of Nebraska; medial Clarendonian of California, Nebraska, South Dakota, Texas, and Florida; Hemphillian to Blancan of Florida; late Hemphillian of Louisiana. As discussed below, *Cormohipparion* is not found yet beyond North America, contrary to Bernor et al. (2003).

TYPE SPECIMEN: Hulbert (1988) gave a definition of the subgenus *Notiocradohipparion* but not of the sister taxon he nominated as the subgenus, *Cormohipparion*. Relative to *Notiocradohipparion*, the subgenus *Cormohipparion* is plesiomorphic in the retention of a short muzzle. The most primitive members of the subgenus *Cormohipparion* (*C. goorisi* and *C. quinni*) have the derived condition of a strongly pocketed posterior extent of the DPOF, and all members of this subgenus are derived in having the IOF located anteriorly, above the P3 or the P3–P4 boundary, and closely associated with the anterior or anteroventral edge of the DPOF. In this combination of characters, at least, members of the subgenus *Cormohipparion* differ from approximately contemporaneous other taxa: *Parahippus leonensis*, *Merychippus insignis*, *M. shirleyi*, *"M." primus*, *"M." tertius*, *Parapliohippus carrizoensis*, *Acritohippus stylodontus*, *Scaphohippus sumani*, *"M." coloradense*, *P. mirabilis* (list from Hulbert and MacFadden, 1991: fig. 15; note that other species in this figure are known only from dentitions; *Parapliohippus carrizoensis* and *Acritohippus stylodontus* is from Kelly, 1995; *Scaphohippus sumani* is from Pagnac, 2006).

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

AGE: Likely medial Clarendonian.

DEFINITION OF *CORMOHIPPARION*: Note that this definition does not depend on the number of OTUs in *C. occidentale*, *s.l.* This definition is taken from Woodburne (1996b) and therefore is modified from MacFadden (1984) and Hulbert (1987): Mesodont to hypsodont hipparion. The mean TRL ranges from about 116 mm to 140 mm. The unworn or little-worn M1MSHT ranges from about 34 mm to 66 mm (table 3B). The DPOF is prominent with a relatively well-developed and usually continuous anterior rim, with the IOF located above P3, the P2–P3 boundary, or the P3–P4 boundary and consistently very close to the anteroventral tip of the DPOF. Posteriorly, this fossa has a well-developed and pocketed rim. In general, the fossa is oval or teardrop-shape in outline and situated far anterior of the orbit, resulting in a wide POB. The anterior tip of the lacrimal bone enters into the rear of the DPOF (primitive species) or does not reach the rear of the fossa (advanced species). The DPOF is lost or severely reduced in advanced species of *C. (Notiocradohipparion)*, such as *C. (N.). emsliei* (Hulbert, 1987). The DP1 is relatively large and persistent into the adult condition, except in more derived species, where it tends to be smaller and not to persist into adult wear, or it tends to be limited to females. The protocone is isolated (except in P2) until very late wear, with a spur in plesiomorphic taxa. The protocone becomes ovate to elongate-oval in shape in evolved species. The P2 anterostyle is well developed; P2 is slightly (plesiomorphously) longer to much longer than other cheek teeth. The pli caballin is prominent; it is usually multiple (2 or more plis) in premolars and single in molars. Fossette borders are moderately to very complex (especially the opposing borders of pre- and postfossettes). The anterior border of the prefossette is increasingly complex in derived taxa. The lower cheek teeth generally possess protostylids (except *C. goorisi*).

*Cormohipparion occidentale* (Leidy), 1856
figures 9–11, 13; tables 2–8

TYPE SPECIMEN: ANSP 11287, four left and one right upper cheek teeth (fig. 9D). See Skinner and MacFadden (1977: 919, fig. 4D) and Osborn (1918: 176, fig. 140). According to Osborn (1918: 176), these are RP2–3, M2, and LP3. Another specimen, ?RM1 (Skinner and MacFadden, 1977), is not specifically discussed, nor is it part of the cast series (AMNH 10794) in the AMNH.

TYPE LOCALITY: Probably from along Little White River, South Dakota, a possible correlate of the XMas-Kat quarries in Nebraska (Skinner and Johnson, 1984).

AGE: Clarendonian, likely late medial Clarendonian.

DISTRIBUTION: ?Late medial Clarendonian of South Dakota; late medial Clarendonian of north-central Nebraska (XMas-Kat, Machaerodus, and Hans Johnson quarries).

DESCRIPTION OF TYPE SPECIMEN: This is based on casts of ANSP 11287 in the AMNH and on Osborn (1918: 177, fig. 140), Skinner and MacFadden (1977), and MacFadden (1984). The material is considered to represent four right cheek teeth and a single left upper molar, RP2, RP3, ?RM1, RM2 and LP3, with P2–M2 illustrated as reversed in figure 9D. As indicated in table 4A, the teeth are interpreted to be in about middle to one-third wear, with mesostyle heights ranging from about 30 mm (P2) to 41 mm (M2). The enamel pattern is of moderate complexity, with 3–5 plis on the anterior border of the prefossette, 4–7 plis on the posterior border of the prefossette, 3–5 plis on the anterior border of the postfossette, and 1 pli on the posterior border of the postfossette. The protocone is ovate to elongate-oval, nearly flat to slightly concave lingually, and nearly flat to slightly convex labially. The hypoconal groove is simple and open and lacks a hypoconal spur. The pli caballin is most complex in the premolars (2–3) and single in the only molar. The pli caballin is directed somewhat posterolingually in all of these teeth, except for M2, where it is slightly anterolingually directed. The pre- and post-

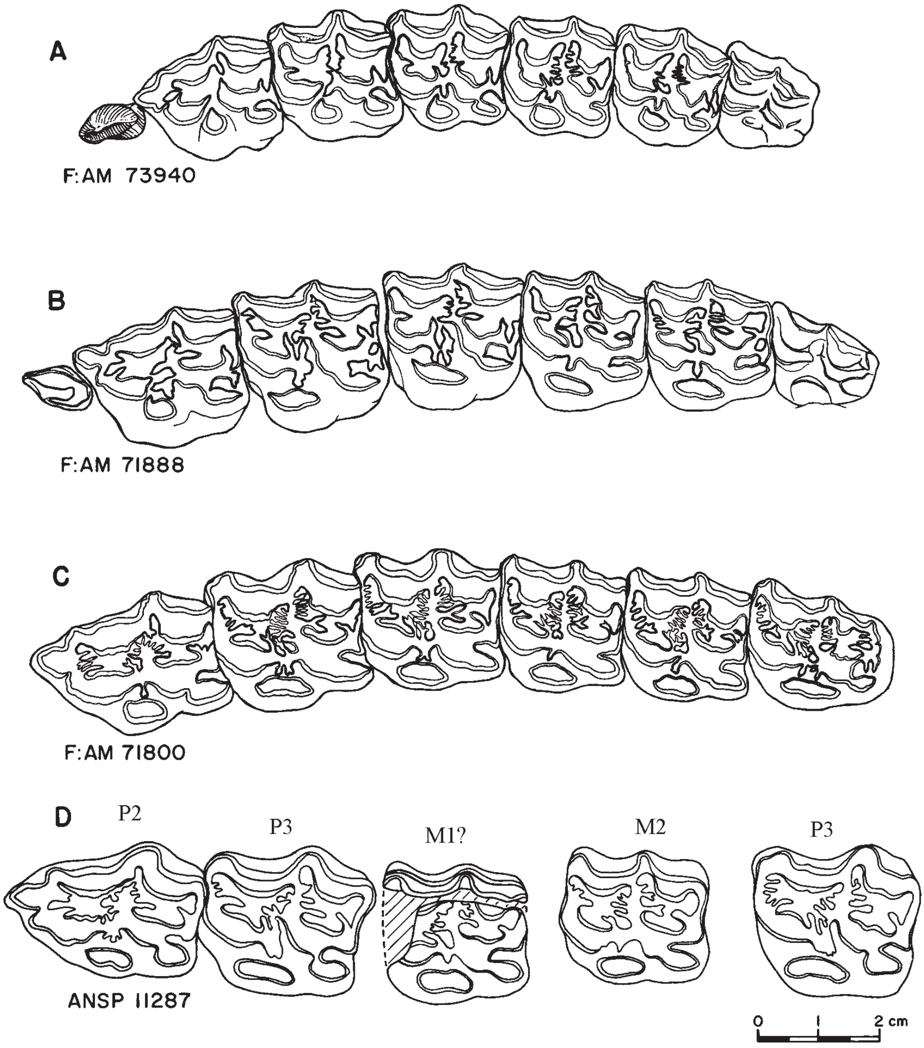


Fig. 9. Upper cheek tooth dentition of *Cormohipparion*. **A,** *C. goorisi*, type, F:AM 73940, LdP1, P2–M3, Trinity River Pit 1, early Barstovian, Texas. **B,** *C. quinni*, type, F:AM 71888, LdP1, P2–M3, Devil's Gulch Horse Quarry, late Barstovian, Nebraska. **C,** *C. occidentale*, F:AM 71800, RP2, P3, ?M1, M2, reversed, LP3, XMas-Kat quarries, medial Clarendonian, Nebraska. **D,** *C. occidentale*, type, ANSP 11287, Little White River, early Clarendonian, South Dakota. After Skinner and MacFadden (1977: fig. 4).

fossettes are united along their labial margins in P2. Based on the crown height of M2 (table 4A), the unworn MSTHT for these cheek teeth appears likely to have been in the range of 50–65 mm, based on other material referred to *C. occidentale*. The pre- and postfossette of P2 are confluent labially.

The type material was compared with specimens from F:AM locality Hollow Horn Bear Quarry, South Dakota, as potentially representative of the area from which the type materials are thought to have been collected. As discussed above, this site apparently is correlative with the Minnechaduza Fauna (figs. 2, 7), and, as described below, F:AM 71880 (fig. 8B) therefrom has a more plesiomorphic molar and lacrimal morphology compared with examples of *C. occidentale*. F:AM 71880 is herein referred to *C. fricki*, n.sp., as are the other specimens from the Hollow Horn Bear Quarry (table 4B).

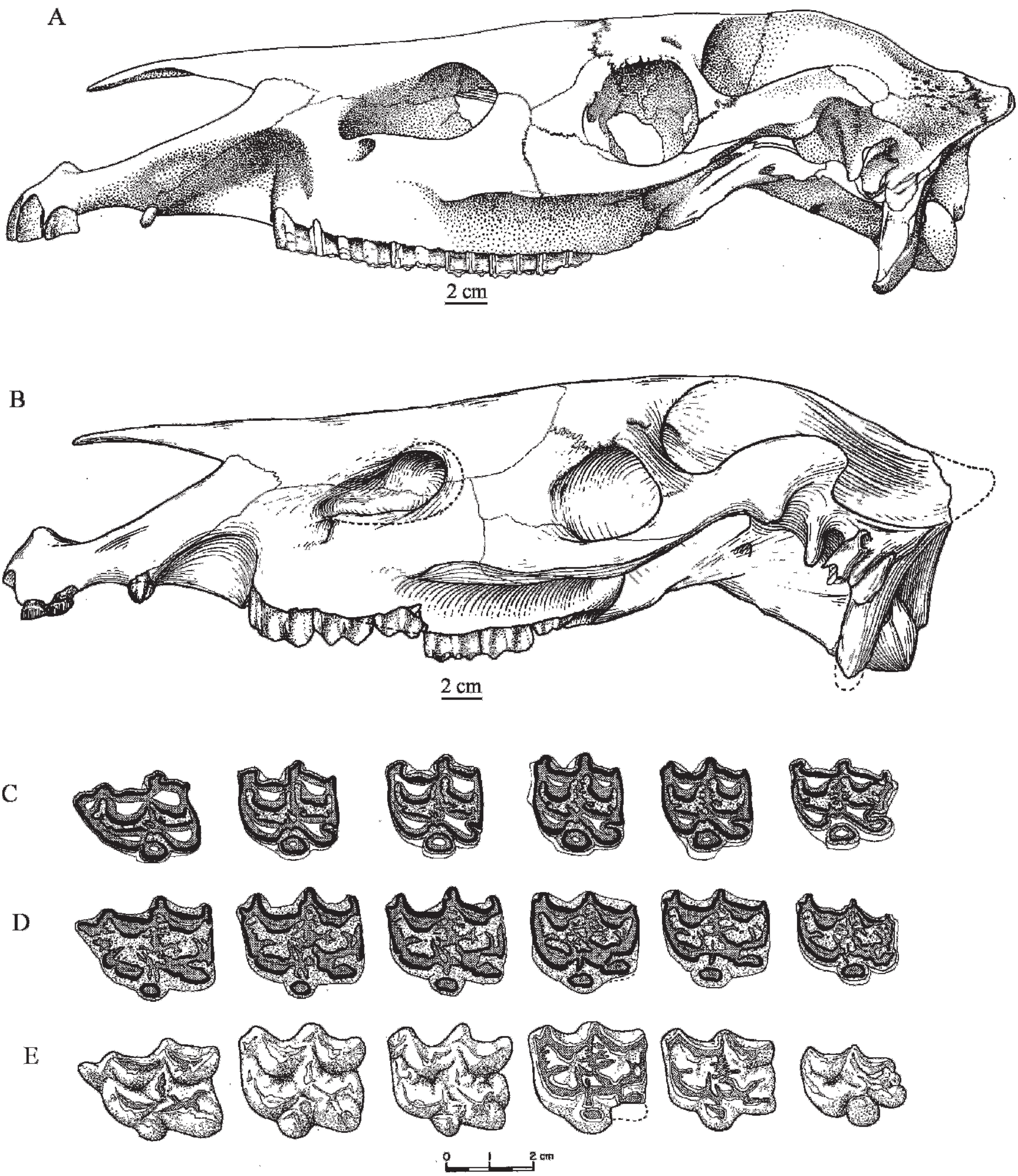


Fig. 10. *Cormohipparion occidentale*, referred. **A,** F:AM 71800, XMas-Kat Quarry, Merritt Dam Member, Ash Hollow Formation, Cherry County, Nebraska, lateral view of cranium. After MacFadden (1984: fig. 131). See figure 7C for upper cheek tooth dentition. **B–E,** F:AM 71801. **B,** lateral view of cranium, after MacFadden (1984: fig. 132). **C–E,** cross-section and occlusal pattern of left upper cheek tooth dentition. **C,** near base of tooth. **D,** approximate middle of tooth. **E,** occlusal surface of tooth. After MacFadden (1984: fig. 18).

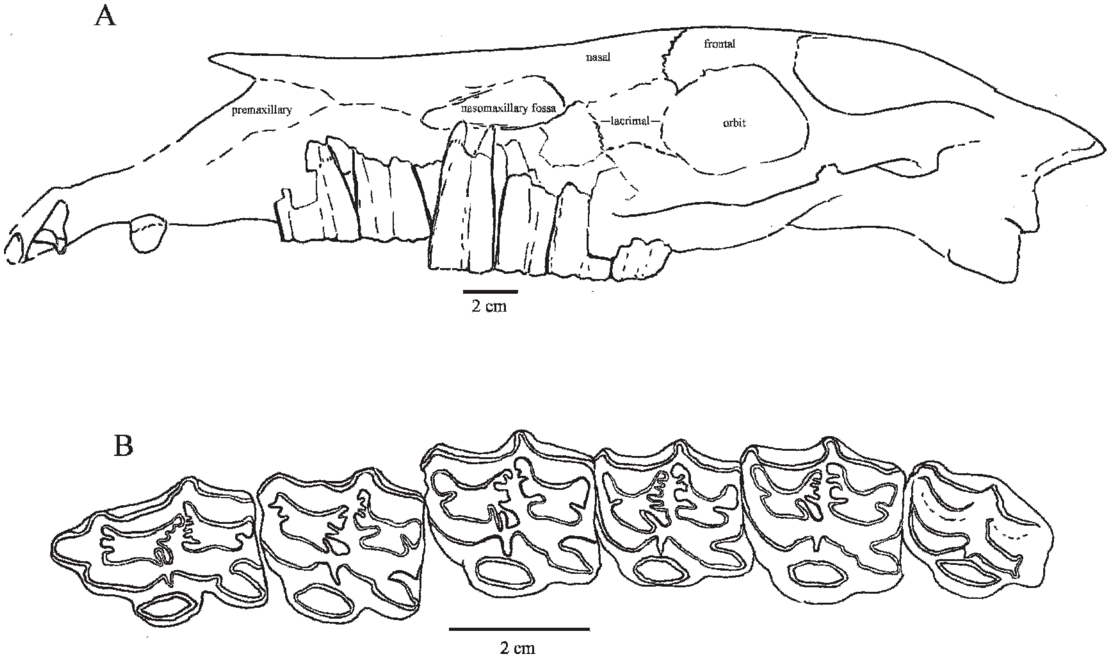


Fig. 11. *Cormohipparion* cf. *occidentale*. F:AM 71872, ?Thin Elk Formation, South Dakota, early Clarendonian. **A,** lateral view of cranium showing tall-crowned upper cheek teeth. **B,** occlusal view of left upper cheek teeth.

Specimens possibly from the Thin Elk Formation, F:AM 71872 and AMNH 10869 (table 4C), are higher crowned than seen in *C. fricki*, n.sp.; show a more derived dental morphology (more elongate protocones) than F:AM 71880 (table 4B); and are considered to be chronologically younger than specimens from the Hollow Horn Bear Quarry. These same specimens are morphologically comparable to the type material of *C. occidentale* and suggest that both the Thin Elk Formation and the type material are younger than taxa from the Minnechaduza-equivalent interval (see Webb, 1969). If the Thin Elk Formation provenance of F:AM 71872 and AMNH 10869 can be verified, the presence of abundant garnet crystals in both the Thin Elk Formation and the Merritt Dam Member of the Ash Hollow Formation (there associated with the XMas-Kat and Machaerodus quarries) also would be consistent with the age interpretations explored here.

The type of *C. occidentale* also was compared with a sample of *Neohipparion affine* (following MacFadden, 1984), as this taxon also has an upper cheek tooth morphology in which an elongate, isolated protocone is prominent (contrary to species of *Hipparion* and *Nannippus* as summarized in MacFadden, 1984). Specimens with dentitions in crania that also preserve the facial morphology are represented, in part, by AMNH 141218 (fig. 12A–B) from the Hollow Horn Bear Quarry and by F:AM 111728 (MacFadden, 1984: fig. 66; fig. 12C–D), F:AM 111729 (MacFadden, 1984: fig. 67), and F:AM 132652–132656 from the MacAdams Quarry, Clarendon beds, Texas. As shown in figures 12B and 12D, the elongate and lingually concave protocone of these specimens is similar to that shown in the type of *C. occidentale*. These specimens all differ, however (table 4D), in the distinctly simpler fossette border morphology, the single pli caballin in premolars as well as molars, the anterior orientation of this pli caballin in premolars as well as molars, the more lingually slanted axis of the hypoconal groove in the premolars overall, and the generally less prominent pli protoconule of the premolars as well as the molars. The

TABLE 5

**Measurements (mm) of Crania of *Cormohipparion occidentale*, Late Medial Clarendonian, Nebraska and South Dakota**

| | Character[a] | | | | | |
|---|---|---|---|---|---|---|
| Specimen | 1, muz | 2, pal | 3, popl | 4, basc | 5, comb | 6, tsl |
| ***C. occidentale*; XMas-Kat Quarries, Merritt Dam Member, Ash Hollow Formation, Nebraska** | | | | | | |
| F:AM 71800 ♀ | 110.7 | 109.6 | 95.7 | 80.1 | 170.3 | 395.7 |
| F:AM 71801 ♂ | 102.2 | 109.0 | 94.2 | 88.8 | 181.5 | 402.6 |
| F:AM 71803 ♂ | 102.8 | | | | 200.8 | 376.4 |
| F:AM 71806 ♀ | 111.1 | 116.8 | | | | |
| F:AM 71807 | | | | | | |
| F:AM 71808 | | | | | | |
| F:AM 71809 ♀ | | | | | | |
| F:AM 71810 | | | | | | |
| F:AM 71813 ♀ | | | | | | |
| F:AM 71814 ♂ | | | | | | |
| F:AM 71868 ♂ | 103.4 | 109.4 | | | | |
| Range | 102.2–111.1 | 109.9–116.8 | 94.2–95.7 | 80.1–88.8 | 170.3–200.8 | 376.4–402.6 |
| Mean | 106.0 | 111.2 | 95.0 | 84.5 | 184.2 | 391.6 |
| SD | 4.46 | 3.74 | 1.06 | 6.15 | 15.43 | 13.58 |
| CV | 4.20 | 3.36 | 1.12 | 7.28 | 8.38 | 3.47 |
| *N* | 5 | 4 | 2 | 2 | 3 | 3 |
| ***Cormohipparion occidentale*; Machaerodus Quarry, Merritt Dam Member, Ash Hollow Formation, Nebraska** | | | | | | |
| F:AM 71832 ♂ | 103.7 | 89.4 | 99.8 | 87.2 | 182.8 | 336.0 |
| F:AM 71834 ♀ | 103.3 | 70.2 | | | | |
| F:AM 71835 | | | | | | |
| F:AM 71844 ♂ | 99.1 | | | | | |
| F:AM 71831 ♂ | 99.3 | 90.9 | | | | |
| Range | 99.1–103.7 | 70.2–90.0 | | | | |
| Mean | 101.4 | 83.5 | 99.8 | 87.2 | 182.8 | 336.0 |
| SD | 2.49 | 11.54 | | | | |
| CV | 2.46 | 13.83 | | | | |
| *N* | 4 | 3 | 1 | 1 | 1 | 1 |
| ***C. occidentale*; Hans Johnson Quarry, Merritt Dam Member, Ash Hollow Formation, Nebraska** | | | | | | |
| F:AM 71855 ♂ | 120.0 | | | | | |
| F:AM 71856 ♂ | | 98.0 | 98.2 | 85.1 | 175.6 | |
| F:AM 71857 ♀ | 100.2 | 105.9 | 80.1 | 88.4 | 163.7 | 370.2 |
| F:AM 71858 ♀ | 106.9 | 101.8 | 89.1 | 82.1 | 172.3 | 383.2 |
| F:AM 71860 ♂ | 105.7 | 82.2 | | | | |
| F:AM 71861 ♀ | | | | | | |
| F:AM 71862 ♀ | 108.8 | 100.2 | | | | |
| Range | 100.2–120.0 | 82.2–105.9 | 80.1–98.2 | 82.1–88.4 | 163.7–175.6 | 370.2–383.2 |
| Mean | 108.3 | 97.6 | 89.1 | 85.2 | 170.5 | 376.7 |
| SD | 7.27 | 9.09 | 9.05 | 3.15 | 6.14 | 9.19 |
| CV | 6.71 | 9.31 | 10.16 | 3.70 | 3.60 | 2.44 |
| *N* | 5 | 5 | 3 | 3 | 3 | 2 |
| ***Cormohipparion* cf. *occidentale*; Ed Ross Ranch Quarry, ?Thin Elk Formation, South Dakota** | | | | | | |
| F:AM 71872 ♂ | 111.5 | | | | 161.5a | 380.0a |

TABLE 5
(*Continued*)

| Specimen | Character[a] 7, upl | 8, uml | 9, tcl | 12, choa | 13, palw | 14, sntw |
|---|---|---|---|---|---|---|
| ***C. occidentale*; XMas–Kat Quarries, Merritt Dam Member, Ash Hollow Formation, Nebraska** | | | | | | |
| F:AM 71800 ♀ | 77.4 | 64.1 | 140.3 | 33.7 | 54.9 | 30.3 |
| F:AM 71801 ♂ | | | | 29.6 | 52.1 | 37.3 |
| F:AM 71803 ♂ | 77.1 | 66.0 | 141.9 | 33.4 | 55.5 | 34.1 |
| F:AM 71806 ♀ | 75.8 | 62.9 | 139.9 | | 57.7 | 30.2 |
| F:AM 71807 | 87.8 | 73.5 | 158.8 | | | |
| F:AM 71808 | | 66.4 | | | | |
| F:AM 71809 ♀ | 76.6 | 62.7 | 139.8 | | | |
| F:AM 71810 | | 70.0 | | | | |
| F:AM 71813 ♀ | 82.2 | 69.2 | 149.5 | | | |
| F:AM 71814 ♂ | | 65.5 | | | | |
| F:AM 71868 ♂ | | | | 35.7 | | 34.1 |
| Range | 75.8–87.8 | 62.7–73.5 | 139.8–141.9 | 29.6–35.7 | 52.1–57.7 | 30.2–37.3 |
| Mean | 79.5 | 66.7 | 145.0 | 33.1 | 55.1 | 33.2 |
| SD | 4.66 | 3.60 | 7.69 | 2.55 | 2.31 | 2.99 |
| CV | 5.86 | 5.39 | 5.30 | 7.69 | 4.19 | 9.02 |
| *N* | 6 | 9 | 6 | 4 | 4 | 5 |
| ***C. occidentale*; Machaerodus Quarry, Ash Hollow Formation, Nebraska** | | | | | | |
| F:AM 71832 ♂ | 69.8 | 59.8 | 130.0 | 29.5 | 49.0 | 32.0 |
| F:AM 71834 ♀ | 67.0 | 62.0 | 125.2 | | 59.9 | 31.4 |
| F:AM 71835 | 80.4 | 67.7 | 146.7 | | | |
| F:AM 71844 ♂ | 76.2 | 65.8 | 139.1 | | | |
| F:AM 71831 ♂ | | | | | | 33.0 |
| OR | 67.0–80.4 | 59.8–67.7 | 125.2–146.7 | | 49.0–59.9 | 31.4–33.0 |
| Mean | 73.4 | 63.8 | 135.3 | 29.5 | 54.5 | 32.1 |
| SD | 6.08 | 3.58 | 9.57 | | 7.71 | 0.81 |
| CV | 8.28 | 5.61 | 7.07 | | 14.16 | 2.52 |
| *N* | 4 | 4 | 4 | 1 | 2 | 3 |
| ***C. occidentale*; Hans Johnson Quarry, Ash Hollow Formation, Nebraska** | | | | | | |
| F:AM 71855 ♂ | 68.0 | 62.2 | 129.3 | | | |
| F:AM 71856 ♂ | 72.8 | 63.3 | 134.2 | 33.0 | 56.6 | 36.4 |
| F:AM 71857 ♀ | 73.9 | 61.7 | 134.7 | 38.2 | 58.0 | 35.8 |
| F:AM 71858 ♀ | 70.3 | 61.3 | 128.7 | 28.5 | 51.2 | 28.6 |
| F:AM 71860 ♂ | 74.3 | 62.5 | 135.8 | 39.2 | 62.7 | 38.8 |
| F:AM 71861 ♀ | 78.0 | 64.0 | 140.1 | | 60.9 | 38.0 |
| F:AM 71862 ♀ | 81.8 | | | | | |
| Range | 68.0–81.8 | 61.7–63.3 | 128.7–140.1 | 28.5–39.2 | 51.2–62.7 | 28.6–38.8 |
| Mean | 74.2 | 62.5 | 133.8 | 34.7 | 57.9 | 35.5 |
| SD | 4.62 | 1.00 | 4.26 | 4.96 | 4.43 | 4.05 |
| CV | 6.23 | 1.61 | 3.19 | 14.29 | 7.66 | 11.40 |
| *N* | 7 | 6 | 6 | 4 | 5 | 5 |
| ***Cormohipparion* cf. *occidentale*; Ed Ross Ranch Quarry, ?Thin Elk Formation, South Dakota** | | | | | | |
| F:AM 71872 ♂ | | 66.2 | | 26.5 | | 30.8a |

TABLE 5
(*Continued*)

| Specimen | Character[a] | | | | | |
|---|---|---|---|---|---|---|
| | 15, wmuz | 18, fwd | 19, trgl | 22, in | 25, snh | 28, orl |
| ***C. occidentale*; XMas–Kat Quarries, Ash Hollow Formation, Nebraska** | | | | | | |
| F:AM 71800 ♀ | 48.3 | 133.9 | 135.1 | 54.7 | 74.1 | 55.1 |
| F:AM 71801 ♂ | 55.5 | 134.0 | 139.2 | | 78.9 | 57.6 |
| F:AM 71803 ♂ | 47.4 | 119.2 | 144.3 | | 78.5 | 60.0 |
| F:AM 71806 ♀ | 45.3 | | | | 79.9 | |
| F:AM 71807 | | | | | | |
| F:AM 71808 | | | | | | |
| F:AM 71809 ♀ | | | | | | 56.3 |
| F:AM 71810 | | | 140.0 | 73.0 | | |
| F:AM 71813 ♀ | 50.9 | | | | | |
| F:AM 71814 ♂ | 54.0 | | | | | |
| F:AM 71868 ♂ | 46.9 | | | | | |
| Range | 45.3–50.9 | 119.2–134.0 | 135.1–144.3 | 54.7–73.0 | 74.1–79.9 | 55.1–60.0 |
| Mean | 49.8 | 129.0 | 139.7 | 63.9 | 77.9 | 57.3 |
| SD | 3.83 | 8.52 | 3.77 | 12.94 | 2.57 | 2.10 |
| CV | 7.70 | 6.60 | 2.70 | 20.27 | 3.30 | 3.67 |
| *N* | 7 | 3 | 4 | 2 | 4 | 4 |
| ***C. occidentale*: Machaerodus Quarry, Ash Hollow Formation, Nebraska** | | | | | | |
| F:AM 71832 ♂ | 47.1 | 129.2 | 148.6 | 67.2 | 80.0 | 49.8 |
| F:AM 71834 ♀ | 46.9 | 137.8 | | | 81.0 | 51.3 |
| F:AM 71835 | | | | | | |
| F:AM 71844 ♂ | | | | | | |
| F:AM 71831 ♂ | 47.8 | | | | 67.0 | |
| Range | 46.9–47.8 | 129.2–137.8 | | | 67.0–81.0 | 49.8–51.3 |
| Mean | 47.3 | 133.5 | 148.6 | 67.2 | 76.0 | 50.55 |
| SD | 0.47 | 6.08 | | | 7.81 | 1.06 |
| CV | 1.00 | 4.56 | | | 10.28 | 2.30 |
| *N* | 3 | 2 | 1 | 1 | 3 | 2 |
| ***C. occidentale*; Hans Johnson Quarry, Ash Hollow Formation, Nebraska** | | | | | | |
| F:AM 71855 ♂ | | | | | | 53.6 |
| F:AM 71856 ♂ | 54.3 | 124.0 | 130.8 | | 85.6 | 55.8 |
| F:AM 71857 ♀ | 52.3 | 141.3 | 142.3 | | | 54.2 |
| F:AM 71858 ♀ | 47.3 | 143.3 | 137.6 | 63.2 | 85.4 | 57.7 |
| F:AM 71860 ♂ | 54.7 | | | | | 53.8 |
| F:AM 71861 ♀ | 37.5 | | | | | |
| F:AM 71862 ♀ | 47.0 | | | 61.5 | | |
| Range | 37.5–54.7 | 124.0–143.3 | 130.8–142.3 | 61.5–63.2 | 85.4–85.6 | 53.6–57.7 |
| Mean | 48.9 | 136.2 | 136.9 | 62.4 | 85.5 | 55.0 |
| SD | 6.49 | 10.61 | 5.78 | 1.20 | 0.14 | 1.73 |
| CV | 13.28 | 7.79 | 4.22 | 1.93 | 0.17 | 3.14 |
| *N* | 6 | 3 | 3 | 2 | 2 | 5 |
| ***Cormohipparion* cf. *occidentale*; Ed Ross Ranch Quarry, ?Thin Elk Formation, South Dakota** | | | | | | |
| F:AM 71872 ♂ | 48.7 | 126.0a | | | | |

TABLE 5
(*Continued*)

| Specimen | Character[a] | | | | | |
|---|---|---|---|---|---|---|
| | 29, orh | 30, nis | 31, fac | 32, pobl | 33, dpof | 34, iof |
| ***C. occidentale*; Xmas–Kat Quarries, Ash Hollow Formation, Nebraska** | | | | | | |
| F:AM 71800 ♀ | 49.2 | 113.5 | 149.4 | 39.7 | 71.3 | 59.2 |
| F:AM 71801 ♂ | 47.5 | 118.5 | 157.6 | 46.1 | 62.4 | 54.7 |
| F:AM 71803 ♂ | 44.8 | 100.9 | 160.6 | 45.5 | 71.8 | 61.0 |
| F:AM 71806 ♀ | | | 158.5 | 42.2 | 75.2 | 69.0 |
| F:AM 71807 | | | | | | |
| F:AM 71808 | | | | | | |
| F:AM 71809 ♀ | 45.0 | | | 49.5 | 71.5 | 68.2 |
| F:AM 71810 | | | | | | |
| F:AM 71813 ♀ | | | | | | |
| F:AM 71814 ♂ | | | | | | |
| F:AM 71868 ♂ | | 113.8 | 163.7 | 47.3 | 70.3 | 52.8 |
| Range | 45.0–49.2 | 100.9–118.5 | 149.4–163.7 | 39.7–49.5 | 62.4–75.2 | 52.8–69.0 |
| Mean | 46.6 | 111.7 | 158.0 | 45.1 | 70.4 | 60.8 |
| SD | 2.11 | 7.54 | 5.33 | 3.55 | 4.27 | 6.72 |
| CV | 4.53 | 6.75 | 3.37 | 7.87 | 6.06 | 11.05 |
| *N* | 4 | 4 | 5 | 6 | 6 | 6 |
| ***C. occidentale*: Machaerodus Quarry, Ash Hollow Formation, Nebraska** | | | | | | |
| F:AM 71832 ♂ | 48.8 | 115.3 | 147.5 | 40.4 | 71.2 | 64.0 |
| F:AM 71834 ♀ | 45.3 | | | 36.5 | 62.1 | 65.6 |
| F:AM 71835 | | | | | | |
| F:AM 71844 ♂ | | | | | | |
| F:AM 71831 ♂ | | 109.0 | | 44.0 | 62.8 | 55.5 |
| Range | 45.3–48.8 | 109.0–115.3 | | 36.5–44.0 | 62.1–71.2 | 55.5–65.6 |
| Mean | 47.1 | 112.2 | 147.5 | 40.3 | 65.4 | 61.7 |
| SD | 2.47 | 4.56 | | 3.75 | 5.06 | 5.43 |
| CV | 5.26 | 3.98 | | 9.31 | 7.48 | 8.80 |
| *N* | 2 | 2 | 1 | 3 | 3 | 3 |
| ***Cormohipparion occidentale*; Hans Johnson Quarry, Ash Hollow Formation, Nebraska** | | | | | | |
| F:AM 71855 ♂ | | 115.9 | | 45.8 | | 60.8 |
| F:AM 71856 ♂ | 49.5 | | 140.6 | 39.8 | 60.2 | 65.0 |
| F:AM 71857 ♀ | 49.5 | 116.5 | 153.7 | 48.0 | 69.5 | 61.2 |
| F:AM 71858 ♀ | 46.5 | 113.8 | 159.5 | 38.5 | 73.6 | 66.0 |
| F:AM 71860 ♂ | 49.2 | | | 42.2 | 68.7 | 57.2 |
| F:AM 71861 ♀ | | | | 38.5 | 74.6 | 65.3 |
| F:AM 71862 ♀ | | 116.4 | | 49.8 | 63.7 | 56.9 |
| Range | 46.5–49.5 | 113.8–116.5 | 140.6–159.5 | 38.5–49.8 | 60.2–74.6 | 56.9–66.0 |
| Mean | 48.7 | 115.7 | 151.3 | 43.6 | 68.4 | 61.8 |
| SD | 1.46 | 1.26 | 9.68 | 5.00 | 5.59 | 3.80 |
| CV | 2.99 | 1.09 | 6.40 | 11.47 | 8.17 | 6.15 |
| *N* | 4 | 4 | 3 | 7 | 6 | 7 |
| ***Cormohipparion* cf. *occidentale*; Ed Ross Ranch Quarry, ?Thin Elk Formation, South Dakota** | | | | | | |
| F:AM 71872 ♂ | | | | 36.7a | 56.0a | |

TABLE 5
(*Continued*)

| Specimen | Character[a] | | | | | |
|---|---|---|---|---|---|---|
| | 35, hdof | 36, fch | 37, ioa | 38, mpof | 39, ldof | 40, medof |
| ***Cormohipparion occidentale*; XMas–Kat Quarries, Merritt Dam Member, Ash Hollow Formation, Nebraska** | | | | | | |
| F:AM 71800 ♀ | 39.3 | 32.0 | 42.7 | 60.5 | 17.3 | 19.2 |
| F:AM 71801♂ | 30.1 | 34.2 | 41.5 | 57.0 | 13.3 | 14.5 |
| F:AM 71803♂ | 29.0 | 34.8 | 33.3 | 52.3 | 21.0 | |
| F:AM 71806 ♀ | 35.4 | 25.8 | | 59.4 | | |
| F:AM 71807 | | 32.8 | 40.5 | | | |
| F:AM 71808 | | | | | | |
| F:AM 71809 ♀ | 33.6 | 30.0 | 38.0 | | | |
| F:AM 71810 | | | | | | |
| F:AM 71813 ♀ | | | | | | |
| F:AM 71814♂ | | | | | | |
| F:AM 71868♂ | | 34.0 | 52.5 | 61.0 | | |
| Range | 29.0–39.3 | 25.8–34.8 | 33.3–52.5 | 52.3–61.0 | 13.3–21.0 | 14.5–19.2 |
| Mean | 33.5 | 31.9 | 41.4 | 58.0 | 17.2 | 16.9 |
| SD | 4.16 | 3.16 | 6.37 | 3.56 | 3.85 | 3.32 |
| CV | 12.41 | 9.90 | 15.36 | 6.13 | 22.39 | 19.72 |
| *N* | 5 | 7 | 6 | 5 | 3 | 2 |
| ***C. occidentale*; Machaerodus Quarry, Ash Hollow Formation, Nebraska** | | | | | | |
| F:AM 71832♂ | 43.0 | 23.8 | 41.0 | 62.2 | 14.4 | 17.1 |
| F:AM 71834 ♀ | 48.0 | 20.2 | 32.3 | 58.2 | 11.5 | 17.2 |
| F:AM 71835 | | 31.2 | 38.0 | | | |
| F:AM 71844 | | 25.2 | 35.2 | | | |
| F:AM 71831 | 41.0 | 28.8 | 39.0 | 55.1 | 18.9 | 14.2 |
| Range | 41.0–48.0 | 20.2–31.2 | 32.3–41.0 | 55.1–62.2 | 11.5–18.9 | 14.2–17.2 |
| Mean | 44.0 | 25.8 | 37.1 | 58.5 | 14.9 | 16.2 |
| SD | 3.61 | 4.30 | 3.40 | 3.56 | 3.73 | 1.70 |
| CV | 8.19 | 16.63 | 9.17 | 6.08 | 24.97 | 10.54 |
| *N* | 3 | 5 | 5 | 3 | 3 | 3 |
| ***C. occidentale*; Hans Johnson Quarry, Ash Hollow Formation, Nebraska** | | | | | | |
| F:AM 71855 ♂ | 38.5 | 27.6 | 40.0 | 52.8 | 16.5 | 17.0 |
| F:AM 71856 ♂ | | 30.3 | 45.0 | 48.2 | 14.3 | 16.5 |
| F:AM 71857 ♀ | 42.2 | 27.4 | 39.0 | 51.2 | 23.0 | 16.0 |
| F:AM 71858 ♀ | 43.3 | 22.3 | 36.1 | 51.7 | 8.2 | 15.6 |
| F:AM 71860 ♂ | | 26.1 | 38.1 | 51.3 | 17.7 | 15.0 |
| F:AM 71861 ♀ | | 26.0 | 42.2 | 52.2 | 17.0 | |
| F:AM 71862 ♀ | 43.9 | | 43.9 | 51.8 | 19.7 | 16.0 |
| Range | 38.5–43.9 | 22.3–30.3 | 36.1–43.9 | 48.2–52.8 | 8.2–19.7 | 15.0–17.0 |
| Mean | 42.0 | 26.6 | 40.6 | 51.3 | 16.6 | 16.0 |
| SD | 2.42 | 2.62 | 3.22 | 1.48 | 4.62 | 0.69 |
| CV | 5.77 | 9.86 | 7.93 | 2.88 | 27.75 | 4.33 |
| *N* | 4 | 6 | 7 | 7 | 7 | 6 |
| ***Cormohipparion* cf. *occidentale*, Ed Ross Ranch Quarry, ?Thin Elk Formation, South Dakota** | | | | | | |
| F:AM 71872 ♂ | | | | | 9.1 | |

TABLE 5
(*Continued*)

| Specimen | Wear Class; Remarks |
|---|---|
| ***Cormohipparion occidentale*; XMas–Kat Quarries, Merritt Dam Member, Ash Hollow Formation, Nebraska** | |
| F:AM 71800 ♀ | IV+; M3 well worn; nasals perfect; slight transverse distortion, #18, 19 too small? |
| F:AM 71801 ♂ | III; M3, P4 just erupting; little distortion in cranium; slightly transversely skewed |
| F:AM 71803 ♂ | IV+; M3 erupted; all cranial length measurements approximate |
| F:AM 71806 ♀ | IV; M3 early wear; preorbital and snout distorted; DPOF indistinct anterior rim; dentition relatively simple |
| F:AM 71807 | ?wear class; palatal halves only |
| F:AM 71808 | III; M3 early wear; occiput distorted; palate transversely crushed |
| F:AM 71809 ♀ | IV+; M3 well worn; skull distorted dorsoventrally & transversely; lengths relatively accurate; gaps between P2 and M1 |
| F:AM 71810 | IV+; M3 well worn; cranium badly crushed |
| F:AM 71813 ♀ | IV+; M3 well worn; cranium badly crushed; gaps between P3/P4/M1 |
| F:AM 71814 ♂ | IV+; M3 well worn; cranium badly crushed |
| F:AM 71868 ♂ | II; M2 erupting; skull cracked longitudinally; #11, 12 too wide; anterior rim DPOF relatively indistinct (= juvenile?) |
| ***Cormohipparion occidentale*; Machaerodus Quarry, Merritt Dam Member, Ash Hollow Formation, Nebraska** | |
| F:AM 71832 ♂ | IV+; M3 well worn; cranium generally good condition |
| F:AM 71834 ♀ | IV++; very old; very deep and tall DPOF (#35); DPOF relatively short re: IOF length (#34) |
| F:AM 71835 | IV; M3 in early wear; palate separated |
| F:AM 71844 ♂ | IV; M3 early wear |
| F:AM 71831 ♂ | I; incisors + dP4 present; P2–M2 erupting; facial and snout regions only |
| ***C. occidentale*; Hans Johnson Quarry, Merritt Dam Member, Ash Hollow Formation, Nebraska** | |
| F:AM 71855 ♂ | IV+; M3 well worn; skull laterally crushed, occiput displaced anteriorly, #4 and 6 suspect |
| F:AM 71856 ♂ | IV; M3 worn; cranium skewed, snout twisted |
| F:AM 71857 ♀ | IV+; M3 well worn; cranium transversely skewed |
| F:AM 71858 ♀ | IV+; M3 well worn; cranium slightly crushed, dorsoventrally flattened frontals |
| F:AM 71860 ♂ | IV++; M3 well worn; cranium dorsoventrally crushed; #2 inaccurate, 11, 12 ?too wide, 19 ?too narrow |
| F:AM 71861 ♀ | III; M3 beginning wear; cranium dorsoventrally crushed |
| F:AM 71862 ♀ | III; M3 erupting only; cranium transversely crushed; height measurements too great; occiput distorted |
| ***Cormohipparion* cf. *occidentale*; Ed Ross Ranch, ?Thin Elk Formation, South Dakota** | |
| F:AM 71872♂ | III; M3 beginning wear; cranium dorsoventrally flattened; P2 mesostyle 34.3 mm tall |

[a]Parameter 39 is the length from the rear of the DPOF to the anterior tip of the lacrimal; 40 is the medial depth of the DPOF. All others are shown in figs. 3–5.

a = approximate.

cheek teeth tend to be narrower at comparable stages of wear. Based on these specimens, as well as on other material referred by MacFadden (1984) to *N. affine*, the unworn MSTHT likely was about 55 mm (e.g., F:AM 108236 from the Eli Ash Pit, Cap Rock Member, Ash Hollow Formation, medial Clarendonian, of north-central Nebraska, with very early wear M3 being 52 mm tall, and an early wear M2 and P4 being 54 mm and 52 mm tall, respectively; MacFadden, 1984: fig. 68). F:AM 111728 (MacAdams Quarry, fig. 12E) shows that protostylids are present in p2–m3, as in *C. occidentale* (see below), even in relatively late wear (m1 metaconid and metastylid effectively confluent; MacFadden, 1984: fig. 69).

If the unworn MSTHT of the upper cheek tooth dentition of the type of *C. occidentale* was on the order of 60 mm, as seems likely, it would be beyond the range for all but the XMas-Kat materials and those from Gidley Horse Quarry, Texas, a comparison reinforced by the elongate protocones and fossette border complexity seen in the type material.

The comparisons above validate the operation taken by Skinner and MacFadden (1977) in referring a large sample of late Barstovian and Clarendonian equids to

TABLE 6
**Measurements (mm) of Diastema Length and Canine Position in *Cormohipparion* Species**

| Specimen | Diast. length | Can. loc. | Ratio |
|---|---|---|---|
| *C. occidentale* XMas-Kat Quarry | | | |
| F:AM 71800♀ | 89.0 | 32.0 | 0.36 |
| F:AM 71801♂ | 85.5 | 28.7 | 0.34 |
| F:AM 71803♂ | 83.8 | 27.4 | 0.33 |
| F:AM 71806♀ | 95.4 | 31.6 | 0.33 |
| Range | | | 0.33–0.34 |
| Mean | | | 0.34 |
| SD | | | 0.01 |
| CV | | | 4.37 |
| *N* | | | 4 |
| Machaerodus Quarry | | | |
| F:AM 71832♂ | 87.3 | 27.9 | 0.32 |
| F:AM 71834♀ | 86.0 | 27.2 | 0.32 |
| F:AM 71844♂ | 79.6 | 23.4 | 0.29 |
| F:AM 71831♂ | 79.0 | 26.0 | 0.33 |
| Range | | | 0.29–0.33 |
| Mean | | | 0.31 |
| SD | | | 0.01 |
| CV | | | 4.09 |
| *N* | | | 4 |
| Hans Johnson Quarry | | | |
| F:AM 71855♂ | 105.0 | 35.7 | 0.34 |
| F:AM 71857♀ | 105.0 | 25.5 | 0.24 |
| F:AM 71858♀ | 83.5 | 27.5 | 0.33 |
| F:AM 71860♂ | 85.0 | 23.0 | 0.27 |
| F:AM 71861♀ | 76.0 | 22.0 | 0.29 |
| F:AM 71862 ♀ | 90.0 | 31.0 | 0.34 |
| Range | | | 0.24–0.34 |
| Mean | | | 0.29 |
| SD | | | 0.04 |
| CV | | | 12.8 |
| *N* | | | 6 |

Remarks: Can. loc. = distance between rear of I3 and the anterior alveolus for the canine. F:AM 71831 in wear class I; F:AM 71801, 71861, 71862 in wear class III; F:AM 71800, 71803, 71806, 71832, 71834, 71844, 71855, 71857, 71858, 71860 in wear class IV or above. F:AM 71984 snout proportions likely representative of remnant preserved in F:AM 71891. F:AM 141219 is adult skull; relatively short Canine-I3 diastema.

TABLE 6
(*Continued*)

| Specimen | Diast. length | Can. loc. | Ratio |
|---|---|---|---|
| *Cormohipparion matthewi* | | | |
| Xmas Quarry | | | |
| F:AM 71802 ♀ | 71.8 | 23.6 | 0.33 |
| F:AM 71804♀ | 74.5 | 25.7 | 0.34 |
| F:AM 71805♂ | 70.3 | 21.4 | 0.30 |
| Range | | | 0.30–0.34 |
| Mean | | | 0.33 |
| SD | | | 0.02 |
| CV | | | 5.11 |
| *N* | | | 3 |
| *Cormohipparion fricki* | | | |
| MacAdams Quarry | | | |
| F:AM 73920♂ | 62.0 | 20.0 | 0.32 |
| F:AM 73914♀ | 78.0 | 25.0 | 0.32 |
| F:AM 73915♂ | 58.0 | 15.0 | 0.26 |
| F:AM 73912♂ | 72.5 | 21.0 | 0.29 |
| F:AM 73913♂ | 85.0 | 21.5 | 0.25 |
| F:AM 73921 | 80.0 | 24.2 | 0.30 |
| Range | | | 0.25–0.32 |
| Mean | | | 0.29 |
| SD | | | 0.03 |
| CV | | | 10.3 |
| *N* | | | 6 |
| *Cormohipparion johnsoni* | | | |
| Burge Quarry | | | |
| F:AM 71894 | 63.0 | 16.5 | 0.26 |
| F:AM 125899 | 75.0 | 23.0 | 0.31 |
| F:AM 71891 | imm. | imm. | imm. |
| Range | | | 0.26–0.31 |
| Mean | | | 0.29 |
| SD | | | 0.03 |
| CV | | | 7.87 |
| *N* | | | 2 |
| *Cormohipparion merriami* | | | |
| June Quarry | | | |
| F:AM 141219♀ | 79.0 | 21.0 | 0.27 |

Remarks: F:AM 71891 very immature (imm.); F:AM 71894 in wear class I; F:AM 73913, 73914 in wear class II; F:AM 71805, 73920 in wear class III; F:AM 71802, 73915, 73912, 72921 in wear class IV; F:AM 71804 above wear class IV.

*Cormohipparion* and some of these to *C. occidentale* based on the associated dental features described above and the distinctive morphology of the DPOF. This also is consistent with the action taken by MacFadden (1984) in restricting the nomen *Neohipparion* to specimens referred by him to *N. affine*, *N. coloradense*, *N. trampasense*, *N. leptode*, *N. eurystyle*, and *N. gidleyi.*

REVISED DIAGNOSIS: Based on the type and referred material, within the subgenus *Cormohipparion*, *C. occidentale* is distinguished from *C. goorisi* and *C. quinni* (fig. 9) in larger cranial (and presumably

TABLE 7

**Measurements (mm) of Upper Cheek Tooth Dentition of *Cormohipparion occidentale*, Merritt Dam Member, Ash Hollow Formation, Medial Clarendonian, Nebraska**

Height is at mesostyle; boldface specimens used in plication count statistics; a = approximate; rel. = relatively.

| P2 | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | | | | | | Protocone | | | | |
| Specimen | Height | Length | Width | Ratio | Index | Length | Width | Ratio | Pli caballin | Hypoconal groove |
| XMas-Kat Quarry | | | | | | | | | | |
| **F:AM 71868♂** | 43.3 | 32.4 | 24.4 | 0.75 | unworn | | | | | |
| **F:AM 71801♂** | 42.0a | 32.0 | 23.5 | 0.73 | ?:?:?:? | | | | | |
| **F:AM 71807** | 39.0 | 34.2 | 25.6 | 0.75 | 6:7:5:3 | 7.3 | 3.8 | 0.52 | 1 | open; simple |
| **F:AM 71810** | 29.0 | 30.6 | 25.5 | 0.83 | 6:9:5:2 | 8.0 | 4.0 | 0.50 | 2 | open; simple |
| **F:AM 71800♀** | 25.2 | 30.0 | 20.5 | 0.68 | 6:7:7:3 | 6.6 | 2.9 | 0.44 | 2 | narrow; simple |
| **F:AM 71808** | | | | | | | | | | |
| F:AM 71809 | 15.9 | 29.8 | 21.4 | 0.72 | 4:4:3:1 | 7.6 | 4.4 | 0.58 | 2 | narrow; simple |
| F:AM 71813♀ | 14.6a | 29.9 | 23.5 | 0.79 | 2:3:3:1 | 7.7 | 4.2 | 0.55 | 1 | narrow; simple |
| Range | | 29.8–34.2 | 20.5–24.4 | 0.72–0.83 | | 6.6–8.0 | 2.9–4.4 | 0.44–0.58 | | |
| Mean | | 31.3 | 23.5 | 0.75 | 6:8:6:3 | 7.3 | 3.9 | 0.52 | 2 | |
| SD | | 1.66 | 1.94 | 0.05 | | 0.50 | 0.58 | 0.05 | | |
| CV | | 5.31 | 8.27 | 6.42 | | 6.80 | 15.1 | 10.1 | | |
| *N* | 7 | 7 | 7 | 7 | 3 | 5 | 5 | 5 | 3 | 5 |
| Hans Johnson Quarry | | | | | | | | | | |
| **F:AM 71862♀** | 34.5a | barely worn | | | 3:8:6:2? | | | | | not formed |
| **F:AM 71861♀?** | 32.0a | 28.6 | 21.9 | 0.77 | 3:3:3:1 | 6.3 | 3.0 | 0.48 | 2 | open; rel. narrow |
| **F:AM 71860♂** | 27.0a | 28.7 | 22.5 | 0.78 | 6:5:7:1 | 7.4 | 3.3 | 0.45 | 2 | open |
| F:AM 71857♀? | 17.0a | 28.7 | 21.3 | 0.74 | 2:3:4:1 | 7.5 | 3.7 | 0.49 | 1 | narrow |
| F:AM 71858♀ | 12.7 | 25.3 | 21.7 | 0.86 | 3:4:3:1 | 5.0 | 3.0 | 0.60 | 3 | open |
| F:AM 71856♂ | 11.0 | 27.9 | 22.6 | 0.81 | 1:7:5:1 | 6.7 | 4.5 | 0.67 | 1 | narrow |
| F:AM 71855♂ | 12.0 | 27.0 | 23.0 | 0.85 | 0:0:0:0 | | | | 0 | narrow; short |
| Range | | 25.3–28.7 | 21.3–23.0 | 0.74–0.86 | | 5.0–7.3 | 3.1–4.0 | 0.45–0.67 | | |
| Mean | | 27.7 | 22.2 | 0.80 | 4:5:5:1 | 6.6 | 3.5 | 0.54 | 2 | |
| SD | | 1.35 | 0.64 | 0.05 | | 1.01 | 0.63 | 0.10 | | |
| CV | | 4.87 | 2.88 | 5.82 | | 15.4 | 18.0 | 17.7 | | |
| *N* | 7 | 6 | 6 | 6 | 3 | 5 | 5 | 5 | 2 | 7 |
| Machaerodus Quarry | | | | | | | | | | |
| **F:AM 71831♂** | 39.0a | | | | | | | | | |
| **F:AM 71844♂** | 31.0a | 27.3 | 21.9 | 0.80 | 4:6:4:2 | 6.1 | 3.4 | 0.56 | 1 | open |
| **F:AM 71835** | 30.0a | 31.7 | 23.1 | 0.73 | 6:6:2:1 | 8.3 | 3.1 | 0.37 | 3 | spurred |
| F:AM 71832♂ | 12.5 | 27.5 | 22.5 | 0.82 | 3:3:5:1 | 6.8 | 4.0 | 0.59 | 2 | open |
| F:AM 71834♀ | 7.5 | 25.0 | 21.5 | 0.86 | no pattern | | | | | |
| Range | | 25.0–31.7 | 21.5–23.1 | 0.73–0.86 | | 6.1–8.3 | 3.1–4.0 | 0.37–0.59 | | |
| Mean | | 27.9 | 22.3 | 0.80 | 5:6:3:1 | 7.1 | 3.5 | 0.51 | 2 | |
| SD | | 2.79 | 0.70 | 0.05 | | 1.12 | 0.46 | 0.12 | | |
| CV | | 10.01 | 3.15 | 6.83 | | 15.9 | 13.1 | 22.9 | | |
| *N* | 5 | 4 | 4 | 4 | 2 | 3 | 3 | 3 | 2 | 3 |

Remarks: dP1/P2 length ratios: F:AM 71861, 0.3. dP1 very small in F:AM 7163, 71833; F:AM 71857, 0.3. dP1 absent in F:AM 71844, 71859, 71802, 71804, 71805; F:AM 71858, 0.3.

Estimated unworn crown heights (MSTHT) for the XMas-Kat Quarry sample of Cormohipparion occidentale are: P2 43 mm; P3 50 mm; P4 52 mm; M1 66 mm; M2 ?65 mm; M3 ?45 mm. Unworn MSTHTs for the same tooth positions in the sample from Machaerodus and Hans Johnson quarries likely are similar to those from XMas-Kat Quarry.

TABLE 7
(*Continued*)

| P3 | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | | | | | | Protocone | | | | |
| Specimen | Height | Length | Width | Ratio | Index | Length | Width | Ratio | Pli caballin | Hypoconal groove |
| XMas-Kat Quarry | | | | | | | | | | |
| **F:AM 71868♂** | 50.0 | 28.6 | 27.5 | 0.96 | unworn | | | | | |
| **F:AM 71801♂** | 46.5a | 27.5 | 26.0 | 0.95 | ?:?:?:? | | | | | |
| **F:AM 71807** | 41.0a | 28.0 | 29.5 | 1.05 | 4:9:9:4 | 9.9 | 4.2 | 0.42 | 3 | open; simple |
| **F:AM 71810** | 32.0a | 26.4 | 28.0 | 1.06 | 6:9:8:2 | 8.3 | 3.8 | 0.46 | 2 | spurred |
| **F:AM 71800♀** | 31.0a | 25.2 | 24.3 | 0.96 | 5:10:8:1 | 9.5 | 4.3 | 0.45 | 2 | narrow; simple |
| **F:AM 71808** | 30.5 | 25.5 | 25.8 | 1.01 | 6:13:5:1 | 8.3 | 3.0 | 0.36 | 2 | open; simple |
| F:AM 71809 | 20.5a | 24.3 | 24.4 | 1.00 | 3:10:8:1 | 8.4 | 3.9 | 0.46 | 3 | open; simple |
| F:AM 71813♀ | 22.0a | 25.4 | 25.9 | 1.02 | 2:7:6:1 | 8.0 | 4.5 | 0.56 | 2 | open; simple |
| Range | | 24.3–28.6 | 24.3–29.5 | 0.95–1.06 | | 8.0–9.9 | 3.0–4.5 | 0.36–0.56 | | |
| Mean | | 26.4 | 26.4 | 1.00 | 5:10:7:2 | 8.7 | 4.0 | 0.45 | 2 | |
| SD | | 1.52 | 1.80 | 0.04 | | 0.77 | 0.53 | 0.07 | | |
| CV | | 5.78 | 6.79 | 4.26 | | 8.83 | 13.5 | 14.4 | | |
| *N* | 8 | 8 | 8 | 8 | 4 | 6 | 6 | 6 | 4 | 6 |
| Hans Johnson Quarry | | | | | | | | | | |
| **F:AM 71862♀** | 39.0a | 25.7 | 24.1 | 0.94 | 3:5:5:1? | 9.5 | 1.8 | 0.19 | 2 | not formed |
| **F:AM 71861♀?** | 33.0a | 24.4 | 24.7 | 1.01 | 4:3:4:1 | 9.6 | 3.5 | 0.36 | 2 | open |
| **F:AM 71860♂** | 31.0a | 24.2 | 25.5 | 1.05 | 3:7:7:2 | 9.4 | 4.2 | 0.45 | 2 | open |
| F:AM 71857♀? | 17.0a | 23.3 | 24.0 | 1.03 | 1:4:5:1 | 8.5 | 4.2 | 0.49 | 2 | narrow |
| F:AM 71858♀ | 11.0a | 23.1 | 24.3 | 1.05 | 1:5:7:1 | 6.9 | 3.5 | 0.51 | 3 | spurred |
| F:AM 71856♂ | 10.0a | 23.2 | 25.2 | 1.09 | 1:6:5:2 | 7.7 | 4.2 | 0.55 | 2 | narrow |
| F:AM 71855♂ | 11.0 | 21.1 | 23.8 | 1.13 | 1:3:0:1 | 8.1 | 4.4 | 0.54 | 2 | narrow |
| Range | | 21.1–25.7 | 23.8–25.5 | 0.94–1.13 | | 7.7–9.6 | 1.8–4.4 | 0.19–0.55 | | |
| Mean | | 23.6 | 24.5 | 1.04 | 3:6:5:1 | 8.5 | 3.7 | 0.44 | 2 | |
| SD | | 1.42 | 0.64 | 0.06 | | 1.03 | 0.91 | 0.13 | | |
| CV | | 6.04 | 2.62 | 5.74 | | 12.1 | 24.6 | 28.9 | | |
| *N* | 7 | 7 | 7 | 7 | 3 | 7 | 7 | 7 | 3 | 7 |
| Machaerodus Quarry | | | | | | | | | | |
| **F:AM 71831♂** | | | | | | | | | | |
| **F:AM 71844♂** | 40.0a | 24.9 | 22.5 | 0.90 | 4:8:6:1 | 9.2 | 3.5 | 0.38 | 2 | open |
| **F:AM 71835** | 39.0a | 26.5 | 25.6 | 0.97 | 6:6:7:2 | 10.0 | 3.1 | 0.31 | 3 | spurred |
| F:AM 71832♂ | 15.0a | 21.6 | 25.9 | 1.20 | 2:11:8:1 | 7.5 | 4.0 | 0.53 | 3 | open |
| F:AM 71834♀ | 13.0a | 23.0 | 24.6 | 1.07 | none | 7.4 | 5.3 | 0.72 | 0 | short to absent |
| Range | | 21.6–26.5 | 22.5–25.9 | 0.90–1.20 | | 7.4–10.0 | 3.1–5.3 | 0.31–0.72 | | |
| Mean | | 24.3 | 24.7 | 1.03 | 5:7:7:1 | 8.5 | 4.0 | 0.48 | 2 | |
| SD | | 2.15 | 1.54 | 0.13 | | 1.28 | 0.96 | 0.18 | | |
| CV | | 8.94 | 6.34 | 12.5 | | 15.1 | 24.1 | 37.1 | | |
| *N* | 4 | 4 | 4 | 4 | 2 | 4 | 4 | 4 | 2 | 4 |

body) size; in higher crowned cheek teeth; in having a more complex enamel pattern in the upper cheek teeth; in dP1 being reduced to absent; in lower cheek teeth with stronger protostylids; in a cranium with the DPOF having a generally teardrop shape (dorsoventrally much higher posteriorly than anteriorly); and in the lacrimal not reaching the rear of the DPOF.

