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AN UNUSUALLY DIVERSE NORTHERN BIOTA FROM THE MORRISON FORMATION (UPPER JURASSIC), BLACK HILLS, WYOMING

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Theme Issue

An Ecosystem We Thought We Knew—

The Emerging Complexities of the Morrison Formation

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Cover

A few of the elements from the Little Houston Quarry biota represented by individual fossils. Left to right and by approximate row top to bottom: ***Nanosaurus*** *femur; seed; dromaeosaurid tooth; unionid bivalve shell imprint; salamander vertebra;* ***Nanosaurus*** *tooth;* ***Docodon*** *jaw;* ***Theriosuchus*** *jaw; abelisauroid(?) tooth; and* ***Cteniogenys*** *jaw.*

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An Unusually Diverse Northern Biota from the Morrison Formation (Upper Jurassic), Black Hills, Wyoming

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ABSTRACT

The Little Houston Quarry in the Black Hills of Wyoming contains the most diverse vertebrate fauna in the Morrison Formation (Upper Jurassic) north of Como Bluff and the second-most diverse in the entire formation, after Reed's Quarry 9. The deposit was an occasionally reactivated abandoned river channel, in interbedded green mudstone and laminated green-gray siltstone above a channel sandstone. The dinosaur material is densely distributed and is disarticulated to articulated, with several associated skeletons. The biota contains charophytes, horsetails, a possible seed fern, possible conifers, gastropods, two types of unionoid bivalves, diplostracans ("conchostracans"), a malacostracan, ray-finned fish, lungfish, a frog, salamanders, two types of turtles, rhynchocephalians, a lizard, choristoderes, two types of crocodyliforms, a pterosaur, *Allosaurus* and several types of small theropods including *Tanycolagreus*? and probable dromaeosaurids, numerous *Camarasaurus* and a diplodocine sauropod, a stegosaur, the neornithischian *Nanosaurus*, and the mammals *Docodon*, *Amblotherium*, and a multituberculate. Among these taxa, one of the unionoid bivalves, an atoposaurid crocodyliform, and the species of *Amblotherium*, which appear to be new and unique to the locality so far. The *Docodon* material may represent the first occurrence of *D. apoxys* outside of its type area in Colorado. Additionally, small, unusual theropod tooth types reported here may represent the first Late Jurassic occurrence of cf. *Richardoestesia* in North America and a possible abelisauroid, respectively.

INTRODUCTION

The Morrison Formation (Upper Jurassic) has been known as a massively productive unit for large dinosaurs since the second half of the nineteenth century (Dodson and others, 1980; Ostrom and McIntosh, 1999). Microvertebrate taxa were identified in the formation relatively early on (Marsh, 1879; Gilmore, 1910, 1928) but large samples of such taxa were restricted to only a handful of sites until relatively recently. Work from the past few years has suggested that microvertebrate taxa, and specifically aquatic and semi-aquatic taxa, may be more abundant in the formation than commonly appreciated (Foster and Trujillo, 2004; Foster and Heckert, 2011; Foster and McMullen, 2017) and that the Morrison may show some paleobiogeographic zonation based on these small taxa and their preferred environments for habitat and preservation (Chure and Evans, 1998; Foster and Trujillo, 2000; Foster and others, 2006; Foster and McMullen, 2017). Paleobiogeo-

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graphic zonation is also becoming apparent for some groups of dinosaurs within the Morrison.

The Black Hills have yielded Morrison Formation taxa since O.C. Marsh (1890a) described the first specimen of *Barosaurus*, which had been partially collected by Marsh with J.B. Hatcher in 1889 (Marsh sent G.R. Wieland to collect more of the specimen in 1898). Smithsonian (USNM) and American Museum (AMNH) crews collected diplodocid and camarasaurid specimens from the Sturgis, South Dakota, area around 1900–1901, and the South Dakota School of Mines and Technology (SDSM) collected mostly sauropod material from sites near Spearfish and Blackhawk, South Dakota, and adjacent to Inyan Kara Creek in Wyoming, although theropods, turtles, and crocodyliforms were found at some sites (Foster, 1996a, 1996b; Foster and Chure, 2000). More than a dozen vertebrate localities are now known from the Black Hills (Foster, 1992, 1996a, 1996b, 2003; Maltese and others, 2018), and the most productive of these so far is the Little Houston Quarry, west of Sundance in Crook County, Wyoming (figure 1; Foster, 1993, 2001; Foster and Martin, 1994). The Little Houston Quarry was first developed in June 1991 and was worked annually through 2000 by the SDSM and from 2004–2011 by SDSM and the Museums of Western Colorado. The most diverse fauna of vertebrates known from the northern part of the Morrison Formation is found in the Little Houston Quarry. This paper describes the richness of that fauna and several unique taxa from it that may be endemic to northern parts of the formation minimally and possibly to the Black Hills specifically.

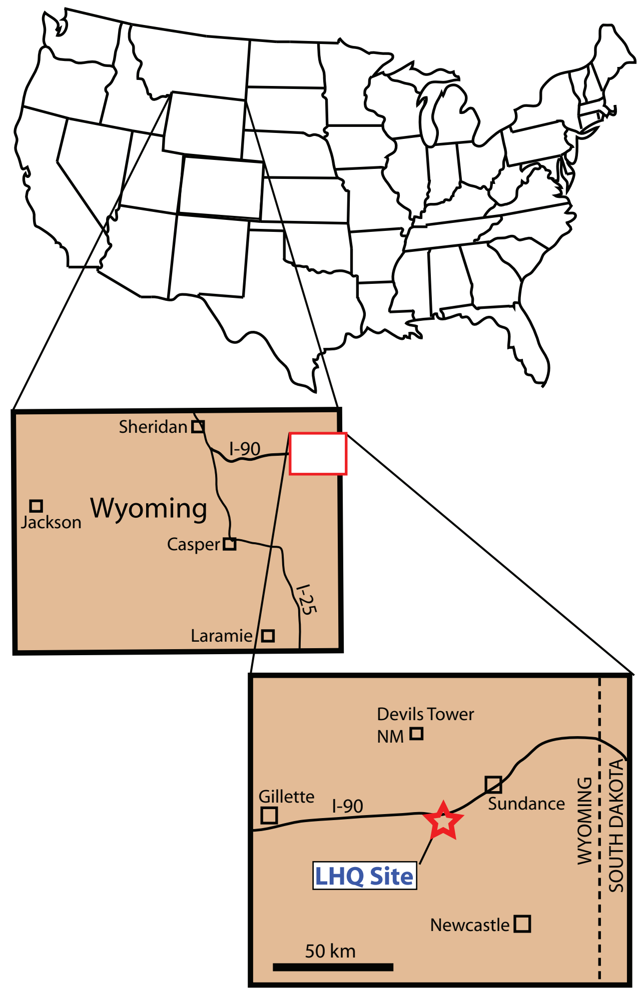

Figure 1. Location of the Little Houston Quarry (red star) on the northwestern edge of the Black Hills in Crook County, northeastern Wyoming, and within the United States.

INSTITUTIONAL ABBREVIATIONS

AMNH–American Museum of Natural History, New York, New York; FMNH–Field Museum of Natural History, Chicago, Illinois; MWC–Museums of Western Colorado, Dinosaur Journey, Fruita, Colorado; SDSM–South Dakota School of Mines and Technology, Museum of Geology, Rapid City, South Dakota; USNM–National Museum of Natural History, Smithsonian Institution, Washington, D.C.; EBG–Field numbers of Darrin Pagnac for 1996–2000 field seasons, uncatalogued material at SDSM; JRF–Field numbers of John Foster for 1991–2000 field seasons, uncatalogued material at SDSM.

GEOLOGIC SETTING AND LOCALITY

The Morrison Formation in the northwestern Black Hills is unusually thin (~24 m; Mapel and Pillmore, 1963) compared to most outcrops of the unit farther south and west, and it consists of red, gray, and green, non-smectitic mudstones (Tank, 1956) with only a few thin, lenticular and laterally restricted sandstone beds (Foster, 1992; Turner and Peterson, 1999). In the eastern and southeastern Black Hills the lower member of the formation consists of an eolian sandstone (the Unkpapa Sandstone Member; Szigeti and Fox, 1981) that is overlain by an unnamed light gray to green silty mudstone facies that probably represents wet environments bordering the Unkpapa dune field to the south. Most of the fossil sites in the Morrison of the eastern and southeastern Black Hills occur in this latter facies (Foster, 1996b). In the northwestern Black Hills, the red, gray, and green mudstones have a more "traditional" appearance for the Morrison Formation, aside from the overall thinness, the lack of smectitic mudstones, and the very thin and restricted channel sandstones (Foster, 1992; Foster and Martin, 1994).

The Little Houston Quarry consists of two pits, the main and mammal (figures 2A, 3A, and 3B), in the same abandoned channel deposit, separated laterally by approximately 70 m but easily correlated visually, as the channel cut down into variegated mudstones exposed on either side (Foster and Martin, 1994). The matrix of the quarry is an interbedded interval of green claystone and thinly laminated siltstone with abundant bone fragments and clayballs (figure 2B), which rests immediately above a thin, convex-bottomed channel sandstone. Laterally, the deposit matrix and the bone material are

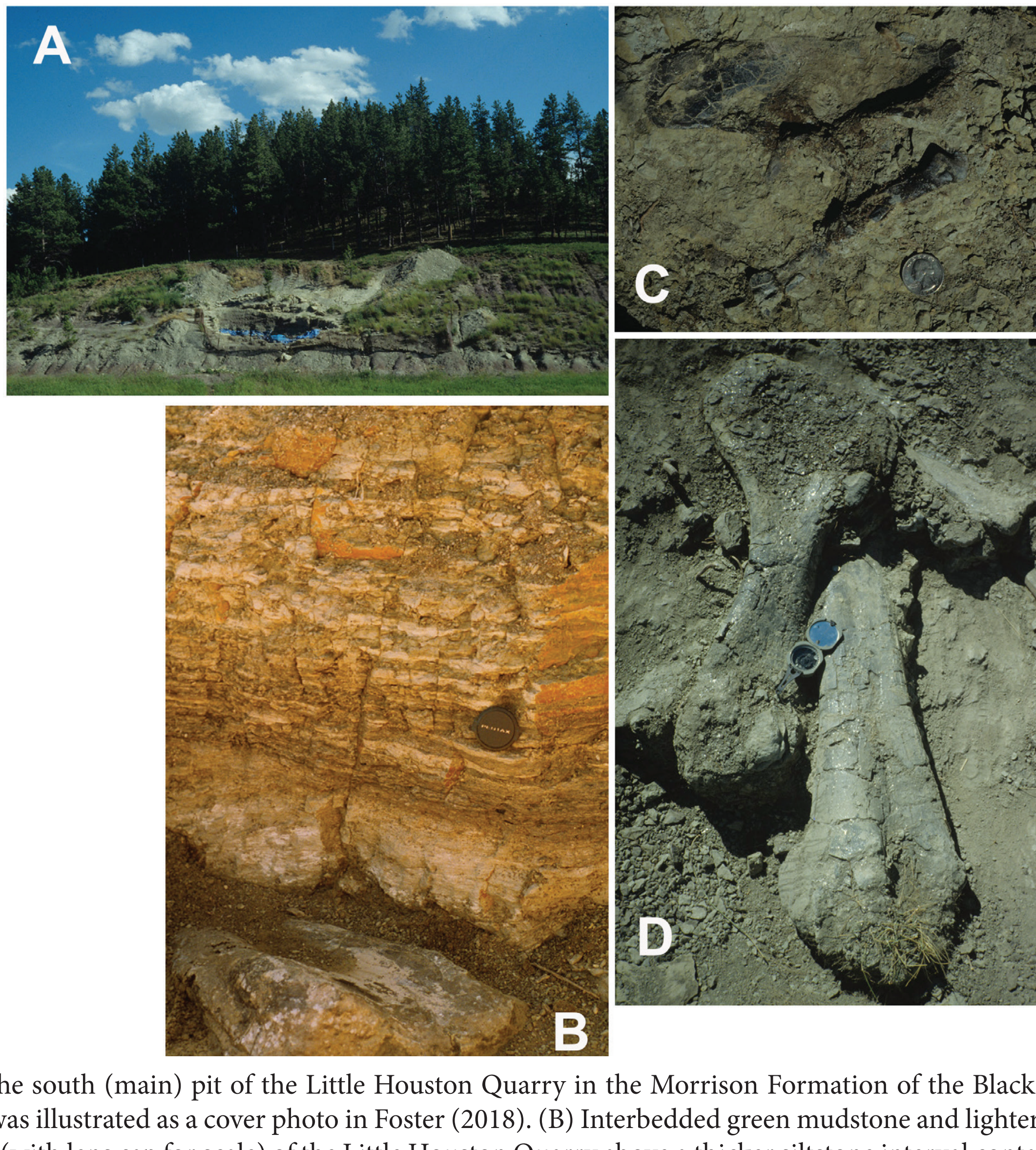

Figure 2. (A) The south (main) pit of the Little Houston Quarry in the Morrison Formation of the Black Hills. The north (mammal) pit was illustrated as a cover photo in Foster (2018). (B) Interbedded green mudstone and lighter green-gray laminated siltstone (with lens cap for scale) of the Little Houston Quarry above a thicker siltstone interval containing a sauropod humerus. (C) Ilium and metatarsal of an associated juvenile *Allosaurus jimmadseni* skeleton (see Foster and Chure, 2006) at the Little Houston Quarry. U.S. quarter for scale. (D) Left humerus of *Camarasaurus* and femur of diplodocine(?) at the Little Houston Quarry, Brunton indicating north.

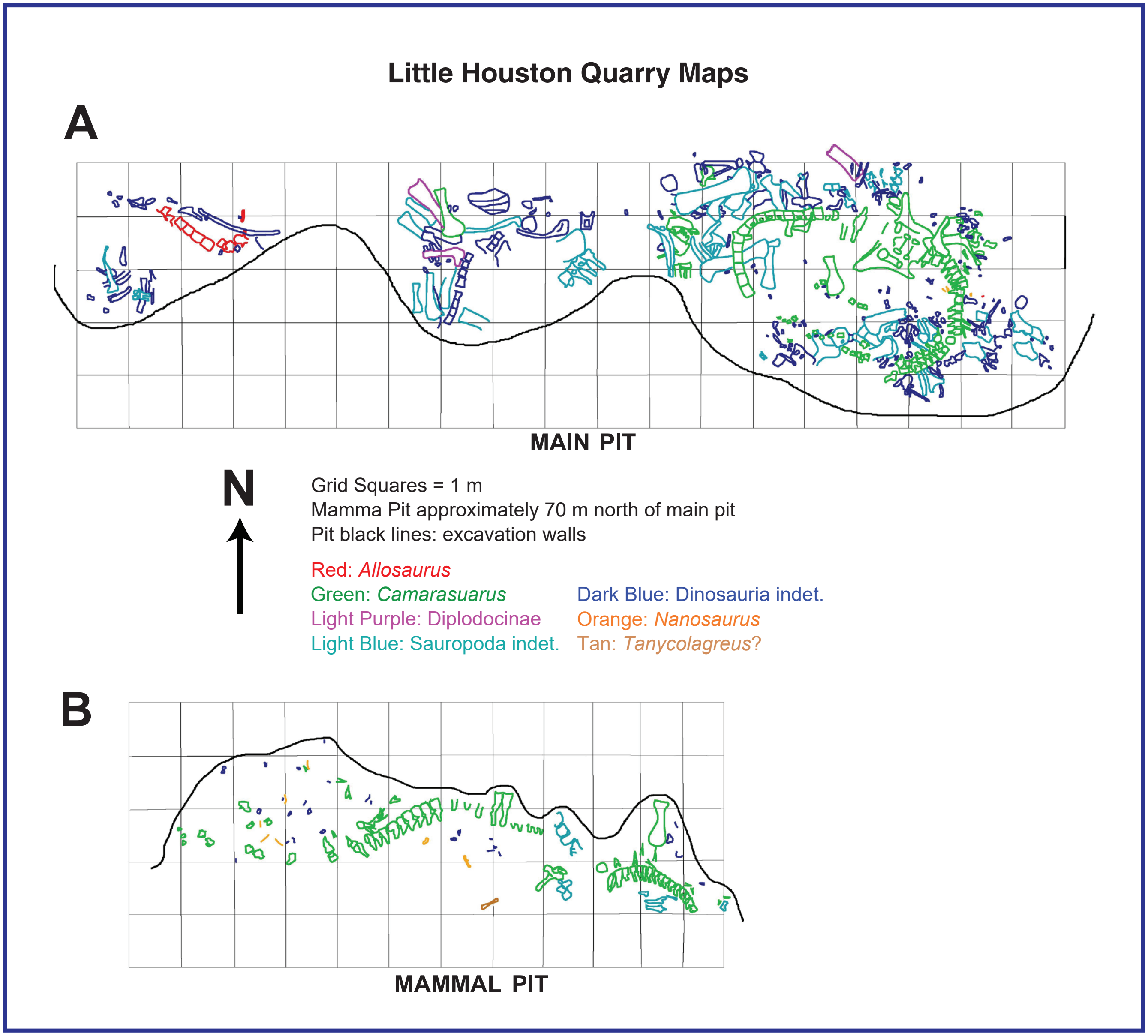

Figure 3. Quarry maps of the Little Houston Quarry. (A) Map of main pit. (B) Map of mammal pit. Each map grid square = 1 m.

restricted to the layers above the channel, which is up to 20 m wide. Dinosaur material at the site is largely associated to articulated (figures 2C and 2D), with a significant number of isolated elements as well. Microvertebrate material is mixed in with the same layers as the articulated dinosaur elements, often concentrated in two 1- to 10-cm-thick layers separated vertically by 15 to 30 cm within the interbedded mudstone and laminated siltstone above the channel sandstone.

