Chapter 16

Craniodental Analysis of *Merychippus insignis* and *Cormohipparion goorisi* (Mammalia, Equidae), Barstovian, North America

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ABSTRACT

The morphology and dimensional parameters of the cranium and upper and lower cheek tooth dentition of the early Barstovian aged three-toed horse, *Merychippus insignis*, the genotypic species, are analyzed based on specimens from Echo Quarry in the Olcott Formation of western Nebraska. Specimens of early Barstovian age from the Trinity River Pit 1 quarry, Texas, and of late Barstovian age from Deep Creek, Nebraska, are utilized to corroborate the association of upper and lower dentitions of the Echo Quarry sample to *Merychippus insignis*. A revised definition of *Cormohipparion* is utilized. *Cormohipparion goorisi* is characterized on the basis of cranial and dental information based on material from Trinity River Pit 1, Texas (early Barstovian). Based on these species, *Merychippus* and *Cormohipparion* are distinctly different taxa.

INTRODUCTION

This report is one of a number (e.g., Woodburne, 1996a) designed to review the species of *Cormohipparion* Skinner and MacFadden (1977), MacFadden and Skinner (1981), and MacFadden (1984) as part of an appraisal of the morphologic and taxonomic basis of the Old World ''*Hipparion* Datum'' involving the ancestry of *Hippotherium primigenium* from deposits of Vallesian age (ca. 9–11.2 Ma) in Europe (e.g., Garces et al., 1997; Steininger et al., 1996; Woodburne, 1996b). The present work focuses on the nominally oldest (ca. 15 Ma; early Barstovian, Texas; figs. 16.1, 16.2) and morphologically most plesiomorphic species of *Cormohipparion*, *C. goorisi* MacFadden and Skinner (1981; Woodburne, 1996a), in comparison with *Merychippus insignis* Leidy 1857 (ca. 16–15 Ma; early Barstovian, Nebraska; Skinner and Taylor, 1967).

In addition to utilizing the cranial and mandibular parameters (figs. 16.3–16.6) identified during the course of the *Hipparion* Conference, held at the American Museum of Natural History, New York, in 1981 (Eisenmann et al., 1988), I document and evaluate morphological characters of the upper and lower cheek-tooth dentitions of *M. insignis* and *C. goorisi*, as well. Until now, the lower dentition of *M. insignis* had not been described, although Hulbert and MacFadden (1991) placed *M. insignis* in a cladogram in which features of the lower dentition were utilized. Furthermore, in that the Trinity River Pit 1 quarry sample that produced *Cormohipparion goorisi* also includes material potentially referable to other species, I briefly comment on some of those specimens. Both in terms of the latter and to determine the morphology likely to have been present in the lower dentition of *M. insignis*, it was necessary to determine what species or specimens should be considered as merychippine and which should not. The allocation of some Texas crania and upper

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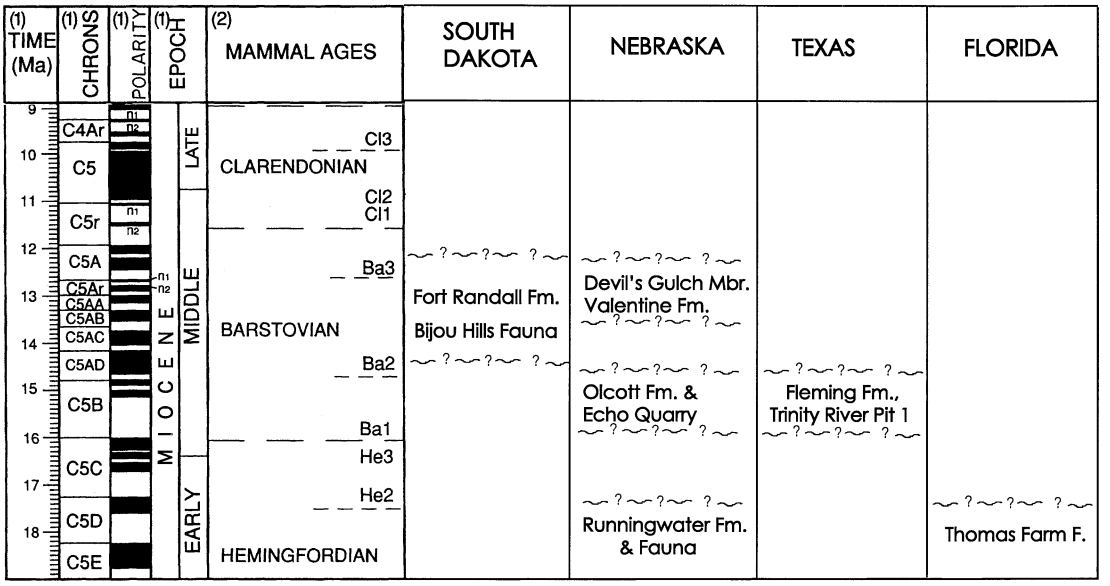


Fig. 16.1. Correlation chart of rock and faunal units discussed in the text: (1) from Berggren et al. (1995), (2) after Woodburne and Swisher (1995); rock and faunal units this paper.

and lower dentitions as merychippine is corroborated by material from the Valentine Formation, Nebraska. The section on methodology utilizes specimens from the Devil's Gulch Member of the Valentine Formation in Nebraska and Trinity River Pit 1, Texas, where associated crania, mandibles, and their dentitions verify the allocation to *Merychippus insignis* of isolated mandibles from Echo Quarry, Nebraska, the main hypodigm of that species. *M. insignis* is characterized here on the basis of the Echo Quarry sample. The other Nebraskan and Texas examples likely are not conspecific with *M. insignis* at Echo Quarry, and are the subject of future phyletic analysis.

Hulbert (1989) and Hulbert and MacFadden (1991) advocated removing *C. goorisi* from *Cormohipparion*, but that suggestion is not followed here (Woodburne, 1996a). For purposes of simplicity, taxa referred (Hulbert, 1987b) to either *Cormohipparion s.s.* (*C. sphenodus* [= *C. quinni* in part; Woodburne, 1996a]; *C. occidentale*) or to the subgenus *Notiocradohipparion* Hulbert 1988 [*C. (N.) ingenuum, C. (N.) plicatile* and *C. (N.) emsliei*] are not considered further.

Abbreviations

Morphological:

DPOF	Dorsal preorbital fossa (= lacrimal or nasomaxillary fossa on the side of the face anterior to the orbit; does not distinguish explicitly between LAF and NMF; after MacFadden, 1984).
hypsodont	Equidae in which the unworn mesostyle crown height for P2–M3 is greater than 35 mm.
IOF	Infraorbital foramen.
LAF	Lacrimal fossa. The posterior portion of the DPOF if two fossae can be distinguished. Occurs primarily on the lacrimal, but may be expressed partially on the adjacent nasal and maxillary bones.
mesodont	Equidae in which the unworn mesostyle crown height is between 10 and 30 mm.
NMF	Nasomaxillary preorbital fossa. The portion of the DPOF anterior to the lacrimal bone. This is the DPOF of most taxa because the LAF commonly is lost evolutionarily.
POB	Preorbital bar, or the space on the face between the orbit and the DPOF.

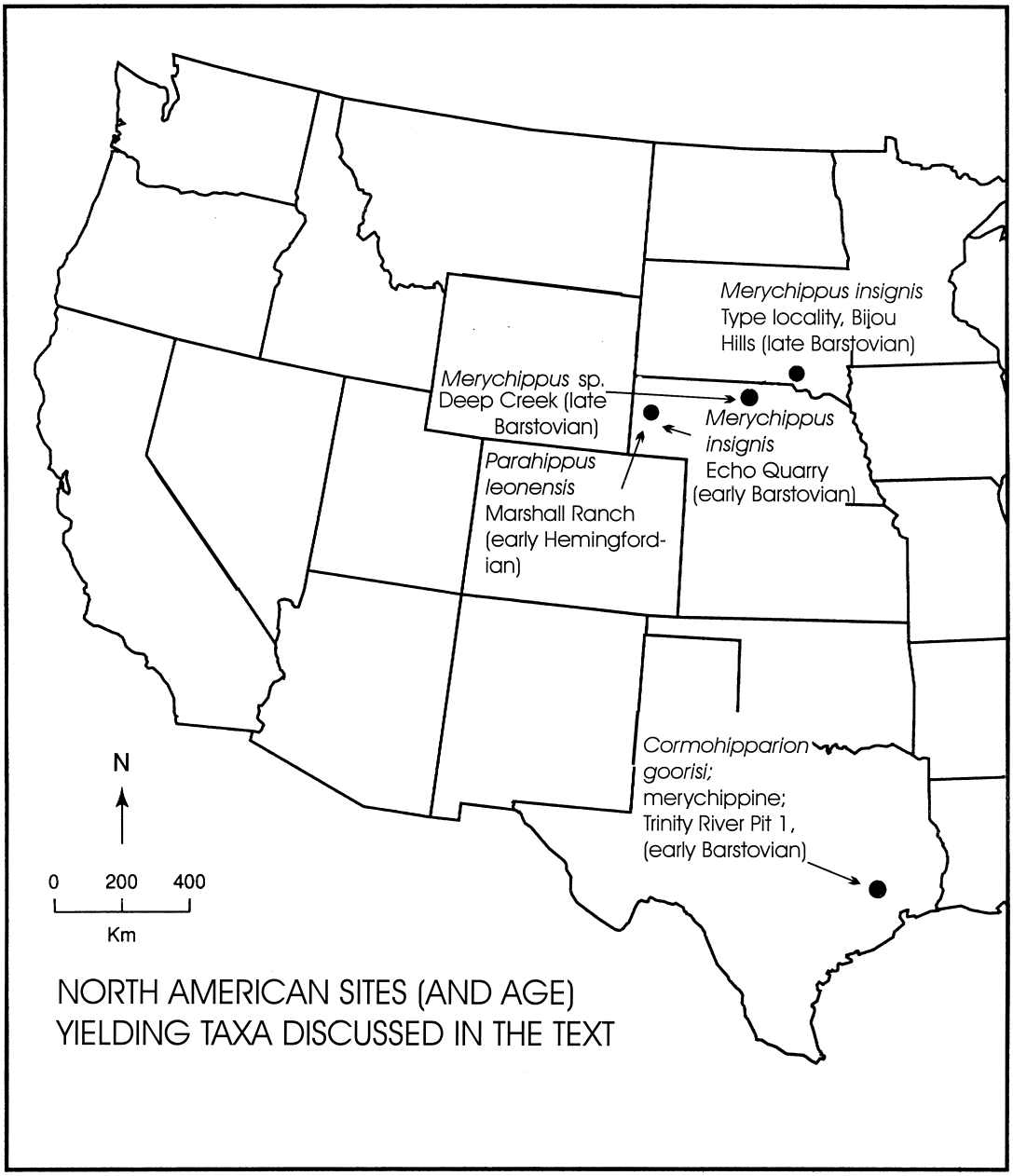


Fig. 16.2. Map of sites producing taxa (and age) discussed in the text.

INSTITUTIONAL:

AMNH Department of Vertebrate Paleontology, American Museum of Natural History, New York.

ANSP Academy of Natural Sciences, Philadelphia.

F:AM Frick: American Mammals in the AMNH collections.

TMM Texas Memorial Museum, University of Texas, Austin.

UF Florida Museum of Natural History, Gainesville.

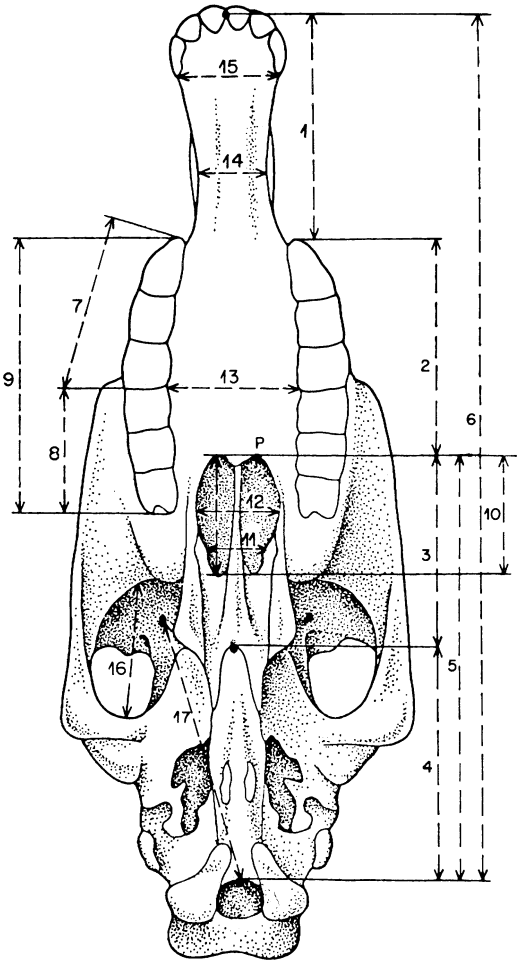


Fig. 16.3. Diagram showing location of cranial measurements. After Eisenmann et al. (1988).

CHRONOLOGICAL AND OPERATIONAL:

Ma	Megaannum in the radioisotopic time scale (e.g., 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 a fossil species.

TAXONOMIC CONCEPTS

This paper utilizes the general phyletic framework of Miocene Equidae presented in Hulbert and MacFadden (1991). For the purposes of this discussion, *Parahippus leonensis* is the out-group taxon relative to *Merychippus insignis*, and *Cormohipparion goorisi*, with *C. goorisi* being the most derived. *C. goorisi* is retained in the genus *Cormohipparion* rather than as a species of ''*Merychippus*.'' *M. insignis* is the only species of *Merychippus* formally discussed.

MERYCHIPPUS INSIGNIS: The following characterization is based on contrasting the Echo Quarry sample of *Merychippus insignis* with *Parahippus leonensis* and *C. goorisi*. As indicated in figure 13 of Hulbert and MacFadden (1991), *C. goorisi* [''*M.*'' *goorisi*] is more derived than *M. insignis* and both are more derived than *Parahippus leonensis*. I utilize information from the lower dentition as derived from the Echo Quarry sample here allocated to *M. insignis*. As discussed below, this allocation is consistent with the morphology found in lower dentitions and mandibles associated with crania from Trinity River Pit 1, Texas, and Deep Creek, Nebraska.

As figured below, *Merychippus insignis* is a mesodont equid that differs from *Parahippus leonensis* in: larger cranial size, longer muzzle, nasal notch more deeply retracted (to about midway between C1 and P2, vs. about above C1), POB ca. 17 mm wide (vs. about 7 mm or less), DPOF distinctly expressed with dorsal, posterior, ventral, and (palpable) anterior borders (vs. less distinct); the DPOF is (slightly) pocketed posteriorly (vs. unpocketed) and is relatively short (ca. 64 mm vs. ca. 72 mm) in comparison to the cheek tooth row length (ca. 116 mm vs. 92 mm); the anterior end of the DPOF is located above P3 (rather than above P2); the posterior portion of the DPOF is short (ca. 15 mm) compared to the anterior part (ca. 50 mm), in contrast to the two parts being about equally long in *P. leonensis*; the vertical ridge that separates the two parts of the DPOF is thus located above M1 rather than above P4; the IOF is located above the P4/M1 boundary versus above P3; the bisector of the rear of the IOF lies 13–17 mm above an anterior projection of the facial crest (rather than being only about 7 mm above it); the lacrimal is dorsoventrally broad and extends into the rear of the DPOF for a distance of about 8 mm, versus about 20; upper cheek teeth are mesodont, ca. 24–27 mm tall at the mesostyle in the unworn condition, versus

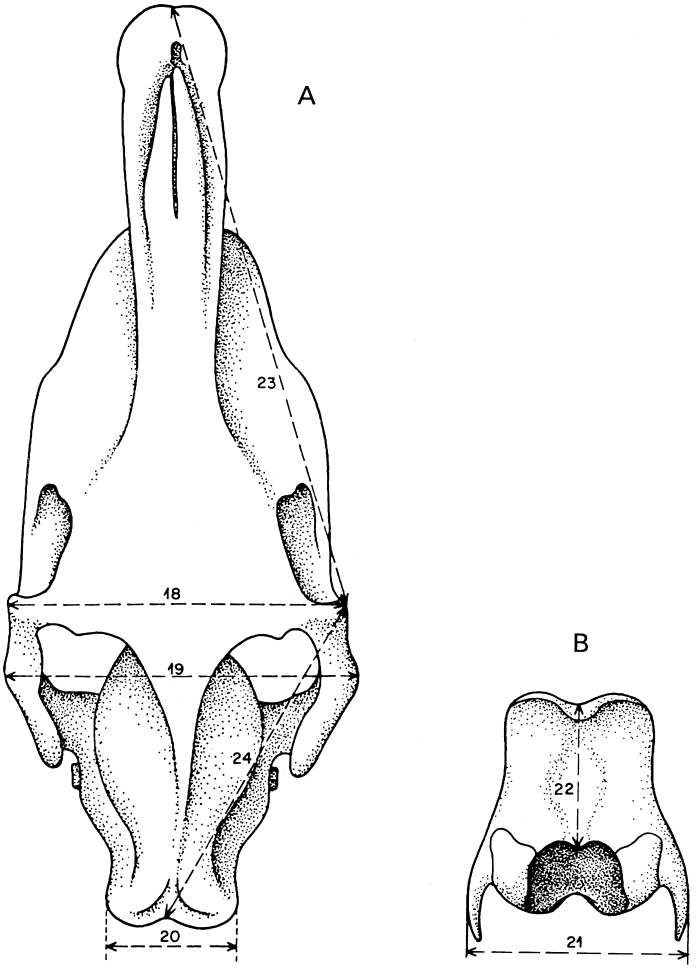


Fig. 16.4. Diagram showing location of cranial measurements. After Eisenmann et al. (1988).

ca. 16 mm or less; the protocone is uniformly connected to the protoloph in P2 except in earliest wear, but remains isolated until latest wear in other cheek teeth (versus being confluent with the protoloph in all teeth after midwear); fossette borders are moderately complex in the upper half of the cheek tooth crown (vs. simpler), with as many as four but usually two plications on the opposing faces of the pre- and postfossettes (vs. rarely more than two, except in very early wear), and at least one pli commonly present on the distal borders of these fossettes (vs. rarely present); protocones are uniformly (and persistently; late wear) spurred (as in *P. leonensis*, but in early wear only); those of the premolars are nearly circular, whereas those of the molars are more elongate (vs. uniformly circular in mature wear); the hypoconal groove commonly has a single plication (vs. smooth or lost early in *P. leonensis*); dp1 is rarely preserved in the lower cheek tooth dentition (vs. commonly present); metaconids and metastylids are subequal in size and mostly have rounded outlines and are separated by deeper but U-shaped linguaflexids (vs. smaller, and with shallower linguaflexids); protostylids are developed on p3–m2 in later wear and are usually little more than an angulate bend in the enamel at the pertinent part of the tooth (as in *P. leonensis*, but only developed faintly and in later wear).

The suite of characters present in *Merychippus insignis* includes a number of ple-

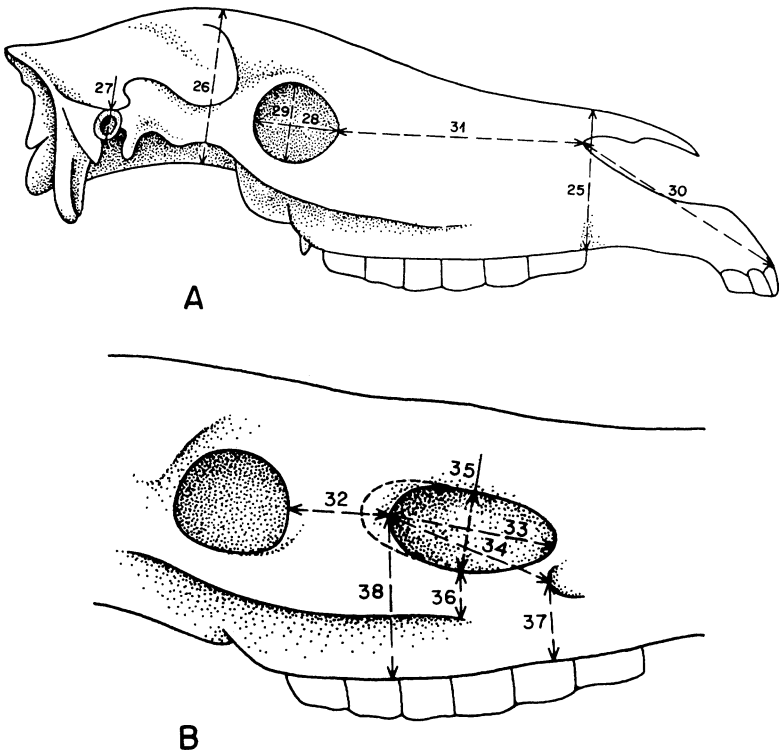
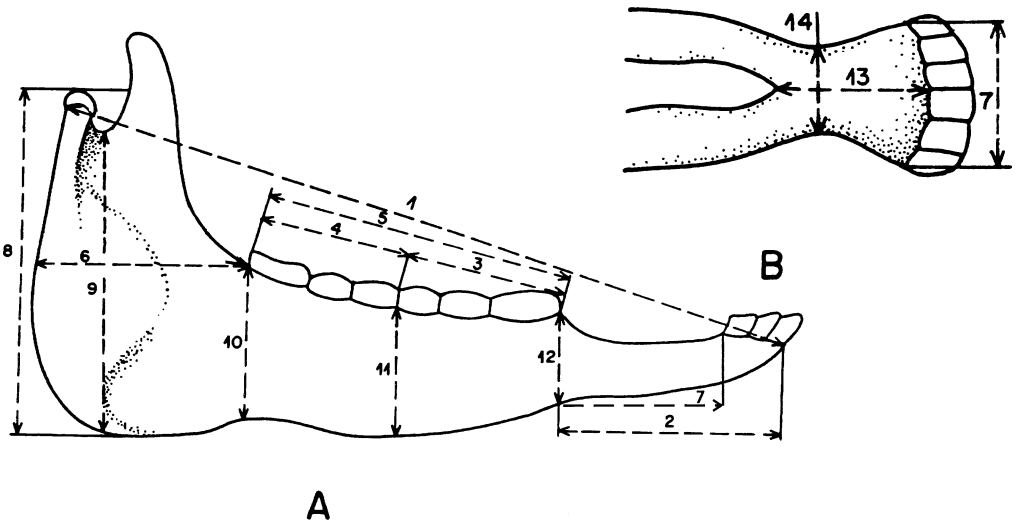


Fig. 16.5. Diagram showing location of cranial measurements. After Eisenmann et al. (1988). **A,** Lateral view. **B,** Close-up of facial region, lateral view.

siomorphic ones relative to more derived taxa, such as *C. goorisi*, for example, POB still relatively short; DPOF still relatively moderately developed; lacrimal dorsoventrally tall; lacrimal still penetrates DPOF; dP1 larger (table 16.1); protocone connected to protoloph in P2; protocones with persistent spur; metaconids/metastylids subequal in size with premolar ectoflexids early penetrating the isthmus. The DPOF/IOF character states described above are distinct in *M. insignis* relative to both *C. goorisi* and *P. leonensis.*

MERYCHIPPINE: This concept is utilized for mesodont to hypsodont Neogene equids that resemble *Merychippus insignis* wherein the DPOF has well-defined posterior, dorsal, ventral, and at least palpably (but not sharply as in *C. goorisi*) distinctive anterior borders; the IOF is located above the P4/M1 boundary, about aligned with the lower boundary of the orbit, and occurs distinctly below the well-defined ventral boundary of the DPOF (figs. 16.7–16.10). *Well-defined* is taken to mean that the fossa border forms a definite shoulder, so that the IOF opens well lateral to, and below, the medial surface of the DPOF, in contrast to, for example, *P. leonensis* (fig. 16.7) where the IOF is much farther forward and the DPOF much less well defined, and in contrast to *C. goorisi* where the IOF is both anterior in position and located very close to the much more strongly defined anterior portion of the ventral border of the DPOF. A malar fossa is absent. None of the other taxa referred by Hulbert and MacFadden (1991) as ''*Merychippus,*'' including ''*M. goorisi*'' has this combination of features where relevant cranial material is known (''*M.*'' *primus*, ''*M.*'' *intermontanus*, ''*M.*'' *carrizoensis*, ''*M.*'' *tertius*, ''*M.*'' nr. *sejunctus*, ''*M.*'' *coloradense*, ''*M. goorisi*''). ''*M.*'' *gunteri* is represented only by dental remains and cannot be directly compared in this context, but Hulbert and MacFadden (1991: fig. 10)



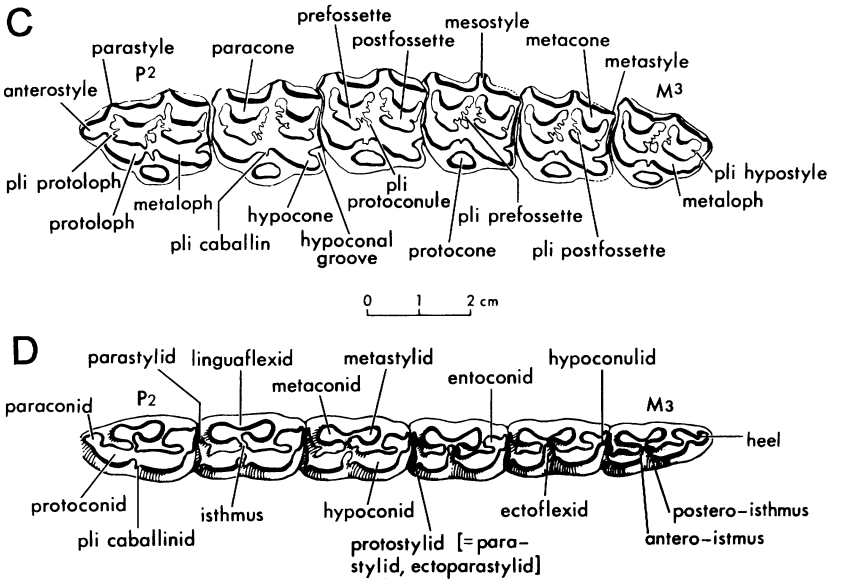


Fig. 16.6. Diagram of measurements and dental terminology. **A,** Measurements of mandible. **B,** Symphysis of mandible. **C,** Upper cheek tooth dental terminology. **D,** Lower cheek tooth dental terminology. A and B after Eisenmann et al. (1988). C and D after MacFadden (1984).

show ''*M.*'' *gunteri* as a sister taxon to *Parahippus leonensis* and below all other ''*Merychippus*'' on their cladogram. Aside from the above, two other samples representing species-rank taxa are referred to herein as merychippine: a sample from the early Barstovian Trinity River Pit 1 fauna, of Texas, and that from a Deep Creek, Ne-

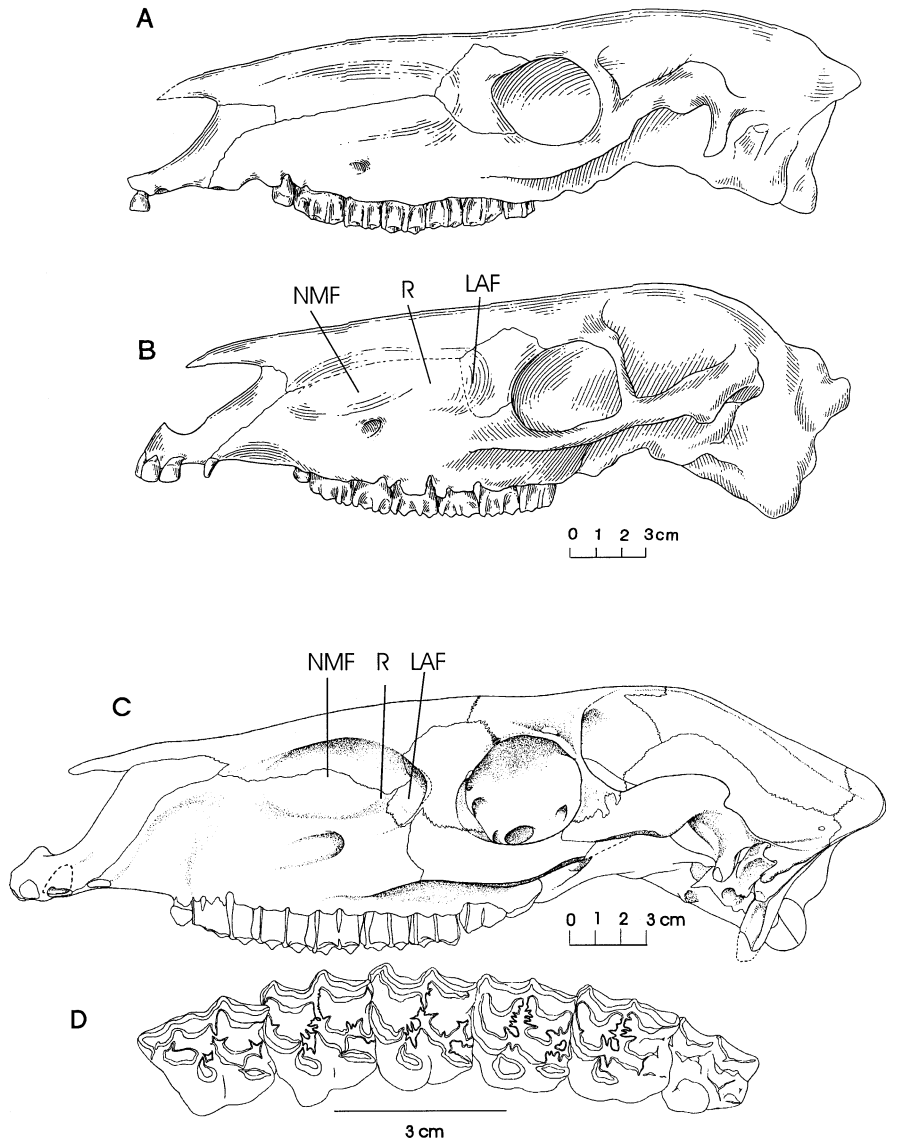


Fig. 16.7. Lateral views of crania of *Parahippus leonensis* (**A, B**) and *Merychippis insignis* (**C**), and occlusal view of left upper cheek tooth series of *M. insignis* (**D**). A (Thomas Farm, Florida; early Hemingfordian) and B (Marshall Ranch, Nebraska; early Hemingfordian) after Hulbert and MacFadden (1991); C and D (Echo Quarry, Nebraska; early Barstovian) after Skinner and Taylor (1967). A is a composite based on UF 56000 and UF 103753. B is based on F:AM 109857. C and D are based on F:AM 87001. R = ridge separating LAF from NMF.

braska, site in the Valentine Formation (late Barstovian). In addition to having the relevant cranial features, this material demonstrates the association of cranial and upper dental features with those of the mandible and lower dentition.