With respect to other members of the *C. occidentale* group, *C. occidentale*, *s.s.*, is distinguished in having 4–5 plis on the anterior border of the molar prefossette. The molar posterior border of the prefossette

TABLE 7
(*Continued*)

P4

| Specimen | Height | Length | Width | Ratio | Index | Protocone Length | Protocone Width | Protocone Ratio | Pli caballin | Hypoconal groove |
|---|---|---|---|---|---|---|---|---|---|---|
| Xmas-Kat Quarry | | | | | | | | | | |
| **F:AM 71868♂** | 52.3 | 27.5 | 26.0 | 0.95 | unworn | | | | | |
| **F:AM 71801♂** | barely erupted | | | | | | | | | |
| **F:AM 71807** | | 26.7 | 28.1 | 1.05 | 6:6:8:5 | 9.2 | 3.4 | 0.37 | 2 | open |
| **F:AM 71810** | 35.5 | 26.1 | 26.8 | 1.03 | 6:10:7:2 | 8.3 | 4.0 | 0.48 | 3 | spurred |
| **F:AM 71800♀** | | 24.0 | 24.0 | 1.00 | 6:10:7:1 | 8.4 | 4.2 | 0.50 | 2 | open |
| **F:AM 71808** | 39.2 | 23.6 | 25.9 | 1.10 | 8:11:7:2 | 7.5 | 3.0 | 0.40 | 3 | open; narrow |
| F:AM 71809 | 20.0a | 22.0 | 24.6 | 1.12 | 4:10:7:1 | 8.6 | 3.9 | 0.45 | 4 | open |
| F:AM 71813♀ | | 24.3 | 25.4 | 1.05 | 5:7:8:1 | 8.2 | 4.0 | 0.49 | 2 | open |
| Range | | 22.0–27.5 | 24.0–28.1 | 1.00–1.12 | | 7.5–9.2 | 3.0–4.2 | 0.37–0.50 | | |
| Mean | | 24.9 | 25.8 | 1.01 | 7:9:7:2 | 8.4 | 3.8 | 0.45 | 3 | |
| SD | | 1.72 | 1.36 | 0.06 | | 0.55 | 0.45 | 0.05 | | |
| CV | | 6.90 | 5.28 | 5.59 | | 6.62 | 12.1 | 11.8 | | |
| *N* | 5 | 7 | 7 | 7 | 4 | 6 | 6 | 6 | 4 | 6 |
| Hans Johnson Quarry | | | | | | | | | | |
| **F:AM 71862♀** | | 23.0 | | | barely worn | | | | | not formed |
| **F:AM 71861♀?** | | 23.5 | 24.9 | 1.06 | 3:6:4:1 | 9.8 | 3.7 | 0.38 | 3 | open; simple |
| **F:AM 71860♂** | | 22.5 | 24.8 | 1.10 | 8:6:6:1 | 8.7 | 1.7 | 0.20 | 2 | open |
| F:AM 71857♀? | | 21.5 | 22.7 | 1.06 | 2:8:6:1 | 9.7 | 4.2 | 0.43 | 2 | narrow |
| F:AM 71858♀ | | 23.0 | 24.2 | 1.05 | 1:6:5:1 | 5.5 | 3.8 | 0.69 | 3 | open |
| F:AM 71856♂ | | 21.4 | 24.6 | 1.15 | 1:8:7:1 | 6.5 | 3.3 | 0.51 | 3 | open |
| F:AM 71855♂ | 11.0a | 19.7 | 23.2 | 1.18 | 1:4:3:1 | 8.2 | 4.1 | 0.50 | 2 | narrow |
| Range | | 19.7–23.5 | 22.7–24.9 | 1.05–1.18 | | 5.5–9.7 | 1.7–4.2 | 0.20–0.69 | | |
| Mean | | 22.1 | 24.1 | 1.10 | 5:6:5:1 | 8.1 | 3.5 | 0.45 | 2 | |
| SD | | 1.31 | 0.91 | 0.05 | | 1.74 | 0.92 | 0.16 | | |
| CV | | 5.95 | 3.79 | 4.88 | | 21.6 | 26.6 | 36.3 | | |
| *N* | 1 | 7 | 6 | 6 | 2 | 6 | 6 | 6 | 2 | 7 |
| Machaerodus Quarry | | | | | | | | | | |
| **F:AM 71831♂** | | 25.1 | 22.5 | 0.90 | 0:10:6:2 | 6.6 | 3.9 | 0.59 | 2 | open; simple |
| **F:AM 71844♂** | | 24.4 | 25.1 | 1.03 | 3:7:5:1 | 9.6 | 2.9 | 0.30 | 2 | open; simple |
| **F:AM 71835** | | 23.9 | 25.3 | 1.06 | 3:8:6:2 | 10.9 | 3.0 | 0.28 | 2 | spurred |
| F:AM 71832♂ | | 21.2 | 24.3 | 1.15 | 2:9:8:1 | 8.8 | 3.7 | 0.42 | 3 | open |
| F:AM 71834♀ | | 22.0 | 24.1 | 1.10 | 0:5:2:1 | 8.3 | 5.1 | 0.61 | 1 | open |
| Range | | 21.2–25.1 | 22.5–25.3 | 0.90–1.15 | | 6.6–10.9 | 2.9–5.1 | 0.28–0.61 | | |
| Mean | | 23.3 | 24.3 | 1.00 | 3:8:6:2 | 8.8 | 3.7 | 0.44 | 2 | |
| SD | | 1.65 | 1.11 | 0.09 | | 1.59 | 0.88 | 0.16 | | |
| CV | | 7.08 | 4.57 | 8.99 | | 18.1 | 23.8 | 35.8 | | |
| *N* | | 5 | 5 | 5 | 3 | 5 | 5 | 5 | 3 | 5 |

has 8–9 plis; the premolar posterior border of the postfossette has 2–3 plis; the molar posterior border of the postfossette has 2–3 plis; the molars usually have two plis caballin; and the orbit is posterior to M3. With a range of about 50–66 mm, the unworn MSTHT for P3–M3 is higher than that for all other species, possibly except *C. skinneri*, n.sp. (table 3B), a segregation strengthened by a comparison of unworn MSTHT for P4/M1 in these samples, as well.

In addition, and as compared in figures 13, 15, 18, 20, 22, and 24, *C. occidentale* has the most deeply incised nasal notch (no. 30) of

TABLE 7
(*Continued*)

| M1 | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | | | | | | Protocone | | | | |
| Specimen | Height | Length | Width | Ratio | Index | Length | Width | Ratio | Pli caballin | Hypoconal groove |
| XMas-Kat Quarry | | | | | | | | | | |
| **F:AM 71868♂** | 58.0a | 26.6 | 24.3 | 0.91 | 2:7:4:? | 9.0 | 2.8 | 0.31 | 3 | narrow; simple |
| **F:AM 71801♂** | | 26.0 | 23.4 | 0.90 | 4:7:7:3 | 5.5 | 3.2 | 0.58 | 2 | narrow; simple |
| **F:AM 71807** | | 25.1 | 26.0 | 1.04 | 3:8:6:3 | 7.5 | 4.3 | 0.57 | 2 | open; narrow |
| **F:AM 71810** | 41.5a | 22.8 | 24.3 | 1.07 | 6:8:7:2 | 8.8 | 3.5 | 0.40 | 2 | open; narrow |
| **F:AM 71800♀** | | 20.4 | 22.3 | 1.09 | 6:9:8:1 | 7.9 | 3.7 | 0.47 | 1 | open; narrow |
| **F:AM 71808** | 36.8 | 20.5 | 22.1 | 1.08 | 1:10:8:1 | 6.1 | 2.9 | 0.48 | 2 | open; narrow |
| F:AM 71809 | | 19.8 | 22.4 | 1.13 | 3:10:8:1 | 8.1 | 4.7 | 0.58 | 4 | open; narrow |
| F:AM 71813♀ | | 21.5 | 23.6 | 1.10 | 3:8:9:1 | 7.9 | 3.7 | 0.47 | 1 | open; narrow |
| Range | | 19.8–26.6 | 22.1–26.0 | 0.90–1.13 | | 5.5–9.0 | 2.8–4.4 | 0.31–0.58 | | |
| Mean | | 22.8 | 23.6 | 1.04 | 4:8:7:2 | 7.6 | 3.6 | 0.48 | 2 | |
| SD | | 2.72 | 1.32 | 0.09 | | 1.23 | 0.66 | 0.10 | | |
| CV | | 11.93 | 5.59 | 8.31 | | 16.1 | 18.2 | 19.9 | | |
| *N* | 3 | 8 | 8 | 8 | 6 | 8 | 8 | 8 | 6 | 8 |
| Hans Johnson Quarry | | | | | | | | | | |
| **F:AM 71862♀** | | 22.5 | 22.2 | 0.99 | 4:7:5:3 | 7.9 | 2.9 | 0.37 | 2 | nearly closed |
| **F:AM 71861♀?** | | 21.0 | 22.3 | 1.06 | 3:7:5:2 | 6.9 | 3.5 | 0.51 | 2 | open; narrow |
| **F:AM 71860♂** | | 20.4 | 23.3 | 1.14 | 3:9:6:1 | 7.6 | 3.2 | 0.42 | 3 | open; narrow |
| F:AM 71857♀? | | 18.9 | 21.6 | 1.14 | 1:10:9:2 | 8.2 | 3.8 | 0.46 | 1 | narrow |
| F:AM 71858♀ | | 19.3 | 21.9 | 1.14 | 1:8:7:2 | 5.6 | 3.5 | 0.63 | 1 | narrow |
| F:AM 71856♂ | | 20.2 | 24.0 | 1.19 | 1:9:8:2 | 6.9 | 2.5 | 0.36 | 1 | narrow |
| F:AM 71855♂ | | 18.7 | 21.8 | 1.17 | 0:6:5:1 | 7.5 | 4.3 | 0.57 | 1 | narrow |
| Range | | 18.7–22.5 | 21.6–23.3 | 0.99–1.19 | | 5.6–8.2 | 2.5–4.3 | 0.36–0.63 | | |
| Mean | | 20.1 | 22.4 | 1.12 | 3:8:5:2 | 7.3 | 3.4 | 0.47 | 2 | |
| SD | | 1.34 | 0.88 | 0.07 | | 0.87 | 0.59 | 0.10 | | |
| CV | | 6.63 | 3.93 | 6.23 | | 12.0 | 17.4 | 21.2 | | |
| *N* | | 7 | 7 | 7 | 3 | 7 | 7 | 7 | 3 | 7 |
| Machaerodus Quarry | | | | | | | | | | |
| **F:AM 71831♂** | | 23.1 | 22.2 | 0.96 | 2:7:8:2 | 6.1 | 2.3 | 0.38 | 3 | open; simple |
| **F:AM 71844♂** | | 21.5 | 22.5 | 1.05 | 2:6:6:2 | 7.5 | 3.5 | 0.47 | 2 | open; simple |
| **F:AM 71835** | | 22.4 | 22.9 | 1.02 | 3:7:8:2 | 9.1 | 2.8 | 0.31 | 2 | narrow |
| F:AM 71832♂ | | 18.3 | 22.2 | 1.21 | 1:8:7:1 | 7.3 | 3.9 | 0.53 | 2 | narrow |
| F:AM 71834♀ | | 18.2 | 22.8 | 1.25 | 1:5:6:1 | 6.2 | 4.8 | 0.77 | 1 | open; narrow |
| Range | | 18.2–23.1 | 22.2–22.9 | 0.96–1.25 | | 6.1–9.1 | 2.3–4.8 | 0.31–0.77 | | |
| Mean | | 20.7 | 22.5 | 1.10 | 2:7:7:2 | 7.2 | 3.5 | 0.49 | 2 | |
| SD | | 2.31 | 0.33 | 0.13 | | 1.22 | 0.97 | 0.18 | | |
| CV | | 11.15 | 1.45 | 11.5 | | 16.8 | 28.1 | 36.5 | | |
| *N* | | 5 | 5 | 5 | 3 | 5 | 5 | 5 | 3 | 5 |

all the other species, and the lacrimal does not extend anteriorly beyond the junction with the maxillo-jugal suture, in contrast to *C. merriami*, n.sp., and *C. johnsoni*, n.sp., but not *C. fricki*, n.sp., *C. matthewi*, n.sp., or *C. skinneri*, n.sp. As in *C. matthewi*, n.sp., the lacrimal in *C. occidentale* extends across about 60% of the POB (table 3A), greater than all other species except *C. skinneri*, n.sp., and *C. johnsoni*, n.sp. *Cormohipparion occidentale* also has a longer muzzle (parameter 1) than all members of the *Cormohipparion* group but *C. merriami*, n.sp. The 1 S.D. (standard deviation) range of the length of

TABLE 7
(*Continued*)

**M2**

| Specimen | Height | Length | Width | Ratio | Index | Protocone Length | Protocone Width | Protocone Ratio | Pli caballin | Hypoconal groove |
|---|---|---|---|---|---|---|---|---|---|---|
| XMas-Kat Quarry | | | | | | | | | | |
| **F:AM 71868♂** | 57.1 | 25.4 | 22.9 | 0.90 | incomplete | | | | | |
| **F:AM 71801♂** | | 26.1 | 21.7 | 0.83 | 3:8:7:? | | | | 1 | unformed |
| **F:AM 71807** | | 24.8 | 24.3 | 0.98 | 3:7:6:2 | 9.6 | 5.0 | 0.52 | 3 | narrow |
| **F:AM 71810** | | 23.4 | 23.4 | 1.00 | 5:8:6:1 | 7.8 | 3.7 | 0.47 | 2 | spurred |
| **F:AM 71800♀** | | 21.0 | 22.0 | 1.05 | 6:9:6:1 | 8.1 | 3.3 | 0.41 | 1 | open; narrow |
| **F:AM 71808** | | 21.5 | 22.1 | 1.03 | 4:10:7:2 | 7.3 | 2.8 | 0.38 | 2 | open; narrow |
| F:AM 71809 | | 20.7 | 22.3 | 1.08 | 4:10:7:1 | 8.4 | 3.3 | 0.39 | 4 | open; narrow |
| F:AM 71813♀ | | 22.5 | 22.7 | 1.01 | 5:9:7:3 | 7.3 | 3.3 | 0.45 | 2 | open; narrow |
| Range | | 20.7–26.1 | 20.1–25.3 | 0.83–1.08 | | 7.3–9.6 | 2.8–5.0 | 0.38–0.52 | | |
| Mean | | 23.2 | 22.7 | 0.98 | 4:8:6:2 | 8.1 | 3.6 | 0.44 | 2 | |
| SD | | 2.08 | 0.85 | 0.08 | | 0.86 | 0.76 | 0.05 | | |
| CV | | 8.98 | 3.76 | 8.20 | | 10.7 | 21.3 | 12.2 | | |
| *N* | 1 | 8 | 8 | 8 | 5 | 6 | 6 | 6 | 5 | 7 |
| Hans Johnson Quarry | | | | | | | | | | |
| **F:AM 71862♀** | | 23.0 | 19.7 | 0.86 | 1:4:5:? | 7.8 | 1.6 | 0.21 | 2 | open; incipient |
| **F:AM 71861♀**? | | 21.8 | 20.4 | 0.94 | 2:6:5:1 | 7.3 | 3.2 | 0.44 | 2 | open |
| **F:AM 71860♂** | | 21.5 | 22.5 | 1.05 | 4:6:5:1 | 8.4 | 2.3 | 0.27 | 2 | open; narrow |
| F:AM 71857♀? | | 20.1 | 21.6 | 1.07 | 2:8:7:2 | 9.1 | 3.5 | 0.38 | 2 | narrow |
| F:AM 71858♀ | | 19.1 | 21.2 | 1.11 | 2:6:6:2 | 5.2 | 3.7 | 0.71 | 2 | narrow |
| F:AM 71856♂ | | 20.3 | 22.3 | 1.10 | 1:8:7:3 | 7.2 | 3.1 | 0.43 | 2 | narrow |
| F:AM 71855♂ | | 18.9 | 21.3 | 1.13 | 0:6:4:1 | 7.4 | 4.8 | 0.65 | 2 | narrow |
| Range | | 18.9–23.0 | 19.7–22.5 | 0.86–1.13 | | 5.2–9.1 | 1.6–4.8 | 0.21–0.71 | | |
| Mean | | 20.7 | 21.3 | 1.04 | 2:5:5:1 | 7.5 | 3.2 | 0.44 | 2 | |
| SD | | 1.50 | 0.99 | 0.11 | | 1.22 | 1.02 | 0.18 | | |
| CV | | 7.24 | 4.66 | 9.78 | | 16.3 | 32.2 | 41.7 | | |
| *N* | | 7 | 7 | 7 | 3 | 7 | 7 | 7 | 3 | 7 |
| Machaerodus Quarry | | | | | | | | | | |
| **F:AM 71831♂** | very early wear | | | | | | | | | not erupted |
| **F:AM 71844♂** | | 22.3 | 20.5 | 0.92 | 3:7:5:3 | 9.2 | 2.5 | 0.27 | 2 | open |
| **F:AM 71835** | | 23.2 | 21.1 | 0.91 | 3:8:6:1 | 10.3 | 3.0 | 0.29 | 2 | narrow; spur |
| F:AM 71832♂ | | 19.8 | 22.5 | 1.14 | 1:11:9:1 | 8.9 | 4.9 | 0.55 | 2 | narrow; short |
| F:AM 71834♀ | | 20.5 | 22.3 | 1.09 | 1:4:5:1 | 7.6 | 4.6 | 0.61 | 1 | open; narrow |
| Range | | 19.8–23.2 | 20.5–22.5 | 0.91–1.14 | | 7.6–10.3 | 2.5–4.9 | 0.27–0.61 | | |
| Mean | | 21.5 | 21.6 | 1.01 | 3:8:6:2 | 9.0 | 3.8 | 0.36 | 2 | |
| SD | | 1.57 | 0.96 | 0.12 | | 1.11 | 1.18 | 0.28 | | |
| CV | | 7.33 | 4.44 | 11.4 | | 12.3 | 31.4 | 40.2 | | |
| *N* | | 4 | 4 | 4 | 2 | 4 | 4 | 4 | 2 | 5 |

the DPOF (no. 33) in *C. occidentale* incorporates the (low) range of this feature seen in *C. merriami*, n.sp., and *C. skinneri*, n.sp., so these populations probably are not distinct in this regard. However, the DPOF is sharply shorter in *C. matthewi*, n.sp., and *C. johnsoni*, n.sp., and its 1 S.D. ranges are much smaller in *C. fricki*, n.sp. None of the other species shows as tall a DPOF (no. 35) as in the Machaerodus and Hans Johnson quarry samples of *C. occidentale*, and only *C. johnsoni*, n.sp., has as short a separation of the DPOF and facial crest (no. 36) as in those two quarry samples of *C. occidentale*.

TABLE 7
(*Continued*)

**M3**

| Specimen | Height | Length | Width | Ratio | Index | Protocone Length | Protocone Width | Protocone Ratio | Pli caballin | Hypoconal groove |
|---|---|---|---|---|---|---|---|---|---|---|
| XMas-Kat Quarry | | | | | | | | | | |
| **F:AM 71868♂** | not erupted | | | | | | | | | |
| **F:AM 71801♂** | erupting | | | | | | | | | |
| **F:AM 71807** | very early wear | | | | | | | | | not formed |
| **F:AM 71810** | | 23.5 | 20.4 | 0.87 | 4:9:5:? | 9.4 | 2.9 | 0.31 | 2 | spurred |
| **F:AM 71800♀** | | 23.7 | 19.2 | 0.81 | 6:6:6:1 | 9.3 | 2.4 | 0.26 | 1 | spurred |
| **F:AM 71808** | | 20.8 | 19.1 | 0.92 | 2:7:2:1 | 8.3 | 2.3 | 0.28 | 2 | open; simple |
| F:AM 71809 | | 21.7 | 19.0 | 0.88 | 4:9:6:1 | 10.4 | 3.6 | 0.35 | 2 | spurred |
| F:AM 71813♀ | | 25.4 | 20.2 | 0.80 | 1:6:7:4 | 8.6 | 3.2 | 0.37 | 3 | spurred |
| Range | | 20.8–25.4 | 19.0–20.4 | 0.80–0.92 | | 8.3–10.4 | 2.3–3.6 | 0.26–0.37 | | |
| Mean | | 23.0 | 19.6 | 0.85 | 4:7:4:1 | 9.2 | 2.9 | 0.30 | 2 | |
| SD | | 1.81 | 0.67 | 0.05 | | 0.82 | 0.55 | 0.05 | | |
| CV | | 7.84 | 3.40 | 5.91 | | 8.9 | 18.9 | 15.1 | | |
| *N* | | 5 | 5 | 5 | 3 | 5 | 5 | 5 | 3 | 6 |
| Hans Johnson Quarry | | | | | | | | | | |
| **F:AM 71862♀** | not erupted | | | | | | | | | |
| **F:AM 71861♀?** | not fully erupted | | | | | | | | | |
| **F:AM 71860♂** | barely erupted | | 16.5 | | | | | | | not formed |
| F:AM 71857♀? | | 22.1 | 18.0 | 0.81 | 3:5:3:1 | 9.1 | 3.2 | 0.35 | 1 | spurred |
| F:AM 71858♀ | | 21.0 | 18.8 | 0.90 | 2:5:4:1 | 7.4 | 3.7 | 0.50 | 2 | open |
| F:AM 71856♂ | | 22.4 | 19.0 | 0.85 | 1:8:6:1 | 7.0 | 1.5 | 0.21 | 3 | open |
| F:AM 71855♂ | | 23.4 | 19.2 | 0.82 | 1:6:4:1 | 8.3 | 3.6 | 0.43 | 2 | closed |
| Range | | 21.0–23.4 | 16.5–19.2 | 0.81–0.90 | | 7.0–9.1 | 1.5–3.6 | 0.21–0.43 | | |
| Mean | | 22.2 | 18.3 | 0.85 | | 8.0 | 3.0 | 0.40 | | |
| SD | | 0.99 | 1.11 | 0.04 | | 0.94 | 1.02 | 0.12 | | |
| CV | | 4.45 | 6.04 | 4.36 | | 11.8 | 34.1 | 32.8 | | |
| *N* | | 4 | 4 | 4 | 0 | 4 | 4 | 4 | 0 | 5 |
| Machaerodus Quarry | | | | | | | | | | |
| **F:AM 71831♂** | not erupted | | | | | | | | | |
| **F:AM 71844♂** | | | 15.7 | | 1:7:5:? | 8.4 | 2.1 | 0.25 | 2 | not formed |
| **F:AM 71835** | 41.0 | | 18.0 | | 1:7:4:? | 8.0 | 2.2 | 0.28 | 2 | not formed |
| F:AM 71832♂ | | 22.4 | 21.2 | 0.95 | 1:8:5:1 | 9.3 | 3.8 | 0.41 | 2 | open |
| F:AM 71834♀ | | 23.5 | 20.6 | 0.88 | 1:7:4:1 | 7.7 | 4.1 | 0.53 | 1 | closed |
| Range | | 22.4–23.5 | 15.7–21.2 | 0.88–0.95 | | 7.7–9.3 | 2.1–4.1 | 0.25–0.53 | | |
| Mean | | 23.0 | 18.9 | 0.91 | 1:7:5:1 | 8.4 | 3.1 | 0.37 | 2 | |
| SD | | 0.78 | 2.53 | 0.05 | | 0.70 | 1.05 | 0.13 | | |
| CV | | 3.39 | 13.41 | 5.42 | | 8.3 | 34.3 | 35.7 | | |
| *N* | 1 | 2 | 4 | 4 | 2 | 4 | 4 | 4 | 2 | 4 |

REFERRED MATERIAL: From Little White River, South Dakota. Medial Clarendonian.

From the Ed Ross Ranch Quarry, ?late medial Clarendonian, ?Thin Elk Formation, Bennett County, South Dakota. F:AM 71872, ♂ skull with right and left C1, P2–M3 (fig. 11).

From Loup Fork beds, ?Clarendonian. AMNH 10869, fragmentary skull with right and left dP2–4, right and left M1, RM2 erupting.

TABLE 7
(*Continued*)

| Specimen | Wear class; remarks |
|---|---|
| *Cormohipparion occidentale*; **Xmas-Kat Quarries, Merritt Dam Member, Ash Hollow Formation, Nebraska** | |
| F:AM 71868 ♂ | DP2–4 in place; P2–4 from crypt; M2 very early wear. Anterior prefossette plis very small mostly. Nearly true crown height of M1 must be ca 66 mm. P2, 43 mm unworn height; P3, 50 mm; P4, 52 mm; M1, 66 mm; M2, ca 63 mm; M3, ?43 mm. |
| F:AM 71801 ♂ | Early juvenile wear; P2–4, M3 erupting; note complex pattern; dP1is absent. Note relatively round protocone on M1. Labial pre- and postfossettes not formed in P2. |
| F:AM 71807 | Early juvenile wear; M3 not fully formed; very complex pattern. P2 pre- and postfossettes separate labially; ovate protocone P2, M1; others more elongate; dP1 is absent. |
| F:AM 71810 | Early adult wear; M3 formed; very complex pattern in all; P2 pre- and postfossettes linked. |
| F:AM 71800 ♀ | Late medial wear; slightly lingually convex protocones in premolars, nearly flat in molars; double pli caballin P2-4; complex pattern in all; pre- and postfossette labially separate in P2. |
| F:AM 71808 | Early medial wear; slightly lingually convex protocones, double pli caballin in P3–M3; complex pattern. |
| F:AM 71809 | Late medial wear; slightly lingually flat to slightly convex protocones, quadruple pli caballin in P2–4; P2 pre- and postfossette separate; fatter protocones in later wear. |
| F:AM 71813 ♀ | Early medial wear; M3 early wear; note complexity; double pli caballinin P2–M3; complex anterior pli prefossettes; 2 plis anterior to small pli protoconule in P4–M2. P2 pre- and postfossettes separate. dP1 is 3.0 mm long. |
| *Cormohipparion occidentale*; **Hans Johnson Quarry, Merritt Dam Member, Ash Hollow Formation, Nebraska** | |
| F:AM 71862 ♀ | Early juvenile wear; M2 barely worn; M3 not erupted. Note moderately complex pattern; elongate protocones, cf. type of *C. occidentale*. P2 with labially separated pre- and postfossette. dP1 8.0 mm long. |
| F:AM 71861 ?♀ | Early adult wear; M3 pattern incomplete; note relatively complex pattern. P2 pre and postfossettes linked labially. Anterior prefossette of P2 cf. type of *C. occidentale*. Lingual penetration of hyposelene disrupts pli caballin. dP1 ca 7.5 mm long. |
| F:AM 71860 ♂ | Early adult wear; M3 pattern incomplete; note relatively complex pattern. P2 pre- and postfossettes separate labially. Note elongate, slanted protocones, lingually concave cf. type of *C. occidentale*. |
| F:AM 71857 ?♀ | Adult wear; M3 pattern complete; still relatively elongate protocones; relatively complex pattern. dP1 is 9.3 mm long. |
| F:AM 71858 ♀ | Late adult wear; protocones still ovate, except M3; triple P3–4, double M2–3 plis caballin; pre- and postfossette P2 labially connected. dP1 7.5 mm long. |
| F:AM 71856 ♂ | Late adult wear; still relatively elongate protocones, not concave lingually; connected in P2, nearly connected in M1. |
| F:AM 71855 ♂ | Late adult wear; broad protocones; protocone connected in P2, nearly in M1; pre- and postfossette P2 obliterated. |
| *Cormohipparion occidentale*; **Machaerodus Quarry, Merritt Dam Member, Ash Hollow Formation, Nebraska** | |
| F:AM 71831 ♂ | Early juvenile wear; M2 barely worn; M3 not erupted. Note relatively simple pattern; more circular protocone M1; short protocone M2, contra type of *C. occidentale*. |
| F:AM 71844 ♂ | Early adult wear; M3 pattern incomplete; note relatively complex pattern. P2 pre- and postfossettes linked labially. |
| F:AM 71835 | Early adult wear; M3 pattern incomplete; note relatively complex pattern. P2 pre- and postfossettes linked labially. Note elongate, slanted protocones, lingually concave cf. type of *C. occidentale*. |
| F:AM 71832 ♂ | Late adult wear; slightly lingually convex protocones premolars ex. P2; protocone connected in P2; riple P3–4, double M1–3 pli caballin; pre- and postfossette P2 labially separate. |
| F:AM 71834 ♀ | Late adult wear; broad protocones; protocone connected in P2, 3, M1; single pli caballins; pre- and postfossette in P2 obliterated. |

TABLE 8

**Measurements (mm) of Lower Mandible and Dentition of *Cormohipparion occidentale*, Ash Hollow Formation, Medial Clarendonian, Nebraska, and Lower Dentition of LACM 138755, Dove Spring Formation, California**

| | | Characters[a] | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| Specimen | Quarry | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 |
| Mandible | | | | | | | | | |
| F:AM 71800 ♀ | XMas-Kat | 359.4 | 83.5 | 71.8 | 69.4 | 138.2 | 92.9 | 84.0 | 169.4 |
| F:AM 71855♂ | Hans Johnson | 344.8 | 103.2 | 61.0 | 62.0 | 122.8 | 101.9 | 88.0 | 148.0a |
| F:AM 71844♂ | Machaerodus | 364.0a | 86.2a | 72.0 | 66.8 | 137.5 | 100.0 | 69.2 | 152.2 |
| | | 9 | 10 | 11 | 12 | 13 | 14 | 16 | 17 |
| F:AM 71800 ♀ | XMas-Kat | 165.8 | 82.5 | 58.8 | 39.1 | 61.3 | 28.2 | 43.4 | 38.8 |
| F:AM 71855♂ | Hans Johnson | 137.0a | 72.0a | 64.8 | 51.5 | 64.0a | 28.2 | 42.8 | 32.2 |
| F:AM 71844♂ | Machaerodus | 146.8 | 78.8 | 60.8 | 40.7 | 58.0a | 35.0a | | 22.0 |

| | | p2 | | p3 | | p4 | | m1 | | m2 | | m3 | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Specimen | Quarry | L | W | L | W | L | W | L | W | L | W | L | W |
| Lower dentition | | | | | | | | | | | | | |
| F:AM 71800 ♀ | Xmas | 25.5 | 13.2 | 23.4 | 14.8 | 23.6 | 14.4 | 21.1 | 12.7 | 21.9 | 12.4 | 25.8 | 11.9 |
| F:AM 71855♂ | Hans Johnson | 25.6 | 14.0 | 23.5 | 15.7 | 24.1 | 15.4 | 22.8 | 14.5 | 22.3 | 13.0 | 22.6 | 11.3 |
| F:AM 71844♂ | Machaerodus | 21.4 | 13.6 | 20.5 | 15.0 | 19.0 | 14.5 | 18.5 | 12.9 | 18.5 | 12.0 | 26.0 | 10.2 |
| LACM 138755 | Dove Spring | 29.5 | 15.0 | 28.4 | 16.1 | 29.1 | 15.1 | 27.5 | 13.8 | 29.6 | 13.6 | 30.0a | 11.3 |

Remarks: [a]Characters shown in figure 6. Character 17 = p2 to mandibular foramen. L = length; W = width; a = approximate. LACM 138755 parastylid is 33.4 mm tall, early wear; ca. 10.1 Ma old; p2 and p3 larger than in *C. occidentale* from Xmas Q.; upper molars MSTHT ca. 50 mm; see LACM 146246, table 19.

From Niobrara River, Merritt Dam Member, Ash Hollow Formation, Cherry County, Nebraska. Late medial Clarendonian.

XMas-Kat quarries. F:AM 71800, nearly complete cranium with right and left I1–3, C, P2–M3, adult female, M3 well worn. F:AM 71801, nearly complete cranium with right and left I2–3, C, P2–M3, sub-adult male, M3 just erupting. F:AM 71803, nearly complete cranium with L I2–3, right and left C, P2–M3, adult male, M3 erupted. F:AM 71806, partial cranium with right and left I1–3, P2–M3, adult female, M3 in medial wear. F:AM 71807, right and left palate with P2–M3, M3 in early wear. F:AM 71808, partial cranium with right and left P3–M3, M3 in early wear. F:AM 71809, partial cranium with right and left P2–M2, LM3, M3 well worn. F:AM 71810, partial cranium with right and left P2–M3, M3 well worn. F:AM 71813, nearly complete cranium with right and left I1–3, RC, right and left P2–M3, adult female, M3 well worn. F:AM 71814, badly crushed cranium with L I2–3, C, right and left P3–M3, adult male, M3 well worn. F:AM 71868, anterior cranium with R I2–3, right and left C, dP2–4, LM1–2 erupting, LP2–4 removed from crypt, juvenile male.

Machaerodus Quarry. F:AM 71831, snout and frontal regions preserved, with right and left I1, L12, right and left C, RdP1, right and left dP4, P2–M3, M1–2 erupting, lower mandibles with right and left i1, Ri3, right and left c, p2–m2, juvenile male, p2 and p3 erupting. F:AM 71832, nearly complete cranium with right and left I3, C, LdP1, right and left P2–M3, adult female, M3 well worn. F:AM 71834, snout and facial region with right and left I1–2, RI3, P2–M3, ancient female, M3 very well worn. F:AM 71835, palate with LP2, right and left P3–M3, adult, M3 in early wear. F:AM 71844, partial snout and palate with R C, P2, right and left P3–M3, adult male, M3 in early wear, and associated left and right mandibles with p2–m3.

Hans Johnson Quarry. F:AM 71855, laterally compressed cranium with right and left I1–2, LI3, C, RP2, right and left P3–M3, adult male, M3 well worn; mandible with

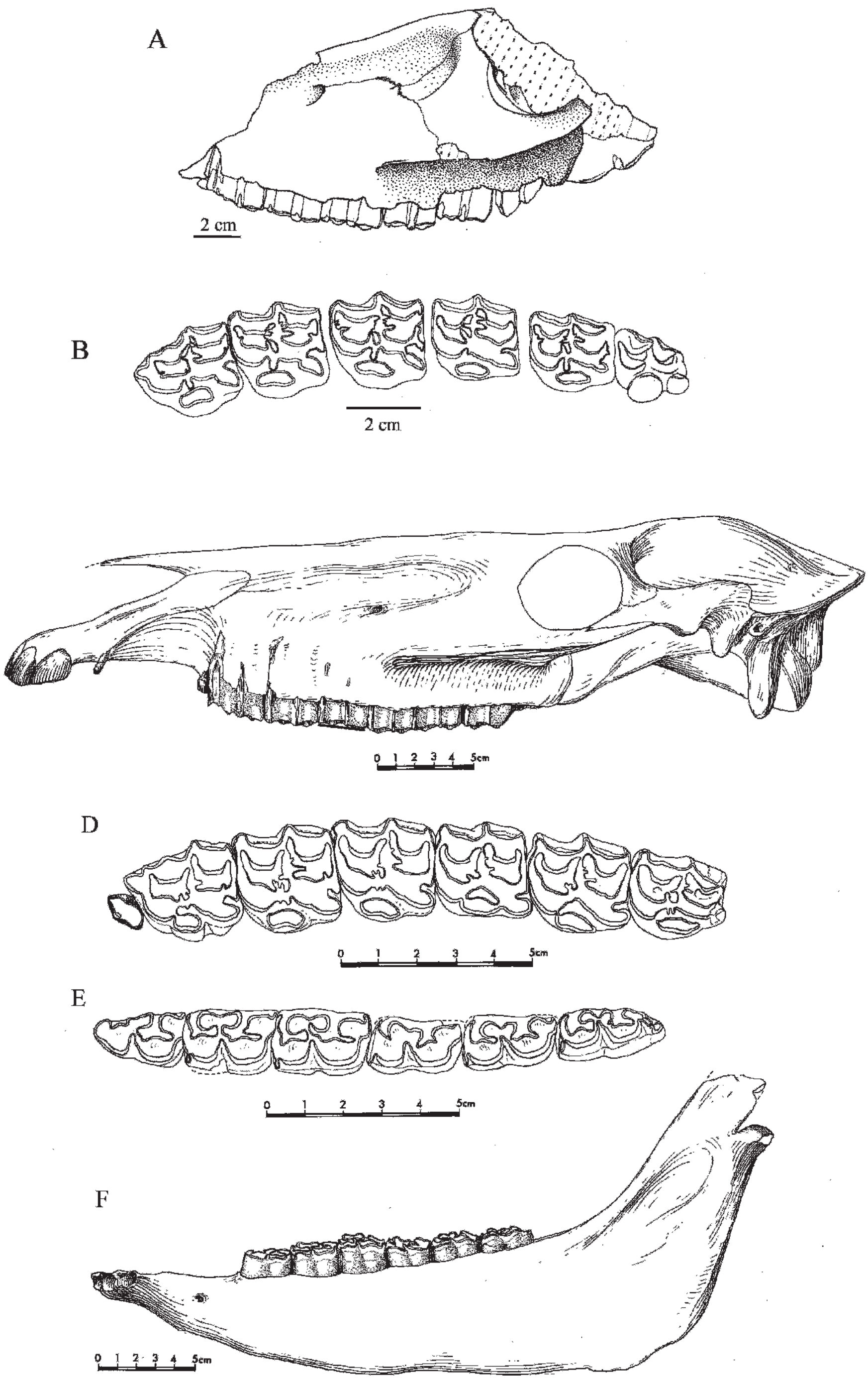


Fig. 12. *Neohipparion affine*. **A–B,** AMNH 141218, Hollow Horn Bear Quarry, Ash Hollow Formation, South Dakota, early Clarendonian. **A,** lateral view of cranium, reversed. **B,** occlusal view of cheek tooth dentition. **C–E,** F:AM 111728, MacAdams Quarry, Clarendon Beds, Texas; early Clarendonian. **C,** lateral view of cranium, reconstructed from both sides, slightly crushed dorsoventrally. **D,** occlusal view of cheek tooth dentition, with dP1. **E**, occlusal view of lower cheek teeth. **F,** lateral view of left mandible. **A** and **B** drawn by Ellen L.Forsyth. **C–E** after MacFadden (1984: figs. 66, 69).

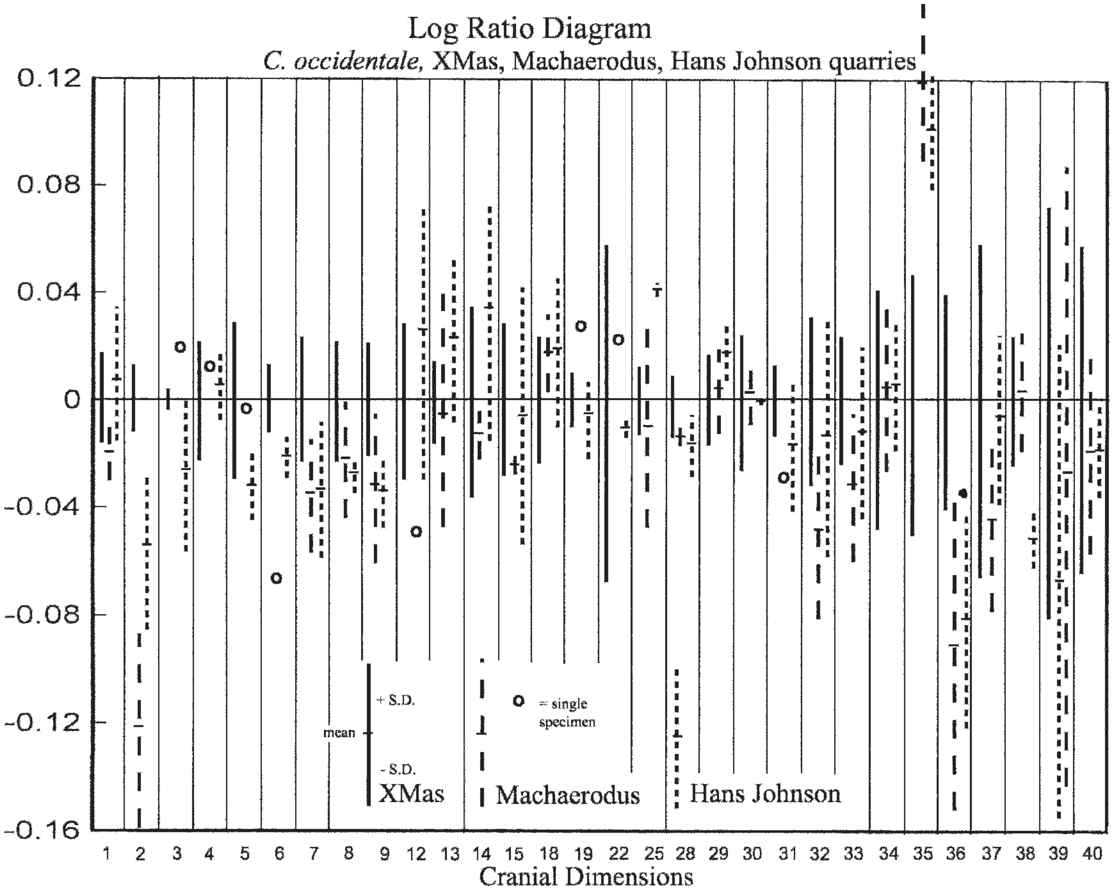


Fig. 13. *Cormohipparion occidentale*. Log-ratio diagrams of cranial dimensions of samples from XMas-Kat, Machaerodus, and Hans Johnson quarries, Merritt Dam Member, Ash Hollow Formation, Nebraska.

right and left i1–3, c, Pp2–m3. F:AM 71856, nearly complete cranium with right and left I1–3, C, P2–M3, adult male, M3 worn. F:AM 71857, nearly complete cranium with right and left I2–3, dP1–M3, adult female, M3 well worn. F:AM 71858, nearly complete cranium with R I1, C, right and left dP1–M3, adult female, M3 well worn. F:AM 71860, partial cranium with L I3, right and left C, P2–M3, adult male, M3 very well worn. F:AM 71861, partial cranium with right and left P2–M3, adult female, M3 beginning wear. F:AM 71862, crushed cranium with right and left I1, right and left I2-3, C, dP1–M3, subadult female, M3 erupting.

Description of Referred Material: The cranium of *C. occidentale* is poorly represented in specimens from localities of medial Clarendonian age in South Dakota. The following description is based on material from the late medial Clarendonian XMas-Kat quarries, herein taken as the most representative of this species (see below). F:AM 71800 is a nearly complete and undistorted cranium of an adult female (fig. 10A). The skull is slightly crushed dorsoventrally but otherwise nearly complete. The parietal region is somewhat depressed; the maxillary overlaps by about 20 mm its normal contact with the nasal bone; and the lower suture of the lacrimal is obscured. The configuration of the face in this area is more accurately represented by F:AM 71801 (fig. 10B). Figure 10A illustrates the generally elongate configuration of the cranium (snout and facial region) typical of late Miocene hypsodont horses. The large DPOF (no. 33, table 5) characteristic of *Cormohipparion* species is clearly shown, as are its strongly demarcated borders. The anterior tip of the DPOF is closely associated with the infraorbital foramen, which is located above the anterior margin of P3 and at a level opposite the lower margin of the orbit, and exemplifies the anteroventral orientation of this fossa (state 0, character 5, table 1). Figure 10B demonstrates the extent to which the DPOF is pocketed in *C. occidentale*, reaching posteriorly about 10 mm to a point internal to the tip of the lacrimal bone; the anterior tip of the lacrimal is about 15 mm posterior to the rear of the DPOF. The lacrimal is not pointed anteriorly, but its anterior edge (maxillo-lacrimal suture) is nearly vertically oriented and approximately aligned with the maxillo-jugal suture. The nasal notch is well developed and extends posteriorly to a point above the anterior margin of P2. The anterior edge of the large orbit is located above the rear of M3 and is well separated from the DPOF by a wide POB (no. 32, table 5). As shown in table 5, the orbit tends to be somewhat longer (no. 28) than high (no. 29). The facial crest is well developed and extends anteriorly to a point above M1. Although crushed in F:AM 71800, F:AM 71801 shows that the frontal region is slightly domed anterior to the parietal crest. The occipital condyles are slightly below the level of the tooth row in lateral view, and the paroccipital processes are strongly developed.

Crania from the Machaerodus and Hans Johnson quarries are comparable to those from XMas-Kat. Figure 13 shows the log-ratio values for the *C. occidentale* samples from the Machaerodus and Hans Johnson quarries relative to that from XMas-Kat. Parameter 4 is a measure of the basicranium and thus of fundamental cranial size. The correspondence between the samples indicates that they are all about the same size. Although the Machaerodus Quarry occasionally is represented by only one specimen (in which case it is assumed that the dimension represents the log mean for its sample), the relatively close correspondence of the log means of all three samples indicates that range of variation (± 1 standard deviation) would overlap extensively. Parameters in which the S.D. range of the XMas-Kat sample overlaps the other two are no. 22 (inion height), no. 30 (nasal notch), no. 34 (IOF relative to rear of DPOF), and no. 37 (IOF height relative to alveolar border). Parameters in which the S.D. range of the XMas-Kat sample is overlapped by the other two (assuming the S.D. range for the sample represented by a single Machaerodus specimen is comparable to that from the Hans Johnson Quarry) are no. 1 (muzzle length), no. 3 (postpalatal length), no. 12 (choanal width), no. 13 (palatal width), no. 19 (transglenoid width), no. 25 (muzzle height; assumes a greater range for the Hans Johnson sample), no. 31 (facial length; log mean only in Machaerodus Quarry; includes no. 2 in part), no. 32 (POB length), and no. 39 (lacrimal tip to rear of DPOF; see also table 3A). Parameters in which the Machaerodus and Hans Johnson samples are smaller or shorter than, and beyond the S.D. range of, the XMas-Kat sample are no. 2 (palatal length), no. 6 (total cranial length, in part includes no. 2), and no. 36 (facial crest below DPOF; inversely correlated with no. 35). Parameters in which the Machaerodus and Hans Johnson samples are slightly shorter or lower (but at least partly within the S.D. range of) XMas-Kat are no. 5 (foramen magnum to rear of palate; combines nos. 3 and 4), no. 7 (premolar length; includes no. 2 in part), no. 8 (molar length; includes no. 2 in part), no. 9 (premolar-molar length; includes no. 2 in part), and no. 28 (orbital length). Parameters in which the Machaerodus and Hans Johnson samples are much greater or higher than the S.D. range of XMas-Kat are no. 35 (DPOF height; inversely correlated with no. 36; DPOF relative to facial crest). Those in which the above two samples are slightly higher than (but S.D. ranges overlap with) that from XMas-Kat are no. 18 (frontal width) and no. 29 (orbital height). In most cases where parameters differ, samples from Machaerodus and Hans Johnson quarries segregate together. In no. 33 (length, DPOF) and no. 38 (height of rear of DPOF relative to alveolar border), the Hans Johnson sample is partly (no. 33) to completely (no. 38) shorter than that from Machaerodus and XMas-Kat. In nos. 14–15, the S.D. range for the Machaerodus sample is overlapped by that from XMas-Kat, but the Hans Johnson sample overlaps that from XMas-Kat.

Except for parameter 2 (which likely is associated in part with nos. 7–9 and possibly with nos. 31, 33, and 34), no. 6 (in part includes no. 2), no. 36 (inversely correlated with no. 35), cranial parameters of the three quarry samples are generally similar. Thus, even though the three quarry samples are within about one mile of each other (Skinner and Johnson, 1984: fig. 16) and are nominally correlative, it appears that the Machaerodus and Hans Johnson samples have a slightly shorter face/palate and slightly taller DPOF than does the sample from XMas-Kat. As indicated in table 5, both sexes are represented in each of the three quarry samples, so these differences cannot be ascribed to sexual dimorphism. The possible significance of this is discussed below. In having the greatest number of specimens (table 5), the sample from XMas-Kat quarries is taken herein as the most representative of *C. occidentale* from Nebraska.

The upper incisors are well developed and ovate in cross section, with I3 tapering laterally. All have cement-filled infundibula. Lengths for I1–3 are 15.5 mm, 16 mm, and 15 mm, respectively; widths are 9.8 mm, 9 mm, and 8.4 mm. In F:AM 71800, the canine is relatively small, indicating the female sex of the specimen (in contrast to its much larger size in F:AM 71801; table 6). The canine is located 32 mm posterior to the rear of I3, or 36% of the length of the diastema (table 6) between I3 and P3. DP1 is absent in this as well as in all adult XMas-Kat quarry specimens. As indicated in table 6, the canine is located about 34% of the length (mean) of the diastema in XMas-Kat and Hans Johnson material and about 31% of the length in Machaerodus Quarry specimens.

As considered from all quarry sites, the upper cheek tooth dentition is relatively complex. Protocones tend to be elongate, but only P3 and P4 have protocones with slightly lingually concave borders at this stage of wear. As indicated in table 7, there are two plis caballin in both the premolars and molars; fossette borders are relatively complex, except for the posterior border of the postfossette (usually with 2 plis only). Although some specimens of *C. quinni* in early wear stages show multiple plications on the anterior border of the prefossette (Woodburne, 1996b), this trait is especially characteristic of the *C. occidentale* group, with mean counts of three or more in most samples of P2–M1 (table 7). Overall, the sample from XMas-Kat Quarry has the most complex fossette borders at all tooth positions relative to the samples from the Machaerodus and Hans Johnson quarries. The fossette borders of P2, P3, and M2 appear to be more complex in the Machaerodus samples than in the Hans Johnson samples, with the reverse being the case for P4 and M1. M3 is not considered relevant in this regard as being poorly represented in the adult state.

The dP1 is absent from all adult skulls at the XMas-Kat quarries regardless of sex. The upper dentition of *C. occidentale* from the XMas-Kat quarries is relatively complex and high crowned (table 3B). As reconstructed from table 7, the unworn P2 is about 43 mm tall; P3 is 50 mm; P4 is 52 mm; M1 likely was about 66 mm; M2 was 65 mm; and M3 probably was about as tall as P2 (ca. 45 mm). At about medial wear (25–40 mm; table 7, excluding F:AM 71809, F:AM 71813), and as indicated in figures 9C and 10D, the mean plication count for P2 is about 6:8:6:3. In P3, this is 5:10:7:2; in P4, 7:9:7:2; in M1, 4:8:7:2; in M2, 4:8:6:2; and in M3, 4:7:4:1. For the entire sample, the protocone tends to be relatively elongate to subrounded (narrower in M2–3; table 3C), and the hypoconal groove is open and not spurred. The anterior border of the prefossette is relatively complex (more than 3 plis), commonly with many plications that are of small amplitude rather than there being a smaller number of relatively deep plis; the pli caballin is double or more in premolars and typically double in molars. Of eleven specimens, the P2 pre- and postfossette score is confluent in three specimens, separate in four specimens, and not applicable in four specimens.

FROM MACHAERODUS QUARRY: The dP1 is absent in all (two) adult male skulls and one adult female. It is present in one adult female skull. The upper dentition of *C. occidentale* from the Machaerodus Quarry is somewhat smaller than the sample from XMas-Kat Quarry and slightly less complex.

The unworn cheek tooth crown height is difficult to assess in the available sample. Based on F:AM 71844, P3 in an adult stage of wear is about 40 mm tall (table 7). M3 (very early wear) is 41 mm tall in F:AM 71835 (table 7), so the unworn crown height would have been at least 43 mm. This is comparable to the MSTHT in the XMas-Kat and Hans Johnson samples, so it is likely that the other cheek teeth were about as tall as in those samples. In about medial wear (ca. 30 mm; F:AM 71844, F:AM 71835, table 7), complexity in P2 reaches a mean of 5:6:3:1; in P3, 5:7:7:1; in P4, 3:8:6:2; in M1, 2:7:7:2; in M2, 3:8:6:2; and in M3, 1:7:5:1. With regard to the entire sample, the protocone tends to be elongate in the premolars but somewhat more ovate in the molars; the protocone retains a slight lingual concavity into later wear; the hypoconal groove is about equally spurred as un-spurred and open; the anterior border of the prefossette tends to be relatively complex and well delineated in medial wear, especially in the premolars; and the pli caballin is typically double in both premolars and molars but tends to be somewhat more complex in the premolars. Overall, the upper cheek teeth are less complex than in the XMas-Kat Quarry sample. The sample apparently is about as hypsodont as that in the Hans Johnson Quarry. Of five specimens, the pre- and postfossette of P2 score confluent in two, separate in one, and not applicable in two.

FROM HANS JOHNSON QUARRY: The dP1 is absent in all three adult male skulls and is present in all four adult female skulls. The upper dentition of *C. occidentale* from the Hans Johnson Quarry is relatively complex and high crowned. The unworn P2 is about 45 mm tall, judging from the very early wear stage of F:AM 71862 (table 7), and P3 is likely about 50 mm tall, judging from the very early wear in F:AM 71862 and compared with materials from the XMas-Kat quarries. On the same basis, likely unworn crown heights for P4 are 52 mm; M1 likely was about 64 mm; M2 was about 65 mm; and M3 probably was about as tall as P2 (ca. 45 mm). At about medial wear (25–40 mm; F:AM 71862, F:AM 71861, F:AM 71860, table 7), the plication count for P2 is about 4:5:5:1; for P3, 3:6:5:1; for P4, 5:6:5:1; for M1, 3:8:5:2; and for M2, 2:5:5:1. M3 is not represented at this wear interval. In the total sample, the protocone tends to be relatively elongate (table 3C) and lingually concave; the hypoconal groove is open and not spurred. The anterior border of the prefossette is relatively complex (3 or more plis in P2–M1), usually being represented by relatively deep plications rather than by a larger number of plications having a very shallow amplitude, and the pli caballin is double or more in premolars, typically double in molars. Overall, the dentition of the Hans Johnson sample is most similar to that of the type of *C. occidentale* than any other sample under study here. This similarity includes, in F:AM 71861 and F:AM 71860, the disconnection of the pli caballin from the hypoconal selene, with that selene penetrating labially to incorporate or lie in proximity with the pli protoconule, also as seen in P3 of the holotype. Of seven specimens, the pre- and postfossette in P2 score confluent in three, separate in three, and not applicable in one.

FROM ED ROSS RANCH QUARRY, SOUTH DAKOTA: F:AM 71872 from ?late medial Clarendonian sites (referred by Skinner and MacFadden to Hollow Horn Bear Quarry [*sic*]), apparently in the Thin Elk Formation (♂ skull with right and left C1, P2–M3; fig. 11; tables 3A, 4C, 5), also indicates the presence of taxa with the morphology of *C. occidentale* in this district of South Dakota. The unworn MSTHT likely was in the range of 60 mm (table 4C). The cranial morphology shows that the ratio of facial length of the lacrimal (nos. 32, 39, table 5) to the length of the POB (no. 32, table 5) is relatively large (0.75; table 3A), and the ratio of the length of the lacrimal tip to the rear DPOF (no. 39, table 5) to the POB length is generally comparable (0.25; table 3A) to the later Clarendonian taxa *C. occidentale* or *C. skinneri*, n.sp. AMNH 10869, also possibly from the Thin Elk Formation, has an unworn MSTHT (M1) of about 65 mm (table 4C). As indicated above, this material is a likely correlate of that from the XMas-Kat quarries. P2 pre- and postfossettes are confluent on the right side of F:AM 71872 and separate on its left side; in AMNH 10869, the condition is separate.

The mandible of *C. occidentale* at the XMas-Kat Quarry is represented by F:AM

71800. As shown in MacFadden (1984: fig. 135) and table 8 (nos. 10–12), this female mandible is relatively shallow below the cheek tooth row. The symphysis extends for about half the length of the diastema from p2 to c1. The mandibular foramen is sited about halfway in the diastemal region. The lower incisors are arranged in an arcuate fashion and display cement-filled infundibula. The lower canine is nearly directly posterior to i3. The lower cheek tooth dentition is relatively slender in overall proportions. Protostylids are present on all cheek teeth except p2 and take the shape of a labially projected enamel loop. The metaconids and metastylids are well developed, of equal size, and essentially subrounded, except in p2, where the metaconid is slightly smaller than the metastylid and subtriangular. *C. occidentale* differs from *C. quinni* in the clear separation of p2 metaconid and metastylid and in their larger and subequal size, whereas in *C. quinni* the metaconid tends to be larger than the metastylid and both cuspids are relatively smaller. The labial margins of the protoconid and hypoconid are relatively flat in p2 and p3 but more convex in the remaining cheek teeth. A single pli caballinid is present in each of the premolars but not in the molars. The ectoflexids are labial in position in all cheek teeth and do not penetrate the metaconid–metastylid isthmus. The linguaflexid is relatively shallow in premolars and deeper in molars, but still sub V-shaped rather than U-shaped.

F:AM 71844, from the Machaerodus Quarry, is similar overall to F:AM 71800. The diastema in this male mandible is slightly shorter than in F:AM 71800, but other dimensions are comparable (table 8). The rear of the symphysis is about level with the anterior border of the mandibular foramen instead of being located posterior to the foramen in F:AM 71800. F:AM 71844 is in a slightly earlier wear stage than F:AM 71800, as judged by the less worn heel of m3. This may account for the otherwise unusual penetration of the isthmus by the ectoflexid in p2, p3, and m1–3 in the Machaerodus specimen and the overall less prominently developed metaconids and metastylids. Woodburne (2003: 402) indicates that the penetration of lower premolar isthmuses by the ectoflexid is a plesiomorphic trait that is found in *Merychippus insignis* but not, for example, in *C. goorisi*. As indicated in the present report, this trait is typically absent in juvenile or adult (but not ancient) specimens of other species of *Cormohipparion*, so its presence in F:AM 71844 apparently is an atavistic occurrence.

F:AM 71855, from the Hans Johnson Quarry, is a male in late wear. The mandible is somewhat crushed dorsoventrally, but its overall dimensions (table 8) appear comparable to those of the other two specimens. As in F:AM 71844, the symphysis ends anterior to the mandibular foramen, which is located near the mid-length of the diastema. The cheek teeth in F:AM 71855 show that the ectoflexids penetrate the isthmus in late wear on all cheek teeth. Ectoflexids are present in all teeth except p2 but are nearly obscured by wear in p3–m1.

### ***Cormohipparion matthewi***, new species
figures 14–15; tables 2–3, 6, 8–10

TYPE SPECIMEN: F:AM 71802, nearly complete skull with right and left I1–3, C, P2–M3, female, late adult wear.

TYPE LOCALITY: XMas-Kat quarries, Merritt Dam Member, Ash Hollow Formation, Cherry County, Nebraska.

AGE: Medial Clarendonian.

DISTRIBUTION: Xmas-Kat quarries, north-central Nebraska.

DESCRIPTION OF TYPE SPECIMEN: The cranium of F:AM 71802 (fig. 14) generally resembles that of *C. occidentale* (fig. 10). It is slightly crushed dorsoventrally and medially above the facial crest. The frontals are slightly domed above the dorsal skull profile above the nasal bones. The canine is situated about two-thirds of the length of the diastema anterior to P2. The DPOF is relatively small (short in length as well as height; nos. 33 and 35, table 9) and appears to have been pocketed to a depth of about 13 mm posterior to the rear of the DPOF and, thus, anterior to the tip of the lacrimal. The IOF is located above the anterior half of P3 and below the anterior end of the DPOF, as in *Cormohipparion* generally. The anterior end of the orbit is located above M3 rather than posterior to it. The lacrimal is blunt anteri-

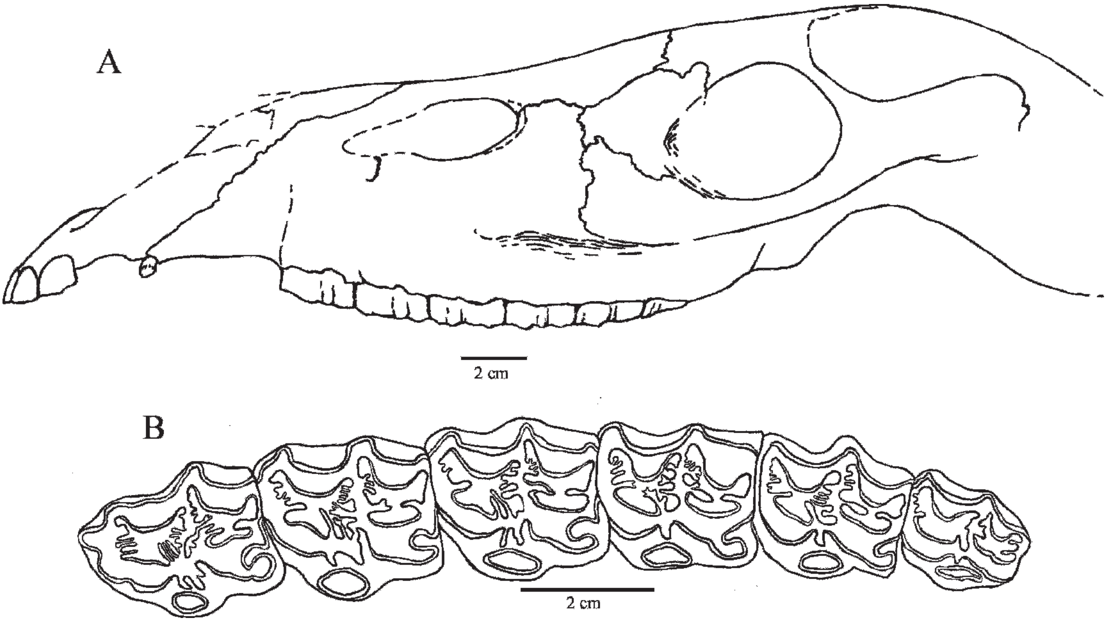


Fig. 14. *Cormohipparion matthewi*. F:AM 71802, XMas-Kat quarries, Merritt Dam Member, Ash Hollow Formation, Cherry County, Nebraska. **A,** lateral view of cranium. **B,** occlusal view of upper cheek tooth dentition.

orly, with its anterior end being about aligned with the maxillo-jugal suture rather than extending anteriorly from that point. It extends across about 60% of the POB (length 2, table 3A). The anterior tip of the lacrimal is about 20 mm posterior to the rear of the DPOF so that the facial extent of the lacrimal is about 27.5 mm, or 40%, of the DPOF (length 1, table 3A). DP1 appears to be absent. As indicated in table 10, P2 is at least 35 mm tall, and P3 is at least 33 mm tall. Based on the hypodigm, the cheek teeth appear to have been 40–45 mm tall in the unworn condition (table 3B), in contrast to 50–66 mm in *C. occidentale*. The fossette plications appear to have been relatively complex, as discussed below, but not as complex as in *C. occidentale*.