Dinosaur material in the quarry is abundant and densely concentrated, with up to 25% of material in articulation (figures 3A and 3B; for articulation percent comparison with other localities see Foster and others, 2018). *Camarasaurus* elements are particularly abundant, with sections of at least four adult individuals in articulation.

MATERIAL AND METHODS

Fossil material was collected from the Little Houston Quarry each summer continuously from 1991 to 2000 and again from 2004 to 2011, principally by the SDSM's Museum of Geology but also by the MWC (Foster, 1992, 1993, 1996a, 1996b, 2001, 2018; Foster and Martin, 1994; Martin and Foster, 1998; Pagnac, 1998; Foster and Trujillo, 2000, 2018; Foster and others, 2018). The biota consists of at least 35 taxa, including four plants, five invertebrates, and 26 vertebrates (table 1). Foster (2001) assessed the relative abundances and taphonomy of taxa found through the 2000 field season, but the full biota has never been described or illustrated in detail.

Specimens were compared to existing museum collections and published illustrations of other material. Theropod tooth terminology used in tooth descriptions incorporates terms of Hendrickx and others (2015) whereas that for mammals utilizes those of Kielan-Jaworowska and others (2004). Cladistic analysis utilized Mesquite 3.0 and TNT 1.5.

Table 1. Biota list of taxa known from the Little Houston Quarry, Morrison Formation, Crook County, Wyoming.

- PLANTAE
  - **Chlorophyta**
    - Charophyta indet.
  - **Polypodiopsida**
    - Equisetales
      - *Equisetum* sp.
  - **Polysporangiophytes**
    - Tracheophytes
      - Pteridospermatophyta?
  - **Gymnosperma? Indet.**
- METAZOA
  - **Mollusca**
    - Gastropoda
      - *Amplovalvata* sp.
    - Bivalvia
      - Unionidae indet. ("*Unio*" *stewardi*?)
      - Unionida indet., new genus?
  - **Arthropoda**
    - Malacostraca?
      - Crayfish?
    - Diplostraca
      - "conchostracans"
  - **Chordata**
    - **Osteichthyes**
      - Actinopterygii
        - Actinopterygii indet. Scale type A
        - Actinopterygii indet. Scale type B
        - Actinopterygii indet. Scale type C
      - Sarcopterygii
        - Dipnoi
          - *Ceratodus fossanovum*
    - **Amphibia**
      - Anura indet.
      - Caudata indet.
    - **Reptilia**
      - Testudinata
        - *Dinochelys whitei*
        - *Glyptops plicatulus*
        - Testudinata indet.
      - Rhynchocephalia
        - *Opisthias*?
      - Squamata
        - cf. *Paramacellodus*
      - Archosauria
        - Choristodera
          - *Cteniogenys antiquus*
        - Crocodylomorpha
          - Crocodyliformes
            - Atoposauridae
              - *Theriosuchus morrisonensis*
            - Goniopholididae? indet.
          - Crocodyliformes indet.
        - Archosauria indet.
        - Pterosauria
          - Pterosauria indet.
        - Dinosauria
          - Saurischia
            - Theropoda
              - Tetanurae
                - Allosauroidea
                  - *Allosaurus jimmadseni*
                - Coelurosauria
                  - *Tanycolagreus*?
                  - Dromaeosauridae indet.
            - Theropoda Indet.
              - Tooth type A (cf. *Richardoestesia*?)
              - Tooth type B
              - Tooth type C
              - Tooth type D (abelisauroid?)
              - Tooth type E
            - Sauropoda
              - Diplodocidae
                - Diplodocinae indet.
              - Macronaria
                - Camarasauridae
                  - *Camarasaurus* sp.
          - Ornithischia
            - Thyreophora
              - Stegosauridae indet.
            - Neornithischia
              - *Nanosaurus agilis*
    - **Mammalia**
      - Docodonta
        - *Docodon* cf. *apoxys*
      - Multituberculata
        - Allodontidae indet.
      - Dryolestida
        - Dryolestidae
          - *Amblotherium megistodon* n. sp.

SYSTEMATIC PALEONTOLOGY

PLANTAE
Chlorophyta
Charophyta Indet.

Three charophyte oogonia have been found in the Little Houston Quarry over the years, but all were lost in the course of study due to unfortunate laboratory mishaps before they could be photographed. There are at least six genera of charophytes known from the Morrison Formation, and they have been reported at least from the Piedmont area of the Black Hills (South Dakota), in addition to the unidentified taxa reported from Little Houston here (Schudack and others, 1998).

Polypodiopsida
Equisetales

Equisetum sp.

One plant specimen (JRF 95153) has been identified as a stem of a relatively large horsetail, probably *Equisetum* (figure 4A). Horsetail fossils are relatively common in the Morrison Formation, both in Wyoming and the Colorado Plateau (Tidwell and others, 1998, 2006; Ash and Tidwell, 1998), and this fossil represents one of the larger specimens reported from the unit.

Polysporangiophytes
Tracheophytes
Pteridospermatophyta?

One specimen (JRF 9411) represents a small, well preserved seed less than 2 mm in diameter (figure 4B). It appears to consist of a complete seed with ribbed integument, possibly from an indeterminate seed fern (C. Gee, University of Bonn, written communication, 2018).

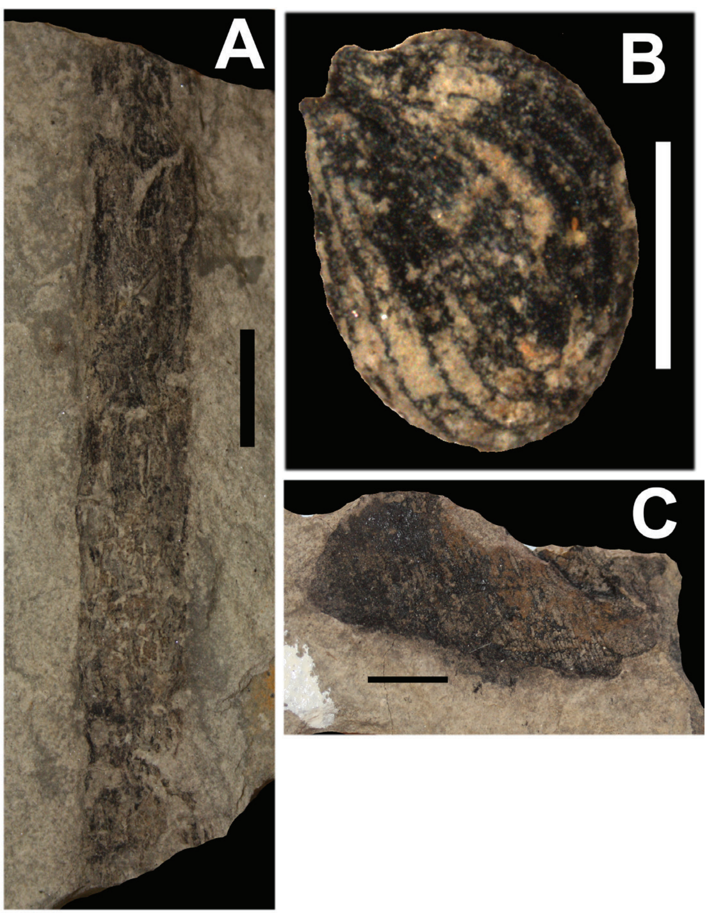

Figure 4. Representative plant material from the Little Houston Quarry. (A) Horsetail stem *Equisetum* sp., JRF 95153, scale bar = 1 cm. (B) Seed of possible pteridospermatophyte (seed fern), JRF 9411, scale bar = 1 mm. (C) Carbonized impression of possible cone scale or cycadophyte leaf-scale, SDSM 25305, scale bar = 1 cm.

Gymnospermae? indet.

Carbonized, roughly rectangular (and sometimes relatively thick) plant fragments (represented by SDSM 25305, figure 4C) are the most abundant plant material in the deposit. It is unclear what element or taxon these represent, although one hypothesis is that they are partial cone or seed scales of conifers (e.g., Tidwell, 1998; Eckenwalder, 2009) or, alternatively, cycad leaf-scales such as those of *Cycadolepis* (e.g., Tidwell and others, 1998).

METAZOA
Mollusca
Gastropoda
Amplovalvata sp.

Several gastropods have been found in the Little Houston Quarry, and at least one of these (JRF 9359; figure 5A) appears to belong to the genus *Amplovalvata* (Yen, 1952; Evanoff and others, 1998), although it is not well preserved enough to identify to species.

Bivalvia
Unionida
Unionidae indet.

Specimens of unionids are relatively abundant in the deposit, and most are preserved as impressions in the siltstone matrix; however, one specimen from the underlying sandstone preserves the shell nearly intact. None of these specimens is well preserved enough to be certain of their identifications within Unionidae, but one large (~8 cm) specimen (figure 5B) and the one preserving shell material (figures 5C and 5D) may represent "*Unio*" *stewardi* or "*U.*" *felchi*, and either "*Unio*" sp. or possibly *Vetulonaia*, respectively (Branson, 1935; Evanoff and others, 1998).

Unionida indet., new genus?

Most abundant in the Little Houston Quarry, however, is an unusual unionoid consisting of very elongate shell valves and often preserved as impressions of articulated but open shells (figures 5E and 5F). Unionids with this degree of relative elongation (up to 4.6:1) have

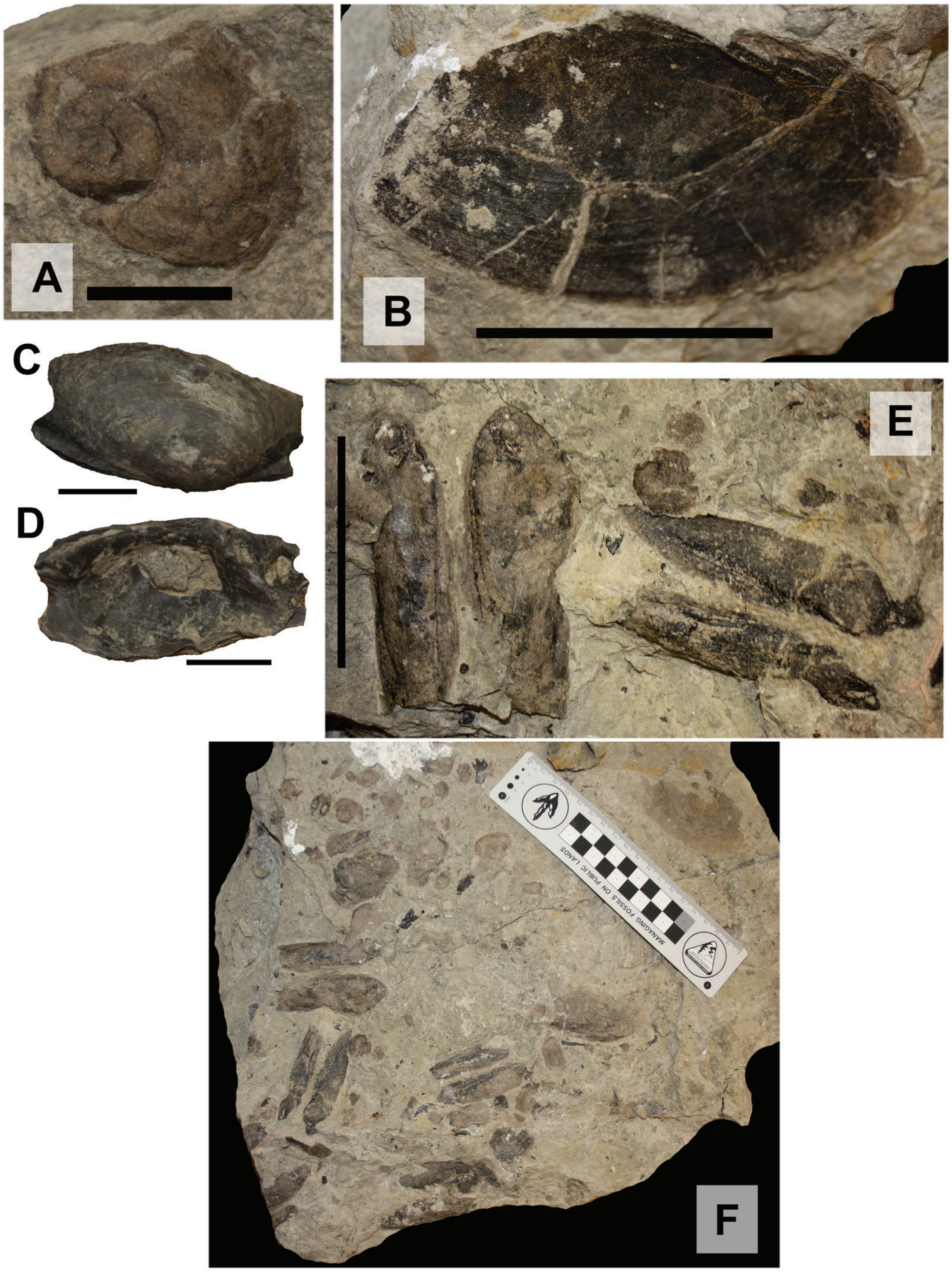

Figure 5. Representative Little Houston Quarry Mollusca. (A) Impression of gastropod *Amplovalvata* sp., JRF 9359, scale bar = 1 cm. (B) Impression of indeterminate unionoid, scale bar = 5 cm. (C and D) Indeterminate unionoid shell, scale bars = 1 cm. (E) Impressions of indeterminate elongate unionoids, scale bar = 5 cm. (F) Overview of same slab as in (E), showing additional specimens, scale bar in cm. (B to F) all SDSM unnumbered.

not previously been reported from the Morrison Formation (Branson, 1935; Yen, 1952; Evanoff and others, 1998; Good, 2004). Among modern unionoids such elongate shell dimensions are known in several genera of the families Unionidae and Mycetopodidae (Anderson, 2014), and these taxa live in a range of freshwater environmental settings, including in muds and sands or firm grounds of rivers or oxygenated to dysoxic lake beds. Further identification of this taxon in the Little Houston Quarry will require additional material.

Arthropoda

Malacostraca?

One small specimen (MWC 5640) appears to be the incomplete posterior walking leg of a small crayfish or other malacostracan (figure 6). The specimen is less than 1 cm long and appears to consist of three to five podomeres, including a spinose dactylus, the propodus, and carpus, but the nature of the more proximal elements is unclear. The leg is similar in size to an isolated, more anterior walking appendage from the Fruita Paleontological Area in western Colorado illustrated by Hasiotis and others (1998); the limbs of a nearly complete crayfish from the Mygatt-Moore Quarry in western Colorado, illustrated by Foster and others (2018), are too poorly preserved to compare.

Diplostraca

Several diplostracans (previously referred to as "conchostracans;" Martin and Davis, 2001) have been found in the quarry (e.g., JRF 9521, not figured), but they are very rare. Previous studies of Morrison diplostracans indicate that there are at least four taxa, mostly in Colorado and Utah (Lucas and Kirkland, 1998).

Chordata

Osteichthyes

Actinopterygii indet.

Actinopterygian fish are represented by many elements from the Little Houston Quarry, including numerous upper and lower jaw fragments (figure 7), and three types of scales similar to those illustrated from other sites by Kirkland (1998) and Foster and Heckert (2011). The scales include abundant, tiny ganoid scales (figures 7A and 7B), whereas the jaw elements include a diverse sample of upper and lower elements, with almost no two the same (figures 7C to 7I). One fish specimen appeared in the field to be an operculum and pectoral fin of a large amioid, but this specimen has not yet been prepared.