METHODOLOGY

All samples discussed here are compared by means of the cranial and mandibular parameters (figs. 16.3–16.6) advocated by participants of the 1981 *Hipparion* Conference

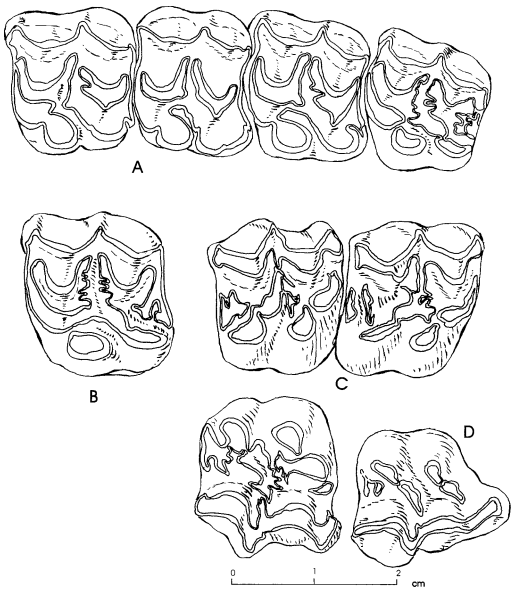


Fig. 16.8. Upper cheek tooth dentition of *Parahippus leonensis*, Thomas Farm, early Miocene, Gilchrist County, Florida. **A,** F:AM 22682, left P4–M3. **B–D,** F:AM 22682. **B,** LM2, early wear. **C,** RP4–M1, early wear. **D,** LP3–P4, very early wear.

held at the American Museum of Natural History, New York (Eisenmann et al., 1988). Furthermore, the Echo Quarry (early Barstovian) sample of *Merychippus insignis* was thoroughly studied in terms of the dental characters shown at various upper cheek tooth crown heights. Rather than assigning a particular tooth to a predetermined wear stage (e.g., Van Valen, 1964), the mesostyle crown height of each tooth was either measured directly or estimated in comparison with other specimens whose crown height is known or the ontogenetic development of which is relatively well established. Unless directly known, crown heights of M1–3 are the most ambiguous.

Lower dentitions are more problematic because samples consist largely of specimens still implanted in the mandible. In this case, specimens were assorted into wear classes that progressed from immature to mature, and comparisons of the various quarry samples were made between specimens of individual wear classes. Both of these techniques, not necessarily new (e.g., Downs, 1961), enhance the validity of making morphological comparisons with other teeth in the tooth row, or to those of other species, as discussed further below. With these data in hand, a comparable analysis was made of the less abundant hypodigm of *Cormohipparion goorisi*, some other specimens from Trinity River Pit 1, and another sample from Deep Creek, Nebraska, regarded as of merychippine affinity.

Comments on ''Standardized'' Methodologies

The data developed in these dental analyses show that each of the upper cheek teeth of *Merychippus insignis* has its own range with respect to the crown (mesostyle) heights at which the greatest enamel complexity is displayed, and that these individualities must be kept in mind when comparing teeth of this taxon with homologues of other species. Students of equid evolution are commonly advised to place most reliance on cheek tooth data acquired from, for example, the ''approximate middle 1/3 stage-of-wear'' (e.g., Bernor et al., 1990), or that data should be segregated into four wear stages of equal thickness (e.g., Eisenmann et al., 1988: 18). These operations recognize that the occlusal pattern in equid cheek teeth becomes simplified with wear, and that the pattern most useful in phyletic analysis commonly is found in earlier wear stages. The present analysis suggests that it is better to specify the crown height at which each tooth of a particular taxon is most complex (or displays its potentially most representative morphology; e.g., Downs, 1961), and that taxa be compared only at homologous tooth loci (all P2s, rather than P2s and M3s), at least in the beginning of the analysis, with complexity (representative morphology) intervals being kept in mind, and compared as well. If taxon A has only a narrow range in crown height with respect to its most important morphological display, and taxon B has a very different range, that difference could be significant in and of itself. Obviously, if the data are not acquired originally, they can never be retrieved.

Another convention recommended by the *Hipparion* Conference (Eisenmann et al.,

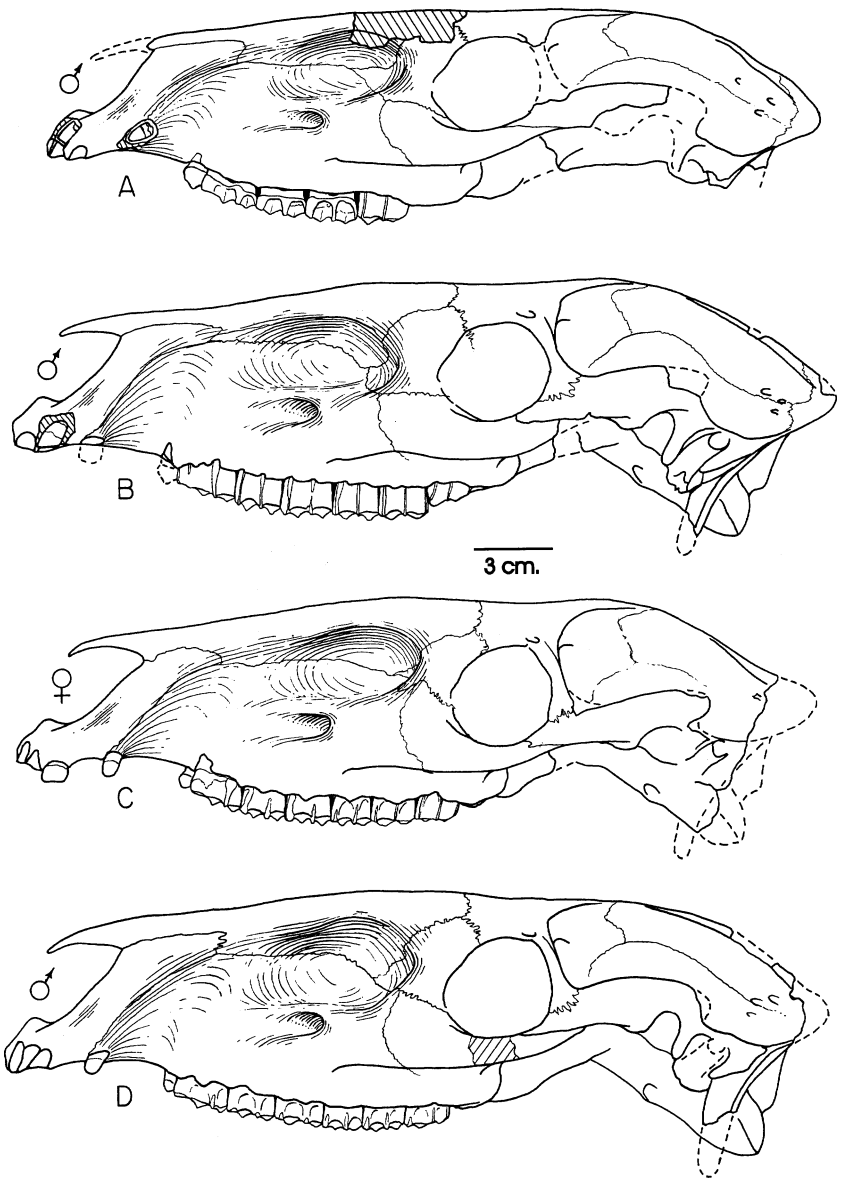


Fig. 16.9. Lateral views of referred crania of *Merychippus insignis*, Echo Quarry, Olcott Formation, Nebraska (early Barstovian). **A,** F:AM 87000; **B,** F:AM 87001; **C,** F:AM 87004; **D,** F:AM 87005. After Skinner and Taylor (1967).

1988: 18) is to measure the length and width of isolated upper cheek teeth of hipparions and other mesodont to hypsodont horses at 1 cm above the coronal base. As is evident from data presented herein, most of the coronal complexities of the upper cheek tooth dentition and other details thought to be of phylogenetic significance in these merychippines and primitive *Cormohipparion* (not to mention the large number of nominally higher-crowned and otherwise more derived taxa) have disappeared by that degree of wear. If genetic control as to the range in crown height showing the most important morphological features bears any direct relationship to length/width dimensions, then arbitrarily

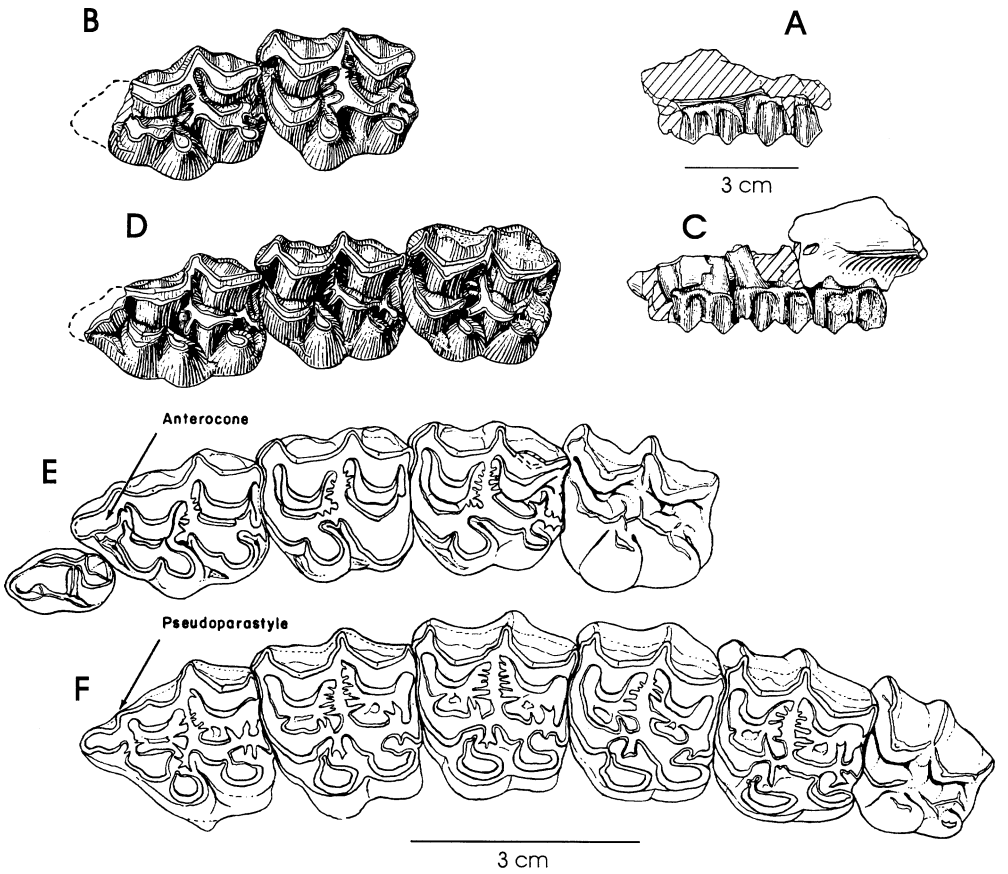


Fig. 16.10. *Merychippus insignis*. **A, B,** Type, dP2–3, reversed, ANSP 11276; from the Bijou Hills, South Dakota. A, Lateral view. B, Occlusal view. **C, D,** dP2–4, reversed, F:A.M. No 87006; from Echo Quarry, Nebraska. C, Lateral view. D, Occlusal view. Note cement on dP4. **E,** Left dP1–4 and M1. Occlusal view, F:AM No. 87000, Echo Quarry, Nebraska, arrow at anterocone. **F,** P2–M3, reversed, occlusal view, F:AM 87002; Echo Quarry, Nebraska. Arrow at pseudoparastyle. After Skinner and Taylor (1967; fig. 5).

measuring length/width at 1 cm may not be the phylogenetically most informative height at which to obtain those dimensions.

The Lower Dentition of *Merychippus insignis*

Skinner and Taylor (1967: 19) did not describe the lower dentition of *Merychippus insignis* from Echo Quarry (Olcott Formation), Nebraska, because no lower mandibles and dentitions were definitely associated with cranial material. In his study of mesodont horses of late Hemingfordian and Barstovian age, Evander (1985) allocated unassociated mandibular and lower cheek tooth material to a number of quarry samples of such taxa based effectively on indices of gross size. For this study, I began with the sample allocated by Evander (1985) to *Merychippus insignis* from Echo Quarry, arranged the specimens according to progressive wear stages (see below; independent of the stages devised by Evander, 1985), compiled morphometric and morphologic data, and evaluated the results. These were then checked against specimens considered to pertain to *Merychippus s.s.* from a late Barstovian sample from the Devil's Gulch Member of the Valentine Formation, Nebraska, and an early Barstovian sample from the Trinity River Pit 1, Texas.

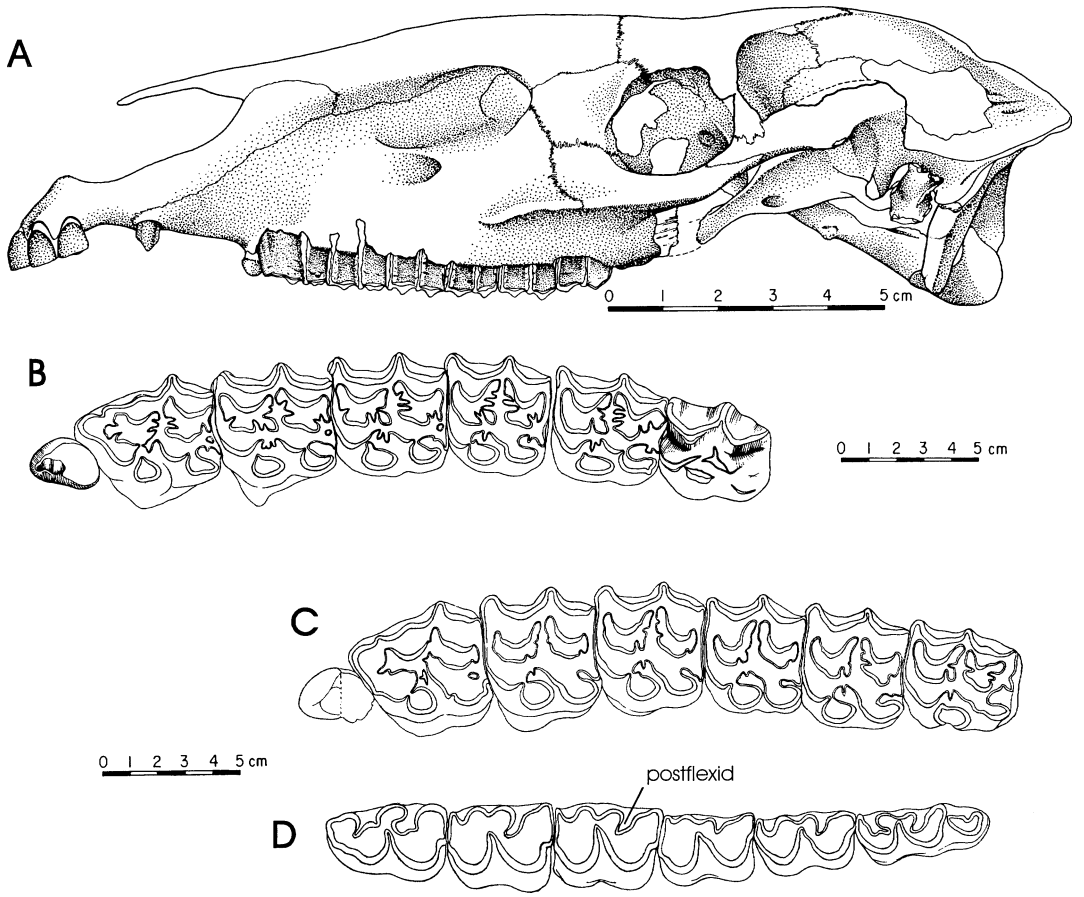


Fig. 16.11. *Merychippus* sp. (**A**), left lateral view of cranium, and (**B**) occlusal view of left cheek teeth, F:AM 126899. **C,** occlusal view of left upper cheek tooth series. **D,** occlusal view of left lower cheek tooth series, F:AM 126900. All from F:AM Deep Creek locality, Devils' Gulch Member, Valentine Formation, late Barstovian, Nebraska.

Based on these studies (below) the sample from the Trinity River Pit 1 represents at least three taxa, of which one is *Cormohipparion goorisi* (originally described by MacFadden and Skinner, 1981). The others include a lower-crowned taxon with dental and cranial characters comparable to those of *Merychippus insignis,* and another taxon under study by Evander (1985). Both dentally and cranially the latter is sufficiently different from either of the other two Trinity River Pit 1 taxa and from *Merychippus insignis* as to be removed from further consideration.

A somewhat higher-crowned mesodont taxon from the Devil's Gulch Member of the Valentine Formation (fig. 16.11) also resembles the Trinity River Pit 1 *Merychippus s.s.* and is distinguishable from contemporary species with equally to more hypsodont, but morphologically different dentitions and morphologically different crania referred (Tedford et al., 1987: 169) to *Pseudhipparion retrusum, Calippus, Pliohippus, Cormohipparion, Protohippus,* or *Neohipparion* (e.g., MacFadden, 1984; Hulbert, 1986, 1987a, 1987b, 1988, 1989; Webb and Hulbert, 1986; see above).

Both at Trinity River Pit 1, Texas, and the F:AM locality from the Devil's Gulch Member of the Valentine Formation, Nebraska, mesodont horses having unworn upper cheek tooth crown heights of about 25–36 mm or less (comparable to *M. insignis*) are the exception rather than the rule. By ruling out an

allocation to one of the other taxa cited above based on cranial and dental features typical of merychippines, the lower dentition of such mesodont horses can be used to indicate the morphology to be expected in the lower cheek tooth dentition of *Merychippus insignis*. As discussed more fully below, I note that both Barstovian samples (Fleming Fm., Texas; Valentine Fm., Nebraska) are different relative to *M. insignis* in certain cranial characters, but otherwise the upper and lower cheek tooth dentitions resemble those (upper) teeth originally allocated as, and the lower teeth here referred to, *M. insignis*. In their mesodont crown height and other dental features (moderately complex upper molar fossette borders, persistently (into late wear) spurred protocones, and the deep penetration of the lower premolar ectoflexids) these samples differ from contemporary Barstovian species that pertain to other genera.

Specimens Utilized for Comparative Purposes

This section lists specimens from the Devil's Gulch member of the Valentine Formation, Nebraska, and the Fleming Formation (Trinity River Pit 1), Texas. Collectively they are important in corroborating the allocation of lower dentitions from Echo Quarry, Nebraska, to *Merychippus insignis*, in showing that *Cormohipparion goorisi* (fig. 16.12) is derived relative to *Merychippus s.s.*, and in documenting the allocation of certain cranial, dental, and mandibular specimens from Trinity River Pit 1 to *Merychippus s.s.* rather than to *C. goorisi*.

Devil's Gulch Member, Valentine Formation, Nebraska: AMNH 126899, nearly complete ♂ cranium (fig. 16.11A), laterally crushed and skewed, lacking left zygomatic arch, both paroccipital processes, with R&L I1–3, canines, dP1, P2–M3, in relatively early wear (M3 having breached enamel only on protocone and protoloph). AMNH 126900, partial ♂ cranium, dorsoventrally crushed, lacking virtually all of the right side and neurocranial portion of both sides, with L canine, LdP1, P2–M3 in late wear (protocone of P3 and M2 showing incipiently confluent protocone with the protoloph) and associated left mandible lacking symphyseal region, but having the mandibular and ascending rami, with p2–m3 in late wear stage, and no evidence of dp1 ever having been present (fig. 16.11C, D).

Comments: This material is briefly described to set out the reasons for considering the Deep Creek taxon to be included as a merychippine and to list the characters of its lower dentition that are relevant to corroborating the allocation of Echo Quarry specimens to *Merychippus insignis*. Further descriptions will be given in a revision of *Merychippus s.s.* now in progress.

AMNH 126900, with the cheek teeth in adult wear (fig. 16.11C, D) shows (table 16.2) that the P2 mesostyle is 15.6 mm tall. The p2 protoconid is about 12.3 mm tall (table 16.3). The hypoconulid of m3 is still distinct from the hypolophid (fig. 16.11D). Merychippine affinity is shown by ovoid and still spurred protocones on P4–M3 (fig. 16.11B), with the premolar protocones being more nearly circular than those of the molars, the presence of single pli caballins, the remnants of a reasonably complex fossette plication pattern, relatively large dP1 (ca. 14 mm long; fig. 16.11B, C), a remnant DPOF comparable to, but medially deeper (#40; table 16.4 vs. table 16.5) than that of the Echo Quarry sample of *M. insignis*, and the IOF being located above the P4/M1 boundary (see cranium of AMNH 126899; fig. 16.11A). In addition to the medially deeper (but still only slightly pocketed) DPOF, this specimen differs from the Echo Quarry sample of *M. insignis* in having the P2 protocone confluent with the protoloph [vs. isolated from it at virtually all ontogenetic wear stages in *M. insignis*], but the merychippine characters of the Deep Creek material are emphasized here.

The merychippine traits are better expressed by AMNH 126899. In addition to the features described above, the better preserved DPOF (fig. 16.11A;) more clearly resembles that of the Echo Quarry sample of *M. insignis* (figs. 16.7, 16.9). In spite of the wider POB (table 16.4), the lacrimal penetrates the DPOF (fig. 16.11A), which is proportionately smaller than in *M. insignis* (compare tables 16.4, 16.5). The upper cheek tooth dentition of AMNH 126899 is in an earlier stage of wear (fig. 16.11A, B) than the previous specimen (fig. 16.11C). The P2

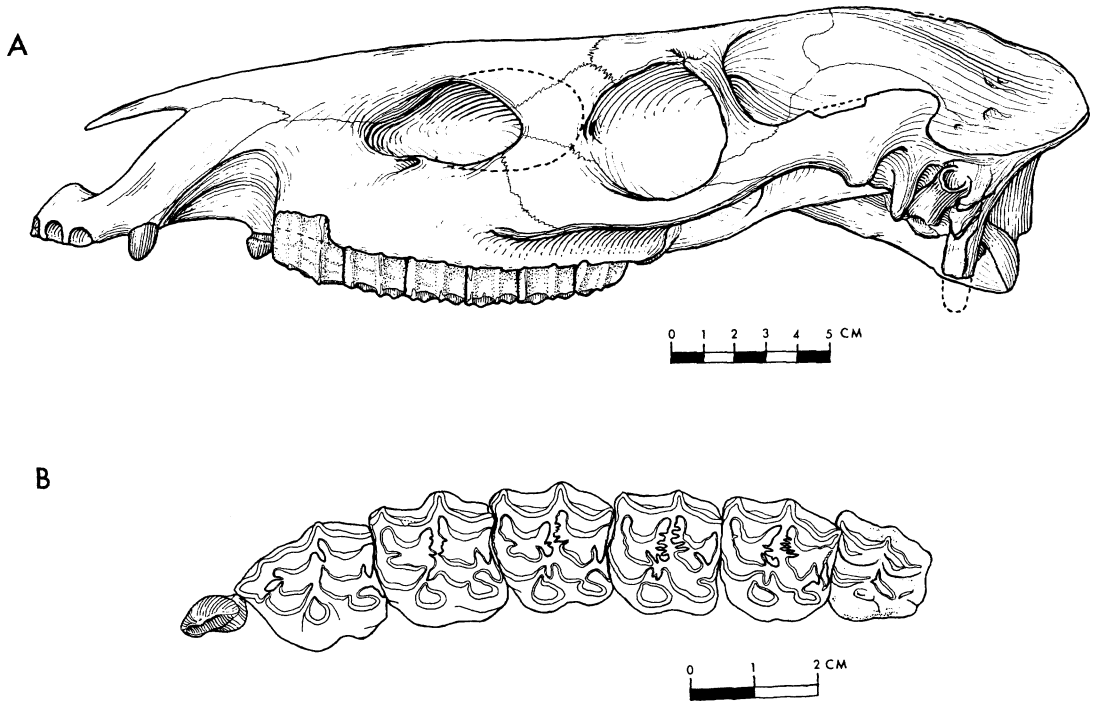


Fig. 16.12. *Cormohipparion goorisi*, F:AM 73940, holotype, Trinity River Pit 1, Fleming Formation, early Barstovian, San Jacinto County. Texas. **A,** Lateral view of cranium with lacrimal shown as penetrating the rear of the DPOF (see text). **B,** Occlusal view of left cheek tooth dentition.

mesostyle in AMNH 126899 is 25 mm tall, M3 shows only incipient wear, and confirms the presence of spurred protocone, the moderately complex fossette plication pattern, the double pli caballins on the premolars, the isolated protocone of P2, and the relatively large dP1 (11.2 mm long = 58% length of P2; table 16.1; note that the length of dP1 is about 53% that of P2 in merychippines, but much less, ca. 45% in *Cormohipparion goorisi*). In addition to its overall larger size and isolated P2 protocone, AMNH 126899 differs from the Echo Quarry sample of *M. insignis* in that the nasal notch is retracted to a position above dP1, the POB is wider, and the DPOF proportionately smaller. I emphasize the merychippine similarities of the Deep Creek, Echo Quarry, and Trinity River samples, rather than these differences.

The lower dentition of the merychippine from the Valentine Formation is represented by the associated lower ramus of AMNH 126900 (fig. 16.11D). Although incomplete, this specimen is relatively shallow below p2 (31.0 mm) and has been restored as being relatively shallow below the boundary between m2 and m3 (ca. 47 mm; table 16.6B). Whether or not this restoration is absolutely correct, enough of the actual bone is preserved to warrant the interpretation that this was a relatively slender-jawed form, comparable to, even though absolutely larger than, *Merychippus insignis* (table 16.7).