DIAGNOSIS: Based on the type and referred material, and as indicated in figure 15 and in comparison with figure 13, *C. matthewi* differs from *C. occidentale* in the greater length of the postpalatal dimension of the cranium (no. 3), and thus somewhat greater length of no. 5 (which includes no. 3). Effectively, all other measured parameters in *C. matthewi* are smaller, narrower, or shorter than in *C. occidentale*. This is exemplified by the shorter muzzle (no. 1) in *C. matthewi*. The palatal length (no. 2) and total cranial length (no. 6) in *C. matthewi* is also smaller than in *C. occidentale* from XMas-Kat Quarry but not in the samples from the Machaerodus and Hans Johnson quarries. Similarly, the cheek-tooth lengths (nos. 7–9) in *C. matthewi* are at the lower end of the range for these features in the XMas-Kat Quarry sample of *C. occidentale* but more in line with those from the Machaerodus and Hans Johnson quarries. The snout in *C. matthewi* is much narrower (no. 14) than in *C. occidentale* and all other species of the *C. occidentale* group except *C. johnsoni*, n.sp., which is even narrower. *C. matthewi* has the narrowest transglenoid dimension (no. 19) of any species discussed here. The snout (no. 25) is relatively much shorter vertically in *C. matthewi*, *C. johnsoni*, n.sp., and *C. fricki*, n.sp., than in *C. occidentale* or the other species. The nasal notch is relatively less developed in *C. matthewi*, *C. johnsoni*, n.sp., *C. merriami*, n.sp., *C. fricki*, n.sp., and *C. skinneri*, n.sp., compared with *C. occidentale*. The DPOF (no. 33) is sharply shorter in *C.*

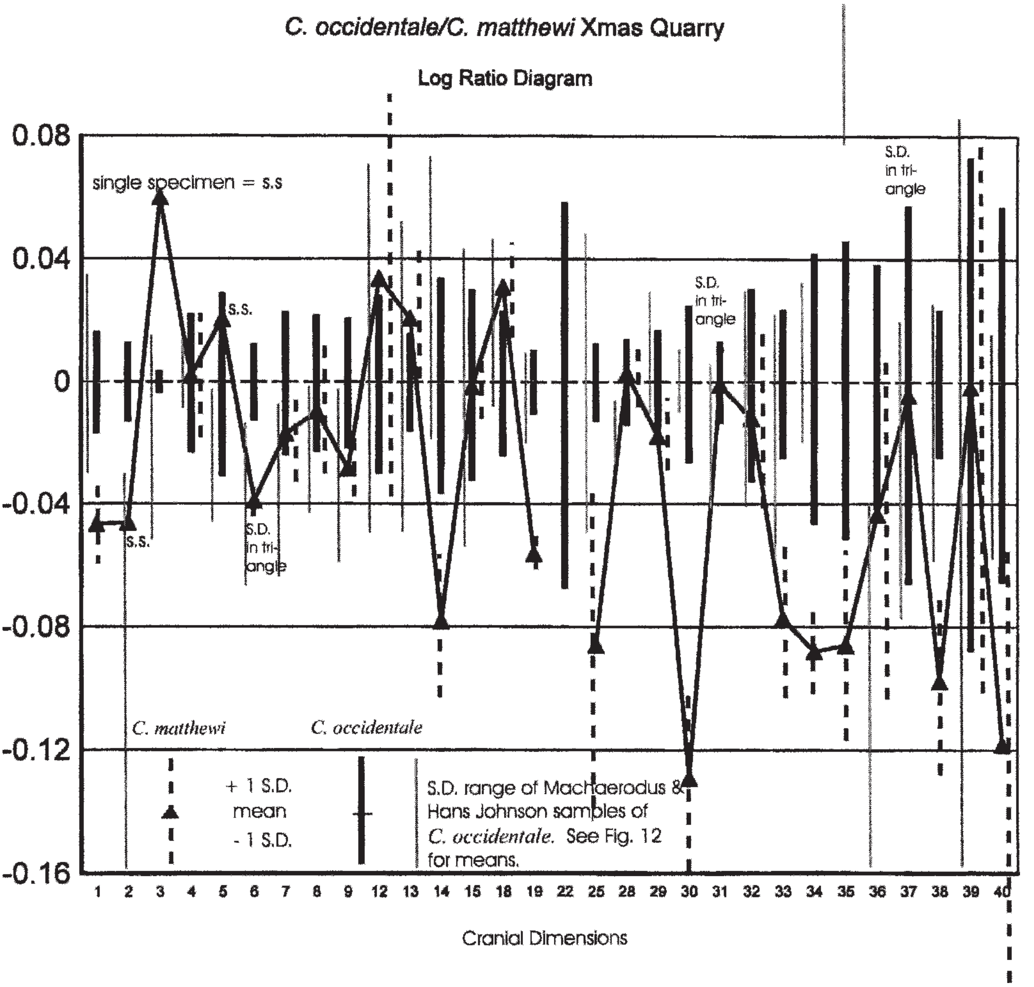


Fig. 15. Log-ratio diagram of cranial dimensions of *Cormohipparion matthewi* compared with *C. occidentale*, XMas-Kat quarries, Merritt Dam Member, Ash Hollow Formation, Cherry County, Nebraska.

*matthewi* and *C. johnsoni*, n.sp., and the S.D. ranges are shorter in *C. fricki*, n.sp., and *C. merriami*, n.sp. The separation of the IOF relative to the rear of the DPOF (no. 34) is much less in *C. matthewi* compared with *C. occidentale* or the other species, except *C. johnsoni*, n.sp., and the DPOF is much shorter vertically (no. 35) in *C. matthewi* than in *C. occidentale*. The rear of the DPOF is nearer the alveolar border (no. 38) in *C. matthewi* than in *C. occidentale* and is exceeded in this only by *C. johnsoni*. C. *matthewi* has a much shallower DPOF (no. 40) than any other species.

The unworn dentition is not represented; overall plications are less numerous in medial adult wear; and protocones are perhaps somewhat more elongate, but the sample is small. The unworn MSTHT for the upper cheek teeth is estimated at 40–45 mm (tables 3B, 10).

Referred Material: From XMas-Kat quarries, eastern Cherry County, Nebraska (Skinner and Johnson, 1984: 315, fig. 16). F:AM 71804, nearly complete skull, RI3, right and left P2–M3, female, adult wear. F:AM 71805, partial cranium, RI2–3, right and left C, P2–M3, male, early adult wear.

TABLE 9

**Measurements (mm) of Cranial Parameters for *Cormohipparion matthewi*, Merritt Dam Member, Ash Hollow Formation, medial Clarendonian Nebraska**

| | Characters[a] | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| Specimen | 1, muz | 2, pal | 3, popl | 4, basc | 5, comb | 6, tsl | 7, upl | 8, uml | 9, tcl | 12, choa | 13, palw |
| **Xmas-Kat Quarry** | | | | | | | | | | | |
| F:AM 71802 ♀ | 94.3 | 100.0 | 109.0 | 80.7 | 193.1 | 359.8 | 79.8 | 63.8 | 140.8 | 28.0 | 53.7 |
| F:AM 71804 ♀ | 99.4 | | | 89.0 | | 356.1 | 73.0 | 69.6 | 131.4 | 40.4 | 58.5 |
| F:AM 71805 ♂ | 92.1 | | | | | | 76.5 | 62.2 | 135.4 | 38.9 | 61.0 |
| Range | 92.1–99.4 | | | 80.7–89.0 | | 356.1–359.8 | 73.0–79.8 | 62.2–69.6 | 131.4–140.8 | 28.0–40.4 | 53.7–61.0 |
| Mean | 95.3 | 100.0 | 109.0 | 84.9 | 193.1 | 358.0 | 76.4 | 65.2 | 135.9 | 35.8 | 57.7 |
| SD | 3.75 | | | 5.87 | | 2.62 | 3.40 | 3.89 | 4.72 | 6.77 | 3.71 |
| CV | 3.94 | | | 6.92 | | 0.73 | 4.45 | 5.97 | 3.47 | 18.92 | 6.43 |
| *N* | 3 | 1 | 1 | 3 | 1 | 3 | 3 | 3 | 3 | 3 | 3 |
| **Hans Johnson Quarry** | | | | | | | | | | | |
| F:AM 71899 ♀ | | 102.8 | 80.2 | 90.0 | 167.0 | | 69.0 | 58.7 | 126.5 | 36.0a | 60.6 |

| Specimen | 14, sntw | 15, wmuz | 18, fwd | 19, trgl | 25, snh | 28, orl | 29, orh | 30, nis | 31, fac | 32, pobl | 33, dpof |
|---|---|---|---|---|---|---|---|---|---|---|---|
| **Xmas-Kat Quarry** | | | | | | | | | | | |
| F:AM 71802 ♀ | 25.6 | 50.8 | 131.3 | 125.0 | 60.0 | 58.0 | 43.5 | 76.5 | 161.2 | 51.2 | 56.5 |
| F:AM 71804 ♀ | 28.8 | 47.9 | 139.8 | | 57.0 | 55.7 | | 82.4 | 153.6 | 34.0 | 63.7 |
| F:AM 71805 ♂ | 28.8 | 50.0 | 144.6 | 120.4 | 74.6 | 59.2 | 46.0 | 90.0 | 158.1 | 46.3 | 56.6 |
| Range | 25.6–28.8 | 47.9–50.8 | 131.3–144.6 | 120.4–125.0 | 57.0–74.6 | 55.7–59.2 | 43.5–46.0 | 76.5–90.0 | 153.6–161.2 | 34.0–51.2 | 56.5–63.7 |
| Mean | 27.7 | 49.6 | 138.6 | 122.7 | 63.9 | 57.6 | 44.8 | 83.0 | 157.6 | 43.8 | 58.9 |
| SD | 1.85 | 1.50 | 6.74 | 3.25 | 9.42 | 1.78 | 1.77 | 6.77 | 3.82 | 8.86 | 4.13 |
| CV | 6.66 | 3.02 | 4.86 | 2.65 | 17.74 | 3.09 | 3.95 | 8.16 | 2.42 | 20.22 | 7.01 |
| *N* | 3 | 3 | 3 | 2 | 3 | 3 | 2 | 3 | 3 | 3 | 3 |
| **Hans Johnson Quarry** | | | | | | | | | | | |
| F:AM 71899 ♀ | 28.2 | 58.0 | | | | 55.8a | 43.0a | | 147.0 | 47.0a | 53.0 |

| Specimen | 34, iof | 35, hdof | 36, fch | 37, ioa | 38, mpof | 39, ldof | 40, mdof |
|---|---|---|---|---|---|---|---|
| **Xmas-Kat Quarry** | | | | | | | |
| F:AM 71802 ♀ | 49.9 | 26.1 | 32.2 | 41.3 | 45.7 | 21.1 | 10.0 |
| F:AM 71804 ♀ | 51.5 | 30.3 | 23.7 | 40.5 | 42.8 | 17.8 | 15.0 |
| F:AM 71805 ♂ | 47.6 | 26.0 | 30.8 | 41.2 | 50.5 | 12.5 | 13.5 |
| Range | 47.6–51.5 | 26.0–30.3 | 23.7–30.8 | 40.5–41.3 | 42.8–50.5 | 12.5–21.1 | 10.0–13.5 |
| Mean | 49.7 | 27.5 | 28.9 | 41.0 | 46.3 | 17.1 | 12.8 |
| SD | 1.96 | 2.45 | 4.56 | 0.44 | 3.89 | 4.34 | 2.57 |
| CV | 6.66 | 3.02 | 4.86 | 2.65 | 17.74 | 3.09 | 3.95 |
| *N* | 3 | 3 | 3 | 2 | 3 | 3 | 2 |
| **Hans Johnson Quarry** | | | | | | | |
| F:AM 71899 ♀ | 49.9 | 26.1 | 32.2 | 41.3 | 45.7 | 21.1 | 10.0 |

Remarks: [a]Characters are described in detail in table 1. **F:AM 71802**. Wear Class IV; M3 erupted; occiput crushed; #4, 5, 6 likely too small; #16, 17 difficult to define. **F:AM 71804**. Wear Class IV+; M3 erupted; skull slightly crushed dorsoventrally; #4, 6 too long. **F:AM 71805**. Wear Class III; M3 very early wear; occiput missing; cranium slightly skewed; no DPOF anterior rim. **F:AM 71859**. Wear Class IV++; M3 well worn; skull dorsoventrally flattened; anterior end DPOF not rimmed.

TABLE 10

**Measurements (mm) of Upper Cheek Tooth Dentition of *Cormohipparion matthewi*, Merritt Dam Member, Ash Hollow Formation, Medial Clarendonian, Nebraska**

Height is at mesostyle; boldface specimens used in plication count statistics; a = approximate; est. = estimated.

| Specimen | Height | Length | Width | Ratio | Index | Protocone Length | Protocone Width | Protocone Ratio | Pli caballin | Hypoconal groove |
|---|---|---|---|---|---|---|---|---|---|---|
| **P2** | | | | | | | | | | |
| **XMas-Kat Quarry** | | | | | | | | | | |
| **F:AM 71805♂** | 35.0a | 28.4 | 21.6 | 0.76 | 3:9:5:1 | 6.7 | 3.0 | 0.45 | 2 | open; simple |
| **F:AM 71802♀** | 29.0 | 28.9 | 22.5 | 0.78 | 3:7:7:2 | 7.2 | 3.7 | 0.51 | 1 | spurred |
| F:AM 71806♀ | 22.0 | 29.7 | 21.8 | 0.73 | 1:4:6:1 | 7.5 | 4.1 | 0.55 | 2 | open; narrow |
| F:AM 71804♀ | 12.0a | 27.2 | 20.9 | 0.77 | 0:1:3:0 | 7.4 | 3.2 | 0.43 | 0 | open; narrow |
| Range | | 27.2–29.7 | 20.9–22.5 | 0.76–0.78 | | 6.7–7.5 | 3.0–4.1 | 0.43–0.55 | | |
| Mean | | 28.5 | 21.7 | 0.80 | 3:8:6:2 | 7.2 | 3.5 | 0.49 | 2 | |
| SD | | 1.05 | 0.66 | 0.02 | | 0.36 | 0.45 | 0.05 | | |
| CV | | 3.67 | 3.03 | 2.38 | | 4.94 | 14.2 | 11.2 | | |
| *N* | 4 | 4 | 4 | 4 | 2 | 4 | 4 | 4 | 2 | 4 |
| **Hans Johnson Quarry** | | | | | | | | | | |
| F:AM 71863 | 39.0 | barely worn | | | | | | | | not formed |
| **P3** | | | | | | | | | | |
| **XMas-Kat Quarry** | | | | | | | | | | |
| **F:AM 71805♂** | 33.0a | 25.7 | 23.6 | 0.92 | 5:7:6:1 | 8.8 | 3.5 | 0.40 | 3 | spurred |
| **F:AM 71802♀** | 32.0a | 26.2 | 24.7 | 0.94 | 6:9:4:2 | 7.5 | 3.7 | 0.49 | 2 | narrow; simple |
| F:AM 71806♀ | 26.0 | 23.7 | 23.5 | 0.99 | 1:8:6:2 | 8.6 | 3.8 | 0.44 | 2 | open |
| F:AM 71804♀ | 16.0a | 22.9 | 22.6 | 0.99 | 1:5:3:1 | 7.3 | 3.0 | 0.41 | 3 | open; narrow |
| Range | | 22.9–26.2 | 22.6–24.7 | 0.92–0.99 | | 7.3–8.8 | 3.0–3.8 | 0.40–0.49 | | |
| Mean | | 24.6 | 23.6 | 0.96 | 6:8:6:2 | 8.1 | 3.7 | 0.33 | 3 | |
| SD | | 1.58 | 0.86 | 0.04 | | 0.76 | 0.15 | 0.23 | | |
| CV | | 6.41 | 3.65 | 3.69 | | 9.43 | 4.17 | 67.7 | | |
| *N* | 4 | 4 | 4 | 4 | 2 | 4 | 4 | 4 | 2 | 4 |
| **P4** | | | | | | | | | | |
| **XMas-Kat Quarry** | | | | | | | | | | |
| **F:AM 71805♂** | | 23.8 | 22.7 | 0.95 | 1:6:3:1 | 8.0 | 3.3 | 0.41 | 2 | spurred |
| **F:AM 71802♀** | | 24.0 | 23.0 | 0.96 | 3:7:4:1 | 8.9 | 3.3 | 0.37 | 3 | open; simple |
| F:AM 71806♀ | 26.0 est. | 22.4 | 23.7 | 1.06 | 4:8:8:1 | 7.5 | 4.2 | 0.56 | 2 | open |
| F:AM 71804♀ | | 21.5 | 22.3 | 1.04 | 1:5:3:1 | 7.3 | 3.2 | 0.44 | 2 | open |
| Range | | 21.5–24.0 | 22.3–23.7 | 0.95–1.06 | | 7.3–8.9 | 3.2–4.2 | 0.37–0.56 | | |
| Mean | | 22.9 | 22.9 | 1.00 | 2:7:4:1 | 7.9 | 3.5 | 0.45 | 3 | |
| SD | | 1.19 | 0.59 | 0.05 | | 0.71 | 0.47 | 0.08 | | |
| CV | | 5.18 | 2.58 | 5.35 | | 9.00 | 13.4 | 18.3 | | |
| *N* | 1 | 4 | 4 | 4 | 2 | 4 | 4 | 4 | 2 | 4 |

From Machaerodus Quarry, eastern Cherry County, Nebraska (Skinner and Johnson, 1984: 315, fig. 16). F:AM 71833, juvenile cranium, with LI3, LdP1, right and left dP2–4, M1, M2 erupting.

From Hans Johnson Quarry, eastern Cherry County, Nebraska (Skinner and Johnson, 1984: 315, fig. 16). F:AM 71859, nearly complete ♂ skull; snout displaced; dorsoventrally somewhat flattened, laterally expanded, right and left I1–2, LC, right and left P2–M3. F:AM 71863, nearly complete ♀ cranium of immature individual, LI1–3, R, C erupting, right and left dP1–dP4, M1 erupting.

TABLE 10
(*Continued*)

| Specimen | Height | Length | Width | Ratio | Index | Protocone Length | Protocone Width | Protocone Ratio | Pli caballin | Hypoconal groove |
|---|---|---|---|---|---|---|---|---|---|---|
| **M1** | | | | | | | | | | |
| **XMas-Kat Quarry** | | | | | | | | | | |
| **F:AM 71805♂** | | 21.5 | 20.1 | 0.94 | 1:7:5:1 | 5.5 | 3.2 | 0.58 | 1 | narrow; simple |
| **F:AM 71802♀** | | 23.0 | 21.1 | 0.92 | 3:9:6:1 | 6.6 | 3.0 | 0.45 | 1 | open; narrow |
| F:AM 71806♀ | 26.0 est. | 19.0 | 22.4 | 1.18 | 1:7:6:2 | 6.6 | 3.9 | 0.59 | 1 | open; narrow |
| F:AM 71804♀ | | 19.2 | 20.7 | 1.08 | 1:6:5:1 | 6.2 | 3.1 | 0.50 | 2 | open; narrow |
| Range | | 19.2–23.0 | 20.1–22.4 | 0.92–1.18 | | 5.5–6.6 | 3.0–3.9 | 0.45–0.59 | | |
| Mean | | 20.7 | 21.1 | 1.00 | 2:8:6:1 | 6.2 | 3.3 | 0.53 | 1 | |
| SD | | 1.92 | 0.97 | 0.12 | | 0.52 | 0.41 | 0.07 | | |
| CV | | 9.29 | 4.62 | 12.1 | | 8.33 | 12.4 | 12.4 | | |
| *N* | 1 | 4 | 4 | 4 | 2 | 4 | 4 | 4 | 2 | 4 |
| **Hans Johnson Quarry** | | | | | | | | | | |
| F:AM 71863 | 33.0 est | 25.0 | 19.0 | 0.76 | 2:4:5:2 | 7.2 | 3.8 | 0.53 | 2 | open |
| **Machaerodus Quarry** | | | | | | | | | | |
| F:AM 71833 | 36.0 est. | 23.2 | 18.6 | 0.80 | 1:4:?:? | 7.2 | 3.0 | 0.42 | 1 | ?open |
| **M2** | | | | | | | | | | |
| **XMas-Kat Quarry** | | | | | | | | | | |
| **F:AM 71805♂** | | 21.4 | 19.8 | 0.93 | 1:8:6:1 | 5.8 | 2.4 | 0.41 | 1 | open |
| **F:AM 71802♀** | | 22.1 | 20.1 | 0.91 | 4:6:4:1 | 6.1 | 3.0 | 0.49 | 1 | narrow |
| F:AM 71806♀ | 27.0 est. | 20.0 | 21.8 | 1.09 | 1:7:6:2 | 7.0 | 3.3 | 0.47 | 1 | open; narrow |
| F:AM 71804♀ | | 19.0 | 20.5 | 1.08 | 1:4:5:1 | 6.4 | 3.1 | 0.48 | 2 | open; narrow |
| Range | | 19.0–22.1 | 19.8–21.8 | 0.91–1.09 | | 5.8–7.0 | 2.4–3.3 | 0.41–0.49 | | |
| Mean | | 20.6 | 20.6 | 1.00 | 3:7:5:1 | 6.3 | 3.0 | 0.47 | 1 | |
| SD | | 1.39 | 0.88 | 0.10 | | 0.51 | 0.39 | 0.04 | | |
| CV | | 6.75 | 4.29 | 9.67 | | 8.10 | 13.1 | 7.6 | | |
| *N* | 1 | 4 | 4 | 4 | 2 | 4 | 4 | 4 | 2 | 4 |
| **M3** | | | | | | | | | | |
| **XMas-Kat Quarry** | | | | | | | | | | |
| **F:AM 71805♂** | | | | | Only initial wear | | | | | |
| **F:AM 71802♀** | | 2.10 | 15.7 | 0.75 | 5:3:2:1 | 6.5 | 2.0 | 0.31 | 1 | not formed |
| F:AM 71806♀ | 22.0 | 23.0 | 19.5 | 0.85 | 2:7:4:4 | 6.8 | 3.5 | 0.51 | 1 | open |
| F:AM 71804♀ | | 19.9 | 18.9 | 0.95 | 1:6:5:1 | 7.2 | 3.1 | 0.43 | 2 | open |
| Range | | 19.9–23.0 | 15.7–19.5 | 0.75–0.95 | | 6.5–7.2 | 2.0–3.5 | 0.31–0.51 | | |
| Mean | | 21.3 | 18.0 | 0.85 | 5:3:2:1 | 6.8 | 2.9 | 0.42 | 1 | |
| SD | | 1.57 | 2.04 | 0.10 | | 0.35 | 0.78 | 0.10 | | |
| CV | | 7.38 | 11.33 | 11.91 | | 5.14 | 27.1 | 23.8 | | |
| *N* | 1 | 3 | 3 | 3 | 1 | 3 | 3 | 3 | 1 | 3 |

Remarks:

F:AM 71805; early adult wear; M3 still erupting (relatively simple pattern); Labial pre and postfossettes connected in P2. Cf. type of *C. occidentale* except more circular protocones generally; dP1 is absent.

F:AM 71802; early adult wear; M3 pattern incomplete (relatively complex). P2 pre and postfossettes separated labially; dP1 absent.

F:AM 71806; adult wear; M3 pattern complete; relatively ovate protocones and relatively complex pattern overall; dP1 absent.

F:AM 71804; late adult wear; slightly lingually convex protocones; protocone connected in P2; triple pli caballin P3, double P4–M3; dP1 absent.

F:AM 71863; juvenile; M2 erupting, MSTHT est. 37 mm; dP1–4 present; M1 very early wear. Unworn MSTHT ca. 40–45 mm.

F:AM 71833; juvenile; M1 in early wear, MSTHT ca. 45 mm; M2 erupting; dP1 present, dP1–4 worn.

Description of Referred Material: F:AM 71895 and F:AM 71863 are too crushed to yield significant new morphological information, but F:AM 71804 and F:AM 71805 confirm that the blunt end of the lacrimal is effectively aligned with the nearly vertical maxillo-jugal suture and ends about 18 mm and 13 mm, respectively, posterior to the rear rim of the DPOF (no. 39, table 9). F:AM 71863 is somewhat crushed in this region, but its right side confirms that the lacrimal terminates about 23 mm posterior to the rim of the DPOF. F:AM 71833 is a juvenile cranium and yields no significant information.

DP1 appears to be absent, except in the juvenile cranium F:AM 71833, where the tooth is very well worn and about 9 mm long, and in the equally juvenile cranium F:AM 71863 (female), where the tooth is also worn and only about 5 mm long. DP1 is absent in all adult crania, regardless of sex. Compared with the average length of P2 in the adult specimens from the XMas-Kat quarries (28.6 mm; table 10), the dP1–P2 length ratio would be 0.32–0.18, generally consistent with the late medial Clarendonian age of this sample. The cheek teeth appear to have been 40–45 mm tall in the unworn condition, in contrast to 50–66 mm in *C. occidentale* (tables 3B, 10). As indicated in table 10, the anterior border of the prefossette in *C. matthewi* has a mean of at least 3 plis in P2 (mean of 6), P3, M2, and M3 (mean of 5), but a mean of 2 in P4 and M1. For P2–M2, the posterior border of the prefossette usually has a mean of at least 7 (up to 8) plis, with a mean of 2 in M3. The anterior border of the postfossette usually has a mean of 6 plis in P2, P3, and M1, but a mean of 5, 4, and 2 in M2, P4, and M3. The posterior border of the postfossette has a mean of 2 plis in P2 and P3 but a mean of 1 pli in the other cheek teeth. Regarding the confluence of pre- and postfossettes of P2, the three XMas-Kat specimens are scored as one yes, one no, and one not applicable; for the Machaerodus Quarry, the score is one not applicable; for the Hans Johnson Quarry, the score is one not applicable and one no. Based on the very small sample, it appears that the pre- and postfossettes in P2 may be confluent somewhat less than 50% of the time.

At present, no mandibles or lower dentitions can be directly associated with crania referred to *C. matthewi*.

***Cormohipparion johnsoni***, new species
figures 16–18; tables 2–3, 6, 11–12

Type Specimen: F:AM. 71891, ♂ skull, missing snout and occiput, somewhat crushed dorsoventrally and laterally skewed, dentition in very late wear.

Type Locality: Burge Quarry, Burge Member, Valentine Formation, Nebraska.

Age: Early Clarendonian, Burge Local Fauna, Nebraska.

Distribution: Type locality.

Description of Type Specimen: The basic morphology of the type cranium is as for *C. occidentale*. The left side best preserves the morphology in lateral view (fig. 16). As indicated in table 11, and in comparison with the juvenile cranium F:AM 71894 (fig. 17), the orbit is somewhat attenuated anterodorsally, and its anteroventral portion faces more posterolaterally than otherwise normal. The anteroventral margin of the orbit is less sharply demarcated than in F:AM 71894, for instance. The frontal region of the cranium is depressed in the type, and the postorbital fossa is distorted due to the adjacent lateral wall of the cranium having been displaced somewhat ventrally and laterally. As indicated in figure 16, the lacrimal exits the orbit just anterior to the end of the rugose dorsal orbital border and extends anterodorsally to join the fronto-nasal suture, then descends shallowly anteroventrally toward the rear of the DPOF. The lacrimal extends anteriorly about to the maxillo-jugal suture and nearly reaches, but does not penetrate, the rear of the DPOF. The lacrimo-jugal suture descends posteroventrally to enter the orbit well below the lacrimal foramen. As indicated in table 11, the POB is about 40 mm long. The DPOF is well defined posteriorly. Its dorsal margin extends anteroventrally to the relatively well-defined anterior end, situated above and in close proximity to the IOF. The bony surface of the DPOF is broken so that the canal for the maxillary nerve is exposed posterior to the infraorbital foramen, but the continuous ventral margin of the DPOF can be recognized as it joins the

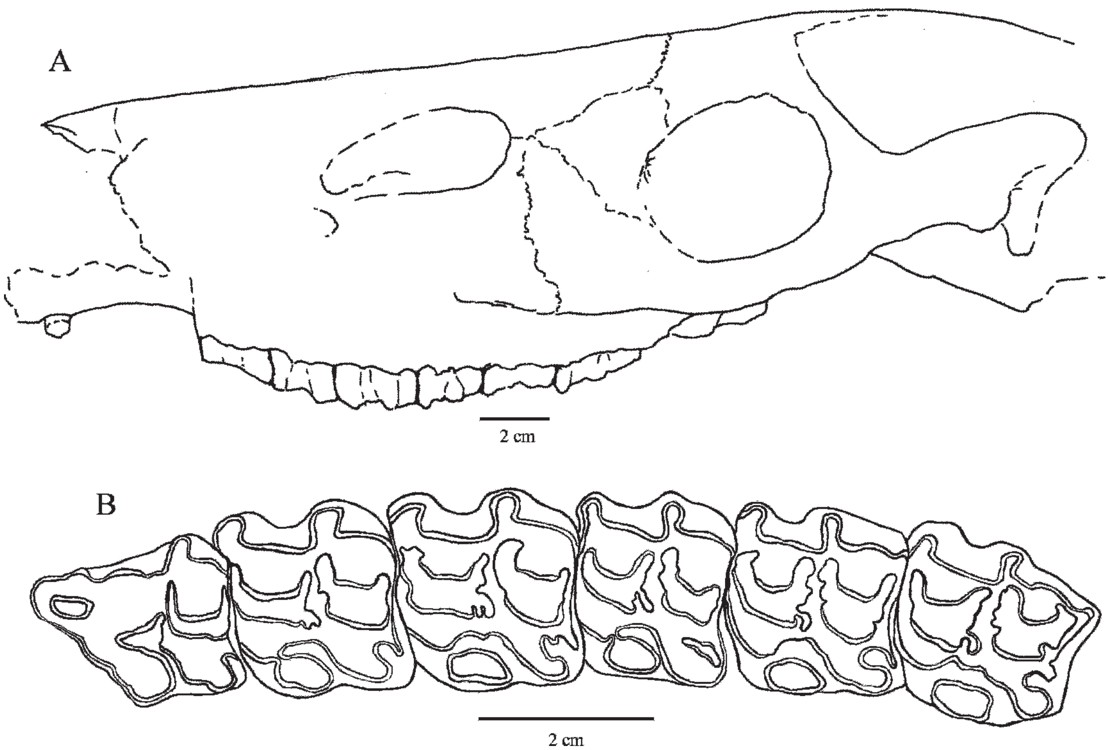


Fig. 16. *Cormohipparion johnsoni*, F:AM 71891, Burge Quarry, Burge Member, Valentine Formation, late Barstovian, Nebraska. **A,** left lateral view of cranium. **B,** occlusal view of right upper cheek tooth dentition.

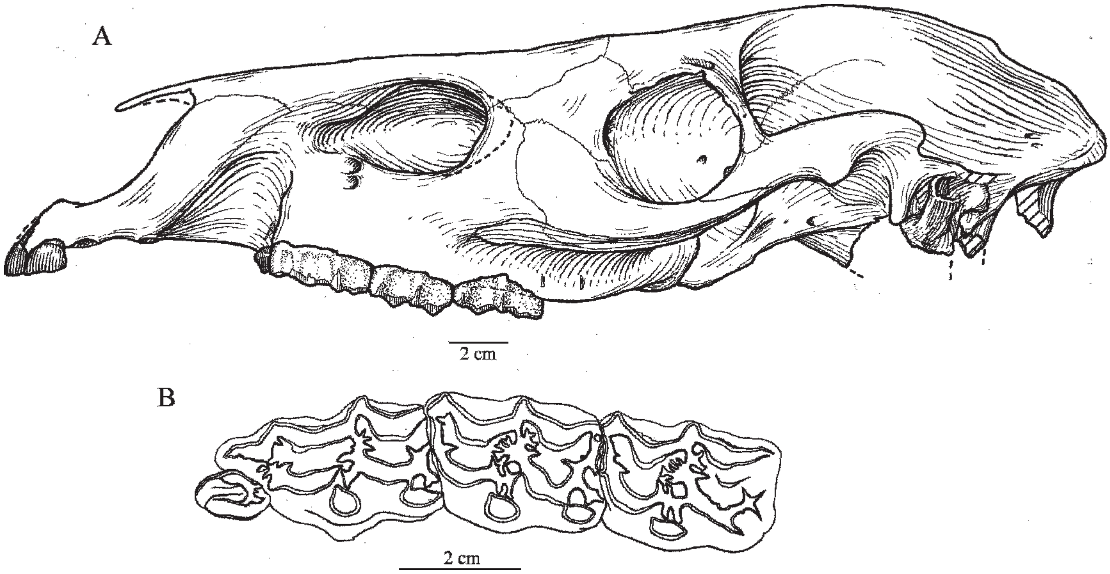


Fig. 17. *Cormohipparion johnsoni*, F:AM 71894, Burge Quarry, Burge Member, Valentine Formation, Cherry County, Nebraska, late Barstovian. **A,** lateral view of juvenile cranium, drawn by S. Gray. **B,** occlusal view of left dP1–P4, drawn by E. L. F.

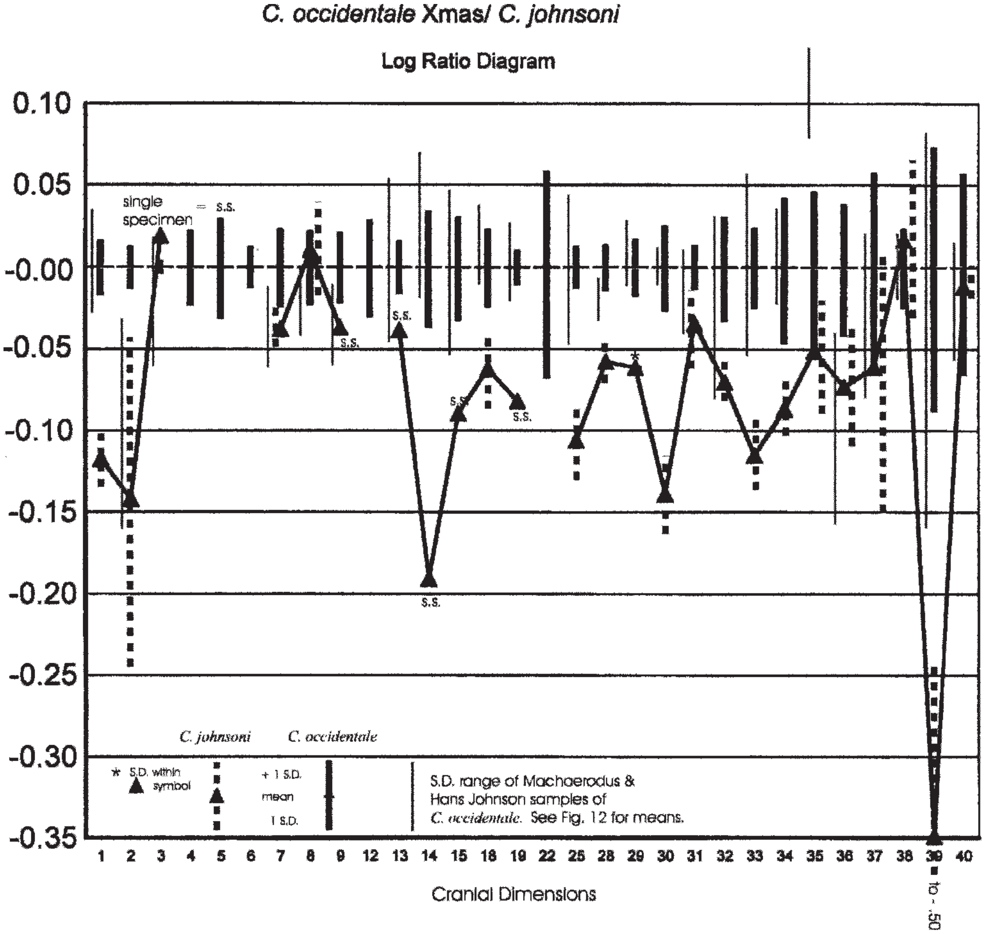


Fig. 18. Log-ratio diagram of cranial dimensions of *Cormohipparion johnsoni* compared with *C. occidentale*, XMas-Kat quarries, Merritt Dam Member, Ash Hollow Formation, Cherry County, Nebraska.

posterior margin of the fossa. The IOF is located about 44 mm (table 11) above the rear half (metacone) of P3 and is aligned about with the orbital bisector. Allowing for distortion, it appears that the DPOF is positioned relatively high on the face, anterior to the orbit in *C. johnsoni*.

In lateral view (fig. 16A), the robust canine of this male cranium can be seen, but the snout anterior thereto is not preserved. As indicated in table 6, it appears that the diastema would have been as extensive as in F:AM 125899 but probably more robust, reflective of its male sex. The basic morphology is similar to that of *C. occidentale*. Roots for dP1 are preserved, but the crown is absent. Due to the advanced age of the specimen, the dental morphology is poorly preserved. That for P2 is virtually obliterated, with the protocone confluent with the protoloph at this advanced stage of wear (MSTHT 10 mm, table 12). In P3, the protocone is confluent to still virtually isolated (left side; fig. 16B); it is barely open to the protoloph in M1 but isolated in all other teeth. Tables 3B and 12 show that the protocone is ovate in all teeth except for M3, where it is more elongate (protocone width to length ratio of 0.47), with M3 preserving a remnant of what likely was a fairly complex fossette border morphology throughout. Due to the late stage of wear shown by this specimen, the teeth are

TABLE 11

**Measurements (mm) of Cranial Parameters for *Cormohipparion johnsoni* and *C. merriami*, Burge Member, Valentine Formation, early Clarendonian Nebraska**

| Specimen | Characters[a] | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| | 1, muz | 2, pal | 3, popl | 4, basc | 5, comb | 6, tsl | 7, upl | 8, uml | 9, tcl | 12, choa | 13, palw |
| ***Cormohipparion johnsoni*, Burge Quarry** | | | | | | | | | | | |
| F:AM 71891 ♂ | | 99.7 | | | | | 68.6 | 68.3 | 133.3 | 32.4 | 50.4 |
| F:AM 71894 ?♀ | 75.2 | 60.7 | 99.2 | | | | | | | | |
| AMNH 125899 ♂ | 86.6 | | | | | | 77.2 | | | | |
| Range | 75.2–86.6 | 60.7–99.7 | | | | | 68.6–77.2 | | | | |
| Mean | 80.9 | 80.2 | 99.2 | | | | 72.9 | 68.3 | 133.3 | 32.4 | 50.4 |
| SD | 8.06 | 27.58 | | | | | 6.08 | | | | |
| CV | 10.00 | 34.39 | | | | | 8.34 | | | | |
| *N* | 2 | 2 | 1 | | | | 2 | 1 | 1 | 1 | 1 |
| | 14, sntw | 15, wmuz | 18, fwd | 19, trgl | 25, snh | 28, orl | 29, orh | 30, nis | 31, fac | 32, pobl | 33, dpof |
| F:AM 71891 ♂ | | | 121.5 | | 66.5 | 52.6 | 39.9 | | 156.9 | 40.3 | 60.3 |
| F:AM 71894 ?♀ | 21.4 | 40.5 | 102.3 | 115.7 | 55.5 | 47.7 | 41.1 | 75.0 | 129.2 | 35.5 | 48.1 |
| AMNH 125899 ♂ | | | | | | | | 87.2 | 151.6 | 39.2 | 53.6 |
| Range | | | 103.3–121.5 | | 55.5–66.5 | 47.7–52.6 | 39.9–41.1 | 75.0–87.2 | 129.2–156.9 | 35.5–40.3 | 48.1–60.3 |
| Mean | 21.4 | 40.5 | 111.9 | 115.7 | 61.0 | 50.2 | 40.5 | 81.1 | 145.9 | 38.3 | 54.0 |
| SD | | | 13.58 | | 7.78 | 3.46 | 0.85 | 8.63 | 14.70 | 2.51 | 6.11 |
| CV | | | 12.13 | | 12.75 | 6.91 | 2.10 | 10.6 | 10.1 | 6.6 | 11.3 |
| *N* | 1 | 1 | 2 | 1 | 2 | 2 | 2 | 2 | 3 | 3 | 3 |
| | 34, iof | 35, hdof | 36, fch | 37, ioa | 38, mpof | 39, ldof | 40, mdof | | | | |
| F:AM 71891 ♂ | 54.2 | 28.0 | 35.6 | 44.0 | 67.5 | 11.1 | 16.0 | | | | |
| F:AM 71894 ?♀ | 44.2 | 33.4 | 19.7 | 27.5 | 53.2 | 5.5 | 16.8 | | | | |
| AMNH 125899 ♂ | 51.0 | 27.9 | 25.7 | 36.5 | | 6.5 | | | | | |
| Range | 44.2–54.2 | 27.9–33.4 | 19.7–35.6 | 27.5–44.0 | 53.2–67.5 | 5.5–11.1 | 16.0–16.8 | | | | |
| Mean | 49.8 | 29.8 | 27.0 | 36.0 | 60.4 | 7.7 | 16.4 | | | | |
| SD | 5.11 | 3.15 | 8.03 | 8.26 | 10.11 | 3.00 | 0.57 | | | | |
| CV | 10.3 | 10.6 | 29.7 | 23.0 | 16.8 | 38.8 | 3.5 | | | | |
| *N* | 3 | 3 | 3 | 3 | 2 | 3 | 2 | | | | |

Remarks:

F:AM 71891; wear class IV+; M3 well worn; skull slightly skewed laterally, transverse dimensions distorted; DPOF with well developed anterior rim.

F:AM 71894; wear class I; dPs erupted; juvenile; most dimensions too small, except 28, 29, 30; DPOF with well developed anterior rim; triangular lacrimal.

AMNH 125899; wear class II; M2 erupting; skull laterally crushed; DPOF with anterior rim; trianglar lacrimal.

[a]Parameters are illustrated in figs. 3–5.

TABLE 11
(*Continued*)

| Specimen | 1, muz | 2, pal | 3, popl | 4, basc | 5, comb | 6, tsl | 7, upl | 8, uml | 9, tcl | 13, palw |
|---|---|---|---|---|---|---|---|---|---|---|
| ***Cormohipparion merriami*, June Quarry and Midway Quarry** | | | | | | | | | | |
| AMNH 141219 ♀ | 104.3 | 120.8 | 95.8 | 84.1 | 168.8 | 396.6 | 85.9 | 69.4 | 153.8 | 59.4 |
| AMNH 141220 ♀ | | | | 66.5 | | | | 59.3 | | |
| F:AM 71893 (**M**) | | | | | | | | | | |
| Range | | | | 66.5–84.1 | | | | 59.3–69.4 | | |
| Mean | 104.3 | 120.8 | 95.8 | 75.3 | 168.8 | 396.6 | 85.9 | 64.4 | 153.8 | 59.4 |
| SD | | | | 12.45 | | | | 7.14 | | |
| CV | | | | 16.5 | | | | 11.1 | | |
| *N* | 1 | 1 | 1 | 2 | 1 | 1 | 1 | 2 | 1 | 1 |

| | 14, sntw | 15, wmuz | 18, fwd | 19, trgl | 22, in | 25, snh | 28, orl | 29, orh | 30, nis | 31, fac | 32, pobl |
|---|---|---|---|---|---|---|---|---|---|---|---|
| AMNH 141219 ♀ | 32.1 | 52.3 | 128.5 | 134.8 | 58.8 | 78.4 | 52.0 | 49.5 | 98.0 | 173.8 | 44.3 |
| AMNH 141220 ♀ | | 45.0 | | | | | 56.6 | 46.3 | | | 35.3 |
| F:AM 71893 (**M**) | | | | | | | 48.4 | 41.5 | | | 36.9 |
| Range | | 45.0–52.3 | | | | | 48.4–56.6 | 41.5–49.5 | | | 35.3–44.3 |
| Mean | 32.1 | 48.7 | 128.5 | 134.8 | 58.8 | 78.4 | 52.3 | 45.8 | 98.0 | 173.8 | 38.8 |
| SD | | 5.16 | | | | | 4.11 | 4.03 | | | 4.8 |
| CV | | 10.6 | | | | | 7.9 | 8.8 | | | 12.4 |
| *N* | 1 | 2 | 1 | 1 | 1 | 1 | 3 | 3 | 1 | 1 | 3 |

| | 33, dpof | 34, iof | 35, hdof | 36, fch | 37, ioa | 38, mpof | 39, ldof | 40, medof |
|---|---|---|---|---|---|---|---|---|
| AMNH 141219 ♀ | 63.8 | 58.3 | 38.8 | 33.8 | 42.5 | 75.8 | 16.9 | 16.5 |
| AMNH 141220 ♀ | 75.0 | 70.0 | 38.0 | 31.5 | | 62.0 | 17.4 | 15.0 |
| F:AM 71893 (**M**) | 51.1 | | 32.0 | 21.0 | | | 9.5 | 17.5 |
| Range | 51.1–75.0 | 58.3–70.0 | 32.0–38.8 | 21.0–33.8 | | 62.0–75.8 | 9.5–17.4 | 16.5–17.5 |
| Mean | 63.3 | 64.2 | 36.3 | 28.8 | 42.5 | 68.9 | 143.6 | 16.3 |
| SD | 11.96 | 8.27 | 3.72 | 6.82 | | 9.76 | 4.42 | 1.26 |
| CV | 18.9 | 12.9 | 10.3 | 23.7 | | 14.2 | 30.3 | 7.7 |
| *N* | 3 | 2 | 3 | 3 | 1 | 2 | 3 | 3 |

Remarks: (**M**) = Midway Quarry. [a]Parameters are illustrated in figs. 3–5.
AMNH 141219; wear class IV; M3 worn; nearly prefect skull; triangular lacrimal does not reach rear of DPOF.
AMNH 141220; wear class V; M3 well worn; skull crushed and cracked; facial region probably OK; subtriangular lacrimal.
F:AM 71893; wear class I; dPs only erupted; cranial dimensions likely small; triangular lacrimal.

TABLE 12

**Measurements (mm) of Upper Cheek Tooth Dentition of *Cormohipparion johnsoni*, Burge Member, Valentine Formation, Early Clarendonian, Nebraska**

**P2**

| Specimen | Height | Length | Width | Ratio | Index | Protocone Length | Protocone Width | Protocone Ratio | Pli caballin | Hypoconal groove |
|---|---|---|---|---|---|---|---|---|---|---|
| F:AM 71894 ?♀ | juvenile | no | data | | | | | | | |
| **F:AM 125899** ♀ | 36.7 | 27.6 | 21.0 | 0.76 | no data | 7.3 | 3.9 | 0.53 | 1 | open; spurred |
| **F:AM 119095** | | | | | | | | | | |
| F:AM 71891 ♂ | 10.0 | 27.6 | 20.9 | 0.76 | 0:0:0:0 | 8.9 | 6.5 | 0.73 | 0 | open; simple |
| Range | | | 20.9–21.0 | | | 7.3–8.9 | 3.9–6.5 | 0.53–0.73 | | |
| Mean | | 27.6 | 21.0 | 0.76 | | 8.1 | 5.2 | 0.63 | 1 | |
| SD | | | 0.07 | | | 1.13 | 1.84 | 0.14 | | |
| CV | | | 7.34 | | | 14.0 | 35.4 | 21.9 | | |
| *N* | 2 | 2 | 2 | 2 | 0 | 2 | 2 | 2 | 2 | 2 |

Remarks: Height is at mesostyle; boldface specimens used for plication statistics. Index unknown, F:AM 71891 too low crowned; a = approximate.

F:AM 125899 crown heights from original data; other dimensions and plication counts taken from second level of sectioned teeth.

F:AM 71894 dP1 length is 10.4; width is 6.8.

F:AM 125899 dP1 length is 8.2; width is 4.8. Ratio of dP1 length/M1 length is 0.30.

**P3**

| Specimen | Height | Length | Width | Ratio | Index | Protocone Length | Protocone Width | Protocone Ratio | Pli caballin | Hypoconal groove |
|---|---|---|---|---|---|---|---|---|---|---|
| **F:AM 125899** ♀ | 42.2 | 25.8 | 25.0 | 0.97 | 1:4:4:1 | 9.4 | 3.8 | 0.40 | 1 | open, spurred |
| **F:AM 119095** | 36.7 | 24.0 | 22.4 | 0.93 | 1:7:4:1 | 7.6 | 4.3 | 0.57 | 3 | spurred |
| F:AM 71891 ♂ | 11.6 | 23.5 | 22.6 | 0.96 | 0:1:1:0 | 7.7 | 5.0 | 0.65 | 0 | open; simple |
| Range | | 23.5–25.8 | 22.6–25.0 | 0.93–0.97 | | 7.6–9.4 | 3.8–5.0 | 0.40–0.65 | | |
| Mean | | 24.4 | 23.3 | 0.95 | 1:5:4:1 | 8.2 | 4.4 | 0.54 | 2 | |
| SD | | 1.63 | 1.70 | 0.01 | | 1.20 | 0.85 | 0.17 | | |
| CV | | 6.66 | 7.27 | 0.54 | | 14.6 | 19.4 | 32.1 | | |
| *N* | 3 | 3 | 3 | 3 | 2 | 3 | 3 | 3 | 2 | 3 |
| **P4** | | | | | | | | | | |
| **F:AM 125899** ♀ | 48.6 | 24.8 | 23.5 | 0.95 | 1:6:5:1 | | | | 2 | unworn |
| **F:AM 119095** | 39.0a | 23.4 | 22.5 | 0.96 | 1:6:4:1 | 7.8 | 4.0 | 0.51 | 3 | open; simple |
| F:AM 71891 ♂ | 14.3 | 22.6 | 25.8 | 1.14 | 1:2:2:1 | 7.9 | 4.5 | 0.57 | 1 | open; simple |
| Range | | 22.6–24.8 | 23.5–25.8 | 0.95–1.14 | | 7.8–7.9 | 4.0–4.5 | 0.51–0.57 | | |
| Mean | | 23.6 | 23.9 | 1.02 | 1:6:5:1 | 7.9 | 4.25 | 0.54 | 3 | |
| SD | | 1.56 | 1.63 | 0.14 | | 0.07 | 0.35 | 0.04 | | |
| CV | | 6.59 | 6.82 | 13.5 | | 0.90 | 8.32 | 7.42 | | |
| *N* | 3 | 3 | 3 | 3 | 2 | 2 | 2 | 2 | 2 | 3 |

very low crowned. Cranial dimensions are summarized in table 11.

DIAGNOSIS: Based on the type and referred material, *Cormohipparion johnsoni* is distinguished from all other species of the subgenus *Cormohipparion* in having an unworn mesostyle crown height of 40–50 mm (table 3B). In addition, figure 18 in comparison with figure 13 indicates that *C. johnsoni* differs from *C. occidentale* and the other species in having a much shorter muzzle (no. 1) and narrower muzzle at the I3

TABLE 12
(*Continued*)

| Specimen | Height | Length | Width | Ratio | Index | Protocone Length | Protocone Width | Protocone Ratio | Pli caballin | Hypoconal groove |
|---|---|---|---|---|---|---|---|---|---|---|
| **M1** | | | | | | | | | | |
| **F:AM 125899 ♀** | 42.4 | 24.2 | 23.2 | 0.96 | 1:6:6:1 | 9.9 | 3.7 | 0.37 | 1 | narrow; simple |
| **F:AM 119095** | 38.5 | 20.3 | 20.7 | 1.02 | 1:7:5:1 | 7.4 | 4.0 | 0.54 | 1 | open; simple |
| F:AM 71891 ♂ | 10.3 | 20.4 | 24.0 | 1.18 | 0:2:1:0 | 7.8 | 4.9 | 0.63 | 0 | open; simple |
| Range | | 20.4–24.2 | 20.7–24.0 | 0.96–1.18 | | 7.4–9.9 | 3.7–4.9 | 0.37–0.63 | | |
| Mean | | 21.6 | 22.6 | 1.05 | 1:6:6:1 | 8.4 | 4.2 | 0.51 | 1 | |
| SD | | 2.22 | 1.72 | 0.10 | | 1.34 | 0.62 | 0.13 | | |
| CV | | 10.28 | 7.61 | 10.7 | | 16.1 | 14.9 | 25.1 | | |
| *N* | 3 | 3 | 3 | 3 | 2 | 3 | 3 | 3 | 2 | 3 |
| **M2** | | | | | | | | | | |
| **F:AM 125899 ♀** | 45.6 | 21.8 | 20.6 | 0.94 | 0:6:8:1 | 9.0 | 3.4 | 0.38 | 1 | open; simple |
| **F:AM 199095** | 40.5a | 21.8 | 20.5 | 0.94 | 1:6:4:4 | 7.0 | 3.5 | 0.50 | 1 | open; simple |
| F:AM 71891 ♂ | 10.1 | 21.7 | 24.6 | 1.13 | 0:2:1:1 | 8.0 | 4.9 | 0.61 | 2 | open; simple |
| Range | | 21.7–21.8 | 20.6–24.6 | 0.94–1.13 | | 7.0–9.0 | 3.4–4.9 | 0.38–0.61 | | |
| Mean | | 21.8 | 21.9 | 1.01 | 1:6:6:3 | 8.0 | 3.9 | 0.50 | 1 | |
| SD | | 0.06 | 2.34 | 0.11 | | 1.00 | 0.84 | 0.12 | | |
| CV | | 0.3 | 10.7 | 10.9 | | 12.5 | 21.3 | 23.6 | | |
| *N* | 3 | 3 | 3 | 3 | 2 | 3 | 3 | 3 | 2 | 3 |
| **M3** | | | | | | | | | | |
| **F:AM 125899 ♀** | | | | | | | | | | |
| **F:AM 119095** | 37.0 | 20.0 | 16.5 | 0.83 | 1:?7:3:? | 7.4 | 3.6 | 0.49 | 1 | open; simple |
| F:AM 71891 ♂ | 18.0 | 25.0 | 21.7 | 0.87 | 1:5:2:2 | 9.4 | 4.3 | 0.46 | 1 | open; simple |
| Range | | 20.0–25.0 | 16.5–21.7 | 0.83–0.87 | | 7.4–9.4 | 3.6–4.3 | 0.46–0.49 | | |
| Mean | | 22.5 | 19.1 | 0.85 | 1:7:3:1 | 8.4 | 4.0 | 0.47 | 1 | |
| SD | | 3.54 | 3.68 | 0.03 | | 1.41 | 0.50 | 0.02 | | |
| CV | | 15.7 | 19.3 | 3.6 | | 16.8 | 12.5 | 4.4 | | |
| *N* | 2 | 2 | 2 | 2 | 1 | 2 | 2 | 2 | 1 | 2 |

Remarks:

F:AM 71894; juvenile, dP1–4 well worn.

F:AM 125899; early wear; dP1 relatively small, worn. Occlusal pattern not developed except on M1, where is very early. Unworn MSTHT 45–50 mm.

F:AM 119095; early to medial wear; M3 not maturely developed, shows relatively complex fossette borders; M2 in very early wear. Unworn MSTHT likely 45–50 mm.

F:AM 71891; very late wear; protocone isolated in P4, M2–3; M3 retains elongate premolar and pattern complexity.

(no. 15). *C. johnsoni* differs from the XMas-Kat sample of *C. occidentale*, but from not the Machaerodus and Hans Johnson samples, in the shortness (no. 2) and lesser palatal breadth (no. 13) and in having shorter premolars (nos. 7, 9). It differs from all samples of *C. occidentale* in the diminished breadth of the frontals (no. 18) and transglenoid region (no. 19) and from all other species in these parameters, as well (except for no. 19 in *C. matthewi*). *C. johnsoni* also has smaller orbit (nos. 28–29) than in any other species of the group, as perhaps befits its plesiomorphic status (see below). The POB is shorter in *C. johnsoni* and *C. merriami*, n.sp., than in the other species. The DPOF (no. 33) is sharply shorter in *C. johnsoni* (and *C. matthewi*) and ranges to a comparably small size in *C. merriami*, n.sp., and *C. fricki*, n.sp. The separation of the IOF relative to the rear of the DPOF (no. 34) is much less in *C. johnsoni* as compared with *C.*

*occidentale* or the other species, except *C. matthewi*, and the lacrimal nearly reaches the rear of the DPOF (no. 39) and extends across about 80% of the POB (table 3A), in contrast to any other species.

Especially as regards parameters 2 and 39, the very large range for the standard deviation is influenced by the small number of specimens, and the overall smaller dimensions can be related to the overall smaller size of the skull of *C. johnsoni* compared with *C. occidentale*. Still, the very diminished size of parameters 14 (narrow diastema) and 39 (tip to rear of DPOF; table 11) is noteworthy, as is the fact that other parameters are near or contained within the range of those in *C. occidentale* (fig. 18): no. 7, premolar row length; no. 8, molar row length; no. 12, choanal width; no. 31, facial length; no. 35, height of DPOF relative to the facial crest; no. 36, relative position of the facial crest and DPOF; no. 37, relative height of the IOF from the alveolar row; no. 38, height of rear of DPOF relative to alveolar row; and no. 40, medial depth of DPOF.

*Cormohipparion johnsoni* (fig. 18) differs from *C. matthewi* (fig. 15) in having a much shorter snout and palate (nos. 1–3) in contrast to comparably sized premolar and molar rows (nos. 7–9). *C. johnsoni* also has a narrower palate (no. 13); a greatly narrower diastemal region (no. 14) and muzzle (no. 15); a much narrower frontal width (no. 18); and a narrower transglenoid width (no. 19). In contrast to an equally high snout (no. 25) and equally incised nasal notch (no. 30) relative to *C. matthewi*, *C. johnsoni* has a smaller orbit (nos. 28–29), a shorter facial region (no. 31), a relatively shorter POB (no. 32), and a somewhat shorter DPOF (no. 33). However, the IOF location relative to the DPOF is similar (no. 34) in *C. johnsoni* and *C. matthewi*, but *C. johnsoni* has a taller DPOF (no. 35), a diminished separation of the facial crest from the DPOF (no. 36), a decreased separation between the IOF and alveolar border (no. 37), a greater separation between the DPOF and alveolar border (no. 38), a lacrimal that is very close to the rear of the DPOF (no. 39; table 11), and a medially deeper DPOF (no. 40).

In comparison with *C. merriami*, n.sp. (fig. 20), *C. johnsoni* (fig. 18) has a much shorter snout and palate (nos. 1–2); a much shorter premolar and molar row (nos. 7–9); a much narrower palate (no. 13), diastemal region (no. 14), muzzle (no. 15), frontal region (no. 18) and transglenoid region (no. 19); a much smaller snout (no. 25); a smaller orbit (no. 29); a shallower nasal notch (no. 30); and a much shorter facial region (no. 31). Whereas the POB is comparable (no. 32) in the two species, *C. johnsoni* has a much shorter DPOF (no. 33); a decreased separation between the IOF and rear of the DPOF (no. 34); a much reduced DPOF height (no. 35); a somewhat diminished separation of the facial crest and DPOF (no. 36); and of the IOF relative to the alveolar border (no. 37), a more normative (cf. *C. occidentale*) separation of the alveolar border and rear of DPOF (no. 38); a lacrimal anterior tip very close to the rear of the DPOF (no. 39, table 11); and a comparable DPOF medial depth.

In addition to overall size and crown height, as well as dental complexity, *C. johnsoni* differs from *C. quinni* in the more anterior position of the DPOF, reflected in the fact that the lacrimal barely reaches, but does not penetrate, the DPOF. *C. johnsoni* is the most plesiomorphic member of the *C. occidentale* group.

Referred Material: F:AM 71894, nearly complete immature ?♀ cranium, with dP1–4 present and well worn. F:AM 125899, laterally compressed cranium with occipital region obscured, right and left C, dP1–M2; M3 not erupted. F:AM 119095, right maxilla with P3–M3.

Description of Referred Material: F:AM 71894 (fig. 17) is useful in demonstrating the presence of dP1 as a relatively small, but still functional, tooth (table 12). The deciduous premolars are in an early stage of wear, with the pattern not fully developed on dP2 or dP4. The dP3 and dP4 show double plis caballin and complex opposing borders of the pre- and postfossette. F:AM 125899 indicates that the ratio of the length dP1 to the length of P2 is 0.3 (table 12).

In lateral view (fig. 17), the well-developed and strongly demarcated DPOF is clearly visible, as is the wide POB and the pointed lacrimal that terminates a short distance posterior to the rear of the DPOF (5.5 mm, no. 39, table 11). Although not as well shown, a similar arrangement for the lacrimal is interpreted to have obtained in the type and in F:AM 125899, with the anterior tip of the lacrimal 11 mm posterior to (type) or 6.5 mm to the rear of the DPOF (F:AM 125899).

F:AM 125899 and F:AM 119095 indicate that the unworn cheek tooth MSTHT dimensions apparently were about 45–50 mm (tables 3B, 12). The cheek teeth of F:AM 125899 were removed from the cranium under the direction of the late Morris F. Skinner, and measurements were taken before they were sectioned at three intervals at progressively deeper levels in each tooth. The tooth segments were preserved by being glued to a plate of glass. From these segments it can be seen that M3 is completely unworn and is not furnished with a cement cover, as are the other teeth. The MSTHT for M3 is not available (encased in matrix). P4, the next tooth in the wear progression, shows only incipient wear on its highest crests and is 48.6 mm tall. In further order of increasing wear, P2 MSTHT is 36.7 mm; P3 is 42.2 mm; M2 is 45.6 mm; and M1, with a nearly complete wear pattern, is 42.4 mm tall. It is likely that M1 originally was about as tall as P4. Based on its currently unworn state, the MSTHT for P4 appears to have been no greater than 50 mm. Based on F:AM 125899, the unworn MSTHT for upper cheek teeth in *C. johnsoni* appears to have been 40–50 mm. These parameters are basically verified by AMNH 119095 (table 12), which also shows the moderate complexity of the pre- and post-fossettes. In P3–M3, the anterior border of the prefossette and posterior border of the postfossette typically have a single pli (mean value, table 12). In P3, opposing borders of the pre- and postfossette have mean values of 5 and 4 plis, respectively. In P4, comparable values are 6 and 5; in M1 and M2, 6 and 6; and in M3, the values are 7 and 3. The protocones are ovate to slightly elongate and ovate, with somewhat flattened lingual borders in P3 and P4 but lingually rounded in the molars. As indicated in table 3C, the mean width-to-length ratios for the cheek teeth of *C. johnsoni* are generally similar to those for *C. merriami*, n.sp., and generally wider (at or above 50% in P2–M2) than in all other species of the *C. occidentale* group. AMNH 119095 displays a pli protoconule that is isolated from the posterolingual border of the prefossette in early wear of P3–4 and a large and distinct loop in this position in M1–3. The pre-and postfossettes were separated from one another in P2 of F:AM 125899. Plis caballin are more complex (mean value of 2, table 12) in the P3 and P4 compared with the other cheek teeth. The hypoconal groove is usually simple (bears a spur in the juvenile P2 and P3 in F:AM 71984). In early wear (F:AM 125899), P2 shows separated pre- and postfossettes, but in late wear (type specimen) these fossettes are confluent.