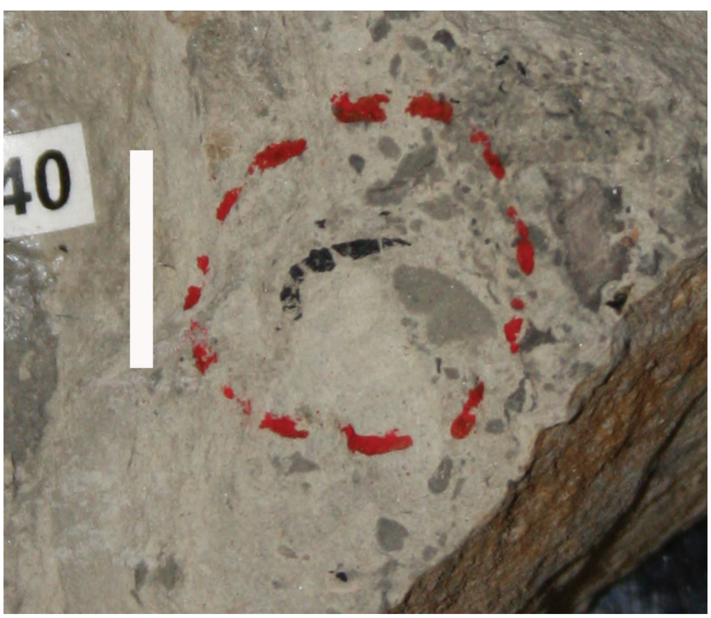

Figure 6. Crayfish walking leg from Little Houston Quarry, MWC 5640, scale bar = 1 cm.

Dipnoi

Ceratodus fossanovum

There are a number of species of lungfish known from the Morrison Formation, including *Ceratodus fossanovum*, *Ceratodus robustus*, and *Potamoceratodus guentheri* (Kirkland, 1987, 1998; Pardo and others, 2010), each best distinguished on tooth plate morphology.

Lungfish are known from several specimens at the Little Houston Quarry, including a left dentary and tooth plate (figure 7J), along with several isolated tooth plates. The tooth plates of most of these specimens, including that of the left lower jaw (MWC 6505), are most similar to *Ceratodus fossanovum* in having a more obtuse inner angle, lower ridges, and a lingual crushing surface; *C. fossanovum* is also known from Quarry 9 at Como Bluff and from Ninemile Hill, Wyoming (Kirkland, 1998; Trujillo, 1999).

Amphibia

Anura indet.

Frogs are represented by a single distal half of a humerus with the preserved shaft and trochlea (figure 8A); this specimen is just over 6 mm long and is the only evidence of frogs from the Morrison Formation north of Como Bluff, Wyoming. The Morrison contains a pelobatid frog and the discoglossid *Enneabatrachus* at Quarry 9 and the pipoid *Rhadinosteus* at Dinosaur National Monument (Evans and Milner, 1993; Henrici, 1998), although this partial humerus cannot be identified more precisely.

Caudata indet.

Salamanders are known from just a handful of

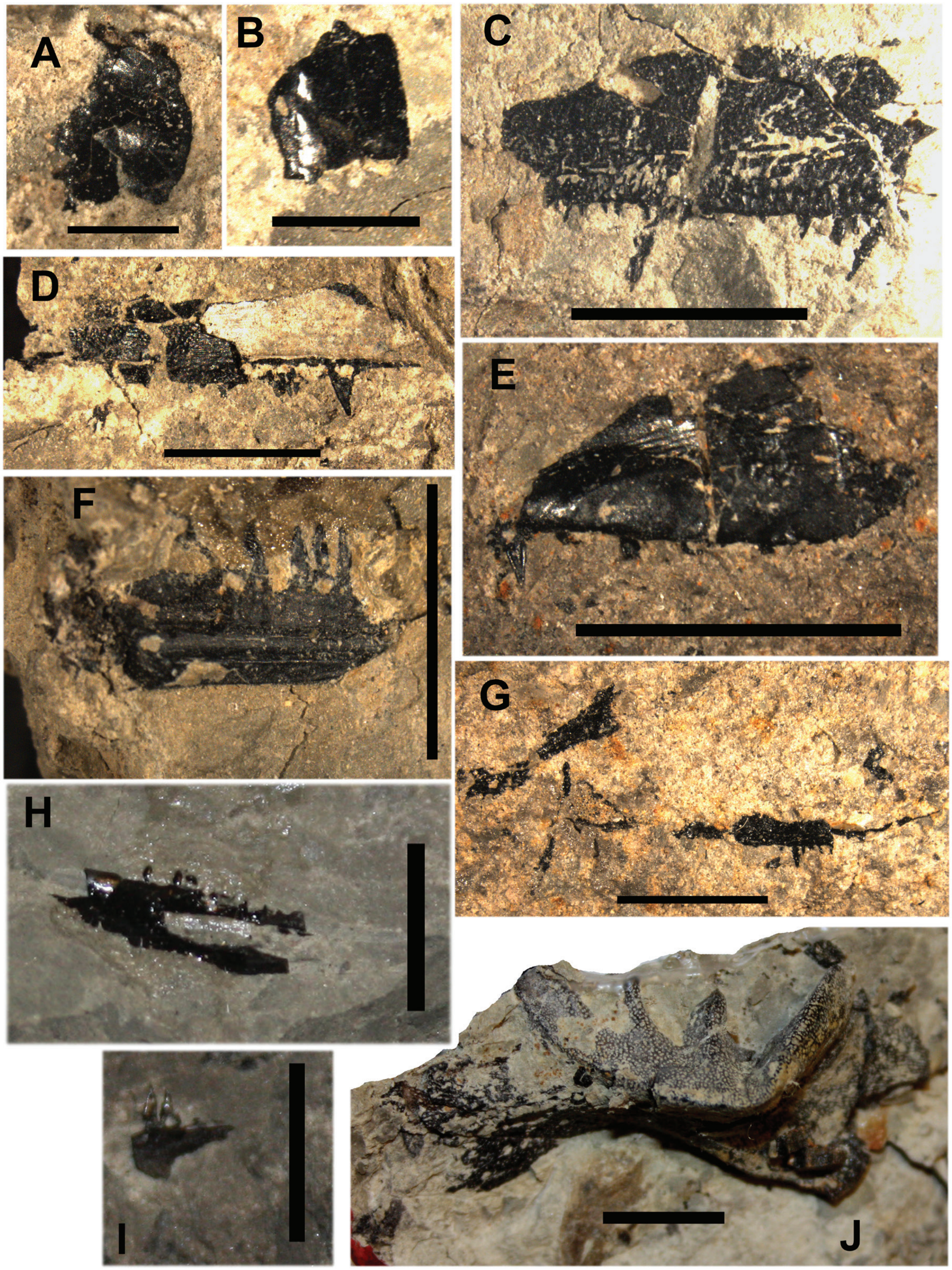

Figure 7. Representative Little Houston Quarry osteichthyan fish fossils. (A) Ganoid scale, JRF 9470. (B) Ganoid scale, JRF 9588. (C) Maxilla(?) fragment with teeth, JRF 95232. (D) Maxilla(?) fragment with teeth, JRF 9529. (E) Maxilla(?) fragment, JRF 9572. (F) Dentary(?) fragment with teeth, JRF 95138. (G) Maxilla(?) fragment, SDSM specimen. (H) Dentary(?) fragment with teeth, MWC 5762. (I) Jaw fragment with two teeth, MWC 5779. (J) Lungfish *Ceratodus fossanovum*, left dentary and tooth plate, MWC 6505. Scale bars A and B = 2 mm; all other scale bars = 1 cm.

strongly amphicoelous vertebrae with dorsoventrally elongate diapophyses (figures 8B to 8G). Most Morrison salamander vertebrae are fairly small, but a few are somewhat larger (Evans and Milner, 1993), suggesting at least two different-sized groups. The specimen illustrated here is of the larger size class (centra ~5 mm length). Some Morrison salamanders such as *Iridotriton* (Evans and others, 2005) are significantly smaller than the taxon illustrated here from the Little Houston Quarry.

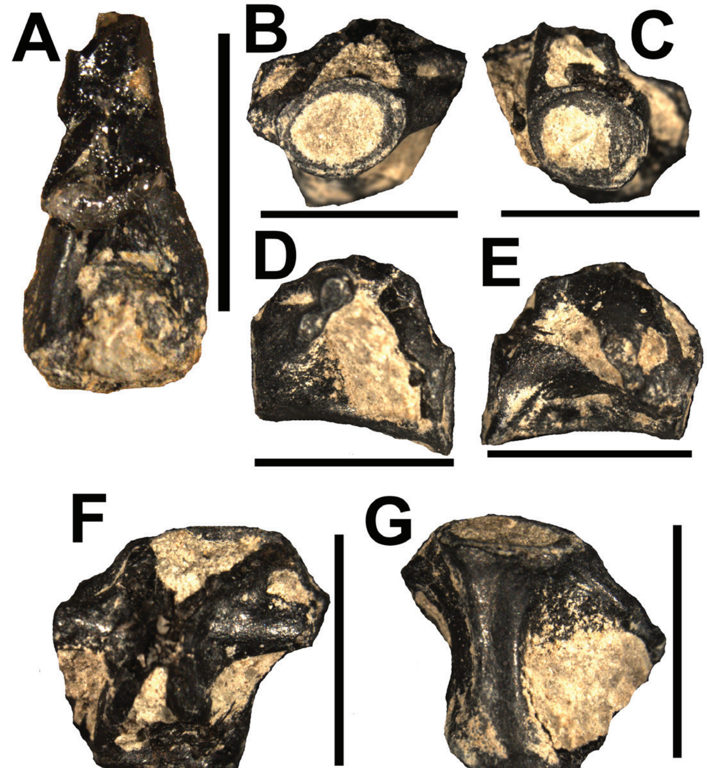

Figure 8. Little Houston Quarry Amphibia. (A) Frog humerus, distal half in anterior view, JRF 9545. (B to G) Caudata (salamander) vertebra in (B) anterior, (C) posterior, (D) left lateral, (E) right lateral, (F) dorsal, and (G) ventral views. All scale bars = 5 mm.

Reptilia

Testudinata

Dinochelys whitei

The relatively smooth-shelled turtle *Dinochelys* (Gaffney, 1979) is the most abundant turtle in the deposit, outnumbering *Glyptops* significantly. Many preserved pleural elements are small and preserved intact and unbroken with unfused sutures, suggesting many of the individuals preserved were juveniles (figures 9A to 9C). At least one shell fragment was found with the laterally radiating dorsal ridges typical of young juveniles (Gaffney, 1979).

Glyptops ornatus

The turtle *Glyptops* is known from a number of shell fragments exhibiting strong sculpturing (Marsh, 1890b; Hay, 1908; figures 9D to 9E); it is far less abundant in the Little Houston Quarry than *Dinochelys*.

Testudinata indet.

Many limb and some axial elements of indeterminate turtles are known from the quarry, including humeri, femora, a tibia, and sacral vertebrae (figures 9F to 9I). These cannot be identified to genus but indicate the abundance of turtles generally in the deposit.

Rhynchocephalia

Opisthias?

The sphenodontian *Opisthias*? is represented by several small dentary fragments, a palatine, and an indeterminate jaw fragment (figures 10A to 10F). The two apparent dentary fragments illustrated here (figures 10C to 10F) are approximately the same size and the first of these (figures 10C and 10D) may be more fragmentary or may represent a morphotype with relatively larger teeth. Rhynchocephalians are numerous in the Morrison Formation (Foster, 2003) though not, as far as we currently recognize, particularly diverse, with three genera currently represented: *Opisthias*, *Theretairus*, and the large, herbivorous *Eilenodon* (Gilmore, 1910; Simpson, 1926; Rasmussen and Callison, 1981; Jones and others, 2018). Recent analyses suggest there may be a previously hidden diversity of rhynchocephalians in the Morrison Formation (DeMar and others, 2018), although the material from the Little Houston Quarry is not complete enough to identify further.

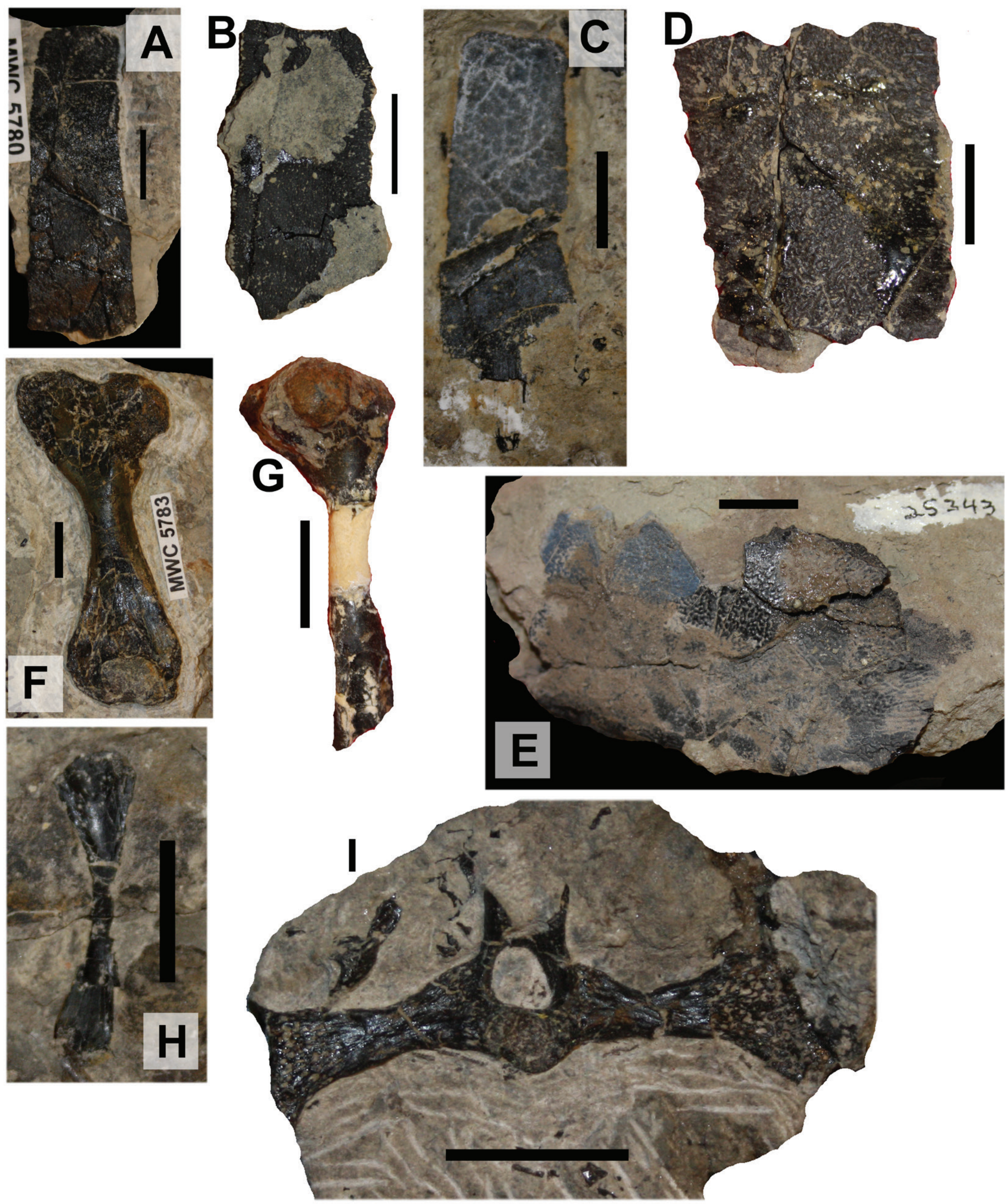

Figure 9. Representative Little Houston Quarry turtles. (A) *Dinochelys* pleural, MWC 5780. (B) *Dinochelys* pleural, SDSM specimen. (C) *Dinochelys* pleural, SDSM specimen. (D) *Glyptops* pleural fragment, SDSM specimen. (E) *Glyptops* pleural fragment, SDSM 25343. (F) Testudinata indet., right humerus, MWC 5783. (G) Testudinata indet., left femur, SDSM 25246. (H) Testudinata indet., tibia(?), JRF 9528. (I) Testudinata indet., sacral vertebra, MWC 5865. All scale bars = 1 cm.

