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REPORT OF A DIVERSE VERTEBRATE BODY FOSSIL ASSEMBLAGE IN THE MAROON FORMATION (CARBONIFEROUS–PERMIAN), EAGLE COUNTY, COLORADO, U.S.A.

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ABSTRACT

The Carboniferous–Permian (C–P) Maroon Formation of western Colorado preserves a paleotropical record of continuous terrestrial sedimentation during Earth's penultimate icehouse-hothouse state change: the "Late Paleozoic Ice Age." In the last twenty years, reports of vertebrate fossils, including tetrapod trackways, have suggested a diverse terrestrial vertebrate fauna adapted to dryland conditions comparable to the famous Permian Tambach vertebrate assemblage of Germany, but body fossils in the formation have remained elusive. Here, we describe the first vertebrate body fossils from the Maroon Formation and discuss them in the contexts of the known ichnoassemblage and C–P environmental change. The vertebrate fossils occur within a sequence of thin carbonate beds in the lower portion of the formation and represent a largely aquatic assemblage. We identify the remains of xenacanth and hybodont chondrichthyans, including the hybodont *Hamiltonichthys*, actinopterygians, including a platysomid and a pygopterid closely comparable to *Progyrolepis*, the lungfish *Sagenodus*, and an amphibamiform temnospondyl (among other rare and isolated tetrapod elements). The assemblage provides biostratigraphic data that may correlate the lower portion of the Maroon Formation to the late Carboniferous and the stratigraphically higher red siltstones to the early Permian (Wolfcampian), and therefore a continuous record of deposition across the C–P boundary. The new assemblage preserves a snapshot of one of the latest known Carboniferous wetland faunas in western Colorado prior to Pangean climate-drying during the peak Late Paleozoic Ice Age.

KEY WORDS: Carboniferous, Colorado, Eagle Basin, Late Paleozoic Ice Age, Pennsylvanian

INTRODUCTION

Carboniferous–Permian (C–P) vertebrate fossils from the southwestern United States have played a key role in understanding the evolution of continental ecosystems following the "collapse" of the long-lived Carboniferous coal swamps (Olson and Vaughn 1970; Sahney et al. 2010; Dunne et al. 2018; Pardo et al. 2019). The classic C–P redbeds in northern New Mexico and Utah, for example, document diverse assemblages of terrestrial tetrapods during progressive climate-drying and the establishment of herbivore-based foodwebs by Permian times, foreshadowing "modern" terrestrial community structure (Olson 1966; Olson and Vaughn 1970). Though lesser known, C–P redbeds in western Colorado were historically among some of the first in the southwest to yield well-preserved vertebrate material during early geological exploration, including the early discoveries of David Baldwin near modern-day Durango in the 1870s and 1880s (Case and Williston 1912) and later systematic collecting in San Miguel, Ouray, and Fremont counties (Lewis and Vaughn 1965; Vaughn 1969, 1972). However, with a few exceptions (e.g., Gee et al. 2021), attention has shifted to more productive localities in Texas, Oklahoma, and New Mexico, making it difficult to put these early finds into context.

Comparisons between these Colorado localities and regions of greater research focus have nevertheless emerged, requiring additional consideration of the C–P beds of western Colorado. One example of this has been the discoveries of well-preserved tetrapod footprints and trackways in the Maroon Bells of Eagle Basin, Colorado, which show similarities to the famous Permian Tambach assemblage of Germany (Voigt et al. 2005, 2021). Both ichnofaunas are dominated by herbivorous diadectid amniotes as well as abundant small-bodied reptiles. Consequently, the shared ichnospecies potentially suggest a widespread C–P terrestrial amniote fauna spanning the entirety of paleotropical Euramerica. Thus, ongoing studies of contemporaneous C–P assemblages in understudied basins—and comparisons of different C–P basins—can further refine our understanding of early continental vertebrate biogeography.