The lower cheek teeth are in an adult wear stage, with the occlusal pattern well worn on p2–m1, the ectoflexid still nearly touching the labial enamel of the metaconid/metastylid on m2–3, and the hypoconulid still separate from the hypolophid of m3. Protostylids are present on m1 and appear to be faintly represented on p3–4, as well (although not shown on fig. 16.11D). Note that, as in *M. insignis* (fig. 16.13) such protostylids are poorly expressed and do not form a major transverse element of the anterior border of the tooth. It is important that, even at this stage of wear, the ectoflexids of p3–4 reach well lingual to, or beyond (p4) the postflexid

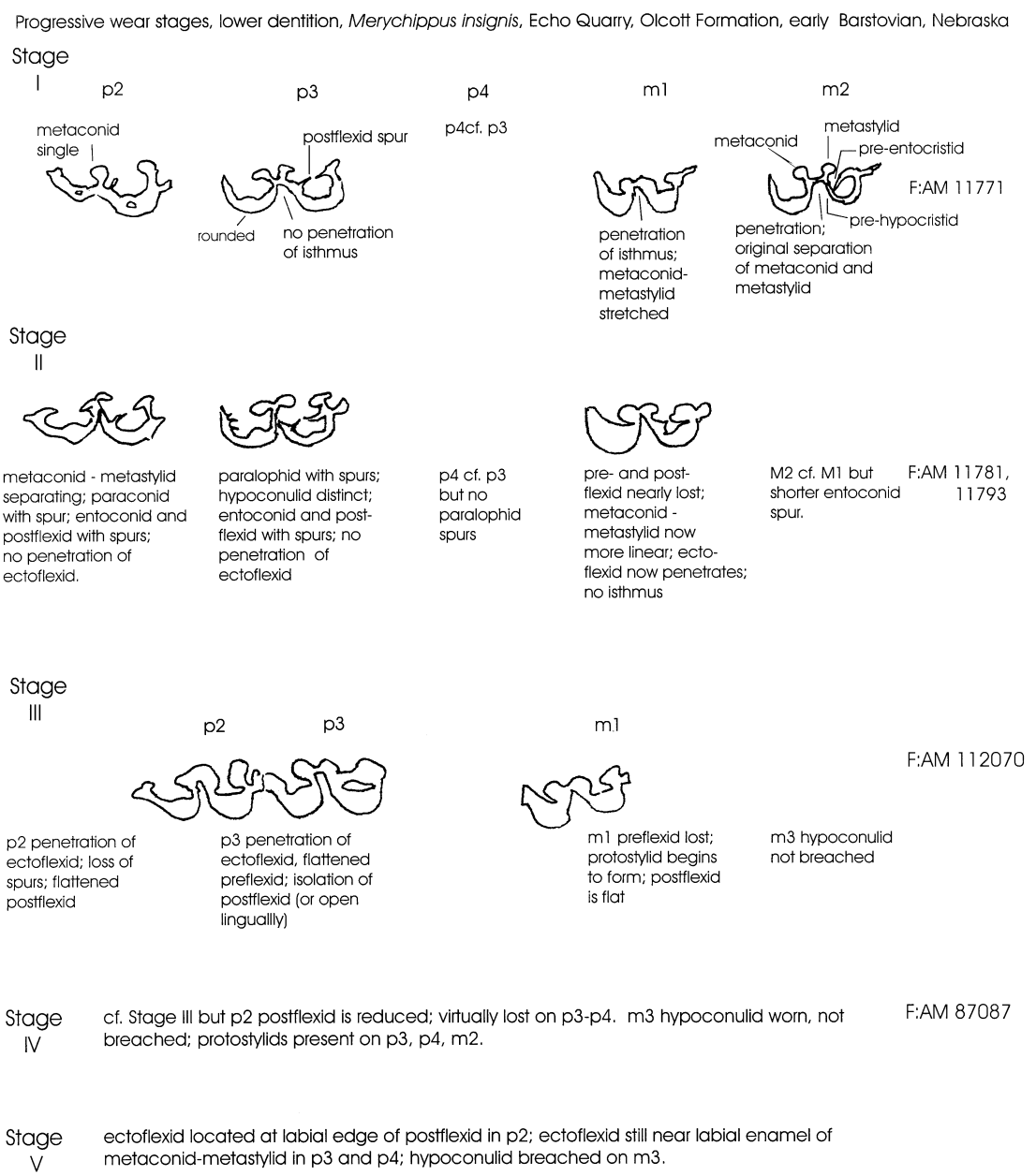


Fig. 16.13. *Merychippus insignis*. Progressive wear stages of lower dentition, based on sample from Echo Quarry, Olcott Formation, Nebraska. Wear stages used to rank progressive ontogenetic ages of mandibles bearing teeth, the heights of which could not be measured directly. See tables 16.6 and 16.7. Note that the ectoflexid in premolars penetrates deeply between the metaconid and metastylid, obviating the development of an isthmus on these teeth, as well as in the molars. This contrasts with *Cormohipparion*, where isthmuses typically are formed in the premolars. Note also that protostylids generally do not form until wear stage IV.

(fig. 16.11D) such that a well-developed isthmus does not seem to have been present in the premolars. Although in a relatively late stage of wear (V or later), p4 of AMNH 126900 preserves the deep lingual penetration of the ectoflexid typical of *M. insignis*.

Discussion: These specimens are referred to as merychippines, and it is likely that the Deep Creek form is specifically distinct from *Merychippus insignis*. Features in which the Deep Creek taxon appears to differ from *M. insignis* include: larger overall size, proportionately somewhat smaller dP1, P2 protocone remaining separate from the protoloph in late wear (e.g., fig. 16.11C), more posteriorly retracted nasal notch, longer POB, concomitantly shorter DPOF, and other features summarized in table 16.4.

Trinity River Pit 1, Fleming Formation, Texas: Fossils from this quarry are of early Barstovian age (e.g., Tedford et al., 1987). The sample includes equid specimens having a cranial and upper cheek tooth morphology similar to that just described for the Devil's Gulch sample. Further, these Trinity River Pit 1 specimens are similar to and different from *M. insignis* in ways comparable to the Devil's Gulch material described above, and also are associated with mandibular rami and lower dentitions in which p2–4 show early penetration of the metaconid/metastylid isthmus by the ectoflexid (fig. 16.13), in contrast to the condition in *Cormohipparion goorisi* (fig. 16.14). Based on these comparisons, those Texas specimens having the morphology just described are referred to *Merychippus s.s.* Furthermore, the Texas *Merychippus s.s.* samples under discussion also have a mandible that is overall more slender and of relatively more uniform depth below the cheek teeth (tables 16.6, 16.7) than in *C. goorisi* (table 16.8; fig. 16.15B). Thus, the three samples, the Texas material allocated as merychippine, the Devil's Gulch material, and specimens herein allocated to *M. insignis*, all are similar to each other in the relatively shallow mandible depth below the cheek teeth and in that the ectoflexid in the lower premolars penetrates deeply between the metaconid and metastylid, in contrast to *C. goorisi* wherein the premolar isthmuses are strongly developed and retained ontogenetically longer (compare figs. 16.13, 16.14, tables 16.6–16.8, 16.9). In that it is possible that more than one specific-rank taxon is represented by the Trinity River Pit 1 *Merychippus s.s.* material, this sample is not treated as a hypodigm. The material is also under study by R.L. Evander, so the comments made here are brief.

Material: F:AM 109883, partial cranium, RdP1, P2–M3; F:AM 109894, partial cranium, RdP1, P2–M3; F:AM 109892, R maxillary fragment, dP1, P2–M3; F:AM 109893, partial cranium, RP2–M3; F:AM 109891, associated cranium, LI2–3, R&L dP1, P2–M3, R&L rami, i1–3, p2–m3; F:AM 109884, partial cranium, RP2–M3; F:AM 109885, R maxillary fragment, P2–M3; F:AM 109874; partial cranium, RdP1, P2–4, M1 erupting; F:AM 107837, partial cranium, RP2–M3; F:AM 109882, RP2–M3; F:AM 109876, RP2–M3; F:AM 113054, R ramal fragment, p2–m3; F:AM 113052, R ramal fragment, p4–m3; F:AM 113053, R ramal fragment, p2–m2; F:AM 113056, L ramal fragment, p2–m3; F:AM 113055, R partial symphysis, ramal fragment, p2–m3; F:AM 113061, L ramal fragment, p2–m3; F:AM 113062, L partial symphysis, ramal fragment, p2–m3; F:AM 113059, L ramal fragment, p2–m3; F:AM 113064, L ramus, angular process and ascending ramus, p3–m3; F:AM 113057, R ramal fragment, p2–m3; F:AM 113060, R partial symphysis, ramal fragment, p2–m3; F:AM 113065, R&L rami, lacking symphysis, R&L p3–m3; F:AM 113070, L partial symphysis, ramus, p2–m3; F:AM 113071, L ramal fragment, p2–m3; F:AM 113066, partial symphysis, R&L rami, R&L i1, Ri2–3, c1, p2–m3, angular process; F:AM 113067, R ramus, p2–m3, angular process, partial ascending ramus; F:AM 113052, R ramal fragment, p4–m3. F:AM 113075, R ramus with symphyseal region, p2–m3.

Features indicating affinity with *Merychippus s.s.* rather than with *Cormohipparion goorisi* (found in the same quarry) include the following.

Crown height. The least worn P2 of the Trinity River Pit 1 merychippine is 16.2 mm tall at the mesostyle (table 16.2); the hypocone is still isolated from the metaloph (i.e., in very early wear). It becomes confluent with the metaloph at 14.5 mm in this sample. In *M. insignis*, the hypocone is confluent

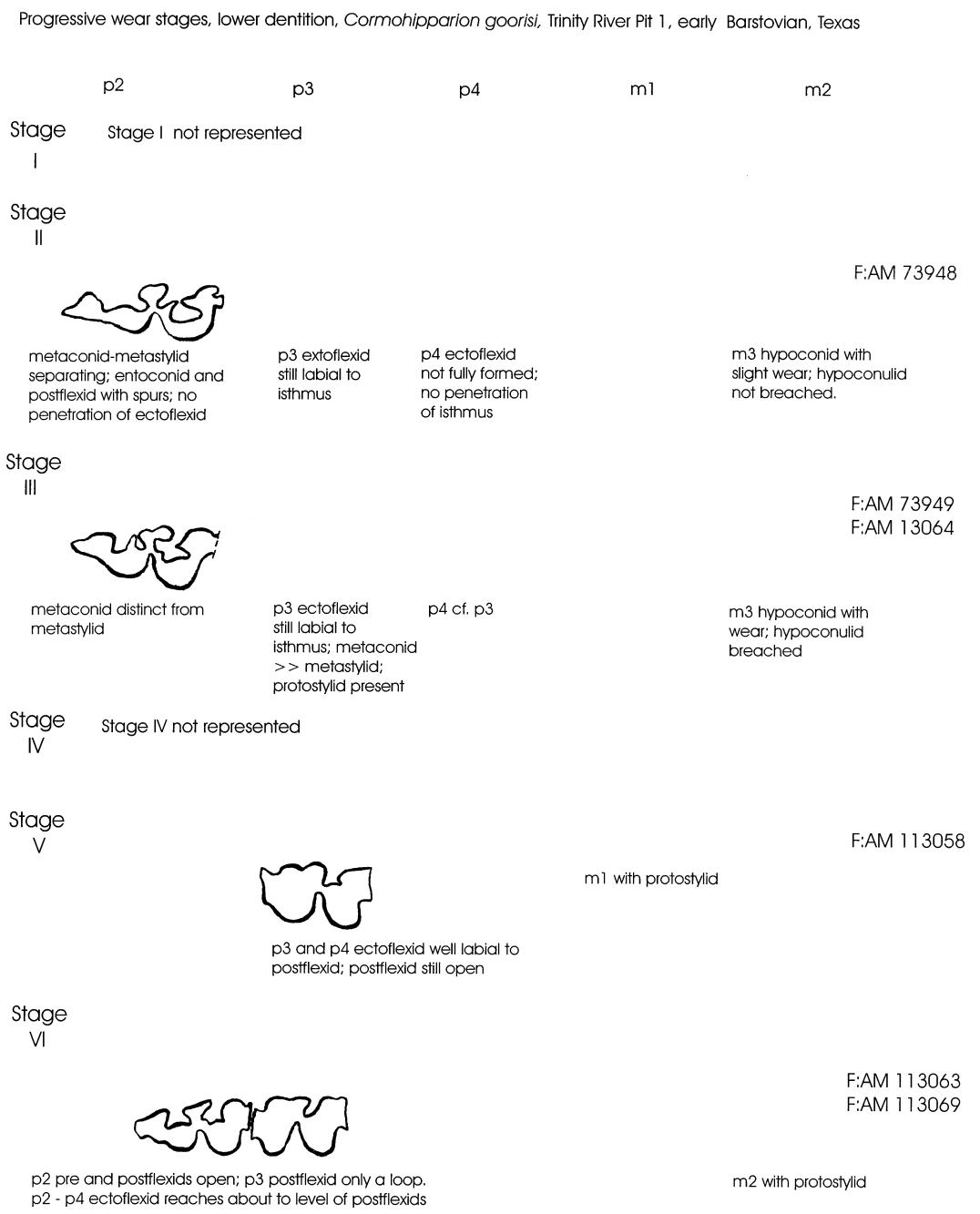


Fig. 16.14. *Cormohipparion goorisi*. Progressive wear stages, lower dentition, Trinity River Pit 1, early Barstovian, Texas. Note that premolar isthmuses are preserved well into late wear, in contrast to *M. insignis* and other taxa referred herein to *Merychippus s.s.*

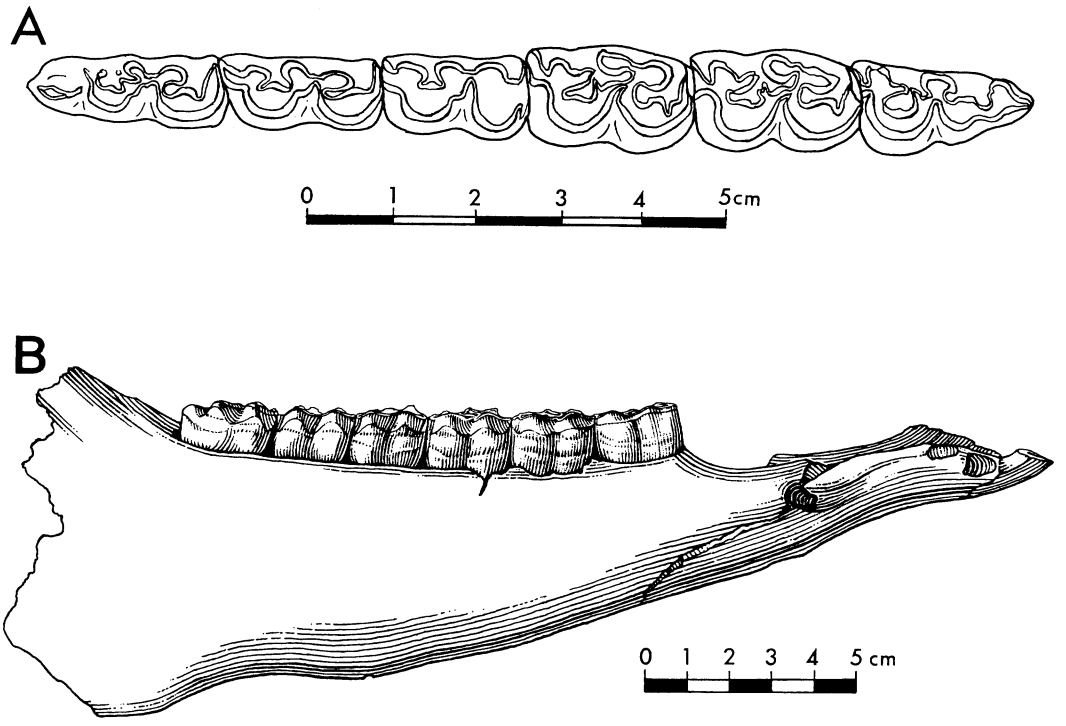


Fig. 16.15. *Cormohipparion goorisi*, F:AM 73940, holotype, Trinity Pit 1, Fleming Formation, early Barstovian, San Jacinto County, Texas. **A,** occlusal view of right lower cheek teeth, p2–m3. **B,** lateral view of dentition and mandible.

with the metaloph at 21 mm in P2. In *C. goorisi*, this occurs at 24 mm. Unworn P2 mesostyle heights for these taxa are 25 mm (*M. insignis*) and 26 mm (*C. goorisi*).

M3 in the merychippine sample is unworn at ca. 20 mm. Comparable figures for *M. insignis* are 24 mm; for *C. goorisi*, 26 mm. Thus, the Texas merychippine is somewhat lower crowned than in *M. insignis* from Nebraska, and much lower crowned than contemporary *C. goorisi*.

Protocone. The protocone of P2 is virtually circular, with a persistent spur in the Trinity River Pit 1 merychippine sample, and otherwise identical to that seen in *M. insignis*. The protocone in P3–4 in the merychippine sample is similar to the condition seen in *M. insignis*.

Fossette borders. P4–M2 fossette borders are less complex in the Trinity River Pit 1 merychippine sample, and the pli prefossette loop is distinctly smaller and less prominent than in *C. goorisi*, and generally similar to *M. insignis*.

DP1 length. This ranges from 10.5 to 15.0 mm (x = 12.5; N = 5) and is intermediate in the Trinity River Pit 1 merychippine sample between *C. goorisi* (smaller) and *M. insignis* (table 16.1).

Segregated according to these characters, the Trinity River Pit 1 merychippine sample shows other features consistent with its referral to *Merychippus s.s.* The lacrimal reaches into the rear of the DPOF (e.g., F:AM 109883, 109894, 109893, 109891, 109884, 109874, 107837). The IOF is located above the posterior part of P4 (or dP4) or the border between P4 and M1 (or dP4 and M1; e.g., F:AM 109883, 109894, 109892, 109893, 109891, 109884, 109885, 107837). IOF location does not show significant ontogenetic variation. When visible, the DPOF is either not pocketed or is only slightly pocketed (e.g., F:AM 109883, 109884, 109891, 109892, 109893, 109894).

Table 16.9 shows a segregation of lower cheek teeth from the Trinity River Pit 1 sample, with specimens compared at similar

wear stages. Those originally referred by MacFadden and Skinner (1981) to *C. goorisi* are distinct from the others, of which F:AM 109891 is associated with a cranium and upper cheek tooth dentition similar to *Merychippus insignis*. The Texas merychippine lower cheek teeth differ from those of *C. goorisi* in maintaining a deep penetration of the premolar isthmuses by their ectoflexids and being ontogenetically precocious in developing premolar and molar protostylids.

In summary, dentally and cranially these particular Trinity River Pit 1 specimens resemble *M. insignis* and other merychippines (e.g., the Deep Creek, Nebraska, material described above), and appear to have a number of cranial characters in common with that taxon. The Texas merychippine differs, at least, from *M. insignis* and from the Deep Creek, Nebraska, form in being still lower crowned.

The Texas specimens also are distinctly lower crowned than those assigned here to *C. goorisi*, have a simpler coronal pattern, and more ovate and distinctly spurred protocones (even into very late wear). In their overall similarity to the dental morphology of *M. insignis*, these Texas specimens are of merychippine type. Similarly, a suite of mandibular rami and lower cheek tooth dentitions differ from those of *C. goorisi* and resemble the merychippine from the Devil's Gulch Member of the Valentine Formation, as discussed above. These Trinity River Pit 1 specimens display strong penetration of premolar isthmuses by the ectoflexids and an ontogenetically earlier development of premolar and molar protostylids in contrast to *C. goorisi*. Associated crania and mandibular rami link the upper and lower cheek tooth features and additionally show that dP1 is relatively long (table 16.1), that the facial region is of *Merychippus s.s.* type (lacrimal penetrates the rear of the DPOF, IOF is located above the P4/M1 boundary and below a well-defined ventral border of the DPOF) and that the mandibular ramus is of relatively even depth from M3–P2.

The above analysis of associated cranial, dental, and mandibular data in the Deep Creek, Nebraska, and Trinity River Pit 1, Texas, samples led to a determination that not only are they referable as merychippines, but also which specimens from Echo Quarry, Nebraska, were referable to *M. insignis* as based originally on the cranium and upper dentition. The appraisal also indicates which of the Texas materials can be confidently allocated to *C. goorisi*. Most of the referrals of material to that species by MacFadden and Skinner (1981) are corroborated herein.

PREVIOUS INVESTIGATIONS

As summarized by Skinner and Taylor (1967), Leidy (1857) based the taxon, *Merychippus insignis*, from Tertiary deposits of the Bijou Hills, South Dakota on ANSP No. 11276, right maxillary fragment with dP2–3. *Merychippus insignis* is the genotypic species of *Merychippus*, and in the intervening years, this horse has come to represent an evolutionary grade that formed the base of the Neogene radiation of progressively hypsodont horses in North America and elsewhere. In important reviews, Stirton (1940) and Hulbert and MacFadden (1991) clearly showed that whereas the overall concept had merit, the genus *Merychippus* was paraphyletic.

Skinner and Taylor (1967) attempted to stabilize the nomen *Merychippus insignis*. After failing to find more informative specimens from the original stratotype (referred by Skinner and Taylor, 1967, to the Fort Randall Formation), a sample from the Echo Quarry of the Olcott Formation (rock unit named by Skinner et al., 1977) of western Nebraska was found to closely match the holotype. The material consists of a number of crania and directly associated and referred upper cheek teeth. Skinner and Taylor (1967) described Leidy's original material of *Merychippus insignis* and the upper cheek tooth dentition and cranium of the Echo Quarry sample. Although not exactly matched, the type of *M. insignis*''can be nearly duplicated'' in the Echo Quarry sample (fig. 16.13), which includes specimens that range from immaturity to old age (Skinner and Taylor, 1967: 19). Whereas Evander (1986) advocated restricting the nomen *Merychippus insignis* to the type material and TMM 31242–100 based largely on the absence there of a protostyle versus its presence in the Echo Quarry sample, Hulbert and MacFadden

(1991) pointed out that the polarity of this and a number of characters is uncertain, that many of these are variable in occurrence, and that the loss or acquisition of a character such as this one may occur independently in more than one equid lineage. I concur with these considerations, and further advocate stabilizing, when reasonably possible, taxonomic names that have long been utilized in the literature. I therefore support the use of the nomen *Merychippus insignis* as defended by Skinner and Taylor (1967) and Hulbert and MacFadden (1991). Based on litho- and biostratigraphic data, the holotype of *M. insignis* is of late Barstovian age, ca. 14 Ma (R.H. Tedford, personal commun., 1989) whereas the Echo Quarry referred material is of early Barstovian age (fig. 16.1), ca. 15 Ma (Tedford et al., 1987: fig. 6.2; Olcott Fm.).

MacFadden and Skinner (1981) named *Cormohipparion goorisi* on the basis of cranial, dental, and mandibular material from the early Barstovian Trinity River Pit 1 locality, Fleming Formation, San Jacinto County, Texas. The taxon was considered as the geologically oldest and morphologically most primitive species of *Cormohipparion* Skinner and MacFadden 1977, based on *Cormohipparion occidentale* (= *Hipparion occidentale* Leidy, 1856) from deposits exposed along the Little White River (Skinner and Taylor, 1967: 18) of late Clarendonian age (see also MacFadden, 1984: 162).

Skinner and MacFadden (1977) showed that *C. occidentale,* commonly referred to the genus *Neohipparion* in previous literature (e.g., Stirton, 1940), differed from *Neohipparion* especially in features of the cranium, but also in having distinctly more complex upper cheek tooth dental patterns. This was followed by MacFadden (1984), who suggested that the most plesiomorphic species of *Neohipparion* is represented by *N. coloradense*. Hulbert (1988, 1989), Webb and Hulbert (1986), and Hulbert and MacFadden (1991) advocated removing the species, *N. coloradense*, from *Neohipparion*, but that does not affect the interpretation that *C. occidentale* is distinct from *Neohipparion*. Woodburne et al. (1981) defined *Cormohipparion sphenodus* that is overall geologically and morphologically intermediate between *C. goorisi* and *C. occidentale*. Woodburne (1996a) renamed this taxon as *Cormohipparion quinni*. One of the results of the present work will be to enlarge upon the characters that define and characterize *C. goorisi* so as to lay the foundation for further analysis of its relationship to other taxa that participated in the adaptive radiation of Miocene hypsodont horses (e.g., Hulbert and MacFadden, 1991).

SYSTEMATIC PALEONTOLOGY

Merychippus insignis Leidy 1857

Figures 16.7, 16.9, 16.10, 16.13, 16.16; tables 16.1, 16.5, 16.7, 16.10–16.19

TYPE SPECIMEN AND LOCALITY: ANSP 11276, maxillary fragment with RdP2–3 from the Fort Randall Formation, Bijou Hills, South Dakota (Skinner and Taylor, 1967: 18).

DISTRIBUTION AND AGE: Late Barstovian, Bijou Hills, South Dakota, and early Barstovian, northwestern Nebraska.

REFERRED MATERIAL: From Echo Quarry, Olcott Formation, Sioux County, Nebraska (Skinner et al., 1977). F:AM 87006, RdP2–4; F:AM 87007, RdP2–4, unerupted P2–M2; F:AM 87009, RdP2–4; F:AM 87010, LdP2–4; F:AM 87015, partial cranium, RdP3, R&L dP4, unerupted RP4, R&L M1–2; F:AM 87000, juvenile ♂ cranium with LdP1, R&L dP2–4, M1; F:AM 87001, ♂ cranium with RdP1, R&L P2–M3; F:AM 87002, ♂ cranium with RP2–M3; F:AM 87003, ♂ cranium with R&L dP1, P2–M3; F:AM 87004, ♂ cranium with R&L dP1, P2–M3; F:AM 87005, elderly ♂ cranium with R&L dP1, P2–M3; F:AM 87008, R maxillary with P2–M3; F:AM 87049, L maxilla with P3–M2; F:AM 87048, L maxilla with P3–M3; F:AM 87050, LP4–M2, M3 in crypt; F:AM 87058, RP4–M3; F:AM 109983, unerupted RP3–4, RM1; F:AM 87056, RP2–M2, M3 in crypt; F:AM 87014, partial cranium with R&L P3–M3; F:AM 87052, LP4–M3; F:AM 109984, RM1–3; F:AM 87042, palate with R&L P2–M3; F:AM 87013, palate with R&L dP1, P2–P3, RP4–M3; F:AM 87041, fragmentary cranium with LP2, M1–3, RP3–M3; F:AM 87022, RP3–M3; F:AM 87035, LM1–3; F:AM 87036, LM1–3; F:AM 87039, LM1–3; F:AM 87037, LM1–3; F:AM 87019, RP3–M2; F:AM 87060, LP4–M3; F:AM 87046, LdP1,

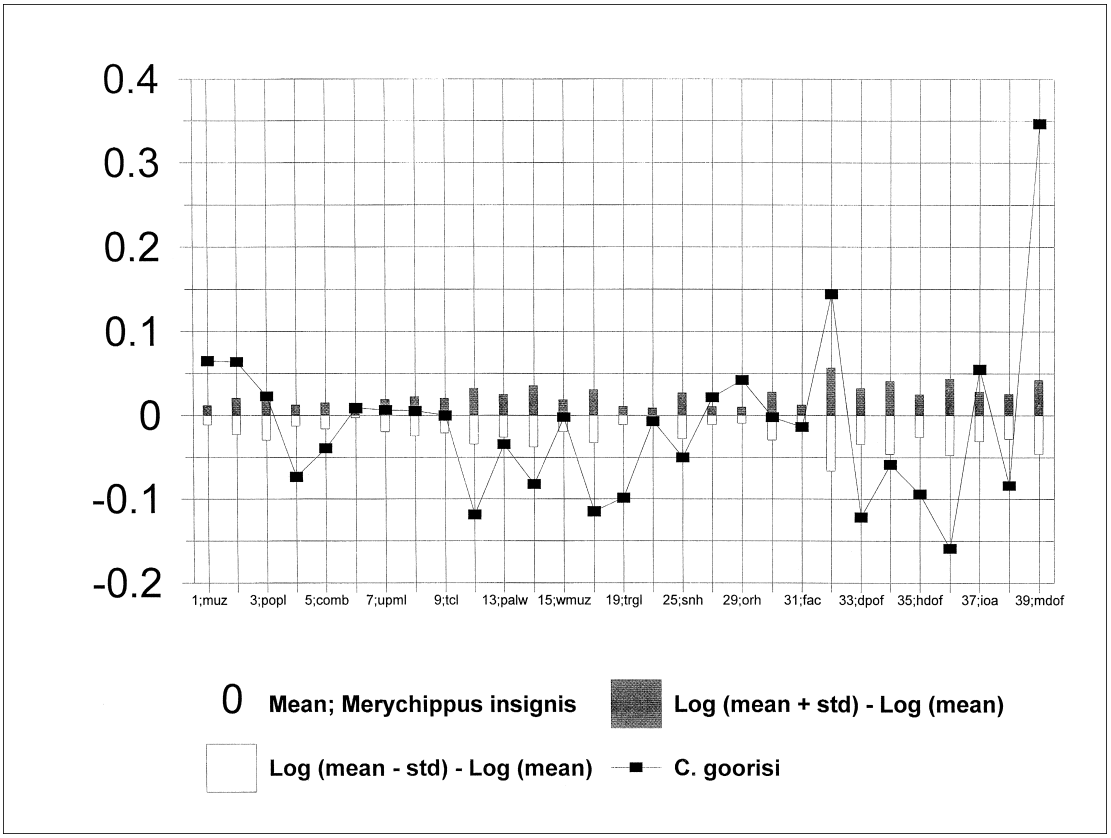


Fig. 16.16. Log-ratio diagram of cranial dimensions of *Merychippus insignis* relative to *Cormohipparion goorisi*, based on tables 16.5 and 16.20.

P2–M3; F:AM 87062, LM1–M3; F:AM 87043, LdP1, P2–M3; F:AM 87047, LP2–M3; F:AM 87057, elderly RdP1, P2–M3; F:AM 110374, RM1–3; F:AM 110387, LP3–M1; F:AM 110389, RP2–4; F:AM 110379, RM1–3; F:AM 87059, RP2–M1; F:AM 87064, LP3–M3; F:AM 87061, LdP1, P2–4; F:AM 87051, LP2–M2; F:AM 87055, palate with R&L dP1–P3, LP4; F:AM 87045, palate with R&L dP1–P2, RP3–M1; F:AM 87030, LdP1, P2, P4–M1; F:AM 87012, palate with R&L P2–M2; F:AM 87016, RP3–M3; F:AM 87023, RP2–M1; F:AM 87029, LP3–M2; F:AM 87028, LP3–M1; F:AM 87032, LdP1, P2–M1; F:AM 87040, LP2–4; F:AM 87034, LP2–M2; F:AM 111771, L ramal fragment, p2–m2; F:AM 87074, R ramal fragment, p2–m3; F:AM 111781, L&R symphysis, L ramal fragment, p2–m1; F:AM 111791, R ramal fragment, p3–m2; F:AM 111793, ♂, R&L symphysis, Li3, ramal fragment, p2–m2; F:AM 112061, R ramal fragment, p3–m3; F:AM 87072, L symphysis, ramal fragment, p2–m3; F:AM 112062, L ramal fragment, p3–m3; F:AM 111794, symphysis, R&L c1, Li3 erupting, Lp2–m2; F:AM 87076, symphysis, erupting R&L i3, R ramal fragment, p2–m2; F:AM 111774, R ramal fragment, p2–m2; F:AM 111780, L ramal fragment, p3–m2; F:AM 111792, L ramal fragment, p3–m2; F:AM 87075, L ramal fragment, p3–m3; F:AM 112070, symphysis, R&L ramal fragment, c1, p2–m3; F:AM 87078, R&L symphysis, angular, condylar and coronoid processes, R&L p2–m3; F:AM 112064, L ramal fragment, p2–m3; F:AM 112066, L ramal fragment, p2–m3; F:AM 112063, L ramal fragment, p2–m3; F:AM 87080, L symphysis, ramal fragment, p2–m3; F:AM 111757, R symphysis, ramal fragment, p2–m3; F:AM 111760, R symphysis, ramal fragment, p2–m3; F:AM 111761, R ramal frag-

ment, p3–m3; F:AM 111759, R ramal fragment, p3–m3; F:AM 112067, L ramal fragment, p2–m3; F:AM 87085, R&L symphysis, ramal fragment, p2–m3; F:AM 111750, L symphysis, ramal fragment, p2–m3; F:AM 87088, ancient R symphysis, ramal fragment, p2–m3; F:AM 111754, R ramal fragment, p2–m3.