Squamata

cf. *Paramacellodus*

Lizards are represented by a single tiny dentary just 6 mm long. It preserves 11 short, blunt teeth suggestive of a scincomorph and is likely a paramacellodid (figure 10G). The scincomorphs of the Morrison Formation include *Paramacellodus*, *Saurillodon*, and *Schillerosaurus* (Prothero and Estes, 1980; Evans and Chure, 1998, 1999). The Little Houston Quarry jaw is not as short and deep as the dentary in *Saurillodon* (Broschinski, 2000) nor apparently as slender (dorsoventrally shallow) as *Schillerosaurus*, but it is similar to several specimens of *Paramacellodus* from Dinosaur National Monument

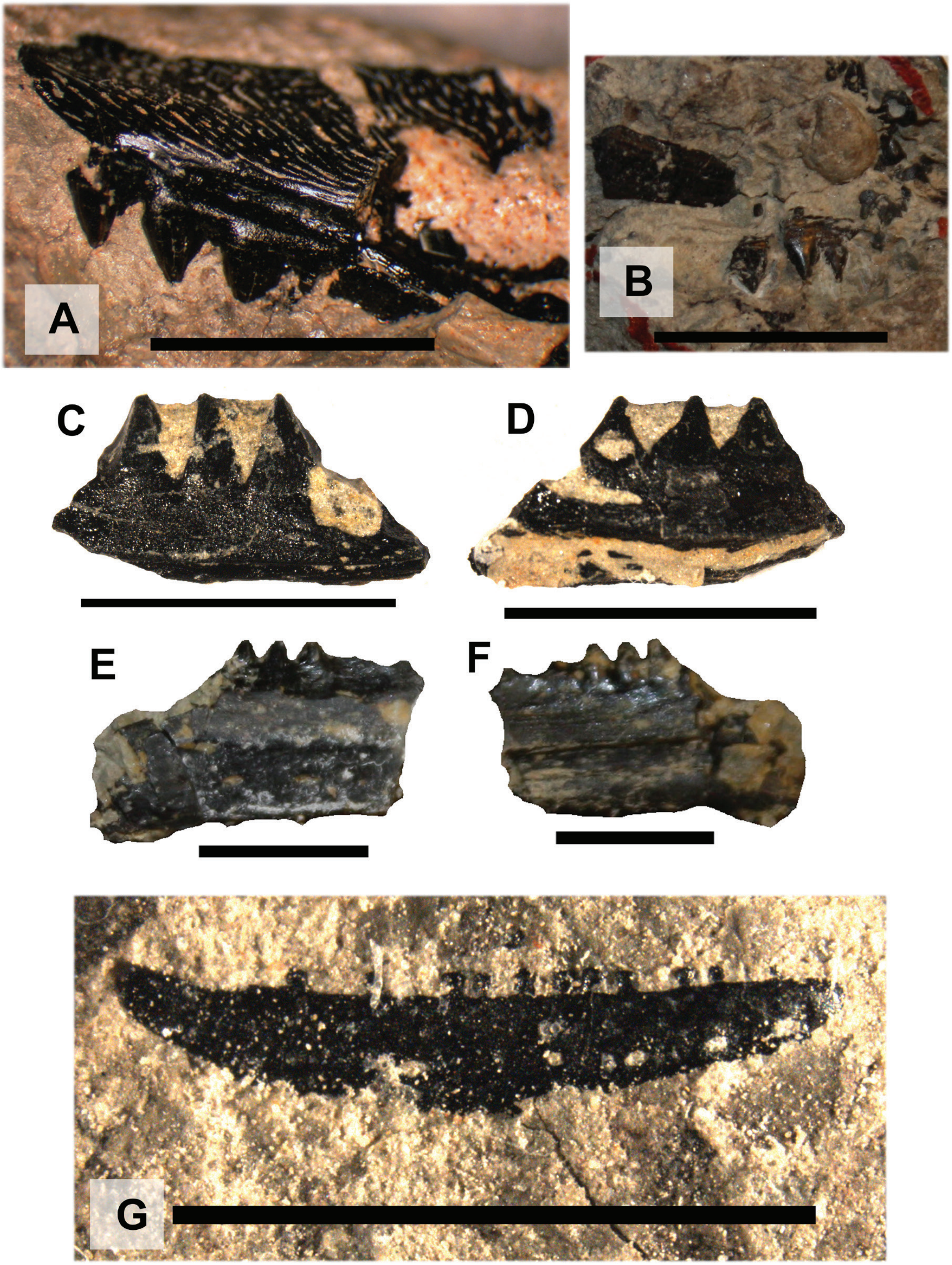

Figure 10. Representative Little Houston Quarry Lepidosauria. (A to F) *Opisthias*?, Rhyncocephalia. (A) Left palatine in lateral view, MWC specimen. (B) Indeterminate jaw fragment in lateral view, MWC specimen. (C and D) Dentary(?) fragment in (C) labial and (D) lingual views, EBG 9833. (E and F) Right dentary fragment (MWC specimen) in (E) labial and (F) lingual views. (G) Small cf. *Paramacellodus* (Scincomorpha, Squamata) right dentary in labial view, JRF 95102. Scale bars = 5 mm.

(Evans and Chure, 1998) in its proportions and overall structure.

Choristodera

Cteniogenys antiquus

Choristoderes are relatively abundant in the deposit, being represented by numerous isolated vertebrae, and several upper and lower jaw fragments (figure 11). *Cteniogenys* was a small (~25 cm long) semiaquatic choristodere common in the Late Jurassic of North America and Europe (Gilmore, 1928; Evans, 1990). It appears to have been significantly more abundant in the eastern and northern parts of the Morrison Formation than it was in what is now the Colorado Plateau region (Chure and Evans, 1998; Foster and Trujillo, 2000).

Crocodylomorpha
Crocodyliformes
Atoposauridae

Theriosuchus morrisonensis

This newly named species of atoposaurid crocodyliform (Foster, 2018) was based on a lower mandible found in the Little Houston Quarry in 2004 (figures 12A to 12C). The jaw indicates an atoposaurid similar to *Theriosuchus pusillus* and *Knoetschkesuchus* was present in at least the northern region of the Morrison Formation.

Goniopholididae? indet.

Several isolated teeth at the site appear to belong to relatively large crocodyliforms, probably goniopholidids (figure 12D). The form and size of the teeth is essentially indistinguishable from goniopholidids from the Morrison Formation, such as *Eutretauranosuchus* and *Amphicotylus* (Mook, 1967; Smith and others, 2010; Allen, 2012).

Crocodyliformes indet.

Relatively abundant and not particularly large crocodyliform osteoderms from the quarry could be those of goniopholidids, although these are not dorsal armor with the rectangular plates and anterior projections typical of that family. These are squarish to almost oval in shape (figures 12E to 12F) and could conceivably belong to any of several families of crocodyliforms.

Archosauria indet.

One tiny premaxilla appears to belong to an indeterminate small archosauromorph (figure 12G). This small specimen has 5 to 6 conical teeth, a tall nasal process, a thick maxillary process, and is anteroposteriorly relatively short.

Pterosauria
Pterosauria indet.

Pterosaurs are represented by a single, elongate tooth with a tall conical and slightly recurved crown, a long root, and an oval to slightly laterally compressed cross section (MWC 5809; figures 12H to 12I). This is a general form typical of some pterosaurs (Wellnhofer, 1991; Witton, 2013), and it is rather similar in overall appearance to an anterior dentary tooth from the Breakfast Bench facies at Como Bluff described by McLain and Bakker (2017). Isolated pterosaur teeth are also preserved at Quarry 9 at Como Bluff (Carrano and Velez-Juarbe, 2006).

Dinosauria
Saurischia
Theropoda
Tetanurae
Allosauroidea

Allosaurus jimmadseni

A juvenile *Allosaurus* partial skeleton from Little Houston Quarry (figure 2C) was described and illustrated by Foster and Chure (2006) and was referred to *A. jimmadseni* by Chure and Loewen (2020). This specimen (SDSM 30510) demonstrated the extreme elongation of the hindlimb relative to ilium length in juveniles of the genus compared with adults. It is also one of the more complete associated skeletons of a very young individual of the genus yet reported, consisting of cervicals, a dorsal, a sacral, both ilia, caudals, an ischium,

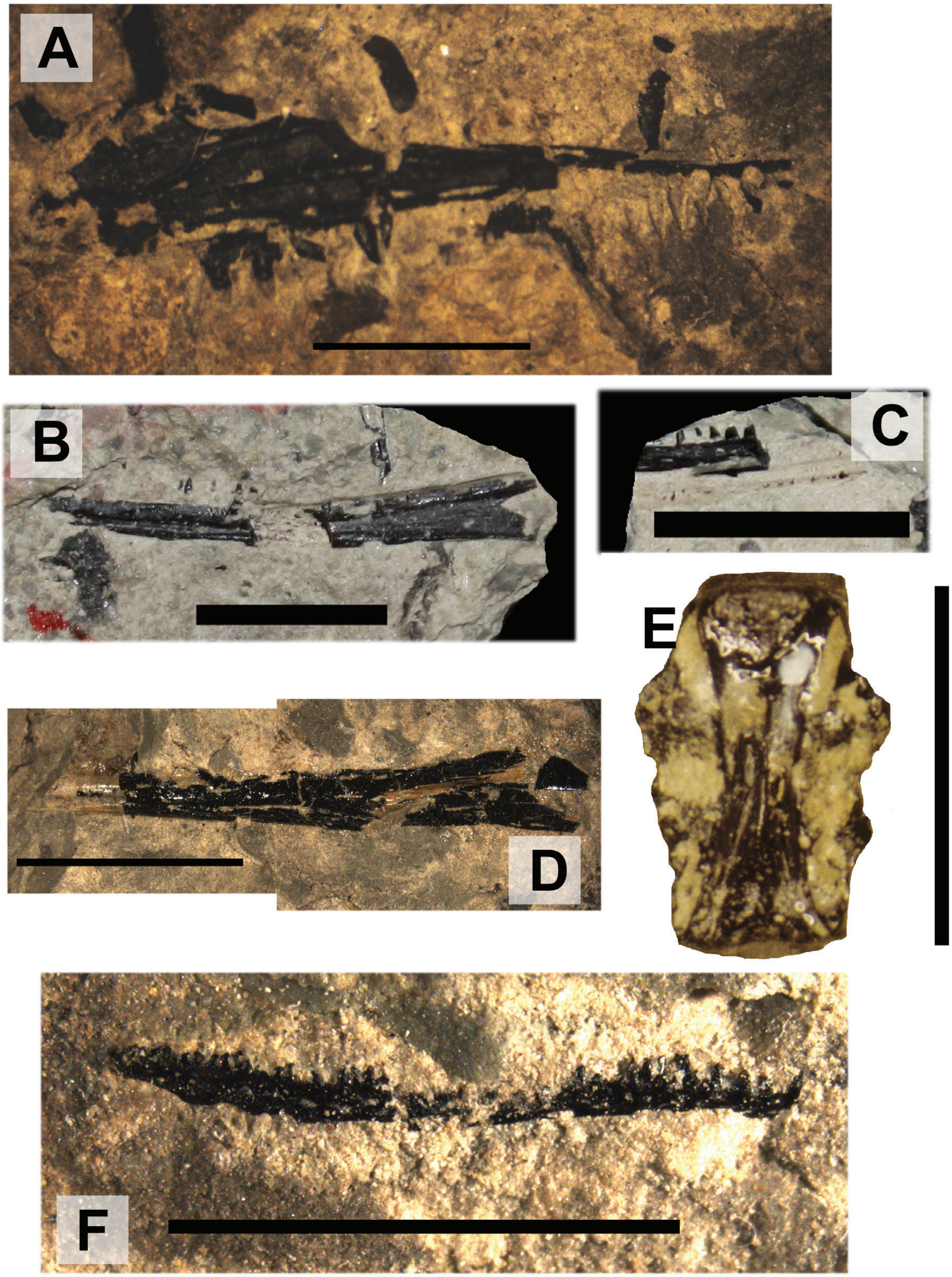

Figure 11. Representative Little Houston Quarry *Cteniogenys* (Choristodera). (A) Left maxilla in labial view, SDSM specimen. (B and C) Right dentary fragment, MWC 6504, in (B) lingual view and fragment with well-preserved teeth (missing from (B) in (C) labial view. (D) Dentary fragment, JRF 95216. (E) Vertebra in dorsal view, SDSM specimen. (F) Dentary with teeth, small individual, JRF 95100. Scale bars = 1 cm, except E = 5 mm.

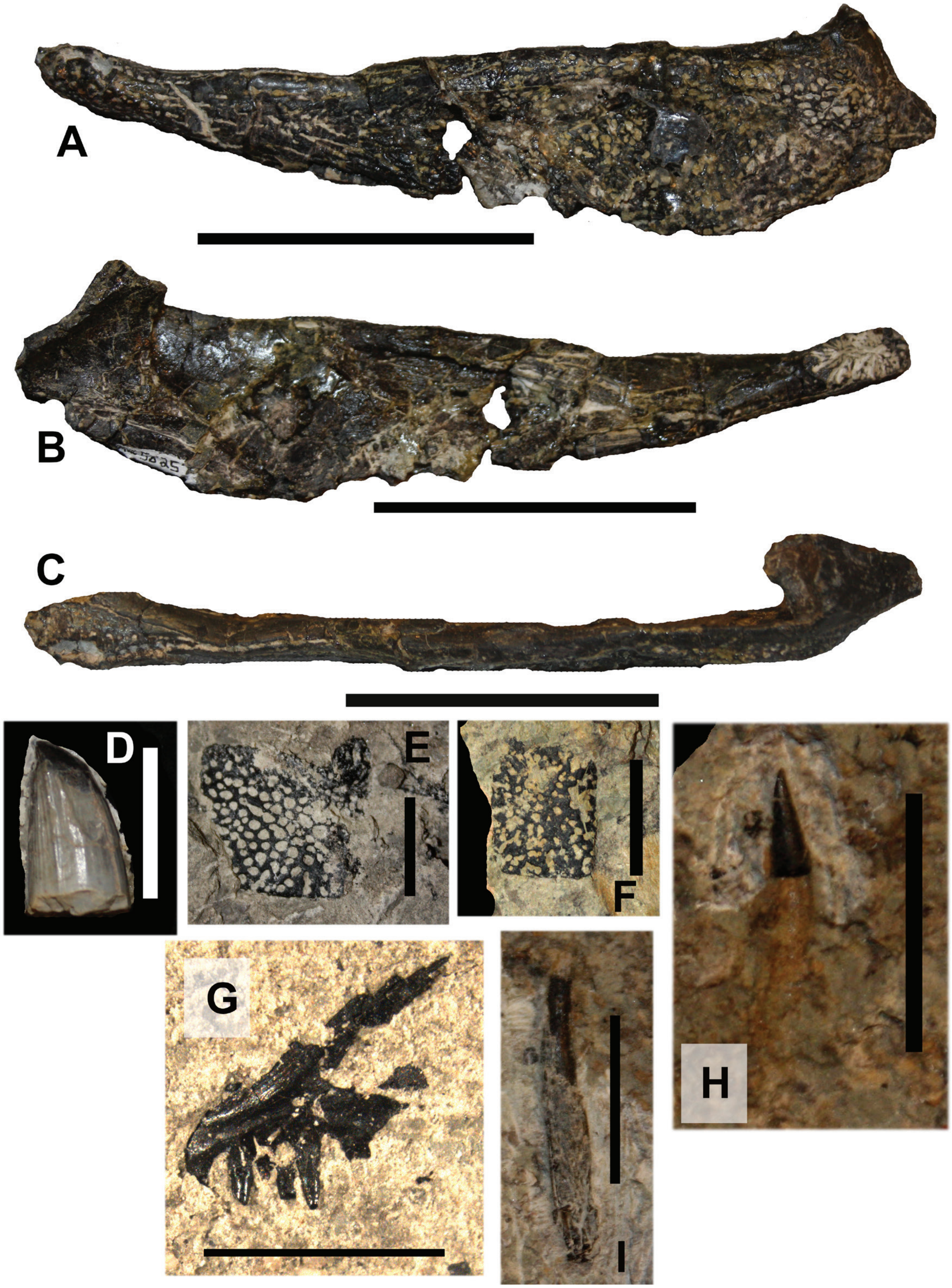

Figure 12. Representative Little Houston Quarry Crocodyliformes, Pterosauria, and Archosauromorpha indet. (A to C) Left mandible of *Theriosuchus morrisonensis*, MWC 5625, in (A) labial, (B) lingual, and (C) occlusal views. (D) Tooth of Goniopholididae(?), SDSM 25337. (E) Osteoderm of Crocodyliformes indet., JRF 9571. (F) Osteoderm of Crocodyliformes indet., JRF 95211. (G) Archosauromorpha indet., premaxilla with teeth in lingual(?) view, JRF 95208. (H and I) Tooth of Pterosauria indet., MWC 5809; tooth tip in H) and base of crown plus root in I). Scale bars: A to C = 5 cm; D to F and H to I = 1 cm; G = 5 mm.

femur, tibia, metatarsals, and manual and pedal phalanges and unguals (Foster and Chure, 2006).

A partial skeleton of an adult *Allosaurus* was also collected from the main pit (figure 3A), consisting of posterior dorsal vertebrae, a sacrum and both ilia, anterior caudal vertebrae, and a femur; preparation of this specimen is still being completed. Several teeth assigned to *Allosaurus* are also known from the quarry (figures 13K and 13L). These are relatively large teeth (~19 to 27 mm crown height) with denticles that are neither as coarse as in *Torvosaurus* nor as fine as in *Ceratosaurus* and with a distinctive cross-sectional shape similar to *Allosaurus* (Madsen, 1976; Madsen and Welles, 2000; Bakker and Bir, 2004). Other elements representing the adult *Allosaurus* from the quarry include a quadrate, premaxilla (Foster and Martin, 1994), dentary fragment, and dorsal and caudal vertebrae.