The Maroon Formation in present-day Colorado was deposited in a low-latitude (5–10° north paleolatitude), north-south trending basin on the northern edge of the central Colorado trough (Scotese 1997; Loope et al. 2004; Soreghan et al. 2014). The basin was geographically situated between the ancestral Front Range to the east, Uncompahgre Highlands to the west, and Sawatch Uplift to the south, forming an isolated drainage system that flowed northward (Johnson 1987b) into what is today the Eagle Basin. As such, the Eagle Basin was apparently cut off from the better-sampled Paleozoic basins of northern New Mexico and Utah, which have yielded abundant vertebrate fossils. Moreover, a lack of biostratigraphically significant fossils, structural complexities, and rapid facies changes in Eagle Basin have hindered work on large-scale stratigraphic correlations (Langenheim 1954). Following the early 2000s discoveries of the tetrapod tracks in the Maroon Bells, systematic surveys and collecting in the upper Maroon Formation were conducted by the Denver Museum of Nature & Science, producing a diverse collection of footprints, trackways, and other ichnofossils (Voigt et al. 2005; Small and Sanders 2007). Notable vertebrate ichnotaxa in the Maroon assemblage included: *Tambachichnium*, *Varanopus*, *Dimetropus*, *Dromopus*, and abundant *Ichniotherium* (a diadectid). The track associations and additional geochronological evidence (e.g., U-Pb ages of detrital zircons; Soreghan et al. 2014) has suggested an early Permian (Wolfcampian) age for the upper Maroon Formation redbeds in the Frying Pan and Aspen sub-basins. Although tracks and traces are abundant and well documented in the Maroon Formation (Voigt et al. 2005, 2021), no vertebrate body fossils have been described to date.

In the summer of 2013, two of the authors (A.K.H. and J.D.P.) discovered a bone-bearing fossiliferous limestone near the base of the Maroon Formation in the Derby Junction area 8 km southwest of Burns, Eagle County, Colorado (Fig. 1). Investigation of the site over subsequent seasons (2014–2017) resulted in the identification of mixed carbonate-siliciclastic cycles with multiple thin limestone beds containing vertebrate material (Small et al. 2017). Prior reports of fossils from this area were limited to surface collected footprints recovered from 'float' and likely originating from the red siltstone facies (Voigt et al. 2005, 2021; Small and Sanders 2007), but the new site contains a unique assemblage of in situ vertebrate body fossils in transitional marine-nonmarine carbonate facies. This assemblage includes a variety of chondrichthyans (including xenacanths and hybodonts), actinopterygians, lungfish, and rare tetrapods (including a small temnospondyl amphibian). Thus, the juxtaposition of fossiliferous limestones and a terrestrial footprint assemblage in Eagle Basin presents a snapshot of adjacent coastal wetland habitats just prior to Permian climate-drying and the ultimate disappearance of these habitats from western basins. This snapshot shows important biogeographic connections to neighboring Carboniferous basins and clarifies the age of the lower portion of the Maroon Formation, while also preserving distinct elements not preserved in the overlying redbed footprint assemblage.

Institutional abbreviations: **CM**, Carnegie Museum of Natural History, Pittsburgh; **DMNH**, Denver Museum of Nature & Science, Denver; **UMNH**, Natural History Museum of Utah, Salt Lake City.

GEOLOGY AND ENVIRONMENT

The Maroon Formation accumulated in a subsiding intracratonic basin situated between salt anticlines associated with the Ancestral Rocky Mountain orogeny (late Paleozoic), although its precise depositional age is poorly constrained. The Maroon Formation was named by