SPECIMENS PROBABLY REFERABLE: These specimens are in a very old or very early ontogenetic stage of wear, and may be confused with other taxa, but likely pertain to the Echo Quarry hypodigm of *Merychippus insignis*. F:AM 87017, RP2–M3; F:AM 110373, LP3–M3; F:AM 87063, LP3–M3; F:AM 71218, RM1–3; F:AM 110376, RM1–3; F:AM 87027, LP4–M3; F:AM 110378, RP4–M3; F:AM 110376, RM1–3; F:AM 110377, RM1–3; F:AM 110375, RP3–M3; F:AM 87038, LM1–3; F:AM 110380, very ancient LdP1, P2–M3; F:AM LP4–M3; F:AM 87043, LP2–M3; F:AM 87028, LP3–M1; F:AM 87054, LP2–4; F:AM 110386, RP4–M2; F:AM 110381, LdP1, P2–M1; F:AM 110388, LP4–M2; F:AM 110385 (very early wear), RP2–4; F:AM 110383 (very early wear), RP4–M2; F:AM 110384, RdP1, P2–4; F:AM 87021, RP3–M2; F:AM 110382 (very early wear), RdP1, P2–4.

SPECIMENS PROBABLY NOT REFERABLE: These specimens, currently catalogued as *Merychippus insignis* from Echo Quarry, probably do not pertain to this species. F:AM 71190, RdP1, P2–M3. M1 in early but nearly adult wear has a mesostyle height of 30 mm and thus originally much taller than typical of unworn M1 in *M. insignis*. Also, for this stage of wear, the protocone tends to be more elongate, the hypocone is too slender, fossette plications are too deep and numerous. F:AM 71216, RP4–M2. P4 is ca. 17 mm tall (mesostyle), but is nearly worn out with a very much simpler enamel pattern than typical of *M. insignis* at this crown height; protocone is confluent with the protoloph in M1 and P4, M2 has very simple fossette patterns, but retains an isolated protocone. F:AM 71227, LdP1, P2–M2 has a 17 mm tall (mesostyle) P2, with the protocone confluent with the protoloph and the protoloph connected by a crochet to the metaloph (never occurs in *M. insignis*; in P3–M1 the protocone is confluent with the protoloph at 18, 17, and 16 mm, respectively (much sooner than in *M. insignis*), and the isolated M2 protocone lacks a spur.

ORIGINAL CHARACTERIZATIONS: (some additions signified by * based on the present study): Leidy (1857) gave no diagnosis, but characterized the (immature) dentition of *M. insignis* as resembling those of ruminants, including those of deer and oreodonts. Based on the referred material from Echo Quarry, Skinner and Taylor (1967: 29–35) characterized, but did not diagnose, *Merychippus insignis* and (with few and minor exceptions) did not otherwise compare it with other equid species. The following is paraphrased and somewhat condensed from Skinner and Taylor (1967: 29–35), with emphasis on features determined to be useful in phyletic analysis by Hulbert and MacFadden (1991). In this context *M. insignis* is a mesodont horse in which the upper cheek teeth consist of a large and functional double-rooted dP1; dP2 and dP3 have prominent mesostyles, weak metastyles, an arcuate protoloph with a single plication between (but not connecting) the paracone and protocone, an incipient anterocrochet present but not uniting with the metaloph, protocone round to tear-shaped, crescentic metaloph with incipient to distinct crochet, and connecting to the anterior base of the metacone and to the hypocone, respectively, distinct hypostyle uniting anteriorly with the metaloph and bearing one or two plis hypostyle in the hypoconal groove. DP4 was not described by Skinner and Taylor (1967), but based on their figure 5 and personal inspection, generally resembles dP3.

The permanent cheek teeth were characterized as being mesodont, moderately curved, and covered by cement, except for the centers of fossettes. The long parastyle of P2 is centrally placed; those of P3–4 are large and overlap the metastyles of the next anterior tooth. Molar parastyles are neither so large nor as overlapping as in the premolars. Premolar mesostyles are stronger than those of the molars. Except for an anterior rib on P2, ribs are weak on all other cheek teeth. On P2 the protoloph connects to the ectoloph posterior to the parastyle, whereas on remaining cheek teeth it connects to the parastyle. The pli protoloph is weakly developed

to absent in all adult teeth. The protoloph is mostly separate from the metaloph on P2, but is usually connected to the metaloph by a crochet on the other teeth. Protocones, elongate and isolated in early wear, connect with the protoloph and become rounded in later wear, and are oriented with their long axis about parallel to the anteroposterior axis of the tooth. Hypocones show changes in shape with wear comparable to the protocones and have a similar orientation. In early wear the fossette borders are moderately complex, the pli caballin is usually double in premolars, single in molars. One or two plications from the hypostyle extend into the hypoconal groove.

The cranium of *M. insignis* (Skinner and Taylor, 1967: 33–35) has a moderate-sized muzzle, the nasal notch (* not specifically mentioned by Skinner and Taylor, 1967) is relatively short (incised to a position above and about midway between C1 and P2); the buccinator fossa is separate from the DPOF; the POB is about 17 mm (*$\bar{x}$ = 17.2, table 16.5, #32) wide and the lacrimal extends anterior to it; the DPOF is ovate, located high on the face, and ends anteriorly above P3. The upper border of the DPOF is sharp, especially at midlength, and the posterior border is sharp and rounded. In contrast, the ventral and anterior borders are shallow to indistinct, although *they are visibly and palpably distinguishable from the adjacent facial surfaces. The DPOF is faintly pocketed, if at all, and a malar fossa is absent. *The DPOF is bipartite, with a shallow ridge located just anterior to the tip of the lacrimal separating an anterior from a posterior portion (fig. 16.7C). *The infraorbital foramen lies low on the face, with the bisector of its posterior border being about 10–12 mm below the DPOF, 17–20 mm above an anterior projection of the facial crest, and above the rear half of P4. The orbit has a distinctly formed anteromedial fossa for the lacrimal sac, with a small lacrimal duct found slightly externally and dorsally that penetrates into the nasal cavity. The frontal bones are flat, not domed, and the lacrimal is prominent, effectively subrectangular in shape in facial expression with a variably tapered or notched anterior tip contained within the rear portion of the DPOF. In ventral view, the muzzle is U-shaped, and palatine fissures are prominent. The posterior nares are widest opposite M2 in adult skulls. The occipital condyles have shallow and wide condyloid fossae.

ADDITIONAL DESCRIPTION AND COMPARISON: A fuller appreciation of the significance of various cranial parameters measured as recommended by the 1981 *Hipparion* Conference (Eisenmann et al., 1988) will follow the measurement of remaining *Cormohipparion* samples. For the present, the following comments can be advanced both as basic data (table 16.5) and in comparison with the cranium of *Cormohipparion goorisi*. Using parameter #4 (combined length of the basioccipital and basisphenoid) as a basilar length indicative of basic cranial and thus body size (e.g., Radinsky, 1984), cranial dimensions of *M. insignis* may be compared with those of *C. goorisi*. Parameter #4 is about 20% longer in *M. insignis* than in *C. goorisi*. Other parameters that are comparably different in the two taxa (with *C. goorisi* being 16–20% smaller; log—0.05 to 0.1, fig. 16.16) include: diastemal width (#14), transglenoid width (#19), DPOF height (#35), and height of rear center of DPOF above the alveolus (#38). Thus, in all the above, *M. insignis* is actually larger than but proportionally similar to *C. goorisi*. This suite is here referred to as Cranial Group 1 to facilitate comparison.

Cranial Group 2 includes parameters in which *M. insignis* is dimensionally about the same as *C. goorisi*. In terms of Group 1, these features actually are about 20% proportionally larger in *C. goorisi*. These parameters include, postpalatal length (#3), total cranial length (#6), length of premolar series (#7), length of molar series (#8), length of combined premolar and molar series (#9), width of muzzle at I3 (#15), inion height (#22), incision of nasal notch (#30), and facial length from orbit to nasal notch (#31).

Cranial parameters in which *C. goorisi* is distinctly larger than *M. insignis* would be proportionally much (27–46%) larger in *C. goorisi*. This suite is referred here to Cranial Group 3. The parameters include: muzzle length (#1), palatal length (#2), length of preorbital bar (#32), height of the IOF above the alveolus (#37), and the distance between the anterior end of the lacrimal and the rear of

the DPOF. In *M. insignis*, the anterior end of the lacrimal actually penetrates beyond the rear of the DPOF by an average of about 8 mm, so the value is a negative figure (#39, table 16.5). In *C. goorisi*, the rear of the DPOF lies about 10 mm anterior to the lacrimal tip.

In summary, it appears that *M. insignis* is a relatively small hipparionine (sensu Hulbert and MacFadden, 1991), with a basilar length (#4) of about 86 mm; the muzzle is short (ca. 67 mm, #1) and relatively wide (ca. 36 mm, #15), the premolar series is slightly longer (ca. 64 mm, #7) than the molar series (ca. 55 mm, #8) and the total cheek tooth length is rather short (ca. 116 mm, #9). The palate is relatively wide (ca. 48 mm, #13, the frontals are flat and relatively wide (ca. 92 mm, #18). The preorbital region of the face is relatively long (ca. 132 mm, #31), and the DPOF relatively long (ca. 64 mm, #33) and medially shallow (9–12 mm as measured in this study), relatively well-defined dorsally, well-defined posteriorly, and weakly defined ventrally and anteriorly; it is faintly, if at all, pocketed posteriorly; the overall rectangularly shaped lacrimal has a pointed anterior tip that extends on average about 8 mm into the rear of the DPOF (#39); the DPOF is relatively high (ca. 37 mm, #35) and located well above (ca. 31 mm, #36) the facial crest; the POB is of moderate size (ca. 17 mm, #32). The IOF is located above the rear of P4, or the boundary between P4 and M1 or, in juvenile specimens, comparably with respect to dP4 and M1, and is virtually below the longitudinal midpoint of the DPOF, irrespective of ontogenetic age.

Description of the Upper Cheek Tooth Dentition: The following remarks are derived from the data obtained for each tooth in the cheek tooth series, and summarized in tables 16.10–16.16. Table 16.10 forms the crown height framework upon which the other data shown in tables 16.11–16.16 were constructed. These record the following data for each tooth position: height (mesostyle) at which the protoloph connects to the metaloph, interval at which the prefossette is displayed (compare the incomplete fossettes in P3 of fig. 16.7D versus P3 in fig. 16.10F) (or lost), comparable data for the postfossette; for opening of the hypocone (isolated in M1, fig. 16.7D, vs. open and connected to metaloph in fig. 16.10F), presence and complexity of the hypoconal groove, isolation versus opening of the protocone to the protoloph, and presence and complexity of the pli caballin, of the pli protoloph, of the pli prefossette, of the pli postfossette and of the pli hypostyle.

A detailed description of the upper cheek teeth is presented in Appendix 1. The salient morphology of the adult upper cheek tooth dentition of *Merychippus insignis* is summarized as follows.

The dP1 is large (table 16.1), double rooted, and persistent into final stages of wear (e.g., F:AM 87032). P2–M3 are mesodont (unworn crown heights range from 24 to 27 mm; tables 16.11–16.16), moderately curved (Skinner and Taylor, 1967), with generally ovate protocones (figs. 16.7, 16.12) that have a strong spur persisting virtually to the end of wear. A stable (= adult) wear pattern is established after about 24% wear in P2, 11% in P3, 15% in P4, 22% in M1, 22% in M2, 12% in M3, and the hypocone connects to the metaloph in early wear. Within the interval of maximum complexity of the occlusal pattern, the pli protoloph is present in 50% (P2), 85% (P3), 53% (P4), 13% (M1), 39% (M2), and 29% (M3) of the specimens.

Although the protocone and hypocone are subequal in size (Skinner and Taylor, 1967), the protocone is always somewhat larger. The protocone is usually subovate in outline, and (as indicated here) is nearly equidimensional in the P2 and P3, with the width/length ratio of the means of the dimensions being 0.90 (P2) and 0.81 (P3). In P4 (0.78), M1 (0.75), and M2 (0.61), the protocone tends to be more elongate (table 16.17). Because of relatively early wear stages represented for many M3s, they were not considered in this analysis.

This report reveals that, whereas the protocone remains distinct from the protoloph until latest wear in all cheek teeth, the hypocone early connects to the metaloph. The protocone remains closed until very late wear (12 mm or below, or at levels consistent with 50% or greater wear). This is best developed in P4, M2, and M3. In P2, some specimens display an open protocone from the 17-mm level (32% wear; table 16.11). For P3 and

M1 (tables 16.12, 16.14) comparable figures are 18 mm (33%) and 16 mm (41%). In all teeth, the protocone retains a spur until it becomes confluent with the protoloph. The protoloph consistently connects via a crochet to the metaloph in all but P2, where the two lophs are uniformly separate until very latest wear.

Within the interval of greatest pattern complexity (tables 16.11–16.16), the pli caballin is present in about 50% of the specimens in P2, 85% in P3, 69% in P4, 97% in M1, 92% in M2, and 32% in M3. When present, the pli caballin is double more frequently in the premolars than in the molars (22% in P2, 57% in P3, and 69% in P4 versus 8% in M1, 4% in M2, and never double in M3).

The pli hypostyle is present in about 94% of the specimens in P2, and is composed of more than a single pli in 29% when present. Comparable figures for the other cheek teeth are: P3, 70% and 5%; P4, 80% and 17%; M1, 84% and 13%; M2, 71% and 0%; and M3, 53% and 44%.

Fossette borders are moderately complex, and opposing margins of the pre- and postfossettes may bear as many as 5–6 plications at 19%–33% wear in P4–M2. The pli protoloph, pli prefossette, pli postfossette, and pli hypostyle are typically present to, and beyond, 50% wear, except in M1, which generally lacks a pli protoloph. Although less frequent and less numerous than on opposing faces of the pre- and postfossettes, P2 and P3 show extra plications on the anterior and posterior faces of those fossettes in 15–70% of cases where such are present. P4, M1, and M3 show no additional crenulations of the pli protoloph, whereas M2 has an extra plication in 10% of such cases. An additional crenulation of the pli hypostyle occurs in about 15% of such cases in P4 and M1, in no cases for M2, and in about 20% in M3. This indicates that there are virtually no crenulations on the anterior border of the prefossette, except for the pli protoloph, and none on the posterior border of the postfossette except for the pli hypostyle in P4–M3. Table 16.18 shows average plication complexity for P2–M3 in the interval of greatest complexity. Virtually all taxonomically important details of the tooth have been lost by the time the teeth are worn to 10–13 mm above the base of the crown.

DESCRIPTION OF THE LOWER CHEEK TOOTH DENTITION: The morphology of the material discussed here from Echo Quarry (Olcott Formation), Nebraska, is consistent with that discussed above for *Merychippus s.s.*, and is of the proper size to successfully occlude with comparably aged (ontogenetically) upper dentitions associated with the crania of *M. insignis*. The description is presented in an ontogenetically developmental sequence, couched, in part, on table 16.19 where the specimens are listed in progressively increasing wear stages. The wear stages used here are generally comparable to those used for the Trinity River Pit 1 specimens. Because of specific differences, however, some morphological details may differ between the two samples.

In wear stage I (e.g., F:AM 111771), the p2 metaconid is single, slightly later bifid into the presumptive metaconid/metastylid (fig. 16.13). A spur from the anterolingual portion of the postflexid extends posterolingually. For p3, the postflexid spur (fig. 16.13) is directed toward an opposing structure from the entoconid (pre-entoconid spur) and, as throughout, the labial margins of the protoconid and hypoconid are rounded and, for all premolars, the ectoflexid does not penetrate the isthmus between the metaconid and metastylid. The p4 is generally similar to p3, but in a more advanced stage of wear. In about equivalently worn m1, the metaconid/metastylid are already distinct, and longitudinally drawn out, whereas in m2, the ectoflexid penetrates the metaconid/metastylid isthmus, and the pre-entocristid extends to the prehypocristid (fig. 16.13).

In stage II (e.g., F:AM 111781, 111793), p2 shows a better developed metaconid and metastylid; a posterolingual spur is present on the paraconid, comparable to that from the prehypocristid and the pre-entoconid spur still is present. Although separate and connected, the metastylid and metaconid are slightly penetrated by the ectoflexid (fig. 16.13). In p3, short-lived spurs occur on the posterolingual border of the paralophid; the hypoconulid is distinct; the ectoflexid does not penetrate the metaconid/metastylid isthmus. The p4 resembles p3 but lacks paralo-

phid spurs. In m1, preflexids and postflexids are nearly absent, and ectoflexid penetrates deeply lingually. The m2 is much like m1 but has a shorter pre-entoconid spur.

In stage III (e.g., F:AM 112070), all premolars show deep penetration into the metaconid/metastylid isthmus by the ectoflexid; above-mentioned spurs are absent; the postflexid is flattened and open (p2) to isolated p3; in m1 the preflexid is essentially lost and the postflexid is flat. The hypoconulid of m3 is still not breached.

In stage IV (e.g., F:AM 87087), the premolar morphology is generally like that of stage III but the p2 postflexid is reduced, and virtually absent on p3–4. Protostylids are present on p3–4, m2, and likely on m1. The hypoconulid of m3 is worn, but dentine not yet exposed.

In stage V (e.g., F:AM 111761), the ectoflexid now is at the labial edge of the postflexid in p2 and still is near the labial enamel of the metaconid/metastylid in p3–4; m3 hypoconulid is breached. In older stages, the dental pattern progressively deteriorates to the extent that the morphological characterization of *Merychippus insignis* is not based on such specimens.

Based on the materials evaluated here, the lower cheek tooth dentition of *Merychippus insignis* is characterized as being relatively small; premolar and molar metaconids/metastylids (when developed in stage II and later) are subequal in size and have rounded enamel borders; the protoconid and hypoconid are rounded in outline; premolar ectoflexids penetrate deeply lingually and only in latest stages of wear terminate at or labial to the pre- or postflexids whereas molars show deeply penetrating ectoflexids at least to wear stage III or IV; premolar and molar protostylids appear at about wear stage III and IV and rarely are more than a visible sharp bend in the enamel pattern at the anterolabial corner of the tooth.

As shown in table 16.7, the mandibular ramus of *M. insignis* is gracile and diminishes only slightly from below the anterior end of m3 to the anterior end of p2. Based on less exhaustive comparisons with other, approximately contemporaneous, taxa, the lower mandible and cheek tooth dentition of *M. insignis* appears to be conservative in the combined character suite of: smaller size, less prominent protostylids, shorter symphysis, rounded protoconid and hypoconid, subequal metaconid/metastylid, rounded outline of metaconid and metastylid with broad, shallow, U-shaped linguaflexid; deep lingual penetration of premolar ectoflexids.

SUMMARY: Based on the information detailed above, *Merychippus insignis* can be characterized on the Echo Quarry sample as: relatively small size with a short muzzle; nasal notch retracted to a position about midway between C1 and P2; a POB that is of intermediate width (e.g., 17 mm); the DPOF faintly but distinctly expressed with definite dorsal, posterior, and ventral borders; the DPOF but slightly pocketed posteriorly and relatively long (ca. 64 mm) in comparison to the cheek tooth row length (ca. 116 mm); the IOF located above the P4/M1 boundary, with the bisector of the rear of the IOF lying about 13–17 mm above the anterior projection of the facial crest; the lacrimal dorsoventrally broad and penetrating the rear of the DPOF for a distance of about 8 mm; dP1 persistently large (ca. 13 mm long), two-rooted, and present into old age; upper cheek teeth mesodont, ca. 25–27 mm tall at the mesostyle in the unworn condition; the protocone uniformly connected to the protoloph in P2 except in earliest wear, but remaining isolated until latest wear in other cheek teeth; fossette borders moderately complex in the upper half of the cheek tooth crown, with as many as four to six but usually two plications on the opposing faces of the pre- and postfossettes; protocones virtually uniformly spurred; those of the premolars nearly circular, whereas those of the molars are more elongate; the hypoconal groove commonly with single plication; dp1 rarely preserved (generally suppressed); metaconids and metastylids subequal in size and mostly with rounded outlines and separated by shallow but U-shaped linguaflexids; premolar ectoflexids early penetrate the metaconid/metastylid isthmuses and maintain a position at or lingual to the pre- or postflexid into late wear; protostylids developed on p3–m2 in later wear and are usually little more than an angulate bend in the enamel at the pertinent part of the tooth; mandibular rami have short

symphyses and are relatively uniform in depth from the anterior end of m3 to p2.

Cormohipparion goorisi MacFadden and Skinner 1981

Figures 16.12, 16.14–16.16; tables 16.8, 16.9, 16.17, 16.18, 16.20–16.28

TYPE SPECIMEN AND LOCALITY: ''F:AM 73490, well preserved skull with alveoli for incisors, right canine and P1, and right and left P2–M3, from Trinity River Pit 1, Fleming Formation, San Jacinto County, Texas Gulf Coastal Plain.'' (MacFadden and Skinner, 1981: 620).

DISTRIBUTION AND AGE: Early Barstovian of the Gulf Coastal Plain of Texas and Florida (ca. 15 Ma; Hulbert and MacFadden, 1991: 36), including material from the Sweetwater Branch site, Arcadia Formation, Polk County, Florida not mentioned by MacFadden and Skinner (1981). The present discussion is limited to the holotype and topotypic material. Comments are not presented as to the affinity of the Sweetwater Branch specimens.

HYPODIGM (* = original hypodigm of MacFadden and Skinner, 1981: 621): *F:AM 73940, holotype ♂ cranium with RC1, RdP1, R&L P2–M3; *F:AM 73941, juvenile cranium with R&L dP2–4; *F:AM 73942, ♀ laterally skewed cranium with R&L dP1 (alveoli), P2–M3; *F:AM 73943, ♀ facial region, with R&L dP1, P2–M3; *F:AM 73944, R&L dP2–4, M1–2, M3 barely erupting; *F:AM 73952, ♀ partial facial region, with R&L I2–3, C1, dP1, P2–M3, LP4–M3; *F:AM 73945, R maxillary fragment with dP2–dP4; *F:AM 73946, R maxillary fragment with dP2–4; *F:AM 73947, R maxillary fragment with dP2–4, erupting M1; F:AM 109875, R maxillary fragment with P2 and P3 in crypt, RdP3–4, M1; F:AM 109886, maxillary fragment with LP3–M3; F:AM 109887, RM1–3; F:AM 109889, LP3–M2; F:AM 109890, RP4–M3; F:AM 73948, R ramus with symphyseal region, Ri2, Lc1, Rp2–m3; F:AM 73949, L ramus with p2–m3; F:AM 113058, L ramus with symphyseal region, p2–m3; F:AM 113063, R&L rami with Rp2–m1, Lp3–m3; F:AM 113068, R ramus with symphyseal region, Rp2–m3; F:AM 113069, L ramus with p2–m3. F:AM 107873, adult skull fragment with RP2–M3, LC1, LP2–4 is here removed from the hypodigm of *C. goorisi* on the basis of IOF being located above the anterior half of M1 in this ontogenetically very old specimen.

ORIGINAL DIAGNOSIS (MacFadden and Skinner, 1981: 621): ''Small hipparion. Cheek teeth mesodont. Protocone rounded with anterior spur. Cheek teeth covered with cement. Skull small relative to hipparions such as species of North American *Hipparion s.s.*, *Neohipparion*, and the other species of *Cormohipparion*. Nasal notch shallow and it extends posteriorly to a position that lies dorsal to the canine. Prominent nasomaxillary fossa lying over P3–M1 with well-developed and continuous anterior and posterior rims. Very deep posterior pocket of fossa that extends almost to the anterior margin of the orbit. Fossa positioned far forward of orbit resulting in a wide preorbital bar. The anterior margin of the lacrimal bone usually does not touch the posterior rim of the fossa [see below]. In the upper cheek teeth, protocones rounded with anterior spur (particularly during early wear stages), fossette borders moderately plicated, pli caballin consists of single or double loops and deep hypoconal groove. In the lower cheek teeth, ectoparastylids [= protostylids of this report] absent or rudimentary, deep ectoflexids, pli caballinid rudimentary or absent, metaconids and metastylids small, rounded, and moderately separated, and moderately developed enamel plications''.

OTHER ORIGINAL COMMENTS: These are excerpted from MacFadden and Skinner (1981) as being useful in broader comparisons. I have verified all features subsequently, with particular additions indicated here by *. In addition to being a mesodont horse (noting that mesodont has not been defined except only vaguely, and that unworn upper cheek teeth of this species range from 26 to 32 mm in height*), *C. goorisi* is additionally characterized as having a shallow nasal notch that is about midway between C1 and P2; the posterior tip of the premaxilla overlies the rear of the buccinator fossa; the postcanine diastema is short; the buccinator fossa is moderately developed (and is separated from the DPOF*); the infraorbital foramen lies over P3 or P4 at or *very near the antero-

ventral margin of the *very well-defined nasomaxillary fossa (DPOF of subsequent usage, and as used in this report); the malar crest is moderately inflated; the malar fossa is absent. The DPOF is teardrop shaped, has well-defined and continuous *dorsal, ventral, and anterior and posterior rims, and is deeply pocketed. The DPOF is anteroposteriorly oriented*. The DPOF is located well forward of the orbit so that the preorbital bar is wide. The anterior edge of the lacrimal bone either ''barely touches'' (e.g., F:AM 73941) or ''does not touch'' (e.g., F:AM 73940) the rear of the DPOF (MacFadden and Skinner, 1981: 622). These statements are open to other interpretation. Woodburne (1996a) reappraised the morphology of these skulls in conjunction with F:AM 73942 and concluded that the anterior tip of the lacrimal extended at least a short distance into the rear of the DPOF as shown in figure 16.12. Of special note, however, is the fact that the jugal makes a rather extensive contact with the lacrimal and reduces the length of the maxillo-lacrimal suture, a feature unique to *C. goorisi*.

ADDITIONAL DESCRIPTION: The following is developed from tables 16.5 and 16.20, based on cranial parameters recommended by the 1981 *Hipparion* Conference (Eisenmann et al., 1988), and indicates some cranial features in which *C. goorisi* differs from *M. insignis*. Using parameter #4 (combined length of basioccipital and basisphenoid) as a basilar length indicative of cranial and thus body size (e.g., Radinsky, 1984), cranial dimensions of *C. goorisi* may be compared with those of *M. insignis*. Parameter #4 is about 20% shorter in *C. goorisi* than in *M. insignis*. Other parameters that are comparably different in the two taxa (with *C. goorisi* being smaller) include: diastemal width (#14), frontal width (#18), trans-glenoid width (#19), occipital height (#22), muzzle height (#25), DPOF length (#33), length from rear of DPOF to IOF (infraorbital foramen; #34), DPOF height (#35), height of DPOF above maxillary (facial) crest (#36), and height of rear center of DPOF above the alveolus (#38). Thus in all the above, *C. goorisi* is actually smaller than, but proportional to, the dimensions found in *M. insignis* Cranial Group 1.

Cranial parameters in which *C. goorisi* is dimensionally about the same as *M. insignis* would actually be proportionally smaller in the merychippine form. These pertain to Cranial Group 2: length of premolar series (#7), length of molar series (#8), length of combined premolar and molar series (#9), width of muzzle at I3 (#15), facial length from orbit to nasal notch (#31).

Cranial parameters in which *C. goorisi* is distinctly larger than *M. insignis* would be proportionally much smaller in the merychippine species. These pertain to Cranial Group 3: muzzle length (#1), palatal width (#13), length of preorbital bar (#32), height of the IOF above the alveolus (#37). In *M. insignis*, the anterior end of the lacrimal penetrates beyond the rear of the DPOF by an average of about 8 mm, so the value is a negative figure (#39, table 16.5). In that the DPOF is pocketed in *C. goorisi*, the anterior tip of the lacrimal touches the rear of the DPOF, giving a value of 0 for #39 in table 16.20).