Coelurosauria

Maniraptora

Tanycolagreus?

A single right metatarsal II, collected from the mammal pit at the Little Houston Quarry, appears to belong to a small theropod (figures 13A and 13B). The metatarsal is too elongate to belong to *Allosaurus* (even a juvenile), *Ceratosaurus*, or *Torvosaurus* and is too robust to be *Coelurus* (Madsen, 1976; Britt, 1991; Madsen and Welles, 2000; Carpenter and others, 2005a) and too large to be *Ornitholestes* or *Koparion* (assuming the latter was as small as its lone tooth suggests). However, this specimen is essentially indistinguishable in proportions and articular end shapes from the metatarsals of *Tanycolagreus* (Carpenter and others, 2005b). The pes of *Stokesosaurus* and *Marshosaurus* is unknown in both. The Little Houston metatarsal is here tentatively identified as *Tanycolagreus*?, possibly the first occurrence of the taxon north of Bone Cabin Quarry in southern Wyoming.

Dromaeosauridae indet.

A single isolated tooth from the quarry (figures 13E to 13G) is small, short, recurved, and laterally compressed (10.8 mm crown height), with strong serrations on the distal carina (4/mm) and only small indistinct serrations on the mesial carina. The distal serrations are slightly hooked apically, and in most of these characters the tooth is similar to those of *Dromaeosaurus*, *Saurornitholestes*, and *Sinornithosaurus* among dromaeosaurids (Currie and others, 1990; Farlow and others, 1991; Fiorillo and Currie, 1994; Xu and Wu, 2001; Larson and Currie, 2013). It is a relatively large tooth at nearly 11 mm, with fine serrations on the distal carina. The tooth dimensions and denticle characteristics are similar to those of possible dromaeosaurid tooth morphotypes 5 and 6 reported from the Middle-Late Jurassic Shishugou Formation of China (Han and others, 2011). Overall tooth shape is also similar to teeth from Guimarota (Late Jurassic of Portugal) referred to *Compsognathus* (Zinke, 1998), although overall size and the distal denticles are both larger in the Little Houston specimen. Hendrickx and Mateus (2014) referred a similar tooth from the Late Jurassic of Lourinhã, Portugal, to *Richardoestesia*, although the Little Houston tooth is approximately twice as large and has much larger denticles on the distal carina. The tooth is less strongly recurved than the Morrison troodontid *Hesperornithoides* (Hartman and others, 2019) and less labiolingually bulbous than the troodontid *Koparion* (Chure, 1994).

Reports of dromaeosaurid-like teeth from the Morrison Formation have been rare, with only two teeth illustrated, from the Dry Mesa Quarry in western Colorado and the Warm Springs Ranch site in northern Wyoming (Britt, 1991; Ikejiri and others, 2006). The occurrence of dromaeosaurid (or at least dromaeosaurid-like) teeth in at least three deposits in the Morrison Formation, plus a number of dromaeosaurid teeth in the Late Jurassic of Portugal, Spain, Germany, Ethiopia, and China (Zinke, 1998; Rauhut, 2000; Van Der Lubbe and others, 2009; Han and others, 2011; Hall and Goodwin, 2011), suggests that this family was rare but certainly present in many areas of the globe during the Late Jurassic. In the Morrison Formation, isolated, partial bones of possible dromaeosaurs were reported by Jensen and Padian (1989), but those are the only non-tooth evidence of the family in the formation. That no well-preserved skeletons of dromaeosaurids have been reported yet from the Late Jurassic may be indicative of their rareness at the time but may more likely be a result of taphonomic bias against smaller, more delicate material.

Figure 13. Representative Little Houston Quarry Theropoda (Dinosauria). (A and B) Right metatarsal II of *Tanycolagreus*?, JRF 95215, in (A) medial and (B) anterior views. (C) Tooth of theropod Tooth Type A (cf. *Richardoestesia*?), JRF 95222, and (D) in close-up showing serrations. (E to G) Tooth of Dromaeosauridae indet., JRF 95188, in (E) lingual(?), (F) labial(?), and (G) in close-up view of serrations. (H) Tooth of theropod Tooth Type B, MWC specimen. (I and J) Tooth of theropod Tooth Type C in (I) labial and (J) lingual views, JRF 9739. (K and L) Teeth of *Allosaurus*, SDSM specimen and JRF 9337. Scale bars: A and B = 10 cm; C, E, F, and H to J = 5 mm; D = 2 mm; G = 1 mm; K and L = 1 cm.

Despite the fragmentary evidence so far, it appears reasonable to conclude that dromaeosaurids were present in the Morrison Formation and that we might expect to find more complete elements in the future.

Theropoda indet.
Tooth Type A (cf. *Richardoestesia?*)

A small (4.1 mm crown height) and laterally compressed tooth (figures 13C to 13D) differs from the dromaeosaurid tooth type described above in having a relatively taller crown, in being less recurved, and in having finer serrations on the distal carina (8/mm) that are shorter with more rectangular and blunt apical profiles. In these characteristics, the tooth type is roughly similar to many teeth assigned to *Richardoestesia* (Currie and others, 1990), a taxon which has been identified from the Late Jurassic of Portugal (Rauhut, 2000; Mateus, 2006; Malafaia and others, 2017). Although the Little Houston Quarry tooth is similar to some illustrated teeth of Cretaceous *Richardoestesia* in being somewhat recurved (Currie and others, 1990), a few Cretaceous and Jurassic specimens are relatively tall and less recurved (see figure 6 in Zinke, 1998; see figure 11.9 in Rauhut, 2000; Longrich, 2008). Larson and Currie (2013) demonstrated the difficulties, in many cases, of distinguishing species of *Richardoestesia* and other small Cretaceous theropod taxa, based on teeth, and this indirectly implies there may be difficulty in referring isolated teeth from other times or geographical areas to the genus. Whatever taxon these possible cf. *Richardoestesia* teeth from the Morrison and elsewhere in the Late Jurassic represent, it is clear that the Morrison and Guimarota faunas, for example, were more diverse in small theropod taxa that was previously apparent and that they likely shared closely related or congeneric taxa with *Richardoestesia*-like teeth.

Tooth Type B

Another isolated small theropod tooth (figure 13H) from the quarry is roughly similar to Tooth Type A above but is less laterally compressed and the nature of the serrations is unclear. Crown height for the specimen is 5.0 mm. In some general ways this tooth appears similar to those of *Coelurus* (Marsh, 1896) and *Ornitholestes* (Carpenter and others, 2005a) and especially to an unidentified theropod tooth type from Guimarota, Portugal (see figures 8A to 8D in Zinke, 1998).

Tooth Type C

Another tooth from the quarry appears to be a small anterior theropod tooth (figures 13I to 13J) with a wear facet and the serrated mesial carina curving distal-lingually; this tooth type may belong to a young *Allosaurus*. It is 5.7 mm in crown height with 3.5 denticles per millimeter.

Tooth Type D (Abelisauroid?)

A somewhat larger theropod tooth type (11 to 30 mm crown height, as preserved) from the quarry is the most unusual and consists of labiolingually thin, unrecurved teeth with slightly constricted crown bases and relatively distally tall serrations with very elongate, basally oriented interdenticular sulci. The first representative of these teeth (figures 14A to 14E) is approximately 11 mm in crown height; in labial or lingual view the mesial and distal carinae both curve symmetrically toward the apex so that the tooth is unrecurved, except for a very slight posterior(?) curvature at the tip. The tooth is labiolingually thin compared to its mesiodistal length and curves slightly lingually toward the apex. The tooth is serrated from apex to crown base along both mesial and distal carinae, and the lower portion of the mesial carina has approximately 5 denticles per millimeter. Each denticle curves slightly apically at its distal end (figure 14E).

The second representative of Tooth Type D is similar in overall shape but the apex is not preserved (figure 14F). It is larger than the first and was probably about 30 mm long when complete. The root of this tooth is missing, suggesting it is a shed tooth, and in lingual view the crown appears to have been very slightly constricted at its base, as in the first tooth described above. Also in lingual view, the mesial and distal carinae both curve symmetrically toward the apex so that the tooth is unrecurved. Despite being partially in matrix, the tooth can be seen in mesial or distal view to be strongly labiolingually compressed relative to its basal length. The serrations are more elongate proximodistally than

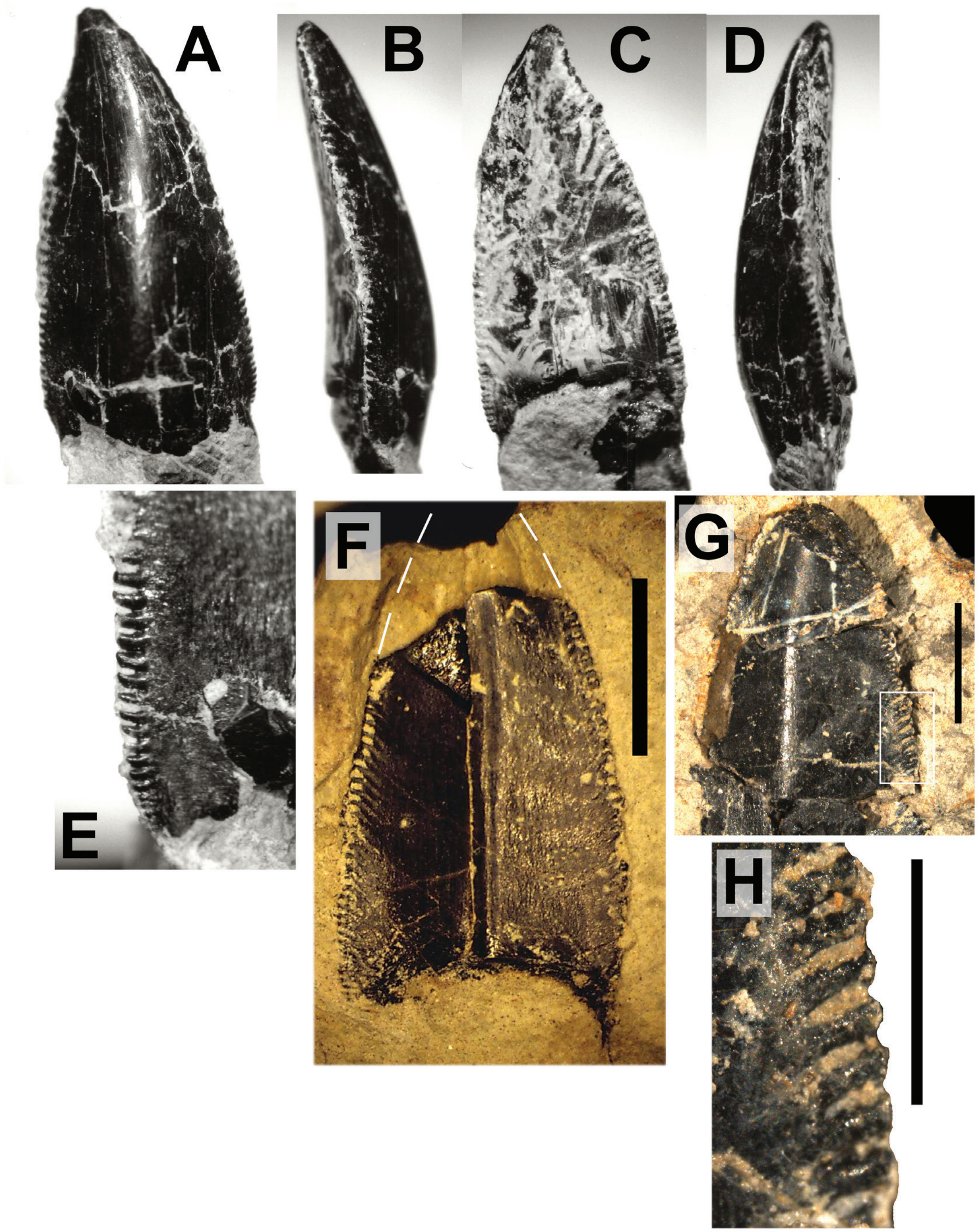

Figure 14. Unusual Little Houston Quarry Theropoda (Dinosauria) teeth. (A to E) JRF 94130. Tooth of theropod Tooth Type D in (A) labial view, (B) distal view, (C) lingual view, and (D) mesial view. JRF 94130 is approximately 11 mm in height. (E) Close-up of denticles of distal carina near base of crown, JRF 94130. (F) Second specimen of theropod Tooth Type D, scale bar = 1 cm. (G) Tooth of theropod Tooth Type E, EBG 9830, in lingual view and (H) with close-up of denticles as marked by white box in G. Scale bars: G = 1 cm; H = 5 mm. (Photos A to E courtesy of National Park Service.)

in most other theropod teeth from the Morrison Formation and the interdenticular sulci are long and distinct. On this larger tooth there are approximately two serration denticles per millimeter; each denticle curves slightly apically at its distal end. The enamel on the lingual surface is relatively smooth and neither concave nor convex, but rather appears to be flat from a subtle central ridge out to the carinae.

These teeth (figures 14A to 14F) share some distinct similarities to the procumbent anterior dentary or premaxillary teeth of the noasaurid abelisauroid *Masiakasaurus* from the Cretaceous of Madagascar (Carrano and others, 2002, figures 5A to 5C of FMNH PR 2180) in being thin, not distally recurved, and in having pinched crown bases in labial or lingual view. The Little Houston Quarry teeth are not as thick nor as lingually curved toward the apex as in FMNH PR 2180, however, and are also similar to FMNH PR 2182 (Carrano and others, 2002, figure 5E), although they are not recurved as in that *Masiakasaurus* specimen. These similarities suggest that the Type D Morrison specimens (figures 14A to 14F) may represent the anterior teeth of an unknown small- to medium-sized abelisauroid or ceratosaurian. In the general characteristics of the serrations and overall shape, Type D teeth are similar to other Late Jurassic teeth referred to abelisaurids from Lourinhã, Portugal (Hendrickx and Mateus, 2014) and to a possible carcharodontosaurid from the Tendaguru Formation of Tanzania (Rauhut, 2011). In overall shape the Little Houston specimens are also similar to lateral dentary teeth from a very small theropod jaw from Guimarota in Portugal (Zinke and Rauhut, 1994).

No teeth of this morphology have previously been reported from the Morrison Formation, and it is unclear if the teeth represent a previously unknown taxon or a currently known taxon for which there is no tooth material. Among the Morrison theropods for which known teeth do not match Tooth Type D are: *Allosaurus*, *Torvosaurus*, *Ceratosaurus*, *Marshosaurus*, *Ornitholestes*, *Coelurus*, *Koparion*, *Hesperornithoides*, and *Tanycolagreus*. Taxa without teeth or with poorly known teeth include *Saurophaganax*, an unidentified abelisauroid(?) (formerly "*Elaphrosaurus*"), *Fosterovenator*, and *Stokesosaurus*. If the similarities of the Type D teeth to those of anterior teeth of *Masiakasaurus* are significant, and if the teeth belong to a known taxon with no or poor tooth representation, the best candidates might be the unidentified abelisauroid or possibly *Fosterovenator*. Finding this tooth type with associated skull material will be key to determining its affinities.

Tooth Type E

A lone tooth somewhat similar to Type D is also known; it is thicker, shorter, and lingually more convex (figures 14G and 14H), though it possesses similarly elongate serration denticles (figure 14C). These serrations are coarser than in Type D, too, however (1.75/mm); the denticles appear to be angled apically and to have slightly enlarged rather than apically curved distal ends, both unlike Type D. The crown height is 25 mm. This tooth type appears to be that of an anterior tooth, and the apparently distally enlarged denticles are similar to some referred teeth of abelisaurids (Hendrickx and Mateus, 2014), but beyond that it is difficult to identify.

Sauropoda
Diplodocidae
Diplodocinae indet.

Diplodocine sauropods are represented at the Little Houston Quarry by only rare elements including a pubis and at least one complete, slender femur (figures 2D and 3A). The pubis is slender and has an enlarged ambiens process as with diplodocines such as *Diplodocus* and *Barosaurus* (Hatcher, 1901; McIntosh, 1990; Ostrom and McIntosh, 1999).

Macronaria
Camarasauridae
Camarasaurus sp.

Camarasaurus is represented by at least six or possibly seven individuals, including four articulated vertebral series: a set of anterior to mid caudals and a set of posterior dorsals and most of a tail from the mammal pit (both in figure 3B); and a partial mid-tail and a nearly complete vertebral column from anterior cervicals to the tip of the tail from the main pit (both in figure 3A). In addition to these four individuals, there is a partial hind foot of a juvenile, a partial skull of a large individual found near (but probably not belonging to) the nearly complete vertebral column (figure 3A), and a hatchling to very young juvenile represented by a tiny tooth. The *Camarasaurus* material from the Little Houston Quarry cannot be assigned to one species (Pagnac, 1998), in part because the dorsal vertebrae of the most complete specimen do not clearly exhibit diagnostic features due to post-depositional crushing. Most anterior caudal vertebrae, however, appear to have only mildly expanded neural spines, suggesting possible affinity to *C. lentus* (Ikejiri, 2005).