At present, no mandibles or lower dentitions can be directly associated with crania referred to *C. johnsoni*.

DISCUSSION: As discussed below, *C. johnsoni* is the basal member of the *C. occidentale* group.

***Cormohipparion merriami***, new species
figures 19–20; tables 2–3, 6, 11, 13

*Neohipparion* cf. *coloradense* Webb 1969: 98.

TYPE SPECIMEN: AMNH 141219, nearly perfect ♀ skull, right and left I3, C, dP1–M3 in about mid wear.

TYPE LOCALITY: June Quarry, Burge Member, Valentine Formation, Nebraska.

AGE: Early Clarendonian, Burge Local Fauna, Nebraska.

DISTRIBUTION: Midway Quarry, Burge Member, Valentine Formation, Nebraska.

DESCRIPTION OF TYPE SPECIMEN: AMNH 141219 is generally similar to *C. occidentale* in basic skull morphology (fig. 19A). The IOF is situated above the anterior half of P3 and below the anterior end of the DPOF, as is typical of the *C. occidentale* group of *Cormohipparion*. The anterior edge of the orbit is located above M3 rather than more posteriorly, as in *C. occidentale*. The lacrimal is pointed anteriorly and extends about 11 mm anteriorly beyond the maxillo-jugal suture but ends about 15 mm (mean value) posterior to (and does not reach) the rear of the DPOF (no. 39, table 11). It appears that the DPOF is pocketed posteriorly to about the anterior tip of the lacrimal. In contrast to *C. occidentale* as represented by the XMas-Kat

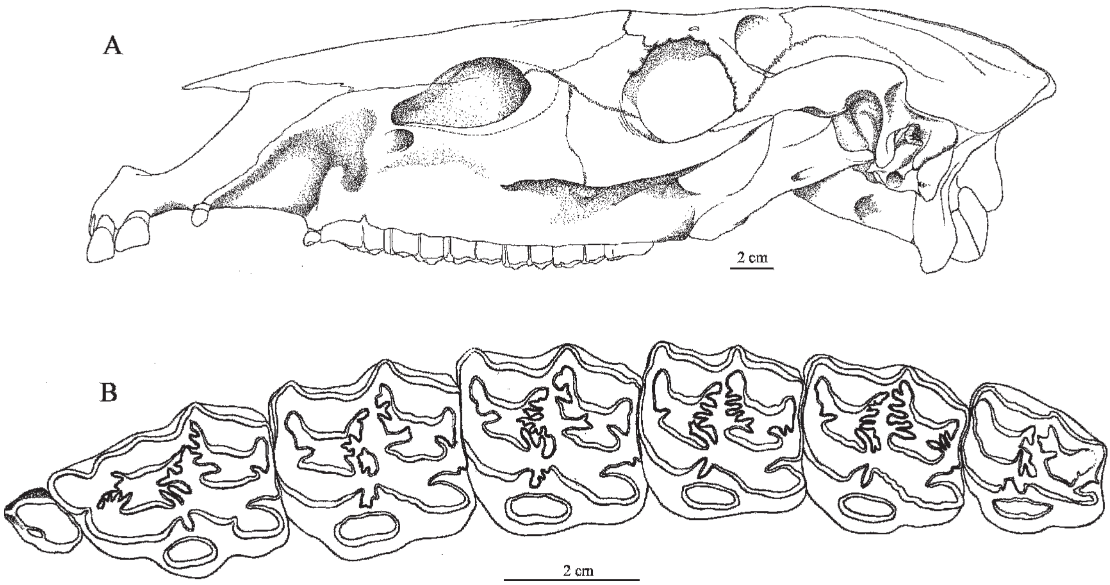


Fig. 19. *Cormohipparion merriami*, AMNH 141219, Burge Quarry, Valentine Formation, Nebraska, late Barstovian. **A,** left lateral view of cranium. **B,** occlusal view of upper cheek tooth dentition, drawn by E. L. F.

sample, the MSTHT is estimated as having been ca. 55 mm (i.e., much lower crowned; tables 3B, 13); dP1 is present (the ratio of the length of dP1 to the length of P2 is 0.37) in the type specimen but apparently has been lost in the juvenile cranium F:AM 71893. As indicated in table 3C, the protocones are relatively wider than in all members of the *C. occidentale* group except for *C. johnsoni.* Whereas P2 is subovate, the protocone in the other cheek teeth is more elongate (fig. 19B). Fossette plications are discussed in conjunction with the referred material (see below).

DIAGNOSIS: Based on the type and referred material, *Cormohipparion merriami* is distinguished from other species of the subgenus *Cormohipparion* in having lacrimal that extends anteriorly beyond the maxillo-jugal suture but still does not reach the rear of the DPOF. The MSTHT is relatively low (ca. 55 mm) in *C. merriami*; the protocones are relatively wide and not so elongate. As indicated in figure 20 and in comparison with figure 13, *C. merriami* is greater than (or likely would range much higher than) all other species in length of palate (no. 2) and has a relatively greater premolar (no. 7) and thus cheek tooth (no. 9) length than in *C. occidentale* (unknown in *C. johnsoni*), with the exception of the palate and cheek teeth of *C. skinneri*, n.sp. *Cormohipparion merriami* tends to have a smaller orbit than in *C. occidentale* (nos. 28–29) and all other species, except for *C. johnsoni*, in which the orbit is still smaller. The nasal notch in *C. merriami* is less strongly incised than in *C. occidentale* (no. 30) but more so than in all other species. The facial length (no. 31) apparently is (or likely would range) larger than in *C. occidentale* and all other species except *C. skinneri*, n.sp. The POB (no. 32) tends to be shorter in *C. merriami* than in *C. occidentale* and all species except the comparably sized *C. johnsoni*.

REFERRED MATERIAL: From June Quarry, Burge Member, Valentine Formation, Nebraska. AMNH 141273, left maxillary fragment with dP1–dP3; AMNH 141274, right upper cheek tooth row in very early wear, P2–M3 and LM2; AMNH 141272, right upper cheek tooth row in medial wear, P3–M3.

From Midway Quarry, Burge Member, Valentine Formation, Nebraska. AMNH 141220, old adult, cracked and crushed skull

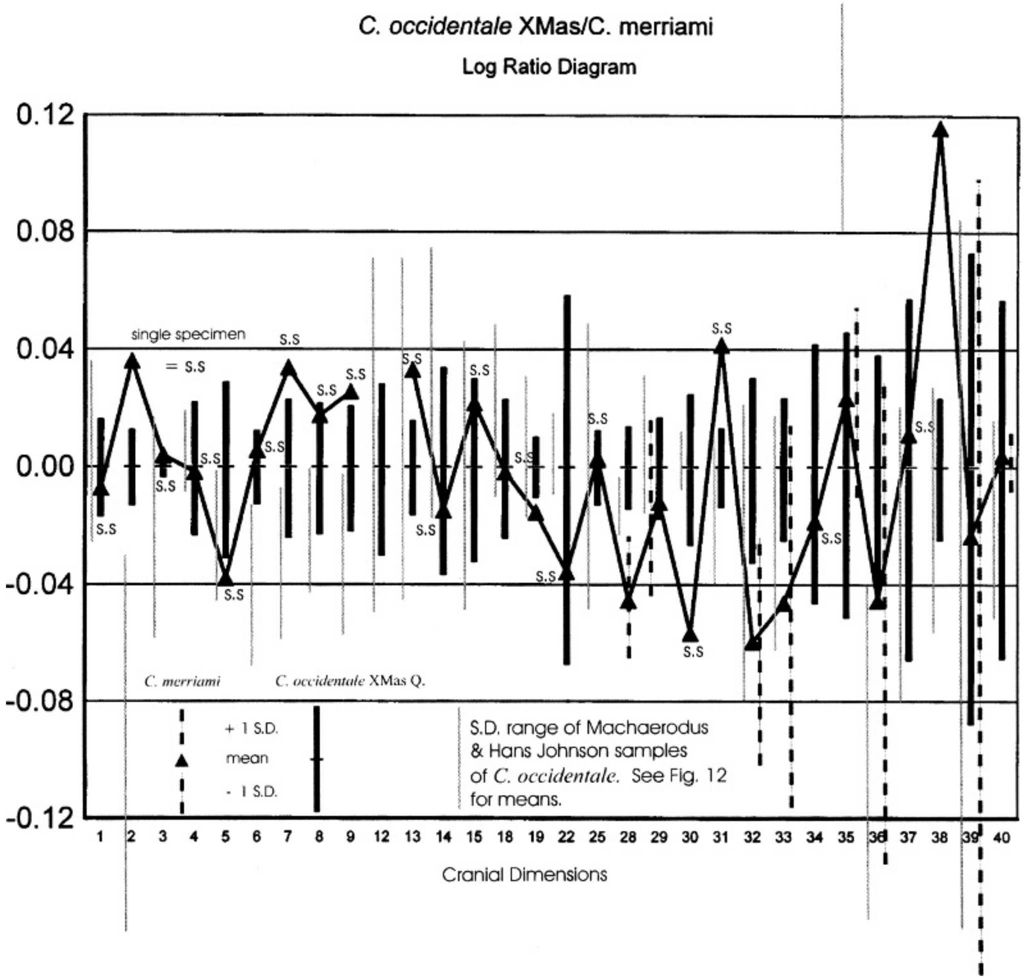


Fig. 20. Log-ratio diagram of cranial dimensions of *Cormohipparion merriami* compared with *C. occidentale*, XMas-Kat quarries, Merritt Dam Member, Ash Hollow Formation, Cherry County, Nebraska.

with relatively intact facial region; F:AM 71893, juvenile partial cranium LI1–2, right and left I3, alveoli for the canines, right and left dP2–4 erupted and worn to the degree that the enamel pattern is almost completely developed; right and left M1 are barely exposed above the gum line. The cranium is largely undistorted but lacks the occipital region and paroccipital processes. F:AM 71983 also shows the triangular lacrimal bone seen in the type and is similar in that the lacrimal does not reach the rear of the DPOF.

Description of Referred Material: The partial cranium AMNH 141220 retains the muzzle but lacks the intervening nasal elements to the cheek teeth, and the skull itself is conspicuously cracked, with most of the left side of the facial region missing. Overall, AMNH 141220 appears similar to the type skull. The POB is intact and shows the lacrimal as about subtriangular in aspect, with its anterior end about 17 mm posterior to the rear of the DPOF (no. 39, table 11), comparable to that of the type specimen. The DPOF in AMNH 141220 is somewhat longer than in the type and somewhat shorter dorsoventrally but otherwise similar, with the differences (including the apparently greater DPOF-IOF distance, no. 34) due

TABLE 13
**Measurements (mm) of Upper Cheek Tooth Dentition of *Cormohipparion merriami*, and *Cormohipparion* sp.**

**P2**

| Specimen | Height | Length | Width | Ratio | Index | Protocone Length | Protocone Width | Protocone Ratio | Pli caballin | Hypoconal groove |
|---|---|---|---|---|---|---|---|---|---|---|
| ***Cormohipparion merriami*, Burge Quarry, Early Clarendonian, Nebraska** | | | | | | | | | | |
| **AMNH 141274** | 38.0 | 32.9 | 23.8 | 0.72 | 3:3:3:1 | 8.3 | 4.8 | 0.58 | 1 | open; spurred |
| **AMNH 141219** ♀ | 33.5 | 32.8 | 23.5 | 0.72 | 6:6:4:1 | 7.6 | 4.8 | 0.63 | 1 | open; simple |
| AMNH 141220 | 18.2 | 26.0 | 23.5 | 0.90 | 1:3:2:0 | 7.8 | 6.3 | 0.81 | no data | open; simple |
| Range | | 26.0–32.9 | 23.5–23.8 | 0.72–0.90 | | 7.6–8.3 | 4.8–6.2 | 0.58–0.81 | | |
| Mean | | 30.6 | 23.6 | 0.80 | 5:5:4:1 | 7.9 | 5.3 | 0.67 | 1 | |
| SD | | 9.96 | 0.17 | 0.11 | | 0.36 | 0.87 | 0.12 | | |
| CV | | 12.9 | 0.7 | 13.6 | | 4.6 | 16.3 | 17.9 | | |
| *N* | 3 | 3 | 3 | 3 | 2 | 3 | 3 | 3 | 2 | 3 |
| ***Cormohipparion* sp., Punchbowl Formation, Early Clarendonian, Valyermo, California** | | | | | | | | | | |
| LACM 150080 | 29.5 | 32.2 | 26.7 | 0.83 | 4:6:4:2 | 7.3 | 5.8 | 0.79 | 4 | open; spurred |

Remarks: Height is at mesostyle; boldface specimens used in plication count statistics; a = approximate. In AMNH 141219, the dP1 = 12.1 long; ratio with length of P2 = 0.37.

AMNH 141274 very early wear; M3 almost unworn; crown heights likely 45–55 mm. tall.

AMNH 141219 early adult wear; relatively elongate protocones, except ovate in P2; relatively complex fossette patterns early wear.

AMNH 141272 about early 1/4 wear; relatively complex.

AMNH 141220 old adult; relatively late wear.

LACM 150080 P2 protocone connected to protoloph at about 50% wear; pre- and postfossettes confluent.

**P3**

| Specimen | Height | Length | Width | Ratio | Index | Protocone Length | Protocone Width | Protocone Ratio | Pli caballin | Hypoconal groove |
|---|---|---|---|---|---|---|---|---|---|---|
| ***Cormohipparion merriami*, Burge Quarry, Early Clarendonian, Nebraska** | | | | | | | | | | |
| **AMNH 141274** | 39.3 | 26.0 | 26.8 | 1.03 | 5:12:6:2 | 9.5 | 4.3 | 0.45 | 2 | open; simple |
| **AMNH 141219** ♀ | 33.0 | 32.5 | 26.7 | 0.82 | 1:10:5:1 | 9.4 | 4.3 | 0.46 | 3 | slight spur |
| **AMNH 141272** | 32.3 | 25.0 | 25.0 | 1.00 | 1:9:6:1 | 8.8 | 4.3 | 0.49 | 3 | open; slight spur |
| AMNH 141220 | 20.2 | 21.7 | 24.3 | 1.12 | 1:3:1:0 | 8.1 | 4.8 | 0.59 | 0 | open; simple |
| Range | | 21.7–32.5 | 24.3–26.8 | 0.82–1.12 | | 8.1–9.5 | 4.3–4.8 | 0.45–0.59 | | |
| Mean | | 26.3 | 25.7 | 0.99 | 2:10:6:1 | 9.0 | 4.4 | 0.50 | 3 | |
| SD | | 4.52 | 1.25 | 0.13 | | 0.65 | 0.25 | 0.07 | | |
| CV | | 17.2 | 4.9 | 12.6 | | 7.2 | 4.7 | 13.1 | | |
| *N* | 4 | 4 | 4 | 4 | 3 | 4 | 4 | 4 | 3 | 4 |
| ***Cormohipparion* sp., Punchbowl Formation, Early Clarendonian, Valyermo, California** | | | | | | | | | | |
| LACM 150080 | 25.4 | 27.1 | 26.1 | 1.04 | 3:15:4:2 | 8.0 | 5.2 | 0.65 | 4 | open; simple |

largely to the cracked and distorted condition in AMNH 141220.

The upper cheek tooth dentition displayed by the referred material includes the presence of dP1 in AMNH 141273, in association with a strongly worn dP2–3, so that its persistence in the adult condition as shown by the type specimen is to be expected. In AMNH 141273, dP1 is 9.8 mm long and 6 mm wide, somewhat smaller than the dimensions (12.1 mm and 6.7 mm) in the type. As indicated in table 13, the ratio of the length of dP1 to the length of P2 is 0.37 in the type. AMNH 141274 is the least worn of the

TABLE 13
(*Continued*)

| Specimen | Height | Length | Width | Ratio | Index | Protocone Length | Protocone Width | Protocone Ratio | Pli caballin | Hypoconal groove |
|---|---|---|---|---|---|---|---|---|---|---|
| **P4** | | | | | | | | | | |
| ***Cormohipparion merriami*, Burge Quarry, Early Clarendonian, Nebraska** | | | | | | | | | | |
| **AMNH 141274** | 39.3 | 26.7 | 26.2 | 0.98 | 4:11:7:1 | 9.7 | 4.7 | 0.48 | 2 | spurred |
| **AMNH 141219** ♀ | 29.2 | 26.2 | 27.0 | 1.03 | 1:11:5:1 | 9.3 | 4.3 | 0.46 | 3 | slight spur |
| **AMNH 141272** | 33.5 | 25.6 | 25.5 | 1.00 | 2:7:6:2 | 8.8 | 4.3 | 0.49 | 3 | open; slight spur |
| AMNH 141220 | 20.0 | 21.4 | 23.5 | 1.10 | 1:6:2:0 | 8.7 | 3.9 | 0.45 | 2 | open, simple |
| Range | | 21.4–26.7 | 23.5–27.0 | 0.98–1.10 | | 8.3–9.7 | 3.9–4.7 | 0.45–0.49 | | |
| Mean | | 24.4 | 25.3 | 1.03 | 2:10:6:1 | 8.9 | 4.2 | 0.47 | 3 | |
| SD | | 2.43 | 1.50 | 0.05 | | 0.47 | 0.33 | 0.02 | | |
| CV | | 9.9 | 5.9 | 5.0 | | 5.2 | 7.8 | 4.1 | | |
| *N* | 4 | 4 | 4 | 4 | 3 | 4 | 4 | 4 | 3 | 4 |
| ***Cormohipparion* sp., Punchbowl Formation, Early Clarendonian, Valyermo, California** | | | | | | | | | | |
| LACM 150080 | 25.0 | 25.6 | 26.8 | 1.05 | 3:9:5:1 | 7.8 | 5.1 | 0.65 | 2+ | open; simple |
| **M1** | | | | | | | | | | |
| ***Cormohipparion merriami*, Burge Quarry, Early Clarendonian, Nebraska** | | | | | | | | | | |
| **AMNH 141274** | 33.7 | 21.9 | 24.3 | 1.11 | 1:6:6:1 | 8.3 | 4.2 | 0.51 | 1 | narrow; simple |
| **AMNH 141219** ♀ | 34.0a | 22.3 | 24.4 | 1.09 | 1:7:6:2 | 9.1 | 4.1 | 0.45 | 1 | narrow; simple |
| **AMNH 141272** | 33.0a | 22.8 | 23.5 | 1.03 | 1:7:9:1 | 8.5 | 4.2 | 0.49 | 1 | narrow; simple |
| AMNH 141220 | | 18.8 | 22.2 | 1.18 | 1:6:2:0 | 7.0 | 4.1 | 0.59 | 1 | narrow; simple |
| Range | | 18.8–22.8 | 22.2–24.4 | 1.03–1.18 | | 7.0–9.1 | 4.1–4.2 | 0.45–0.59 | | |
| Mean | | 21.3 | 23.4 | 1.10 | 1:7:7:1 | 8.2 | 4.1 | 0.51 | 1 | |
| SD | | 1.81 | 1.02 | 0.06 | | 0.89 | 0.06 | 0.06 | | |
| CV | | 8.5 | 4.4 | 5.6 | | 10.8 | 1.4 | 11.4 | | |
| *N* | 3 | 4 | 4 | 4 | 3 | 4 | 4 | 4 | 3 | 4 |
| ***Cormohipparion* sp., Punchbowl Formation, Early Clarendonian, Valyermo, California** | | | | | | | | | | |
| LACM 150080 | 30.0+ | 23.5 | 26.0 | 1.11 | 1+:13:8:3 | 8.6 | 5.1 | 0.59 | 2 | narrow; simple |
| **M2** | | | | | | | | | | |
| ***Cormohipparion merriami*, Burge Quarry, Early Clarendonian, Nebraska** | | | | | | | | | | |
| **AMNH 141274** | 42.2 | 24.0 | 23.3 | 0.97 | 4:11:4:2 | 8.3 | 4.6 | 0.55 | 1 | open; simple |
| **AMNH 141219** ♀ | 38.0a | 24.3 | 24.5 | 1.01 | 1:8:5:3 | 8.9 | 4.2 | 0.47 | 1 | slight spur |
| **AMNH 141272** | 32.3a | 23.6 | 22.7 | 0.96 | 1:9:6:1 | 8.1 | 4.5 | 0.56 | 1 | open; simple |
| AMNH 141220 | | 19.9 | 21.7 | 1.09 | 0:6:4:0 | 8.2 | 4.5 | 0.55 | 1 | open; simple |
| Range | | 19.9–24.3 | 21.7–24.5 | 0.96–1.09 | | 8.1–8.9 | 4.2–4.6 | 0.47–0.56 | | |
| Mean | | 22.6 | 23.0 | 1.02 | 2:9:5:2 | 8.4 | 4.4 | 0.53 | 1 | |
| SD | | 2.05 | 1.17 | 0.06 | | 0.36 | 0.17 | 0.04 | | |
| CV | | 9.1 | 5.1 | 5.8 | | 4.3 | 3.9 | 7.7 | | |
| *N* | 3 | 4 | 4 | 4 | 3 | 4 | 4 | 4 | 3 | 4 |
| ***Cormohipparion* sp., Punchbowl Formation, Early Clarendonian, Valyermo, California** | | | | | | | | | | |
| LACM 150080 | 27.7 | 22.2 | 25.5 | 1.15 | 3?8:6?:2 | 8.0 | 4.7 | 0.58 | 3 | narrow; simple |

available specimens and suggests that the unworn MSTHT for the cheek tooth dentition was likely 45–55 mm tall, with P4 and M1 having been 52–55 mm tall (table 3). The upper cheek tooth protocones were uniformly elongate and ovate, except in P3 and P4, where the lingual border is essentially flat (or slightly concave) and, in late wear of P2,

TABLE 13
(*Continued*)

| M3 | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | | | | | | Protocone | | | Pli | Hypoconal |
| Specimen | Height | Length | Width | Ratio | Index | Length | Width | Ratio | caballin | groove |
| ***Cormohipparion merriami*, Burge Quarry, Early Clarendonian, Nebraska** | | | | | | | | | | |
| **AMNH 141274** | 40.5 | 21.5a | 19.3a | | | | | | | |
| **AMNH 141219** ♀ | 24.0a | 22.9 | 18.8 | 0.82 | 0:4:3:1 | 8.4 | 3.4 | 0.40 | 1 | |
| **AMNH 141272** | 27.5a | 24.1 | 19.9 | 0.83 | 3:7:?:? | 7.7 | 4.0 | 0.52 | 2 | spurred |
| AMNH 141220 | | 20.7 | 19.7 | 0.95 | 0:6:4:1 | 7.5 | 3.5 | 0.47 | 1 | spurred |
| Range | | 20.7–24.1 | 18.8–19.9 | 0.82–0.95 | | 7.5–8.4 | 3.4–4.0 | 0.40–0.52 | | |
| Mean | | 22.6 | 19.5 | 0.87 | 2:6:3:1 | 7.9 | 3.6 | 0.46 | 1 | |
| SD | | 1.72 | 0.59 | 0.07 | | 0.47 | 0.32 | 0.06 | | |
| CV | | 7.6 | 3.0 | 8.6 | | 6.0 | 8.9 | 12.4 | | |
| *N* | 3 | 4 | 4 | 3 | 2 | 3 | 3 | 3 | 3 | 2 |

where the protocone is connected to the protoloph in AMNH 141220. As indicated in tables 3C and 13, the mean width-to-length ratios are 0.67, 0.50, 0.47, 0.51, 0.53, and 0.46 for P2–M3. The type (left side, but not the right side) and AMNH 141274 show that the pre- and postfossettes are confluent labially in P2 in relatively early wear (16% and 25% wear, respectively), but in late wear (AMNH 141220) these fossettes are separate.

Tables 2 and 13 show that the fossette borders overall are simpler than in *C. occidentale* or *C. matthewi*. The mean values in table 13 indicate that *C. merriami* has a more complex plication pattern than *C. johnsoni* (table 12). In table 13, it can be seen that the anterior border of the prefossette in P2 has a mean value of 5 plis, but in all other cheek teeth this is reduced to 2 plis or 1 pli (M1). In premolars, the posterior border of the prefossette contains a mean value of 5–10 plis; in the molars, this feature is represented by 6–9 plis. Remaining mean values for fossette plications are anterior border of the postfossette 4–6 in premolars and 3–7 in molars. The mean value of the plis in the posterior border of the postfossette is a single pli in all cheek teeth but M2 (where the mean value is 2).

DISCUSSION: Webb (1969) discussed the morphology of a sample from Burge Quarry, Valentine Formation, Nebraska, allocated to *Neohipparion* cf. *coloradense*. MacFadden (1984) reviewed the species referable to *Neohipparion* and defined *N. coloradense* as having an MSTHT of 35–43 mm, a simple cheek tooth occlusal pattern, and a relatively ovate protocone. These aspects of Webb's Burge sample (MSTHT 47–52 mm; cheek teeth with relatively complex occlusal pattern, and a more elongate protocone) are most similar to *C. merriami* as herein defined and characterized.

*C. merriami* is comparable to *C. johnsoni* in retaining dP1 into the adult condition but more advanced in being taller crowned and in the greater complexity of the fossette borders of the upper cheek teeth. It also is of larger size than *C. johnsoni*, with which it was contemporaneous. See below for further discussion of *C. merriami* relative to the other species of the *C. occidentale* group.

At present, no mandibles or lower dentitions can be directly associated with crania referred to *C. merriami*.

### ***Cormohipparion fricki***, new species
figures 8, 21–22; tables 2–3, 6, 14–15

TYPE SPECIMEN: F:AM 73912, partial skull with right and left C–M3, adult male, M3 well worn.

TYPE LOCALITY: MacAdams Quarry, Clarendon beds, Texas.

AGE: Medial Clarendonian, Nebraska, Texas, South Dakota.

DISTRIBUTION: Type locality and Hollow Horn Bear Quarry, Ash Hollow Formation undifferentiated (Skinner and Johnson,

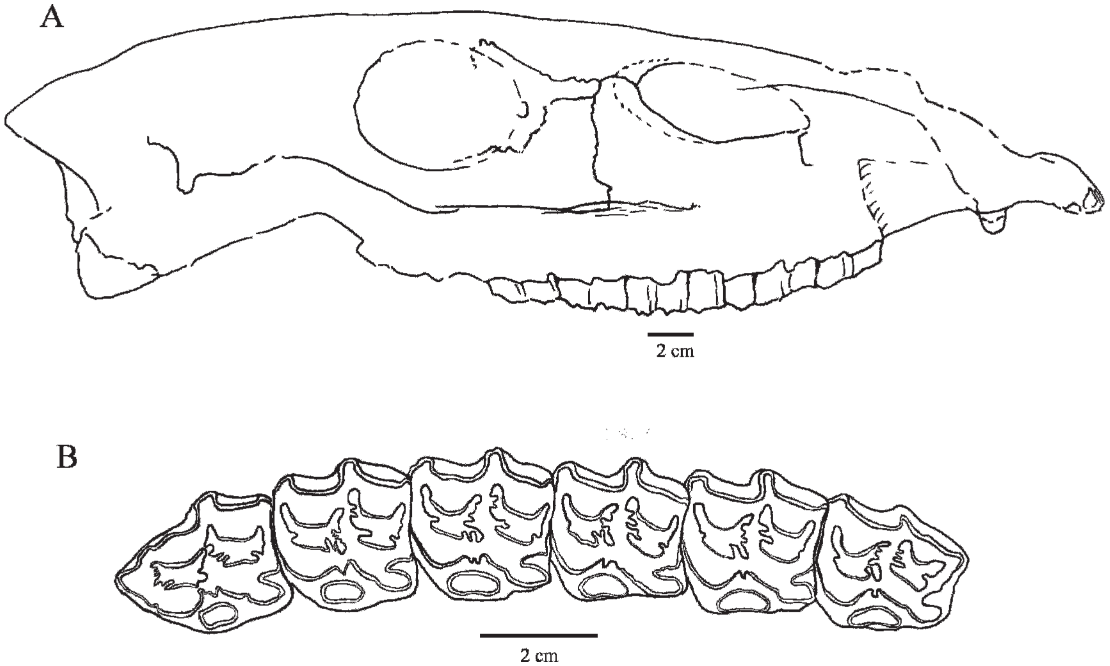


Fig. 21. *Cormohipparion fricki*, F:AM 73912, MacAdams Quarry, Clarendon beds, Texas, medial Clarendonian. **A,** lateral view of craniuim. **B,** occlusal view of upper cheek tooth dentition.

1984; figs. 2A, 3; table 1), Todd County, South Dakota.

DESCRIPTION OF TYPE SPECIMEN: As indicated in figure 21, the specimen is relatively complete. The nasal bones above the snout are missing, as are the upper borders of the orbits. The cranium is slightly depressed by postmortem action, so that certain cranial width dimensions are exaggerated. In comparison, F:AM 71800 from the XMas-Kat sample is somewhat less distorted. The upper cheek tooth dentition is well preserved. The overall quality of F:AM 73912 qualifies its being chosen for the type specimen, even though some others (e.g., F:AM 73920) better preserve the incisors.

In overall morphology, the cranium of *C. fricki* is comparable to that of many contemporaneous equids. The nasal notch appears to have been located about midway between the canine and the anterior tip of P2, but the relatively elongate facial region as compared with, for example, *C. quinni* (Woodburne, 1996b), is shown by the anterior margin of the orbit being located above the rear portion of M3 in adult wear. In lateral view (fig. 21A), the profile overall is relatively regular, with the dorsal surface (lacking the nasal bones) being gently curved. Although depressed postmortem, the frontal bones do not appear to have been dome-like. The orbits are relatively large (nos. 28–29; table 14) and the POB (no. 32) is relatively wide. The DPOF is thus well anterior to the orbit and is higher posteriorly than anteriorly but not as distinctly teardrop shaped as, for instance, in the XMas-Kat taxon. As in *Cormohipparion* generally, the IOF is located just below the anteroventral margin of the DPOF, slightly posterior to the actual anterior end of the fossa, as is the usual case. The anterior end of the DPOF is not as pronounced as typically seen in XMas-Kat materials of *Cormohipparion*. The anteriorly wide POB is reflected in the lacrimal usually being exposed on the posterior one-half of the preorbital bar (length 2, table 3A; no. 39, table 14) and not entering the rear of the DPOF, as in *C. quinni*. In the type, dorsoventral compression of the facial region results in the ventral boundary of the lacrimal being distorted. Based on other specimens,

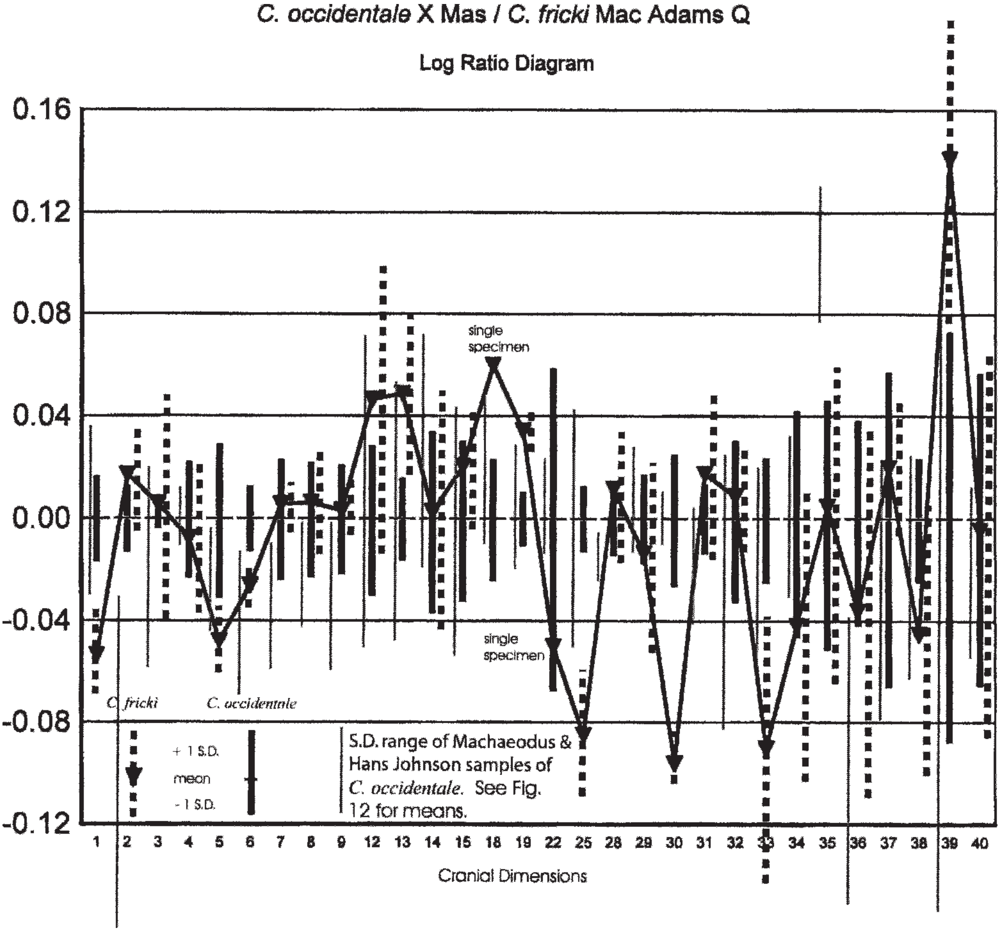


Fig. 22. Log-ratio diagram of cranial dimensions of *Cormohipparion fricki* compared with *C. occidentale*, XMas-Kat quarries, Merritt Dam Member, Ash Hollow Formation, Cherry County, Nebraska.

the morphology of the lacrimal would resemble that in F:AM 71800 (fig. 8A), further described below, rather than being narrowed anteriorly. As in *C. quinni* and the XMas-Kat materials, the facial crest ends about in alignment with the premolar/molar boundary at an elevation approximately midway between the alveolar border and the ventral margin of the DPOF. In spite of the wider POB, the DPOF is still situated about as in *C. quinni*; the rear of the DPOF is still located about above the mesostyle of M1. In the type and other specimens of *C. fricki*, the lacrimal is approximately as long as in *C. quinni*, so that the extension of the POB appears to have taken place between the lacrimal tip and the rear of the POB. This is reflected in dimension no. 32 being essentially twice that in *C. quinni* (table 14, in comparison with table 16, no. 32, in Woodburne, 1996b), even though the facial length of the lacrimal is about 34 mm in *C. fricki* versus about 25 mm in *C. quinni*.

In ventral aspect, the incisor arcade is smoothly rounded (best seen in F:AM 73920), the incisors having cement-filled infundibula (also in F:AM 73910). The canines are situated about midway between I3 and P2 (fig. 21A). DP1 is absent in this adult skull. Premolars are larger than the molars and tend to have a somewhat more complex enamel pattern, comparable to the general

TABLE 14
**Measurements (mm) of Cranial Parameters for *Cormohipparion fricki*, Medial Clarendonian, Texas and South Dakota**
Characters are illustrated in figures 3–5.

**MacAdams Quarry, Texas**

| | Characters | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| Specimen | 1, muz | 2, pal | 3, popl | 4, basc | 5, comb | 6, tsl | 7, upl | 8, uml | 9, tcl | 12, choa | 13, palw |
| F:AM 73920 ♂ | 89.0 | | | 76.0 | | 367.8 | 78.9 | 64.8 | 142.8 | 34.6 | 62.0 |
| F:AM 73914 ♀ | 91.8 | | | | | | | | | | 54.5 |
| F:AM 73915 ♂ | 87.3 | 108.5 | 103.2 | 86.0 | 161.4 | 361.3 | 80.3 | 64.0 | 142.8 | 42.8 | 67.0 |
| F:AM 73912 ♂ | 94.3 | 115.5 | 89.2 | 87.0 | 168.5 | 377.0 | 81.8 | 72.4 | 151.3 | 33.1 | 62.1 |
| F:AM 73938 | | | | | | | | | | | |
| F:AM 73913 ♂ | 106.0 | 116.3 | | | | | 82.8 | | | | 62.3 |
| F:AM 73921 ♀ | 94.0 | 122.3 | | | | | 78.7 | 68.4 | 147.4 | | |
| F:AM 73925 | | | | | | | | 68.5 | | | |
| Range | 87.3–106.0 | 108.5–122.3 | 89.2–103.2 | 76.0–78.0 | 161.4–168.5 | 361.3–377.0 | 78.7–82.8 | 64.0–72.4 | 142.8–151.3 | 33.1–42.8 | 54.5–67.0 |
| Mean | 93.7 | 115.7 | 96.2 | 83.0 | 165.0 | 368.7 | 80.5 | 67.6 | 146.1 | 36.8 | 61.6 |
| SD | 6.61 | 6.56 | 9.90 | 6.08 | 5.02 | 7.89 | 1.79 | 3.37 | 4.10 | 5.22 | 4.49 |
| CV | 7.05 | 4.89 | 10.3 | 7.33 | 3.04 | 2.14 | 2.22 | 4.98 | 2.81 | 14.18 | 7.28 |
| *N* | 6 | 4 | 2 | 3 | 2 | 3 | 5 | 5 | 4 | 3 | 5 |
| **Hollow Horn Bear Quarry, South Dakota** | | | | | | | | | | | |
| F:AM 71880 ♂ | | | | | | | 78.6 | 62.8 | 118.3 | 28.3 | 57.5 |

**MacAdams Quarry, Texas**

| | Characters | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| Specimen | 14, sntw | 15, wmuz | 18, fwd | 10, trgl | 22, in | 25, snh | 28, orl | 29,orh | 30, nis | 31, fac | 32, pobl |
| F:AM 73920 ♂ | 39.5 | 49.3 | | | | 60.0 | | | 90.3 | | |
| F:AM 73914 ♀ | 30.0 | 51.6 | | | | 65.0 | | | 86.5 | 168.3 | 44.0 |
| F:AM 73915 ♂ | 33.3 | 48.9 | | 149.0 | | 67.0 | 54.8 | 48.2 | 92.1 | 150.8 | 43.0 |
| F:AM 73912 ♂ | 29.6 | 53.8 | 148.1 | 153.2 | 56.9 | | 57.8 | 44.8 | 89.0 | 174.2 | 48.5 |
| F:AM 73938 | | | | | | | | | | | |
| F:AM 73913 ♂ | 33.2 | 56.5 | | | | | 61.5 | 40.0 | | | 47.5 |
| F:AM 73921 ♀ | 34.8 | 52.8 | | | | | | | | | 47.7 |
| F:AM 73925 | | | | | | | 61.0 | 47.8 | | | 45.0 |
| Range | 29.6–39.5 | 48.9–56.5 | | 149.0–153.2 | | 60.0–67.0 | 54.8–61.5 | 40.0–48.2 | 86.5–92.1 | 150.8–174.2 | 43.0–48.5 |
| Mean | 33.4 | 52.2 | 148.1 | 151.1 | 56.9 | 64.0 | 58.8 | 45.2 | 89.5 | 164.4 | 46.0 |
| SD | 3.61 | 2.87 | | 2.97 | | 3.61 | 3.12 | 3.78 | 2.36 | 12.17 | 2.25 |
| CV | 10.81 | 5.49 | | 1.97 | | 5.63 | 5.30 | 8.37 | 2.63 | 7.40 | 4.90 |
| *N* | 6 | 6 | 1 | 2 | 1 | 3 | 4 | 4 | 4 | 3 | 6 |
| **Hollow Horn Bear Quarry, South Dakota** | | | | | | | | | | | |
| F:AM 71880 ♂ | | | | | | | | | | | 45.4 |

TABLE 14
(*Continued*)

| **MacAdams Quarry, Texas** | | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| | Characters | | | | | | | |
| Specimen | 33, dpof | 34, iof | 35, hdof | 36, fch | 37, ioa | 38, mpof | 39, ldof | 40, medof |
| F:AM 73920 ♂ | 47.0 | 48.0 | 28.2 | 28.2 | 45.6 | | | |
| F:AM 73914 ♀ | 53.5 | 49.5 | 34.0 | 22.5 | 40.6 | 42.7 | 24.2 | 16.9 |
| F:AM 73915 ♂ | 58.0 | | 33.8 | 26.5 | 44.7 | 47.5 | | 19.2 |
| F:AM 73912 ♂ | 65.0 | 64.5 | 33.4 | 29.2 | 46.3 | 51.4 | 19.5 | 19.8 |
| F:AM 73938 | 69.0 | | 41.8 | 25.5 | | | | 14.6 |
| F:AM 73913 ♂ | 56.0 | 52.2 | 39.8 | 31.5 | 43.5 | 58.0 | 28.5 | 12.2 |
| F:AM 73921 ♀ | 53.0 | | 30.8 | 35.5 | | 54.2 | 22.8 | 17.4 |
| F:AM 73925 | 56.0 | 62.0 | 29.0 | 36.5 | 39.4 | 60.0 | 24.0 | |
| Range | 47.0–69.0 | 48.0–64.5 | 28.2–41.8 | 22.5–36.5 | 39.4–46.3 | 42.7–60.0 | 19.5–28.5 | 12.2–19.8 |
| Mean | 57.2 | 55.2 | 33.9 | 29.4 | 43.4 | 52.3 | 23.8 | 16.7 |
| SD | 6.96 | 7.52 | 4.83 | 4.82 | 2.79 | 6.50 | 3.23 | 2.87 |
| CV | 12.17 | 13.61 | 14.28 | 16.38 | 6.42 | 12.43 | 13.58 | 17.17 |
| *N* | 8 | 5 | 8 | 8 | 6 | 6 | 5 | 6 |
| **Hollow Horn Bear Quarry, South Dakota** | | | | | | | | |
| F:AM 71880 ♂ | 52.5 | 50.8 | 28.9 | 26.4 | 39.2 | 62.3 | 23.0 | 15.3 |

TABLE 15
**Measurements (mm) of Upper Cheek Tooth Dentition of *Cormohipparion fricki* MacAdams Quarry, Clarendon Beds, Early Clarendonian, Texas**

**P2**

| Specimen | Height | Length | Width | Ratio | Index | Protocone Length | Protocone Width | Protocone Ratio | Pli caballin | Hypoconal groove |
|---|---|---|---|---|---|---|---|---|---|---|
| **F:AM 73913** ♂ | 41.0a | 29.4 | 23.0 | 0.78 | ?:?:?:? | 8.8 | 4.1 | 0.47 | 2 | |
| **F:AM 73920** ♂ | 40.0a | 29.9 | 23.3 | 0.78 | 2:5:3:2 | 8.2 | 3.8 | 0.46 | 3 | spurred |
| **F:AM 73925** | 32.5a | 31.4 | 23.0 | 0.73 | 1:5:3:1 | 8.1 | 4.0 | 0.49 | 2 | spurred |
| **F:AM 73921** ♀ | 26.6a | 29.1 | 23.5 | 0.81 | 2:3:3:1 | 9.0 | 4.0 | 0.44 | 2 | open; simple |
| **F:AM 73915** ♂ | 26.4 | 30.0 | 23.0 | 0.77 | ?:8:6:2 | 6.2 | 3.9 | 0.63 | 2 | spurred |
| F:AM 73912 | 24.3a | 32.3 | 23.2 | 0.72 | 2:2:3:1 | 8.2 | 3.9 | 0.48 | 2 | open; simple |
| Range | | 29.1–32.3 | 23.0–23.5 | 0.72–0.81 | | 6.2–9.0 | 3.8–4.1 | 0.44–0.63 | | |
| Mean | | 30.4 | 23.2 | 0.76 | 2:5:4:1 | 8.1 | 4.0 | 0.49 | 2 | |
| SD | | 1.24 | 0.21 | 0.03 | | 0.99 | 0.10 | 0.07 | | |
| CV | | 4.09 | 0.89 | 4.36 | | 12.28 | 2.66 | 13.6 | | |
| *N* | 6 | 6 | 6 | 6 | 4 | 6 | 6 | 6 | 6 | 5 |

Remarks: Height is at mesostyle; boldface specimens used in plication count statistics; a = approximate. In comparison with *C. occidentale, C. fricki* material is lower crowned and less complex. F:AM 73920; dP1 = 12.3 long; ratio with length of P2 = 0.41. F:AM 73913; dp1 = 10.8 long; ratio with length of P2 = 0.38.

**P3**

| Specimen | Height | Length | Width | Ratio | Index | Protocone Length | Protocone Width | Protocone Ratio | Pli caballin | Hypoconal groove |
|---|---|---|---|---|---|---|---|---|---|---|
| **F:AM 73913** ♂ | 45.5a | 27.7 | 25.6 | 0.92 | ?:?:?:? | 11.6 | 4.1 | 0.35 | 3 | |
| **F:AM 73920** ♂ | 42.0a | 25.7 | 26.2 | 1.02 | 1:6:6:3 | 8.5 | 4.2 | 0.49 | 2 | spurred |
| **F:AM 73925** | 35.0a | 28.9 | 25.3 | 0.88 | 3:9:7:1 | 10.2 | 3.6 | 0.35 | 1 | narrow; simple |
| **F:AM 73921** ♀ | 26.2a | 24.9 | 24.8 | 1.00 | 1:6:3:1 | 10.0 | 4.0 | 0.40 | 2 | open; simple |
| **F:AM 73915** ♂ | 31.5a | 25.0 | 25.2 | 1.00 | 4:12:6:2 | 7.5 | 3.8 | 0.51 | 2 | spurred |
| F:AM 73912 | 23.7a | 25.9 | 25.8 | 1.00 | 1:7:3:1 | 8.1 | 4.0 | 0.49 | 2 | open; simple |
| Range | | 24.9–28.9 | 24.8–26.2 | 0.88–1.02 | | 7.5–11.6 | 3.6–4.2 | 0.35–0.51 | | |
| Mean | | 26.4 | 25.5 | 0.97 | 2:9:5:2 | 9.3 | 4.0 | 0.43 | 2 | |
| SD | | 1.60 | 0.49 | 0.06 | | 1.54 | 0.22 | 0.07 | | |
| CV | | 6.09 | 1.93 | 5.89 | | 16.56 | 5.49 | 16.9 | | |
| *N* | 6 | 6 | 6 | 6 | 4 | 6 | 6 | 6 | 6 | 5 |

**P4**

| Specimen | Height | Length | Width | Ratio | Index | Protocone Length | Protocone Width | Protocone Ratio | Pli caballin | Hypoconal groove |
|---|---|---|---|---|---|---|---|---|---|---|
| **F:AM 73913** ♂ | | | | | | | | | | |
| **F:AM 73920** ♂ | 37.0a | 24.6 | 25.7 | 1.04 | 1:8:3:3 | 9.2 | 3.7 | 0.40 | 2 | open |
| **F:AM 73925** | | 27.3 | 25.0 | 0.92 | 1:8:5:2 | 10.4 | 3.7 | 0.36 | 2 | narrow; simple |
| **F:AM 73921** ♀ | | 24.2 | 25.7 | 1.06 | 1:6:4:1 | 9.6 | 4.5 | 0.47 | 2 | open |
| **F:AM 73915** ♂ | 31.0a | 25.5 | 25.2 | 0.99 | 3:6:6:3 | 7.5 | 3.8 | 0.51 | 2 | spurred |
| F:AM 73912 | | 26.1 | 26.1 | 1.00 | 1:7:3:1 | 10.0 | 4.4 | 0.44 | 2 | open; narrow |
| Range | | 24.2–27.3 | 25.0–26.1 | 0.92–1.04 | | 7.5–10.4 | 3.7–4.5 | 0.36–0.51 | | |
| Mean | | 25.5 | 25.5 | 1.00 | 1:7:4:2 | 9.3 | 4.0 | 0.43 | 2 | |
| SD | | 1.23 | 0.44 | 0.06 | | 1.12 | 0.40 | 0.06 | | |
| CV | | 4.83 | 1.72 | 5.70 | | 12.01 | 9.86 | 13.40 | | |
| *N* | 5 | 5 | 5 | 5 | 4 | 5 | 5 | 5 | 4 | 5 |

TABLE 15
(*Continued*)

| Specimen | Height | Length | Width | Ratio | Index | Protocone Length | Protocone Width | Protocone Ratio | Pli caballin | Hypoconal groove |
|---|---|---|---|---|---|---|---|---|---|---|
| **M1** | | | | | | | | | | |
| **F:AM 73913 ♂** | | 27.0 | 24.7 | 0.91 | 2:7:6:1 | 9.5 | 3.9 | 0.41 | 1 | narrow; simple |
| **F:AM 73920 ♂** | 32.0a | 23.0 | 22.0 | 0.96 | 3:7:5:3 | 8.3 | 4.0 | 0.48 | 1 | open; narrow |
| **F:AM 73925** | | 22.8 | 23.3 | 1.02 | 2:11:10:2 | 8.9 | 4.1 | 0.46 | 1 | open; narrow |
| **F:AM 73921 ♀** | | 21.5 | 23.8 | 1.11 | 1:3:3:1 | 9.5 | 4.8 | 0.51 | 1 | open; narrow |
| **F:AM 73915 ♂** | | 21.0 | 21.3 | 1.01 | 2:9:8:3 | 6.5 | 3.6 | 0.55 | 1 | open; narrow |
| F:AM 73912 | | 22.9 | 25.0 | 1.09 | 1:5:4:1 | 9.6 | 4.4 | 0.46 | 1 | open; narrow |
| Range | | 21.0–27.0 | 21.3–25.0 | 0.91–1.11 | | 6.5–9.6 | 3.6–4.8 | 0.41–0.55 | | |
| Mean | | 23.0 | 23.4 | 1.02 | 2:7:6:2 | 8.7 | 4.1 | 0.48 | 1 | |
| SD | | 2.11 | 1.47 | 0.07 | | 1.19 | 0.42 | 0.05 | | |
| CV | | 9.17 | 6.29 | 7.33 | | 13.68 | 10.11 | 10.10 | | |
| *N* | 1 | 6 | 6 | 6 | 5 | 6 | 6 | 6 | 5 | 6 |
| **M2** | | | | | | | | | | |
| **F:AM 73913 ♂** | | 26.0 | 22.6 | 0.87 | 3:5:5:? | 9.0 | 3.2 | 0.36 | 1 | open |
| **F:AM 73920 ♂** | 30.0a | 22.7 | 21.0 | 0.93 | 4:8:4:1 | 8.9 | 3.5 | 0.39 | 2 | open; narrow |
| **F:AM 73925** | | 24.6 | 22.0 | 0.89 | 2:8:7:1 | 10.3 | 4.4 | 0.43 | 1 | narrow |
| **F:AM 73921 ♀** | | 22.4 | 23.7 | 1.06 | 1:6:3:1 | 9.4 | 4.8 | 0.51 | 1 | open; narrow |
| **F:AM 73915 ♂** | | 21.0 | 20.1 | 0.96 | 1:8:6:1 | 6.5 | 3.0 | 0.46 | 1 | spurred |
| F:AM 73912 | | 24.7 | 25.3 | 1.02 | 1:2:4:1 | 9.9 | 4.1 | 0.41 | 1 | open; narrow |
| Range | | 21.0–26.0 | 20.1–25.3 | 0.87–1.06 | | 6.5–10.3 | 3.0–4.8 | 0.36–0.51 | | |
| Mean | | 23.6 | 22.5 | 0.96 | 2:7:5:1 | 9.0 | 3.8 | 0.43 | 1 | |
| SD | | 1.84 | 1.87 | 0.07 | | 1.34 | 0.71 | 0.05 | | |
| CV | | 7.82 | 8.34 | 7.75 | | 14.84 | 18.57 | 12.70 | | |
| *N* | 1 | 6 | 6 | 6 | 5 | 6 | 6 | 6 | 5 | 6 |
| **M3** | | | | | | | | | | |
| **F:AM 73913 ♂** | erupting | | | | | | | | | |
| **F:AM 73920 ♂** | 28.0a | | | | | | | | | |
| **F:AM 73925** | | 21.0 | 20.1 | 0.96 | 4:5:4:? | 10.2 | 3.3 | 0.32 | 1 | not formed |
| **F:AM 73921 ♀** | | 23.4 | 21.4 | 0.92 | | 9.2 | 4.3 | 0.47 | 1 | open; narrow |
| **F:AM 73915 ♂** | | 22.2 | 18.2 | 0.82 | 4:7:3:2 | 6.8 | 3.0 | 0.44 | 1 | closed |
| F:AM 73912 | | 24.7 | 21.5 | 0.87 | 1:5:4:1 | 10.1 | 3.4 | 0.34 | 1 | open; simple |
| Range | | 21.0–24.7 | 18.2–21.5 | 0.82–0.96 | | 6.8–10.2 | 3.0–4.3 | 0.32–0.47 | | |
| Mean | | 22.8 | 20.3 | 0.89 | 4:6:4:2 | 9.1 | 3.5 | 0.39 | 1 | |
| SD | | 1.56 | 1.54 | 0.06 | | 1.58 | 0.56 | 0.07 | | |
| CV | | 6.96 | 7.58 | 6.62 | | 17.43 | 15.99 | 18.5 | | |
| *N* | 1 | 4 | 4 | 4 | 2 | 4 | 4 | 4 | 3 | 4 |

Remarks: F:AM 73913; late juvenile wear; M3 erupting, dP4 still in place; note complex pattern; only M1 fully formed. Labial pre- and postfossettes are not formed. dP1 is 11.3 long; ratio with length P2 is 0.39.

F:AM 73920; early adult wear; M3 in early wear; note complexity, double pli caballin P2–M2; complex anterior pli prefossettes; 2 plis and small pli protoconule in P4–M2. P2 pre and postfossettes separate labially. dP1 present.

F:AM 73925; early medial wear; M3 not fully formed; note very complex pattern. P2 pre- and postfossettes linked labially.

F:AM 73921; late medial wear; slightly lingually convex premolar protocones; double pli cabllin P2–4; 1 pli anterior to pli protoconule in all teeth; pre- and postfossettes in P2 free labially.

F:AM 73915; early medial wear; M3 not quite fully formed; note very complex pattern and short and relatively wide protocones; P2 pre- and postfossettes separate labially.

F:AM 73912; late medial wear; slightly lingually convex protocones; double pli caballin P2–4; 1 pli anterior to pli protoconule in all teeth; pre-and postfossette labially free in P2; P3–M1 with two plis anterior to small pli protoconule.

situation in the *C. occidentale* group. The dentition in F:AM 73912 (fig. 21B) is in a relatively mature state of wear (P2 seems to be more than half worn; table 15), but the bifid versus the single pli caballin distinguishes premolars from molars. At this wear stage, the pre- and postfossettes of P2 are separate rather than confluent along their labial margins; cheek tooth protocones are elongate and isolated but relatively broad and slightly concave lingually in the premolars versus nearly flat in the molars.

The lower dentition and mandible is not represented in the type material of *C. fricki*.

DIAGNOSIS: Based on the type and referred material, *C. fricki* (fig. 22) has a much shorter muzzle (no. 1) than *C. occidentale* and, apparently, *C. merriami*, but not *C. matthewi* or *C. skinneri*, n.sp., and is longer than in *C. johnsoni*. *Cormohipparion fricki* has a much longer palatal region than in the Machaerodus and Hans Johnson samples of *C. occidentale*, *C. matthewi* and *C. johnsoni*, and a shorter overall cranial length (no. 6) than *C. merriami*, *C. skinneri*, n.sp., *C. matthewi* and the XMas-Kat (but not Machaerodus or Hans Johnson samples) of *C. occidentale*. The choanae and palate are somewhat wider (nos. 12–13) in *C. fricki* than in *C. occidentale*. *C. fricki* apparently is much wider across the frontals (no. 18) than any other species and is wider across the glenoid fossae (no. 19) than *C. occidentale*, *C. matthewi*, *C. johnsoni*, and *C. merriami* but not *C. skinneri*, n.sp. The snout (no. 25) is relatively much shorter vertically in *C. fricki* and *C. matthewi* than in *C. occidentale* or the other species. The nasal notch is less incised than in *C. occidentale* (no. 30) in common with all other species, to varying degrees. The DPOF (no. 33) ranges much smaller in *C. fricki* than in all but *C. johnsoni* and *C. matthewi*, and the rear of the DPOF is much farther from the tip of the lacrimal (no. 39) in *C. fricki* than in all other species (tables 5, 9, 11, 16).

Relative to *C. matthewi* (fig. 15), the cranium of *C. fricki* (fig. 22) differs in having a longer palate (no. 2), a somewhat greater cheek tooth length (nos. 7–9), a somewhat wider palate (no. 13), a distinctly greater separation between the IOF and rear of the DPOF (no. 34), and a much greater separation of the anterior tip of the lacrimal and rear of DPOF (no. 39, table 9 versus table 14). *C. fricki* also differs in having relatively shorter palatal fenestrae (no. 3), a shorter postpalatal region (no. 5), a distinctly wider diastemal region (no. 14), a relatively wider muzzle (no. 15), an apparently wider frontal region (no. 18) and transglenoid width (no. 19), a higher DPOF (no. 35) and IOF-alveolar border distance (no. 37), and a medially deeper DPOF (no. 40). The two species are comparable in snout length (no. 1) and height (no. 25), basicranial length (no. 4), total cranial length (no. 6), choanal width (no. 12), orbital dimensions (nos. 28–29), nasal notches (no. 30), facial lengths (no. 31), POBs (no. 32), and DPOF lengths (no. 33) and facial crest elevation (no. 36), and DPOF-alveolar border distance (no. 38).

*Cormohipparion fricki* (fig. 22) differs from *C. johnsoni* (fig. 18) in having a distinctly longer muzzle (no. 1) and palate (no. 2), longer premolar (no. 7) and cheek tooth (no. 9) lengths, longer facial region (no. 31) and POB (no. 32), and a longer IOF–DPOF distance (no. 34), as well as larger orbits (no. 28). The lacrimal is much more widely separated from the rear of the DPOF (no. 39, table 11, versus table 14), and the IOF is more widely separated from the alveolar border (no. 37). *C. fricki* also differs from *C. johnsoni* in having a wider palate (no. 13), diastema (no. 14), muzzle (no. 15), fontal region (no. 18), and transglenoid width (no. 19). Relative to *C. johnsoni*, *C. fricki* has a greater vertical dimension for the DPOF (no. 35), as well as vertical separation of the IOF from the alveolar border (no. 37), in contrast to the DPOF actually lying nearer the alveolar border (no. 38). *C. fricki* and *C. johnsoni* are comparable in snout height (no. 25), postpalatal dimensions (no. 3), molar lengths (no. 8), relatively short length of the DPOF (no. 33), depth of nasal notches (no. 30, probably in general context to no. 25), and medial depth of the DPOF (no. 40).

In comparison with *C. merriami* (fig. 20), *C. fricki* (fig. 22) differs in having a much shorter muzzle (no. 1) and palate (no. 2) and overall cranium (no. 6), a somewhat shorter facial region (no. 31), a much lower snout height (no. 25), somewhat longer (no. 28) but equally tall (no. 29) orbits, a distinctly longer

TABLE 16

**Measurements (mm) of Cranial Parameters for *Cormohipparion skinneri*, Gidley Horse Quarry, Clarendon Beds, Medial Clarendonian, Texas**

Characters illustrated in figures 3–5.

| | Characters | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| Specimen | 1, muz | 2, pal | 3, popl | 4, basc | 5, comb | 6, tsl | 7, upl | 8, uml | 9, tcl | 12, choa | 13, palw |
| F:AM 73909 ♂ | 97.4 | 118.2 | 89.8 | 80.5 | 170.8 | 395.9 | 87.8 | 71.8 | 156.4 | 37.9 | 59.0 |
| Mean | 97.4 | 118.2 | 89.8 | 80.5 | 170.8 | 395.9 | 87.8 | 71.8 | 156.4 | 37.9 | 59.0 |
| *N* | 6 | 4 | 2 | 3 | 2 | 3 | 5 | 5 | 4 | 3 | 5 |

| Specimen | 14, sntw | 15, wmuz | 18, fwd | 19, trgl | 22, in | 25, snh | 28, orl | 29, orh | 30, nis | 31, fac | 32, pobl |
|---|---|---|---|---|---|---|---|---|---|---|---|
| F:AM 73909 ♂ | 34.9 | 55.4 | 131.5 | 159.1 | 54.2 | 78.3 | 58.2 | 46.8 | 79.0 | 185.9 | 52.0 |
| F:AM 73910 ♂ | | | | | | | 55.7 | 60.5 | 99.0 | 162.7 | 45.5 |
| Range | | | | | | | 55.7–58.2 | 46.5–60.5 | 79.0–99.0 | 162.7–185.9 | 45.5–52.0 |
| Mean | 34.9 | 55.4 | 131.5 | 159.1 | 54.2 | 78.3 | 57.0 | 53.7 | 89.0 | 174.3 | 48.8 |
| SD | | | | | | | 1.77 | 9.69 | 14.14 | 16.40 | 4.60 |
| CV | | | | | | | 3.10 | 18.06 | 15.89 | 15.89 | 9.43 |
| *N* | 1 | 1 | 1 | 1 | 1 | 1 | 2 | 2 | 2 | 2 | 2 |

| Specimen | 33, dpof | 34, iof | 35, hdof | 36, fch | 3, ioa | 38, mpof | 39, ldof | 40, medof |
|---|---|---|---|---|---|---|---|---|
| F:AM 73909 ♂ | 64.2 | 60.3 | 37.1 | 42.2 | 45.2 | 73.2 | 18.7 | 21.8 |
| F:AM 73910 ♂ | 60.4 | 73.5 | 41.6 | 26.5 | 35.8 | 81.6 | | 9.5 |
| Range | 60.4–64.2 | 60.3–73.5 | 37.1–41.6 | 26.5–42.2 | 35.8–45.2 | 73.2–81.6 | | 9.5–21.8 |
| Mean | 62.3 | 66.9 | 39.4 | 34.4 | 40.5 | 77.4 | 18.7 | 15.7 |
| SD | 2.69 | 9.33 | 3.18 | 11.10 | 6.65 | 5.94 | | 8.70 |
| CV | 4.31 | 13.95 | 8.07 | 32.32 | 16.41 | 7.67 | | 55.57 |
| *N* | 2 | 2 | 2 | 2 | 2 | 2 | 1 | 2 |

POB (no. 32), and an apparently greater separation of the lacrimal from the rear of the DPOF (no. 39; table 11 versus table 15). *C. fricki* also differs from *C. merriami* in having a distinctly wider frontal (no. 18) and transglenoid region (no. 19). These two species are comparable in postpalatal length (no. 3), basicranial length (nos. 4–5), cheek tooth lengths (nos. 7–9; slightly shorter in *C. fricki*), palatal width (no. 13), muzzles (no. 15), likely diastemal width (no. 14), low inion height (no. 22), and small nasal notch incision (no. 30). Based on an overlap in 1 S.D. ranges, the two species apparently are comparable in having a similar DPOF length (no. 33), IOF positions (no. 34), DPOF heights (no. 35), facial crest–DPOF positions (no. 36), IOF–alveolar border distances (no. 37), and IOF–DPOF distances (no. 38). Also, the DPOFs are comparably deep medially (no. 40).