In summary, it appears that *C. goorisi* is a relatively small hipparionine (*sensu* Hulbert and MacFadden, 1991), with a basilar length (#4) of about 72 mm, versus 86 in *M. insignis*; the muzzle is short (ca. 77 mm, about 10 mm longer than in *M. insignis*; #1) and relatively wide (ca. 36 mm, vs. 36 in *M. insignis*), premolar series is slightly longer (ca. 64 mm, #7) than the molar series (ca. 55 mm, #8) and the total cheek tooth length is rather short (ca. 116 mm, #9 in both species). The palate is relatively wide in both (ca. 46–48 mm, #13), the frontals are flat and relatively wide (ca. 101, vs. 92 mm, #18). The preorbital region of the face is relatively long (ca. 128, vs. 132 mm, #31), the DPOF relatively shorter (ca. 50 vs. 64 mm, #33), medially moderately deeper (23 mm vs. 9–12 mm; column 40, table 16.20 vs. table 16.5), well defined dorsally, posteriorly, ventrally and anteriorly versus mostly less well defined overall, except posteriorly; DPOF is strongly (= nearly to orbit) versus faintly, if at all, pocketed posteriorly; the overall triangularly versus rectangularly shaped lacrimal reaches the rear margin of DPOF (#39); the DPOF is relatively shallower dorsally (ca. 29 vs. 37 mm, #35) and located less dorsally above (ca. 22 vs. 31 mm, #36) the facial crest; the

POB is wide (ca. 24 vs. 17 mm, #32). The IOF is located above P3 or the P3–P4 boundary (or dP3–dP4 boundary), versus above P4 or the P4–M1 (or dP4–M1 boundary), and is virtually below the anterior portion versus the longitudinal midpoint of the DPOF, irrespective of ontogenetic age.

THE UPPER CHEEK TOOTH DENTITION: The following remarks are derived from the data obtained for each tooth in the cheek tooth series, and summarized in tables 16.21–16.27. These show that the upper dentition of *C. goorisi* is sparsely represented, there being no examples of the lower half of each tooth. Estimated unworn crown heights are: P2, 26 mm; P3, 27 mm; P4, 34 mm; M1, 34 mm, M2, 30 mm; M3 26 mm. Due to the small sample size, the detailed analysis accomplished for *M. insignis* is not attempted here. The following general remarks apply for *C. goorisi*.

The upper cheek tooth dentition of *Cormohipparion goorisi* is characterized by having incisors with cement-filled cups (infundibula; MacFadden and Skinner, 1981); dP1 is of moderate size, although smaller than in *M. insignis* (mean = 10.9 mm; table 16.1), two-rooted, and persistent until late ontogenetic age; P2–M3 are mesodont; unworn crown height from P2–M3 ranges about 26–34 mm; P2 protoloph connects to the metaloph (table 16.22) at about 30% wear (contra *M. insignis*; isolated until very late wear; table 16.11).

Other salient comparisons with *M. insignis* include: In P2 the pli prefossette is present after about 19% wear, with the posterior border of the prefossette scoring from 2.67 (total sample; $N = 3$) in *C. goorisi*. This is three times the mean complexity as compared to *M. insignis* (0.88; table 16.18). For P3 (table 16.23), the pli prefossette is present after 15% wear, commonly bifid, and associated with 2–4 additional plis. The posterior border of the prefossette scores at 4.25, considerably more complex than in *M. insignis* (1.32; table 16.18). Comparable statements for P4 (table 16.24) are: present after about 20% wear, mostly bifid, the fossette border scoring 5.00 (more than twice as complex as in *M. insignis*, 1.81, table 16.18); for M1 (table 16.25), pli prefossette is present, after about 32% wear, and associated with 1–5 plis, posterior fossette border scores at 3.25, again more complex than in *M. insignis* (2.74, table 16.18); for M2 (table 16.26), pli prefossette is present after ca. 20% wear, associated with 1–3 plis, posterior fossette border scores 3.40, about twice the complexity of *M. insignis* (1.81, table 16.18); for M3 (table 16.27), pli prefossette is present (sometimes bifid) after ca. 4% wear, is associated with 3–4 additional plis, with the posterior fossette border scoring as 3.60, almost three times more complex than in *M. insignis* (1.00, table 16.18).

The pli postfossette in P2 is present, after 19% wear) and commonly associated with additional plis, with the anterior border of the postfossette scoring at 2.00. This is more complex than comparable figures for *M. insignis* (1.21; table 16.18). For P3, the pli postfossette is present after 15% wear, the anterior fossette border scoring 2.00 (about comparable to *M. insignis*, 1.81); for P4, the pli postfossette is present (except in the unworn state) and associated with 1–4 additional plis; anterior fossette border scores 3.43, about 35% more complex than seen in *M. insignis* (2.21); for M1 the pli postfossette is present after ca. 32% wear, associated with 1–5 additional plis, its anterior fossette border scoring 3.42, distinctly more complex than in *M. insignis* (2.32); for M2, pli postfossette is present after about 20% wear, associated with 1–3 additional plis, with its anterior fossette border scoring 2.88, more complex than in *M. insignis* (1.87); for M3, the pli postfossette is mostly present, associated with 1–3 additional plis, the anterior fossette border scoring 3.00, three times more complex than in *M. insignis* (0.93).

The pli hypostyle is present in about 79% of all specimens in adult wear and is rarely composed of more than a single pli.

The pli caballin is present in about 50% of the specimens in P2, and in 90–100% of the specimens in the other cheek teeth with adult wear. It is doubled more frequently in the premolars than in the molars (50% in P2, 20% in P3, 42% in P4 versus 29% in M1, 13% in M2, and never double in M3, as represented here).

The protocone remains closed until about 45–56% wear for those teeth (P3, M1) in which it is shown to be open eventually to

the protoloph, and except for earliest wear (especially in P2) never has an anterolabial spur, in distinct contrast to *M. insignis*. P2 protocones average more nearly circular than those of P3–M3. The prominent pli prefossette loop projects well beyond the posterior border of the postfossette, and is commonly bifid at its terminal tip, especially on P3–M3.

Virtually all taxonomically important details of the tooth are still present into later wear where this can be shown (P4, 59%; M1, 68%; M2, 57%; all minimum figures).

The premolars and molars are relatively tall for a mesodont horse, with unworn crown heights being about 26 (P2), 27 (P3), 34 (P4), 34 (M1), 30 (M2), and 26 mm (M3). For *M. insignis*, comparable unworn crown heights are 25, 26, 27, 24 (?27), 28, and 24 mm.

The fossette borders are relatively complex, especially in P4–M2, with up to 6, 6, and 4 plications on the posterior border of the prefossette, respectively, and 5, 6, and 4 on the anterior border of the postfossette. The pli prefossette is commonly bifid or trifid. The enamel loop that outlines the pli prefossette is very large and conspicuous, sometimes forming an isolated enamel lake, and is commonly bifid at its posterolingual tip. The posterior border of the prefossette is always significantly more complex than in *M. insignis*, as is the anterior border of the postfossette (possible exception of P2). The protocone is subovate in P2, but more elongate in P3–M2, and the associated spur is neither as prominent nor as persistent with wear as in *M. insignis*.

THE LOWER CHEEK TOOTH DENTITION: The lower incisors have cement-filled cups, and dp1 is absent (MacFadden and Skinner, 1981). The cheek tooth dentition (table 16.28) is described as an ontogenetic sequence in table 16.9 and figure 16.14. Based on other Trinity River Pit 1 specimens, the earliest wear stage includes specimens in which the metaconid/metastylid of p2 is still single, the postflexid is still open lingually, and m3 is in very early wear. No specimens of *C. goorisi* are represented at this stage.

In stage II, (e.g., F:AM 73948), the hypoconid of m3 is breached, and the hypoconulid is slightly worn; the metaconid and metastylid of p2 are beginning to be separate, and the p2 postflexid is nearly closed lingually. A preentocristid extends anterolabially toward a posterolingually directed spur from the anterior part of the prehypocristid. The ectoflexid does not penetrate the metaconid/metastylid isthmus. In p3 and p4, the ectoflexid still is labial to the isthmus.

In stage III (e.g., F:AM 73949), the metaconid is distinct from the metastylid in p2, a preentocristid and remnant opposing spur from the anterior part of the prehypocristid still is present, and a spur within the preflexid extends toward the metaconid. In p3, the postflexid is slightly open, the hypoconid of m3 is worn, the hypoconulid breached. In p3 and p4 the ectoflexid still is labial of the metaconid/metastylid isthmus, and protostylids are present in p3–m1.

Stage IV is not represented. In stage V, the postflexid is still open in p3–4 (p2 not represented; e.g., F:AM 113058), and the ectoflexid still is well labial of the postflexid (not penetrating the isthmus) in p3.

In stage VI, p2 pre- and postflexids are open; in p3 the postflexid is an isolated loop; premolar ectoflexids still reach only to about the level of the postflexids; protostylids are present on p3–m1.

In stage VII (e.g., F:AM 113069), premolar ectoflexids are still about at or slightly labial to the postflexids; protostylids are present from p3–m2.

As shown in table 16.9, the premolar ectoflexids in *C. goorisi* never penetrate the isthmus of the metaconid/metastylid to the degree seen in a Trinity River Pit 1 *Merychippus s.s.*, and the development of protostylids appears to be retarded by about one wear stage relative to that merychippine form. Otherwise the two taxa are similar in overall appearance, with the rounded shape and subequal size of the metaconids and metastylids, the shallow and U-shaped linguaflexid, and the rounded labial borders of the protoconid and hypoconid.

As shown in tables 16.7 and 16.8 and figure 16.15, the mandible of *C. goorisi* is attenuated anteriorly from m3 to p2 more than in *M. insignis*.

SUMMARY: Based on the information detailed above, *Cormohipparion goorisi* can be characterized on the basis of the Trinity River Pit 1 sample as: relatively small size with

a short muzzle; nasal notch retracted to a position about midway between C1 and P2; relatively wide POB (e.g., 24 mm) and DPOF distinctly expressed with strongly defined anterior, dorsal, posterior, and ventral borders; the DPOF is strongly pocketed posteriorly (virtually to a position opposite the anterior edge of the orbit), but its facial expression is relatively short (ca. 48 mm) in comparison to the cheek tooth row length (ca. 116 mm); the IOF is located above the P3/P4 boundary, at or very close to the anteroventral rim of the DPOF; the lacrimal is dorsoventrally narrow and reaches the rear of the DPOF; dP1 is of moderate size (ca. 10 mm long, but shorter than in *M. insignis*), two-rooted, and present into old age; upper cheek teeth are mesodont (but taller than in *M. insignis*, ca. 26–34 tall at the mesostyle in the unworn condition); the protocone is isolated from the protoloph in P2 except in late wear, as in the other cheek teeth; fossette borders are relatively complex in the upper half of the cheek tooth crown, with as many as six but usually four plications on the opposing faces of the pre- and postfossettes; the pli prefossette loop is usually conspicuously large and bifid posterolingually; protocones are virtually uniformly not spurred; those of P2 are nearly circular, whereas those of the other premolars and molars are more elongate; the hypoconal groove commonly lacks plications; dp1 is not preserved in the lower cheek tooth dentition; metaconids and metastylids are subequal in size and mostly have rounded outlines and are separated by shallow but U-shaped linguaflexids; premolar ectoflexids virtually never penetrate the metaconid/metastylid isthmuses and maintain a position at or labial to the pre- or postflexid throughout wear; protostylids are developed on p3–m1 in later wear and are usually little more than an angulate bend in the enamel at the pertinent part of the tooth; mandibular rami have short symphyses and become markedly shallower in depth from the anterior end of m3 to p2.

In comparison with *Merychippus insignis*, *Cormohipparion goorisi* differs in all of the above-mentioned traits. If the relative position for these taxa is that shown in Hulbert and MacFadden (1991; *C. goorisi* is more derived), the changes involved in comparing *M. insignis* and *C. goorisi* appear to involve modifications that result in a taxon with a somewhat shorter basicranium, having undergone negative allometry with respect to characters allocated to Cranial Group 1 (above), undergone positive allometry with respect to characters allocated to Cranial Group 2, and especially with respect to those in Cranial Group 3, developed a more hypsodont and complex cheek tooth dentition, a lower jaw that is more attenuated anteriorly, and a lower cheek tooth dentition in which the premolar ectoflexids penetrate the metaconid/metastylid isthmus, and develop protostylids on p3–m3 by wear stage III, rather than at wear stage IV in *M. insignis*.

ANCESTRY OF *CORMOHIPPARION GOORISI*: Based on the foregoing, *C. goorisi* is strongly different both cranially and dentally from *Merychippus insignis*. If each species can be said to stand at the base of its respective clade, then it seems clear that the generic-rank taxa that they each represent are phyletically separate, and that neither was the ancestor of the other. Further, the posterior location of the IOF in conjunction with its plesiomorphic mesodont cheek-tooth dentition separates *M. insignis* and other merychippine species from all other mesodont to hypsodont equids of late Hemingfordian to Barstovian age. Based on specimens surveyed here, and others under review, the merychippine fossil record is limited to the Barstovian.

SUMMARY

Given *Parahippus leonensis* as an outgroup taxon for comparison with mesodont to hypsodont horses of late Hemingfordian and younger age, the main points developed in this report are:

1. *Merychippus insignis* is a relatively small-sized mesodont species that is derived relative to *P. leonensis* in a number of features, including larger cranial size; nasal notch more deeply retracted; wider POB; DPOF with distinct expression, pocketing, proportions and location; distinct position of IOF above the P4/M1 boundary versus above P3; shorter lacrimal facial expression; mesodont upper cheek teeth about 40% taller at the mesostyle in the unworn condition; fossette borders overall more complex; pli caballin persistent; protocones persistently spurred into late wear; dp1 rarely preserved; meta-

conids and metastylids subequal in size, with mostly rounded outlines, and separated by deeper but U-shaped linguaflexids.

2. *Merychippus insiginis* displays many plesiomorphic features relative to more derived Miocene equids, including the persistence of a relatively large dP1; the mesodont cheek tooth dentition; ovoid, spurred protocones (especially on premolars); persistent separation of protoloph and metaloph on P2; early connection of the protocone to the protoloph in P2; metaconids/ metastylids subequal in size; lower premolar linguaflexid early penetration of the isthmus; POB relatively narrow, DPOF only moderately developed, lacrimal dorsoventrally tall, and penetrating the rear of DPOF.
3. At least two other species showing many of the above features suggest that a merychippine clade of Barstovian age may be distinguished from all other late Hemingfordian and Barstovian mesodont to hypsodont equids, pending further review.
4. As exemplified by *Cormohipparion goorisi*, *Cormohipparion* can be defined on the basis of a number of derived features relative to either *Parahippus leonensis* or *Merychippus insignis*.
5. A method is outlined whereby an occlusal dental morphology profile for equid species can be constructed, keyed to actual crown height in upper cheek teeth and relative wear stages for lower cheek teeth. This profile facilitates comparison of dental morphology between fossil equid species.
6. The dental profile developed in (5) is linked to an assessment of cranial and mandibular parameters as recommended at the 1981 *Hipparion* Conference to facilitate a broadly based comparison of *Merychippus insignis* and *Cormohipparion goorisi*.

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APPENDIX 1

Detailed Description of Upper Cheek Tooth Dentition of Echo Quarry Sample of *Merychippus insignis*footn

For P2, the maximum crown height is at least 25 mm. Although no completely unworn specimen was seen, P2 of F:AM 87045 is at least 23.7 mm tall, with the protocone and hypocone well defined. For this sample, P2 crown height (mesostyle) ranged from 23.7 to 9 mm.

As shown in table 16.11, the protoloph remains isolated from the metaloph to at least about 9 mm. The fossette pattern is established at about 19 mm, with the pli protoloph, as many as 3 plis prefossette, as many as 5 plis postfossette, a pli hypostyle, and 2 plis caballin present, and the hypocone confluent with the metaloph. Thus, at least 6 mm or about 24% of the tooth is worn before a relatively stable pattern is exposed (assuming an unworn crown height of 25 mm). This general pattern is maintained until about 13 mm, so maximum complexity occurs at about 19–13 mm (24–48% wear). Within this interval the hypocone remains open; the hypoconal groove is present in about 60% of the specimens, and is relatively complex (2 plis in 50% of the specimens where the feature is present); the protocone is mostly isolated (open in about 22%); the pli caballin is present in about 33%, but bifid in only two of nine specimens; the pli protoloph and pli prefossette are common (50%; 60%) and relatively complex in about 15% and 42%, respectively, in those specimens having the feature. The pli postfossette is present in about 75% of specimens, and relatively complex in 40% of those. The pli hypostyle is present in about 82% of the specimens in the 19–13-mm range, and of those, about 28% are relatively complex. Thus, when present, the pli protoloph is almost always a single loop, but the pli prefossette and pli postfossette are nearly as apt to be double as single, and the pli hypostyle is only slightly less complex. Thus, the part of the crown in which the morphologically most significant data are displayed appears to range in height from about 21 to 13 mm, depending on the feature examined. Taxonomically important coronal details are virtually absent by the time that the tooth has been worn to about 10 mm above its base.

As another measure of enamel pattern complexity, the *Hipparion* Conference (Eisenmann et

al., 1988: 19) recommended calculating the plication frequency of the opposing borders of the pre- and postfosettes. In that context, the posterior border of the prefossette (in the 21–13-mm range) would be scored as 0 in 11 specimens, 1 in 9, 2 in 4, and 3 in 2, or an average score of 0.88 ($N = 26$). Similarly the anterior border of the postfossette would be scored as 0 in 8 specimens, 1 in 9, 2 in 4, 3 in 1, 4 in 1, and 5 in 1 specimen, or an average score of 1.21 ($N = 24$).

P3: Maximum crown height is about 25.6 mm in available specimens (slightly worn in F:AM 87008 at 25.6 mm, unworn in F:AM 87007 at 23.8). In the present sample, P3 crown height (mesostyle) ranged from 25.6 to 9 mm.

As shown in table 16.12, the protoloph connects to the metaloph via the crochet at least by 24 mm, and continues to at least 9 mm. In that interval, 8 of 34 specimens retain an isolated protoloph. The fossette pattern is established at about 24 mm, with the pli protoloph, pli prefossette, pli postfossette, pli hypostyle, and pli caballin present, and the hypocone confluent with the metaloph. Taking the unworn crown height of P3 to be about 27 mm, at least 3 mm or about 11% of the tooth is worn before a relatively stable pattern is exposed. As indicated in table 16.12, the maximum complexity is displayed from 24 to 13 mm, and the pli caballin is commonly present (85%) and bifid (57% of those present) in this interval. When present (78%), the pli protoloph is always a single loop. In the 24–13-mm range, the pli prefossette is present in 76% of the specimens and in those commonly (48%) is either a double or triple loop. Similarly, the pli postfossette is almost always present (82%), and in 70% of those is composed of either two or three and more rarely of four loops. The pli hypostyle is mostly present (70%) in this interval.

The hypocone becomes confluent with the metaloph at about 24 mm and remains so to at least 9 mm. The hypoconal groove has a single plication on its labial margin from 24 to 13 mm (50% of the specimens in that interval), with one specimen showing three labial plications at 20 mm.

The protocone remains generally closed from 24 to 13 mm, although a few specimens (nine) are open from 18 to 13 mm (32% of specimens in the 24–13-mm range). Taxonomically important coronal details are virtually absent by the time that the tooth has been worn to about 10 mm of its base.

The posterior border of the prefossette (in the 24–13-mm range) is scored as 0 in 7 specimens, 1 in 9, 2 in 6, and 4 in 3 specimens ($\bar{x} = 1.32$; $N = 25$). Comparable data for the anterior border of the postfossette are 0 in 5, 1 in 7, 2 in 6, 3 in 6, and 4 in 3 specimens ($\bar{x} = 1.81$; $N = 27$).

P4: Maximum crown height is at least 28 mm in available specimens (e.g., F:AM 87056). This appears to be near the actual unworn crown height of P4. In the present sample, P4 crown height (mesostyle) ranged from 28 to 9 mm. A gap at 17 mm is not represented by material at hand (table 16.13).

The protoloph connects to the metaloph via the crochet at about 26 mm, and continues to at least 9 mm. Five specimens retain a separate protoloph from 25 to 22 mm. The fossette pattern is established at about 23 mm, with the pli protoloph, pli prefossette, pli postfossette, pli hypostyle, and pli caballin present, and the hypocone confluent with the metaloph. If the unworn crown height of P4 actually was about 27 mm, at least 4 mm or about 15% of the tooth is worn before a relatively stable pattern is exposed. Based on table 16.13, the maximum complexity of the occlusal pattern is established at 23 mm and continues to about 13 mm, below which level the protocone is almost consistently open. In the 23–13 mm interval, the pli caballin is nearly always present (93%) and commonly bifid (69% of those present); the pli protoloph is about equally absent or present (53%); the pli prefossette is nearly always present (90%), commonly single, but more complex in 57% of those specimens. Of these, the pli prefossette is composed of two or three loops in 46% of specimens when present, but in only 14% of these is the feature composed of four or five loops. The pli postfossette is nearly always present (89%), and composed of more than a single loop in 88% when present. Of this group, the feature is about equally double or triple (61% combined) and rarely composed of four to six loops (27%).

The protocone remains generally closed until about 13 mm, although one specimen is open at about 15 mm. The hypocone becomes confluent with the metaloph at about 25 mm and remains so to at least 9 mm. The hypoconal groove has a single plication on its labial margin from 24 to 13 mm (55%). Three specimens, 11–9 mm, lack plications on the hypoconal groove, consistent with this late wear stage.

The part of the crown in which the morphologically most significant data are displayed appears to be from about 24 to 13 mm, depending on the feature examined. Taxonomically important coronal details are progressively diminished by the time that the tooth has been worn below about 13 mm.

The posterior border of the prefossette (23–13-mm range) is scored as 0 in 4, 1 in 12, 2 in 6, 3 in 7, 4 in 2, and 5 in 1 specimens ($\bar{x} = 1.81$; $N = 32$). Comparable data for the anterior border of the postfossette are 0 in 6, 1 in 3, 2 in 7, 3 in 8, and 4 in 3, 5 in 1, and 6 in 1 ($\bar{x} = 2.21$; $N = 27$).

M1: Maximum unworn crown height is about 25 mm in available specimens (F:AM 87007 is 24.8 mm tall at the mesostyle and is slightly worn, with enamel breached on the protocone and adjacent structures). The unworn M1 probably actually reached 27 mm to judge from P4 and M2. In the present sample, M1 crown height (mesostyle) ranged from 24.8 to 8 mm (table 16.14).

The protoloph connects to the metaloph via the crochet at about 22 mm, and remains so for the life of the tooth. The fossette pattern is established at about 21 mm, with the pli protoloph, pli prefossette, pli postfossette, pli hypostyle, and pli caballin present, and the hypocone confluent with the metaloph. If the unworn crown height of M1 actually was about 27 mm, at least 6 mm or about 22% of the tooth is worn before a relatively stable pattern is exposed.

The protocone remains generally closed until about 11 mm, although it commonly is open below 16 mm. The hypocone becomes confluent with the metaloph at about 21 mm and remains so to at least 8 mm.

The greatest complexity in occlusal pattern is displayed from 21 to 12 mm, but the hypoconal groove is mostly unmarked in this interval. This feature displays a fold above 18 mm, below which it is effectively absent; a single specimen displays a plication at 13 mm. On the other hand, the pli caballin is almost universally present from 21 to 12 mm (as well as to the 8 mm level). It is mostly a single loop (double in only 8% when present). The pli protoloph is mostly absent (present in 13% of cases). In contrast, the pli prefossette is almost always present (95%) and is two or more loops in 80% of those cases. Of these, a score of two or three loops accounts for 62% of the specimens, with four and five accounting for 7% and 28%, respectively. The pli postfossette is almost always present in the 21–12-mm range (90%). Of those specimens, it is composed of two or more loops in 78% of cases, within which category two are present in 43%, three in 25%, four in 11% and five in 18% of the cases. In the upper range of the interval (20–21 mm), the pli postfossette is composed of as many as five loops. The pli hypostyle is mostly single, but also from 21 to 20 mm is composed of two loops in four specimens.

The part of the crown in which the morphologically most significant data are displayed appears to be from about 21 to 12 mm, depending on the feature examined. Taxonomically important coronal details are virtually absent by the time that the tooth has been worn below about 12 mm of its base.

The posterior border of the prefossette (21–12-mm range) is scored as 0 in 2, 1 in 7, 2 in 9, 3 in 9, 4 in 3, and 5 in 8 specimens ($\bar{x} = 2.74$; $N = 38$). Comparable figures for the anterior border of the postfossette are: 0 in 4, 1 in 8, 2 in 11, 3 in 7, 4 in 3, and 5 in 5 ($\bar{x} = 2.32$; $N = 38$).

M2: Maximum unworn crown height is at least 28 mm in available specimens, with all structures except the hypocone being worn. In the present sample, M2 crown height ranged from 27.8 to 11 mm, with a gap in the data at the 24 and 17-mm levels (table 16.15).

The protoloph connects to the metaloph via the crochet at about 25 mm, and remains so for the life of the tooth. One specimen retains a separate protoloph and metaloph at 22 mm. The fossette pattern is established at about 22 mm, with the pli protoloph, pli prefossette, pli postfossette, pli hypostyle, and pli caballin present, and the hypocone confluent with the metaloph. If the unworn crown height of M2 actually was about 27 mm (allowing for the least worn samples showing some wear on some cusps), at least 6 mm or about 22% of the tooth is worn before a relatively stable pattern is exposed.

The protocone remains closed until about 12 mm. None are open above that level. The hypocone becomes confluent with the metaloph at about 22 mm and remains so to at least 11 mm. The greatest occlusal pattern complexity is established from about 22 to 13 mm. In this interval, the hypoconal groove is about equally smooth or possesses a single plication in 58% of sample; the pli caballin is almost always present (92%; absent in two specimens), and almost never composed of more than a single pli (4% in those present); the pli protoloph is absent more often than present (39%), and when present almost never (10%) more than a single pli; the pli prefossette is mostly present (88%), and single to trifid or quadruple in 85% of the specimens. It is composed of two or more loops in 54% of the sample; of which two loops are present in 17%, three in 50%, four in 25%, and five in 8% of the sample. The pli postfossette is mostly (91%) present; when present it is composed of two or more loops in 91% of the sample, of which two loops comprise 20%, three loops 35%, four loops 25%, and five loops 15%. The pli hypostyle is commonly present (71%) and is invariably single.

The part of the crown in which the morphologically most significant data are displayed appears to be from about 22 to 13 mm, depending on the feature examined. Taxonomically important coronal details are virtually absent by the time that the tooth has been worn below about 13 mm.

The posterior border of the prefossette (22–13-mm range) is scored as 0 in 5, 1 in 10, 2 in 2, 3 in 6, 4 in 3, and 5 in 1 specimens ($\bar{X} = 1.81$; $N = 27$). Comparable data for the anterior border of

the postfossette are 0 in 5, 1 in 7, 2 in 6, 3 in 6, and 4 in 3 specimens ($\bar{x} = 1.81$; $N = 27$).

M3: Maximum unworn crown height is at least 24 mm in available specimens, with all structures except the hypocone being worn. In the present sample, M3 crown height (mesostyle) ranged from 23 to 13 mm, with a gap in the data at 21 and 15 mm.

The protoloph connects to the metaloph via the crochet at about 22 mm, and remains so to at least 13 mm. Eight specimens retain a separate protoloph and metaloph within the range of from about 22 to 17 mm.

The fossette pattern is established at about 22 mm, with the pli protoloph, pli prefossette, and pli postfossette present. If the unworn crown height of M3 actually was about 25 mm (allowing for the least worn samples showing some wear on some cusps), at least 3 mm or about 12% of the tooth is worn before a relatively stable pattern is exposed. As shown in table 16.16, pattern complexities are shown to about 14 mm, so the range over which these attributes are calculated is 22–14 mm. In general, the occlusal pattern of M3 is the least complex of the cheek tooth row.

The protocone is isolated throughout the wear range of the present sample. The hypocone becomes confluent with the metaloph at about 20 mm and remains so to at least 13 mm. Eight specimens retain a closed hypocone in the range of from 20 to 17 mm. The hypoconal groove is usually smooth (data range from 24 to 13 mm), and rarely (6% of those present) has a single plication on its labial margin.

The pli protoloph, pli prefossette, pli postfossette, and pli hypostyle are usually absent in this tooth until about 16 mm, or after about 33% wear, and then are mostly composed of a single loop. Dual or triple loops are present in about 44% when present for the plis prefossette and postfossette. The pli caballin is present in 32% as a single fold.

The part of the crown in which the morphologically most significant data are displayed appears to be from about 20 to 13 mm. The posterior border of the prefossette (20–13-mm range) is scored as 0 in 6, 1 in 5, 2 in 2, and 3 in 2 specimens ($\bar{x} = 1.00$; $N = 15$). Comparable data for the anterior border of the postfossette are 0 in 6, 1 in 5, 2 in 3, and 3 in 1 specimens ($\bar{x} = 0.93$; $N = 15$).

Tables 16.1–16.28

TABLE 16.1

Comparison of Deciduous Premolar (dP1) Length (mm): *Merychippus insignis*, Other Merychippines, and *Cormohipparion goorisi* of the Barstovian

By contrast, in the Early Hemingfordian Runningwater Formation of Nebraska, specimen F:AM 109857, *Parahippus leonensis*, had a length of 11.2, which was 58% of P2 length.