The skull (SDSM 114501) is relatively large and is flattened to some degree with a number of teeth displaced from their alveoli and the premaxillae, for example, displaced dorsoventrally relative to each other (figure 15A). The skull was found underneath two sauropod ribs and near several camarasaurid metacarpals, several meters away from the end of the neck of the most complete *Camarasaurus* vertebral column in the quarry (figures 15B and 3A). The skull appears to have been too large to go with the neck and skeleton, however. The associated juvenile hind foot consists of the left metatarsals I, IV, and V, plus two unguals, and a phalanx (figure 15C; Foster, 1996a). A 5 mm-long tooth crown with partial root (JRF 9584) appears to belong to a very young camarasaurid and has an apical wear facet suggesting some use (figures 15D and 15E). This tooth has the general shape of most adult camarasaurid teeth (Ostrom and McIntosh, 1999), although the enamel surface appears to be smoother.

Ornithischia

Thyreophora

Stegosauridae indet.

A thin, plate-like bone with surficial grooves appears to be the dermal plate of a stegosaur (SDSM 25300; figure 16). The plates of *Stegosaurus* and *Hesperosaurus* are generally similar in structure, although their shapes differ somewhat, with those of the latter often lower and more oval-shaped (Carpenter and others, 2001; Maidment and others, 2015). The Little Houston Quarry specimen here is too incomplete to identify with one or the other genus, but its overall morphology appears to be that of some type of stegosaurian plate. *Hesperosaurus* has recently been reported at a number of northern localities in the Morrison Formation, appearing to be relatively more abundant there compared with the possibly more southern *Stegosaurus* (Maidment and others, 2018), and raising the possibility that SDSM 25300 may be *Hesperosaurus*, although there is no way to confirm this yet.

Neornithischia

Nanosaurus agilis

Small neornithischians are represented by relatively abundant material including a dentary with 13 teeth (Peirce, 2006; Carpenter and Galton, 2018; figure 16A), isolated anterior and lateral teeth (figures 17B and 17C), some vertebrate (figure 17D), a humerus (figure 17E), a pubis (figure 17K), a tibia of an adult (figure 17J), and a number of femora ranging in length from just a few centimeters to approximately 20 cm (figures 17F to 17I). The teeth are entirely of the "*Othnielosaurus*" type (Galton, 2007), and no "*Drinker*" type teeth (Bakker and others, 1990) have been found. Carpenter and Galton (2018) pointed out that both types of teeth have been found in the same jaw in some instances and synonymized both taxa with *Nanosaurus agilis* (Marsh, 1877; Galton, 1983). One unusual anterior tooth with root is preserved (figures 17L and 17M), though it has not been fully prepared yet.

Mammalia

Multituberculata

Allodontidae indet.

SDSM 26912 is a relatively large, partial right multituberculate dentary with p4 and m1 from the main pit of the Little Houston Quarry (figure 18A). The specimen was probably about 23 mm long when complete, with a p4 length of 2.6 mm. The coronoid process is intact, and the posterior part of the jaw consists of bone and an impression in matrix. The m1 is worn labially but appears to have had two rows of three cusps. The dentary anterior to the p4 is missing but is represented by an impression in the matrix for part of its length. The specimen was identified as *Psalodon*? *marshi* in its first description by Martin and Foster (1998); that species is also known from Quarry 9 at Como Bluff (Simpson, 1929). This specimen was the first mammal found at the Little Houston Quarry.

SDSM 26912 differs from *Ctenacodon serratus* and *C. scindens* in the larger size of the p4, the larger overall size of the jaw, the relatively smaller m1 (compared with p4), and the slightly greater ratio of the depth of the dentary below p4 to the dentary length (table 2;

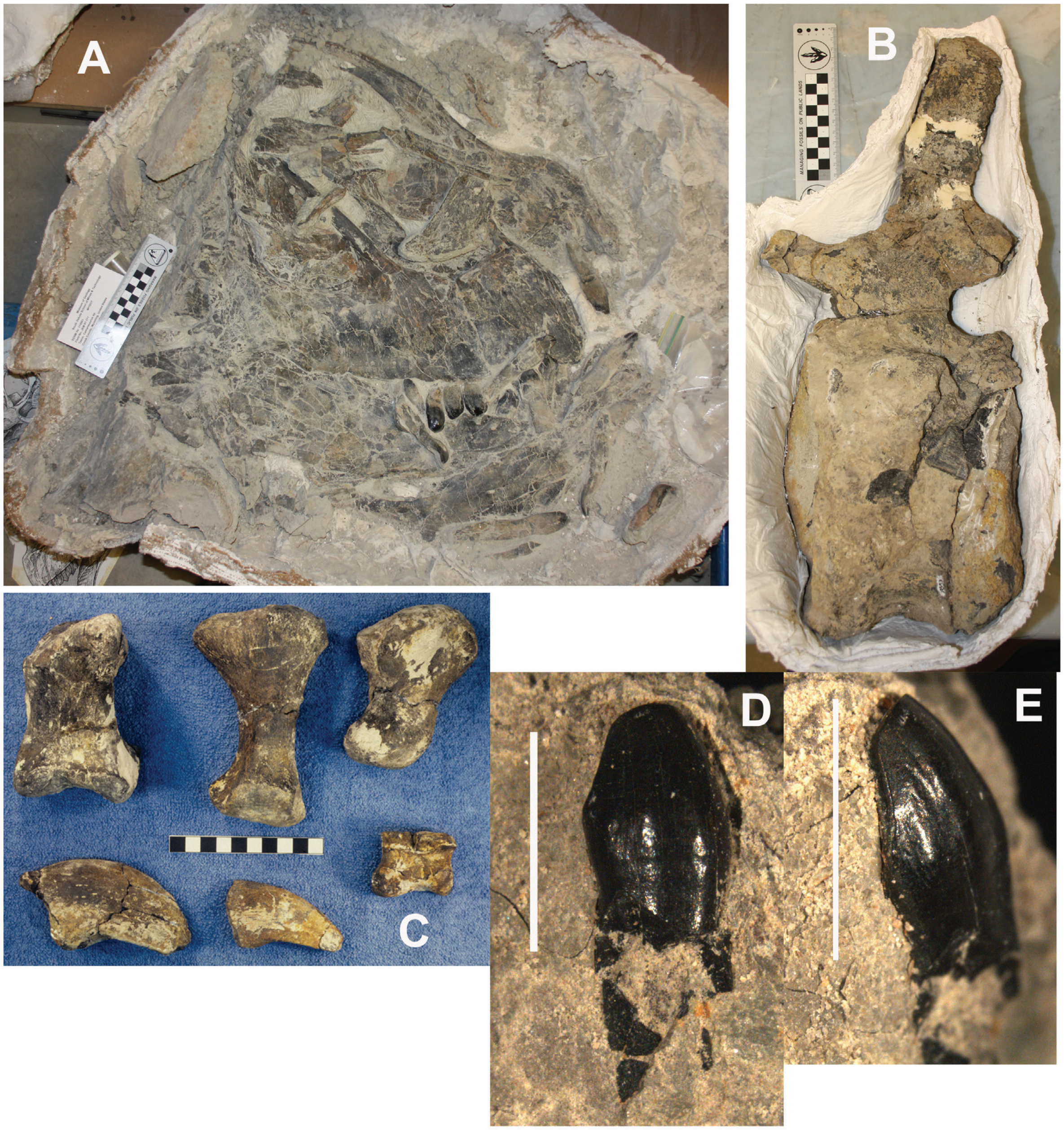

Figure 15. Representative Little Houston Quarry *Camarasaurus* (Dinosauria, Sauropoda). (A) Skull in right lateral view, SDSM 114501, showing displaced teeth and offset of premaxilla. (B) Left lateral view of caudal vertebra, SDSM 35943, from mammal pit specimen. (C) Partial foot of juvenile individual including metatarsals I, IV, and V, phalanx, and two unguals, SDSM specimen. (D and E) Tooth of hatchling(?) individual in (D) labial view and (E) distal(?) view showing wear facet. Scale bars in A to C in cm; scale bars in D and E = 5 mm.

Simpson, 1929). The specimen is similar to *Zofiabaatar* (Bakker and others, 1990) in the dentary length, the length of p4, and the dentary depth to length ratio, but it differs from that taxon in having: (1) an m1 relatively not as small (compared with p4), (2) an m1 with two rows of three cusps (as opposed to two of two in *Zofiabaatar*), and (3) a condyle not facing as much dorsally as that taxon (table 2; Carpenter, 1998). SDSM 26912 differs from *Glirodon grandis* in larger overall size and larger p4, in having a smaller m1 compared to p4, and

Figure 16. Dorsal(?) plate fragment of Stegosauridae indet. from the Little Houston Quarry, SDSM 25300. Scale bar = 5 cm.

in having a less robust ramus (table 2; Engelmann and Callison, 1999). As in *Ctenacodon*, the post-coronoid portion of the ramus of SDSM 26912 is also relatively longer than in *Glirodon*.

The specimen is similar to *Psalodon*? *marshi* in the structure of m1 and in having a large p4, but it differs from that taxon in having an m1 smaller relative to p4 and has a seemingly longer, lower dentary with a less convex ventral border in lateral view and apparently with a smaller incisor.

SDSM 26912 appears not to fit well with *P.*? *marshi*, *Ctenacodon*, *Glirodon*, or *Zofiabaatar* and may in fact represent a separate as yet unidentified multituberculate taxon in the Morrison Formation. *P.*? *marshi* itself (e.g., USNM 2684) in fact may represent a taxon closer to *Plagiaulax becklesii* and may not be closely related to *Ctenacodon*.

Docodonta

Docodontidae

Docodon cf. *apoxys*

Several jaw fragments and isolated teeth of *Docodon* have been found since 1993 (Martin and Foster, 1998; Foster and others, 2006), when the first mammal specimens were uncovered. These specimens include at least three dentary fragments (Foster and others, 2006; figure 18B), a maxilla fragment (figure 18F), a large canine (figure 18D), and some isolated molars. The molars of at least one of the specimens are of the type described for *D. apoxys* from Garden Park (Rougier and others, 2015) in having reduced molar size near the posterior end of the dentary, especially in the last molar (as indicated by alveolus size in the case of the Little Houston Quarry specimen). This specimen (SDSM 60480; figures 18B

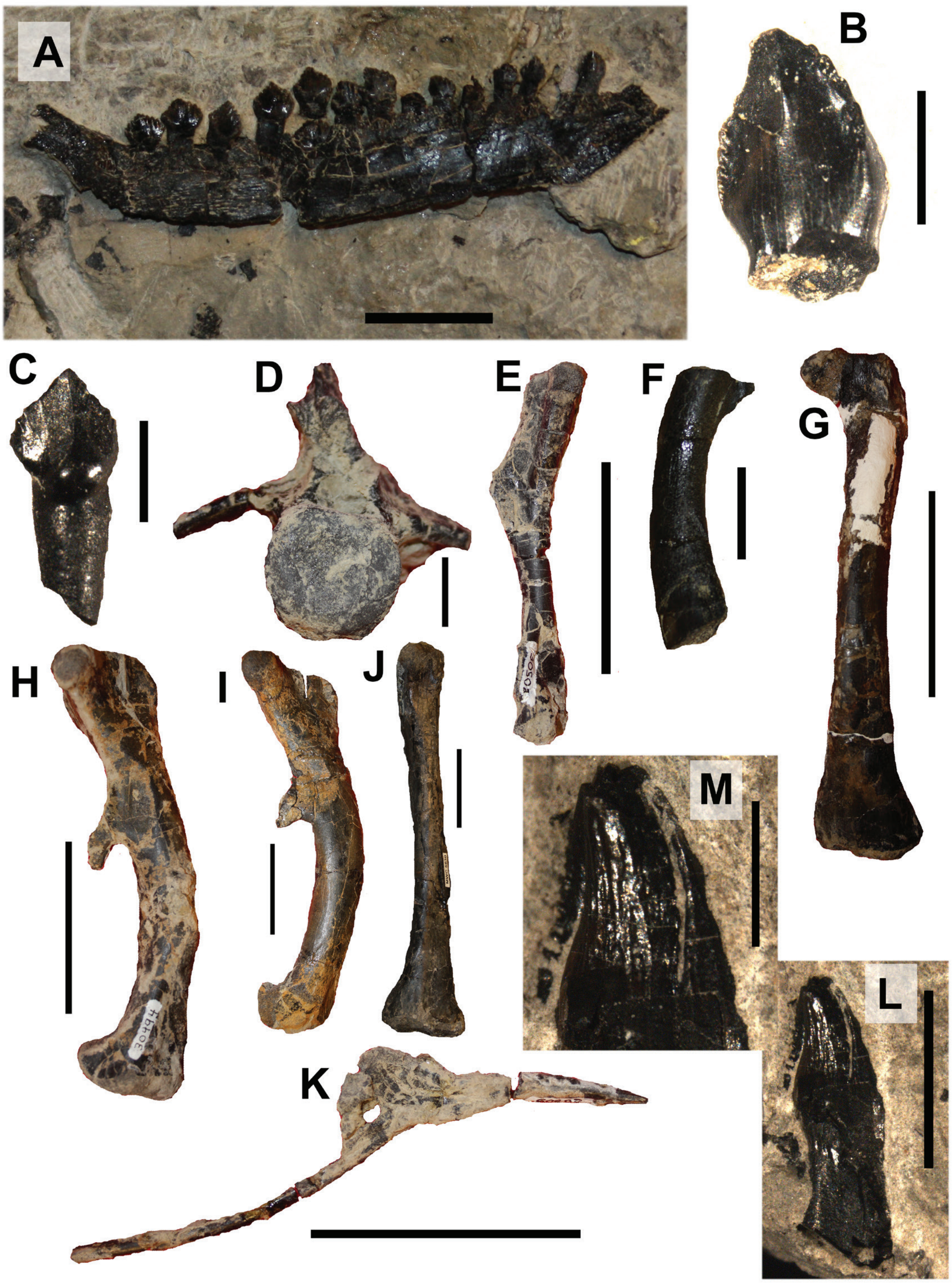

Figure 17. Representative Little Houston Quarry *Nanosaurus* (Dinosauria, Neornithischia). (A) Right dentary with 13 teeth in labial view, MWC 5822. (B) Anterior tooth in lingual view, JRF 95220. (C) Lateral tooth in labial view, JRF 95148. (D) Caudal vertebra in posterior view, SDSM 30496. (E) Right humerus in medial view, SDSM 30502. (F) Tiny femur mid-shaft with partial fourth trochanter, JRF 9822. (G) Left femur in anterior view, SDSM 26913. (H) Complete left femur in medial view, SDSM 30494. (I) Complete left femur of adult in medial view, SDSM 30490. (J) Complete tibia in posterior view, MWC 5630. (K) Right pubis, SDSM 30503. (L and M) Anterior tooth in lingual view and close-up, JRF 95126. Scale bars: A, D, F, and L = 1 cm; B, C, and M = 5 mm; E and G to K = 5 cm.