REFERRED MATERIAL: MacAdams Quarry: F:AM 73913, snout and facial region, right and left I1, LI2, RI3, right and left C, LdP1–M3, RP2–M3, subadult male, M3 erupting. F:AM 73914, partial cranium, LI2, right and left dP1–4, M1, juvenile female, M1 erupting. F:AM 73915, partial cranium, RI2–3, right and left C, P2–M3, adult male, M3 medial wear. F:AM. 73920, a partial cranium with right and left I1–2, LI3, right and left C, dP1–M3, subadult male, M3 early wear. F:AM 73921, snout and facial region, right and left I1–3, C, P2–M3, adult female, M3 well worn. F:AM 73925, facial region, RP3–M3, LP2, M3 early wear. F:AM 73938, cranial fragment.

Hollow Horn Bear Quarry, Ash Hollow Formation undifferentiated (Skinner and Johnson, 1984; figs. 2A, 3; table 1), Todd County, South Dakota: F:AM 71880, partial cranium with right and left P2–M3; F:AM 71881, LdP2–4, M1 erupting; F:AM 71873, juvenile cranium and mandibles with right and left dP1–P4, M1 erupting, right and left dp1–4; F:AM 71874, juvenile palate with right and left dP1–4; F:AM 71875, LP2–M3, late wear; FAM: 71876, R maxilla with dP2–4, M1, M2 erupting; F:AM 71879, dorsally flattened skull with RI1, right and left C1, P2–M3.

Description of Referred Material: Based on the material from MacAdams Quarry, major features of the cranium are comparable to those of the type specimen. The upper cheek tooth dentition is relatively complex (fig. 21B). As indicated in table 15, the tallest P2 is about 41 mm tall and P3 is about 46 mm tall in F:AM 73913, which show an incipiently developed occlusal pattern. Based on this specimen, the unworn MSTHT of P2 likely was about 45 mm and that of P3 was likely about 55 mm, from which it may be suggested that P4–M2 also were about 55 mm tall in the unworn condition, with M3 being somewhat shorter. If this is reliable, it suggests that *C. fricki* was somewhat lower crowned than the XMas-Kat *C. occidentale* (table 3B). The upper cheek tooth dentition of *C. fricki* also appears to have been somewhat less complex than in the XMas-Kat *C. occidentale*, especially as regards the anterior border of the prefossette, which usually bears only 1–2 plis after about medial wear. Similarly, the mean values of plis on the opposing borders of the pre- and postfossettes are 5:4, 9:5, 7:4, 7:6, and 7:5 for P2–M2, respectively, based on the relatively small sample (table 15). The labial margins of the pre- and postfossette in P2 are separate rather than confluent, except for F:AM 73925. The simple morphology of P2 in *C. fricki* contrasts with the more complex morphology in the type of *C. occidentale*. Similarly, the commonly spurred hypoconal groove in P2–4 of *C. fricki* is more complex than in XMas-Kat and in the type of *C. occidentale*.

As indicated in F:AM 73913, dP1 persists into early adult wear in which M3 is in the process of being erupted, but P2–3 are in early phases of wear, with MSTHTs of about 41 mm and 46 mm, respectively (table 15). Based on F:AM 73913 and F:AM 73920, the ratio of the length of dP1 to the length of P2 is 0.38–0.41 (table 15). This compares with a ratio of 0.3 in *C. johnsoni* (table 12), 0.37 in *C. merriami* (table 13), and 0.3 in juvenile XMas-Kat specimens of *C. occidentale* (table 7). DP1 is unknown in adult *C. matthewi* and *C. skinneri*, n.sp. The relatively large size of dP1 in *C. fricki* and *C. merriami* appears to be plesiomorphic in those species. The dP1 is present in about 60% of the specimens from MacAdams Quarry, regardless of sex. It also is absent in both female and male crania.

Upper cheek tooth protocones tend to be relatively elongate as in the type specimen, except in F:AM 73915, where they are shorter (table 15). Premolar plis caballin in *C. fricki* appear to be about as complex as in *C. occidentale* but less complex in the molars (tables 7–8), comparable to the other species of the *C. occidentale* group. Except where not applicable (deciduous premolars; two specimens), the pre- and postfossettes of P2 are about equally confluent or separate in the hypodigm ($N = 3$ for each).

F:AM 71880 (fig. 8) is a partial skull from the Hollow Horn Bear Quarry that preserves the anterior portion of the orbits, the facial region containing the DPOF and palate wherein right and left P2–M3 are retained. As indicated in table 3B, the measured crown height of P2 in F:AM 71880 is within the range for *C. fricki* (table 15). The upper cheek tooth morphology of F:AM 71880 is compatible with that for *C. fricki* (figs. 8B, 21B), considering the earlier wear stage of the Hollow Horn Bear Quarry specimen. The nearly unworn M3 of this specimen is likely to have been about 37 mm tall (table 4B) and about 45 mm in the unworn condition. This suggests that the unworn crown heights of the tallest cheek teeth (P4, M1) would have been on the order of 55 mm, comparable to the MacAdams sample of *C. fricki*. The unworn MSTHT of M1 and M2 in F:AM 71876 is circa 55 mm and 50 mm, respectively (table 3B). Specimens from the Hollow Horn Bear Quarry show a confluent pre- and postfossette in P2 in three specimens (not applicable in four) and separate in none.

F:AM 71880 preserves the facial part of the cranium (fig. 8A), which displays a well-developed DPOF that is situated well anterior to the orbit and to the anterior tip of the lacrimal bone. Note that the lacrimal is separated from the maxillo-nasal suture by a jugo-nasal suture that is about 5 mm long. The lacrimal therefore does not reach the maxillo-nasal suture. The DPOF is slightly pocketed posteriorly and has a well-developed anterior rim adjacent to, but above, the IOF. The IOF is located above the boundary between P2 and P3. Other specimens from the Hollow Horn Bear Quarry (referred material) demonstrate a comparable morphology.

DISCUSSION: Based on these specimens, the unworn crown height for *C. fricki* is on the order of 55 mm for M1 and somewhat less for P2 and M3 (table 3B). The anterior border of the prefossette and the opposing borders of the pre- and postfossettes are relatively complex, even in medial wear (e.g., F:AM 73925, F:AM 73901, F:AM 74915, table 15). For the overall sample, premolar plis caballin tend to be at least double; protocones are ovate, commonly lingually concave, and remain isolated from the protoloph in late wear; at comparable wear stages, cheek teeth tend to be relatively wide. P2 pre- and postfossettes are confluent in all three of the specimens in which it can be appraised (not applicable in four).

Webb (1969: 102) allocated material from Little Beaver B and Little Beaver A sites, Minnechaduza Fauna, Nebraska, to *Neohipparion occidentale*. As revised by Skinner and MacFadden (1977), this species is referable to *Cormohipparion*. In the present revision, the Minnechaduza material is referred to *C. fricki*. This is based chiefly on the crown height of the upper cheek teeth (unworn MSTHT 51–56, according to Webb, 1969: 102). This referral also is compatible with the degree of enamel pattern complexity and the relative elongation of the protocone of the Minnechaduza sample as described by Webb (1969). The Minnechaduza sample does not reach the crown height and enamel complexity characteristic of *C. occidentale* as described herein.

At present, no adult mandibles or lower dentitions can be directly associated with crania referred to *C. fricki*. Based on the crown height of the upper cheek teeth, the confluence of the pre- and postfossettes of P2, the ovate protocone proportions in the upper cheek teeth, general cranial characters, and the retention of dP1, *C. fricki* possesses many features likely prophetic of the North American ancestry of the *Hippotheriuim* Datum. This is discussed further below.

***Cormohipparion skinneri***, new species
figures 23–24; tables 2–3, 6, 16–18

TYPE SPECIMEN: F:AM. 73909, nearly complete undistorted cranium and mandible, with right and left I1–3, C1, P2–M3, right and left i1, Li2–3, right and left c1, Rp2–m3, Lp3–m3.

TYPE LOCALITY: Gidley Horse Quarry, Clarendon beds, Texas.

AGE: Medial Clarendonian, Texas.

DISTRIBUTION: Type locality.

DESCRIPTION OF TYPE SPECIMEN: F:AM 73909 is comparable overall to *C. occidentale*. The type cranium is slightly crushed at the frontal region so that the facial area anterior to the orbit is distorted. The nasal bones and the dorsal border of the facial region are preserved, but the frontal region is somewhat depressed, and the parietals are broken. The lateral surface of the face above the facial crest is depressed so that the lacrimal morphology is somewhat distorted. The dorsal half of the lacrimal is best preserved on the left side. The lower course of this element is partially obscured on the right side, as well. The morphology shown in figure 23A is a composite of both sides. In comparison, F:AM 71800 from the XMas-Kat sample is less distorted. The upper cheek tooth dentition is well preserved, as is the mandible and lower dentition. The angular region of both mandibles is missing (restored), as is the tip of the left coronoid process.

In overall morphology, the cranium of *C. skinneri* is comparable to that of many contemporaneous equids. The nasal notch extends posterior to the canine, but the relatively elongate facial region as compared with, for example, *C. quinni* (fig. 26; see also Woodburne, 1996b) is shown by the anterior margin of the orbit being located above the anterior edge of M3 in adult wear. In lateral view (fig. 23A), the overall profile is relatively regular, with the dorsal surface gently recurved. Although depressed postmortem, the frontal bones do not appear to have been domed dorsally. The orbits are relatively large (table 16), and the POB is relatively wide. The DPOF is thus well anterior to the orbit, is higher posteriorly than anteriorly but not as distinctly teardrop-shaped as, for instance, in the XMas-Kat *C. occidentale*.

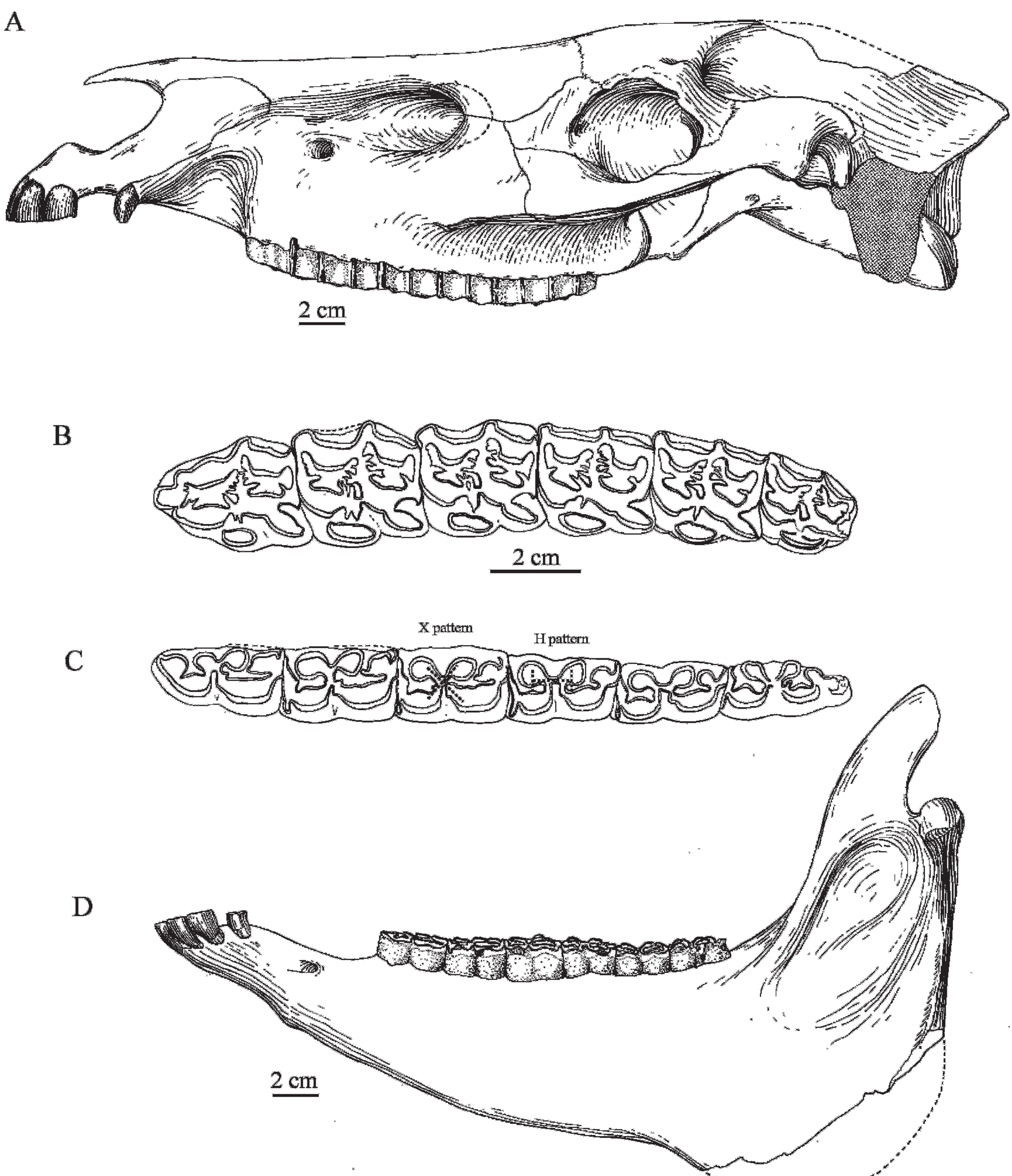


Fig. 23. *Cormohipparion skinneri*, F:AM 73909, Gidley Horse Quarry, Clarendon beds, Texas, medial Clarendonian. **A,** lateral view of cranium, modified from MacFadden (1984: fig. 133A). **B,** occlusal view of right upper cheek tooth dentition, reversed. After MacFadden (1984: fig. 133B). **C,** occlusal view of right lower cheek tooth dentition, reversed. **D,** right lateral view of mandible (reversed). After MacFadden (1984: fig. 136). Note dashed-line X showing the configuration of the metaconid, metastylid, and ectoflexid in P4 (for premolars) and the H pattern on M1 (for M1 and M2).

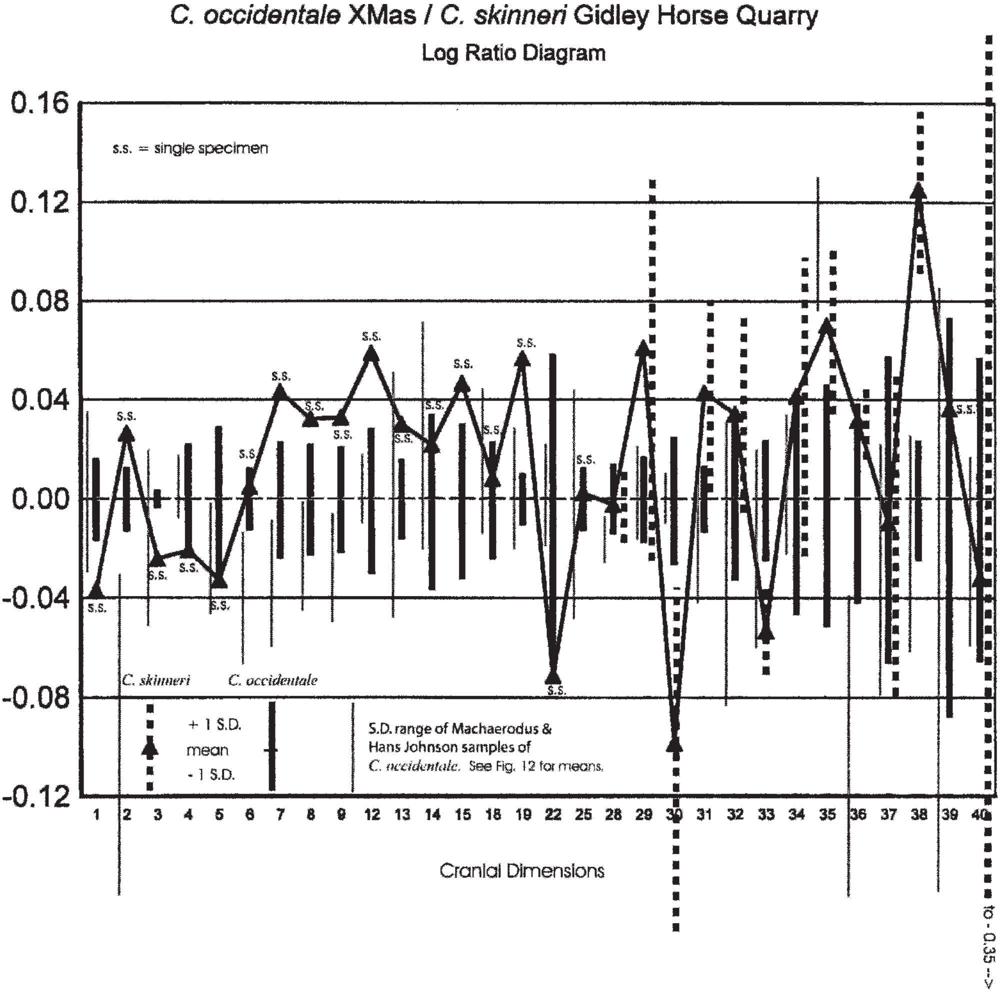


Fig. 24. Log-ratio diagram of cranial dimensions of *Cormohipparion skinneri* compared with *C. occidentale*, XMas-Kat quarries, Merritt Dam Member, Ash Hollow Formation, Cherry County, Nebraska.

As in *Cormohipparion* generally, the IOF is located just below the anteroventral margin of the DPOF, usually slightly posterior to the actual anterior end of the fossa. In *C. skinneri*, the IOF is situated above the rear half of P2, comparable to the condition in *C. fricki*. The anterior end of the DPOF is not as pronounced as typically seen in XMas-Kat materials of *Cormohipparion*. The anteriorly wide POB (no. 32, table 16) is reflected in the lacrimal usually being exposed on the posterior three-fifths of the bar (length 2, table 3A) and not entering the rear of the DPOF, as recorded in *C. quinni*. As in *C. quinni* and the XMas-Kat materials, the facial crest ends above the premolar–molar boundary at an elevation approximately midway between the alveolar border and the ventral margin of the DPOF. In spite of the wider POB, the DPOF is still situated about as in *C. quinni*; the rear of the DPOF still is located essentially above the mesostyle of M1. In *C. skinneri*, the lacrimal is longer than in *C. quinni*, but the extension of the POB appears to have taken place as well between the lacrimal tip and the rear of the POB. This is reflected in dimension no. 32 being about twice that in *C. quinni* (table 16 in comparison with Woodburne, 1996b: table 16 no. 32), even though the facial length of the

TABLE 17

**Measurements (mm) of Upper Cheek Tooth Dentition of *Cormohipparion skinneri* Gidley Horse Quarry, Clarendon Beds, Medial Clarendonian, Texas**

| | | | | | | Protocone | | | Pli | Hypoconal |
|---|---|---|---|---|---|---|---|---|---|---|
| Specimen | Height | Length | Width | Ratio | Index | Length | Width | Ratio | caballin | groove |
| **P2** | | | | | | | | | | |
| **F:AM 73909 ♂** | 30.0a | 33.3 | 25.2 | 0.76 | 4:5:2:1 | 8.2 | 4.4 | 0.54 | 2 | |
| F:AM 73910 | 24.2 | 30.9 | 27.5 | 0.89 | 2:5:3:1 | 8.8 | 4.1 | 0.47 | 3 | narrow; simple |
| Range | | 30.9–33.3 | 25.2–27.5 | 0.76–0.89 | | 8.2–8.8 | 4.1–4.4 | 0.47–0.54 | | |
| Mean | | 32.1 | 26.4 | 0.82 | 4:5:2:1 | 8.5 | 4.3 | 0.50 | 2 | |
| SD | | 1.70 | 1.63 | 0.09 | | 0.42 | 0.21 | 0.05 | | |
| CV | | 5.29 | 6.17 | 11.40 | | 4.99 | 4.99 | 10.00 | | |
| *N* | 2 | 2 | 2 | 2 | 1 | 2 | 2 | 2 | 1 | 2 |
| **P3** | | | | | | | | | | |
| **F:AM 73909 ♂** | 31.0a | 28.8 | 26.8 | 0.93 | 3:7:4:1 | 11.4 | 4.0 | 0.35 | 2 | open; simple |
| F:AM 73910 | 22.2 | 27.9 | 28.0 | 1.00 | 1:5:5:1 | 11.6 | 4.1 | 0.35 | 3 | narrow; simple |
| Range | | 27.9–28.8 | 26.8–28.0 | 0.93–1.00 | | 11.4–11.6 | 4.0–4.1 | | | |
| Mean | | 28.4 | 27.4 | 1.00 | 3:7:4:1 | 11.5 | 4.1 | 0.35 | 2 | |
| SD | | 0.64 | 0.85 | 0.05 | | 0.14 | 0.07 | | | |
| CV | | 2.24 | 3.10 | 4.34 | | 1.23 | 1.75 | | | |
| *N* | 2 | 2 | 2 | 2 | 1 | 2 | 2 | 2 | 1 | 2 |

Remarks: Height is at mesostyle; boldface specimens used in plication count statistics; a = approximate.

| | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| **P4** | | | | | | | | | | |
| **F:AM 73909 ♂** | | 27.2 | 25.5 | 0.94 | 1:8:5:1 | 10.3 | 3.9 | 0.38 | 1 | open; simple |
| F:AM 73910 | 14.8a | 26.8 | 28.0 | 1.04 | 1:5:3:1 | 11.8 | 5.3 | 0.45 | 2 | narrow; simple |
| Range | | 26.8–27.2 | 25.5–28.0 | 0.94–1.04 | | 10.3–11.8 | 3.0–5.3 | 0.38–0.45 | | |
| Mean | | 27.0 | 26.8 | 0.99 | 1:8:5:1 | 11.1 | 4.6 | 0.41 | 1 | |
| SD | | 0.28 | 1.77 | 0.08 | | 1.06 | 0.99 | 0.05 | | |
| CV | | 1.05 | 6.61 | 7.65 | | 9.60 | 21.52 | 12.00 | | |
| *N* | 1 | 2 | 2 | 2 | 1 | 2 | 2 | 2 | 1 | 2 |
| **M1** | | | | | | | | | | |
| **F:AM 73909 ♂** | | 24.3 | 23.9 | 0.99 | 1:5:6:1 | 9.8 | 4.2 | 0.43 | 1 | open; simple |
| F:AM 73910 | 21.0a | 24.6 | 29.2 | 1.19 | 1:7:5:1 | 11.7 | 5.6 | 0.48 | 2 | narrow; simple |
| Range | | 24.3–24.6 | 23.9–29.2 | 0.98–1.19 | | 9.8–11.7 | 4.3–5.6 | 0.43–0.48 | | |
| Mean | | 24.5 | 26.6 | 1.09 | 1:5:6:1 | 10.8 | 4.9 | 0.45 | 1 | |
| SD | | 0.21 | 3.75 | 0.14 | | 1.34 | 0.99 | 0.04 | | |
| CV | | 0.87 | 14.10 | 13.30 | | 12.50 | 20.20 | 7.80 | | |
| *N* | 1 | 2 | 2 | 2 | 1 | 2 | 2 | 2 | 1 | 2 |
| **M2** | | | | | | | | | | |
| **F:AM 73909 ♂** | | 24.5 | 23.2 | 0.95 | 1:6:5:1 | 9.7 | 3.8 | 0.39 | 1 | open; simple |
| F:AM 73910 | | 25.7 | | | 1:7:6:1 | 11.9 | 4.6 | 0.39 | 2 | narrow |
| Range | | 24.5–25.7 | | | | 9.7–11.9 | 3.8–4.6 | | | |
| Mean | | 25.1 | 23.2 | 0.95 | 1:6:5:1 | 10.8 | 4.2 | 0.39 | 1 | |
| SD | | 0.85 | | | | 1.56 | 0.57 | | | |
| CV | | 3.38 | | | | 14.44 | 13.47 | | | |
| *N* | | 2 | 1 | 1 | 1 | 2 | 2 | 2 | 1 | 2 |

TABLE 17
(*Continued*)

| M3 | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | | | | | | Protocone | | | | |
| Specimen | Height | Length | Width | Ratio | Index | Length | Width | Ratio | Pli caballin | Hypoconal groove |
| **F:AM 73909** ♂ | 30.0a | 23.1 | 20.8 | 0.90 | 1:4:4:1 | 9.5 | 2.0 | 0.21 | 1 | spurred |
| F:AM 73910 | | 25.3 | 24.1 | 1.00 | 1:6:4:1 | 13.0 | 3.0 | 0.23 | 2 | modified |
| Range | | 23.1–25.3 | 20.8–24.1 | 0.90–1.00 | | 9.5–13.0 | 2.0–3.0 | 0.21–0.23 | | |
| Mean | | 24.2 | 22.5 | 0.93 | 1:4:4:1 | 11.3 | 2.5 | 0.22 | 1 | |
| SD | | 0.21 | 3.75 | 0.14 | | 1.34 | 0.99 | 0.04 | | |
| CV | | 1.56 | 2.33 | 0.04 | | 2.48 | 0.71 | 0.01 | | |
| *N* | 1 | 2 | 2 | 2 | 1 | 2 | 2 | 2 | 1 | 2 |

lacrimal (nos. 32–39, table 16) is 39 mm in *C. skinneri* versus about 25 mm in *C. quinni*. In contrast to that in *C. fricki*, the lacrimal in *C. skinneri* is blunt anteriorly and nearly vertical. The maxillo-lacrimal and maxillo-jugal sutures thus are effectively aligned with one another. In addition, the lacrimal appears to have been more broadly exposed on the face (length 2, table 3A), and has a blunt, rather than pointed, anterior end. Consequently, the lacrimal does not extend appreciably anterior to the maxillo-jugal suture.

In ventral aspect, the incisor arcade is smoothly rounded, the incisors having cement-filled infundibula. The canines are sited about two-thirds the distance between I3 and P2. DP1 is absent. The premolars are generally larger than the molars and tend to have a slightly more complex enamel pattern (fig. 23B). The dentition of F:AM 73099 is in a mature stage of wear (table 17). With a MSTHT of about 30 mm, P2 seems to be one-quarter worn, if this tooth was about 40 mm tall in the unworn state, comparable to *C. occidentale*. In P2–3, the anterior border of the prefossette is moderately complex (up to 4 plis) but simpler in the more posterior teeth (table 17). The posterior border of the prefossette displays 5–8 plis in the premolars and 4–6 plis in the molars. For the anterior border of the postfossette, comparable numbers are 2–5 plis in the premolars and 4–6 plis in the molars. All have but a single pli on the posterior border of the postfossette. The bifid versus the single pli caballin distinguishes P2, P3, and M1 from the other cheek teeth. At this wear stage, the pre- and postfossettes of P2 are separated rather than confluent along their labial margins; cheek tooth protocones are elongate and isolated but relatively broad and slightly concave labially in both premolars and molars.

The mandibles are well developed, except for missing their angular regions (fig. 23D). As indicated in table 18, the mandible is relatively deep beneath the molars but becomes shallower anteriorly. The lower dentition is remarkable in having a relatively

TABLE 18
**Measurements (mm) of Lower Mandible and Dentition of *Cormohipparion skinneri*, Gidley Horse Quarry, Clarendon Beds, Medial Clarendonian, Texas**

| | Characters[a] | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Mandible | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 10 | 11 | 12 | 13 | 14 | 16 | 17 |
| F:AM 71809 ♀ | 350.0 | 94.0 | 82.0 | 74.7 | 155.7 | 99.0 | 59.4 | 99.0a | 67.0 | 44.0 | 61.3 | 28.2 | 43.4 | 38.8 |

| | p2 | | p3 | | p4 | | m1 | | m2 | | m3 | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Lower dentition | L | W | L | W | L | W | L | W | L | W | L | W |
| F:AM 71809♀ | 30.2 | 15.4 | 26.8 | 17.3 | 26.2 | 18.2 | 26.0 | 15.8 | 25.4 | 13.8 | 28.4 | 12.5 |

[a]Characters shown in figure 6. Character 17 = p2 to mandibular foramen. L = length; W = width; a = approximate.

strong (premolars) to strong (molars) penetration of the isthmus by the ectoflexid (see fig. 6 for terminology). In P3 and P4, the base of the metaconid and metastylid are constricted, respectively, into right and left halves of the upper arms of an "X" pattern, as shown in figure 23C. In M1 and M2, the metaconid and metastylid respectively form the right and left halves on an 'H' pattern, with the cross bar of the H formed by the anteroposteriorly elongate labial end of the ectoflexid (fig. 23C). Protostylids are present on p3–m3. The ectoflexid development is exhibited by a specimen judged to be in adult wear (upper dentition about 25% worn) and is present in all molars, as well as in the premolars. If borne out by additional specimens, if and when recovered, this would represent an evolutionary novelty not found in other species of *Cormohipparion*.

DIAGNOSIS: *Cormohipparion skinneri* is distinguished from all other species of the subgenus *Cormohipparion* in having the characteristic strong development of premolar and molar ectoflexids and the development of the "X" and "H" patterns described above (assuming the type is representative of its species population). As shown in figure 24, *C. skinneri* is represented only by a single specimen in parameters 1–25 and by two specimens in parameters 28–40. Parameters in which *C. skinneri* falls within the range indicated on figure 24 for *C. occidentale* from XMas-Kat Quarry and in figure 13 from the XMas-Kat, Machaerodus, and Hans Johnson quarries are not considered further here. In that context, *C. skinneri* differs from *C. occidentale* in having a somewhat shorter muzzle (no. 1), a somewhat longer palate (no. 2), and a much shorter postpalatal dimension (no. 3), even though the basicranial dimension (no. 4) is similar. *Cormohipparion skinneri* also differs from *C. occidentale* in having longer premolar, molar, and cheek tooth row lengths (nos. 7–9); a wider choanae (no. 12), palate (no. 13), and muzzle (no. 15); and a very much wider transglenoid dimension (no. 19), in spite of the frontal width (no. 18) being comparable. Although the standard deviation for *C. skinneri* overlaps that for *C. occidentale*, *C. skinneri* has a somewhat larger orbit (no. 29), a somewhat longer facial region (no. 31), and a somewhat taller DPOF (no. 35). *Cormohipparion skinneri* also differs from *C. occidentale* in having a much less incised nasal notch (no. 30), a shorter DPOF (no. 33), and a much greater separation of the rear of the DPOF from the alveolar region (no. 38).

In comparison with *C. matthewi* (fig. 15), *C. skinneri* (fig. 24) has a shorter muzzle (no. 1), a much longer palate (no. 2), a much shorter postpalatal dimension (no. 3), a smaller basicranial dimension (nos. 4–5) (but a relatively longer cranium overall [no. 6]), longer cheek tooth row dimensions (nos. 7–9), a wider choanae (no. 12) and palate (no. 13), a much wider snout (no. 14) and muzzle (no. 15) (but a narrower frontal [no. 18] versus a much wider transglenoid region [no. 19]), a much taller snout (no. 25), comparably sized orbits (nos. 28–29), comparably weakly incised nasal notches (no. 30), a somewhat longer facial region (no. 31), a longer POB (no. 32), a comparably short DPOF (no. 33), a much greater separation between the IOF and rear of the DPOF (no. 34) and a much taller DPOF (no. 35), a greater separation of the facial crest and the DPOF (no. 36) (but a comparable separation of the alveolar border and IOF [no. 37]), a very much taller DPOF relative to the alveolar border (no. 38), a somewhat greater separation of the anterior tip of the lacrimal and rear of the DPOF (no. 39; table 16), and a somewhat medially deeper DPOF (no. 40).

In comparison with *C. merriami* (fig. 20), *C. skinneri* (fig. 24) has a somewhat shorter muzzle (no. 1), a comparable palatal length (no. 2); a shorter postpalatal (no. 3) and basicranial region (no. 4); and a comparable dimension no. 5, overall skull length (no. 6), cheek tooth rows (nos. 7–9), and palatal width (no. 13), but a relatively wider snout (no. 14) and muzzle (no. 15). In contrast, the frontals are comparably wide (no. 18), but the transglenoid dimensions are distinctly greater (no. 19) and the inion height smaller (no. 22) in *C. skinneri*, with the snout height (no. 25) being comparable in the two species. The orbit is somewhat smaller in *C. merriami* (nos. 28–29); the nasal notch is somewhat more incised (no. 30); and the facial region is longer (no. 31). The two species have a comparably short POB (no. 32) and DPOF (no. 33), whereas the IOF location (no. 34), DPOF height (no. 35), and facial crest–DPOF separation (no. 36, strongly) are greater in *C. skinneri*. The IOF–alveolar border separation (no. 37) and DPOF–alveolar border separation (no. 38) are comparable in the two species, whereas the DPOF is farther from the lacrimal (no. 39, table 16), but the DPOF is shallower in *C. skinneri*.

In comparison with *C. johnsoni* (fig. 18), *C. skinneri* (fig. 24) has a longer muzzle (no. 1) and palate (no. 2); a shorter postpalatal dimension (no. 3); longer cheek tooth rows (nos. 7–9); a wider palate (no. 13), snout (no. 14), muzzle (no. 15), frontal (no. 18), and transglenoid (no. 19); a taller snout (no. 25); and larger orbits (nos. 28–29), but a comparably little incised nasal notch (no. 30). The facial region (no. 31) and POB (no. 32) are longer in *C. skinneri*, but the DPOF (no. 33) is comparably short in the two species. The IOF location (no. 34), DPOF height (no. 35), facial crest–DPOF separation (no. 36), IOF–alveolar border separation (no. 37), DPOF–alveolar border separation (no. 38), and separation of DPOF and anterior lacrimal tip (no. 39; much greater; see table 16) are greater, but the medial DPOF depth (no. 40) is smaller, in *C. skinneri*.

In comparison with *C. fricki* (fig. 22), *C. skinneri* (fig. 24) has a similarly short snout (no. 1), similar palatal length (no. 2), shorter postpalatal dimension (no. 3), and somewhat shorter basicranium (nos. 4–5), but a somewhat longer skull overall (no. 6). The cheek tooth rows are longer in *C. skinneri* (nos. 7–9), but the choanae (no. 12) and palates (no. 13) are about equally wide in the two species. *Cormohipparion skinneri* has a somewhat wider snout (no. 14) and muzzle (no. 15) but a much narrower frontal (no. 18) and a slightly wider transglenoid dimension (no. 19), as well as a slightly lower inion height (no. 22). *Cormohipparion skinneri* has a great deal taller snout (no. 25) and a somewhat longer orbit (no. 29), but a comparably weakly incised nasal notch (no. 30). The facial region (no. 31), POB (no. 32), and DPOF (no. 33, relatively short) are about equally long in the two species, but the IOF is relatively more anterior (no. 34), the DPOF is taller (no. 35), the facial crest is farther from the DPOF (no. 36) (but the IOF is nearer the alveolar border [no. 37]), the DPOF is farther from the alveolar border (no. 38), the anterior tip of the lacrimal is much nearer the rear of the DPOF (no. 39, table 16), and the DPOF is medially shallower (no. 40) in *C. skinneri*.

REFERRED MATERIAL: F:AM 73910, distorted cranium with right and left I1, LI2–3, right and left P2–M3. Gidley Horse Quarry, Clarendon beds, Texas.

DESCRIPTION OF REFERRED MATERIAL: F:AM 73910 is badly distorted in having been crushed dorsoventrally and skewed labially. It seems to have the same basic morphology as in the type specimen, including a lacrimal that is narrower anteriorly than at the orbit but that appears to be blunt anteriorly. At this mature stage of wear (P2 appears to be about one-half its unworn MSTHT), the cheek tooth protocones still are elongate and isolated. In P3 and P4, the lingual margin of the protocone is slightly concave; otherwise, this protocone border is slightly convex to flat in the other teeth. Plis caballin are more complex (trifid) in P2 and P3 than in P4–M3 (bifid, table 17). The dP1 is absent in these adult crania.

DISCUSSION: As developed further below, *C. skinneri* is most similar to *C. occidentale*, with which it is contemporaneous, but differs in the features indicated in the Diagnosis. The Texan occurrence of *C. skinneri* relative to the more northern distribution of *C. occidentale* suggests that *C. skinneri* may have pertained to a population characteristic of a southern province.

### *Cormohipparion* sp.

Two samples are referred to *Cormohipparion* sp., unallocated. The first is LACM 150080, from Punchbowl Formation, Devil's Punchbowl, Valyermo, California. The second is derived from the Dove Spring Formation, El Paso Basin, California.

VALYERMO: The locality (V, fig. 1) and stratigraphic setting for LACM 150080 are presented in Woodburne (2005). As discussed there, the complexity of the fossette borders and cheek tooth plis caballin, the subovate outline of the protocone (rather than very elongate; fig. 25) and its likely moderate unworn MSTHT (ca. 50–55 mm) are prophetic of the morphology displayed in upper

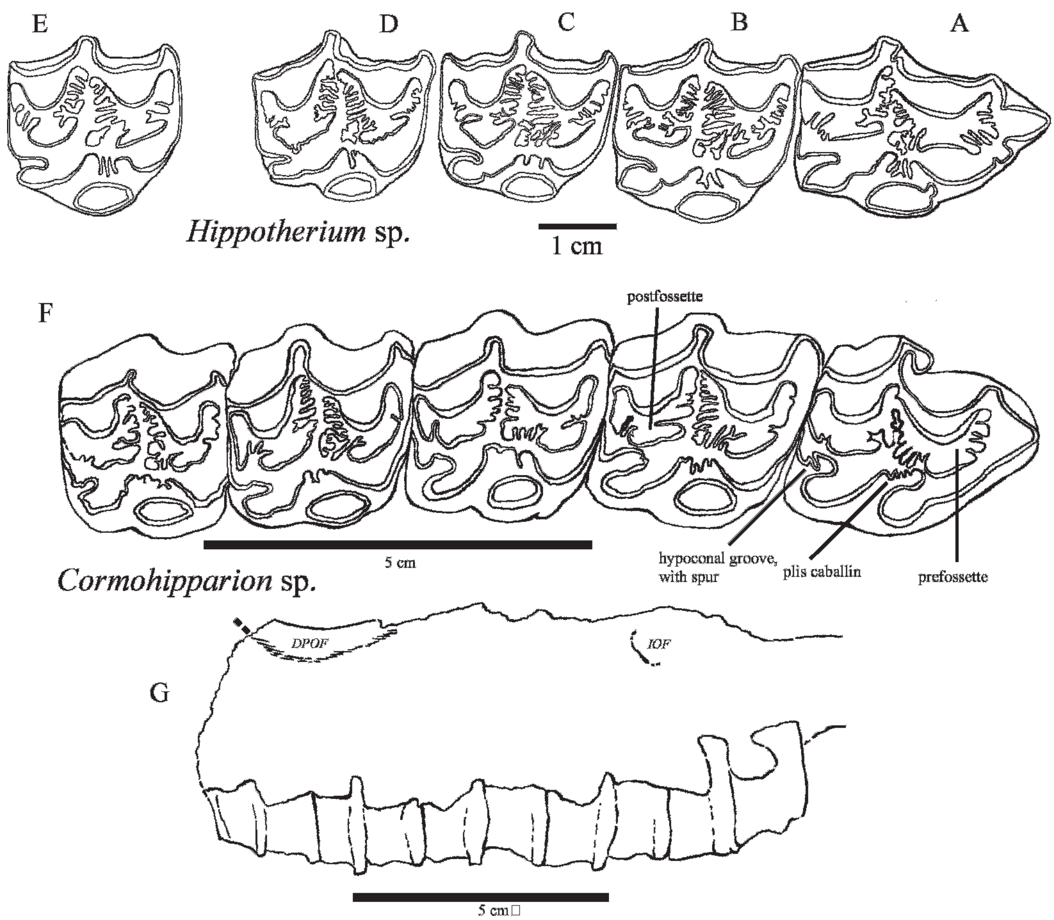


Fig. 25. *Hippotherium* and *Cormohipparion*. **A–D,** *Hippotherium* sp., Pannonian C?, Mariathal, Austria. **E,** *Hippotherium* sp., Pannonian C, Gaiselberg, Austria. **F–G,** *Cormohipparion* sp., Punchbowl Formation, LACM 7502, medial Clarendonian, California. **A,** PIUW 3504/3, LP2, reversed. **B,** PIUW 3540/97, LP3, reversed. **C,** PIUW 3540/54, LP4, reversed. **D,** PIUW 3540/136, RM1. **E,** NHMW 0024/26, RM2. **F,** partial palate with right and left P2–M2, occlusal view. Preservation of the specimen apparently masks the complexity of the plis caballin in P4–M2. **G,** right lateral view of partial palate, showing remnant of posteroventral border of DPOF and the IOF located above the anterior root of P3.

cheek teeth of *Hippotherium primigenium*. LACM 150080 seems to be morphologically the closest to the Old World taxon among North American samples. Note that the preservation of the specimen apparently masks the complexity of the plis caballin in P4–M2. The connection of the protocone to the protoloph in P2 at about 50% wear may be a relatively plesiomorphic retention, but, as discussed below, it also occurs in other species of *Cormohipparion* as well as in Old World material referred to *Hippotherium* sp. and *H. primigenium*. In the current report, the age of LACM 150080 is suggested as medial Clarendonian, although an early Clarendonian age cannot be ruled out.

As indicated in tables 13 and 21 and in figure 25, the complexity of the fossette borders (especially at the posterior border of the prefossette and the anterior border of the postfossette in P3 and M1) rivals or exceeds that of *C. occidentale* as well as samples of *Hippotherium primigenium*. At the same time, the ovate protocones and their width-to-length ratios are generally comparable to those seen in samples of *H.*

TABLE 19

**Upper and Lower Cheek Tooth Parameters, *Cormohipparion* sp., Dove Spring Formation, El Paso Basin, Medial Clarendonian, California**

| | | | | | | | Prot. | | | Hyp. | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Loc. | Spec. | Tooth | Hgt. | L | W | Ratio | L | W | Rat. | L | W | Index | Prot. is.? | Pli cab. | Hypoconal groove |
| 1745 | 55685 | RP3 | 32.5 | 27.0 | | | 7.7 | 3.7 | 0.48 | 5.8 | 4.5 | 1:10:4:1 | yes | 1 | open; simp. |
| 1743 | 59647 | RP2 | 16.5 | | 24.2 | | 9.7 | 4.8 | 0.50 | | | 2:3:2:1 | yes | 1 | ?open; simp. |
| 3431 | 59647 | RP3 | 37.0 | 25.7 | 24.2 | 0.94 | 8.6 | | | 4.4 | 3.6 | 1:6:5:1 | yes | 1 | open; simp. |
| 5097 | 146415 | LP4 | 35.0 | 26.2 | 20.5 | 0.94 | 8.2 | 4.4 | 0.54 | 4.3 | 2.9 | 3:10:7:2 | yes | 2 | open; simp. |
| 4785 | 140854 | LP2 | 32.6 | | | | 5.4 | 3.7 | 0.69 | 7.0 | 4.0 | ?:4:4:1 | yes | 2 | open; simp. |
| 4785 | 140854 | LP3 | 36.8 | 27.7 | 23.4 | 0.84 | 5.8 | 3.8 | 0.66 | 5.9 | 3.3 | 2:9:6:1 | yes | 1 | open; simp. |
| 4785 | 140854 | LP4 | 42.1 | | | | | | | | | 1:7:6:2 | ? | ? | open; simp. |
| 4785 | 140854 | LM1 | 42.0 | 23.8 | 14.5 | 0.61 | 5.1 | 2.8 | 0.55 | 4.1 | 2.9 | 1:5:6:2 | yes | 1 | open; simp. |
| 4785 | 140854 | LM2 | 34.9 | 20.5 | 20.8 | 1.01 | 5.4 | 3.2 | 0.59 | 4.0 | 3.3 | 1:5:7:1 | yes | 1 | open; simp. |
| 3440 | 149667 | RM3 | 28.2 | 25.0 | 20.2 | 0.81 | 7.7 | 3.4 | 0.44 | 4.1 | 2.5 | 1:8:6:2 | yes | 2 | open; wide |
| 3439 | 148905 | RP3 | 37.4 | 26.0 | | | 8.7 | 3.6 | 0.41 | | | 1:6:4:1 | ? | 3 | open; simp. |
| 5732 | 146246 | LP4? | 45.0 | | | | 10.5 | 5.6 | 0.53 | | | | | | |

| | | | p2 | | p3 | | p4 | | m1 | | m2 | | m3 | | Unworn |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | Hgt. | L | W | L | W | L | W | L | W | L | W | L | W | height |
| 5732 | 138755 | 33.4 | 29.5 | 15.0 | 28.4 | 16.1 | 29.1 | 15.1 | 27.5 | 13.8 | 29.6 | 13.6 | 30.0 | 11.5 | 50.5 |

Stratigraphic distribution of key localities:

1745 = ca. 11.7 Ma; in Chron C5r; upper 1/3 Member 3 of Dove Spring Fm., between ashes 4 & 5.

1743 = ca. 11.7 Ma; in Chron C5r; upper 1/3 Member 3 of Dove Spring Fm., between ashes 4 & 5.

5732 = ca. 11.0 Ma; likely in uppermost Chron C5r; between basalts in Member 4 of Dove Spring Fm., above unconformity.

5097 = ca. 10.8 Ma; in lower 3rd Chron 5. Middle part of Dove Spring Fm., ca lower 1/3 Member 5, between ashes 7 & 8.

3431 = ca. 10.7 Ma; in lower 3rd Chron 5. Midlde part of Dove Spring Fm., ca lower 1/3 Member 5, between ashes 8 & 9.

4785 = ca. 10.3 Ma; in middle Chron 5. Middle part of Dove Spring Fm., middle 1/3 Member 5, between ashes 9 & 10.

Abbreviations:

Loc. = locality; Spec. = specimen; Hgt. = height; L = length; W = width; Prot. = protocone; Hyp. = hypocone; cab. = caballin; is.? = isolated; simp. = simple.

*primigenium*. The confluence of the pre- and postfossettes in P2 is seen also in those taxa, as well as in other species of *Cormohipparion*, apparently most abundantly in *C. fricki*.

El Paso Basin: Whistler and Burbank (1992) described the litho-, magneto-, and biostratigraphy and geochronology of the fossiliferous succession of the Dove Spring Formation of the El Paso Basin, California (E, fig. 1). Whistler and Burbank (1992: fig. 4) recorded *C. occidentale* as occurring from the base of the *Cupidinimus avawatzensis*/*Paracosoryx furlongi* Assemblage Zone to just within the base of the *Paronychomys*/*Osteoborus diabloensis* Assemblage Zone. Based on the specimens discussed below, this range is modified to about 11.8–10.3 Ma, as shown in figure 2. All of the specimens are isolated teeth (or, in one case, in a lower mandible) and have no associated cranial material. Thus, for the purposes of this report, the specimens are allocated as *Cormohipparion* sp. but, as also discussed below, it appears unlikely that they would pertain either to *C. occidentale* as defined herein or to the Valyermo taxon.

As summarized in table 19, these teeth overall are of larger size, greater dental complexity, and, likely, taller unworn MSTHT than *Hipparion forcei* and *Hipparion tehonense*, as documented by MacFadden (1984), which also occur in the Dove Spring Formation (Whistler and Burbank, 1992: fig. 4). The lower dentition, LACM 138755, shows protostylids present in p3–m3, also characteristic of *Cormohipparion.* Most show elongate protocone proportions, with only LACM 140854 being more nearly ovate than elongate. In general, crown height (in which the unworn MTSHT could have been on the

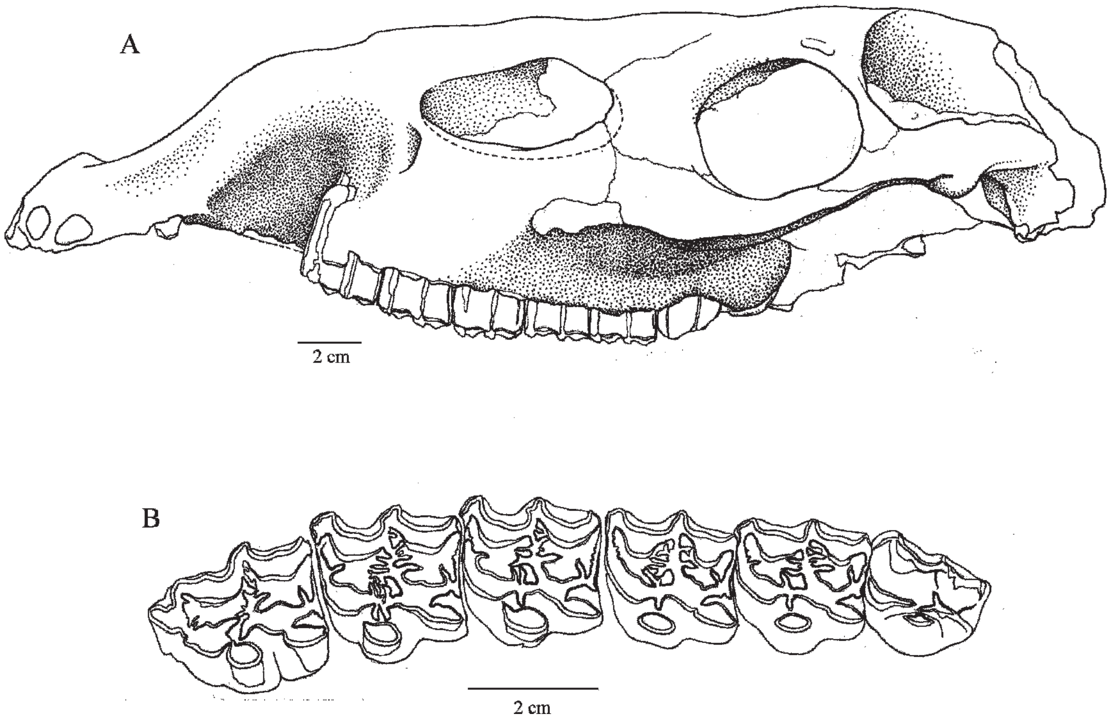


Fig. 26. *Cormohipparion quinni*, AMNH 108535, MacAdams Quarry, Clarendon beds, Texas, medial Clarendonian. **A,** left lateral view of cranium. **B,** occlusal view of left P2–M3.

order of 50–55 mm), protocone index, and fossette complexity in these specimens is similar to the XMas-Kat materials of *C. matthewi*, but further material from each site is needed before a more definite comparison can be made. In that the material spans an interval of nearly 1 m.y., it is possible that more than one taxon could be represented.

*Cormohipparion quinni*
figure 26; table 20

Figure 26 shows a lateral view of AMNH 108535 from MacAdams Quarry, Clarendon beds, Texas. This specimen also was figured as *C. sphenodus* by MacFadden (1984: fig. 127). Woodburne (1996b) replaced *C. sphenodus* with *C. quinni*. The purpose of illustrating this specimen in the current context is to affirm the presence of this species, with its characteristically short POB (no. 32, table 20) and lacrimal eroded by the rear of the DPOF, as well as relatively simpler cheek tooth dentition, in contrast to the *C. occidentale* group of taxa described here. F:AM 108535 confirms the presence of this species in the MacAdams Quarry sample, and the persistence of this species, as shown in figure 2, is contemporaneous with medial Clarendonian descendants of the speciation event responsible for the genesis of the *C. occidentale* group of taxa.

## RESULTS

Figures 13, 15, 18, 20, 22, and 24 show that the basicranial length (no. 4) of *C. occidentale* is comparable to that of all other species (unknown in *C. johnsoni*; possibly somewhat longer than in *C. skinneri*), so if this is a general indicator of cranial and body size (Radinsky, 1989), other dimensions in these species might be comparable. As indicated here, however, this does not seem to have been the case, with some exceptions. Thus, the total cranial length (no. 6) for all species is about within the range for *C. occidentale*, as are the premolar (no. 7), molar (no. 8), and cheek tooth (no. 9) lengths and the choanal width (no. 12).

TABLE 20
**Cranial Measurements (mm) of *Cormohipparion quinni*, MacAdams Quarry, Clarendon Beds, Medial Clarendonian, Texas**

| | Character[a] | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| | 2, pal | 3, popl | 7, upl | 8, uml | 9, tcl | 12, choa | 13, palw | 14, sntw |
| F:AM 108535 ♀ | 88.3 | 89.8 | 70.2 | 59.0 | 127.5 | 39.2 | 56.7 | 35.2 |
| | Character[a] | | | | | | | |
| | 15, wmuz | 18, fwd | 25, snh | 28, orl | 29, orh | 31, fac | 32, pobl | 33, dpof |
| F:AM 108535 | 51.4 | 117.0 | 67.3 | 53.0 | 45.3 | 127.0 | 27.7 | 57.5 |
| | Character[a] | | | | | | | |
| | 34, iof | 35, hdof | 36, fch | 37, ioa | 38, mpof | 39, ldof | 40, medof | |
| F:AM 108535 ♀ | 58.5 | 36.0 | 27.0 | 36.2 | 60.0 | –3.0 | 17.0 | |
| | Remarks | | | | | | | |
| F:AM 108535 ♀ | Occiput missing; M3 very early wear; see fig. 26. Specimen now broken in ventral part of DPOF and anterior lacrimal. #12–15 ?too wide on specimen = DV slightly crushed | | | | | | | |

[a]Characters are described in detail in table 1.

Although generally low in *C. matthewi*, *C. merriami*, and *C. johnsoni*, the length of the POB (no. 32) in these species is about within the range of *C. occidentale*, which embraces the dimensions of *C. fricki* and *C. skinneri*, as well. All species are comparable in separation of the IOF from the alveolar border (no. 37).

*Cormohipparion matthewi* differs from *C. occidentale* in the shorter muzzle (no. 1), the greater length of the postpalatal dimension of the cranium (no. 3), and thus the somewhat greater length of no. 5 (which includes no. 3). The palatal length (no. 2) and total cranial length (no. 6) in *C. matthewi* also are smaller than in *C. occidentale* from XMas-Kat Quarry but not the samples from the Machaerodus and Hans Johnson quarries. Similarly, the cheek tooth lengths (nos. 7–9) in *C. matthewi* are at the lower end of the range for these features in the XMas-Kat Quarry sample of *C. occidentale* but more in line with those from the Machaerodus and Hans Johnson quarries. The snout in *C. matthewi* is much narrower than in *C. occidentale* and all other species except *C. johnsoni*, which is even narrower. *C. matthewi* has the narrowest transglenoid dimension (no. 19) of any species discussed here. The snout (no. 25) is relatively much shorter vertically in *C. matthewi*, *C. johnsoni*, and *C. fricki* than in *C. occidentale* or the other species. The nasal notch is relatively less developed in *C. matthewi*, *C. johnsoni*, *C. merriami*, *C. fricki*, and *C. skinneri* as compared with *C. occidentale*. The DPOF (no. 33) is sharply shorter in *C. matthewi*, and *C. johnsoni* and ranges shorter in *C. fricki* and *C. merriami*. The separation of the IOF relative to the rear of the DPOF (no. 34) is much less in *C. matthewi* as compared with *C. occidentale* or the other species, except *C. johnsoni*, and the DPOF is much shorter vertically (no. 35) in *C. matthewi* than in *C. occidentale*. The rear of the DPOF is nearer the alveolar border (no. 38) in *C. matthewi* than in *C. occidentale* and is exceeded in this only by *C. johnsoni*. *C. matthewi* has a much shallower DPOF (no. 40) than any other species of the *C. occidentale* group.

*Cormohipparion johnsoni* differs from *C. occidentale* and the other species in having a much shorter muzzle (no. 1) that is also narrower at the I3 (no. 15). It differs from the XMas-Kat sample of *C. occidentale*, but not from the Machaerodus and Hans Johnson samples, in having a shorter (no. 2) and narrower (no. 13) palate, and in having shorter premolars (nos. 7, 9). *C. johnsoni* differs from all samples of *C. occidentale* in the diminished breadth of the frontals (no. 18) and transglenoid region (no. 19) and from all other species in these parameters, as well (except for no. 19 in *C. matthewi*). *C. johnsoni* also has smaller orbit (nos. 28–29), as perhaps befits its plesiomorphic status within the group (see below). The POB is shorter in *C. johnsoni* and *C. merriami* than in the other species. The DPOF (no. 33) is sharply shorter in *C. johnsoni* (and *C. matthewi*) and ranges to a comparably small size in *C. merriami* and *C. fricki*. The separation of the IOF relative to the rear of the DPOF (no. 34) is much less in *C. johnsoni* as compared with *C. occidentale* or the other species, except *C. matthewi*, and the lacrimal nearly reaches the rear of the DPOF (no. 39, table 11), in contrast to any other species.

*Cormohipparion merriami* is greater than (or likely would range much higher than) all other species in length of palate (no. 2) and has a relatively greater premolar (no. 7) and, thus, cheek tooth (no. 9) length than in all species other than *C. skinneri*. *C. merriami* tends to have a smaller orbit than in *C. occidentale* (nos. 28–29) and all other species, except *C. johnsoni*, in which the orbit is still smaller. The nasal notch in *C. merriami* is less strongly incised than in *C. occidentale* (no. 30) but more so than in all other species. The facial length (no. 31) apparently is (or likely would range) larger than in *C. occidentale* and all other species except *C. skinneri*. The POB (no. 32, table 11) tends to be shorter in *C. merriami* than in *C. occidentale* and all species except the comparably sized *C. johnsoni*.

*Cormohipparion fricki* has a much shorter muzzle (no. 1) than *C. occidentale* and, apparently, *C. merriami* but not *C. matthewi* or *C. skinneri*; the muzzle is longer than in *C. johnsoni*. *Cormohipparion fricki* has a much longer palatal region than in the Machaerodus and Hans Johnson samples of *C. occidentale*, *C. matthewi*, and *C. johnsoni* and a shorter overall cranial length (no. 6) than *C. merriami*, *C. skinneri*, *C. matthewi*, and the XMas-Kat (but not Machaerodus or Hans Johnson) samples of *C. occidentale*. The choanae and palate are somewhat wider (nos. 12–13) in *C. fricki* than in *C. occidentale*. *Cormohipparion fricki* apparently is much wider across the frontals (no. 18) than any other species and is wider across the glenoid fossae (no. 19) than *C. occidentale*, *C. matthewi*, *C. johnsoni*, and *C. merriami* but not *C. skinneri*. The snout (no. 25) is relatively much shorter vertically in *C. fricki* and *C. matthewi* than in *C. occidentale* or the other species. The nasal notch is less incised than in *C. occidentale* (no. 30), in common with all other species, to varying degrees. The DPOF (no. 33) ranges much smaller in *C. fricki* than in all but *C. johnsoni* and *C. matthewi*, and the rear of the DPOF is much farther from the tip of the lacrimal (no. 39, table 14) in *C. fricki* than in all other species.

*Cormohipparion skinneri* has a longer palate (no. 2) than *C. occidentale*, *C. matthewi*, and *C. johnsoni*; a relatively shorter postpalatal dimension (nos. 3, 5) than the XMas-Kat *C. occidentale* sample, *C. matthewi*, *C. johnsoni*, and *C. merriami*; and an apparently somewhat shorter basicranium (no. 4) than most *C. occidentale*, *C. matthewi*, and *C. fricki*. Cheek tooth lengths (nos. 7–9) in *C. skinneri* are, or likely are, longer than in all other species. The choanae (no. 12) in *C. skinneri* are wider than in *C. occidentale* and *C. matthewi* (unknown in *C. johnsoni* and *C. merriami*). *Cormohipparion skinneri* differs from all species in having a much wider muzzle (no. 15) and in being much wider across the glenoid fossae (no. 19). The orbit is, or likely trends, taller in *C. skinneri* than in any other species. The facial length (no. 31) is greater in *C. skinneri* and *C. merriami* than in all other species. *C. skinneri* has a strong separation of the rear of the DPOF and the alveolar border (no. 38, table 17).