	Merychippus insignis Echo Quarry Olcott Fm., Nebraska		Merychippine Trinity River Pit 1 Fleming Fm., Texas		Merychippine Prospect 28 Valentine Fm., Nebraska		*Cormohipparion goorisi* Trinity River Pit 1 Fleming Fm., Texas	
	Specimen	Length	Specimen	Length	Specimen	Length	Specimen	Length
	F:AM 87000	15.3	F:AM 109874	15.0	F:AM 126899	12.0	F:AM 93943	12.0
	F:AM 87001	13.2	F:AM 109883	12.5	F:AM 126900	13.7	F:AM 73942	11.0
	F:AM 87003	12.7	F:AM 109894	13.1			F:AM 73952	9.8
	F:AM 87004	12.8	F:AM 109891	10.5				
	F:AM 87005	12.0	F:AM 109892	11.3				
	F:AM 87013	14.0						
	F:AM 87032	11.7						
	F:AM 87043	13.5						
	F:AM 87046	13.7						
	F:AM 87057	12.7						
	F:AM 87961	13.5						
	F:AM 87055	14.9						
	F:AM 87045	13.9						
	F:AM 87030	13.9						
Range		11.7–15.3		11.5–15.0		12.0–13.7		9.8–12.0
Mean		13.4		12.5		12.9		10.9
SD		1.00		1.74		1.20		1.10
CV		7.47		13.91		9.36		10.07
N		14		5		2		3
% P2 length		53%; *N*=8		53%; *N*=2		53%; *N*=2		45%; *N*=3
Range, P2 length		48–59		51–54		49–56		39–49

Note: Tooth length proportional to ontogenetic age: longer = younger. dP1 is strongly two-rooted and roots well separated in all merychippine taxa; in *C. goorisi* the roots are smaller and crowded together.

TABLE 16.2

Measurements (mm) of Upper Cheek Tooth Dentition of Texas and Nebraska Merychippines

				Protocone					Protocone					Protocone	
	Height	Length	Width	Height	Length	Height	Length	Width	Height	Length	Height	Length	Width	Height	Length
***Merychippus* sp., Deep Creek, Valentine Formation, Late Barstovian, Nebraska**															
			P2					P3					P4		
F:AM 126899♂	24.8	24.3	19.6	5.0	4.7	28.3	21.8	21.7	6.3	3.6	26.0a	21.2	21.6	5.8	4.0
F:AM 126900♂	15.6	24.3	17.8	5.1	5.0	15.3	21.0	21.9	6.3	4.9	14.5	20.4	22.5	6.1	5.3
Range		24.3	17.8–19.6	5.0–5.1	4.7–5.0		21.0–21.8	21.7–21.9	6.3	3.6–4.9		20.4–21.2	21.6–22.5	5.8–6.1	4.0–5.3
Mean		24.3	18.7	5.1	4.9		21.4	21.8	6.3	4.3		20.8	22.1	6.0	4.7
SD			1.27	0.07	0.21		0.57	0.14		0.92		0.57	0.64	0.21	0.92
CV			6.81	1.40	4.37		2.64	0.65		21.63		2.72	2.89	3.57	19.77
N		2	2	2	2		2	2	2	2		2	2	2	2
			M1					M2					M3		
F:AM 126899♂	22.0a	19.7	20.8	6.1	3.7	—	21.6	20.6	6.3	3.0	31.0a	18.8	17.7	—	—
F:AM 126900♂	12.7	18.3	21.8	6.0	4.0	16.5a	19.4	20.8	6.3	4.3	16.8a	20.4	17.2	6.3	2.7
Range		18.3–19.7	20.8–21.8	6.0–6.1	3.7–4.0		19.4–21.6	20.6–20.8	6.3	3.0–4.3		18.8–20.4	17.2–17.7	6.3	2.7
Mean		19.0	21.3	6.1	3.9		20.5	20.7	6.3	3.65		19.6	17.5	6.3	2.7
SD	1.00	0.71		0.07	0.21		1.56	0.14		0.92		1.13	0.35		
CV	5.21	3.32	1.69	5.51			7.59	0.68		25.19		5.77	2.03		
N	2	2	2	2			2	2	2	2		2	2	1	1

(continued)

TABLE 16.2
Continued

	Height	Length	Width	Protocone Height	Protocone Length	Height	Length	Width	Protocone Height	Protocone Length	Height	Length	Width	Protocone Height	Protocone Length
Merychippine, Trinity River Pit 1, Fleming Formation, Early Barstovian, Texas															
	P2					P3					P4				
F:AM 109874	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
F:AM 109882	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
F:AM 109876	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
F:AM 109883♂	14.4	23.1	19.5	5.2	5.3	12.7	18.0	20.3	6.3	4.4	13.2	18.9	20.4	6.2	4.5
F:AM 109894	16.2	25.8	19.1	4.2	4.3	17.6	21.4	21.0	6.0	4.1	18.6	21.0	20.3	5.9	4.1
F:AM 109885	—	—	—	—	—	19.1	20.0	—	—	—	19.0a	18.5	—	—	—
F:AM 109884	10.8	22.5	19.4	—	—	11.1	18.5	21.0	5.5	5.2	11.2	18.7	21.3	5.6	5.0
Range		22.5–25.8	19.1–19.5	4.2–5.2	4.3–5.3	—	18.0–21.4	20.3–21.0	5.5–6.3	4.1–5.2	—	18.5–21.0	20.3–21.3	5.6–6.2	4.1–5.0
Mean		23.8	19.3	4.7	4.8		19.5	20.8	5.9	4.6		19.3	20.7	5.9	4.5
SD		1.76	0.21	0.71	0.71		1.54	0.4	0.4	0.57		1.16	0.55	0.3	0.45
CV		7.39	1.08	15.04	14.73		7.90	1.95	6.81	12.45		6.03	2.67	5.08	9.95
N		3	3	2	2		4	3	3	3		4	3	3	3
	M1					M2					M3				
F:AM 109874	16.0a	20.7	—	—	—	—	—	—	—	—	—	—	—	—	—
F:AM 109882	17.0a	20.1	—	—	—	—	—	—	—	—	—	—	—	—	—
F:AM 109876	19.0	20.8	—	—	—	—	—	—	—	—	—	—	—	—	—
F:AM 109883♂	11.1	18.2	20.0	5.5	5.1	12.1	17.6	19.3	5.8	4.4	13.7	17.7	15.6	—	—
F:AM 109894	13.7	19.9	20.1	6.2	4.3	17.5	19.8	16.8	—	—	19.8	17.7	—	—	—
F:AM 109885	18.0a	17.8	17.8	—	—	18.0a	18.6	15.2	—	—	—	—	—	—	—
F:AM 109884	10.0	15.3	20.6	5.8	5.0	12.3	16.8	19.4	6.0	4.3	13.7	16.2	17.3	5.3	3.5
Range		15.3–20.8	17.8–20.6	5.5–6.2	4.3–5.1		16.8–19.8	15.2–19.4	5.8–6.0	4.3–4.4		16.2–17.7	15.6–17.3	5.3	3.5
Mean		19.0	19.6	5.8	4.8		18.2	17.7	5.9	4.4		17.2	16.5	5.3	3.5
SD		1.9	1.24	0.35	0.44		1.30	2.04	0.14	0.07		0.86	1.2		
CV		10.01	6.34	6.02	9.08		7.12	11.52	2.40	1.63		5.34	7.31		
N		7	4	3	3		4	4	2	2		3	2	1	1

Note: Height is at mesostyle; a = approximate.

TABLE 16.3

Measurements (mm) of Lower Cheek Tooth Dentition of Texas and Nebraska Merychippines

	p2		p3		p4		m1		m2		m3	
	Length	Width	Length	Width	Length	Width	Length	Width	Length	Width	Length	Width
Trinity River Pit 1, Fleming Formation, Early Barstovian, Texas												
F:AM 113054	20.2	11.1	17.5	12.7	18.4	11.6	17.0	11.1*	18.6	9.9	20.7	9.4
F:AM 113052	—	—	—	—	18.7	13.0	19.2	12.2*	19.6	10.4	18.9	8.7
F:AM 113053	20.5	10.9	20.2	12.9	19.9	13.7	18.1	12.1*	19.4	10.8	—	—
F:AM 113056	19.8	11.7	19.6	14.5*	20.1	14.8*	17.8	13.0*	20.8	11.9	21.5	9.7
F:AM 113055	19.5	11.8	19.5	13.9	20.0	14.5	18.1	12.7*	19.7	11.4	21.2	9.7
F:AM 113061	20.6	11.5	19.6	13.3*	20.5	13.8	18.4	12.5*	19.7	11.4	21.9	10.3
F:AM 113062	21.1	12.7	19.7	13.8*	21.3	14.7*	19.8	14.1*	19.0	12.0*	21.9	11.0
F:AM 113059	19.7	11.2	20.7	12.0*	19.5	13.5*	17.0	12.2*	18.6	11.0*	21.1	9.7
F:AM 113064	—	—	19.0	12.4*	19.4	12.9*	15.9	10.5*	17.9	10.3*	21.9	9.1
F:AM 113057	20.3	12.0	19.9	13.6*	20.2	13.4*	18.5	12.2*	20.4	11.2*	22.3	10.3
F:AM 113060	18.7	10.6	17.5	13.0*	—	—	—	—	—	—	—	—
F:AM 113065	—	—	18.3	13.4	18.3	13.1*	15.9	12.7*	17.0	10.5*	21.8	8.2
F:AM 113070	21.5	12.8	18.4	15.0*	18.2	14.8*	17.8	14.0*	18.2	12.9*	—	—
F:AM 113071	—	—	16.2	13.8*	17.1	13.0*	16.2	—*	16.0	—*	—	—
F:AM 113066	19.8	13.7	17.8	14.8*	18.2	15.2*	16.1	12.5*	17.2	12.2*	21.5	10.7
F:AM 113067	19.3	12.1	17.3	13.6*	18.1	13.6*	15.9	11.7*	16.0	10.7*	21.7	9.9
F:AM 109891	19.9	12.9	17.5	13.7*	17.2	13.5*	16.2	12.2*	17.3	10.9*	21.9	9.7
F:AM 113075	18.0	12.0	17.5	13.7*	18.2	13.3*	16.0	11.9*	17.1	11.0*	22.3	9.6
Range	21.1–18.0	13.7–10.6	20.7–16.2	15.0–12.0	20.5–17.1	14.8–11.6	19.8–15.9	14.1–10.5	20.8–16.0	12.9–9.9	22.3–18.9	11.0–8.2
Mean	19.9	11.9	18.6	13.5	19.0	13.7	17.3	12.4	18.4	11.2	21.5	9.7
SD	0.91	0.87	1.27	0.80	1.20	0.90	1.27	0.90	1.46	0.79	0.86	0.74
CV	4.56	7.27	6.84	5.89	6.29	6.60	7.36	7.32	7.94	7.05	4.02	7.64
N	14	14	17	17	17	17	17	16	17	16	14	14
Deep Creek, Valentine Formation, Late Barstovian, Nebraska												
F:AM 126900	21.0 p2 12.3 tall	13.9	19.4 p3 13.9 tall	15.1*	19.3	14.8	17.6	13.0*	18.8 m2 13.0 tall	9.9	23.8 m3 11.5 tall	9.4

Note: * indicates presence of protostylid. In this sample (as well as in *M. insignis*), this feature is found in p3–m2. In the Valentine Formation merychippine it occurs in p3–m1. In *C. goorisi* the protostylid also occurs in p3–m2.

TABLE 16.4

Merychippine Cranial Measurements (mm), Deep Creek, Devil's Gulch Member, Valentine Formation, Late Barstovian, Nebraska

	Characters											
	1	2	3	4	5	6	7	8	9	15	28	29
F:AM 126899♂	89.8	82.3	87.5	85.6	166.7	328.9	68.8	60.2	125.2	26.2	47.3	38.2
F:AM 126900♂	—	—	—	—	—	—	65.1	57.3	120.6	—	—	—
Range	89.8	82.3	87.5	85.6	166.7	328.9	65.1–68.8	57.3–60.2	120.6–125.2	26.2	47.3	38.2
Mean	89.8	82.3	87.5	85.6	166.7	328.9	67.0	58.8	122.9	26.2	47.3	38.2
SD	—	—	—	—	—	—	2.62	2.05	3.25	—	—	—
CV	—	—	—	—	—	—	3.91	3.49	2.65	—	—	—
N	1	1	1	1	1	1	2	2	2	1	1	1

	Characters										
	30	31	32	33	34	35	36	37	28	39	40
F:AM 126899♂	93.4	130.0a	31.6	59.0	48.2	24.2	48.5	36.0	71.5	–3	15
F:AM 126900♂	—	—	—	—	—	—	—	—	—	—	—
Range	93.4	130.0	31.6	59.0	48.2	24.2	48.5	36.0	71.5	–3	15
Mean	93.4	130.0	31.6	59.0	48.2	24.2	48.5	36.0	71.5	–3	15
SD	—	—	—	—	—	—	—	—	—	—	—
CV	—	—	—	—	—	—	—	—	—	—	—
N	1	1	1	1	1	1	1	1	1	1	1

	Wear class	Remarks
F:AM 126899	III; M3 erupting, slight wear	Lacrimal subtriangular; only slightly penetrates DPOF; DPOF with slight anterior rim; skull relatively large (e.g., #1, 2, 3, 5, 7, 8, 9) compared to *M. insiginis*, but DPOF comparatively smaller (#33, 35). F:AM 126899 skull too laterally crushed to record #10–14, 16–27

Note: Measurements follow Eisenmann et al. (1988). Characters 39 and 40 are new. #39 = length, rear of DPOF to anterior tip of lacrimal. Negative value indicates estimation of amount of lacrimal eroded by rear of DPOF. #40 = medial depth of DPOF.

TABLE 16.5

Cranial Measurements (mm), *Merychippus insignis*, Echo Quarry, Olcott Formation, Early Barstovian, Nebraska

	Characters											
	1	2	3	4	5	6	7	8	9	12	13	14
F:AM 87000*	66.8			5							43.6	21.6
F:AM 87001♂	68.0	70.2	69.5	88.1	146.8	289.9	65.2	57.7	102.2	32.5	52.3	27.4
F:AM 87002♂	64.1	—	—	—	—	—	67.4	56.8	121.1	—	—	26.6
F:AM 87003♂	68.3	78.4	79.3a	83.1a	160.0a	289.7	65.3	57.7	120.2	28.3a	51.0a	28.5
F:AM 87004♀	66.7	69.1	—	—	—	—	59.4	51.8	108.4	30.8a	44.6a	22.0
F:AM 87005♀	69.5	72.2	—	—	152.3	287.0	62.0	51.1	110.0	35.0a	50.0a	26.0
Range	64.1–69.5	69.1–78.4	69.5–79.3	83.1–88.1	146.8–160.8	287.0–289.9	59.4–67.4	51.1–57.7	108.4–120.2	28.3–35.0	44.6–52.3	22.0–28.5
Mean	67.3	72.5	74.4	85.6	153.0	288.9	63.9	55.0	116.0	31.7	49.5	26.1
SD	2.06	4.15	6.93	3.54	6.30	1.62	3.15	3.29	6.23	2.82	3.38	2.48
CV	3.06	5.73	9.31	4.13	4.33	0.56	4.94	5.98	5.37	8.92	6.84	9.49
N	5	4	2	2	3	3	5	5	5	4	5	5

	Characters											
	15	16	17	18	19	21	22	23	24	25	28	29
F:AM 87000*	33.0	—	—	—	113.6	—	—	211.0a	126.3a	42.0	43.8a	40.0a
F:AM 87001♂	38.2	55.6	88.5	100.3a	130.0	—	49.1a	228.6a	125.0a	44.2	46.4	41.3
F:AM 87002♂	34.8	—	—	—	—	—	—	230.0a	—	41.0	46.6	42.7
F:AM 87003♂	37.7	—	—	92.0a	128.8a	72.4	47.2	241.8a	127.3a	47.0	44.9	40.0a
F:AM 87004♀	35.6	—	—	81.5	121.8	—	—	222.7	—	39.0	43.6	42.0
F:AM 87005♀	34.2	—	—	92.2a	128.0a	—	—	226.5	—	42.2	46.0	41.0a
Range	34.2–38.2			81.5–100.3	121.8–130.0		47.2–49.1	222.7–241.8	125.0–127.3	39.0–47.0	43.6–46.6	40.0–42.7
Mean	36.1	55.6	88.5	91.5	127.5	72.4	48.2	230.0	126.2	42.7	45.5	41.4
SD	1.77			7.71	3.66		1.34	7.19	1.63	3.06	1.25	1.02
CV	4.90			8.42	2.88		2.79	3.13	1.29	7.18	2.75	2.47
N	5	1	1	4	4	1	2	5	2	5	6	6

(continued)

TABLE 16.5
Continued

	Characters										
	30	31	32	33	34	35	36	37	38	39	40
F:AM 87000*	60.3a	118.3	13.3	59.2	45.4	38.1	23.8	—	54.0	—	15.2
F:AM 87001♂	59.8	133.8	15.2	64.2	42.4	39.3	29.3	28.5	65.1	–10.3	10.2
F:AM 87002♂	60.8	136.0	21.9	60.1	46.0	36.0	26.2a	26.0a	57.0	–6.5	9.7
F:AM 87003♂	71.0a	128.5	15.9	72.0	52.1	35.0a	31.0a	32.0a	54.7	–14.5	12.2
F:AM 87004♀	67.5	126.6	16.6	57.8	41.0	32.7	32.7	28.0a	56.5	–3.6	9.1
F:AM 87005♀	68.0a	135.0	16.4	65.4	40.0	39.1	36.0a	29.2	59.1a	–6.1	10.6
Range	59.8–71.0	126.6–136.9	15.2–21.9	57.8–72.0	40.0–52.1	32.7–39.3	26.2–36.0	26.0–32.0	54.0–65.1	–3.6 to –14.5	9.1–12.2
Mean	65.4	132.2	17.2	63.9	44.3	36.4	31.0	28.7	58.5	–8.2	10.4
SD	4.87	4.40	2.68	5.47	4.92	2.81	3.67	2.18	4.02	4.26	1.71
CV	7.45	3.33	15.60	8.56	11.10	7.71	11.82	7.57	6.87	51.94	11.31
N	6	6	6	6	6	6	6	5	6	5	5

	Wear class	Remarks
F:AM 87000*	I; dPs present only	Juvenile; lacrimal "subrectangular" fossa with slight anterior rim; skull size (e.g., #19, 23, 31) relatively small
F:AM 87001	III; M3 erupting	Lacrimal "rectangular"; fossa with slight anterior rim
F:AM 87002	III; M3 erupting	Lacrimal more "triangular"; fossa with slight anterior rim; hypocone especially anteroposteriorly oriented
F:AM 87003	III; M3 erupted, slight wear	Lacrimal "subrectangular"; fossa with slight anterior rim; hypocone especially anteroposteriorly oriented
F:AM 87004	III; all teeth in wear	Lacrimal dorsoventrally shallow anteriorly, cf. F:AM 87002; fossa with slight anterior rim. Skull relatively small (e.g., #9, 18, 19, 33, 35)
F:AM 87005	IV; all teeth worn	Lacrimal "rectangular"; fossa with slight anterior rim; hypocone especially anteroposteriorly oriented

*F:AM 87000, a juvenile specimen, was not included in the statistical analysis. Character 1 was measured to dP2.

TABLE 16.6
Measurements (mm) of Mandible of Texas and Nebraska Merychippines

	Characters									p2 to mandibular foramen	Wear stage
	3	4	5	6	10	11	12	14	15		
A. Trinity River Pit 1, Texas; Fleming Formation, early Barstovian											
F:AM 113054	55.7	56.5	112.0	—	49.7	41.7	31.2	—	—	10.0	I
F:AM 113052	—	57.9	—	—	53.7	46.0	—	—	—	—	I
F:AM 113053	59.0	—	—	—	—	39.6	29.0	—	—	—	II
F:AM 113056	59.6	58.8	112.4	—	59.4	40.5	—	—	—	—	II
F:AM 113055	58.5	57.5	116.5	—	44.9	38.6	25.7	—	17.5	15.1	II
F:AM 113061	61.0	60.5	120.6	—	51.8	46.0	31.1	—	—	—	II
F:AM 113062	61.6	60.1	121.3	—	48.5	41.4	32.3	20.8	18.7	7.5	II
F:AM 113059	58.6	58.0	116.9	—	54.8	44.1	29.3a	—	—	—	III
F:AM 113064	—	56.1	—	—	44.0	39.5	28.0	—	—	19.5	III
F:AM 113057	60.8	60.5	121.0	—	55.1	47.2	—	—	—	—	IV
F:AM 113060	—	—	—	—	—	—	29.0	—	—	8.9	IV
F:AM 113065	—	56.0	—	—	50.1	40.5	30.6	—	—	8.3	V
F:AM 113070	57.3	—	—	—	—	39.0	27.2	23.0	18.7	6.8	VI
F:AM 113071	—	—	—	—	48.8	46.3	—	—	—	—	VII
F:AM 113066	55.6	55.0	110.8	—	47.1	43.2	31.3	—	—	9.0a	VII
F:AM 113067	55.2	54.1	108.9	—	53.3	45.7	33.1	—	23.7	8.2	VII
F:AM 109891	54.5	54.4	109.0	—	48.2	42.0	31.1	18.0	24.0	10.9	II
F:AM 113075	—	—	—	—	—	—	—	—	—	14.2	VII
Range	54.5–61.6	54.1–60.5	108.9–121.3		44.0–59.4	38.6–47.2	25.7–33.1	18.0–23.0	17.5–24.0	6.8–19.5	
Mean	58.1	57.3	114.9		50.7	42.6	29.9	20.6	20.5	10.8	
SD	2.44	2.22	4.94		4.26	2.93	2.11	2.51	3.08	3.91	
CV	4.20	3.87	4.30		8.42	6.89	7.06	12.17	15.01	36.36	
N	12	13	10		14	16	13	4	5	11	
B. Deep Creek, Nebraska; Valentine Formation, late Barstovian											
F:AM 126900	61.5	59.5	120.5	92.6a	47.0a	45.8a	30.5	—	—	—	VII

Note: Protostylid present only on p3–m1, contrary to the Trinity River Pit 1 sample, in which this feature also is found on m2.

TABLE 16.7

Measurements (mm) of Mandible, *Merychippus insignis*, Echo Quarry, Olcott Formation, Early Barstovian, Nebraska

	Characters											p2 to mandibular foramen	Wear stage
	3	4	5	6	8	9	10	11	12	14	15		
F:AM 111771	59.2	—	—	—	—	—	—	42.5	30.1	—	—	—	
F:AM 87074	58.5	59.7	118.0	—	—	—	48.5	38.8	25.5	—	—	—	
F:AM 87076♂	58.7	—	—	—	—	—	54.0	40.7	32.4	23.1	17.7	3.0	
F:AM 111781♀	62.6	—	—	—	—	—	—	41.5	25.8	—	—	3.4	I
F:AM 111793♂	61.2	—	—	—	—	—	—	—	30.0	22.9	17.3	10.0	I
F:AM 111791	59.0	—	—	—	—	—	—	—	—	—	—	—	I
F:AM 112061	59.2	54.2	113.9	—	—	—	47.7	40.9	28.7	—	—	—	I
F:AM 87072♂	60.4	54.3	115.0	—	—	—	47.2	42.5	29.7	20.0	22.2	—	I
F:AM 112062	—	54.5	—	—	—	—	50.1	37.4	—	—	—	—	I
F:AM 111794♂	61.0	—	—	—	—	—	50.1	38.3	26.2	20.2	19.7	2.0	I
F:AM 111774	62.5	—	—	—	—	—	—	—	—	—	—	—	I
F:AM 111780	—	—	—	—	—	—	48.7	37.5	—	—	—	—	I
F:AM 111792	—	—	—	—	—	—	51.8	29.1	—	—	—	—	I
F:AM 87075	—	56.6	—	—	—	—	—	44.2	—	—	—	—	I
F:AM 112070♂	62.5	60.2	119.2	83.0	143.2	136.2	55.2	45.4	30.7	27.0	16.8–28.5	8.0	II
F:AM 87078♀	63.4	58.9	121.5	87.4	151.1	129.9	54.0	47.4	28.7	23.4	17.9	9	II
F:AM 112064	56.9	56.3	112.9	—	—	—	52.2	40.0	28.1	—	—	—	II
F:AM 112066	58.5	56.6	115.0	—	—	—	54.7	42.7	29.0	—	—	—	II
F:AM 112063	58.0	54.5	110.5	88.3	137.3	132.0	49.3	43.0	30.8	—	—	—	II
F:AM 87080♀	56.8	56.5	113.0	77.5	138.0	131.8	51.0	42.0	29.7	19.7	20.5	9.5	I
F:AM 111757	54.1	53.7	107.7	—	—	—	—	43.9	29.6	18.7	28.5	13.9	V
F:AM 111760	—	57.7	—	—	—	—	51.2	48.0	30.1	—	17.0	17.5	V
F:AM 111761	—	54.2	—	—	—	—	51.7	46.7	30.9	—	—	9.3	V
F:AM 111759	—	58.3	—	—	—	—	56.4	52.4	35.2	—	—	19.5	V
F:AM 111767	—	56.5	—	—	—	—	53.7	42.7	—	—	—	—	V
F:AM 87085	53.7	54.0	109.1	84.0	—	137.1	49.2	39.9	33.7	19.3	28.0	14.4	V
F:AM 111750	60.8	60.4	119.3	—	—	—	55.7	49.5	37.7	18.9	20.0	19.9	V
F:AM 87088	55.2	54.0	108.7	—	—	—	50.9	42.8	32.8	19.0	19.5	7.7	VI
F:AM 111754	58.4	54.1	112.6	—	—	—	46.7	40.0	29.2	—	—	—	V
Range	53.7–63.4	53.7–60.2	113.0–121.5	77.5–88.3	137.3–157.1	129.9–137.1	46.7–56.4	29.1–52.4	25.5–37.7	18.7–23.4	16.8–28.5	2.0–19.9	
Mean	59.1	56.3	114.0	84.0	142.4	133.4	51.4	42.3	30.2	21.1	20.45	10.5	
SD	2.73	2.27	4.28	4.28	6.37	3.09	2.85	4.56	2.89	2.64	4.00	5.84	
CV	4.61	4.04	3.75	5.09	4.47	2.32	5.55	10.78	9.58	12.50	19.57	55.56	
N	21	20	14	5	4	5	22	26	22	11	12	14	

TABLE 16.8

Measurements (mm) of Mandible of *Cormohipparion goorisi*, Trinity River Pit 1, Fleming Formation, Early Barstovian, Texas

	Characters									Wear
	2	3	4	5	10	11	12	14	15	stage
F:AM 73948	—	60.6	59.7	108.9	52.0	45.5	32.5	—	—	II
F:AM 73949	—	53.0	53.5	107.3	57.2	48.9	31.1	—	27.7	III
F:AM 113058	68.2	—	57.4	—	55.0	44.0	29.2	24.1	21.2	V
F:AM 113063	—	49.9	52.7	—	52.9	47.8	29.8	19.5	21.0	VI
F:AM 113069	—	—	55.1	—	55.2	46.9	—	—	—	VII
F:AM 113068	—	55.5	55.5	109.8	52.1	45.9	32.0	—	19.5	VII
Range	68.2	53.0–60.6	52.7–59.7	107.3–109.8	52.0–57.2	45.5–48.9	29.2–32.5	19.5–24.1	16.5–27.7	
Mean	68.2	54.8	55.7	108.4	54.1	46.5	30.9	21.8	22.4	
SD		4.52	2.57	0.95	2.07	1.74	1.41	3.25	3.65	
CV		8.26	4.62	0.88	3.83	3.75	4.55	14.92	16.32	
N	1	4	6	3	6	6	5	2	3	

Note: #15 = length from p2 to rear of symphysis, not an angle between the condyle and tooth row as in Eisenmann et al. (1988).