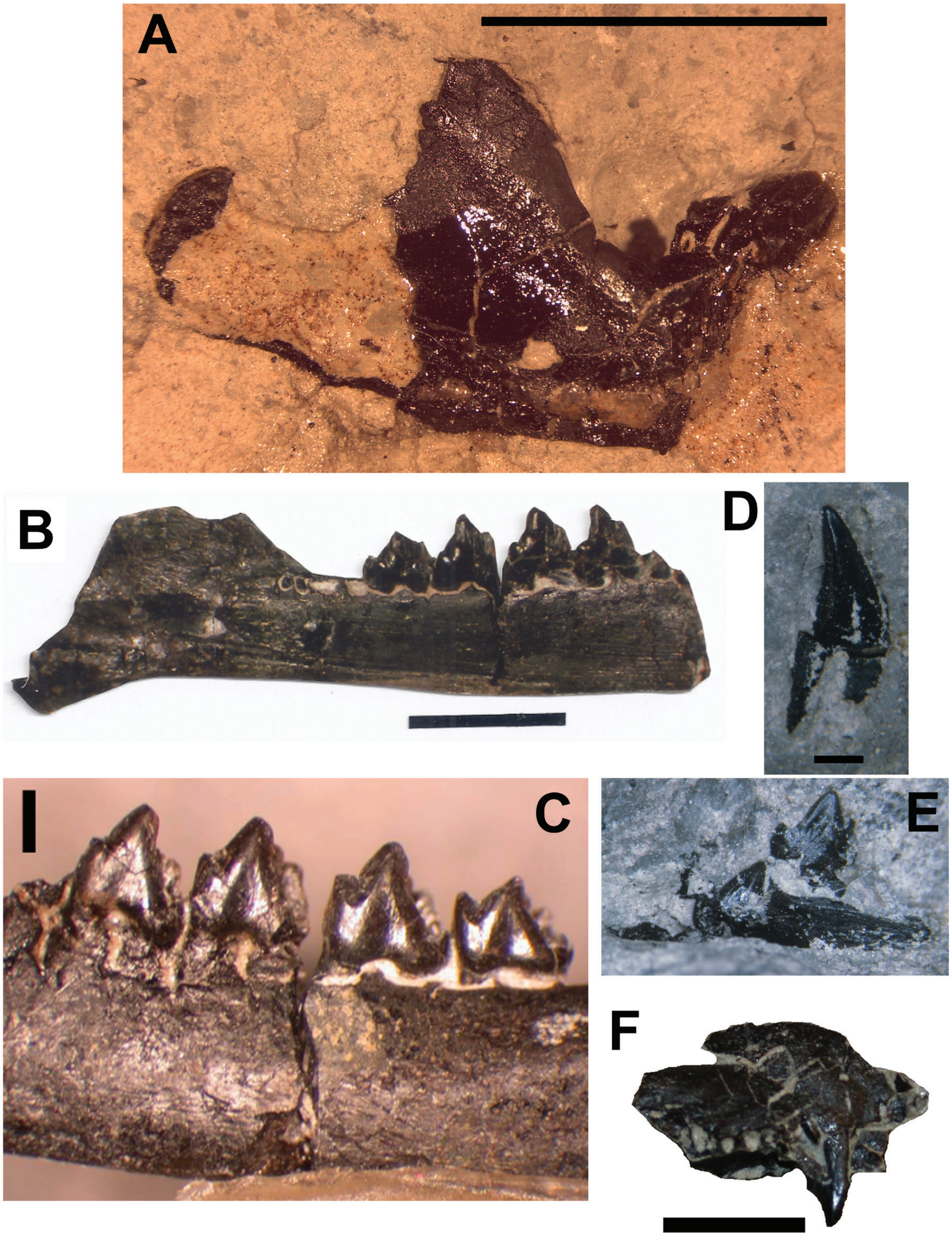

Figure 18. Little Houston Quarry multituberculate and docodont mammals. (A) Partial right dentary with p4 and m1, in labial view, assigned to Allodontidae indet., SDSM 26912. Scale bar = 1 cm. (B to F) *Docodon*. (B) Partial left dentary of *Docodon* cf. *apoxys*, SDSM 60480, in lingual view, with m2–5(?) and alveoli for m6 and m7. Scale bar = 5 mm. (C) Close-up labial view of molars m2–m5(?) of jaw in B (SDSM 60480). Scale bar = 1 mm. (D) Canine tooth in lingual(?) view, SDSM specimen. Scale bar = 1 mm. (E) Jaw fragment with lower molar, incoming more distal molar(?), and some dentary bone, SDSM specimen. Molar length ~2 mm. (F) Left maxilla fragment with canine, MWC specimen, in lingual view. Scale bar = 5 mm.

Table 2. Comparison of features of various species and specimens of jaws of multituberculate mammals from the Morrison Formation.

	Ctenacodon	*Psalodon? marshi*	*Zofiabaatar pulcher*	*Glirodon grandis*	SDSM 26912
Dentary Length	17.5	Incomplete	23	17.3	**~23.3**
Length p4	1.65	3	2.6	1.9	**2.6**
Length p4:m1	1.4	1.43	1.98	1.5	**1.72**
Dentary depth at p4: Dentary length	0.192	Incomplete	0.257	0.297	**0.235**
m1 cusps	2 rows of 3	2 rows of 3	2 rows of 2	2 rows of 3	**2 rows of 3**
Dentary ramus deeper under coronoid	No	No	Yes	No	**No**
Dentary condyle facing	Posteriorly	Posteriorly	Posterodorsally	Posterodorsally	**Posteriorly**
References	Simpson, 1928, 1929	Simpson, 1929	Bakker and others, 1990; Carpenter, 1998; Kielan-Jaworowska and others, 2004	Engelmann and Callison, 1999	**This report**

and 18C) consists of a partial left dentary with m2–5(?) and alveoli for m6 and m7 of reduced size (especially m7). This specimen would be the first occurrence of *D. apoxys* outside of its type area in Garden Park, Colorado. *Docodon* is well known from a number of sites in Wyoming (Quarry 9 and others) and eastern Colorado (Small and Marsh-Felch Quarries, Garden Park) (Simpson, 1928; Kielan-Jaworowska and others, 2004), although it is absent from the Morrison of the Colorado Plateau (Foster and others, 2006).

Cladotheria
Dryolestida
Dryolestidae
Amblotherium
Amblotherium megistodon, sp. nov.
Figure 19

LSID. urn:lsid:zoobank.org:pub:A69FB058-C18B-4AAF-BC4B-EE68E3682561.

Type Specimen

SDSM 148545, left dentary preserved in labial view with p2–p4 and m1–m3 in place.

Type Locality

Little Houston Quarry (mammal pit), Crook County, Wyoming (Foster and Martin, 1994; Foster, 2001).

Type Horizon

Morrison Formation undifferentiated; thin local Morrison section of only ~23 m (Mapel and Pillmore, 1963); thickness and intraformational correlation with other localities in Wyoming unknown.

Etymology

From Greek μεγίστ (megist) meaning "largest" + όδόυ (odon) meaning "tooth," in reference to the much larger overall size compared with other species of *Amblotherium* (*A. gracile* and *A. pusillum*), especially as reflected in the teeth.

Diagnosis

Amblotherium species with isometrically larger dentary and teeth than other species of the genus (m3 up to 87% longer than in other species; 1.5 mm mesiodistal length compared with average of 0.80 mm in *A. pusillum* and *A. gracile*) and differing from other species of the genus in having roots of unequal size in m1 and m2 as well as more distal molars; other characters match generic diagnosis of *Amblotherium*.

Description and Identification

SDSM 148545 is a mostly complete left dentary with p2–p4 and m1–m3 (figure 19) and is a dryolestid, as indicated by the enlarged and bean-shaped mesial alveolus and reduced, oval-shaped distal alveolus of m4. The dentary is 21.97 mm long as preserved and is missing only the anterior end (incisors and full canine alveoli not preserved), posterior tip, and upper coronoid process. The jaw is in a piece of matrix with the labial and occlusal surfaces exposed, and preparation has exposed the lingual sides of the preserved teeth. The six

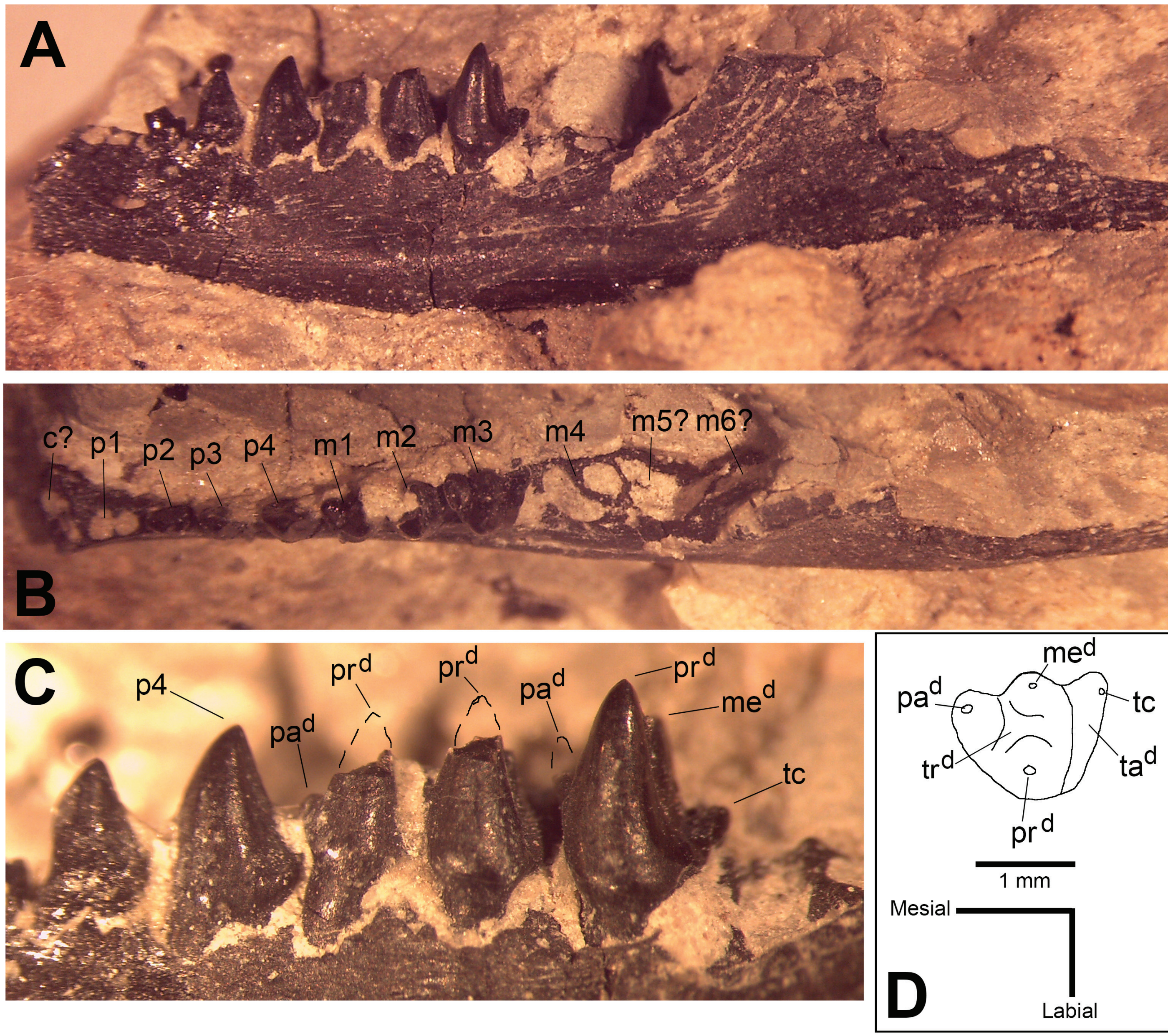

Figure 19. Dryolestid mammal *Amblotherium megistodon* n. sp., SDSM 148545, holotype, left dentary, Little Houston Quarry. (A) Labial view showing p2–p4 and m1–m3. Total length of specimen as preserved is 21.97 mm. (B) Occlusal view showing teeth and alveoli (as labelled) from partial canine(?) alveolus to m6(?). (C) Close-up view of p3–m3 in labial view with cusps labelled. Length of m3 = 1.5 mm. Protoconid cusp heights (m1 and m2) reconstructed from field photos. (D) Tracing of photo of m3 in occlusal view showing features and proportions. Abbreviations for C and D: me^d = metaconid, pa^d = paraconid, pr^d = protoconid, p4 = premolar 4, tc = talonid cusp, ta^d = talonid, tr^d = trigonid.

preserved teeth include p2–p4 and m1–m3, and the alveolus for p1 is exposed too (figure 19). The alveoli for m5 and m6 are poorly preserved due to partial crushing and are positioned partly lingual to the base of the coronoid process, suggesting the individual is a juvenile (Martin, 1999, 2000).

The cusps of the molars are sharp and slender (figure 19C). The molars differ from those of *Laolestes* in not having a bifid metaconid, in not having the paraconid and talonid cusp positioned internal to the metaconid (figures 19B and 19D), and in having an essentially erect (not slightly procumbent) paraconid. The premolars lack the anterior accessory cusp characteristic of *Dryolestes* (other than *D. leirensis*), and the molars differ from those of *Dryolestes* in having a more erect rather than procumbent paraconid (m3 cusp reconstruction in figure 19C based on pre-damage preliminary images). The jaw matches *Amblotherium* in having: (1) a slender ramus, (2) molars with an erect paraconid close to the height of the metaconid, (3) molars with a weak external cingulum, and (4) a coronoid with a low-sloping anterior edge (Simpson, 1928, 1929; Kielan-Jaworowska and others, 2004).

The slenderness of the ramus in SDSM 148545 is indicated by the ratio of the maximum jaw depth to the reconstructed jaw length, and the ratio is similar to *Amblotherium* (SDSM 148545 only 4.5% lower than other species of *Amblotherium*; see table 3). This dentary slenderness ratio also differentiates the Little Houston dentary from *Dryolestes* and *Laolestes* (ratio 19.7% lower than in *Dryolestes*; ratio 24.3% lower than in *Laolestes*). Molar size differs relative to jaw depth in SDSM 148545 and *Amblotherium* versus *Dryolestes* and *Laolestes*, with the latter genera having relatively lower crowned molars. The ratio of the crown height of m3 to the depth of the dentary below m3 ranges from means of 0.366 and 0.362 for *Dryolestes* and *Laolestes*, respectively, to 0.707 and 0.657 for *Amblotherium* and SDSM 148545 (table 3). *Amblotherium* (including SDSM 148545) demonstrates a more dramatic increase in molar crown height from position m1 to m3 compared to *Dryolestes* and *Laolestes*, as indicated by the ratio of m3 crown height to that of m1 (table 3).

SDSM 148545 differs from other species of *Amblotherium* in having a dentary length and molar mesial-distal length more similar to *Dryolestes* (table 3). The lengths of m3 in *Dryolestes* and SDSM 148545 are approximately 1.5 mm in each case, whereas the mean of four specimens of *A. pusillum* and *A. gracile* is 0.80 mm (Simpson, 1928, 1929), a size increase of approximately 87.5% from other species of *Amblotherium* to *A. megistodon* (SDSM 148545). The Little Houston Quarry jaw also differs from other species of *Amblotherium* in having the roots of m1 and m2 being unequal in size, as in the positions from m3 back; in some specimens of other species the first two molars have "normal" roots of equal size.

Phylogenetic analysis, incorporating the matrix of Rougier and others (2012) and adding two characters (appendix), places SDSM 148585 among dryolestids in a polytomy with *Amblotherium* (based on *A. pusillum* and *A. gracile*), *Comotherium*, and *Laolestes+Groebertherium*, with *Dryolestes* as a sister taxon to the clade (figure 20). The unresolved nature of the *Comotherium-Amblotherium*-SDSM 148545 polytomy is likely caused by missing data in SDSM 148545, particularly in the less well preserved posterior dentary region and in the lack of upper jaws. In Rougier and others (2012) this relationship (minus SDSM 148545) was resolved as *Dryolestes*+(*Comotherium*+([*Amblotherium*+(*Laolestes+Groebertherium*)]). *Comotherium* was described as a dryolestid (Prothero, 1981) but has since been classified as a paurodontid by others (Martin, 1999; Kielan-Jaworowska and others, 2004).

Discussion

The jaw length as preserved (~22 mm) suggests a mass estimate for *Amblotherium megistodon* of 33.2 g, compared with estimates of 25.9 g for other species of *Amblotherium*, 71.3 g for *Laolestes*, and 103.7 g for *Dryolestes* (Foster, 2009). However, the facts that SDSM 148545 appears to be a juvenile and that the length of m3 is essentially the same as in adult *Dryolestes* suggest that the adult animal likely would have approached *Laolestes* and *Dryolestes* in mass. At the very least, the complete dentary of SDSM 148545, with the missing anterior and posterior ends restored, was likely close to 26 mm long, a length indicating a possible mass of 54.5 g (formula of Foster, 2009), a size making *A. megistodon* the ninth largest mammal in the Morrison mammal fauna (of 22). *Amblotherium gracile*, in contrast, is the sixth smallest in the group.

Amblotherium comprises the species *A. gracile* from the Upper Jurassic Morrison Formation and *A. pusillum* from the Upper Jurassic-Lower Cretaceous Purbeck Group of England (Simpson, 1928, 1929; Martin, 1999, 2000; Kielan-Jaworowska and others, 2004; Ave-

Table 3. Comparison of features of various dryolestid mammal jaws from the Morrison Formation. All measurements in mm.