## Phyletic Analysis

Figure 27 shows the result of a parsimony analysis based on the matrix in table 2, analyzed via PAUP 4.0b10 (Swofford, 2001), as explained above. The cladogram is a consensus of two trees with a length of 106, a consistency index of 0.792, a retention index of 0.815, and a homoplasy index of 0.208. The results indicate that *Cormohipparion* is a coherent clade, with *C. goorisi* being the most plesiomorphic, the *C. occidentale* group the most derived, and *C. quinni* in an intermediate position. This corroborates the analysis provided by MacFadden (1984) but is at variance with that proposed by Hulbert (1988) and Hulbert and MacFadden (1991)

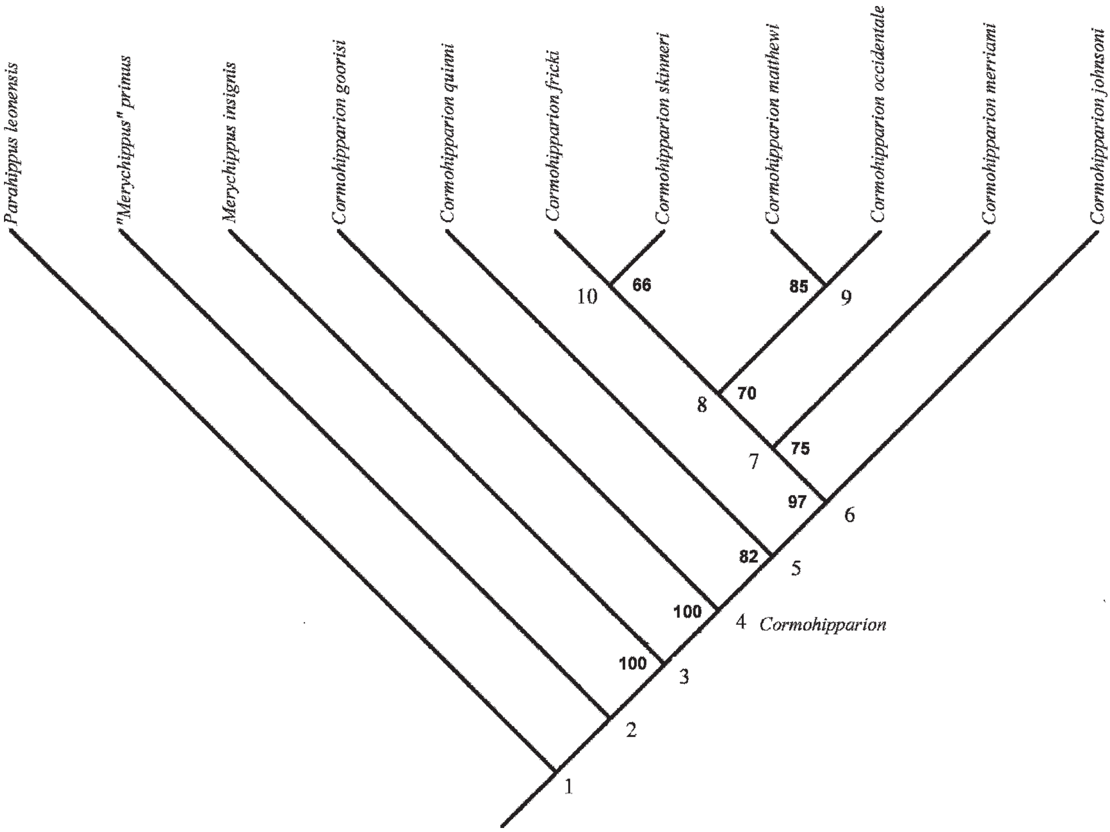


Fig. 27. Cladogram of species of *Cormohipparion*, with outgroups of *Parahippus leonensis*, *"Merychippus" primus*, *M. insignis.* Tree length is 93; Consistency Index is 0.849; Retention Index is 0.770; Homoplasy Index is 0.208. Bootstrap values are in boldface. Based on a character distribution analysis via MacClade 4.08.

Node 1 is the outgroup, *Parahippus leonensis*.

Node 2 shows that *"M." primus* can be distinguished by the lacrimo-jugal and maxillo-lacrimal sutures forming a right angle (15:0).

At Node 3, the mesodont taxa *M. insignis* + *Cormohipparion* are distinguished by having an anteriorly oriented nasomaxillary fossa (5:1); maxillo-lacrimal and naso-lacrimal sutures form an acute angle (**14:2**); P2 protocone connecting to the protoloph in late wear (50–60%; 20:4); premolar anterior postfossette plis are 2–3 (25:1); molar anterior postfossette plis are 2–3 (26:1); molar pli caballin is usually single (30:1); protocone is isolated from, rather than connected to, the protoloph (34:1); and the orbit is positioned above M3 (38:1).

*Merychippus insignis* is distinguished by having the IOF above P4 (10:2); the length ratio of dP1–P2 is about 50% (17:1); the hypoconal groove in the cheek teeth has 1–2 plis (33:1).

At Node 4 (*Cormohipparion*), the lacrimal fossa is absent (1:1); the anterior end of the lacrimal fossa thus is absent (4:2); the IOF is aligned with the lower one-third of the orbit (12:1); the lacrimal is pointed anteriorly (13:1); the upper premolars have 4–5 plis in the posterior border of the prefossette (23:2); the upper molars have 4–5 plis in the posterior border of the prefossette (24:2); the lower premolar ectoflexid retracts from the metaconid/metastylid in early wear (31:1); and the IOF is located below the anterior end of the nasomaxillary fossa (37:1)

*C. goorisi* is distinguished by having the P2 protocone connect to the protoloph within 40–50% wear (20:3); the lower premolar isthmus is not developed in early wear (32:1).

At Node 5, there are 4–5 plis in the premolar anterior border of the postfossette (25:2); the premolar pli caballin is usually double **(29:2)**; and the protocone lacks a spur (**35:1**).

wherein *C. goorisi* is considered a species of *"Merychippus."* This was discussed by Woodburne (1996b), with *C. goorisi* retained as a species of *Cormohipparion*, a hypothesis followed here. The present study also indicates that *C. quinni* persisted into deposits of early medial Clarendonian age, contemporaneous with *C. fricki* of the *C. occidentale* group (fig. 2). Still, the geochronologic succession of *C. goorisi*, *C. quinni*, and the *C. occidentale* group is compatible with the phyletic analysis of figure 27.

Figure 27 also indicates that *C. johnsoni* is the most plesiomorphic species of the *C. occidentale* group and that *C. johnsoni* and the coeval *C. merriami* are more plesiomorphic than are the other four species of this group, compatible with their geochronologic positions (fig. 2). *Cormohipparion fricki* and *C. skinneri* form a species pair that collectively is a sister taxon to the species pair represented by *C. matthewi* and *C. occidentale*. Figure 2 shows that *C. skinneri*, *C. matthewi*, and *C. occidentale* are virtually contemporaneous at this level of resolution, whereas *C. fricki* is geologically older than all of the other three.

Features that unite the *C. occidentale* group include those of node 6 of figure 27. The morphology characterized here (and for *C. johnsoni*) is one of still relatively small cranial size, but lengthening of the face has produced sufficient separation of the orbit and rear of the DPOF that the lacrimal now is fully exposed on the face, even though its is separated from the DPOF by a very short distance (12:2, node 6, fig. 27). As part of a general reduction in importance of dP1, its length ratio with P2 is about 30% (17:3, node 6, fig. 27) versus nearly 40% in *C. quinni* (Woodburne, 1996b: 27). (In *C. johnsoni*, this ratio is 0.30; in *C. merriami*, 0.36; in *C. fricki*, 0.38–0.41; in *C. occidentale*, 0.10 [XMas-Kat Quarry] and 0.26–0.32 [Hans Johnson Quarry]. In *C. matthewi*, dP1 is unknown or

←

*C. quinni* is distinguished by the maxillo-lacrimal and lacrimo-jugal sutures forming a right angle (15:0); the isthmus being developed in the lower premolars (32:2); and the hypoconal groove having 1–2 plis (33:1).

At Node 6, the base of the *C. occidentale* group, the rear of the DPOF is separated from the anterior tip of the lacrimal by 5 mm or more (12:2); the length ratio of dP1–P2 is about 30% (17:3); the protocone of P2 connects to the protoloph only in late wear (> 70%; 20:5); and in the molars the posterior margin of the postfossette has **6–7 plis (24:3)**.

*C. johnsoni* is distinguished by having the IOF aligned about with the orbital bisector (11:2); the lower margin of the lacrimal is smooth and forms no angle, so that the lacrimal is pointed anteriorly (**14:3**); and the orbit is situated posterior to M3 (38:2).

At Node 7, the MSTHT for the unworn upper molars is 50–57 mm (18:5); the premolars have 6–7 plis in the posterior border of the prefossette (23:3).

*C. merriami* is distinguished by having a lacrimal that is pointed anteriorly, having a linear ventral border (13:2); the molar pli caballin is usually triple (29:3).

At Node 8, dP1 is mostly absent (present in only early ontogenetic stages; 17:4).

At Node 9, the maxillo-lacrimal and naso-lacrimal sutures form an obtuse angle (14:0); the posterior border of the premolar prefossette has 8–9 plis (23:4); and the anterior border of the premolar postfossette has 4–5 plis (25:3).

*C. matthewi* is distinguished by having a lower premolar ectoflexid that penetrates the space between the metaconid and metastylid (31:0).

*C. occidentale* is distinguished in having 4–5 plis on the anterior border of the molar prefossette (22:2); the molar posterior border of the prefossette has 8–9 plis (24:4); the premolar posterior border of the postfossette has 2–3 plis (27:1); the molar posterior border of the postfossette has 2–3 plis (28:1); the molars usually have two plis caballin (30:2); and the orbit is posterior to M3 (38:2).

At Node 10, the IOF is located above P2 (36:1).

*C. fricki* is distinguished by having a palpable anterior rim of the DPOF (8:1); molars have 2–3 plis on the anterior border of the prefossette (22:1); the protocone retains a spur (**35:0**); and the orbit is posterior to M3 (38:2).

*C. skinneri* is distinguished by having the lower premolar ectoflexid make an X pattern with the metaconid/metastylid (31:2).

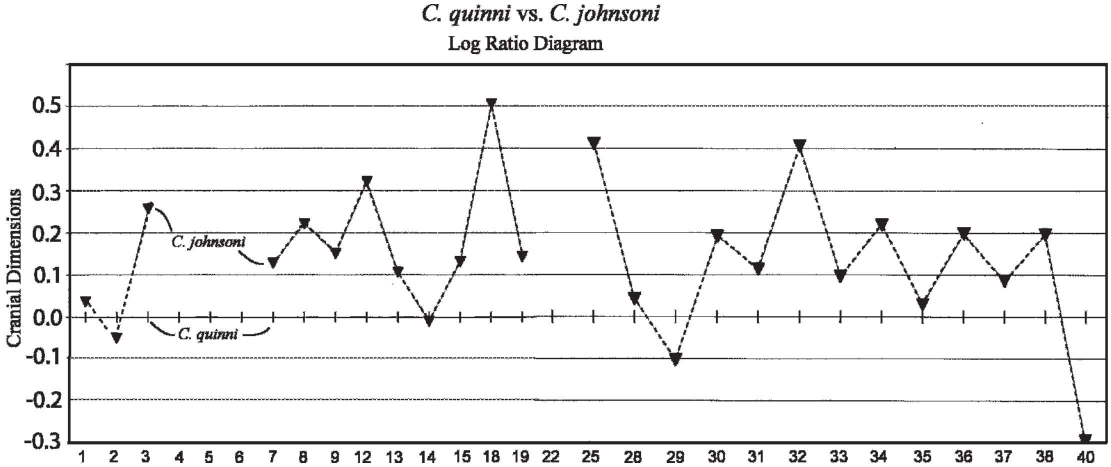


Fig. 28. Log-ratio diagram of cranial dimension of *C. johnsoni* in comparison with *C. quinni*. Data for *C. quinni* from Woodburne (1996b).

absent, and in *C. occidentale*, dP1 is present virtually only in females.) The protocone on P2 is now isolated from the protoloph until late wear (greater than 70%, 20:5), and an emphasis on enamel pattern complexity is seen in the increase to 4–5 plis on the posterior margin of the molar postfossettes (24:3).

As the most plesiomorphic species of the *C. occidentale* group (figs. 16–18, 27), *C. johnsoni* has relatively low-crowned upper cheek teeth (MSTHT for P3–M3 is in the range of 40–50 mm, with that for P4/M1 being about 45–50 mm; table 3B). Still, the relative hypsodonty of the dentition is reflected in the fact that the IOF is about aligned with the orbital bisector (11:2, node 6, fig. 27). The protocone tends to be wider and less elongate in this species and in *C. merriami* compared with all others, except *C. quinni* (table 3C). Although a measure of the overall cranial size (nos. 4, 6) is not available, the small size of the muzzle region (nos. 1, 30, table 11) likely includes an influence of the general cranial size of this species.

In comparison with *C. quinni*, the unworn MSTHT for P3–M3 is similar (table 3B), but perhaps slightly taller. However, *C. johnsoni* (fig. 28) overall is somewhat larger (parameters no. 7–9 [cheek teeth]; 13, 15, and 19 [palate, snout, and glenoid width]; 30 and 31 [nasal notch and facial length]; 33 and 35 [DPOF length and height], 36 and 37 [DPOF height from facial crest and IOF from alveolus], and 38 [DPOF–alveolus]). *C. quinni* is noticeably larger in parameter nos. 3 (postpalatal length) and 12 (choanal width) and is even larger in 18 (frontal width), 25 (snout height), and 32 (DPOF length). Concomitantly, however, *C. johnsoni* has a very much shallower DPOF (no. 40) than in *C. quinni*. Parameter no. 39 is not shown on figure 28 because the anterior tip of the lacrimal is eroded by the rear of the DPOF in *C. quinni* (Woodburne, 1996b).

*Cormohipparion merriami* is more derived than *C. johnsoni* in being higher crowned (MSTHT is about 55 mm, estimated at 52–55 mm for P4/M1; table 3B; 18:5, node 7, fig. 27); in the greater complexity of the posterior border of the premolar prefossette (23:3, node 7, fig. 27); and in the lacrimal being more widely separated from the rear of the DPOF (fig. 15; table 3A), but it is still plesiomorphic compared with other elements of the *C. occidentale* group in retaining relatively ovate protocones (table 3C) and a relatively small orbit (nos. 28–29, fig. 16), and a relatively short POB (no. 32). In addition, derived features of *C. merriami* are indicated in the diagnosis.

The remaining species of the *C. occidentale* group differ from the previous two in that the dP1 usually is lost in the adult dental state (17:4, node 8, fig. 27). As summarized in table 3C, the protocone shape apparently now is more elongate than previously in that all of the species above node 8 show this morphology, in contrast to the more ovate condition in antecedent species. Except for an apparent reversal in MSTHT of *C. matthewi* (table 3B), species above node 8 also are higher crowned than the antecedent two, and all also have a longer POB (no. 32, figs. 14, 16, 19, 21, 23).

In the line leading to *C. occidentale* and *C. matthewi*, there is an apparent reversal to an obtuse angle formed by the maxillo-lacrimal and lacrimo-jugal sutures (14:0, node 9, fig. 27). This is associated with an increase in fossette pattern complexity, with the premolar posterior prefossette plis in premolars increasing to 8–9 (23:4, node, 9, fig. 27) and anterior postfossette plis increasing to 4–5 (25:3, node 9, fig. 27). On average, the premolar protocones of these two species appear to be somewhat less elongate than in *C. fricki* and *C. skinneri* (table 3C).

The overall cranial length for *C. matthewi* (no. 6, fig. 15) is less than that for at least the XMas-Kat Quarry sample of *C. occidentale*, and in most dimensions in which it differs from all samples of *C. occidentale*, *C. matthewi* is smaller. A strongly diminished snout (nos. 14, 25, 30) is among the most trenchant differences for *C. matthewi* in contrast to *C. occidentale* (comparable to *C. johnsoni*); another is a general diminution of DPOF parameters (nos. 33–35, 38, 40). However, *C. matthewi* is comparable to *C. occidentale* in basicranial length (nos. 4–5); cheek tooth lengths (nos. 7–9; one S.D. ranges overlap); choanal (no. 12), snout (no. 13), muzzle (no. 15), and frontal (no. 18) width; orbit size (nos. 28–29); facial length (no. 31); facial crest (no. 36) and IOF (no. 37) positions; and lacrimal development (no. 39).

Concomitantly, *C. occidentale* differs from *C. matthewi* in many cranial parameters being larger, in addition to a much taller unworn MSTHT (table 3B) but, in addition to basicranial length (no. 4), the parameters in which the two species are comparable indicate that their differences are not based on allometry.

In the line leading to *C. fricki* and *C. skinneri*, the IOF has moved forward to lie above P2 (36:1, node 10, fig. 27). These species also have a somewhat smaller basicranial dimension (no. 4, figs. 22, 24), and the premolar protocones appear to be somewhat more elongate on average (table 3C).

The cheek tooth crown height in *C. fricki* apparently is lower than in *C. skinneri* (table 3B) and the cheek teeth are apparently somewhat shorter (nos. 7–9, figs. 22, 24); the snout is less elevated (no. 25, figs. 22, 24); the orbit apparently is not as tall (no. 29); the facial region is apparently somewhat shorter (no. 31); the rear of the DPOF is slightly less well defined (8:1, node 10, fig. 27); and the POB and DPOF parameters (nos. 32–36, 38) are somewhat smaller, but the molar anterior prefossette plis increase to 2–3 (22:1, node 10), M3 is located anterior to the orbit (38:2, node 10), the frontals are wider (no. 18, figs. 22, 24); the IOF is farther from the alveolar border (no. 37); the DPOF is much more distant from the lacrimal (no. 39, table 5); and the DPOF is deeper (no. 40).

The skull is somewhat longer in *C. skinneri* (no. 6, figs. 22, 24), which might be related to those parameters in which *C. fricki* is smaller (see above), but not those in which *C. fricki* is larger. The MSTHT in *C. skinneri* apparently is greater than in *C. fricki* (table 3B), and cheek tooth protocones apparently are even more elongate (table 3C). In addition, *C. skinneri* is unique in the penetration of the ectoflexid of the lower cheek teeth (31:2; fig. 27).

*Cormohipparion occidentale*, *s.s.*, is the best represented species of the *C. occidentale* group in the samples available here. It epitomizes the morphology to which many past references have been made (e.g., Webb, 1969; Skinner and MacFadden, 1977; MacFadden, 1984), even though some of these specimens are herein assigned to different species (*C. fricki*). The unworn cheek tooth crown height of *C. occidentale* surpasses that of any other species, perhaps with the exception of the much less well represented *C. skinneri* from Texas. In addition, the overall cranial and mandibular morphology of *C. occidentale* is a useful proxy for the general *C. occidentale* group for the purposes of general comparisons with other ungulates. At the same time, it is too specialized to be considered as a participant of the *Hippotherium* Datum.

## Speciation within *Cormohipparion occidentale*

Figure 13 indicates that the quarry samples of *C. occidentale* from the Machaerodus and Hans Johnson quarries differ from that of the XMas-Kat quarries in having a shorter facial region of the cranium (nos. 2, 6), which apparently influences somewhat smaller dimensions in cheek tooth row lengths (nos. 7–9), and that these samples also show a taller DPOF (no. 35) apparently associated with a diminished separation between the DPOF and facial crest (no. 36). Furthermore, the sample from the Hans Johnson Quarry appears to have a diminished separation of the DPOF from the alveolar border (no. 38).

According to the data and inferences presented in Skinner and Johnson (1984: 314–215, 320, 345), the XMas-Kat and Machaerodus quarries are contemporaneous. Both occur below the Machaerodus Ash and below a unit of cross-bedded channel sands (fig. 7); both occur in sediments that contain distinctive crystals of garnet similar to those in the Thin Elk Formation, South Dakota, apparently derived from a source in the Black Hills of South Dakota. Although the Hans Johnson Quarry contains neither the Machaerodus Ash nor the garnet crystals, it is considered stratigraphically equivalent to the XMas-Kat quarries (Skinner and Johnson, 1984: 307).

The XMas-Kat Quarry sample of *C. matthewi* (fig. 14) shows a similar disposition of characters no. 2, 6–9, and 36, as seen in the Machaerodus and Hans Johnson samples of *C. occidentale*, so it may be that these specimens were derived from a portion of the overall species population of *C. occidentale* in which these features were preserved as relict from the split at node 9 of the cladogram (fig. 27). It also may be possible to account for the condition of Hans Johnson parameter 38 in this way. Inasmuch as parameter 4 (basicranial length) is comparable among the three quarry samples of *C. occidentale*, it appears that the specimens were of the same basic cranial size, and that size is not a factor in accounting for the diminished values of other parameters. Those parameters vary independently of no. 4 dimensions in the other species of the *Cormohipparion* group (figs. 18, 20, 22, 24), which seems to obviate an allometric size-dependent relationship here. None of the other *Cormohipparion* group samples available here show the distribution of parameter no. 35 seen in the Machaerodus and Hans Johnson quarries, so the increased height of the DPOF that this entails seems to be a unique derivation of yet unknown phyletic significance.

Alternatively, it may be possible that the Machaerodus and Hans Johnson samples are not exactly contemporaneous with that of the XMas-Kat Quarry, with a parsimonious interpretation being that the Hans Johnson sample is relatively the oldest, and that from the Machaerodus Quarry being intermediate in age between the Hans Johnson and XMas-Kat quarries. Another parsimonious interpretation could be that the samples from the three quarries are part of a biologically contemporaneous polymorphic population. Unfortunately, the samples of *C. matthewi* from these same three quarries are insufficient to enable a comparative appraisal of its morphologic distribution, and the samples of the other species of the *C. occidentale* group are likewise limited.

Figure 29 indicates that relative to *C. quinni*, the *C. occidentale* group contains at least six speciation events that were developed during an interval of about 1.5 m.y. (figs. 2, 29). Depending on the actual ages of the *C. skinneri*–*C. fricki* and *C. occidentale*–*C. matthewi* splits, four of those events could have originated in a relatively narrow time interval at about 12 Ma. Based on the known record, *C. johnsoni* and *C. merriami* were contemporaneous and sympatric at about 12.5–12 Ma; *C. skinneri*, *C. occidentale*, and *C. matthewi* were contemporaneous, if not all sympatric, from about 11.5–11 Ma; and *C. occidentale* and *C. matthewi* persisted sympatrically to about 10 Ma. Based on the phyletic analyses, it appears unlikely that the sympatric species pairs should be reconsidered as potential parts of the same species population, not only in the context of their respective diagnoses and characterizations, but also in light of the subpopulation variation shown by the Machaerodus and Hans Johnson samples of *C. occidentale*.

As summarized in Woodburne (2004b), Clarendonian faunas existed during the early part of a cooling trend subsequent to the

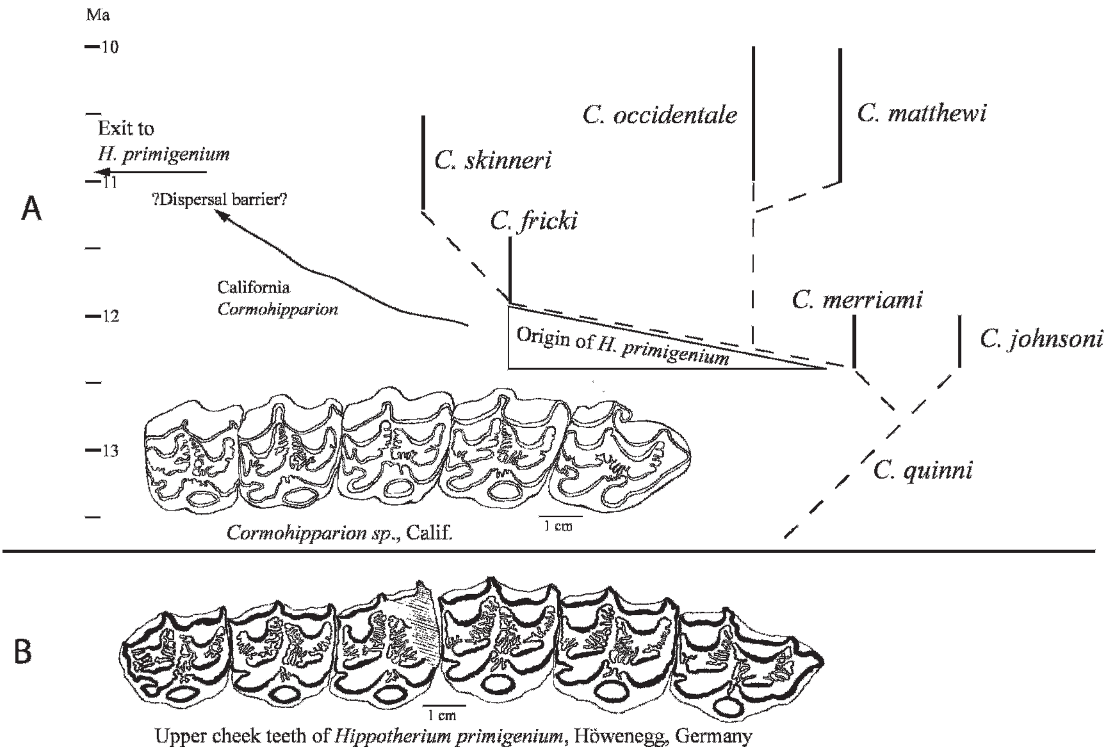


Fig. 29. **A,** chronogram of species of *Cormohipparion* showing window for time of origin of *H. primigenium*-like morphology between the biochrons of *C. merriami* and *C. fricki*, the exit of *H. primigenium*-like morphology at ca. 11.3 Ma, and the age of *Cormohipparion* sp. from California (illustrated below), thought to be close to the species population that dispersed to the Old World. The ?Dispersal barrier? refers to the high sea-level that lowered at about 11.3 MA (Ta3 of Haq et al., 1988; modified by Hardenbol et al., 1998). **B,** upper cheek tooth dentition of *Hippotherium primigenium* from Höwenegg, Germany, HLMD 1081. After Sondaar (1961), fig. 21A.

Mid-Miocene climatic optimum and after the time of initial differentiation of the mesodont ancestors of a variety of hypsodont horse lineages (MacFadden and Hulbert, 1988; Hulbert and MacFadden, 1991). The Clarendonian was a time when grasslands were becoming widely spread in the Great Plains region as seasonal precipitation decreased (dry in winter) (Graham, 1999: 250–266) and, especially in the Great Plains, the diversity of hypsodont, three-toed horses was at its peak (MacFadden, 1998). The *C. occidentale* group apparently participated in this expansion, as well, with *C. occidentale* and *C. skinneri* arguably the most highly evolved of that radiation. The taxa recognized in this study apparently raise the hipparion species richness by two for the 12 Ma interval of Hulbert (1993: table 4A; *C. quinni* persists; *C. johnsoni* and *C. merriami* are new, with one of the last two not being counted because it is already represented in Hulbert's analysis by *C. occidentale*). In the same fashion, Hulbert's (1993: table 4A) count of hipparion species richness for the 10 Ma and 9 Ma intervals would rise by three (*C. skinneri*, *C. matthewi*, and *C. quinni* persisting; *C. occidentale* already counted). Taken broadly, the peak in hipparion species diversity apparently characterized much, if not all, of the Clarendonian rather than there having been a peak in the late Barstovian (ca. 14 Ma of Hulbert, 1993) and mid Hemphillian (ca. 7 Ma). If the analysis of Hayek et al. (1992) in dental microwear is corroborated by mesowear analysis (e.g., Kaiser and Solounias, 2003: 341), it would appear that *C. occidentale*, at least, was adapted to a grazing-to-mixed-feeding strategy during a time when climatic cooling (Zachos et al. 2001) was producing a more open regional habitat in much of the North American Great Plains region (e.g., Graham, 1999).

## ORIGIN OF THE *HIPPOTHERIUM* DATUM

Woodburne (1996a) discussed the anatomy of the *Hippotherium* Datum, an event that witnessed the dispersal from North America to Eurasia of a hipparionine horse that gave rise there to a major radiation of hypsodont, as compared to brachyodont, three-toed horses. The following section incorporates new data on relevant Old World samples as to the morphology characteristic of the first immigrants from the New World.

The sequence at Valles-Penedes, Spain, contains the stratotype of the Vallesian mammal age in the Old World (Crusafont-Pairo, 1951; Garcés et al., 2003), considered to be about 10.7–10.8 Ma old based on the age of the local FAD of *Hippotherium* at Nombrevilla. Sondaar (1961) studied the *Hippotherium* from Nombrevilla, nominated by him as *H. koenigswaldi*. In comparison with the type species of *Hippotherium*, *H. primigenium* Meyer 1829 from Eppelsheim, Germany, the dentition of *H. koenigswaldi* differed in being of somewhat larger size, in having fewer ectostylids in the adult lower cheek teeth (20% vs. 23%), and in the protostylids being more strongly developed and connecting to the protoconid at an earlier stage of wear than in *H. primigenium*. *H. koenigswaldi* also had a slightly less complex enamel plication pattern in the upper molars and a more ovate protocone. Measurements by the present author on isolated cheek teeth of *Hipparion* (here considered to be *Hippotherium*) *koenigswaldi*, from Nombrevilla, indicate MSTHT ranges from 56–62 mm (table 21) and absolutely unworn teeth would be somewhat taller, likely 58–64 mm in P4 and M1. This indicates that *H. koenigswaldi* is somewhat higher crowned than *H. primigenium*, where P4 and M1 unworn MSTHT are about 55–58 mm tall in the samples from Eppelsheim (range is 49–58 mm; table 21), and perhaps only about 52 mm tall in the sample from Höwenegg). The circa 10.7–10.8 Ma age for the Nombrevilla site is consistent with Woodburne's (1996a) interpretation that *H. koenigswaldi* is derived relative to *H. primigenium* and that the latter is somewhat older (ca. 11.3 Ma, based on stratigraphic relationships in the Pannonian Basin, Vienna). As discussed below, the material of Pannonian C age in the Vienna Basin (Gaiselberg, Atzelsdorf) and possibly of Pannonian C age (Mariathal) is designated as *Hippotherium* sp. in recognition of its somewhat conservative morphology (lower crowned, generally simpler fossette plication pattern, confluence of pre- and postfossettes in P2) in contrast to *H. primigenium* from Eppelsheim and Höwenegg. Whereas an age of about 10.3 Ma is reasonable for the Höwenegg material (Swisher, 1996), that of Eppelsheim is unknown except that it most likely is younger than Pannonian C (ca. 11.3 Ma), likely no younger than the material from Höwenegg, and possibly coeval with *H. koenigswaldi*.

To address the question of the ancestry of *H. primigenium*, relevant collections were examined in the Naturhistorisches Museum, Vienna; the Senckenberg Museum, Frankfurt; the Hessisches Landesmuseum, Darmstadt; and the Staatliches Museum für Naturkunde, Karlsruhe. The Viennese material includes specimen from the Pannonian C site of Gaiselberg, Austria (Daxner-Höck, 1996) considered to be the chronologically oldest material in the Old World (Woodburne, 1996a). In addition, samples from Atzelsdorf and from Mariathal, Austria, were examined because Atzelsdorf is considered also to be of Pannonian C age (Daxner-Höck, personal commun., 2005), and Mariathal produced a very well-represented population from a single site. Unfortunately, the exact age of the sample is not known, other than Pannonian C or Pannonian E (Daxner-Höck, personal commun., 2005), also according to whom there are no *Hippotherium* samples of Pannonian D age in the Vienna Basin. All of the Pannonian material discussed here is correlated to MN 9 in the European mammalian time scale, about 11.1–9.3 Ma (e.g., Woodburne, 1996a). In tables 22 and 23, teeth in boldface are considered to represent the adult range from which statistical analyses are obtained.

As indicated above, the materials treated here from Gaiselberg, Atzelsdorf, and Mariathal, Austria, are designated as *Hippotherium* sp. (tables 21–22). Whereas these samples are considered part of the phyletic group of which *H. primigenium* is the major element (and some of which have been so named [Bernor et al., 1988]), they are considered here to be somewhat conservative in their upper cheek tooth morphology relative to specimens from the Dinotherium Sands at Eppelsheim, Germany. Isolated crania from Inzersdorf and Laarberg, Austria, also are assigned here to *Hippotherium* sp. (tables 22, 24; see also Bernor et al., 1988), based on their apparently relatively low MSTHT and generally conservative dental pattern. Whether these samples ultimately are considered within or separate from *H. primigenium* awaits a fuller consideration of that question than can be provided here.

The Eppelsheim material represents the sample to which the nomen *Hippotherium primigenium* originally was assigned (Meyer, 1929). The associated skulls, dentitions, and postcranial skeletons from Höwenegg, Germany, also are considered conspecific with *H. primigenium* (Sondaar, 1961; Bernor et al., 1997).

The Gaiselberg sample of *Hippotherium* sp. is relatively limited, especially in the adult wear range (**boldface**; table 22). It displays unworn upper cheek MSTHTs on the order of 50 mm, and P4 at least may have been as tall as 55 mm. The protocone is subovate to ovate in shape in most stages of wear (fig. 25E). Of the seventeen specimens in the sample, five (30%) have flat or concave lingual borders of the protocone. Of those five only one (**NMHW 00224/17**) has a narrow protocone width-to-length ratio (0.41), comparable to those found in North American species of *Cormohipparion* with elongate and lingually flat protocones (*C. occidentale*, *C. skinneri*, *C. matthewi*), as summarized in table 3C. All other protocones in the Gaiselberg sample show width-to-length ratios near or greater than 0.50, typical of taxa with ovate protocones (*C. johnsoni*, *C. merriami*). This is consistent with the present thesis that the early members of the *H. primigenium* lineage were derived from a North American taxon similar to *C. fricki*, antecedent to the origination of *C. occidentale*. In this context, there is now no basis for the proposal articulated in Bernor et al. (1988) and other publications, such as Bernor et al. (2003), that the presence of lingually flat protocones in samples of *H. primigenium* reflects affinity with *C. occidentale* as represented by specimens from the XMas-Kat sample thereof. As shown in the present report, the generally scarce presence of protocones with flat lingual borders in species of *Cormohipparion*, as well as in *H. primigenium*, is best interpreted as a reflection of intraspecific, including ontogenetic, variation.

Table 21 indicates that the mean width-to-length ratios in the Gaiselberg sample are P2, 0.56; P3, 0.68; P4, 0.45; M1, 0.57; and M2, 0.55. These ratios are generally comparable to those of other Old World samples in table 21.

The pli protoconule in the Gaiselberg sample commonly is distinct; it is also mostly smooth (fig. 25E) and thus considerably simpler than the morphology seen in *H. primigenium* from Höwenegg (fig. 29B) and *H. koenigswaldi* (Sondaar, 1961). Note that NHMW 17 of Bernor (1988: fig. 9) shows a simple bifurcation of the pli protoconule. Whereas this occasionally occurs in the Gaiselberg sample, the specimen illustrated in Bernor et al. (1988) is not the same specimen with that number in table 22 and apparently pertains to a tooth not seen during the present analysis.

The limited sample suggests (table 21) that the plication count for P2 is 4:10:6:3; for P3, 6:9:8:3; for P4, 4:12:8:1 (early wear); for M1, 4:8:6:2; and for M2, 5:11:8:2. These numbers are average figures for teeth in adult wear (between 40–20 mm tall). In general, those mean figures are slightly less complex than in *H. primigenium* from Eppelsheim and Höwenegg and somewhat more complex than in all species of *Cormohipparion* except the geologically younger *C. occidentale*, which approaches, but does not meet, the Gaiselberg sample in this regard. Of the North American samples, that of *Cormohipparion* sp. from California is most generally comparable to that of Gaiselberg (fig. 15E–F), but the small number of specimens in the Gaiselberg and California samples should be kept in mind. As shown in table 21, the pre- and postfossettes

TABLE 21

**Dental Statistics of Upper Cheek Teeth of *Hippotherium* and *Cormohipparion* Species**

| | | | P2 prot. | | | P2 pre- and postfossette confluence | | |
|---|---|---|---|---|---|---|---|---|
| Species/site | Correlated age | MSTHT | Ratio L/W | Plication index | *N* | Approx. % | *N* | Remarks |
| *H. koenigswaldi* | 10.7 Ma | 56–62 | 0.67 | 9:6:5:4 | | 10? | 18 | personal obs., rarely confluent |
| *H. primigenium* | | | | | | | | |
| Höwenegg | 10.3 Ma | 45–52 | 0.56 | 9:12:12:4 | 3 | 0 | 3 | fossettes separate |
| Eppelsheim | | 49–58 | 0.66 | 7:11:10:4 | 12 | 18 | 22 | fossettes rarely confluent |
| HLMD | | | | | | | | |
| Eppelsheim | | 45–58 | 0.67 | 7:10:10:3 | 6 | 20 | 10 | fossettes rarely confluent |
| SENCK | | | | | | | | |
| *Hippotherium* sp. | | | | | | | | |
| Inzersdorf | Pannonian D/E | 40–50 | 0.76 | 5:8:7:3 | 1 | 0 | 1 | single specimen; separate |
| Mariathal | Pannonian ?C/E | 44–56 | 0.56 | 8:9:6:3 | 5 | 90 | 10 | fossettes confluent |
| Atzelsdorf | Pannonian C | ?50 | | 5:8:5:2 | 1 | ?100 | 1 | too few specimens; ?confluent |
| Gaiselberg | Pannonian C; 11.3 Ma | 50–55 | 0.56 | 4:10:6:3 | 3 | 100 | 3 | fossettes confluent |
| *Cormohipparion* | | | | | | | | |
| *C. quinni* | RRQ; 12–13.5 Ma | 34–45 | 0.63 | 1:3:3:1 | 4 | ? | 4 | figs. in Woodburne (1996b) |
| *C. quinni* | DGHQ; 12–13.5 Ma | 40–45 | 0.61 | 1:2:2:1 | 9 | 50 | 7 | " |
| *C. johnsoni* | 12.5 Ma | 40–50 | 0.63 | | 2 | 50? | 2 | too few specimens; ?ca. 50% |
| *Cormohipparion* sp. | Punchbowl Fm; 12 Ma | ?45–50 | 0.79 | 4:6:4:2 | 1 | 100 | 1 | single specimen; confluent |
| *C. merriami* | 12.5 Ma | 45–55 | 0.67 | 5:5:4:1 | 3 | 60+? | 3 | small number of specimens |
| *C. fricki* | 12 Ma | 50–55 | 0.49 | 2:5:4:1 | 6 | 75 | 9 | confluence about 75% |
| *C. skinneri* | 10.5 Ma | ?60 | 0.50 | 4:5:2:1 | 1 | 0 | 1 | single specimen; separate |
| *C. matthewi* | 10–11 Ma | 40–45 | 0.49 | 3:8:6:2 | 4 | 50 | 4 | confluence about 50% |
| *C. occidentale* | XMas Q., 10–11 Ma | 50–66 | 0.52 | 6:8:6:3 | 7 | 50 | 7 | confluence about 50% |
| *C. occidentale* | Mach. Q., 10–11 Ma | 50–66 | 0.50 | 5:6:3:1 | 4 | 60 | 3 | too few specimens, ?ca. 50% |
| *C. occidentale* | H. John. Q., 10–11 Ma | 50–66 | 0.54 | 4:5:5:1 | 6 | 50 | 6 | confluence about 50% |

TABLE 21
(*Continued*)

| Species/Site | P3 prot. | | | P4 prot. | | | M1 prot. | | | M2 prot. | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | L/W ratio | Plication index | *N* | L/W ratio | Plication index | *N* | L/W ratio | Plication index | *N* | L/W ratio | Plication index | *N* |
| *H. koenigswaldi* | 0.60 | 10:12:9:3 | 35 | 0.55 | 6:10:8:3 | 24 | 0.54 | 4:10:9:4 | 26 | 0.50 | 5:10:9:3 | 18 |
| *H. primigenium* | | | | | | | | | | | | |
| Höwenegg | 0.44 | 8:12:9:3 | 3 | 0.50 | 9:12:11:3 | 3 | 0.51 | 8:12:10:5 | 3 | 0.41 | 6:10:7:4 | 3 |
| Eppelsheim HLMD | 0.57 | 6:10:9:3 | 10 | 0.58 | 7:12:9:4 | 14 | 0.60 | 7:12:9:3 | 7 | 0.51 | 6:10:14:3 | 2 |
| Eppelsheim SENCK | 0.65 | 8:14:11:5 | 3 | 0.87 | 5:13:4:4 | 4 | 0.72 | 8:15:8:5 | 4 | 0.60 | 5:11:8:5 | 2 |
| *Hippotherium* sp. | | | | | | | | | | | | |
| Inzersdorf | 0.45 | 6:7:7:2 | 1 | 0.49 | 6:8:5:4 | 1 | 0.57 | 8:12:9:3 | 1 | 0.48 | 6:7:7:6 | 1 |
| Mariathal | 0.54 | 7:12:10:3 | 26 | 0.51 | 6:13:9:3 | 14 | 0.50 | 6:11:9:3 | 9 | 0.47 | 4:10:6:6 | 1 |
| Atzelsdorf | | | 1 | 0.52 | 2:7:5:3 | 1 | | 4:10:6:1 | 1 | | | 1 |
| Gaiselberg | 0.68 | 6:9:8:3 | 2 | 0.45 | 4:12:8:1 | 2 | 0.57 | 4:8:6:2 | 2 | 0.55 | 5:11:8:2 | 3 |
| *Cormohipparion* | | | | | | | | | | | | |
| *C. quinni* | 0.52 | 1:5:5:1 | 4 | 0.50 | 1:5:5:1 | 4 | 0.51 | 1:5:4:1 | 4 | 0.50 | 1:4:5:1 | 4 |
| *C. quinni* | 0.43 | 3:4:5:1 | 9 | 0.49 | 1:5:5:2 | 9 | 0.50 | 1:5:4:1 | 9 | 0.47 | 2:5:4:1 | 9 |
| *C. johnsoni* | 0.54 | 1:5:4:1 | 2 | 0.54 | 1:6:5:1 | 2 | 0.51 | 1:6:6:1 | 2 | 0.50 | 0:6:6:3 | 2 |
| *Cormohipparion* sp. | 0.65 | 3:15:4:2 | 3 | 0.65 | 3:9:5:1 | 1 | 0.59 | 1?:13:8:3 | 1 | 0.58 | 3?:8:6?:2 | 1 |
| *C. merriami* | 0.50 | 2:10:5:1 | 3 | 0.47 | 2:10:6:1 | 3 | 0.51 | 1:7:7:1 | 3 | 0.53 | 2:9:5:2 | 3 |
| *C. fricki* | 0.43 | 2:9:5:2 | 6 | 0.43 | 1:7:4:2 | 6 | 0.48 | 2:7:6:2 | 6 | 0.43 | 2:7:6:1 | 6 |
| *C. skinneri* | 0.35 | 3:7:4:1 | 1 | 0.41 | 1:8:5:1 | 1 | 0.45 | 1:5:6:1 | 1 | 0.39 | 1:6:5:1 | 1 |
| *C. matthewi* | 0.33 | 6:8:6:2 | 4 | 0.45 | 2:7:4:1 | 4 | 0.53 | 2:8:6:1 | 4 | 0.47 | 3:7:5:1 | 4 |
| *C. occidentale* | 0.45 | 5:10:7:2 | 8 | 0.50 | 7:9:7:2 | 7 | 0.48 | 4:8:7:2 | 8 | 0.44 | 4:8:6:2 | 8 |
| *C. occidentale* | 0.48 | 5:7:7:1 | 4 | 0.44 | 3:8:6:3 | 4 | 0.49 | 2:7:7:2 | 5 | 0.43 | 3:8:6:2 | 5 |
| *C. occidentale* | 0.44 | 3:5:5:1 | 7 | 0.45 | 5:6:5:1 | 7 | 0.47 | 3:8:5:2 | 7 | 0.44 | 2:5:5:1 | 7 |

Remarks: RRQ = Railway Quarry, Crookston Bridge Member, Valentine Formation, Nebraska.
DGHQ = Devil's Gulch Horse Quarry, Devil's Gulch Member, Valentine Formation, Nebraska.
Time range for *Cormohipparion quinni* based on this report, not on presence in RRQ and DGHQ alone (ca. 13.5 Ma).
Punchbowl. Fm. = Punchbowl Formation, Valyermo, California.
Mach. Q. = Machaerodus Quarry.
H. John. Q. = Hans Johnson Quarry.
HLMD = Hessisches Landesmuseum, Darmstadt, Germany.
SENCK = Senckenberg Museum, Frankfurt, Germany.

TABLE 22

**Measurements (mm) of Upper Cheek Tooth Dentition of Hippotherium sp., Pannonian Basin, Austria**

Height is at mesostyle; boldface specimens used in plication count statistics; ** = early wear; con. = concave; sl. = slightly; unw. = unworn; vew. = very early wear.

**A. Gaiserberg** Pannonian C.

| Specimen | Height | Length | Width | Ratio | Index | Protocone Length | Protocone Width | Protocone Ratio | Pli caballin | Hypoconal groove | Protocone shape |
|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | | | **P2** | | | | | | |
| **NHMW 00224/18** | 33.0 | 31.5 | 21.9 | 0.70 | ?:?:?:3 | 8.3 | 4.5 | 0.54 | 3 | open; narrow | oval |
| **NHMW 00224/19** | 30.0 | 30.8 | 23.2 | 0.75 | 5:10:6:3 | 8.3 | 4.5 | 0.54 | 2 | open; narrow | flat |
| **NHMW 00124/11** | 21.0 | 29.2 | | | 3:10:?:2 | 7.9 | 4.6 | 0.58 | 2 | open; simple | oval |
| Range | | 2.92–31.5 | 21.9–23.0 | 0.70–0.75 | | 7.9–8.3 | 4.5–4.6 | 0.54– | | | |
| Mean | | 30.5 | 22.6 | 0.73 | 4:10:6:3 | 8.2 | 4.5 | 0.56 | 2 | | |
| SD | | 1.18 | 0.92 | 0.04 | | 0.23 | 0.06 | 0.02 | | | |
| CV | | 3.87 | 4.08 | 6.66 | | 2.83 | 1.27 | 4.17 | | | |
| *N* | 3 | 3 | 2 | 2 | 2 | 3 | 3 | 3 | 3 | 3 | 3 |
| | | | | | **P3** | | | | | | |
| **NHMW 00224/14** | 35.5 | 26.0 | 23.9 | 0.92 | 6:9:8:3 | 6.1 | 4.4 | 0.72 | 3 | open; simple | sl. ovate |
| **NHMW 00224/20** | 22.0 | 24.5 | 23.4 | 0.96 | 6:9:6:3 | 7.8 | 5.0 | 0.64 | 3 | open | oval |
| NHMW 00224/11 | 16.0 | 24.8 | 24.8 | 1.00 | 2:9:6:1 | 10.3 | 5.3 | 0.51 | 2 | open; simple | oval |
| NHMW 00224/23 | 16.0 | 25.0 | 24.7 | 1.00 | 1:11:7:1 | 9.5 | 5.6 | 0.59 | 1 | worn | oval |
| Range | | 24.5–26.0 | 23.4–23.9 | 0.92–0.96 | | 6.1–7.8 | 4.4–5.0 | 0.64–7.2 | | | |
| Mean | | 25.3 | 23.7 | 0.94 | 6:9:8:3 | 7.0 | 4.7 | 0.68 | 3 | | |
| SD | | 1.06 | 0.35 | 0.03 | | 1.20 | 0.42 | 0.06 | | | |
| CV | | 4.20 | 1.49 | 2.70 | | 17.3 | 9.03 | 8.33 | | | |
| *N* | 2 | 2 | 2 | 2 | 2 | 2 | 2 | 2 | 2 | 2 | 2 |
| | | | | | **P4** | | | | | | |
| **NHMW 00224/16** | 49.0 | 27.5 | 22.5 | 0.82 | 1:10:9:1 | 8.3 | 4.0 | 0.48 | 2 | open; narrow | sl. ovate |
| **NHMW 00224/17** | 44.0 | 28.0 | 24.4 | 0.87 | 6:12+:6:? | 8.8 | 3.6 | 0.41 | 3 | no data | flat |
| Range | | 27.5–28.0 | 22.5–24.4 | 0.82–0.87 | | 8.3–8.8 | 3.6–4.0 | 0.41–0.48 | | | |
| Mean | | 27.8 | 23.6 | 0.84 | 4:12:8:1** | 8.6 | 3.8 | 0.45 | 3 | | |
| SD | | 0.35 | 1.34 | 0.04 | | 0.35 | 0.28 | 0.05 | | | |
| CV | | 1.27 | 5.73 | 4.46 | | 4.14 | 7.44 | 11.60 | | | |
| *N* | 2 | 2 | 2 | 2 | 2 | 2 | 2 | 2 | 2 | 2 | 2 |

TABLE 22
(*Continued*)

| Specimen | Height | Length | Width | Ratio | Index | Protocone Length | Protocone Width | Protocone Ratio | Pli caballin | Hypoconal groove | Protocone shape |
|---|---|---|---|---|---|---|---|---|---|---|---|
| **M1** | | | | | | | | | | | |
| NHMW 00224/15 | 45.0 | 22.8+ | 22.8 | | 3:7:4:3 | 8.3 | 4.6 | 0.55 | 2 | narrow; simple | sl. ovate |
| **NHMW 00224/22** | 32.0 | 25.7 | 24.6 | 0.96 | 4:10:8:3 | 8.7 | 5.2 | 0.60 | 3 | open; narrow | concave |
| **NHMW 00224/13** | 25.0 | 25.5 | 23.5 | 0.92 | 3:7:4:1 | 8.9 | 4.8 | 0.54 | 2 | open | sl. concave |
| NHMW 00224/25 | 19.0 | 22.4 | 24.7 | 1.10 | 2:10:8:2 | 10.0 | 6.0 | 0.60 | 1 | open; narrow | oval |
| Range | | 25.5–25.7 | 23.5–24.6 | 0.92–0.96 | | 8.7–8.9 | 4.8–5.2 | 0.54–0.60 | | | |
| Mean | | 25.6 | 24.1 | 0.94 | 4:8:6:2 | 8.8 | 5.0 | 0.57 | 2 | | |
| SD | | 0.14 | 0.78 | 0.03 | | 0.14 | 0.28 | 0.04 | | | |
| CV | | 0.55 | 3.23 | 2.68 | | 1.61 | 5.66 | 7.26 | | | |
| *N* | 2 | 2 | 2 | 2 | 2 | 2 | 2 | 2 | 2 | 2 | 2 |
| **M2** | | | | | | | | | | | |
| **NHMW 00224/26** | 32.0 | 22.6 | 23.3 | 1.03 | 4:12:9:4 | 9.1 | 5.7 | 0.63 | 3 | open; pinched | oval |
| **NHMW 00224/24** | 27.0 | 25.8 | 26.8 | 1.04 | 6:12:10:1 | 8.7 | 4.2 | 0.48 | 2 | narrow | oval |
| **NHMW 00224/21** | 25.0 | 26.0 | 24.5 | 0.94 | 6:10:5:2 | 10.2 | 5.6 | 0.55 | 2 | narrow | sl. concave |
| Range | | 22.6–26.0 | 23.3–26.8 | 0.94–10.4 | | 8.7–1.02 | 4.2–5.6 | 0.48–0.63 | | | |
| Mean | | 24.8 | 24.9 | 1.00 | 5:11:8:2 | 9.3 | 5.2 | 0.55 | 2 | | |
| SD | | 1.91 | 1.78 | 0.56 | | 0.78 | 0.84 | 0.07 | | | |
| CV | | 7.69 | 7.15 | 5.34 | | 8.32 | 16.23 | 13.00 | | | |
| *N* | 3 | 3 | 3 | 3 | 3 | 3 | 3 | 3 | 3 | 3 | 3 |
| **M3** | | | | | | | | | | | |
| NHMW 00224/10 | 16.0 | 15.9 | 22.2 | 1.40 | 2:6:6:1 | 9.4 | 4.7 | 0.50 | 2 | open; narrow | sl. ovate |

**B. Mariathal**, Pannonian ?C/E

**P2**, unworn MSTHT likely 44 mm

| Specimen | Height | Length | Width | Ratio | Index | Lingual complexity | Protocone Length | Protocone Width | Protocone Ratio | Pli caballin | Hypoconal groove | Protocone shape |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| PIUW 3540/14 | 44.0a | | | | | | | | | | | |
| PIUW 3540/1 | 43.0 | 33.6 | 21.2 | 0.63 | 7:?:?:? | 0;0;0;0 | 7.9 | 4.7 | 0.59 | ? | v. early wear | oval |
| PIUW 3540/5 | 40.0 | 33.3 | 24.0 | 0.72 | 8:12:6:7 | 0;0;0;0 | 9.2 | 4.3 | 0.47 | 3 | narrow; early | oval |
| PIUW 3540/6 | 40.0 | 33.0 | 21.8 | 0.66 | 6:6?:5?:1 | 0;0;0;0 | 8.2 | 5.3 | 0.65 | ? | incomplete | flat |
| PIUW 3540/2 | 36.7 | 31.4 | 22.8 | 0.73 | 3:3:3:2 | 0;0;0;0 | 6.8 | 4.0 | 0.59 | 2 | open; spur | oval |

TABLE 22
(*Continued*)

**B. Mariathal**, Pannonian ?C/E

**P2**, unworn MSTHT likely 44 mm

| | | | | | | | Protocone | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Specimen | Height | Length | Width | Ratio | Index | Lingual complexity | Length | Width | Ratio | Pli caballin | Hypoconal groove | Protocone shape |
| **PIUW 3540/9** | 32.5 | 31.2 | 23.0 | 0.74 | 5:9:4:3 | 0;0;0;1 | 7.9 | 4.5 | 0.57 | 2 | long; narrow | oval |
| **PIUW 3540/4** | 31.3 | 33.1 | | | 8:4:4:2 | 0;0;1;0 | 9.0 | 4.2 | 0.50 | 3 | open | oval |
| **PIUW 3540/10** | 30.0 | 31.2 | 24.4 | 0.78 | 7:9:5:3 | 1;0;1;0 | 7.9 | 4.6 | 0.58 | 3 | open | flat |
| **PIUW 3540/3** | 29.5 | 33.1 | 22.9 | 0.69 | 9:13:8:3 | 0;0;1;0 | 9.7 | 4.5 | 0.46 | 4 | open | sl. oval |
| **PIUW 3540/7** | 29.5 | 34.7 | 25.6 | 0.74 | 9:11:7:3 | 0;0;1;0 | 7.4 | 5.0 | 0.68 | 4 | open; narrow | oval |
| PIUW 3540/315 | 23.0 | 32.6 | 23.8 | 0.73 | 5:9:5:2 | 0;0;1;0 | 6.2 | 5.2 | 0.84 | 3 | open; narrow | oval |
| PIUW 3540/8 | 22.5 | 31.3 | 25.0 | 0.80 | 6:10:5:3 | 0;0;1;0 | 8.6 | 5.0 | 0.58 | 3 | narrow | sl. oval |
| PIUW 3540/11 | 21.0 | 31.0 | 22.2 | 0.72 | 3:8:5:3 | 0;0;0;0 | 8.0 | 4.2 | 0.50 | 3 | open; narrow | sl. oval |
| PIUW 3540/316 | 20.7 | 32.7 | 23.9 | 0.73 | 7:5:4:2 | 0;0;0;0 | 8.0 | 5.0 | 0.60 | 2 | open; narrow | sl. oval |
| PIUW 3540/317 | 15.8 | 32.1 | 23.2 | 0.72 | 5:7:3:1 | 0;0;0;0 | 8.0 | 5.2 | 0.70 | 2 | open; narrow | sl. oval |
| Range | | 31.2–34.7 | 21.2–25.6 | 0.63–0.80 | | | 7.4–9.7 | 4.2–5.3 | 4.6–0.68 | | | |
| Mean | | 32.7 | 24.3 | 0.74 | 8:9:6:3 | 0;0;1;0 | 8.3 | 4.6 | 0.56 | 3 | | |
| SD | | 1.48 | 1.35 | 0.04 | | | 1.01 | 0.29 | 0.08 | | | |
| CV | | 4.54 | 5.57 | 4.99 | | | 12.29 | 6.12 | 14.7 | | | |
| *N* | 5 | 5 | 4 | 4 | 5 | 5 | 5 | 5 | 5 | 5 | | |

Remarks: PIUW 3540/3 has spur on protocone. PIUW 3540/8 protocone connects to protoloph.

TABLE 22
(*Continued*)

**P3**, unworn MSTHT likely 55 mm.

| Specimen | Height | Length | Width | Ratio | Index | Lingual complexity | Protocone Length | Protocone Width | Protocone Ratio | Pli caballin | Hypoconal groove | Protocone shape |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| PIUW 3540/14 | 44.0a | | | | | | | | | | | |
| PIUW 3540/1 | 43.0 | 33.6 | 21.2 | 0.63 | 7:?:?:? | 0;0;0;0 | 7.9 | 4.7 | 0.59 | ? | v. early wear | oval |
| PIUW 3540/5 | 40.0 | 33.3 | 24.0 | 0.72 | 8:12:6:7 | 0;0;0;0 | 9.2 | 4.3 | 0.47 | 3 | narrow; early | oval |
| PIUW 3540/6 | 40.0 | 33.0 | 21.8 | 0.66 | 6:6?:5?:1 | 0;0;0;0 | 8.2 | 5.3 | 0.65 | ? | incomplete | flat |
| PIUW 3540/2 | 36.7 | 31.4 | 22.8 | 0.73 | 3:3:3:2 | 0;0;0;0 | 6.8 | 4.0 | 0.59 | 2 | open; spur | oval |
| **PIUW 3540/9** | 32.5 | 31.2 | 23.0 | 0.74 | 5:9:4:3 | 0;0;0;1 | 7.9 | 4.5 | 0.57 | 2 | long; narrow | oval |
| **PIUW 3540/4** | 31.3 | 33.1 | | | 8:4:4:2 | 0;0;1;0 | 9.0 | 4.2 | 0.50 | 3 | open | oval |
| **PIUW 3540/10** | 30.0 | 31.2 | 24.4 | 0.78 | 7:9:5:3 | 1;0;1;0 | 7.9 | 4.6 | 0.58 | 3 | open | flat |
| **PIUW 3540/3** | 29.5 | 33.1 | 22.9 | 0.69 | 9:13:8:3 | 0;0;1;0 | 9.7 | 4.5 | 0.46 | 4 | open | sl. oval |
| **PIUW 3540/7** | 29.5 | 34.7 | 25.6 | 0.74 | 9:11:7:3 | 0;0;1;0 | 7.4 | 5.0 | 0.68 | 4 | open; narrow | oval |
| PIUW 3540/315 | 23.0 | 32.6 | 23.8 | 0.73 | 5:9:5:2 | 0;0;1;0 | 6.2 | 5.2 | 0.84 | 3 | open; narrow | oval |
| PIUW 3540/8 | 22.5 | 31.3 | 25.0 | 0.80 | 6:10:5:3 | 0;0;1;0 | 8.6 | 5.0 | 0.58 | 3 | narrow | sl. oval |
| PIUW 3540/11 | 21.0 | 31.0 | 22.2 | 0.72 | 3:8:5:3 | 0;0;0;0 | 8.0 | 4.2 | 0.50 | 3 | open; narrow | sl. oval |
| PIUW 3540/316 | 20.7 | 32.7 | 23.9 | 0.73 | 7:5:4:2 | 0;0;0;0 | 8.0 | 5.0 | 0.60 | 2 | open; narrow | sl. oval |
| PIUW 3540/317 | 15.8 | 32.1 | 23.2 | 0.72 | 5:7:3:1 | 0;0;0;0 | 8.0 | 5.2 | 0.70 | 2 | open; narrow | sl. oval |
| Range | | 31.2–34.7 | 21.2–25.6 | 0.63–0.80 | | | 6.2–9.7 | 4.0–5.3 | 0.5–0.8 | | | |
| Mean | | 32.7 | 24.3 | 0.74 | 8:9:6:3 | 0;0;1;0 | 8.2 | 4.6 | 0.6 | 3 | | |
| SD | | 1.48 | 1.35 | 0.04 | | | 1.01 | 0.29 | 0.08 | | | |
| CV | | 4.54 | 5.57 | 4.99 | | | 12.3 | 6.3 | 14.7 | | | |
| *N* | | 5 | 4 | 4 | 5 | 5 | 5 | 5 | 5 | 5 | | |

Remarks: PIUW 3540/3 has spur on protocone. PIUW 3540/8 protocone connects to protoloph.