TABLE 16.9

Comparison of Lower Dentitions: *Cormohipparion goorisi* and Trinity River Pit 1 Merychippines, Early Barstovian, Texas

Wear stage	Description	*Cormohipparion goorisi*	Trinity River Pit 1 merychippine
I	Early wear; single tubular metaconid/metastylid on p2; postflexid on p2 open; very early wear on m3	No specimens	F:AM 113054, F:AM 113052 • p2 ectoflexid penetrates nearly to labial margin of metaconid/metastylid • p3 isthmus long; ectoflexid extends to labial margin of metaconid/metastylid • p4 ectoflexid penetrates isthmus between metaconid/metastylid; postflexid complex; protoconid ca. 25.5 mm tall • m1 protostyid present
II	m3 hypoconid breached; slight abrasion on hypoconulid; p2 metaconid/metastylid beginning to separate; postflexid nearly closed	F:AM 73948 • p3 ectoflexid still labial to isthmus • p4 ectoflexid not fully formed; still would not penetrate isthmus • m1 with protostylid exposed	F:AM 113053, F:AM 113056, F:AM 113055 • p3–m2 ectoflexid penetrates isthmus to lingual enamel of metaconid/metastylid • posteflexid simple • protostylids on p3–m2 • metaconid = metastylid in occlusal size
III	p2 metaconid distinct from metastylid; p3 postflexid nearly closed, but still not as isolated lake; m3 hypoconid worn; hypoconulid open	F:AM 73949 • p3–p4 ectoflexid not in isthmus, but penetrates about to postflexid loop in p4 • metaconid ≫ metastylid, or = in later wear	F:AM 113059, F:AM 113064 • p3–p4 ectoflexid penetrates far lingually in isthmus • metaconid = metastylid in occlusal size • protostylids developed on p3–m2
IV	p3 metaconid/metastylid lose distinction; postflexid flattened	No specimens	F:AM 113057, F:AM 113060 • p3 ectoflexid still deeply penetrates isthmus, within 1.2 mm of metaconid/metastylid enamel • ectostylids developed on p3–m2 • metaconid = metastylid in occlusal size
V	p2?, p3–p4 postflexid still open and persistent	F:AM 113058 • p3 ectoflexid well labial of postflexid • protostylid present on m1	F:AM 113065 • p3–p4 ectoflexid opposite pre- and postflexids • protostylids developed on p3–m2
VI	p2 pre- and postflexids open; p3 postflexid only a loop of enamel	F:AM 113063 • p3 ectoflexid well labial of postflexid • m1 with protostylid exposed	F:AM 113070 • p2–p4 ectoflexid still lingual to postflexid • protostylids developed on p3–m2
VII	p2–p4 ectoflexid still about at or slightly labial to postflexids; protostylids developed on p3–m2	F:AM 113069 • see description	F:AM 113071, F:AM 113066, F:AM 113067, F:AM 109891 • see description

Note: With respect to these wear classes, note that *C. goorisi* is retarded in time of penetration of isthmus and other features of premolars and in development of ectostylids on premolars and molars (i.e., posterior progression) in comparison to the Trinity River Pit 1 merychippine. This probably reflects the greater hypsodonty of *C. goorisi.*

TABLE 16.10

Measurements (mm) of Upper Cheek Dentition of *Merychippus insignis*, Echo Quarry, Olcott Formation, Early Barstovian, Nebraska

	P2					P3					P4				
				Protocone					Protocone					Protocone	
	Height	Length	Width	Height	Length	Height	Length	Width	Height	Length	Height	Length	Width	Height	Length
F:AM 87001♂	20.9	26.1	20.8	4.1	2.2	20.7a	21.8	22.0	5.6	2.0	20.7	21.1	21.0	5.3	3.0
F:AM 87002♂	19.4	26.3	20.0	4.8	3.8	21.0a	21.8	23.0	6.3	4.1	20.0	21.4	22.3	6.3	3.8
F:AM 87003♂	19.3	26.4	19.8	5.3	4.0	19.8	21.8	22.0	6.1	5.1	19.8	20.4	22.8	6.4	4.1
F:AM 87004♀	12.5	23.6	17.3	4.2	4.2	13.1	19.9	21.6	5.4	5.0	11.7	19.2	21.7	6.0	4.8
F:AM 87005♂	9.6	25.2	21.3	—	—	12.5a	20.2	25.6	—	—	12.4	19.5	23.3	—	—
F:AM 87007	21.8	23.6	18.2	—	—	23.8	21.1	21.0	—	—	25.9	21.0	19.9	—	—
F:AM 87008	21.5	24.7	17.6	—	—	25.6	22.3	20.7	—	—	24.5	21.4	19.0	—	—
F:AM 87049	—	—	—	—	—	25.0a	19.9	18.3	—	—	25.0a	20.3	17.4	—	—
F:AM 87048	—	—	—	—	—	24.0a	21.8	—	—	—	23.0a	20.0	19.3	—	—
F:AM 87050	—	—	—	—	—	—	—	—	—	—	24.0a	20.4	19.0	5.2	3.1
F:AM 87058	—	—	—	—	—	—	—	—	—	—	21.2	20.4	19.9	—	—
F:AM 87056	21.0a	23.8	18.3	—	—	25.0a	20.8	19.3	—	—	28.0	20.0	19.4	—	—
F:AM 87014	—	—	—	—	—	—	—	—	—	—	26.2	21.0	20.2	—	—
F:AM 87052	—	—	—	—	—	—	—	—	—	—	22.5a	20.4	21.0	5.0	3.6
F:AM 109984	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
F:AM 87042	15.3	24.0	18.9	4.4	4.4	16.3	19.7	21.8	6.1	5.2	15.5	19.7	21.7	6.4	4.6
F:AM 87013	14.8a	24.8	17.8	4.2	3.9	20.0a	20.4	19.8	5.7	3.8	19.0a	20.8	19.9	5.7	3.9
F:AM 87041	17.1	26.5	18.8	—	—	13.2	—	21.4	5.1	4.9	14.5a	19.8	20.9	5.3	5.0
F:AM 87035	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
F:AM 87036	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
F:AM 87039	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
F:AM 87037	—	—	—	—	—	11.6a	19.5	21.2	—	—	—	—	—	—	—
F:AM 87019	—	—	—	—	—	—	—	—	—	—	11.0a	19.5	21.8	—	—
F:AM 87060	—	—	—	—	—	—	—	—	—	—	18.0	21.3	20.2	5.8	4.5
F:AM 87046	16.8	23.7	18.1	4.9	4.8	19.4	20.0	19.0	5.8	4.3	20.0a	20.3	19.7	6.1	4.0
F:AM 87062	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
F:AM 87043	19.0	23.0	17.5	4.3	3.6	22.5	20.4	19.9	5.5	4.1	22.0a	19.3	19.1	6.0	3.5
F:AM 87047	16.0	22.4	17.7	4.9	4.6	18.2	19.9	19.5	5.5	4.5	18.0	19.0	20.9	5.6	4.0

(continued)

TABLE 16.10
Continued

	P2					P3					P4				
				Protocone					Protocone					Protocone	
	Height	Length	Width	Height	Length	Height	Length	Width	Height	Length	Height	Length	Width	Height	Length
F:AM 87057	13.8	23.4	18.8	4.4	5.3	15.0	19.0	21.0	5.3	5.2	16.0	18.7	21.3	5.8	4.3
F:AM 87022	—	—	—	—	—	12.7	20.1	21.5	5.8	5.0	11.7	20.3	21.8	6.0	5.0
F:AM 110374	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
F:AM 110387	—	—	—	—	—	19.6	19.7	17.3	—	—	22.0a	19.1	16.7	—	—
F:AM 110389	17.9	23.3	17.3	6.3–4.1	3.1	19.0a	20.9	18.8	6.4	4.2	20.0a	19.5	19.2	6.0	3.2
F:AM 110379	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
F:AM 87059	14.2	21.2	19.9	5.1	4.9	14.5a	20.3	21.3	6.3	6.0	15.7	20.3	21.7	6.0	5.1
F:AM 87064	—	—	—	—	—	13.3	—	19.9	—	—	13.0	20.3	22.6	—	—
F:AM 87061	16.0	24.3	18.7	5.0	4.2	18.0a	21.0	20.8	5.8	4.9	15.7a	20.2	21.3	6.6	5.1
F:AM 87051	16.2	25.2	19.0	—	—	18.3	20.5	20.4	5.7	5.3	15.7	20.1	21.8	6.4	5.0
F:AM 87055	12.8	23.9	18.8	—	—	13.5	20.8	21.4	—	—	11.8	19.5	22.1	—	—
F:AM 87045	23.7	24.5	17.7	—	—	24.1	22.1	19.5	—	—	24.9	21.3	19.8	—	—
F:AM 87030	15.6	24.3	18.6	5.6	5.1	—	—	—	—	—	18.0	20.0	20.8	6.4	4.8
F:AM 87012	20.9	23.5	17.3	—	—	22.3	22.1	19.9	—	—	23.0a	20.2	19.7	—	—
F:AM 87016	—	—	—	—	—	16.7	20.3	22.0	5.8	4.8	14.5a	20.2	22.1	6.3	5.2
F:AM 87023	19.3	23.9	19.4	—	—	22.5a	21.4	21.4	—	—	18.5a	20.2	21.0	—	—
F:AM 87029	—	—	—	—	—	13.9	17.9	19.5	—	—	14.8	18.3	19.9	—	—
F:AM 87028	—	—	—	—	—	11.0	19.9	20.3	5.5	5.5	11.3	19.7	19.8	5.5	5.2
F:AM 87023	20.9	24.2	18.0	—	—	22.9a	20.8	20.3	—	—	19.5a	20.1	21.1	—	—
F:AM 87032	11.6	22.4	17.0	—	—	9.3	18.5	20.9	—	—	9.0	18.8	21.7	—	—
F:AM 87040	14.6	23.3	19.0	5.0	4.4	15.5	20.2	21.0	6.4	5.2	15.2	19.8	21.3	5.2	4.8
F:AM 87034	16.0	24.3	18.5	—	—	16.8a	21.0	21.7	—	—	16.3a	20.6	21.6	—	—
Range		26.5–21.2	21.3–17.0	6.3–4.1	5.3–2.7		22.3–17.9	25.6–17.3	6.4–5.1	6.0–2.6		21.4–18.3	23.3–16.7	6.6–5.2	5.2–3.0
Mean		24.1	18.6	4.8	4.2		20.5	20.7	5.8	4.7		20.1	20.7	5.9	4.3
SD		1.24	1.08	0.60	0.80		1.02	1.47	0.38	0.85		0.75	1.39	0.46	0.72
CV		5.15	5.80	12.48	19.13		5.00	7.11	6.60	18.22		3.71	6.72	7.87	16.57
N		28	28	15	15		34	35	19	19		42	42	21	21

(continued)

TABLE 16.10
Continued

	M1					M2					M3				
				Protocone					Protocone					Protocone	
	Height	Length	Width	Height	Length	Height	Length	Width	Height	Length	Height	Length	Width	Height	Length
F:AM 87001♂	20.2	19.5	20.8	6.0	4.5	21.0a	20.1	20.0	6.1	3.8	—	—	—	—	—
F:AM 87002♂	16.4	20.6	22.6	7.0	3.3	21.0a	20.5	21.7	7.0	3.3	21.1	—	—	—	—
F:AM 87003♂	17.9	20.1	19.1	7.2	3.6	21.7	20.3	18.2	7.3	3.4	21.5a	—	—	—	—
F:AM 87004♀	12.7	17.3	20.2	5.8	5.0	18.3a	17.9	—	5.5	3.5	18.2	17.2	—	—	—
F:AM 87005♂	16.0	17.4	22.9	—	—	13.5	17.8	21.5	—	—	13.5a	18.0	19.4	—	—
F:AM 87007	24.8	20.7	19.2	—	—	27.8	20.2	18.6	—	—	—	—	—	—	—
F:AM 87008	21.3	21.3	19.5	—	—	25.0	20.0	19.5	—	—	23.3	19.2	—	—	—
F:AM 87049	21.0a	19.6	19.1	—	—	25.5	18.7	15.8	—	—	—	18.3	—	—	—
F:AM 87048	19.0a	21.1	19.9	5.8	3.9	21.0a	21.3	17.6	—	—	—	—	—	—	—
F:AM 87050	20.0a	18.9	19.6	6.1	4.2	22.0a	19.1	16.7	—	—	—	—	—	—	—
F:AM 87058	19.8a	19.0	19.2	5.8	3.2	20.0a	19.3	17.0	—	—	—	18.5	—	—	—
F:AM 87056	24.0a	19.1	19.1	—	—	22.0a	18.9	16.3	—	—	—	—	—	—	—
F:AM 87014	20.2	20.2	18.6	—	—	25.1	19.2	17.5	—	—	22.3	18.2	—	—	—
F:AM 87052	19.0a	19.0	20.7	5.5	4.8	21.0a	20.8	18.3	5.2	3.3	22.2	18.2	—	—	—
F:AM 109984	16.9	20.0	20.0	5.2	4.0	18.3a	20.0	17.2	—	—	18.5	18.3	—	—	—
F:AM 87042	15.3	18.3	19.8	6.3	4.8	19.0a	17.8	19.2	—	—	—	16.4	19.8	—	—
F:AM 87013	13.8	—	—	—	—	16.0a	19.5	18.2	—	—	—	18.8	—	—	—
F:AM 87041	12.8	17.5	20.7	5.2	4.6	13.2	17.4	19.9	5.6	4.5	17.0	17.8	16.5	—	—
F:AM 87035	13.0	17.8	20.2	5.7	6.0	15.0a	17.8	18.7	6.1	3.3	17.4	—	—	—	—
F:AM 87036	9.8	17.3	21.0	—	—	15.0	17.8	19.9	—	—	18.0a	19.4	18.2	—	—
F:AM 87039	9.0	17.3	21.3	—	—	12.5	18.2	20.5	—	—	16.0a	18.4	17.9	—	—
F:AM 87037	13.6	17.9	21.0	—	—	19.0a	18.4	19.8	—	—	22.0a	17.4	15.1	—	—
F:AM 87019	10.2	16.5	21.0	—	—	11.5a	17.6	19.8	—	—	—	—	—	—	—
F:AM 87060	13.7	18.7	20.2	5.7	4.2	16.0a	19.5	19.0	6.1	3.7	—	19.0	15.7	—	—
F:AM 87046	17.5	18.0	18.9	5.9	3.8	18.0a	18.5	18.3	6.3	3.3	20.0a	17.0	14.8	—	—
F:AM 87062	14.8	17.6	19.1	5.8	4.2	17.9	18.4	18.9	6.2	4.4	19.8	18.7	15.6	—	—
F:AM 87043	16.5	18.2	19.3	6.5	4.3	19.0a	19.0	17.3	6.0	2.3	20.0a	17.4a	—	—	—
F:AM 87047	13.9	18.0	21.0	6.2	4.3	17.9	19.1	19.1	6.5	3.7	—	16.5	—	—	—

(continued)

TABLE 16.10
Continued

	M1					M2					M3				
				Protocone					Protocone					Protocone	
	Height	Length	Width	Height	Length	Height	Length	Width	Height	Length	Height	Length	Width	Height	Length
F:AM 87057	13.7	17.6	19.8	5.6	4.3	15.9	17.7	19.7	6.2	4.0	19.3	18.0	16.7	—	—
F:AM 87022	12.0	18.5	20.7	5.5	4.6	14.0	18.7	19.3	6.0	4.0	16.0a	18.0	15.7	—	—
F:AM 110374	9.6	16.5	20.2	—	—	11.0	16.9	21.0	—	—	13.0a	18.4	18.0	—	—
F:AM 110387	18.9	18.9	17.3	—	—	—	—	—	—	—	—	—	—	—	—
F:AM 110389	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
F:AM 110379	14.7	17.7	20.8	6.2	4.8	18.0a	18.8	20.0	6.5	3.8	20.0a	17.1	15.6	—	—
F:AM 87059	11.7	17.8	—	5.2	4.4	—	—	—	—	—	—	—	—	—	—
F:AM 87064	12.3	18.0	21.0	6.6	—	13.2	17.9	20.1	5.2	4.6	13.8	17.9	20.0	6.5	4.2
F:AM 87061	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
F:AM 87051	12.4	17.0	21.1	6.3	5.5	13.8	17.6	21.3	6.5	4.9	—	—	—	—	—
F:AM 87055	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
F:AM 87045	22.1	20.3	18.4	—	—	—	—	—	—	—	—	—	—	—	—
F:AM 87030	15.5	17.6	20.1	6.4	4.8	—	—	—	—	—	—	—	—	—	—
F:AM 87012	21.0a	20.5	19.3	—	—	22.3	19.0	16.9	—	—	—	—	—	—	—
F:AM 87016	13.4	16.6	19.9	5.4	4.4	19.4	17.8	20.7	6.1	4.9	19.4	19.1	17.9	3.8	3.8
F:AM 87023	17.8a	19.2	21.8	—	—	—	—	—	—	—	—	—	—	—	—
F:AM 87029	11.3	15.5	18.8	—	—	12.8a	16.4	17.7	—	—	—	—	—	—	—
F:AM 87028	10.7	17.2	20.9	6.0	4.9	—	—	—	—	—	—	—	—	—	—
F:AM 87023	17.8a	19.2	19.8	—	—	—	—	—	—	—	—	—	—	—	—
F:AM 87032	10.3	17.0	20.2	—	—	—	—	—	—	—	—	—	—	—	—
F:AM 87040	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
F:AM 87034	12.8	18.9	20.4	—	—	14.8a	19.3	20.1	—	—	—	—	—	—	—
Range		21.3–15.5	22.9–17.3	7.2–5.0	6.0–3.3		21.3–16.4	21.7–15.8	7.3–5.2	4.9–2.3		19.4–16.4	20.0–15.1	6.5–3.8	4.2–3.8
Mean		18.5	20.1	6.0	4.4		18.8	19.0	6.1	3.8		18.0	17.1	5.2	4.0
SD		1.36	1.08	0.52	0.62		1.12	1.51	0.54	0.66		0.80	1.74	1.35	0.28
CV		7.39	5.38	8.86	14.11		5.98	7.96	8.86	17.41		4.46	10.17	26.21	7.07
N		45	44	26	25		38	37	18	18		25	15.1	2	2

Note: Height is at mesostyle; a = approximate.

TABLE 16.11

Elements of Dental Pattern Relative to Crown Height, *Merychippus insignis*, Echo Quarry, Olcott Fm., Early Barstovian, Nebraska: P2

Ht (mm)	Protoloph-metaloph	Pre-fossette	Post-fossette	Hypocone opens	Hypoconal grv plicat	Protocone opens	Pli caballin	Pli protoloph	Pli prefossette	Pli postfossette	Pli hypostyle	
24		–	–	–	+	–	–	–	–	–	–	Wear has begun on protocone
22	NEVER CONNECTS							– +				
		– +	–	– +	+ --	–	----	---	-- +,2	--- 2	--- +	Hypocone conn. to metaloph
			– +	+	--	–			+			
20									–			
		– +	+	+	– +,2	--	-- +,2	---	++ --- +,3	– 4,5	+++	↑
									++ –			
			+	+	2	–	+		++ –	+	+	Fossette pattern
18				–		–	–	–	+ –	– +	2	established and interval of
				+	– +	+	–	–	–	–	– 2	maximum
		+		+	2	– +	–		+	++	+++,2 +	complexity
16		+	+	+	– +	+	-- +	--	+,2	2,3	+,3 +,2,3	↓
		+	+	+	– 2	--	2	--	2	2,2	2,2 ++	to
		+				+			++			13 mm
		–	– +	+	2,2	--	++	–		++	– + ++	↓
14		–	–	+	+	–	+	–		+	+ +	
		–	+		+	–	–	–	–	–	+	
			+	+	+	–	–	–	+	+	2	
		–	–		+		+	–	–	–	–	
12		–		+	+	–						
		–	–	+	–	+	–	–	–	–	–	Protocone conn. to protoloph
10												
		–	–	+		+	–	–	–	–	–	
8												

Note: Protoloph remains isolated from metaloph until extremely late wear; unworn height of tooth is somewhat greater than 24 mm; fossette pattern is established after about 24% wear; protocone remains isolated until about 48% wear; maximum complexity established at about 24% wear, and maintained until about 48% wear, below which taxonomically useful features tend to be lost.

Key: Hypocone opens = isolation (–) or confluence (+) of hypocone and metaloph; Hypoconal grv plicat = plications in hypoconal groove; Protocone opens = isolation (–) or confluence (+) of protocone and protoloph; Pli caballin = score for pli caballin: absence (–), presence (+), and number of plications if more than one; Pli protoloph, Pli prefossette, Pli postfossette, and Pli hypostyle = scores for pli protoloph, pli prefossette, pli postfossette, and pli hypostyle, respectively. Numbers in (–) columns = additional number of specimens lacking the feature in question.

TABLE 16.12

Elements of Dental Pattern Relative to Crown Height, *Merychippus insignis*, Echo Quarry, Olcott Fm., Early Barstovian, Nebraska: P3

Ht (mm)	Protoloph-metaloph	Pre-fossette	Post-fossette	Hypocone opens	Hypoconal grv plicat	Protocone opens	Pli caballin	Pli protoloph	Pli prefossette	Pli postfossette	Pli hypostyle	
26	–	–	–	–	–	–	–	–	–	–	–	Wear begins on protocone
	––	––	––	––	––	––	––	––	––	––	––	
24	– +	– +	– +	– +	– +	––	– +	– +	– +	– +	– +	Protoloph conn. to metaloph; fossette pattern and interval of maximum complexity established, and continues to 13 mm
	–	+ –		+ –		–	+	+	+ –		–	
	–– ++	– ++	– ++	+++	–– +	–––	+,2	– ++	– ++	– 3,3	–– 4	
22												
	++	+	+	+	+	–	2	+	2	5	+	
	+++	–	–	–	–	–	2	–		–	–	
20	+	+	+	+	3	–	–	+	3	3	+	
	– +	+	+	+ –	+	–	2	+	*	3	+	
	+++	+++	+++	+++ –	++	––	+,2,2	+++	+,3,*3	+,4,4	+++	
	+	+	+	+	+ –	+	2	+	2	+	+	
18	+	+	+	+	+	+	2	–	++,2	2,3	+	
	– +	++	++	++ ––		++ –	+	++ –	+	+,2	++	
	+	++	++	++	++	––	2	+	2	2 –		
16												
	+	+	+	+	+	+	2	+ –		2	+	
	–	+	+	+ –	–		+	+ –		–	–	
	+	+	+	+	+ –		2	+	2	+	+	
14	+	+	+	+ –		+	+ –		3	3	+	Protocone conn. to protoloph
	+	+	+	+	+	+	+,2	++ –	+,2	2,4	++	
	+++	+++	+++	+++ –––		–– ++	++,2	– ++	++	++,2	– ++	
	+	++	++	++ ––		+ –	–	–	–	+	–	
12												
	– +	++	++	++ ––	lake	– +	– +	–	– +	– ++	––	
10												
	+	+	+	+ –	flat	+	+	–	+	2	+	
8												

Note: Protoloph is mostly connected to metaloph; unworn height of tooth is somewhat greater than 26 mm; fossette pattern is established after about 11% wear; protocone remains isolated until about 59% wear, but some specimens show a breached protocone at 34% wear; maximum complexity established at about 11% wear, and maintained until about 50% wear, below which taxonomically useful features tend to be lost.

Key: See table 16.11 for explanation of notation. * indicates one or three loops anterior to pli prefossette.

TABLE 16.13

Elements of Dental Pattern Relative to Crown Height, *Merychippus insignis*, Echo Quarry, Olcott Fm., Early Barstovian, Nebraska: P4

Ht (mm)	Protoloph-metaloph	Pre-fossette	Post-fossette	Hypocone opens	Hypoconal grv plicat	Protocone opens	Pli caballin	Pli protoloph	Pli prefossette	Pli postfossette	Pli hypostyle	
28												
	+	+	+	–	–	–	+	–	3	–	–	Pattern begins
26												Proto. conn. meta.
	–+	–+	–+	–+	––+	–––	–+	–+	–+	–––	–+	Still some
	–	–	–	–	–	–	–	–	–	–	–	unworn
24	+	–	–	+	+	–	+	–	–	–	–	
	––++	–++	–++	–––	–––	–––	–++	––+	–3,2	–3,2	–++	Pattern shows
	+	+	+	+	+	–	+	+	2	3	+	interval of
22	–+	++	++	++	++	––	2,2	++	2,3	–4	++	maximum
												complexity
	+	+	+	+	+	–	2	–	3	5	+	established,
	+	–	–	+	–	–	2	–	–	–	–	and continues
20	+++	+++	+++	+++	–++	–––	–2,2	+++	3,4,5	+,6,4	+++	to 13 mm
	+++	+++	+++	+++	–++	–––	+,2,2	––+	++,3	–2,3	––+	
	+	+	+	+	+	–	2	–	3	4	+	
	+	–	–	+	+	–	+	–	–	–	–	
18	+++	+++	+++	+++	–++	–––	2,2,2	+++	+,2,4	4,3,3	+++	
	+	+	+	+	–	–	+	–	+	3	+	
16	+	+	+	+	–	–	2	+	+	+	+	
	+++	+++	+++	+++	–++	–––	2,2,2	–++	++,2	2,3,3	++,2	
	++	++	++	++	++	––	2,2	–+	+,3	2,6	–2	
	+	+	+	+	–	–+	+++	–––	+++	+,2,2	+,2	
14	+	+	+	+	+	–	2	+	2	3	+	Protocone conn.
												to protoloph
	+	+	+	+	+	–	2	–	+	2	2	
	+	++	++	++	––	+–	––	–	–	–	–	
12	++	++	++	++	–+	–+	++	–+	+,4	++	++	
	+	+	+	+	–	+–	+	–	+	2	+	
	+	+	+	+	–	+	+	–	2	2	–	
10												
	+	+	+	+	–	+	+	–	+	+	–	
8												

Note: Protoloph is mostly connected to metaloph; unworn height of tooth is somewhat greater than 27 mm; fossette pattern is established after about 15% wear; protocone remains isolated until about 57% wear; maximum complexity established at about 18% wear, and maintained until about 54% wear, below which taxonomically useful features tend to be lost.

Key: See table 16.11 for explanation of notation.

TABLE 16.14

Elements of Dental Pattern Relative to Crown Height, *Merychippus insignis*, Echo Quarry, Olcott Fm., Early Barstovian, Nebraska: M1

Ht (mm)	Protoloph-metaloph	Pre-fossette	Post-fossette	Hypocone opens	Hypoconal grv plicat	Protocone opens	Pli caballin	Pli protoloph	Pli prefossette	Pli postfossette	Pli hypostyle	
24												Likely unworn crown height 27 mm
22	+	+	+	–	–	–		+	–	3	+	–	
	+ –	–	+		–	–	–	–	–	–	–	–	
	– ++++ –	+++++ –	++++	––	+++ -----	+ ----	–	++++	––	+ +,3,5,4	– 3,3,4,5	++,2,2	Pattern shows interval of maximum of complexity established and continues to about 12 mm
	++	++	++	––	–	+ ––		++	––	5,5	5,3	+,2	
20	+++	+++	+++	––	+ –	++ ---		+++	---	3,5,5	5,5,5 –	+,2	
	+	+	+		+	+ –		+	–	3	3	+	
	+++ –	++ –	++		+++ –	+,2 ---		++,2	––	+ – 3,3	– 2,2 –	++	
18	+++	+++	+++		+++ –	++ ---		++,2	––	+ 5,5,5	2,2,3	+++	
	+	+	+		+	+ –		+	–	3	2	+	
	+	+	+		+ –	–		+		+	4	+	
	++	++	++		++ ––	––		++	––	4,3	2,4	++	
16	++	++	++		++ ––		++	++	––	– + –	+ ––		
	+	+	+		+ –	–		+	–	2	2	+	
	+	+	+		+ –		+	+	–	4	2	+	
	+	+	+		+ –		+	+	–	2	2	+	
14	+++	+++	+++		+++ ---	–	++	+++	---	+,2,2	+,2,4	+++	
	++	++	++		++ ––		++	++	––	++	+,2	++	Protocone connects to protoloph
	++	++	++		++ –	+ –	+	+,2	– +	+,2	+,3 –	+	
	++++	++++	++++		++++ 4–	––	++	++	4–	2,2,2,3	++,2,3 –	+++	
12	++	++	++		++ ––	–	+	++	––	2,3 –	++	++	
	+	+	+		+ –	–		+	–	+	2	+	
	+	+	+		+ –		+	+	–	2	2	+	
	+	+	+		+ –	–		+	–	+	+ –		
10	++	++	++		++ ––		++	++	––	+,2	++ ––		
	+	+	+		+ –		+ –	–	–	–	–		Fossettes lose pattern
	+	+	+		+ –		+	+	–	+	+ –		
	+	+	+		+ –		+	+	–	2	+ –		
8													

Note: Protoloph is mostly connected to metaloph; unworn height of tooth is about 27 mm; fossette pattern is established after about 22% wear; protocone remains isolated until about 62% wear, but some connect to protoloph by 41% wear; maximum complexity established at about 22% wear, and maintained until about 52% wear, below which taxonomically useful features tend to be lost.

Key: See table 16.11 for explanation of notation.

TABLE 16.15

Elements of Dental Pattern Relative to Crown Height, *Merychippus insignis*, Echo Quarry, Olcott Fm., Early Barstovian, Nebraska: M2

Ht (mm)	Protoloph-metaloph	Pre-fossette	Post-fossette	Hypocone opens	Hypoconal grv plicat	Protocone opens	Pli caballin	Pli protoloph	Pli prefossette	Pli postfossette	Pli hypostyle	
28												
26												
	–	–	–	–	–	–	–	–	–	–	–	
	++	––	––	––	––	––	––	––	––	––	––	Wear on all cusps except hypocone
24												
	+	–	–	–	–	–	+	–	–	–	–	
22	– +	––	––	––	––	––	++	––	––	––	––	
	+	+	+	+	+	–	+	+	4	5	+	Pattern
	++++	– +++	– +++	–– ++	––– +	–––––	++++	––– +	– 2,4,5	3,4,5	–– ++	complexity established
20	+	+	+	–	–	–	+	–	3	3		and continues
	+++	+++	+++		+++ –	++ –––	+++	–– +	+,3,4	+,3,4	– ++	to
	++	++	++	–	+ –	+ ––	++	+,2	++	2,3	++	about
18	++	++	++		++	++ ––	– 2	– ++	+,3	3,4	++	13 mm
16	++	++	++		++ –	+ ––		++ –	+ +,3	4,5	++	
	++	++	++		++	++ ––		++ –	+ +,3	+,4	– +	
	++	++	++		++	++ ––		++ ––	– +	– 3	– +	
	+	+	+		+ –	–		+ –	+	2	+	
14	++	++	++		++ –	+ ––		++ ––	+,3	2,3	– +	
	+	+	+		+ –	–		+ –	–	–		
	++	++	++		++ –	+ ––	–	+ –	+ +,2	2,3	++	
	+	+	+		+ –	–		+ –	–	+	+	
12	+	+	+		+	+	+	+ –	2	+	+	
	+	+	+		+ –	–		+ –		+	+	
	+	+	+		+ –	–		+ –		2	+	
10												

Note: Protoloph is mostly connected to metaloph; unworn height of tooth probably is about 28 mm; fossette pattern is established after about 22% wear; protocone remains isolated at least to about 59% wear, but in one specimen is connected to protoloph at 56% wear; maximum complexity established at about 22% wear, and maintained until about 52% wear, below which taxonomically useful features tend to be lost.