	Dryolestes	***Laolestes***	***Amblotherium***	**SDSM 148545**
Dentary Length	30.5 (Gui Mam 130/75)	27.5 (YPM 13719)	18.2 (BMNH 47752)	~22.0
Length m3	1.5	1.25	0.8	1.5
Dentary depth: length	0.132	0.14	0.111	~0.106
Height m3: Dentary depth (mean)	0.366 (N=3)	0.362 (N=2)	0.707 (N=4)	0.657
Height m3:m1 (mean)	1.29 (N=4)	1.14 (N=1)	1.65 (N=3)	1.38

rianov and others, 2013, 2014). *Amblotherium gracile* includes *A. debile* and *Miccylotyrans* (Averianov and others, 2013) and is known from Como Bluff (Quarry 9 and Chuck's Prospect), Dinosaur National Monument (Rainbow Park), and Garden Park (Marsh-Felch) in the Morrison Formation. *Amblotherium megistodon* is then a second species within the Morrison Formation. In addition to partial jaws of *Amblotherium gracile* from Quarry 9 at Como Bluff (Simpson, 1929), several referred lower molars from the Rainbow Park microvertebrate sites at Dinosaur National Monument were described by Engelmann and Callison (1998). These latter teeth were small and of an "*A. debile*" size of 0.62 to 0.72 mm length, in contrast to *A. megistodon*'s molar length of ~1.5 mm

The presence of a species of *Amblotherium* in the Morrison Formation that is more than 87% larger than *A. gracile* suggests that either there were two co-existing and niche-partitioned species present in the region during the Late Jurassic or that the genus underwent body-size evolution over the course of Morrison times. Because of the inability to correlate the very thin Morrison Formation of the Black Hills to other, thicker sections in Wyoming or elsewhere, it is unclear if *A. megistodon* represents a larger contemporary of *A. gracile* or if it represents an anagenetic change in body size within *Amblotherium* through some part of the ~7 million years of the formation. If the latter, it is even unclear whether the change in body size would have been an increase or decrease. On the other hand, a larger but contemporaneous species in the northern part of the Morrison Formation could indicate some degree of paleobiogeographic segregation within the genus, but this is not yet conclusive.

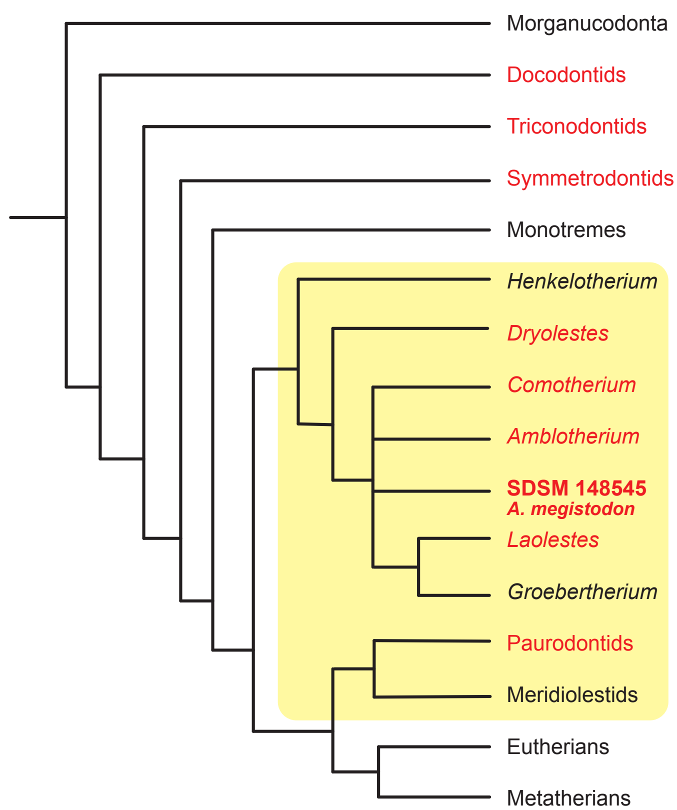

Figure 20. Simplified phylogenetic tree based on strict consensus of 12 MTPs from analysis of 60 taxa and 319 characters (length = 1226), showing relationships of SDSM 148545 (*Amblotherium megistodon*) and other dryolestids. Red text indicates taxa with representatives in the Morrison Formation; yellow box indicates traditional Dryolestida.

BONE MODIFICATIONS

Many of the sauropod bones from the Little Houston Quarry (but far fewer of the bones of smaller taxa such as neornithischians) possess a few to near-complete covering of surficial pits, especially along the shafts of long bones (figure 21). These pits are similar to those described as being caused by low pH soil conditions or alternatively by boring dermestid beetles or their larvae (Fiorillo, 1998; Britt and others, 2008; Bader and others, 2009). Most sauropod limb elements from the Little Houston Quarry have at least some of these pits, and a number of elements are almost completely covered in them. These modifications suggest at least some subaerial exposure or burial in acidic soils for many of the sauropod elements from the site.

THEROPOD(?) TRACKS

Several small, tridactyl dinosaur tracks of a *Grallator*-like morphology were found in a sandstone block displaced from just below the quarry level (figure 22), and these were described by Foster and Lockley (1995). These tracks probably represent small theropod dinosaurs, though some may possibly have been made by small neornithischians.

DISCUSSION

Paleoenvironmental Setting

The Little Houston Quarry contains a very dense deposit of vertebrate material ranging in size from large sauropod dinosaurs to microvertebrates in thin and laterally restricted layers of an elongate, ribbon-shaped deposit above a channel sandstone (figure 23). The deposit is laterally restricted to the space between visible edges incised into variegated floodplain mudstones and is much longer than wide ("ribbon" geometry). The transition from a thin and laterally restricted channel sandstone (with mud clasts) into the quarry interval of interbedded green claystone and sometimes laminated, clay-ball bearing siltstone (figure 2B), similarly laterally restricted, and then into pure floodplain mudstone, all suggests a gradually in-filling abandoned channel that was occasionally reactivated during floods (Foster, 2001; e.g., Miall, 2010). The quarry layer itself probably represents the laminated fill unit of a fully disconnected channel (e.g., Toonen and others, 2012), and most well-preserved microvertebrate bone elements within the deposit are probably parautochthonous to autochthonous (Behrensmeyer, 1988; Foster, 2001; Rogers and Brady, 2010).

Taphonomy

The Little Houston Quarry contains microvertebrate material in great abundance and in relatively highly defined layers but with a high degree of disarticulation (~100%) and fragmentation, and its lithology consists of siltstone with heterogeneous clasts of clay balls and small bone fragments (Foster, 2001). It thus represents a broad Type 1 pond deposit taphofacies for microvertebrate remains in the Morrison Formation, along with

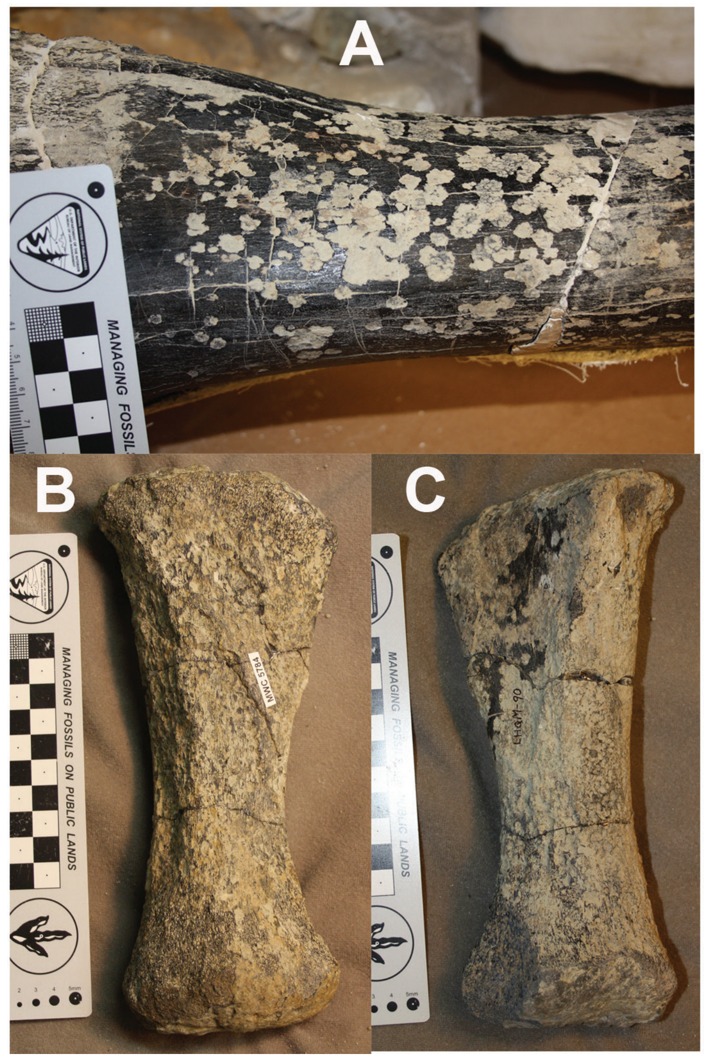

Figure 21. Modifications of sauropod dinosaur bones from the Little Houston Quarry. (A) Pitting on shaft of sauropod ulna SDSM 35952. (B and C) Near-total coverage by pitting on a sauropod metapodial MWC 5784. Scale bars in cm.

Figure 22. Tridactyl (theropod?) dinosaur track on sandstone slab from channel just below Little Houston Quarry (see Foster and Lockley, 1995). Scale bar numbered in inches.

the Small Quarry at Garden Park, Colorado, and Quarry 9 at Como Bluff, Wyoming (Foster, 2001, 2003). This taphofacies contrasts markedly with broad Type 2 pond deposits typical of the Morrison Formation of the Colorado Plateau, the latter consisting of usually "clean" grayish mudstone with a very low-density deposit of sometimes articulated or associated material, including whole or partial skeletons of microvertebrates such as mammals and sphenodontians (Foster 2001, 2003); localities of this type include the Callison and Tom's Place sites at the Fruita Paleontological Area, Colorado (Callison, 1987; Kirkland, 2006), Rainbow Park 94 and 96, Dinosaur National Monument (Evans and Chure, 1998, 1999; Evans and others, 2005), Wolf Creek, Colorado (Wood, 1986), and Cisco Mammal Quarry, Utah (Davis and others, 2018). Matrix samples from Little Houston, Small Quarry, and Quarry 9 placed side by side can be almost indistinguishable from each other and would presumably represent somewhat similar pond settings, although the details of their respective settings differ. The Little Houston Quarry, situated on top of a channel sand, appears to represent the in-filling of an abandoned channel pond (Foster, 2001), whereas Quarry 9, the main fossiliferous lens of which was under a sandstone (Carrano and Velez-Juarbe, 2006), probably represents a floodplain pond followed by avulsion of a main river channel. The Small Quarry microvertebrate layer is just below a crevasse-splay sandstone series (Rougier and others, 2015) and was probably in a floodplain pond and apparently near a river channel as well.

So far, Type 1 pond deposits (Little Houston, Small Quarry, Quarry 9) are restricted to the northern and eastern parts of the Morrison Formation, and Type 2 deposits (FPA, Rainbow Park, Wolf Creek, and Cisco Mammal) are only known from the Colorado Plateau region in the Morrison. This taphofacies segregation may reflect the relative abundance differences in the occurrences of turtles and semi-aquatic crocodyliforms between the Colorado Plateau and areas north and east (Foster and McMullen, 2017), the north- and east-restricted distributions of possibly semi-aquatic mammalian and archosauromorph taxa in *Docodon* and *Cteniogenys* (Chure and Evans, 1998; Foster and Trujillo, 2000; Foster and others, 2006), and geologic evidence suggesting a higher water table and wetter surface conditions during Morrison times in areas that are now parts of Wyoming and eastern Colorado (Turner and Peterson, 2004). The Little Houston Quarry therefore helps characterize the faunas of the northern and eastern "wet" setting of the Morrison Formation.

In contrast to the microvertebrate material, up to 25% of dinosaur material in the quarry is in articulation, although the dinosaur material is part of the same dense accumulation as the small taxa. Almost uniquely, microvertebrate remains occur in among the articulated and disarticulated dinosaur remains as well, with some mammal jaws from the mammal pit being found centimeters away from an articulated series of *Camarasaurus* caudals.

Paleobiodiversity

With at least 26 vertebrate taxa preserved (and 35

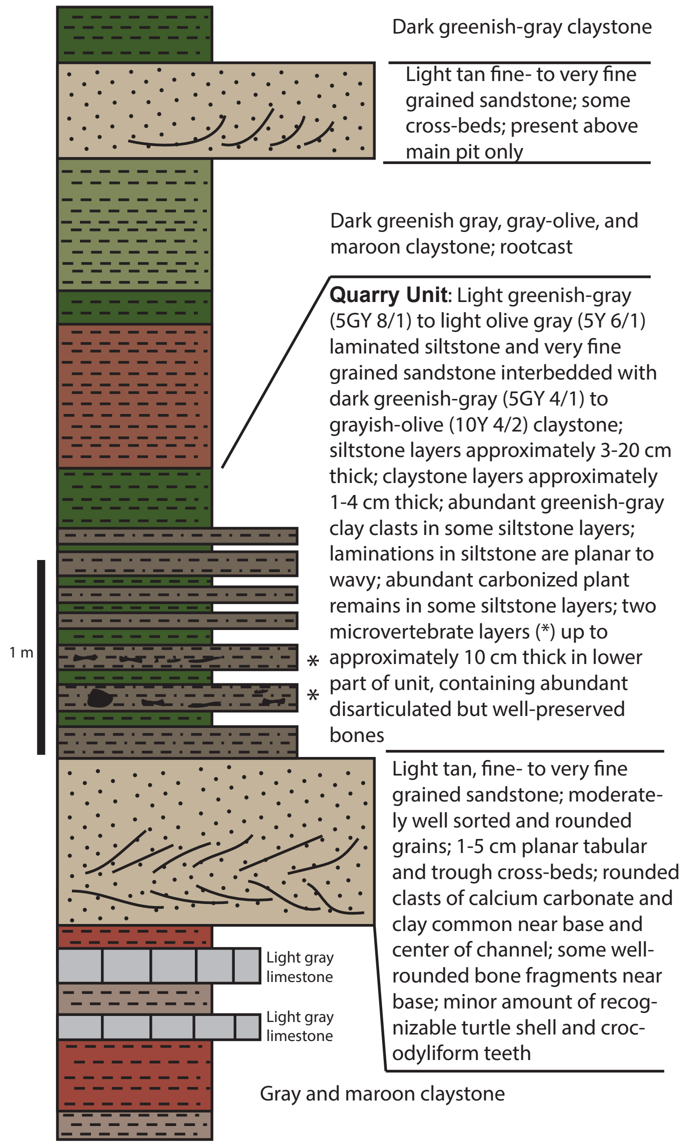

Figure 23. Stratigraphic section of Morrison Formation exposure at the Little Houston Quarry showing position of main bone layers (*) above thin channel sandstone.

taxa total), the biota from the Little Houston Quarry is the second-most diverse single locality in the Morrison Formation after Reed's Quarry 9 (Foster, 2003), the latter at 76 species (72 vertebrates; Carrano and Velez-Juarbe, 2006). The Little Houston Quarry represents the most diverse Morrison Formation locality north of Como Bluff, Wyoming, and it is important for studying what seems to be a newly recognized "northern fauna" of the unit (e.g., Maidment and others, 2018). The Little Houston Quarry is followed closely in vertebrate diversity by the Dry Mesa Quarry of Colorado, and then several others.

Beyond the shared taphonomic characteristics, the biota of the Little Houston Quarry shares with Quarry 9 and the Small Quarry several faunal similarities: (1) a relative abundance of *Docodon* specimens among the mammalian genera (Little Houston and Small appear to specifically share the species *D. apoxys*); (2) a relative abundance of *Cteniogenys* (so far absent at Small); (3) actinopterygian fish represented by vertebrae, teeth, and jaw fragments; (4) the lungfish *Ceratodus fossanovum* (Little Houston and Quarry 9 at least); and (5) relatively abundant turtles and semi-aquatic crocodyliforms. These are taxa and patterns that are absent or rare in Type 2 deposits on the Colorado Plateau.

Most of the diversity at the Little Houston Quarry is among microvertebrate taxa, and several of the species are particularly rare in other parts of the Morrison Formation. Among these latter taxa are the potentially new, elongate unionid bivalves (figures 5E and 5F), the first occurrence of the atoposaurid crocodyliform *Theriosuchus* in the Morrison Formation (figures 12A to 12C), several unusual small theropod tooth types (figures 13 and 14), a new species of *Amblotherium* (figure 19), and the first occurrence of the mammal *Docodon apoxys* outside its type locality (figure 18). The abundance of aquatic and semi-aquatic taxa in the deposit reflects the abandoned channel pond setting. The diversity of the biota is probably not unusual for the paleoenvironment of the northern Morrison Formation but more likely is a product of preservation in a highly concentrated deposit.

The Morrison Formation of the Black Hills of Wyoming and South Dakota may preserve even more taxa than are currently known, including possibly new species, but it has been difficult to fully compare the biota from the area to other parts of Wyoming and the Colorado Plateau due to the thinness of the unit in the Black Hills and the apparent lack of smectitic mudstones, both preventing lithostratigraphic correlations or radiometric age comparisons (e.g., Turner and Peterson, 1999; Trujillo and Kowallis, 2015). The diverse biota present at the Little Houston Quarry, and the unusual taxa preserved there, suggest that the region may yet hold even more information about the apparent "northern fauna" of the Morrison Formation.

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