TABLE 22
(*Continued*)

**P4**, unworn MSTHT likely 56 mm.

| Specimen | Height | Length | Width | Ratio | Index | Lingual complexity | Protocone Length | Protocone Width | Protocone Ratio | Pli caballin | Hypoconal groove | Protocone shape |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| PIUW 3540/70 | 52.5 | 28.4 | 23.2 | 0.82 | ?:?:?:? | 0;0;0;0 | 7.1 | 2.7 | 0.38 | ? | ? | flat |
| PIUW 3540/60 | 47.5 | 27.3 | 22.6 | 0.83 | ?:?:?:? | 0;0;0;0 | 8.1 | 3.8 | 0.47 | 2 | slighty ovate | sl. oval |
| PIUW 3540/62 | 47.0 | 27.3 | 24.6 | 0.90 | 6:12:?:? | 0;0;0;0 | 9.1 | 3.6 | 0.40 | 2?+ | open, v.early | flat |
| PIUW 3540/65 | 46.0 | 27.4 | 23.3 | 0.85 | 4:7:5:1 | 0;0;0;0 | 8.2 | 3.8 | 0.46 | 5 | open; spur | sl. oval |
| PIUW 3540/71 | 44.5 | 25.9 | 23.4 | 0.90 | 4:9:5:1 | 0;0;0;0 | 10.2 | 4.9 | 0.48 | 2 | open; narrow | sl. oval |
| PIUW 3540/61 | 41.2 | 25.5 | 22.7 | 0.89 | 3:8:3:2 | 0;0;0;0 | 8.2 | 3.9 | 0.48 | 2 | open | flat |
| PIUW 3540/47 | 40.3 | 24.3 | 23.9 | 0.98 | 5:9:6:2 | 0;0;1;0 | 9.5 | 4.1 | 0.43 | 2 | open; narrow | sl. oval |
| **PIUW 3540/45** | 39.8 | 26.8 | 25.7 | 0.96 | 7:15:12:2 | 1;0;1;0 | 8.0 | 4.8 | 0.58 | 2 | open; narrow | sl. oval |
| **PIUW 3540/46** | 38.9 | 24.6 | 23.0 | 0.93 | 5:11:8:3 | 0;1;1;0 | 8.3 | 3.9 | 0.47 | 3 | open; narrow | flat |
| **PIUW 3540/72** | 37.0 | 24.6 | 24.6 | 1.00 | 6:12:11:3 | 1;0;1;1 | 8.9 | 4.6 | 0.52 | 3 | open; narrow | sl. oval |
| **PIUW 3540/64** | 36.4 | 23.7 | 23.9 | 1.01 | 7:14:9:4 | 1;1;1;0 | 8.2 | 4.4 | 0.54 | 2 | open; narrow | sl. oval |
| **PIUW 3540/68** | 35.7 | 23.3 | 23.2 | 1.00 | 7:12:7:4 | 1;1;1;0 | 8.6 | 5.0 | 0.58 | 3 | narrow | sl. oval |
| **PIUW 3540/48** | 32.8 | 22.7 | | | 7:15:10:2 | 1;1;1;1 | | | | 3 | open; narrow | sl. oval |
| **PIUW 3540/44** | 32.5 | 22.1 | 21.5 | 0.97 | 6:13:10:4 | 1;1;1;1 | 8.1 | 3.9 | 0.48 | 2 | open; narrow | sl. oval |
| **PIUW 3540/54** | 31.7 | 23.3 | 22.2 | 0.95 | 4:14:9:3 | 1;1;1;0 | 7.5 | 4.3 | 0.45 | 2 | open; narrow | sl. oval |
| **PIUW 3540/67** | 31.5 | 24.9 | 24.6 | 0.99 | 9:12:9:3 | 1;1;1;1 | 7.7 | 3.9 | 0.51 | 3 | open | sl. oval |
| **PIUW 3540/59** | 31.1 | 22.7 | 21.6 | 0.95 | 5:9:7:3 | 0;1;1;0 | 7.5 | 3.6 | 0.48 | 2 | open; narrow | oval |
| **PIUW 3540/73** | 30.8 | | 22.8 | | 4:11:10:3 | 0;0;1;0 | 7.8 | 4.5 | 0.58 | 2 | open; narrow | sl. oval |
| **PIUW 3540/63** | 29.7 | 21.2 | 22.5 | 1.06 | 7:14:8:4 | 1;1;1;1 | 9.0 | 4.1 | 0.46 | 2 | open; narrow | sl. oval |
| **PIUW 3540/50** | 28.0 | 23.6 | 24.0 | 1.02 | 5:13:10:2 | 0;1;1;1 | 8.2 | 4.2 | 0.51 | 3 | open; narrow | sl. oval |
| **PIUW 3540/52** | 25.6 | 21.8 | 21.6 | 0.99 | 7:12:9:4 | 1;1;1;1 | 8.6 | 4.2 | 0.49 | 3 | open; narrow | sl. oval |
| PIUW 3540/66 | 24.5 | | 23.3 | | 2:9:8:2 | 0;1;0;0 | 9.2 | 4.8 | 0.52 | 2 | open | sl. oval |
| PIUW 3540/55 | 17.8 | 24.7 | 24.4 | 0.99 | 6:10:8:1 | 0;0;1;0 | 8.9 | 4.9 | 0.55 | 1 | open; narrow | flat |
| Range | | 21.2–26.8 | 21.5–25.7 | 0.93–1.06 | | | 7.5–9.0 | 3.4–4.8 | 0.45–0.60 | | | |
| Mean | | 23.5 | 23.2 | 0.99 | 6:13:9:3 | 1;1;1;1 | 8.13 | 4.12 | 0.51 | 2 | | |
| SD | | 1.49 | 1.32 | 0.03 | | | 0.48 | 0.40 | 0.04 | | | |
| CV | | 6.37 | 5.71 | 3.53 | | | 5.91 | 9.61 | 8.68 | | | |
| *N* | 23 | 13 | 13 | 12 | 14 | 14 | 13 | 13 | 13 | 14 | | |

TABLE 22
(*Continued*)

| Specimen | Height | Length | Width | Ratio | Index | Lingual complexity | Protocone Length | Protocone Width | Protocone Ratio | Pli caballin | Hypoconal groove | Protocone shape |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| **M1**, unworn MSTHT likely 55 mm. | | | | | | | | | | | | |
| PIUW 3540/146 | 52.9 | 27.3 | 22.7 | 0.83 | ?:?:?:? | 0;0;0;0 | 10.4 | | | | | |
| PIUW 3540/143 | 48.9 | 24.8 | 22.1 | 0.89 | 4:10:5:1? | 0;0;0;0 | 10.0 | 4.0 | 0.40 | 2 | open | sl. oval |
| PIUW 3540/134 | 47.7 | 23.4 | 19.8 | 0.85 | 6:5:4:2 | 0;0;0;0 | 7.7 | 3.2 | 0.42 | 3 | open | flat |
| PIUW 3540/129 | 46.1 | 24.4 | 21.3 | 0.87 | 5:5:4:2 | 0;0;0;0 | 8.3 | 3.5 | 0.42 | 2 | open; narrow | sl. oval |
| PIUW 3540/141 | 44.8 | 24.4 | 20.8 | 0.85 | 6:10:6:2 | 0;0;0;0 | 8.7 | 3.7 | 0.42 | 2 | open | flat |
| PIUW 3540/144 | 44.0 | 25.3 | 22.8 | 0.90 | 4:7:6:5 | 0;0;0;0 | 7.5 | 3.8 | 0.51 | 2 | open | oval |
| **PIUW 3540/140** | 43.0 | 26.3 | 24.2 | 0.92 | 7:11:7:5 | 0;1;1;0 | 9.5 | 4.3 | 0.45 | 2 | open; narrow | sl. oval |
| **PIUW 3540/130** | 36.8 | 23.3 | 22.4 | 0.96 | 7:10:10:3 | 1;1;1;1 | 7.5 | 3.7 | 0.49 | 4 | open; narrow | flat |
| **PIUW 3540/145** | 37.7 | 21.6 | 23.4 | 1.08 | 6:11:9:3 | 0;1;0;0 | 8.5 | 3.7 | 0.44 | 3 | open; narrow | sl. oval |
| **PIUW 3540/139** | 36.5 | 24.5 | 23.6 | 0.96 | 9:16:9:4 | 1;1;1;0 | 9.1 | 4.2 | 0.46 | 3 | open; narrow | oval |
| **PIUW 3540/138** | 35.9 | 23.4 | 21.4 | 0.91 | 6:12:8:2 | 1;1;1;1 | 6.9 | 4.0 | 0.58 | 2 | open; narrow | oval |
| **PIUW 3540/131** | 35.8 | 24.1 | 23.3 | 0.97 | 4:10:11:2 | 1;1;0;0 | 8.9 | 4.7 | 0.53 | 3 | open | sl. con. |
| **PIUW 3540/147** | 34.2 | 23.0 | 22.0 | 0.96 | 8:11:7:4 | 1;1;0;0 | 8.6 | 4.0 | 0.47 | 2 | open; narrow | flat |
| **PIUW 3540/135** | 33.7 | 24.1 | 23.4 | 0.97 | 6:9:9:1 | 0;0;1;1 | 8.7 | 4.5 | 0.52 | 2 | narrow | oval |
| **PIUW 3540/136** | 29.2 | 24.1 | 22.4 | 0.93 | 4:10:7:3 | 0;1;1;1 | 7.9 | 4.5 | 0.57 | 2 | narrow | oval |
| PIUW 3540/137 | 24.3 | 23.3 | 22.3 | 0.96 | 5:10:9:3 | 0;0;1;0 | 8.2 | 4.5 | 0.55 | 3 | narrow | oval |
| PIUW 3540/379 | 15.6 | 23.7 | 23.3 | 0.96 | 1:8:10:1 | 0;1;1;0 | 9.0 | 4.5 | 0.50 | 2 | open | oval |
| Range | | 21.6–26.3 | 21.4–24.2 | 9.1–1.08 | | | 6.9–9.5 | 3.7–4.7 | 0.44–0.58 | | | |
| Mean | | 23.9 | 22.9 | 0.96 | 6:11:9:3 | 1;1;1;0 | 8.4 | 4.2 | 0.50 | 3 | | |
| SD | | 1.37 | 0.89 | 0.05 | | | 0.82 | 0.36 | 0.05 | | | |
| CV | | 5.33 | 3.91 | 5.18 | | | 9.78 | 8.53 | 10.40 | | | |
| *N* | 17 | 9 | 9 | 9 | 9 | 9 | 9 | 9 | 9 | 9 | | |
| **M2**, unworn MSTHT likely 55 mm. | | | | | | | | | | | | |
| PIUW 3540/158 | 52.5 | 26.0 | 20.3 | 0.78 | early | early | 8.8 | 3.7 | 0.42 | ? | ? | sl. oval |
| PIUW 3540/159 | 47.0 | 23.8 | 18.6 | 0.78 | | | | | | 2 | nearly unw. | sl. oval |
| **PIUW 3540/322** | 45.0 | 23.9 | 21.0 | 0.88 | 4:10:6:6 | 0;0;0;0 | 8.1 | 3.8 | 0.47 | 2 | narrow; vew. | sl. oval |
| PIUW 3540/136 | 24.6 | 22.6 | 22.6 | 1.00 | 5:11:11:3 | 0;0;0;0 | 8.8 | 4.2 | 0.48 | 2 | narrow | sl. oval |
| Range | | | | | | | | | | | | |
| Mean | | 23.9 | 21.0 | 0.88 | 4:10:6:6 | 0;0;0;0 | 8.1 | 3.8 | 0.47 | 2 | | |
| SD | | | | | | | | | | | | |
| CV | | | | | | | | | | | | |
| *N* | 4 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | | |

TABLE 22
(*Continued*)

**M3**, unworn MSTHT likely 55 mm.

| Specimen | Height | Length | Width | Ratio | Index | Protocone Length | Protocone Width | Protocone Ratio | Pli caballin | Hypoconal groove |
|---|---|---|---|---|---|---|---|---|---|---|
| **PIUW 3540/23** | 36 | 24.1 | 21.8 | 0.91 | 7:10?:6?:4 | 7.8 | | | 2 | open; narrow |
| **PIUW 3540/47** | 33 | 23.6 | 19.1 | 0.81 | 5:8:7:4 | 7.8 | 3.8 | 0.49 | 2 | open |
| Range | | 23.6–24.1 | 19.1–21.8 | 0.81–0.90 | | | | | | |
| Mean | | 23.9 | 20.5 | 0.86 | 6:9:7:4 | 7.8 | 3.8 | 0.49 | 2 | |
| SD | | 0.35 | 1.91 | 0.07 | | | | | | |
| CV | | 1.48 | 9.34 | 7.86 | | | | | | |
| *N* | 2 | 2 | 2 | 2 | 2 | 2 | 1 | 1 | 2 | 2 |

**C. Laarberg**, Pannonian E.

| Specimen | Height | Length | Width | Ratio | Index | Protocone Length | Protocone Width | Protocone Ratio | Pli caballin | Hypoconal groove | Protocone shape |
|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | | | | **P2** | | | | | |
| NHMW 1842.VII.6 | 32.0 | 31.2 | 24.4 | 0.78 | 4:12:10:3 | 7.6 | 5.0 | 0.66 | 3 | open | flat |
| | | | | | | **P3** | | | | | |
| NHMW 1842.VII.6 | 35.0 | 26.5 | 25.6 | 0.97 | 9:12:8:2 | 8.8 | 4.9 | 0.56 | 3 | open | flat |
| | | | | | | **P4** | | | | | |
| NHMW 1842.VII.6 | 38.0 | 25.8 | 25.0 | 0.97 | 8:10:6:2 | 7.7 | 4.0 | 0.52 | 2+ | open | flat |
| | | | | | | **M1** | | | | | |
| NHMW 1842.VII.6 | 42.0a | 23.5 | 25.6 | 1.09 | 8:15:9:5 | 8.0 | 4.2 | 0.53 | 2 | open | oval |
| | | | | | | **M2** | | | | | |
| NHMW 1842.VII.6 | | 24.0 | 24.2 | 1.01 | 8:7:6:6 | 7.8 | 3.7 | 0.47 | 2+ | open | flat |
| | | | | | | **M3** | | | | | |
| NHMW 1842.VII.6 | 28.0a | 23.6 | 20.0 | 0.85 | ?:?:?:? | 8.8 | 3.0 | 0.34 | 2? | wide; early wear | flat |

TABLE 23
**Measurements (mm) of Upper Cheek Teeth of *Hippotherium primigenium*, Höwenegg and Eppelsheim, Germany**

**A. Höwenegg**; Karlsruhe sample

**P2**, unworn MSTHT likely 52 mm.

| | | | | | | Lingual | Protocone | | | Pli | Hypoconal | Protocone |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Specimen | Height | Length | Width | Ratio | Index | complexity | Length | Width | Ratio | caballin | groove | shape |
| **SMNK Ho B** | 39.5 | 32.0 | 18.7 | 0.58 | | | 6.0 | 3.7 | 0.62 | | | s. oval |
| **SMNK Ho A** | 32.4 | 33.4 | 25.0 | 0.75 | 10:12:12:3 | 0;0;1;1 | 7.6 | 4.0 | 0.53 | 4 | open; narrow | oval |
| **SMNK Ho 1** | 30.0 | 35.0 | 27.3 | 0.78 | 8:11:11:5 | 1;1;1;1 | 7.8 | 4.3 | 0.55 | 5 | open | oval |
| SMNK Ho C | 29.0a | 32.5 | 24.5 | 0.75 | 6:6:2:1 | 0;0;0;0 | 7.6 | 4.6 | 0.61 | 2 | open; hy. spur | oval |
| Range | | 32.0–35.0 | 18.7–27.3 | 0.58–0.78 | | | 6.0–7.8 | 3.7–4.6 | 0.53– | | | |
| Mean | | 33.5 | 23.7 | 0.70 | 9:12:12:4 | 1;1;1;1 | 7.1 | 4.0 | 0.57 | 5 | | |
| SD | | 1.50 | 4.45 | 0.11 | | | 0.99 | 0.30 | 0.05 | | | |
| CV | | 4.49 | 18.81 | 14.9 | | | 13.83 | 7.5 | 8.26 | | | |
| *N* | 4 | 3 | 3 | 3 | 2 | 2 | 3 | 3 | 3 | 2 | | |

Remarks: Height is at mesostyle; boldface specimens used in plication count statistics. SMNK Ho B dP1/P2 width ratio is 0.48. ln. = long. sl. con. = slightly concave; con. = concave; narr. = narrow; ov. = ovate; immat; = immature; e.wr. = early wear; tr.= triangular; incomp. = incomplete. s. oval = slight oval; s. ovate = slightly ovate; sl. tr. = slightly triangular. PPSep, PPS = pre- and postfossettes separate; PPCon, PPC= pre- and postfossettes connected; hy. = hypocone; * = elongate protocone.

**P3**, unworn MSTHT likely 52 mm.

| | | | | | | Lingual | Protocone | | | Pli | Hypoconal | Protocone |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Specimen | Height | Length | Width | Ratio | Index | complexity | Length | Width | Ratio | caballin | groove | shape |
| **SMNK Ho B** | 39.9 | 27.5 | 24.0 | 0.87 | | | 7.4 | 3.5 | 0.47 | | | sl. con. |
| **SMNK Ho A** | 38.2 | 27.0 | 28.3 | 1.05 | 7:10:7:2 | 1;0;1;0 | 8.7 | 3.6 | 0.41 | 3 | open | flat |
| **SMNK Ho 1** | 30.5 | 28.2 | 29.2 | 1.04 | 8:14:11:4 | 1;1;1;1 | 8.0 | 3.5 | 0.44 | 6 | open; narrow | oval |
| SMNK Ho C | 37.0a | 28.2 | 26.7 | 0.95 | 8:7:3:1 | 0;1;0;0 | 7.8 | 4.5 | 0.58 | 3 | open; narrow | oval |
| Range | | 27.0–28.2 | 24.0–29.2 | 0.87–1.05 | | | 7.4–8.7 | 3.5–3.6 | 0.41–0.47 | | | |
| Mean | | 27.6 | 27.2 | 0.99 | 8:12:9:3 | 1;1;1;1 | 8.0 | 3.5 | 0.44 | 4 | | |
| SD | | 0.60 | 2.78 | 0.10 | | | 0.65 | 0.06 | 0.03 | | | |
| CV | | 2.19 | 10.23 | 9.93 | | | 8.10 | 1.63 | 6.75 | | | |
| *N* | 4 | 3 | 3 | 3 | 2 | 2 | 3 | 3 | 3 | 2 | | |

TABLE 23
(*Continued*)

| Specimen | Height | Length | Width | Ratio | Index | Lingual complexity | Protocone Length | Protocone Width | Protocone Ratio | Pli caballin | Hypoconal groove | Protocone shape |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| **P4**, unworn MSTHT likely 52 mm. | | | | | | | | | | | | |
| **SMNK Ho B** | 46.0 | 26.0 | 33.4 | 1.28 | | | 7.3 | 3.3 | 0.45 | | | sl. con. |
| **SMNK Ho A** | 37.2a | 26.9 | 27.5 | 1.02 | 7:11:11:3 | 1;0;1;0 | 8.5 | 4.0 | 0.47 | 4 | open; narrow | flat |
| **SMNK Ho 1** | 34.0a | 28.6 | 29.0 | 1.01 | 11:14:10:3 | 1;1;1;1 | 8.1 | 4.6 | 0.57 | 6 | open; narrow | oval |
| SMNK Ho C | 28.0 | 27.4 | 25.7 | 0.94 | 3:7:8:1 | 0;0;0;0 | 8.4 | 3.9 | 0.46 | 2 | open; immat. | sl. tr. |
| Range | | 26.0–28.6 | 27.5–33.4 | 1.01–1.28 | | | 7.3–8.5 | 3.3–4.6 | 0.45–0.57 | | | |
| Mean | | 27.2 | 30.0 | 1.11 | 8:12:11:3 | 1;1;1;1 | 8.0 | 4.0 | 0.50 | 5 | | |
| SD | | 1.32 | 3.07 | 0.15 | | | 0.61 | 0.65 | 0.06 | | | |
| CV | | 4.86 | 10.23 | 13.90 | | | 7.67 | 16.4 | 12.5 | | | |
| *N* | 4 | 3 | 3 | 3 | 2 | 2 | 3 | 3 | 3 | 2 | | |
| **M1**, unworn MSTHT likely 52 mm. | | | | | | | | | | | | |
| **SMNK Ho B** | 38.8 | 24.6 | 23.2 | 0.94 | 8:9:6:3 | 0;0;0;0 | 7.5 | 4.0 | 0.53 | 4 | open; narrow | oval |
| **SMNK Ho A** | 33.0a | 22.4 | 24.2 | 1.08 | 6:11:9:4 | 1;1;1;1 | 8.0 | 4.1 | 0.51 | 4 | open | sl. ovate |
| **SMNK Ho 1** | 29.5 | 25.2 | 25.9 | 1.08 | 9:16:24:9 | 1;1;1;1 | 8.7 | 4.7 | 0.54 | 3 | open; narrow | oval |
| SMNK Ho C | | 24.6 | 24.8 | 1.01 | 4:10:6:4 | 0;0;1;0 | 9.4 | 4.5 | 0.48 | 4 | open | oval |
| Range | | 22.4–25.2 | 23.2–25.9 | 0.94–1.08 | | | 7.5–8.7 | 4.0–4.7 | 0.51–0.54 | | | |
| Mean | | 24.1 | 24.4 | 1.03 | 8:12:10:5 | 1;1;1;1 | 8.1 | 4.3 | 0.53 | 4 | | |
| SD | | 1.47 | 1.37 | 0.08 | | | 0.60 | 0.38 | 0.01 | | | |
| CV | | 6.13 | 5.59 | 7.65 | | | 7.42 | 8.87 | 2.73 | | | |
| *N* | 3 | 3 | 3 | 3 | 3 | 3 | 3 | 3 | 3 | 3 | | |
| **M2**, unworn MSTHT likely 50 mm. | | | | | | | | | | | | |
| **SMNK Ho B** | 42.0 | 32.2 | 23.0 | 0.71 | 6:8:6:1 | 0;0;0;0 | 7.4 | 3.1 | 0.42 | 2 | open; narrow | oval |
| **SMNK Ho A** | 30.5a | 24.1 | 23.0 | 0.95 | 6:11:8:4 | 1;1;1;1 | 8.0 | 3.2 | 0.40 | 5 | open; narrow | flat |
| **SMNK Ho 1** | 35.0a | 25.7 | 25.2 | 0.98 | 7:11:8:7 | 1;1;1;1 | 8.8 | 3.7 | 0.42 | 7 | open; narrow | oval |
| SMNK Ho C | 25.0a | 24.2 | 22.6 | 0.93 | 6:10:7:4 | 1;0;0;0 | 7.3 | 4.3 | 0.59 | 3 | open | oval |
| Range | | 24.1–32.2 | 23.0–25.2 | 0.71–0.98 | | | 7.4–8.8 | 3.1–3.7 | 0.40–0.42 | | | |
| Mean | | 27.3 | 23.7 | 0.88 | 6:10:7:4 | 1;1;1;1 | 8.1 | 3.3 | 0.41 | 4 | | |
| SD | | 4.29 | 1.27 | 0.15 | | | 0.70 | 0.32 | 0.01 | | | |
| CV | | 15.7 | 5.35 | 16.6 | | | 8.70 | 9.64 | 2.76 | | | |
| *N* | 3 | 3 | 3 | 3 | 3 | 3 | 3 | 3 | 3 | 3 | | |

TABLE 23
(*Continued*)

| Specimen | Height | Length | Width | Ratio | Index | Lingual complexity | Protocone Length | Protocone Width | Protocone Ratio | Pli caballin | Hypoconal groove | Protocone shape |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| **M3**, unworn MSTHT likely 45 mm. | | | | | | | | | | | | |
| **SMNK Ho B** | 33.0a | 33.3 | 27.4 | 0.82 | | | 7.3 | 2.8 | 0.38 | | | triangular |
| **SMNK Ho A** | 34.8a | 23.0 | 20.6 | 0.90 | 4:10:6:3 | 0;0;1;0 | 7.0 | 3.1 | 0.44 | 2 | open; spur | sl. ovate |
| **SMNK Ho 1** | 30.0 | 26.0 | 22.0 | 0.85 | 5:9:6:2 | 0;0;1;0 | 9.5 | 4.5 | 0.47 | 4 | open; narrow | oval |
| SMNK Ho C | 21.0a | 18.8 | 16.1 | 0.86 | incomp. | incomp. | 7.0 | 4.2 | 0.60 | ? | incomplete | oval |
| Range | | 23.0–33.3 | 20.6–27.4 | 0.82–0.90 | | | 7.0–9.5 | 2.8–4.5 | 0.38–0.47 | | | |
| Mean | | 27.4 | 23.3 | 0.86 | 5:9:6:3 | 0;0;1;0 | 7.9 | 3.5 | 0.43 | 3 | | |
| SD | | 5.30 | 3.59 | 0.04 | | | 1.37 | 0.91 | 0.05 | | | |
| CV | | 19.3 | 15.4 | 4.35 | | | 17.2 | 26.2 | 10.6 | | | |
| *N* | 3 | 3 | 3 | 3 | 2 | 2 | 3 | 3 | 3 | 2 | | |
| **B. Eppelsheim**; Darmstadt sample | | | | | | | | | | | | |
| **P2**, unworn MSTHT likely about 50 mm. | | | | | | | | | | | | |
| HLMD Din. 2987 | 45.0a | shows little worn tooth | | | | | | | | | | |
| HLMD Din. 2976 | 44.0 | shows little worn tooth | | | | | | | | | | |
| HLMD Din. 2756 | 40.2 | 34.2 | 23.6 | 0.69 | 6:4:3:2 | 0;0;0;0 | 6.3 | 4.4 | 0.70 | 2 | open | oval |
| HLMD Din. 2932 | 40.0 | shows little worn tooth | | | | | | | | | | conc. |
| HLMD Din. 2696 | 36.7 | shows unworn crown about 46 mm | | | | | | | | | | sl. con. |
| HLMD Din. 3005 | 35.0a | | | | PP Sep. | | | | | | | |
| HLMD Din. 2934 | 33.5 | 29.9 | 22.7 | 0.76 | PP Conn. | | | | | | | sl. ovate |
| **HLMD Din.2686** | 32.8 | 30.8 | 23.5 | 0.76 | 7:11:8:3 | 0;0;1;0 | 6.7 | 4.5 | 0.67 | 2 | open; narr. | oval |
| HLMD Din. 2933 | 30.0a | | | | PP Sep. | | | | | | | oval |
| HLMD Din. 2658 | 30.0a | | | | PP Sep. | | | | | | | flat |
| **HLMD Din.2858** | 29.5 | | | | PP Conn. | | | | | | | |
| **HLMD Din.2518** | 29.4 | 35.0 | 23.0 | 0.65 | 11:12:11:9 | 1;1;1;1 | 6.3 | 4.6 | 0.73 | 3 | open; PPS | sl. oval |
| **HLMD Din.2440** | 29.3 | 32.6 | 22.5 | 0.69 | 9:15:11:3 | 0;0;0;0 | 7.4 | 3.8 | 0.51 | 4 | open; PPS. | oval |
| **HLMD Din.2902** | 28.6 | 31.0 | 24.2 | 0.78 | PP Conn. | | | | | | | sl. oval |
| **HLMD Din.2439** | 28.2 | 31.7 | 25.2 | 0.79 | 10:12:10:3 | 1;1;1;0 | 6.6 | 4.4 | 0.67 | 3 | open; PPC | oval |
| **HLMD Din.2695** | 27.6 | 31.4 | 24.2 | 0.77 | 7:7:8:2 | 0;0;1;0 | 7.0 | 4.1 | 0.60 | 2 | open; PPC | |
| **HLMD Din.2923** | 27.0 | 33.5 | 24.7 | 0.74 | PP Sep. | | | | | | | sl. con. |
| **HLMD Din.2663** | 26.5 | 29.8 | 22.4 | 1.08 | 11:11:8:2 | 1;0;0;1 | 6.0 | 4.0 | 0.70 | 3 | open; PPS | oval |
| **HLMD Din.2698** | 26.5 | 23.6 | 24.1 | 1.02 | 6:12:11:5 | 1;1;1;1 | 6.3 | 4.2 | 0.67 | 3 | open; PPS | oval |
| **HLMD Din.2904** | 25.7 | 32.1 | 25.6 | 0.80 | PP Sep. | | | | | | | sl. con. |
| **HLMD Din.2557** | 24.8 | 22.7 | 23.6 | 1.04 | 5:7:7:3 | 0;0;1;1 | 6.8 | 4.8 | 0.71 | 2 | open; PPC | |
| **HLMD Din.2447** | 24.3 | 31.9 | 24.3 | 0.76 | 7:15:8:4 | 1;0;1;1 | 6.5 | 4.8 | 0.74 | 4 | open; PPC | oval |

TABLE 23
(*Continued*)

**B. Eppelsheim**; Darmstadt sample

**P2**, unworn MSTHT likely about 50 mm.

| Specimen | Height | Length | Width | Ratio | Index | Lingual complexity | Protocone Length | Protocone Width | Protocone Ratio | Pli caballin | Hypoconal groove | Protocone shape |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| **HLMD Din.2443** | 23.6 | 31.4 | 23.3 | 0.74 | 7:9:11:12 | 1;0;1;0 | 7.0 | 4.9 | 0.70 | 2 | open; PPS | oval |
| HLMD Din. 2438 | 22.2 | 31.5 | 23.3 | 0.74 | 5:10:9:3 | 0;0;0;0 | 8.2 | 4.2 | 0.51 | 2 | open; PPS | oval |
| HLMD Din. 2997 | 19.0 | 32.6 | 23.3 | 0.71 | PP Conn. | late wear | | | | | | oval |
| HLMD Din. 2973 | 15.5 | 28.7 | 0.86 | | PP Sep. | late wear | | | | | | oval |
| HLMD Din. 2697 | 13.0 | | | | PP Sep. | late wear | | protocone connected | | | | oval |
| Range | | 22.7–35.0 | 22.5–25.6 | 0.66–1.08 | | | 6.0–8.2 | 3.8–4.9 | 0.51–0.73 | | | |
| Mean | | 30.6 | 23.9 | 0.82 | 7:11:10:4 | 1;0;1;1 | 6.7 | 4.4 | 0.67 | 3 | | |
| SD | | 3.54 | 0.97 | 0.14 | | | 0.41 | 0.38 | 0.07 | | | |
| CV | | 11.6 | 4.05 | 16.7 | | | 6.18 | 8.51 | 10.3 | | | |
| *N* | 27 | 13 | 12 | 12 | 11 | 10 | 10 | 10 | 10 | 10 | | |

**P3**, unworn MSTHT likely 52 mm.

| Specimen | Height | Length | Width | Ratio | Index | Lingual complexity | Protocone Length | Protocone Width | Protocone Ratio | Pli caballin | Hypoconal groove | Protocone shape |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| HLMD Din. 2683 | 47.0a | 26.0 | 23.1 | 0.89 | 7:? :? :1 | 0;?;?;0 | 6.4 | 3.7 | 0.58 | 3 | open; e.wr. | ovate |
| HLMD Din. 2701 | 45.0 | 25.6 | 23.6 | 0.92 | 8:12:9:4 | 1;1;0;0 | 7.3 | 4.1 | 0.56 | 2 | narr; e.wr. | ovate |
| **HLMD Din.2882** | 39.7 | 26.5 | 26.0 | 0.98 | 8:7:7:2 | 0;0;1;1 | 7.0 | 3.8 | 0.54 | 2 | wide | sl. tr. |
| **HLMD Din.2479** | 34.6 | 25.7 | 23.8 | 0.93 | ? :? :? :4 | ?;1;1;0 | 6.2 | 4.3 | 0.69 | 4 | open | oval |
| **HLMD Din.2449** | 32.3 | 27.2 | 23.2 | 0.85 | 5:12:11:4 | 0;1;1;1 | 7.1 | 3.8 | 0.54 | 4 | open; narr. | flat |
| **HLMD Din.2711** | 30.5 | 22.9 | 21.8 | 0.95 | 8:11:12:6 | 1;1;1;1 | 6.5 | 4.2 | 0.65 | 2 | open | ovate |
| **HLMD Din.2482** | 28.3 | 25.8 | 24.8 | 0.96 | 8:10:9:4 | 1;1;1;1 | 9.4 | 4.5 | 0.48 | 3 | open; narr. | flat |
| **HLMD Din.2550** | 28.2 | 23.6 | 22.4 | 0.95 | 4:9:9:2 | 0;1;1;0 | 6.3 | 4.3 | 0.68 | 3 | open | ovate |
| **HLMD Din.2924** | 28.0 | 25.7 | 23.9 | 0.93 | 5:14:7:1 | 0;1;0;0 | 8.8 | 4.5 | 0.51 | 2 | narrow | sl. con. |
| **HLMD Din.2575** | 27.3 | 24.9 | 25.4 | 1.02 | 5:10:8:1 | 0;1;1;0 | 8.9 | 4.8 | 0.54 | 3 | open | sl. ovate |
| **HLMD Din.2520** | 26.0a | 27.0 | 26.3 | 0.97 | 6:16:? :7 | 1;0;0;1 | 8.8 | 4.0 | 0.45 | 3 | open | ovate |
| **HLMD Din.2579** | 23.7 | 22.8 | 23.5 | 1.03 | 6:10:9:2 | 0;1;1;0 | 7.8 | 4.5 | 0.58 | 3 | open | ovate |
| HLMD Din. 2552 | 21.5 | 25.5 | 24.4 | 0.96 | 1:8:6:1 | 0;0;0;0 | 8.0 | 5.2 | 0.65 | 1 | open | ovate |
| HLMD Din. 2548 | 20.6 | 25.5 | 27.2 | 1.07 | 4:15:14:2 | 1;1;1;1 | 8.3 | 5.2 | 0.63 | 4 | open | ovate |
| HLMD Din. 2925 | 17.0 | | | | | Protocone isolated in late wear; also in 2554 | | | | | | |
| HLMD Din. 2554 | 13.5 | 25.5 | 25.5 | 10.0 | 3:9:4:1 | 0;0;0;0 | 10.1 | 5.8 | 0.57 | 1 | open | ovate |
| Range | | 22.8–26.5 | 21.8–26.0 | 0.85–1.03 | | | 6.2–9.4 | 3.8–4.5 | 0.45–0.69 | | | |
| Mean | | 25.2 | 24.1 | 0.96 | 6:10:9:3 | 0;1;1;1 | 7.7 | 4.3 | 0.57 | 3 | | |
| SD | | 1.62 | 1.49 | 0.05 | | | 1.21 | 0.33 | 0.08 | | | |
| CV | | 6.41 | 6.20 | 5.27 | | | 15.8 | 7.65 | 14.6 | | | |
| *N* | 16 | 10 | 10 | 10 | 10 | 10 | 10 | 10 | 10 | 10 | | |

TABLE 23
(*Continued*)

**P4**, unworn MSTHT likely 55 mm.

| Specimen | Height | Length | Width | Ratio | Index | Lingual complexity | Protocone Length | Protocone Width | Protocone Ratio | Pli caballin | Hypoconal groove | Protocone shape |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| HLMD Din. 2710 | 52.0 | 27.0 | 22.7 | 0.84 | | | | | | | | |
| HLMD Din. 1079 | 49.0 | | | | | | | | | | | |
| HLMD Din. 2689 | 49.0 | 25.9 | 20.7 | 0.80 | 2:6:3:1 | 0;0;0;0 | 6.1 | 2.9 | 0.48 | 2 | open; narr. | ovate |
| HLMD Din. 2953 | 45.0 | | | | | | | | | | | |
| HLMD Din. 2944 | 44.2 | 29.5 | 26.2 | 0.89 | 4:6:5:1 | 0;0;0;0 | 7.9 | 4.1 | 0.52 | 2 | not formed | oval, in. |
| **HLMD Din.2680** | 38.1 | 25.1 | 21.9 | 0.87 | 7:11:8:5 | 1;1;1;1 | 6.1 | 3.9 | 0.64* | 2 | open; narr. | ovate |
| **HLMD Din.2484** | 37.5 | 28.5 | 26.7 | 0.94 | 9:14:12:3 | 1;0;1;0 | 7.4 | 4.1 | 0.55 | 3 | open; narr. | flat |
| **HLMD Din.2576** | 33.0 | 27.4 | 25.4 | 0.93 | 8:16:9:2 | 1;1;1;0 | 8.4 | 4.4 | 0.52 | 4 | open; narr. | sl. ovate |
| **HLMD Din.2556** | 32.4 | 26.8 | 26.2 | 0.98 | 8:? :10:4 | 1;?;1;1 | 9.2 | 4.5 | 0.49 | 3 | open | ovate |
| **HLMD Din.2943** | 32.2 | 24.0 | 25.4 | 1.06 | 7:11:9:3 | 1;1;1;1 | 8.2 | 3.9 | 0.48 | 3 | open | ovate |
| **HLMD Din.2445** | 31.9 | 24.5 | 23.2 | 0.95 | 9:7:6:1 | 1;0;1;0 | 7.1 | 4.1 | 0.58 | 3 | ?; PPS | oval |
| **HLMD Din.3013** | 31.0 | 23.6 | 24.0 | 1.02 | 6;13:10;4 | 1;1;1;0 | 8.3 | 4.2 | 0.51 | 2 | open; narr. | ovate |
| **HLMD Din.2572** | 29.9 | 25.6 | 24.9 | 0.97 | 7:14:12:3 | 1;1;1;1 | 8.4 | 4.7 | 0.56 | 3 | open | sl. ovate |
| **HLMD Din.2869** | 29.2 | 22.2 | 23.5 | 1.06 | 2:12:7:2 | 0;1;1;1 | 8.2 | 4.5 | 0.55 | 3 | narrow | sl. ovate |
| **HLMD Din.2553** | 28.7 | 26.3 | 25.1 | 0.95 | 8:14:15:8 | 1;1;1;1 | 6.9 | 4.0 | 0.58 | 5 | open, narr. | sl. ovate |
| **HLMD Din.1057** | 27.0 | 24.0 | 24.5 | 1.02 | 4:14:11:5 | 1;1;1;1 | 6.8 | 4.8 | 0.71 | 3 | open, narr. | ovate |
| **HLMD Din.2684** | 24.2 | 22.3 | 23.9 | 1.07 | 4:12:9:3 | 1;1;1;1 | 7.3 | 4.9 | 0.67 | 3 | open, narr. | ovate |
| **HLMD Din.2980** | 23.5 | 23.0 | 25.2 | 1.10 | 5:11:12:6 | 1;1;1;1 | 8.0 | 4.8 | 0.60 | 4 | open; narr. | ovate |
| **HLMD Din.2975** | 21.2 | 24.7 | 24.6 | 1.00 | 7:12:10:3 | 1;1;1;1 | 7.7 | 5.0 | 0.65 | 3 | open, narr. | ovate |
| HLMD Din. 2755 | 20.8 | 24.2 | 25.3 | 1.05 | 3:8:6:1 | 0;0;1;0 | 8.8 | 5.0 | 0.57 | 3 | open; narr | ovate |
| Range | | 22.2–28.5 | 21.9–26.7 | 0.87–1.07 | | | 6.1–9.2 | 3.9–5.0 | 0.48–0.71 | | * = narrow protocone | |
| Mean | | 24.9 | 24.6 | 0.99 | 7:12:9:4 | 1;1;1;1 | 7.7 | 4.4 | 0.58 | 3 | | |
| SD | | 1.89 | 1.25 | 0.06 | | | 0.82 | 0.38 | 0.07 | | | |
| CV | | 7.60 | 5.07 | 6.43 | | | 10.7 | 8.70 | 12.0 | | | |
| *N* | 20 | 14 | 14 | 14 | 14 | 14 | 14 | 14 | 14 | 14 | | |

TABLE 23
(*Continued*)

| Specimen | Height | Length | Width | Ratio | Index | Lingual complexity | Protocone Length | Protocone Width | Protocone Ratio | Pli caballin | Hypoconal groove | Protocone shape |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| **M1**, unworn MSTHT likely 58 mm. | | | | | | | | | | | | |
| HLMD Din. 2978 | 54.0a | 27.4 | 21.3 | 0.78 | | | | | | | | |
| HLMD Din. 2447 | 50.2 | 26.7 | | | | | | | | | open | unknown |
| HLMD Din. 2483 | 47.7 | 28.5 | 21.9 | 0.77 | | | | | | | | |
| HLMD Din. 2926 | 43.5 | | | | | | | | | | | |
| **HLMD Din. 2437** | 38.9 | 27.3 | 24.2 | 0.89 | 5:8:9:3 | 1;1;1;0 | 8.4 | 4.6 | 0.55 | 4 | open | oval |
| **HLMD Din. 2486** | 35.6 | 25.3 | 24.5 | 0.97 | 7:14:11:1 | 1;0;1;0 | 7.7 | 4.3 | 0.56 | 2 | open | sl. ovate |
| **HLMD Din. 2682** | 35.6 | 25.8 | 25.0 | 0.97 | 4:15:9:2 | 0;1;1;0 | 8.3 | 4.0 | 0.48 | 3 | narrow | sl. con. |
| **HLMD Din. 2947** | 30.2 | 22.5 | 23.6 | 1.05 | 9:13:8:5 | 1;1;1;1 | 8.2 | 4.1 | 0.50 | 2 | open | oval |
| **HLMD Din. 2487** | 29.7 | 21.6 | 23.7 | 1.10 | 6:12:11:5 | 1;1;1;1 | 5.7 | 4.1 | 0.72 | 2 | open; narr | oval |
| **HLMD Din. 2478** | 29.0 | 24.5 | 23.1 | 0.94 | 7:10:8:5 | 0;0;1;1 | 6.5 | 4.1 | 0.63 | 4 | open; narr. | oval |
| **HLMD Din. 2448** | 25.8 | 25.0 | 24.3 | 0.97 | 8:13:9:3 | 0;1;1;0 | 6.2 | 4.7 | 0.76 | 3 | open | oval |
| HLMD Din. 2712 | 22.3 | 24.3 | 23.8 | 0.98 | 1:11:9:1 | 0;0;1;0 | 8.1 | 4.5 | 0.56 | 3 | open | oval |
| HLMD Din. 2600 | 16.7 | 21.4 | 23.3 | 1.09 | 0:10:9:1 | 0;0;1;0 | 8.4 | 5.4 | 0.64 | 2 | narrow** | oval |
| HLMD Din. 2967 | 8.5 | 23.0 | 23.8 | 1.03 | protocone begins opening at very late wear | | | | | | | |
| Range | | 21.6–27.3 | 23.1–25.0 | 0.89–1.05 | | | 5.7–8.4 | 4.0–4.7 | 0.48–0.76 | | ** = prot. still isolated | |
| Mean | | 24.5 | 24.1 | 0.98 | 7:12:9:3 | 1;1;1;0 | 7.3 | 4.3 | 0.60 | 3 | | |
| SD | | 1.95 | 0.63 | 0.07 | | | 1.13 | 0.28 | 0.11 | | | |
| CV | | 7.93 | 2.64 | 7.05 | | | 15.4 | 6.44 | 17.8 | | | |
| *N* | 14 | 7 | 7 | 7 | 7 | 7 | 7 | 7 | 7 | 7 | | |
| **M2**, unworn MSTHT likely 55 mm. | | | | | | | | | | | | |
| HLMD Din. 2875 | 50.0 | 25.5 | | | | | | | | | | |
| HLMD Din. 3175 | 46.5 | 25.2 | 23.3 | 0.93 | 7:8:7:5 | 0;0;0;0 | 7.3 | 3.7 | 0.51 | 1 | open; narr. | sl. ov. * |
| HLMD Din. 2700 | 39.5 | 27.3 | 22.5 | 0.82 | 3:8:6:2 | 0;0;0;0 | 8.9 | 3.5 | 0.39 | 3 | open; spur | flat * |
| **HLMD Din. 2485** | 39.3 | 23.6 | 22.6 | 0.96 | 6:14:8:2 | 1;1;1;1 | 8.0 | 3.9 | 0.49 | 4 | open, narr. | sl. ovate |
| **HLMD Din. 2694** | 25.2 | 22.3 | 23.2 | 0.96 | 5:?:12:3 | 1;1;1;0 | 8.4 | 4.5 | 0.54 | 4 | narrow | sl. ovate |
| Range | | 22.3–23.6 | 22.6–23.2 | | | | 8.0–8.4 | 3.9–4.5 | 0.49–0.54 | | ** = prot. still isolated | |
| Mean | | 22.3 | 22.9 | 0.96 | 6:14:10:3 | 1;1;1;1 | 8.2 | 4.2 | 0.52 | 4 | | |
| SD | | 0.92 | 0.42 | | | | 0.28 | 0.42 | 0.03 | | | |
| CV | | 4.00 | 1.85 | | | | 3.45 | 10.1 | 6.66 | | | |
| *N* | 5 | 2 | 2 | 2 | 2 | 2 | 2 | 2 | 2 | 2 | | |

TABLE 23
(*Continued*)

| Specimen | Height | Length | Width | Ratio | Index | Lingual complexity | Protocone Length | Protocone Width | Protocone Ratio | Pli caballin | Hypoconal groove | Protocone shape |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| **M3**, unworn MSTHT likely 49 mm. | | | | | | | | | | | | |
| HLMD Din. 2909 | 47.0 | | | | | | | | | | | |
| HLMD Din. 2677 | 45.5 | | | | | | | | | | | |
| HLMD Din. 2665 | 42.8 | | | | | | | | | | | |
| HLMD Din. 2883 | 40.0 | | | | | | | | | | | |
| HLMD Din. 2667 | 38.7 | | | | | | | | | | | |
| HLMD Din. 2584 | 35.2 | | | | | | | | | | | |
| HLMD Din. 2887 | 37.7 | 24.3 | 21.6 | 0.89 | | | | | | | open | long |
| HLMD Din. 2555 | 32.0 | | | | | | 8.4 | 3.5 | 0.42 | 2 | open; narr. | flat |
| **HLMD Din. 2444** | 31.0 | 23.6 | 20.4 | 0.86 | 8:8:7:3 | 1;0;1;1 | 7.4 | 3.7 | 0.50 | 3 | open; PPS | ov. long |
| **HLMD Din. 2486** | 27.1 | 22.0 | 22.8 | 1.04 | 4:9:11:4 | 0;0;0;1 | 7.4 | 4.0 | 0.54 | 2 | open; narr. | ovate |
| Range | | 22.0–23.6 | 20.4–22.8 | 0.86–1.04 | | | | 3.7–4.0 | 0.50–0.54 | | ** = prot. still isolated | |
| Mean | | 22.8 | 21.6 | 0.95 | 6:8:9:4 | 1;0;1;1 | 7.4 | 3.9 | 0.52 | 3 | | |
| SD | | 1.13 | 1.70 | 0.12 | | | | 0.21 | 0.03 | | | |
| CV | | 4.96 | 7.86 | 12.8 | | | | 5.51 | 5.51 | | | |
| *N* | 10 | 2 | 2 | 2 | 2 | 2 | 2 | 2 | 2 | 2 | | |
| **C. Eppelsheim**; Senckenberg sample | | | | | | | | | | | | |
| **P2**, unworn MSTHT likely 45 mm. | | | | | | | | | | | | |
| PW/2000/10155-LS | 42.2 | 32.9 | 21.5 | 0.65 | | | | | | | | |
| PW/2000/10133-LS | 42.0 | 35.9 | 23.1 | 0.64 | | | | | | | | |
| PW/2000/10167-LS | 41.2 | 34.1 | 25.2 | 0.74 | 6:13:10:5 | 0;0;1;0 | 7.5 | 4.1 | 0.55 | 2 | open; PPS | ln. ov. |
| PW/2000/10161-LS | 37.5 | 35.3 | 23.7 | 0.67 | 8:9:8:3 | 0;0;1;1 | 7.4 | 5.1 | 0.69 | 4 | open; PPS | ovate |
| PW/2000/10231-LS | 36.0a | | | | | | | | | | | |
| PW/2000/10175-LS | 35.1 | 35.6 | 23.8 | 0.67 | 7:3:2:3 | 0;0;0;0 | 6.8 | 4.9 | 0.72 | 1 | open; PPC | ovate |
| **PW/2000/10169-LS** | 33.0 | 33.2 | 24.9 | 0.75 | 7:11:12:4 | 0;1;1;1 | 8.0 | 4.8 | 0.60 | 2 | open; PPS | ovate |
| **PW/2000/10107-LS** | 31.8 | | 24.0 | | 8:11:9:5 | 0;1;1;1 | 6.5 | 4.0 | 0.62 | 1 | open; PPS | ovate |
| **PW/2000/10091-LS** | 31.0a | | | | 5:12:7:3 | 0;1;1;0 | 6.4 | 5.3 | 0.82 | 2 | open; PPS | ovate |
| **PW/2000/10082-LS** | 31.0a | 32.1 | 24.4 | 0.76 | 7:9:12:2 | 1;0;0;0 | 6.9 | 4.5 | 0.65 | 3 | open | ovate |
| **PW/2000/10083-LS** | 28.6 | 22.7 | 23.5 | 1.04 | 10:10:10:2 | 1;1;1;1 | 6.9 | 4.2 | 0.61 | 4 | open; PPS | oval |
| PW/2000/10109-LS | 23.7 | 32.7 | 25.4 | 0.78 | 5:6:9:3 | 0;0;1;0 | 7.0 | 5.0 | 0.70 | 1 | narr; PPS | oval |
| PW/2000/10176-LS | 18.4 | 31.7 | 24.5 | 0.77 | 5:6:4:2 | 0;0;0;0 | 8.4 | 5.5 | 0.66 | 3 | open; PPC | oval |
| Range | | 22.7–33.2 | 23.5–25.4 | 0.75–1.04 | | | 6.4–8.0 | 4.0–5.3 | 0.60–0.82 | | | |
| Mean | | 30.2 | 24.4 | 0.83 | 7:10:10:3 | | 7.0 | 4.6 | 0.67 | 2 | | |
| SD | | 5.00 | 0.74 | 0.14 | | | 0.57 | 0.49 | 0.09 | | | |
| CV | | 16.6 | 3.04 | 16.5 | | | 8.18 | 10.6 | 13.2 | | | |
| *N* | 13 | 3 | 4 | 3 | 5 | | 5 | 5 | 5 | 5 | | |

TABLE 23
(*Continued*)

| Specimen | Height | Length | Width | Ratio | Index | Lingual complexity | Protocone Length | Protocone Width | Protocone Ratio | Pli caballin | Hypoconal groove | Protocone shape |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| **P3**, unworn MSTHT likely 58 mm. | | | | | | | | | | | | |
| PW/2000/10222-LS | 51.5 | 27.8 | 27.8 | 1.00 | 7:?6:?6:2 | 0;0;0;0 | 7.3 | 4.2 | 0.58 | ? | open | sl. ovate |
| **PW/1998/10001-LS** | 33.6 | 27.1 | 27.0 | 1.00 | 6:14:11:3 | 1;1;1;1 | 6.7 | 5.2 | 0.78 | 5 | open | ovate |
| **PW/2000/10133-LS** | 33.3 | 24.2 | 26.2 | 1.08 | 8:18:12:6 | 1;1;0;0 | 7.5 | 4.2 | 0.56 | 3 | narrow | ovate |
| **PW/2000/10164-LS** | 29.0 | 25.2 | 27.3 | 1.08 | 8:12:10:5 | 1;1;1;1 | 7.3 | 4.7 | 0.64 | 4 | open | ovate |
| **PW/2000/10174-LS** | 24.0a | 24.1 | 24.3 | 1.08 | 8:12:12:4 | 1;1;1;1 | 7.5 | 4.6 | 0.61 | 5 | open | ovate |
| PW/2000/10077-LS | 23.0a | | | | 3:10:6:1 | 0;0;1;0 | 8.0 | 5.1 | 0.84 | 2 | open | ovate |
| Range | | 24.1–27.1 | 24.3–27.3 | 1.00–1.08 | | | 6.7–7.5 | 4.2–5.2 | 0.56–0.78 | | | |
| Mean | | 25.2 | 26.2 | 1.04 | 8:14:11:5 | 1;1;1;1 | 7.3 | 4.7 | 0.65 | 4 | | |
| SD | | 1.39 | 1.35 | 0.05 | | | 0.38 | 0.41 | 0.09 | | | |
| CV | | 5.53 | 5.15 | 4.49 | | | 5.22 | 8.80 | 14.2 | | | |
| *N* | 6 | 4 | 4 | 4 | 4 | | 4 | 4 | 4 | 4 | | |
| **P4**, unworn MSTHT likely 59 mm. | | | | | | | | | | | | |
| PW/2000/10149-LS | 48.5 | 27.1 | 26.7 | 0.99 | 6:15:?11:4 | 0;0;0;1 | 7.1 | 4.3 | 0.61 | 4 | open | ovate |
| PW/2000/10180-LS | 47.1 | 27.1 | 23.0 | 1.08 | | | | | | | long. trian. | sl. ovate |
| **PW/2000/?????-LS** | 38.5 | 25.8 | 25.0 | 0.97 | 4:11:9:3 | 0;1;1;0 | 6.7 | 4.7 | 0.71 | 1 | open | ovate |
| **PW/2000/10158-LS** | 37.0 | 23.9 | 24.2 | 1.01 | 8:13:9:4 | 1;1;1;1 | 7.4 | 4.5 | 0.61 | 4 | open | ovate |
| **PW/10178/10081-LS** | 37.0 | 22.5 | 25.5 | 1.08 | 5:12:11:3 | 1;1;1;1 | 7.2 | 4.4 | 1.08 | 5 | open | sl. ovate |
| **PW/10178/10078-LS** | 27.0 | 23.9 | 23.1 | 0.97 | 4:14:10:4 | 1;1;1;1 | 7.3 | 4.2 | 1.08 | 2 | open | ovate |
| Range | | 22.5–25.8 | 23.1–25.5 | 0.97–1.08 | | | 6.7–7.4 | 4.2–4.7 | 0.61–1.08 | | | |
| Mean | | 24.0 | 24.5 | 1.01 | 5:13:4:4 | 1;1;1;1 | 7.2 | 4.5 | 0.87 | 3 | | |
| SD | | 1.35 | 1.05 | 0.05 | | | 0.31 | 0.21 | 0.25 | | | |
| CV | | 5.64 | 4.28 | 5.27 | | | 4.35 | 4.68 | 28.6 | | | |
| *N* | 6 | 4 | 4 | 4 | 4 | | 4 | 4 | 4 | 4 | | |

TABLE 23
(*Continued*)

| Specimen | Height | Length | Width | Ratio | Index | Lingual complexity | Protocone Length | Protocone Width | Protocone Ratio | Pli caballin | Hypoconal groove | Protocone shape |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| **M1**, unworn MSTHT likely is 59 mm. | | | | | | | | | | | | |
| PW/2000/10162-LS | 51.5a | | | | | | | | | | | |
| PW/2000/10000-LS | 44.0 | 25.5 | 22.0 | 0.86 | 7:7:7:2 | 0;0;0;0 | 7.1 | 3.7 | 0.52 | 3 | open | sl. ovate |
| PW/1998/10073-LS | 37.8 | | | | 7:10:9:3 | 0;0;1;0 | 7.3 | 4.1 | 0.56 | 3 | open | oval |
| **PW/2000/10207-LS** | 36.6 | 23.8 | 22.4 | 0.94 | 5:15:9:6 | 0;1;1;1 | 6.3 | 4.0 | 0.63 | 3 | open | ovate |
| **PW/2000/10200-LS** | 31.0 | 24.9 | 25.3 | 1.02 | 9:17:13:3 | 1;1;1;1 | 7.4 | 3.8 | 0.51 | 4 | open | s. conc. |
| **PW/2000/10068-LS** | 29.1 | 22.6 | 24.7 | 1.08 | 7:14:11:6 | 1;1;1;1 | 7.8 | 5.0 | 0.64 | 5 | open | oval |
| **PW/2000/10189-LS** | 22.5 | 27.0 | 27.0 | 1.00 | 12:?15:?:4 | 1;1;?;1 | 8.4 | 5.5 | 0.65 | 5 | open | ovate |
| Range | | 22.6–27.0 | 22.4–27.0 | 0.94–1.08 | | | 6.3–8.4 | 3.8–5.5 | 0.51–1.08 | | | |
| Mean | | 24.6 | 24.9 | 1.01 | 8:15:8:5 | 1;1;1;1 | 7.5 | 4.6 | 0.72 | 4 | | |
| SD | | 1.87 | 1.91 | 0.06 | | | 0.89 | 0.81 | 0.25 | | | |
| CV | | 7.61 | 7.65 | 5.65 | | | 11.8 | 17.7 | 34.3 | | | |
| *N* | 6 | 4 | 4 | 4 | 4 | | 4 | 4 | 4 | 4 | | |
| **M2**, unworn MSTHT likely 57 mm. | | | | | | | | | | | | |
| PW/2000/10173-LS | 52.0 | 27.8 | 24.4 | 0.88 | 4:8:4:3 | 0;0;0;0 | 7.3 | 3.9 | 0.52 | 1 | open | oval |
| PW/2000/10224-LS | 49.7 | 25.0 | 21.5 | 0.86 | | | | | | | | oval |
| PW/1998/10074-LS | 48.8a | totally unworn | | | | | | | | | | |
| **PW/2000/10148-LS** | 36.0 | 23.3 | 22.6 | 0.97 | 4:11:8:6 | 0;0;1;0 | 7.8 | 4.4 | 0.56 | 2 | open | ovate |
| **PW/2000/10186-LS** | 31.0 | 24.2 | 24.4 | 1.01 | 5:11:7:4 | 0;0;0;0 | 7.1 | 4.5 | 0.63 | 3 | open | ovate |
| Range | | 23.3–24.2 | 22.6–24.4 | 0.97–1.01 | | | 7.1–7.8 | 4.4–4.5 | 0.56–0.63 | | | |
| Mean | | 23.8 | 23.5 | 0.99 | 5:11:8:5 | 0;0;1;0 | 7.5 | 4.5 | 0.60 | 3 | | |
| SD | | 0.64 | 1.91 | 0.03 | | | 0.50 | 0.07 | 0.05 | | | |
| CV | | 2.68 | 7.65 | 2.74 | | | 6.64 | 1.59 | 8.23 | | | |
| *N* | 5 | 2 | 2 | 2 | 2 | 2 | 2 | 2 | 2 | 2 | | |

TABLE 23
(*Continued*)

**M3**, unworn MSTHT likely 57 mm.

| Specimen | Height | Length | Width | Ratio | Index | Lingual complexity | Protocone Length | Protocone Width | Protocone Ratio | Pli caballin | Hypoconal groove | Protocone shape |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| PW/2000/10157-LS | 49.5 | very early wear | | | | | | | | | | |
| PW/2000/10151-LS | 34.5 | 23.6 | 20.2 | 0.86 | 8:11:8:7 | | 6.2 | 3.1 | 0.50 | 2 | open | ovate |
| **PW/2000/10111-LS** | 32.5 | 23.0 | 20.2 | 0.88 | 3:15:7:4 | 1;1;1;0 | 8.0 | 4.0 | 0.50 | 3 | open | ovate |
| **PW/2000/10088-LS** | 27.2 | 23.5 | 20.3 | 0.86 | 5:8:8:3 | 1;1;0;1 | 6.7 | 4.4 | 0.66 | 1 | open | ovate |
| **PW/2000/10163-LS** | 17.6 | 20.7 | 21.8 | 1.08 | 4:10:8:3 | 1;1;1;0 | 7.6 | 5.0 | 0.66 | 1 | open | ovate |
| PW/2000/10206-LS | 7.6 | 26.4 | 21.4 | 0.81 | 6:12:7:4 | 1;1;0;0 | 8.7 | 5.3 | 0.61 | 4 | ? | ovate |
| Range | | 20.7–23.5 | 20.2–21.8 | 0.86–1.08 | | | 6.7–8.0 | 4.0–5.0 | 0.50–0.66 | | | |
| Mean | | 22.4 | 20.8 | 0.94 | 4:10:8:3 | 1;1;1;0 | 7.4 | 4.5 | 0.60 | 2 | | |
| SD | | 1.49 | 0.90 | 0.12 | | | 0.67 | 0.50 | 0.09 | | | |
| CV | | 6.67 | 4.32 | 12.9 | | | 8.96 | 11.3 | 15.0 | | | |
| *N* | 6 | 3 | 3 | 3 | 3 | 3 | 3 | 3 | 3 | 3 | | |

of P2 are typically confluent, also as seen in the California taxon and as found in virtually all other species of *Cormohipparion*, with perhaps *C. fricki* displaying the greatest frequency of this morphology among those other species.

For an even more limited sample at Atzelsdorf (table 21), plication counts are P2, 5:8:5:2 (late wear); P3, not represented; P4, 2:7:5:3; M1, 4:10:6:1; and M2, not represented. The sample is too small to indicate likely MSTHT for the upper cheek teeth, but a dimension comparable to that from Gaiselberg seems warranted. The single p2 shows that the pre- and postfossettes are confluent.

The taxon from Mariathal, Austria, is well represented. Overall, the upper cheek tooth morphology (fig. 25A–D) resembles that of *H. primigenium* from Höwenegg (fig. 29B) but is less complex. Based on the Mariathal sample (tables 21–22), P2 has an unworn crown height of about 44 mm. The width of the tooth is relatively narrow in early wear but gains mature breadth after about 17% wear (PIUW 3540/6). The pli caballin and hypoconal groove are not complete in this early-wear-stage tooth, however. Overall, the pre- and postfossettes remain connected labially throughout wear (table 21). The lingual border of protocone becomes relatively flat at about 17% wear, but in most cases (tables 21–22) the protocone is slightly ovate to ovate rather than flat (mean protocone width-to-length ratio of 0.56). The lingual border of the protocone is flat in only one of five adult specimens and in one other specimen in early wear, out of a total sample of fifteen specimens (table 22). In all but two instances (one adult; protocone slightly ovate; **PIUW 3504/3**, fig. 25A), the protocone width-to-length ratio is 0.50 or greater.