Key: See table 16.11 for explanation of notation.

TABLE 16.16

Elements of Dental Pattern Relative to Crown Height, *Merychippus insignis*, Echo Quarry, Olcott Fm., Early Barstovian, Nebraska: M3

Ht (mm)	Protoloph-metaloph	Pre-fossette	Post-fossette	Hypocone opens	Hypoconal grv plicat	Protocone opens	Pli caballin	Pli protoloph	Pli prefossette	Pli postfossette	Pli hypostyle	
24	–	–	–	–	–	–	–	–	–	–	–	Unworn
	––	––	––	––	––	––	––	––	––	––	––	
22	– +	– +	– +	––	––	––	––	– +	– +	– 3	––	Slight protocone wear
	–	–	–	–	–	–	–	–	–	–	–	
20	– ++	– ++	– ++	–– +	–––	–––	–– +	–– +	– +	– 2,3	––– 2,3	
	+	–	–	–	–	–	–	–	–	–	–	
	+	–	–	–	–	–	+	–	–	–	–	
	–	–	–	–	–	–	–	–	–	–	–	
18	– +	– +	– +	– +	–– +	––	– +	––	– +	– +	– +	+ Protocone wear developed
	–	–	–	–	–	–	–	–	–	–	–	
	+	+	+	–	–	–	–	–	3	2	–	
16	++	++	++	++	––	––	++	++	++	++		+,2
	+	+	+	+	–	–	–	–	+	+	–	
14	+	+	+	+	+	–	+	+	2	2		+
	+	+	+	+		–	+	–	+	+		+
12												

Note: Protoloph is mostly connected to metaloph; unworn crown height probably 24 mm; fossette pattern is established after about 12% wear; protocone remains isolated until at least 46% wear; maximum complexity established by 12% wear and maintained at least to 46% wear.

Key: See table 16.11 for explanation of notation.

TABLE 16.17

Comparison of Mean Protocone Dimensions of Selected Mesodont Horses

	Length					Width				Length					Width			
Tooth	Range	Mean	SD	*N*	L/W	Range	Mean	SD	*N*	Range	Mean	SD	*N*	L/W	Range	Mean	SD	*N*
	***Merychippus insignis,* Ft. Randall Formation, Late Barstovian, Nebraska**									**Merychippine, Fleming Formation, Early Barstovian, Texas**								
P2	4.1–6.3	4.8	0.6	15	0.90	2.7–5.3	4.3	0.7	15	4.4–5.2	4.7	0.71	2	0.98	4.3–5.3	4.8	0.71	2
P3	5.1–6.5	5.8	0.4	19	0.81	2.8–6.3	4.7	0.7	19	5.5–6.3	5.9	0.40	3	0.77	4.1–5.2	4.6	0.57	3
P4	5.2–6.6	6.0	0.4	21	0.78	3.0–5.2	4.7	0.6	21	5.6–6.2	6.9	0.45	3	0.76	4.1–5.0	4.5	0.45	3
M1	5.2–7.2	6.0	0.5	21	0.75	3.3–6.0	4.5	0.6	21	5.0–6.2	5.7	0.61	3	0.84	4.3–5.1	4.8	0.44	3
M2	5.2–7.3	6.2	0.5	17	0.61	2.3–4.5	3.9	0.7	17	5.8–6.0	5.9	0.14	2	0.75	4.3–4.4	4.4	0.07	2
	***Merychippus* sp., Valentine Formation, Late Barstovian, Nebraska**									***Cormohipparion goorisi,* Fleming Formation, Early Barstovian, Texas**								
P2	5.4–5.0	5.3	0.35	2	0.88	5.0–4.2	4.6	0.56	2	4.2–4.7	4.5	0.25	3	0.93	3.4–5.2	4.8	0.92	3
P3	6.3–6.3	6.3	—	2	0.68	4.9–3.6	4.3	0.92	2	5.5–5.5	5.5	—	3	0.76	3.6–4.7	4.6	0.56	3
P4	6.1–6.1	6.1	—	2	0.72	5.1–3.7	4.4	1.00	2	4.9–5.5	4.9	0.65	3	0.78	3.7–4.1	4.5	0.23	3
M1	6.0–5.8	5.9	0.14	2	0.67	4.0–4.0	4.0	—	2	6.2–6.9	6.2	0.48	4	0.65	3.2–4.8	4.8	0.80	3
M2	6.3–6.3	6.3	—	2	0.59	4.3–3.0	3.7	0.92	2	5.5–6.3	5.9	0.40	3	0.61	3.2–4.2	4.4	0.51	3

TABLE 16.18
Mean Fossette Border Complexity*

	Merychippus insignis		*Cormohipparion goorisi*	
Tooth	Posterior border prefossette	Anterior border postfossette	Posterior border prefossette	Anterior border postfossette
P2	0.88	1.21	2.67	2.00
P3	1.32	1.81	4.25	2.00
P4	1.81	2.21	5.00	3.43
M1	2.74	2.32	3.25	3.42
M2	1.81	1.87	3.40	2.88
M3	1.00	0.93	3.60	3.00

*Average number of plications of the indicated fossette border for specimens of each species within the "complexity interval" determined for each (see text). The fossette borders in *C. goorisi* are more complex overall (in most cases $\geq 2\times$ more complex) than in *M. insignis.* Number of specimens for each tooth position in *M. insignis*: $N = 26, 25, 32, 38, 27$, and 15 (P2–M3). For *C. goorisi,* $N = 3, 4, 6, 8, 10$, and 5, respectively, the distribution of data in terms of crown height suggests that comparisons would be equally distinctive of *C. goorisi,* were a greater number of specimens available.

TABLE 16.19

Measurements (mm) of Lower Cheek Tooth Dentition of *Merychippus insignis*, Echo Quarry, Olcott Formation, Early Barstovian, Nebraska

	p2		p3		p4		m1		m2		m3		Wear
	Length	Width	Length	Width	Length	Width	Length	Width	Length	Width	Length	Width	stage
F:AM 111711	20.2	10.8	19.5	12.1	20.7	11.3	20.2	11.1	21.2	9.7	—	—	I
F:AM 87074	19.1	—	19.7	11.4	19.6	11.8	18.9	11.1	19.0	—	20.4	7.3	I
F:AM 87076	21.0	10.5	20.3	11.7	19.0	11.0	19.8	9.4	20.7	8.7	—	—	I
F:AM 111781	21.8	11.5	21.7	13.0	21.2	13.0	19.0	10.8	—	—	—	—	II
F:AM 111793	21.3	11.8	21.0	12.7	21.6	13.1	18.7	10.1	21.0	9.8	—	—	II
F:AM 111791	—	—	20.1	11.2	20.1	11.5	21.1	10.3	20.2	9.5	—	—	II
F:AM 112061	21.1	11.4	20.0	12.5	18.8	12.2	19.2	10.4	20.1	9.0	—	—	II
F:AM 87072	21.5	11.1	20.7	12.2	20.2	12.7	18.7	9.8	19.5	9.4	—	—	II
F:AM 112062	—	—	21.3	11.1	20.9	10.7	19.2	8.5	19.7	8.9	—	—	II
F:AM 111794	22.0	11.5	21.6	13.1	20.7	12.5	19.3	10.0	19.1	9.3	—	—	II
F:AM 111774	21.7	10.5	20.5	12.7	20.5	11.2	19.7	10.2	20.2	9.1	—	—	II
F:AM 111780	—	—	20.2	12.2	20.0	12.5	19.0	12.1	19.2	9.0	—	—	II
F:AM 111792	—	—	19.4	10.7	18.7	11.5	20.5	10.0	20.5	8.5	—	—	II
F:AM 87075	—	—	19.3	12.5	19.0	12.2	17.2	10.8	18.3	9.3	20.2	8.3	II
F:AM 112070	21.9	11.6	20.6	12.4	20.7	12.7	19.4	11.2*	20.0	9.4	21.0	7.4	III
F:AM 87078	21.5	11.9	20.3	12.5*	20.8	12.4*	17.9	11.2*	18.4	10.2*	22.1	9.5	III
F:AM 112064	18.9	11.7	18.7	12.7*	19.4	13.4*	17.7	12.5*	18.4	11.4*	20.3	9.6	III
F:AM 112066	22.2	12.2	18.3	13.5*	20.0	13.8*	18.0	12.2*	18.6	11.0*	20.1	8.7	III
F:AM 112063	21.2	11.0	19.3	12.3*	18.7	13.0*	18.3	11.3	18.0	10.2*	19.8	8.9	III
F:AM 87087	19.5	10.6	18.1	13.7*	18.7	13.6*	17.0	12.2*	17.8	11.2*	21.5	9.3	IV
F:AM 111757	19.4	10.9	17.5	12.0*	17.1	11.2*	16.0	9.9*	17.7	9.5*	20.3	7.5	V
F:AM 111760	—	—	19.2	11.6*	19.9	11.1*	17.5	9.6*	17.4	—*	21.1	8.6	V
F:AM 111761	—	—	17.3	14.3*	17.7	13.1*	16.2	12.5*	15.9	9.7*	21.1	8.5	V
F:AM 111759	—	—	18.7	13.3*	18.6	12.4*	17.0	10.8*	18.4	9.5*	23.2	10.3	V
F:AM 111767	—	—	18.4	12.4*	18.5	11.8*	16.9	10.2*	17.9	9.8*	22.4	8.2	V
F:AM 87075	18.8	12.5	17.8	13.6*	17.8	12.5*	15.9	11.5*	16.8	10.9*	20.9	9.5	V
F:AM 111750	20.5	12.5	19.4	12.1*	20.0	10.8*	18.0	9.8*	19.0	9.5*	23.0	10.4	V
F:AM 87088	20.3	12.3	18.4	13.7*	17.1	12.8*	15.6	11.9*	16.3	11.0*	22.1	9.5*	V
F:AM 111754	21.6	12.4	19.0	13.5*	18.1	14.0*	15.6	12.5*	17.4	10.7*	22.1	9.3	V
Range	22.2–18.8	21.7–10.5	21.7–18.1	14.3–10.7	21.6–17.1	14.0–10.7	21.1–15.6	12.5–8.5	21.2–15.9	11.4–8.5	23.2–19.8	10.4–7.3	
Mean	20.8	11.5	19.5	12.5	19.5	12.3	18.2	10.8	18.8	9.8	21.3	8.9	
SD	1.10	0.68	1.20	0.87	1.23	0.93	1.51	1.05	1.40	0.81	1.05	0.94	
CV	5.34	5.91	6.13	6.93	6.32	7.57	8.23	9.74	7.43	8.29	4.94	10.54	
N	20	19	29	29	29	29	29	29	28	26	17	17	

Note: * indicates presence of protostylid; in this case from p3–m2 in wear stage III and later.

TABLE 16.20

Measurement (mm) of the Cranium of *Cormohipparion goorisi*, Trinity River Pit 1, Fleming Formation, Early Barstovian, Texas

	Characters											
	1	2	3	4	5	6	7	8	9	12	13	14
F:AM 73940♂	76.6	85.2	78.3	71.8	139.0	294.8	62.5	53.5	111.8	—	45.7	21.6
F:AM 73941*	51.8a	61.6	61.1	—	—	—	—	—	—	24.1	37.3	13.2
F:AM 73942	—	82.5	—	72.7	—	—	65.5	52.6	117.8	—	—	—
F:AM 73943	—	—	—	—	—	—	64.2	57.0	118.5	—	—	—
F:AM 73952♂	79.8	—	—	—	—	—	67.1	59.6	123.0	—	—	—
Range	76.6–79.8	82.5–95.2	78.3	71.8–72.7	139.0	294.8	62.5–67.1	52.6–59.6	111.8–123.0		45.7	21.6
Mean	78.2	83.9	78.3	72.3	139.0	294.8	64.8	55.7	117.8		45.7	21.6
SD	2.26	1.91		0.64			1.95	3.23	4.60			
CV	2.89	2.28		0.88			3.01	5.81	3.91			
N	2	2	1	2	1	1	4	4	4		1	1

	Characters											
	15	18	19	20	21	22	23	24	25	28	29	30
F:AM 73940♂	35.9	70.3	101.4	—	64.0	47.4	225.0	124.6	38.0	47.8	45.6	65.0a
F:AM 73941*	25.3	79.2cr	—	—	—	—	—	—	30.2	—	—	52.1
F:AM 73942	—	—	—	—	—	—	—	—	—	—	—	—
F:AM 73943	—	—	—	—	—	—	—	—	—	—	—	—
F:AM 73952♂	—	—	—	—	—	—	—	—	—	—	—	—
Range	35.9	70.3	101.4		64.0	47.4	225.0	124.6	38.0	47.8	45.6	65.0a
Mean	35.9	70.3	101.4		64.0	47.4	225.0	124.6	38.0	47.8	45.6	65.0a
SD												
CV												
N	1	1	1		1	1	1	1	1	1	1	1

(continued)

TABLE 16.20
Continued

	Characters									
	31	32	33	34	35	36	37	38	39	40
F:AM 73940♂	128.0a	21.9	51.6a	41.3a	31.6	21.6	30.9	48.2	0	23.0a
F:AM 73941*	96.8	18.1	42.7	30.0	31.0	17.0	21.0	33.8	0	13.0a
F:AM 73942	—	—	—	—	—	—	33.3	—	—	—
F:AM 73943	—	—	—	—	—	—	33.7	—	—	—
F:AM 73952♂	—	—	—	—	—	—	—	—	0	—
Range	128.0a	21.9–30.0	45.0–51.6	36.0–41.3	26.0–31.6	21.3–21.6	30.9–33.7	48.2	0	23.0a
Mean	128.0a	26.0	48.3	38.7	28.8	21.5	32.6	48.2	0	23.0a
SD		5.27	4.67	3.75	4.00	0.21	1.51			
CV		22.07	9.66	9.70	13.75	1.00	4.64			
N	1	2	2	2	2	2	3	1	2	1

	Wear class	Remarks
F:AM 73940	III; M3 beginning wear	Slightly skewed transversely; DPOF with strong anterior rim, pocketed posteriorly medial to anterior end of orbit
F:AM 73941*	I; dP2–4 in place	Juvenile; dorsoventral flattening; DPOF with strong anterior rim, pocketed posteriorly medial to anterior end of orbit; dp4 mesostyle height is 13.0
F:AM 73942	III; M3 beginning wear	Transversely skewed, extensively crushed; DPOF with strong anterior rim; pocketed posteriorly
F:AM 73943	III; M3 beginning wear	Transversely crushed; dorsal snout above DPOF separated from ventral part; DPOF pocketed posteriorly
F:AM 73952	III; M3 beginning wear	Dorsoventrally crushed; DPOF pocketed posteriorly

Note: Conventions for characters as in table 16.4; cr = crushed.

*F:AM 73941, a juvenile specimen, was not included in the statistical analyses. Characters 1 and 2 were measured to dP2; character 13 was measured to dP4.

TABLE 16.21

Measurements (mm) of Upper Cheek Tooth Dentition of *Cormohipparion goorisi*, Trinity River Pit 1, Fleming Formation, Early Barstovian, Texas

				Protocone					Protocone					Protocone	
	Height	Length	Width	Length	Width	Height	Length	Width	Length	Width	Height	Length	Width	Length	Width
	P2					P3					P4				
F:AM 73940♂	24.2	23.3	16.7	4.2	3.4	24.8	20.3	18.3	5.5	3.6	27.5	19.7	19.3	5.2	3.7
F:AM 73943♀	20.5	24.4	16.6	4.5	4.0	23.0a	21.0	20.0	5.5	4.3	21.0a	20.1	21.1	5.5	3.7
F:AM 73944	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
F:AM 73942♀	17.7	23.8	18.4	4.7	5.2	23.0a	21.5	20.7	5.5	4.7	24.0a	21.5	20.8	4.9	4.1
F:AM 109875	22.0a	—	—	—	—	29.0	—	—	—	—	—	—	—	—	—
F:AM 109886	—	—	—	—	—	14.8a	19.8	17.3	—	—	16.0a	19.2	20.2	5.8	4.9
F:AM 109887	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
F:AM 109889	—	—	—	—	—	—	—	—	—	—	14.3	18.5	20.1	6.1	4.4
F:AM 109890	—	—	—	—	—	—	—	—	—	—	23.4	21.5	22.2	7.7	4.2
F:AM 73952♂	18.0	25.0	19.8	5.1	4.0	22.5	21.6	21.7	7.2	4.3	27.0a	21.0	22.7	7.1	4.1
Range		25.0–23.3	19.8–16.6	5.1–4.2	5.2–3.4		21.6–19.8	21.7–17.3	7.2–5.5	4.7–3.6		21.5–18.5	22.7–19.3	7.7–7.1	4.9–3.7
Mean		24.1	17.9	4.6	4.2		20.8	19.6	5.9	4.2		20.2	20.9	6.0	4.2
SD		0.74	1.53	0.38	0.76		0.78	1.79	0.85	0.46		1.67	1.20	1.02	0.41
CV		3.05	8.54	8.16	18.19		3.73	9.11	14.35	10.83		5.77	5.75	16.87	10.00
N		4	4	4	4		5	5	4	4		7	7	7	7
	M1					M2					M3				
F:AM 73940♂	23.0a	17.3	18.7	5.8	3.2	24.0a	18.8	16.8	5.5	3.2	26.0a	17.3	—	—	—
F:AM 73943♀	20.0a	18.8	19.2	6.2	4.8	22.0a	19.3	20.0	6.1	4.2	25.4	19.3	16.5	6.0	—
F:AM 73944	29.0	20.0	16.0	—	—	29.0	—	—	—	—	—	—	—	—	—
F:AM 73942♀	21.0a	18.5	21.7	6.9	4.1	23.0a	19.4	21.0	6.3	3.5	24.0a	18.1	16.2	5.4	—
F:AM 109875	33.0	22.0	17.7	—	—	—	—	—	—	—	—	—	—	—	—
F:AM 109886	15.0a	18.5	19.7	6.1	4.8	17.0a	18.3	19.8	6.5	4.1	18.0a	18.5	17.3	5.7	—
F:AM 109887	11.0	17.8	21.7	—	—	14.5	17.4	20.1	6.5	4.5	16.0	17.3	17.0	3.7	—
F:AM 109889	11.2	16.4	19.2	5.8	4.9	13.3	17.0	19.0	6.4	4.8	—	—	—	—	—
F:AM 109890	21.0a	19.3	20.9	7.1	4.2	22.0a	20.1	19.0	6.4	3.1	—	—	—	—	—
F:AM 73952♂	22.0a	19.2	21.8	6.8	4.4	21.0a	20.1	18.8	6.4	3.5	21.0a	19.8	16.1	—	—
Range		22.0–16.4	21.8–16.0	7.1–5.8	4.9–3.2		20.1–17.0	21.0–16.8	6.5–5.5	4.5–3.1		19.8–17.3	17.3–16.1	6.0–3.7	
Mean		18.8	19.7	6.4	4.3		18.8	19.3	6.3	3.9		18.4	16.6	5.2	
SD		1.54	1.92	0.54	0.59		1.16	1.25	0.33	0.63		1.03	0.52	1.03	
CV		8.19	9.74	8.45	13.68		6.18	6.48	5.33	16.19		5.59	3.11	19.80	
N		10	10	8	7		8	8	8	8		6	5	4	

Note: Height is at mesostyle; a = approximate.

TABLE 16.22

Elements of Dental Pattern Relative to Crown Height, *Cormohipparion goorisi*, Trinity River Pit 1, Fleming Fm., Early Barstovian, Texas: P2

Ht (mm)	Protoloph-metaloph	Pre-fossette	Post-fossette	Hypocone opens	Hypoconal grv plicat	Protocone opens	Pli caballin	Pli protoloph	Pli prefossette	Pli postfossette	Pli hypostyle	
26												
24	–	–	–	+	–	–	–	–	–	–	–	Fossette pattern established; proto- + hypocone fully exposed
22												
20	–	+	+	+	+	–	+	+	4	3	2	↑ Complexity interval
18	–	+	+	+	2	–	2	+	2	3	+	
	–	+	+	+	–	–	–	–	2	–	–	Protocone still isolated
16												
14												

Note: Unworn crown height likely at least 26 mm tall; protoloph connected to metaloph only after about 30% wear; fossette pattern established by at least 19% wear; protocone still isolated at about 33% wear.

Key: See table 16.11 for explanation of notation.

TABLE 16.23

Elements of Dental Pattern Relative to Crown Height, *Cormohipparion goorisi*, Trinity River Pit 1, Fleming Fm., Early Barstovian, Texas: P3

Ht (mm)	Protoloph-metaloph	Pre-fossette	Post-fossette	Hypocone opens	Hypoconal grv plicat	Protocone opens	Pli caballin	Pli protoloph	Pli prefossette	Pli postfossette	Pli hypostyle	
26												
	–	+	+	+	–	–	+	+	–	2	2	Wear pattern nearly stabilized
24												
	– +	++	++	++	– +	– –	++	2,2	4,5	+,3	++	
22	+	+	+	+	+	–	2	+	6	3	2	
20												Complexity interval
18												
16												Protocone still isolated
	+	+	+	+	–	+	+	+	2	+	–	Protocone conn. to metaloph
14												

Note: Unworn crown height probably at least 27 mm; pattern nearly established after 15% wear; protocone connects to protoloph at about 45% wear.
Key: See table 16.11 for explanation of notation.

TABLE 16.24

Elements of Dental Pattern Relative to Crown Height, *Cormohipparion goorisi*, Trinity River Pit 1, Fleming Fm., Early Barstovian, Texas: P4

Ht (mm)	Protoloph-metaloph	Pre-fossette	Post-fossette	Hypocone opens	Hypoconal grv plicat	Protocone opens	Pli caballin	Pli protoloph	Pli prefossette	Pli postfossette	Pli hypostyle	
28												Pattern complex
	+	+	+	+	–	–	+	+	2	5	+	
	+	+	+	+	+	–	2	+	5	4	+	
26												
24	+	+	+	+	+	–	+	+	6	3	+	
	+	+	+	+	+	–	2	+	5	4	+	Complexity interval
22												
	+	+	+	+	+	–	+	2	6	3	+	
20												
18												
												Protocone open, pattern still
16	+	+	+	+	–	+	+	–	4	+	+	complex
14	+	+	+	+	–	–	2	+	4	4	+	Protocone isolated, pattern still complex
12												

Note: Unworn crown height likely at least 34 mm; pattern established and complex by 20% wear; protocone connected to protoloph but pattern still complex at 53% wear; protocone also remains isolated with complex pattern at 59% wear.

Key: See table 16.11 for explanation of notation.

TABLE 16.25

Elements of Dental Pattern Relative to Crown Height, *Cormohipparion goorisi*, Trinity River Pit 1, Fleming Fm., Early Barstovian, Texas: M1

Ht (mm)	Protoloph-metaloph	Pre-fossette	Post-fossette	Hypocone opens	Hypoconal grv plicat	Protocone opens	Pli caballin	Pli protoloph	Pli prefossette	Pli postfossette	Pli hypostyle	
34												
	–	–	–	–	–	–	–	–	–	–	–	Slight wear on protocone and ectoloph
32												
30												
	–	–	–	–	–	–	–	–	–	–	–	Very early wear on protocone and ectoloph
28												
26												
24												Pattern complex at least by now
	+	+	+	+	–	–	2	–	6	6	+	
22	+	+	+	+	–	–	+	+	2	4	+	
	++	++	++	++	–	+ ––	++	–	+ 4,4	3,4	++	
20	+	+	+	+	–	–	2	–	6	4	2	
18												
16												
	+	+	+	+	–	+	–	–	2	–	–	Protocone now conn. to protoloph
14												
12												
	++	++	++	++	––	++	++	––	2,4	+,2	– +	Pattern still complex
10												

Note: Unworn height likely at least 34 mm; pattern established at least by 32% wear; protocone opens to protoloph at about 56% wear; pattern still complex to at least 68% wear.
Key: See table 16.11 for explanation of notation.

TABLE 16.26

Elements of Dental Pattern Relative to Crown Height, *Cormohipparion goorisi*, Trinity River Pit 1, Fleming Fm., Early Barstovian, Texas: M2

Ht (mm)	Protoloph-metaloph	Pre-fossette	Post-fossette	Hypocone opens	Hypoconal grv plicat	Protocone opens	Pli caballin	Pli protoloph	Pli prefossette	Pli postfossette	Pli hypostyle	
30												
	–	–	–	–	–	–	–	–	–	–	–	Very early wear on protocone
28												
26												Pattern complex at least by now
24	+	+	+	+	+	–	+	2	3	4	+	
22	++	++	++	++	–	+	––	++	++	4,4,4	2,4	++
	++	++	++	++	––		––	1,2	++	3,4,4	4,4	++
20												
18												
	+	+	+	+	–		–	+	– 3	2	+	
16												
	+	+	+	+	+	–	+	+	3	2	+	
14												Pattern still complex
	+	+	+	+	–		–	+	+	3	2	+
12												

Note: Unworn crown height at least 30 mm; pattern established at least by 20% wear; protocone still isolated and pattern still complex at 57% wear.
Key: See table 16.11 for explanation of notation.

TABLE 16.27

Elements of Dental Pattern Relative to Crown Height, *Cormohipparion goorisi*, Trinity River Pit 1, Fleming Fm., Early Barstovian, Texas: M3

Ht (mm)	Protoloph-metaloph	Pre-fossette	Post-fossette	Hypocone opens	Hypoconal grv plicat	Protocone opens	Pli caballin	Pli protoloph	Pli prefossette	Pli postfossette	Pli hypostyle	
28												
26	–	–	–	–	–	–	–	–	–	–	–	
	+	+	+	–	–	–	–	+	5	4	–	Unworn Protocone breached, hypocone not
24	+	–	–	–	–	–	–	–	–	–	–	
22												Pattern complex at least by this point
	+	+	+	–	–	–	+	–	5	4	–	
20												
18	+	+	+	+	+	–	+	–	4	4	+	
16	+	+	+	+	+	–	+	+	4	3	+	Protocone still isolated, pattern still complex

Note: Unworn crown height about 26 mm; pattern established at least by 4% wear; protocone still isolated at 38% wear.
Key: See table 16.11 for explanation of notation.

TABLE 16.28

Measurements (mm) of Lower Cheek Tooth Dentition of *Cormohipparion goorisi*, Trinity River Pit 1, Fleming Formation, Early Barstovian, Texas

	p2			p3			p4			Wear
	Height	Length	Width	Height	Length	Width	Height	Length	Width	stage
F:AM 73948	13.0+	20.6	11.5	11.9	19.5	13.8	11.8	20.3	13.3	II
F:AM 73949	2.5	18.6	11.4	11.3	17.6	12.8	11.6	17.7	13.0*	III
F:AM 113064	—	20.1	10.8	—	19.6	11.6	—	19.2	11.8	—
F:AM 113058	—	—	—	—	18.7	15.0	—	18.8	16.3*	V
F:AM 113063	—	19.3	13.3	—	18.0	13.9*	—	18.0	12.4*	VI
F:AM 113068	—	19.6	11.0	—	17.5	13.5*	—	18.0	14.4	VII
Range		18.6–20.6	10.8–13.3		17.5–19.6	11.6–13.9		17.7–20.3	11.8–16.3	
Mean		19.6	11.6		18.5	13.4		18.7	13.5	
SD		0.76	0.99		0.93	1.15		0.98	1.61	
CV		3.89	8.56		5.02	8.54		5.25	11.93	
N		5	5		6	6		6	6	
	m1			m2			m3			Wear
	Height	Length	Width	Height	Length	Width	Height	Length	Width	stage
F:AM 73948	12.5	17.0	12.2*	12.7	19.1	10.5	10.4	27.0	9.8	II
F:AM 73949	11.5	17.0	11.4*	—	17.5	10.2	—	18.9	9.2	III
F:AM 113064	—	17.8	9.8	—	18.1	10.0	—	22.2	9.1	—
F:AM 113058	—	17.1	13.8*	—	18.9	13.0	—	21.0	12.0	V
F:AM 113063	—	16.1	12.0*	—	17.1	10.6	—	19.7	9.0	VI
F:AM 113068	—	15.7	12.3*	—	17.4	10.7*	—	20.0	9.3	VII
Range		15.7–17.8	9.8–13.8		17.1–19.1	10.0–13.0		18.9–27.0	9.0–12.0	
Mean		16.8	11.9		18.0	10.8		21.5	9.7	
SD		0.76	1.31		0.83	1.10		2.94	1.15	
CV		4.51	10.96		4.61	10.19		13.70	11.72	
N		6	6		6	6		6	6	

Note: * indicates presence of protostylid; here found in p3–m2.