The fossette pattern is still not fully developed until 27% wear (**PIUW 3540/9**) and shows a relatively large pli protoconule that is plicated both lingually and labially as part of the plication pattern of the prefossette (fig. 25A). The pli protoconule is most commonly connected to, rather than isolated from, the adjacent prefossette. The hypoconal groove is mostly elongate and relatively narrow throughout. The protocone has an aberrant spur in **PIUW 3540/3** at 33% wear (fig. 25A) and makes an also aberrant

TABLE 24
**Measurements (mm) of Crania of *Hippotherium primigenium* from Germany and Austria**

| Specimen | Character[a] 1 | 2 | 3 | 4 | 6 | 7 |
|---|---|---|---|---|---|---|
| ***Hippotherium primigenium*; Höwenegg, Germany; medial Vallesian** | | | | | | |
| SMNK Ho A ♂ | 134.0 | | | | 495.0 | 87.0 |
| SMNK Ho I ♀ | | | | | | 90.0 |
| SMNK Ho B ♂ | | | | | | 86.0 |
| SMNH Ho C ♀ | 139.0 | | | | | 88.0 |
| HLMD Ho V ♀ | 138.0 | 147.0 | 108.0 | 84.0 | 460.0 | 81.0 |
| HLMD Ho M ♂ | 141.0 | | | | | 86.0 |
| HLMD Ho G ♂ | 149.0 | | | | | 83.0 |
| HLMD Ho III | | | | | | 83.0 |
| HLMD Ho E ♀ | | | | | | 81.0 |
| Range | 134.0–149.0 | | | | 460.0–495.0 | 81.0–90.0 |
| Mean | 140.2 | 147.0 | 108.0 | 84.0 | 477.5 | 85.0 |
| SD | 5.54 | | | | 24.75 | 3.16 |
| CV | 3.95 | | | | 5.18 | 3.72 |
| *N* | 5 | 1 | 1 | 1 | 2 | 9 |
| ***Hippotherium* sp.; Inzersdorf, Austria; Pannonian E; medial Vallesian** | | | | | | |
| NHMW A1342 | | | | | | 85.0 |
| ***Hippotherium* sp.; Laarberg, Austria; Pannonian E; medial Vallesian** | | | | | | |
| NHMW 1842[c] ♂ | | 124.0 | | | | 90.0 |

| Specimen | Character[a] 8 | 9 | 13 | 14[b] | 15 | 22[b] |
|---|---|---|---|---|---|---|
| ***Hippotherium primigenium*; Höwenegg, Germany; medial Vallesian** | | | | | | |
| SMNK Ho A ♂ | 72.0 | 163.0 | | 30.0 | 53.0 | 64.0 |
| SMNK Ho I ♀ | 81.0 | 168.0 | | 29.0 | 45.0 | |
| SMNK Ho B ♂ | 71.0 | 161.0 | | | | |
| SMNH Ho C ♀ | 72.0 | 161.0 | | | | |
| HLMD Ho V ♀ | 74.0 | 156.0 | | 34.0 | 35.0 | 77.0 |
| HLMD Ho M ♂ | 82.0 | 164.0 | | | | |
| HLMD Ho G ♂ | 72.0 | 147.0 | | | | |
| HLMD Ho III | 73.0 | 158.0 | | | | |
| HLMD Ho E ♀ | 75.0 | 157.0 | | | | |
| Range | 71.0–82.0 | 147.0–168.0 | | 29.0–34.0 | 35.0–53.0 | 64.0–77.0 |
| Mean | 74.7 | 159.4 | | 31.0 | 44.3 | 70.5 |
| SD | 4.06 | 5.98 | | 2.65 | 9.02 | 9.19 |
| CV | 5.44 | 3.75 | | 8.53 | 20.34 | 13.00 |
| *N* | 9 | 9 | | 3 | 3 | 2 |
| ***Hippotherium* sp.; Inzersdorf, Austria; Pannonian E; medial Vallesian** | | | | | | |
| NHMW A1342 | 68.0 | 153.0 | | | | 57.0 |
| ***Hippotherium* sp.; Laarberg, Austria; Pannonian E; medial Vallesian** | | | | | | |
| NHMW 1842[c] ♂ | 72.6 | 160.0 | 66.0 | 37.0 | 51.5 | |

connection to the protoloph at 49% wear in PIUW 3540/8. The anterior border of the prefossette remains complex (up to 9 plis), at least until about 32% wear in **PIUW 3540/7**, but tends to diminish thereafter. Based on the teeth in this sample, the presence of a bifurcate lingual-most pli on the anterior and posterior surfaces of pre- and postfossettes (**lingual complexity**, recorded for each tooth in tables 22–23) seems to herald the attainment of the adult dentition, and this condition is interpreted to have been achieved

TABLE 24
(*Continued*)

| Specimen | Character[a] 25[b] | 28[b] | 29 | 30 | 31 | 32 |
|---|---|---|---|---|---|---|
| ***Hippotherium primigenium*; Höwenegg, Germany; medial Vallesian** | | | | | | |
| SMNK Ho A ♂ | 108.0 | 71.0 | 47.0 | 122.0 | 180.0 | 46.0 |
| SMNK Ho I ♀ | | | | | | 43.0 |
| SMNK Ho B ♂ | 97.0 | 65.0 | 46.0 | | 225.0 | 57.0 |
| SMNH Ho C ♀ | 104.0 | | | 157.0 | 176.0 | 53.0 |
| HLMD Ho V ♀ | 102.0 | 68.0 | 49.0 | 126.0 | 174.0 | 46.0 |
| HLMD Ho M ♂ | | | | | 213.0 | |
| HLMD Ho G ♂ | | 61.0 | 61.0 | 141.0 | 227.0 | |
| Range | 97.0–108.0 | 61.0–71.0 | 46.0–61.0 | 122.0–157.0 | 174.0–227.0 | 43.0–57.0 |
| Mean | 102.8 | 66.3 | 50.8 | 136.5 | 199.2 | 49.0 |
| SD | 4.57 | 4.27 | 6.95 | 15.93 | 25.18 | 5.79 |
| CV | 4.51 | 6.45 | 13.69 | 11.67 | 12.64 | 11.81 |
| *N* | 4 | 4 | 4 | 4 | 6 | 5 |
| ***Hippotherium* sp.; Inzersdorf, Austria; Pannonian E; medial Vallesian** | | | | | | |
| NHMW A1342 | 94.0 | 51.0 | 51.0 | | 168.0 | 49.0 |
| ***Hippotherium* sp.; Laarberg, Austria; Pannonian E; medial Vallesian** | | | | | | |
| NHMW 1842[c] ♂ | 100.0 | 64.0 | 55.0 | 139.0 | 186.0 | 48.0 |

| Specimen | Character[a] 33 | 34 | 35 | 36[b] | 37[b] | 38[b] |
|---|---|---|---|---|---|---|
| ***Hippotherium primigenium*; Höwenegg, Germany; medial Vallesian** | | | | | | |
| SMNK Ho A ♂ | 65.0 | 73.0 | 43.0 | 24.0 | 52.0 | 62.0 |
| SMNK Ho I ♀ | 80.0 | 83.0 | 53.0 | 27.0 | 45.0 | 75.0 |
| SMNK Ho B ♂ | 94.0 | 98.0 | 55.0 | 16.0 | 47.0 | |
| SMNH Ho C ♀ | 85.0 | 89.0 | 39.0 | 48.0 | 48.0 | 82.0 |
| HLMD Ho V ♀ | 79.0 | | 59.0 | | | 69.0 |
| HLMD Ho III | 80.0 | | 58.0 | 19.0 | | 93.0 |
| Range | 65.0–94.0 | 73.0–98.0 | 39.0–59.0 | 16.0–48.0 | 45.0–52.0 | 62.0–93.0 |
| Mean | 80.5 | 85.8 | 51.2 | 26.8 | 48.0 | 76.2 |
| SD | 9.44 | 10.50 | 8.26 | 12.60 | 2.94 | 11.95 |
| CV | 11.73 | 12.25 | 16.14 | 47.01 | 6.13 | 15.68 |
| *N* | 6 | 4 | 6 | 5 | 4 | 5 |
| ***Hippotherium* sp.; Inzersdorf, Austria; Pannonian E; medial Vallesian** | | | | | | |
| NHMW A1342 | 62.0 | | 50.0 | 17.0 | | 37.0 |
| ***Hippotherium* sp.; Laarberg, Austria; Pannonian E; medial Vallesian** | | | | | | |
| NHMW 1842[c] ♂ | 82.0 | 83.0 | 48.0 | 33.0 | 51.0 | 87.0 |

when this morphology obtains in a majority of the four loci where it may occur (see P3 and P4 of fig. 25B–C for examples). In this zone of maximum development (**PIUW 3540/9–3540/7**, $N = 5$, table 22), the mean plication index is 8:9:6:3. The hypocone is fully formed from **PIUW 3540/9**. In 3540/2 (and higher-crowned teeth; table 22) it still is pinched (= immature), and the lingual-most pli of each fossette border is mostly simple (lingual complexity scored 0;0;0;0, table 22) and not bifurcate.

In that the mature pattern is stable from about 27% wear to about 48% wear, specimens above **PIUW 3540/9** (MSTHT 32.5 mm) and below **PIUW 3540/7** (MSTHT 29.5 mm) on table 22 are not considered in the statistical analysis.

In P3, the unworn crown height likely is 55 mm. The pattern is fully developed,

TABLE 24
(*Continued*)

| Specimen | Remarks |
|---|---|
| ***Hippotherium primigenium*; Höwenegg, Germany; medial Vallesian** | |
| SMNK Ho A ♂ | Adult; MSTHT; P2, 32; P3, 38; P4, 37; M1, 33; M2, 31; M3, 35; Very crushed laterally; bones also fractured |
| SMNK Ho I ♀ | Also numbered as I-53. Adult; P2, 30; P3, 31; P4, 34; M1, 30; M2, 35; M3, 30 |
| SMNK Ho B ♂ | Also numbered as I-154. Subadult; MSTHT; P2, 40; P3, 40; P4, 46; M1, 39; M2, 42; M3, 33 |
| SMNH Ho C ♀ | Young adult; MSTHT not known |
| HLMD Ho V ♀ | Old adult; well preserved; best dimensions; MSTHT not known |
| HLMD Ho M ♂ | Adult; MSTHT not known |
| HLMD Ho G ♂ | Mid-wear adult; MSTHT not known |
| HLMD Ho III | Old adult; MSTHT not known |
| HLMD Ho E ♀ | Old adult; MSTHT not known |
| ***Hippotherium* sp.; Laarberg, Austria; Pannonian E; medial Vallesian** | |
| NHMW 1842[c] ♂ | Laterally crushed skull; restored in plaster. Early adult, relatively complete cranium ant. to (inc.). orbit; meas. of facial and palatal region OK; dentition; occlusal pattern best represented on M1 |

[a]Characters are described in detail in table 1.
[b]Characters 14, 22, 25, 28, 36–38 doubtful due to lateral crushing in all specimens.
[c]A4229, number also provided to this specimen.

although still in an immature state, in the tallest available tooth (PIUW 3540/89; MSTHT 42.5) at about 23% wear. The protocone is isolated at all wear stages up to about 90% wear (PIUW 3540/124, table 22). The protocone tends to be lingually flattened or even concave (PIUW 3540/109; MSTHT 42.3 mm), but in later wear it becomes slightly to clearly ovate. In a sample of thirty-eight teeth, of which twenty-six are in an adult stage of wear, the lingual border of the protocone is flat in eight cases, of which three are adult, and concave in three cases, of which one is an adult. Overall, the protocone (fig. 25B) is slightly ovate to ovate (width-to-length ratio of 0.54) and tends to become larger toward the base of tooth (below 50% wear). The mean protocone width-to-length ratio is 0.54, with the range being from 0.41–0.66 in adult P3. In one case where the protocone is flat, its width-to-length ratio is 0.43 (table 22). The protocone tends to be less elongate and somewhat more ovate by **PIUW 3540/92–PIUW 3540/112** (see table 22).

Pre- and postfossettes are separated by at least 23% wear (PIUW 3540/89 and 109) but still connected in PIUW 3540/110 (24% wear). The fossette plication count decreases sharply below 58% wear (23 mm). In PIUW 3540/114 and 3540/118 (late wear; below 21 mm), the pre- and postfossettes are once again connected labially (62% and 66% wear, respectively). The hypocone is formed and confluent with the metaloph at least by 22% wear (PIUW 3540/89) and remains so for the life of the tooth. The hypoconal groove is narrow in the early record of these teeth but becomes more widely open (less narrow) by about 27% wear (**PIUW 3540/92**; MSTHT 40.2 mm).

The mature wear interval appears to range from about 28% to 58% based on the widely distributed presence of the lingual-most plis of the pre- and postfossettes being bifurcate (or more) and below which the morphology is sharply simplified in conjunction with the simplification of the fossette borders. Thus, specimens above **3540/92** and below **3540/115** in table 22 were not included in the statistical comparisons.

The greatest complexity in enamel pattern is displayed between 40 mm and 23 mm (adult range), during which the hypoconal groove is open but tends to be narrow, and the pli caballin (fig. 25B) displays mostly three loops (range is 3–5; mean is 3). The pli protoconule is present as a distinct, isolated, subrectangular entity in most cases (eighteen), in fourteen of which it is marked by additional plications (on its anterior border). In nine cases (mostly early in the wear series), the pli protoconule is elongate, with four of those in very late wear having one or two plications on the labial border. Within the adult range (**PIUW 3540/92–3540/115**, table 22), the mean plication index is 7:12:10:3. A bifurcate terminal plication pattern for the lingual-most pli on the anterior border of the pre- and postfossette (fig. 25B), respectively, is best displayed in specimens between **PIUW 3540/92** and **3540/115** (with more than one occurrence between the four possible lingual complexity locations [28%–58% wear; table 22]).

In P4, the unworn crown height likely is 56 mm. The pattern incompletely is developed in tallest tooth (PIUW 3540/70 (MSTHT 52.5 mm) at ca. 6% wear. The occlusal pattern is formed, but still too simple, in PIUW 3540/65 at about 18% wear. The enamel pattern is about fully developed in **PIUW 3540/45** (MSTHT 39.8 mm) at circa 29% wear, with the adult range continued to **PIUW 3540/52** (MSTHT 25.6 mm), on table 22, at a wear stage of 44%. Within this range, the protocone is isolated (in fact, at all wear stages). Its lingual border is subovate in all but one of fourteen mature specimens, where it is flat. Of the entire twenty-three specimens in the sample, the protocone is flat only in three less worn specimens, as well as in the most highly worn specimen. The protocone width-to-length ratio ranges from 0.45–0.60 (mean 0.51) in the adult state. All are subovate to ovate in this range.

The hypocone is formed at least by 16% wear (3540/62; MSTHT 47); it is fully confluent with the metaloph by 27% wear (3540/61; MSTHT 41.2) and remains so for the life of the tooth. The greatest complexity in enamel pattern is displayed between 40 mm and 32 mm (adult range; 29–43% wear), within which the hypoconal groove is open, but narrow, and the pli caballin displays mostly two loops (five of fourteen specimens have three loops). The pli protoconule is present as a distinct, isolated, subrectangular feature and only rarely (**PIUW 3540/68**, **PIUW 3540/48**) is marked by additional plications (on its anterior border). The mean plication index is 6:13:9:3. A bifurcate terminal plication pattern for the lingual-most pli on the anterior border of the pre- and postfossette, respectively, is best displayed from **PIUW 3540/64** to **PIUW 3540/52** (37%–54% wear), but the development of this kind of lingual complexity mirrors the wear range of the greatest fossette border complexity (**PIUW 3540/45–PIUW 3540/52**; table 22). Specimens above or below this range are not considered in the statistical analyses (tables 21–22).

In M1, the unworn crown height likely is 55 mm. The enamel pattern is incompletely developed in the tallest tooth (PIUW 3540/146), with very early incipient wear (MSTHT 52.9 mm; 4% wear). Pre- and postfossettes become separated in PIUW 3540/143 (MSTHT 48.9 mm) at 11% wear.

M1 achieves its mature morphology at about 22% wear (**PIUW 3540/140**), with the hypocone opening to the metaloph and plication complexity increasing strongly relative to PIUW 3540/144 (table 22). By 44% wear (**PIUW 3540/139**), the hypocone is fully open to the metaloph, and the triradiate plication pattern for the lingual-most plis in the pre- and postfossettes is now apparent. This morphology carries to **PIUW 3540/136** (47% wear; fig. 25D). The mature wear range is considered to be embraced between **PIUW 3540/140** and **UW 3540/136** (22%–45% wear) in table 22, with specimens above or below that range not considered in the statistical analyses.

The protocone is isolated at all wear stages and is subovate to ovate in most cases; its width-to-length ratio ranges from 0.44–0.58 (mean is 0.50), and its lingual border mostly is subovate to ovate, with two of nine mature range specimens having a flat lingual border and one showing one that is slightly concave. In early wear (PIUW 3540/134 and /141; MSTH 47.7 mm or 13% wear and MSTHT 44.8 mm or 18% wear), the protocone is relatively elongate but shows a more ovate morphology, at least by 20% wear in 3540/144, and is subovate to ovate in the majority of the other specimens (average width-to-length ratio for protocones scored as "oval" is 0.50). The protocone has a flat lingual border in only four of the seventeen specimens available here, taking into account all wear stages. In two of the nine adult examples, the width-to-length ratio is 0.47 and 0.49 (table 22). By about 39% wear (**PIUW 3540/135)**, the protocone begins to become broader and larger, and at about the 44% wear (**PIUW 3540/137**), the intensity of enamel plication diminishes. The hypocone is not fully shaped in PIUW 3540/144 at circa 20% wear, but it is widely open to metaloph in **PIUW 3540/145** at 33% wear (MSTHT 36.7 mm). The hypocone still is slightly constricted in **PIUW 3540/139** and **PIUW 3540/138** at 33–34% wear but thereafter generally is widely confluent with the metaloph.

In the adult wear interval (**PIUW 3540/140–3540/136**, 22%–45% wear), the mean plication index is 6:11:9:3. The plis caballin range from 2–5 (average is 3), and the hypoconal groove is open but narrow. At about 43 mm (22% wear), the plication pattern is characterized by the lingual-most pli of each fossette having a bifurcate or trifurcate internal display, with the maximum development of this feature (lingual complexity, table 22) best developed in the adult wear interval (to 39% wear; **PIUW 3540/147**) but extends to 45% wear (**PIUW 3540/136**, fig. 25D). The pli protoconule is a large element that is commonly isolated from the adjacent part of the prefossette and commonly bears a single pli on either its labial or lingual margin (fig. 25D) or bears one or more plis on its anterior margin. The opposing lingual-most plis of the prefossette extend toward each other and reach within 1.5–2 mm of each other, depending on wear stage (2 mm = early).

The M2 is represented by few specimens and appears to be similar to M1. For M3, there are many specimens, but these were not analyzed except for maximum crown height. 3540/318 is 44.2 mm tall at the mesostyle, with the occlusal pattern in very early wear. It is estimated that the unworn mesostyle height was about 54 mm.

Based on these data, the Mariathal and Gaiselberg samples are similar in the consistent labial connection of the pre- and postfossette in P2. The Mariathal sample may be slightly taller crowned than that from Gaiselberg, and the mean complexity of the fossette borders are slightly greater (tables 21–22). In both samples, the protocone is mostly subovate to ovate, with that of P3 and M1 at Gaiselberg perhaps being somewhat more ovate than at Mariathal, and P4 being the reverse. The pli protoconule is generally persistent and commonly plicated. The lingual-most plis of the pre- and postfossette are commonly bifurcate in the adult condition but are rarely composed of more than two or three branches. With the proviso that the age of the Mariathal sample is not precisely constrained (may be of Pannonian C or E age), and that it may be slightly taller crowned and slightly more complex than that from Gaiselberg, the Mariathal morphology is taken here as representative of the Pannonian C species of *Hippotherium*. As developed below, it may be warranted to separate this species from *H. primigenium*, *s.s.*, from Eppelsheim, and possibly from Höwenegg.

The locality at Eppelsheim, in the Rhine River valley of Germany, contains the type material of the species *Hippotherium primigenium* Meyer 1829. The specimens were derived from the Dinotherium Sands, a local source of construction material. As summarized in Woodburne (1996a), mammals from the Dinotherium Sands are correlated to MN 9, and the Eppelsheim sample of *H. primigenium* is considered likely to have been older than that from Höwenegg (see above and table 21). Two samples from the Dinotherium Sands at Eppelsheim were examined for this study (tables 21, 23). The sample in the HLMD is as large as that from Mariathal; the Senckenberg sample is somewhat smaller. Both samples apparently were recovered from the general area, and the same stratigraphic context, as produced the type of *H. primigenium* (e.g., Franzen et al. 2003b). Franzen, Fejfar, and Storch (2003a) consider that the Dinotherium Sands may be as young as MN 10, based on a consideration of the stage of evolution of two micromammals (*Plesiosorex roosi* and *Crusafontia kormosi*), later than the MN 9 age proposed by Bernor et al. (1996). Resolution of this matter awaits further evidence, and until that is forthcoming, an MN 9 age for the Dinotherium Sands is followed here.

As indicated in table 23, the HLMD sample of *H. primigenium* from Eppelsheim suggests that the unworn MSTHT of P2 was no taller than 50 mm. HLMD Din. 2987 shows that this tooth is at least 45 mm tall at the mesostyle. It is possible that the mature wear stage is reached by about 33 mm, as in

**HLMD Din. 2686.** It is likely that this part of the pattern persists until about 24 mm (**HLMD Din. 2443**), so that the range of this part of the crown is seen from 34% to 52% wear. In almost all cases (and in all pertinent specimens, regardless of wear stage), the pre- and postfossettes are separate; they are connected in only four specimens (out of a possible twenty-two with appropriate pattern available) or 18% (table 21). This is comparable to the frequency of this occurrence in the Eppelsheim collections of the Senckenberg Museum (see below), and compatible with the observations in the sample from Höwenegg (see below), and in distinct contrast to the situation in the samples from Gaiselberg and Mariathal (see above). In the adult wear interval, the lingual plis of the pre- and postfossette typically have some bifurcated examples, but these are not as persistent as in the material from Frankfurt. In virtually all instances, the protocone is ovate or slightly ovate, with examples having a flat lingual surface being restricted to early wear stage material (HLMD Din. 2658). In the HLMD material, the mean ($N$ = 11) plication pattern is 7:11:10:4, more complex than the Vienna Basin material. In this sample, the specimens within the range embraced by **HLMD Din. 2686–HLMD Din. 2443** in table 23 are considered to be adult teeth (34–52% worn). Specimens above or below this range are not considered in the statistical analyses in table 22).

As indicated in table 23, the protocone is represented by twenty-two specimens, of which thirteen are in an adult stage of wear. In all adult cases, the protocone is subovate to ovate, with a width-to-length ratio of 0.5–0.7 and a mean of 0.67. In one early wear individual, the lingual border of the protocone is flat, and in another it is concave, but both are in so early a stage of wear as to be unmeasurable.

For P3, the least worn specimen in the collection is HLMD Din. 2683, with a mesostyle height of about 46 mm. The unworn MSTHT for P3 is estimated at about 52 mm, in being slightly taller than P2 but not as tall as P4. The adult wear pattern is considered to have been developed by about 40 mm (**HLMD Din. 2882**), and to have persisted until about 24 mm (**HLMD Din. 2579**) or within a range of 23% to 54%. Teeth above or below the range embraced by these specimens are not considered in the statistical analyses of table 22. The total sample is composed of sixteen specimens, of which ten are adult. In these, the protocone is usually subovate to ovate, with only a few specimens showing a subtriangular (**HLMD Din. 2882**) to flat lingual border (**HLMD Din. 2482, 2449**; width-to-length ratios of 0.48 and 0.54, respectively) or slightly concave (**HLMD Din. 2924**; width-to-length ratio of 0.51). Overall, the mature stage width-to-length protocone ratio ranges from 0.45–0.69, with a mean of 0.57. The pli protoconule is variably present in this sample but does not reach the prominence seen in the Höwenegg material. The mean plication count is 6:10:9:3 (table 23). This seems comparable to that from Gaiselberg (table 22).

For P4, the least worn tooth in the sample is HLMD Din. 2710, with a mesostyle height of 52 mm. The degree of wear developed on this tooth suggests that the unworn MSTHT for P4 is 55 mm. The adult wear pattern is considered to have been developed by about 38 mm and to have persisted to 21 mm, or within a range of 31% to 62% wear (**HLMD Din. 2680–HLMD Din. 2975**). Specimens above or below the indicated range are not considered in the statistical analyses in table 23. The protocone is usually subovate to ovate in twenty specimens overall, of which fourteen are adult (flat in only one specimen; width-to-length ratio of 0.55). The adult width-to-length protocone ratio ranges from 0.48–0.71, with a mean of 0.58. The disposition of the pli protoconule is compatible with the situation in P3 and M1. The mean plication count ($N$ = 14) is 7:12:9:4, apparently most comparable to that from Mariathal (table 22).

Regarding M1, HLMD Din. 2978 is a nearly unworn tooth with a mesostyle height of 54 mm, and it appears likely that an unworn MSTHT for M1 was about 58 mm. The sample comprises thirteen specimens, of which seven are in the adult stage. The adult wear pattern is considered to have been developed by about 39 mm and persisted to about 26 mm, or a range of 33% to 56% (**HLMD Din. 2437–HLMD Din. 2448**). Specimens above or below the indicated range are not considered in the statistical analyses in table 23. The protocone is slightly ovate or ovate in virtually all specimens, except **HLMD Din. 2682**, where the lingual margin is slightly concave. The width-to-length protocone ratio ranges from 0.48–0.76, with a mean of 0.60 (table 23). The protocone is isolated almost completely to the base of the crown. HLMD Din. 2967 shows that the protocone is just beginning to open to the protoloph at about 8.5 mm, or at a wear level of 86%. As in P4 the lingual complexity of the lingual plis of the pre and postfossettes is less than at Höwenegg. The mean plication count for M1 ($N = 7$) is 7:12:9:3. This sample is about intermediate between those from Mariathal and the Eppelsheim sample at the Senckenberg Museum (table 21).

In M2, HLMD Din. 2875 has a mesostyle height of about 50 mm and suggests that the unworn MSTHT likely was 55 mm. In that context, the adult wear pattern is developed from about 40 mm and persists until at least 25 mm, or a range of 20% to 50% based on this limited sample (**HLMD Din. 2485–HLMD Din. 2694**). The available sample (two adult of five) indicates that the protocone is slightly ovate in all adult specimens of M2. The protocone width-to-length ratio ranges from 0.49 to 0.54 (the mean is 0.51). One specimen in early wear has a flat lingual border of the protocone and a width-to-length ratio of 0.39 (table 23). With the proviso that only two specimens are available for this purpose, the mean plication count (4) in the adult HLMD material appears about comparable to that from Mariathal (imprecise counts) and more complex than that in the Senckenberg collection (table 21).

M3 (HLMD Din. 2909) has a mesostyle height of about 47 mm and indicates that the unworn MSTHT for M3 was about 49 mm. The adult wear pattern was developed by at least 31 mm (57%), but the sample is limited (two adult wear teeth of ten). These indicate that the width-to-length ratio ranges from 0.50 to 0.54 (the mean is 0.5.2). The mean pli caballin count is three.

The Senckenberg sample from the Dinotherium Sands is composed of fewer specimens than that from the HLMD. The P2 unworn MSTHT appears to be about 45 mm (table 23). The least worn teeth in the sample (PW/2000/10155 and 10133) are 42.5 and 42.0 mm tall, respectively, and suggest that the unworn MSTHT would not be greatly taller. The adult wear pattern seems to be represented between 33 mm (**PW/2000/10169**) and 28 mm (**PW/2000/10183**) and lost by about 24 mm (PW/2000/10109), or between about 27% and 47% wear. The mature wear interval is considered bracketed by **PW/2000/10169–PW/2000/10183**. Specimens above and below that range are not considered in the statistical analyses of table 23. Regarding teeth that might have been considered as in the adult state, the hypocone is barely confluent with the metaloph in PW/2000/10167 (41.2 mm), and the hypoconal groove is nearly closed posteriorly, so the tooth is not considered to have achieved a fully adult pattern. The pattern of the anterior border of the prefossette in PW/2000/10161 is still continuous with that from the rear of the anterocone and thus also is still not in the adult state. Only the ectoloph region is preserved in PW/2000/10231, and the mesostyle is incomplete, with the height dimension in table 22 (36a) being derived in part from the base of the parastyle, which has a comparably deep base as the mesostyle. The available enamel pattern in this tooth still is immature in that the structures of the posterior border of the postfossette are not fully developed and the fossette is transversely narrow as compared with the more adult condition, and the pattern in PW10175 also is still immature.

As in other samples, the presence of a bifurcate lingual-most pli on the anterior and posterior surfaces of pre- and postfossettes (lingual complexity) heralds the adult dentition, and this condition is interpreted to have been achieved when this morphology obtains in a majority of the four loci where it may occur. In these teeth, the hypocone is fully confluent with the metaloph, and the fossette borders are the most complex. A possible exception, PW/2000/10109, still has a bifurcate lingual-most pli on the anterior side of the postfossette. As a point of interest, the pli protoconule appears to have been connected to, rather than isolated from, the adjacent border of the prefossette and plicated in the adult condition of P2.

In contrast with material from the Vienna Basin, the pre- and postfossettes appear to be mostly separate, with eight of ten specimens showing pertinent wear patterns of that morphology. In this context, two specimens (**PW/2000/10169**, PW/2000/10183) were scored as separate even though a single enamel band passed between the fossettes. In these cases, plications were present labial to that junction, which is a different pattern relative to the morphology typically found in the connected condition. In the typical situation there tend to be only 6 or fewer plis on the opposing faces of the pre- and postfossettes, with a broadly confluent interval being manifested between the (more lingual) joint connection and the enamel band that represents the labial borders of the paracone and metacone. The Senckenberg sample of *H. primigenium* has an average ($N$ = 6) plication count of 7:10:10:3, most like that from the HLMD collections in table 21.

The protocone is ovate in all thirteen teeth in the sample (of which six are in a mature state). The width-to-length ratio of the protocone ranges from 0.6 to 0.8 (the mean is 0.7), and there are an average of two plis caballin.

P3 MSTHT is best represented by PW/2000/10222 (51.5 mm), and from this tooth it is estimated that the unworn MSTHT would have been about 58 mm. On this basis, the mature wear pattern seems to have been developed from about 34 mm (**PW/1998/10001**) and 24 mm (**PW/2000/10174**), or between 42% and 59% wear, although the adult condition could have been found in earlier wear had specimens been present between 34 mm and 51 mm. Specimens above **PW/1998/10001** and below **PW/2000/10174** are not considered in the statistical analyses in table 23. The pli protoconule seems to have been relatively well developed, generally connected to the prefossette, and plicated. The mean plication count for P3 ($N$ = 4) is 8:14:11:5, possibly most like that from Mariathal in table 21.

The protocone is ovate in all six teeth in the sample (four are in an adult state). The adult width-to-length ratio ranges from 0.56 to 0.78 (the mean is 0.65), and the mean pli caballin count is four.

P4 MSTHT is at least 48.5 mm tall, as shown by PW/2000/10149. This tooth is in early wear, and the completely unworn condition likely would occur at more than 50 mm, with the suggestion based on molars that this reached about 56 mm. On that basis, the adult wear pattern seems to have been developed by about 39 mm (**PW/2000/no number**) and continued to at least 27 mm (**PW/10178/10078**), the sample having no specimens of lower crown height. Thus, the adult wear interval (**PW/2000/no number–PW/10178/10078**) ranges from about 30% to 52% wear. Specimens above that range are not considered in the statistical analyses in table 23. The pli protoconule occurs as both isolated and connected and simple to plicated. This suggests that P3 also likely would have achieved an adult pattern by about 30% wear, and the evidence from P3 also suggests that the adult condition in P4 would have been present until about 60% wear. The mean plication count ($N$ = 4) is 5:13:10:4, possibly most similar to the HLMD sample in table 21.

The protocone is ovate to subovate in all six of the specimens (four are in an adult state). The protocone width-to-length ratio ranges from 0.61–1.08 (the mean is 0.87). The mean pli caballin count is three.

M1 MSTHT is at least 51.5 mm, as shown by PW/2000/10162. This tooth is in very early wear, with the base not complete. It is likely that the completely unworn condition occurred at more than 52 mm and interpretively at about 55–59 mm. If a value of 57 mm is used for comparison, the adult wear pattern occurs between 37 mm and 23 mm, below which the sample is not represented. This indicates an adult wear interval bracketed by **PW/2000/10207–PW/2000/10189**, of about 35% to 53% wear. This is comparable to that for P4 and, for the reasons expressed for P4, it seems likely that the adult pattern in M1 would extend to about 60% wear. The mean plication count for M1 is 8:15:8:5, or more complex overall than the other samples.

The protocone is ovate in all teeth; the width-to-length ratio ranges from 0.51 to 1.08 in the four (of seven) adult teeth, with a mean of 0.72. The mean pli caballin count is four.

M2 MSTHT is at least 52 mm, as shown by PW/2000/10173. This tooth is in an early stage of wear, with the enamel pattern relatively well developed, so it appears most likely that the unworn condition took place somewhat higher than 55 mm, possibly as high as 59 mm. If a value of 57 mm is used for comparison, it appears that the adult wear pattern was in place by about 36 mm (37%) wear (**PW/2000/10148**), at which the pli protoconule was well developed and plicated, but the sample is not available beyond 31 mm (**PW/2000/10186**; 46%) wear (where the pli protoconule is less complicated). The mean ($N = 2$) plication count for M2 is 5:11:8:5, possibly more like the sample from Gaiselberg (table 21).

The protocone is ovate in all teeth (two of five are in an adult state). The width-to-length ratio for the adult protocone ranges from 0.56 to 0.63 (the mean is 0.60). The mean pli caballin count is three.

M3 MSTHT is 49.5 mm tall in PW/2000/10157, in which the pattern is in very early wear and the base of the tooth is not preserved. It is estimated that this tooth was about 57 mm tall in the unworn condition. It appears that the adult pattern was developed from about 33 mm to 18 mm, or between about 42% and 68% wear.

The protocone is ovate in all six (three mature-state) specimens. The adult width-to-length ratio ranges from 0.50 to 0.66, with a mean of 0.60. There is an average of two plis caballin.

Based on the collections studied here, the pli protoconule is relatively persistent in all teeth; it most commonly is well developed, mostly connected to the adjacent border of the prefossette; and usually composed of an anterior and posterior "half" as well as other plications. In P2, the structure is about equally simple (basically no plications) to complex (some or many plications); in the other teeth except M3, the simple condition (no plications) is rare to absent, whereas it is virtually always simple and an isolated circular feature in M3. The pli protoconule appears to be a persistent feature of the entire sample, usually well formed and commonly divided into an anterior and posterior part. In about equal frequencies, the feature is connected to the adjacent part of the prefossette as often as being isolated from it.

The Höwenegg material studied here is limited to four crania with cheek-tooth dentitions. Three of these crania are in an adult state (table 23). The sample shows that pre- and postfossettes in P2 are separated in early wear and that the lingual-most plis of the pre- and postfossettes are complexly subdivided. In addition, this limited sample of adult wear specimens shows that the fossette borders are among the more complex of the other collections summarized in table 21. This suggests a relatively derived status for the Höwenegg material, possibly belied by its apparently low MSTHT values (ca. 45–52; tables 21, 23). The protocone in P2 is uniformly ovate, with width-to-length ratios ranging from 0.5 to 0.6, with a mean of 0.6. There are five plis caballin, on average. P3 and P4 each show one specimen with a lingually flat protocone, one with a lingually concave border, and one that is oval. The width-to-length ratios are 0.41–0.47 (mean, 0.44) in P3, 0.45–0.57 (mean, 0.50) in P4, with an average of four plis caballin in P3 and two in P4. In M1–M3, the protcones are ovate (one is flat in M3), with width-length ratios of 0.51–0.54 (mean, 0.53) in M1, 0.40–0.42 (mean, 0.41) in M2, and 0.38–0.47 (mean, 0.44) in M3. The average pli caballin count is four in M1 and M2 and three in M3.

RESULTS: The Austrian material, mostly (?or completely) recovered from sites correlated with the Pannonian C Stage, appears to be somewhat lower crowned and morphologically conservative relative to German and Austrian specimens allocated as *H. primigenium* and, in Spain, as *H. koenigswaldi*. In that the Eppelsheim sample from the Dinotherium Sands apparently was drawn from the same general site as produced the type specimens of *H. primigenium* Meyer 1829 (Franzen et al., 2003b), the Austrian material may warrant a different, presumably specific, name. Resolution of this taxonomic situation is beyond the scope of the present work, which focuses on the morphology likely to have characterized the colonizers of the Old World as stemming from *Cormohipparion*. The rather limited dental material from sites of Pannonian C age affects the resolution of this question to some degree, but until proved otherwise, the working hypothesis of this report is that the Austrian samples from Gaiselberg, Atzelsdorf, and possibly Mariathal show the upper-cheek-tooth morphology of the geologically oldest representatives of the colonizing population of *Hippotherium*. Further study may reveal the specific allocation of the Inzersdorf and Laarberg crania (tables 22, 24), if different from *Hippotherium* sp. as utilized here. If these two crania (table 24) may be considered to represent the same population, it seems to be have a somewhat shorter muzzle length (no. 1), a possibly smaller upper-molar length (no. 8), a shorter orbit (no. 28), a somewhat shorter facial region (no. 31), and a somewhat shorter DPOF (no. 33) compared with the sample from Höwenegg.

As indicated in table 21, it appears that the unworn MSTHT for P4 and M1 in the samples of Pannonian C age (Gaiselberg, Atzelsdorf), of C/E? age (Mariathal) and of D/E age (Inzersdorf; Daxner-Höck, 1996) is somewhat lower crowned than the *H. primigenium* material from the Dinotherium Sands (Eppelsheim), Germany, and *H. koenigswaldi* from Nombrevilla, Spain. The Höwenegg sample of *H. primigenium* (Germany) is possibly more like the Austrian material in this regard. In addition, the Gaiselberg material also shows that P2 is characterized by having pre- and postfossettes that are connected in their labial portions. The Gaiselberg specimens (represented in fig. 25E) also appear to have a somewhat lower overall plication count than the Eppelsheim sample. The Mariathal (Austrian) material also appears to have a relatively low plication count, and the pre- and postfossettes of P2 also are mostly confluent (table 21), similar to the condition in the Gaiselberg sample. In their similarity to the Gaiselberg and Atzelsdorf material, the specimens from Mariathal also may prove to be of Pannonian C age. Unfortunately, only the Mariathal taxon is represented by a relatively large sample size, and whereas it may be unlikely that the portions of the paleopopulations represented by the specimens from Gaiselberg, Atzelsdorf, and Inzersdorf are fortuitously conservative, caution is still appropriate when assessing their specific allocation. With this caveat accepted, these Austrian specimens are here taken to characterize the morphology of the colonizing taxon, regardless of its name, and to use that morphology to evaluate its possible North American source.

Bernor et al. (1988) reviewed material considered to be derived from Gaiselberg and allocated by those authors to *Hippotherium primigenium*. On this basis, Bernor et al. (1988) suggested that 35% (seven) of twenty Gaiselberg maxillary cheek teeth of *H. primigenium* have an elongate-oval protocone shape, similar to that in *Cormohipparion occidentale*, *s.l.* (essentially the material of *C. occidentale* from the XMas-Kat sample), with three more (15%) having a transitional shape between the oval and lingually flattened protocone morphologies, and that this morphology signified affinity between the two taxa. The frequency of lingually flat protocones obtained here (about 30%; five teeth) for the Gaiselberg sample is comparable to that cited by Bernor et al. (1988). But rather than signifying phyletic affinity to *C. occidentale*, it seems, instead, that the occasional presence of lingually flat protocones in the Gaiselberg (or any other sample of *Hippotherium*) is best considered as endemic to the sample in question and to carry virtually no phyletic information relative to the possible ancestry of this taxon from a North American species of *Cormohipparion*, and specifically not from *C. occidentale* as represented by the XMas-Kat quarries sample.

In addition, some of the specimens utilized by Bernor et al. (1988) actually pertain to a locality (Laarberg) of Pannonian E age rather than from Gaiselberg. Examination of the actual specimen, as well as that in figure 7 of Bernor et al. (1988), indicates that examples with flat protocones occur in RP2, LP4, and right and left M2–3 of the Laarberg skull, NHMW 1842.VII.6 (= A4229; Bernor et al., 1988: fig. 7). P2 and P4 are in mature wear (about 25% worn), but M2 and M3 are in an earlier wear stage. The occlusal pattern on M3 is incompletely formed and so had not achieved a fully developed occlusal pattern. The pattern is obscure in right and left P3 and RP4. In light of its Pannonian E age, the Laarberg specimen appears to be chronologically similar to samples from Höwenegg and Eppelsheim, and the presence of lingually flat protocones is shown to be a limited feature of the upper-cheek-tooth dentition of those two larger samples. In consisting solely of a cranium, the Laarberg sample is of limited use in assessing pattern frequency.

Furthermore, the sparse presence of a lingually flat protocone in the German and in Austrian materials of nominally medial Vallesian age, as well as in the Austrian material of early Vallesian age, suggests that this presumptively elongate-oval pattern was persistent chronologically and was not "rapidly lost" in early Vallesian populations of *H. primigenium*, as proposed by Bernor et al (1988: 439).

Based on this survey, one may conclude that a resemblance in the protocone shape of *H. primigenium* to the morphology found in *C. occidentale* (effectively the XMas-Kat sample) mostly has an intraspecific, including ontogenetic, rather than phyletic source, and that an ovate protocone is typical of the upper-cheek-tooth *H. primigenium* dentition as far as the specimens reviewed here are concerned. The ovate protocone shape found in *C. fricki* combines with other characters to illustrate its potential ancestry (sister taxon) to Old World *Hippotherium*.

In addition to having protocones that were generally ovate (width-to-length ratios at or about 50% in P2–M3), consideration of the morphology of the *Hippotherium* sp. samples from Gaiselberg, Atzelsdorf, and Mariathal, Austria, suggests that the colonizing taxon was relatively low crowned (ca. 50–55 unworn MSTHT), the pre- and postfossettes were confluent labially in P2, the upper-cheek teeth had a relatively low plication index, and plis caballin that ranged between two (most molars) and three (most premolars). Also, to judge from the Austrian specimens from Laarberg and Inzersdorf, as well as from Höwenegg, Germany, dP1 was relatively well developed and persisted into the adult condition. Based on a single skull from Inzersdorf (NHMW 1875.VI.I), the DPOF was relatively large, the POB was relatively wide, and the anterior tip of the lacrimal was found about halfway across the POB. This is generally comparable to the condition figured in the Höwenegg sample in Woodburne and Bernor (1980: fig. 3B), and in fig. 3.1.1.2 in Bernor et al. (1997). In SMNK Hö A, the lacrimal occupies somewhat more than half the length of the POB and has a blunt anterior end in sutural contact with the maxillary. The vertical anterior end of the lacrimal is somewhat longer and more vertically oriented than in, for example, *C. occidentale* (fig. 10B). The lacrimo-nasal suture in *H. primigenium* appears to be more linear and not as concave dorsally, compared with figure 10B. The ventral border of the lacrimal is similar in the two taxa. The shape and sutural relationships, as well as the extent, of the lacrimal bone in the Austrian *Hippotherium* sp. remains of interest in that the morphology for *H. primigenium* described above differs from the more anteriorly attenuated condition displayed by the lacrimal of *C. fricki* (fig. 8A), which is otherwise similar to the Austrian taxon in general crown height, retention of dP1, and high frequency of P2 confluence of the pre- and postfossettes. In being about 11.5–12 Ma old, *C. fricki* is in a chronologically appropriate position to have been the source of the *Hippotherium* Datum of the Old World.

As shown in table 24, the Inzersdorf skull is comparable in measurable dimensions to those from apparently equally young (about medial Vallesian) sites in Austria (Laarberg), but both of these are somewhat smaller in some dimensions compared with the sample from Germany (Höwenegg) and generally compatible with a *C. fricki* size range.

However, *C. fricki* tends to have a more elongate protocone (a width-to-length ratio generally less than 50% in P3–M1; table 15), as also is consistent with all other species of *Cormohipparion* at or above node 8 on figure 30 and in contrast to the "more ovate" ratios in the Gaiselberg sample. It also is important to recognize that, except in *C. fricki*, dP1 is typically absent in adult members of all taxa higher than node 8 in figure 27 and that the Vallesian samples of *Hippotherium* typically retain this tooth, as also seen in *C. merriami*.

*Cormohipparion* sp. from the Punchbowl Formation of California possibly is similar in MSTHT (estimated) to *C. fricki* but is derived (based on the single specimen) in the much more ovate cheek-tooth protocones (width-to-length ratio nearly or greater than 60%) and may be independently derived in this

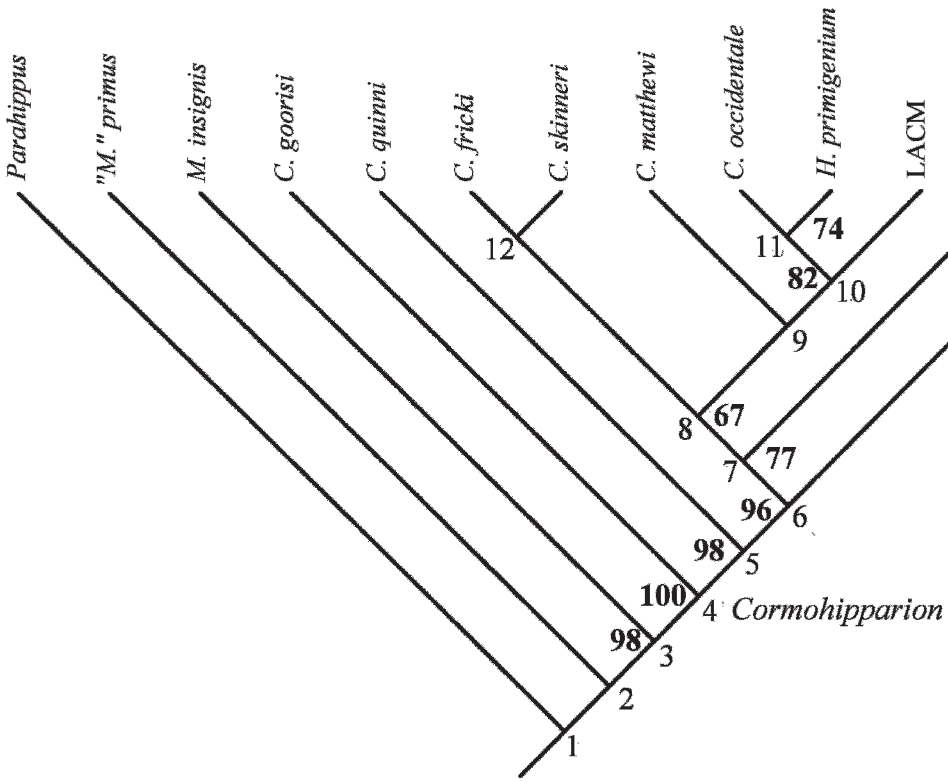


Fig. 30. Cladogram of species of *Cormohipparion*, the LACM specimen, and *Hippotherium primigeniuim* with outgroups of *Parahippus leonensis*, *"Merychippus" primus*, *M. insignis.* Tree length is 124; Consistency Index is 0.742; Retention Index is 0.782; Homoplasy Index is 0.258. Bootstrap values are in boldface. Based on a character distribution analysis via MacClade 4.08. Nodes 1–8 are as in fig. 27.

At Node 9, the maxillo-lacrimal and naso-lacrimal sutures form an obtuse angle (14:0); the posterior border of the premolar prefossette has 8–9 plis (23:4).

*C. matthewi* is distinguished by having a reduced MSTHT to ca. 42 mm (18:3), and a lower premolar ectoflexid that penetrates the space between the metaconid and metastylid (31:0).

At Node 10, the molar posterior prefossette increases to 10 or more (24:5); the premolar postfossette plis increase to 2–3 (27:1); the molar postfossette plis similarly increase to 2–3 (28:1); and the molar pli caballin is usually double (30:2)

The LACM specimen of *Cormohipparion* is distinguished by having reverted to a P2 protocone that attaches to the protoloph within 20–30% wear (20:2); an increase in premolar posterior prefossette plis to 10 or more (23:5); and an increase in premolar plis caballin to 4 (29:4).

Node 11 has no distinguishing characteristics but is the point at which *C. occidentale* and *H. primigenium* diverge from the LACM specimen of *Cormohipparion.*

*H. primigenium* is distinguished by the IOF located above the P2–P3 boundary (10:0); the low position of the IOF relative to the ventral border of the orbit (11:0); the maxillo-lacrimal and naso-lacrimal sutures forming an acute angle (14:1); the maxillo-lacrimal and lacrimo-jugal sutures forming an acute angle; the dP1/P2 length ratio retained at ca. 60% (17:1); and their being 8–9 molar anterior postfossette plis.

*C. occidentale* is distinguished in having an unworn cheek tooth MSTHT 60–66 mm (18:6); their being 8–9 molar posterior prefossette plis (24:4); and the orbit being posterior to M3 (38:2).

At Node 12, the IOF is located above P2 (36:1).

*C. fricki* is distinguished by having a palpable anterior rim of the DPOF (8:1); molars have 2–3 plis on the anterior border of the prefossette (22:1); the protocone retains a spur (35:0); and the orbit is posterior to M3 (38:2).

*C. skinneri* is distinguished by having the lower premolar ectoflexid making an X-pattern with the metaconid/metastylid (31:2).

feature compared with the other species at or above node 8, as also may be the case for plication complexity of P3–M1, again taking into account that this is a single specimen. However, the clear linking of the pre- and postfossettes in P2 of the California specimen has a strong resemblance to the Atzelsdorf, Gaiselberg, and Mariathal samples of *Hippotherium* and distinguishes these samples from the later Vallesian localities of Höwenegg and the majority of specimens from Eppelsheim. Future work may show that the Austrian Pannonian C and E samples pertain to a species distinct from *H. primigenium*, and, perhaps, that the *Cormohipparion* sp. from the Punchbowl Formation should be referred to it. Inspection of *Cormohipparion* samples regarding the morphology of P2 indicates that those that have confluent pre- and postfossettes occur about equally (as opposed to the separated condition) in all species except *C. skinneri*, although the numbers of specimens are small in all samples except for *C. occidentale*, *C. fricki*, and *C. matthewi* (table 21). It appears that more specimens show the confluent versus the separated condition in *C. fricki* (all were confluent in the Hollow Horn Bear Quarry material, and 60% were confluent in the MacAdams Quarry sample). On this basis, it may be suggested tentatively that of all North American samples, this species is most like the Vienna Basin Pannonian C material in that regard. Still, the at least partial absence of dP1 (see below) and more elongate protocones of *C. fricki* tend to argue against close affinity with *Hippotherium*.

Figure 30 is a cladogram of taxa shown in figure 27, with the addition of the LACM specimen of *Cormohipparion* sp. (LACM) and *H. primigenium*. The interrelationships of *Cormohipparion* species are basically those shown in figure 27. The increased plication complexity and crown height relative to *C. matthewi* (node 10) help link *C. occidentale*, *H. primigenium*, and the LACM specimen relative to node 8 or 9, but this means that the loss of dP1 at node 8 would be reversed for *H. primigenium*, where dP1 is not only persistent but large, a plesiomorphic trait otherwise typical of taxa at nodes 6 and 7. The samples are too small for *C. johnsoni* and *C. merriami* to be definitive in this regard, but in *C. occidentale*, dP1 is absent in all adult skulls from the XMas-Kat quarries, regardless of sex, and when dP1 is present in samples from the Machaerodus and Hans Johnson quarries, the tooth is present only in female crania. In *C. fricki*, dP1 is present in about 60% of crania of the adult specimens, regardless of sex, and it is scored as present in figure 30. The absence of dP1 in many specimens of *C. fricki* suggests that the tooth was in the process of being lost from node 8, as was accomplished in *C. skinneri*, *C. matthewi*, and *C. occidentale*. It is plausible that dP1 was present consistently in *C. merriami* and *C. johnsoni*, also given its common presence in *C. quinni*. An increase in premolar pli caballin complexity (score of three; no. 29, table 2) also separates *H. primigenium* from *C. occidentale*. In placing *H. primigenium* as a sister taxon to *C. occidentale*, the analysis apparently is influenced by the likely convergence between these two taxa as regards general size, an approach by *C. occidentale* to the fossette-pattern complexity of *H. primigenium*, and has downplayed the presence of dP1 in *H. primigenium* versus its loss in *C. occidentale*. The phyletic relationships for *H. primigenium* illustrated in figure 29 appear more realistic.

Figure 31 is a log-ratio diagram of cranial parameters of *C. fricki* (table 14) relative to *H. primigenium* as represented by the Höwenegg sample of table 24. Compared with *C. fricki*—and allowing for a potential range of S.D. for these features for which there is only a single specimen, as based on comparison with other samples of the *C. occidentale* group—the Höwenegg sample of *H. primigenium* differs in having a strongly longer muzzle (no. 1), a longer skull overall (no. 6), a higher snout in lateral aspect (no. 25), a longer orbit (no. 28), a more deeply incised nasal notch (no. 30), a longer facial region (no. 31), a longer POB (no. 33), a greater rear DPOF–IOF dimension (no. 34), a greater DPOF height (no. 35), and a greater DPOF–alveolus height (no. 38). The basicranial length (no. 4) is comparable in the two samples (tables 14, 24). Figure 31 also shows that the two taxa have a similar orbital height (no. 29; *C. fricki* is somewhat smaller), so it appears that these differences do not reflect strict allometry relative to basic cranial or

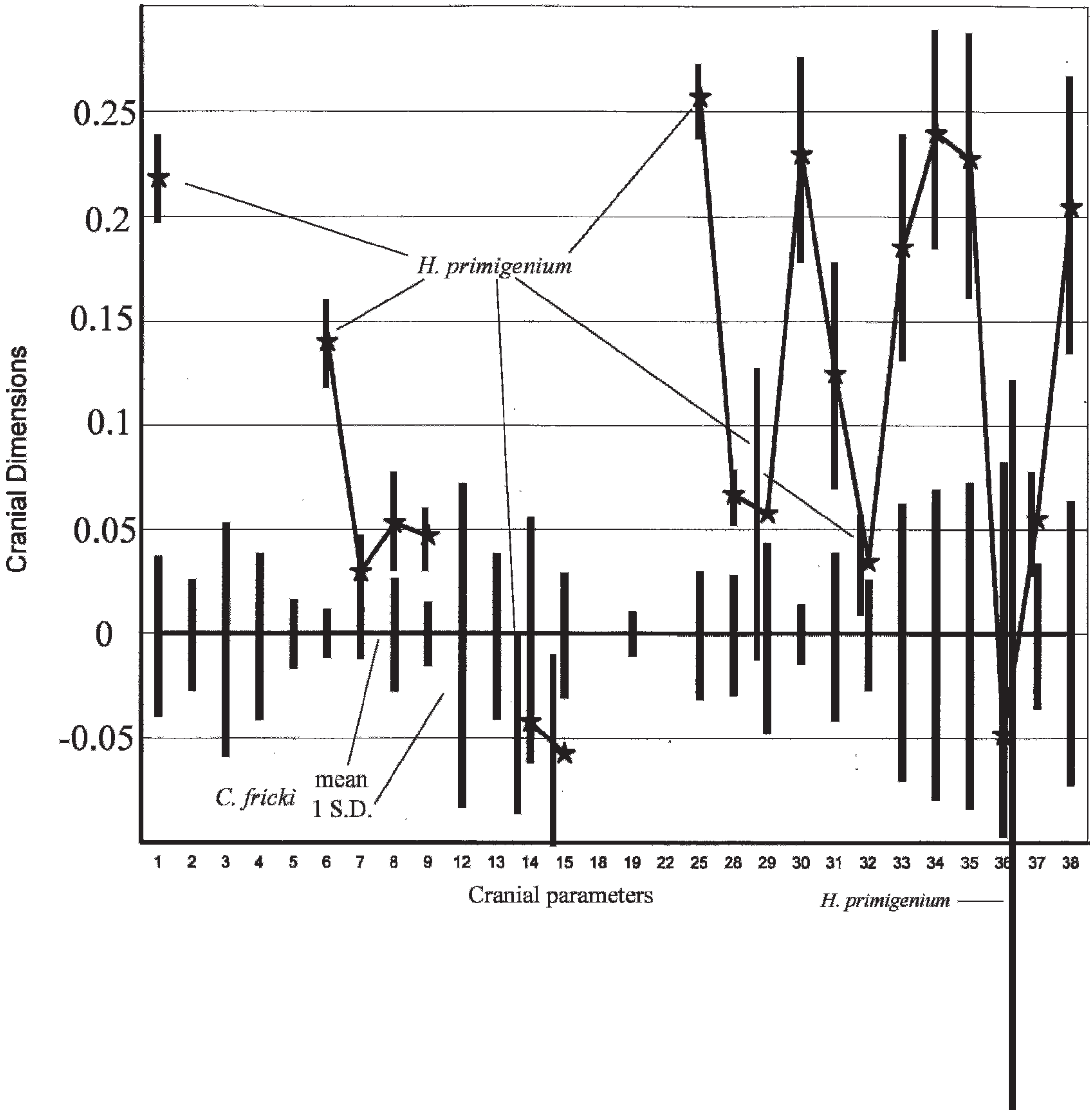


Fig. 31. Log-ratio diagram of cranial parameters of *Hippotheriium primigenium* from Höwenegg, Germany, compared with *C. merriami.* June and Midway quarries, Nebraska.

body size. A similar analysis relative to the other species of *Cormohipparion* suggests that parameters nos. 1, 6, 25, 30 (except for *C. occidentale*), 31 (except for *C. skinneri*), 32 (for *C. occidentale* and *C. skinneri*), 34, and 35 (possibly except for *C. skinneri*) also differ with respect to *H. primigenium*, although not always to the same degree of separation shown for *C. fricki*. Further, as compared with *C. johnsoni*, the longer premolar length (no. 7); longer total cheek-tooth length (no. 9); greater diastemal width of the muzzle (no. 14) and nasal notch (no. 25); and the longer POB (no. 32) in *H. primigenium* possibly reflect an allometric source, given the generally smaller cranial size of *C. johnsoni*. Still, all changes are not equally proportional, and it appears that the cranium of *H. primigenium* differs from that of all species of *Cormohipparion*. This, along with dental features, suggests that the base of the *Hippotherium* radiation in the Old World differs phyletically from members of *Cormohipparion* in North America. As summarized above, the dental features seen in the Gaiselberg, Atzelsdorf, and, possibly, Mariathal samples of *Hippotherium* (as well as the geologically younger samples from Höwenegg and Eppelsheim) are derived in the increased complexity of the enamel pattern of the upper-cheek teeth, including the anterior border of the prefossette and in the number of plis caballin. Future analysis may show whether or not *Hippotherium* is phyletically distinct from *Cormohipparion* and whether the two taxa retain a separate nomenclature.

It is likely that all or most of the features definitive of the *Hippotherium* clade would have been developed in the Old World, so their similarity to some attributes of *C. occidentale*, *s.s.*, must be convergent rather than originally shared. The disparity in phyletic linkage and geologic age of *H. primigenium* versus *C. occidentale* (fig. 29) also indicates a convergent source for such similarities. Whereas features seen in the well-preserved cranial and dental material of *C. occidentale* can provide useful general comparisons with elements of the *Hippotherium* radiation in the Old World, they are of little direct phyletic significance and should be avoided in future phyletic characterizations relative to Old World equids.

It also appears that *Cormohipparion* was restricted to North America, including Mexico (Ferrusquia-Villafranca, 1990). Bernor et al. (2003) nominate *C. sinapensis* from deposits in Turkey that range in age from about 10.5 m.y. to 10.0 m.y. The taxon is based on four specimens from at least three quite separate localities, so very little can be learned about intraspecific variation, regardless of the number of species potentially involved. If it can be considered together, the material indicates a taxon about 13–19% smaller than *H. primigenium*, based on parameters of the cranium, and this may be compatible with the apparently low unworn cheek tooth MSTHT of about 50 mm. Whereas referral of this species to *Cormohipparion* cannot be absolutely ruled out, the available information also supports its assignment to *Hippotherium* (as clearly stated by Bernor et al., 2003). Absent a demonstration of any features phyletically distinctive of *Cormohipparion*, this is followed here, and *C. sinapensis* is not recognized as a species of *Cormohipparion*. This carries the implication that there still is evidence for only a single dispersal event from North America to account for origin of Old World hippotherine horses in the early Vallesian of that region, including deposits of Pannonian C age in Austria.

Further work on the Old World samples discussed here may alter these conclusions, but at present it is reasonable to propose that a taxon with the dentition similar to that of the Punchbowl Formation *Cormohipparion* sp. and having a cranial morphology (and retention of dP1) seen in *C. fricki* was the most likely source of the Old World *Hippotherium* Datum and that it was present in North America at about 11.5–12 Ma (fig. 29). If so, it appears that a taxon with this morphology was prevented from dispersing to the Old World until the major sea level fall at Tb3 transpired at about 11.5 Ma (e.g., Woodburne, 2004b: fig. 8.8). Resolution of this question can be sharpened only by the discovery of associated cranial and dental material of the appropriate age on both sides of the Bering Strait. An important result of the present study is that it is no longer relevant to utilize *C. occidentale* in devising polarities in cranial and dental character states relative to the phyletic origin of *H. primigenium*.

## CONCLUSIONS

The nomen *Cormohipparion occidentale* (*s.l.*) is revised. Specimens formerly allocated to that species are distributed among five others in addition to *C. occidentale*, *s.s.* Collectively, these species range throughout much of western North America during an interval of from about 12.5 Ma to 10 Ma. *Cormohipparion quinni* is a plausible ancestor (sister taxon) of the *C. occidentale* group but also persisted with it until about 12 Ma. During its radiation, elements of the *C. occidentale* group demonstrate an increase in upper cheek tooth crown height and complexity of the enamel pattern, as well as an increase in overall cranial size. The interval of 12.5–10 m.y. witnessed the initiation of a period of climatic cooling and an eventual expansion of vegetation communities toward more open associations, in part showing an increase in grassy areas. Apparently, the *C. occidentale* group developed and maintained a mixed-feeding adaptation to these conditions even while developing very hypsodont upper cheek teeth by about 10 Ma (*C. occidentale*, *s.s.*).

*Cormohipparion johnsoni* is interpreted as the first, most plesiomorphic species of the *C. occidentale* group and is contemporaneous with *C. merriami* at about 12.5–12 Ma. These are followed by *C. fricki* at about 12–11.5 Ma, which demonstrates an increased crown height and complexity of the upper cheek teeth, along with the persistence of dP1 into the adult condition. At least in *C. fricki*, and likely also in *C. merriami* (represented by a much smaller sample), the pre- and postfossettes of P2 commonly were confluent. All of these features are found in early Pannonian C members of *Hippotherium primigenium* of the Old World, and it is likely that a taxon such as *C. fricki* was the most likely source for the Old World dispersal event that resulted in the presence of *H. primigenium*. A specimen of *Cormohipparion* sp. from deposits about 12 Ma old in California is of the proper morphology (enhanced by a significant increase in fossette complexity) to be a member of the dispersal population prior to its exit to the Old World at about 11 Ma.

Subsequent North American species of the *C. occidentale* group lived from about 11 Ma to 10 Ma and convergently approach the enamel pattern complexity found in *Hippotherium* but surpass it in upper cheek tooth crown height and in the almost complete loss of dP1. Two of these species, *C. occidentale*, *s.s.*, and *C. skinneri*, apparently populated a more northern (Great Plains) versus a southern (Texan; *C. skinneri*) district, with *C. occidentale*, *s.s.*, being sympatric with a (?secondarily) smaller taxon, *C. matthewi.* The sample of *C. occidentale*, *s.s.*, from the XMas-Kat quarries of Nebraska differs somewhat in a few cranial and dental parameters from samples from the Machaerodus and Hans Johnson quarries. Whereas the materials from the XMas-Kat and Machaerodus quarries seem contemporaneous on geological grounds, those from the Hans Johnson Quarry are not so securely dated. It is possible that the cranial differences (mainly the size of the preorbital fossa) and dental parameters (the persistence of dP1 into female adult crania) are variations in a somewhat polymorphic population. Alternatively, it is possible that the Hans Johnson sample, at least, might be chronologically somewhat older than that from the XMas-Kat quarries and that the morphological differences represent a more plesiomorphic condition for its specimens.

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