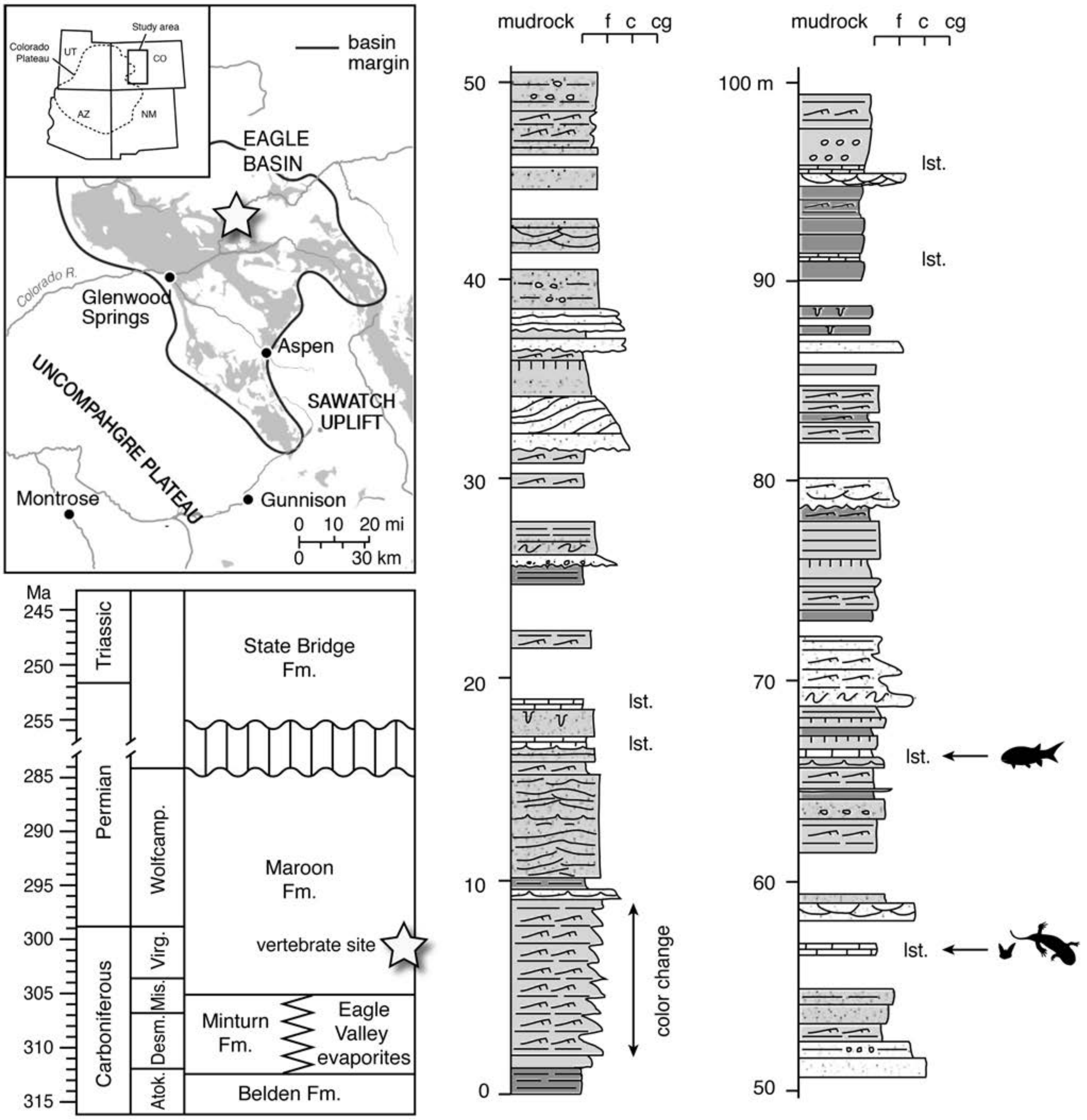

Fig. 1.—Field area and stratigraphic context. Map of the field area in western Colorado (upper left inset). Gray shading represents extent of Carboniferous–Permian redbed outcrops. Star shows location of the vertebrate site. Generalized stratigraphic column with detailed measured section (right) in the Derby Junction area, Eagle County, Colorado, modified from Johnson (1987a). **Abbreviations: Atok.**, Atokan stage; **Desm.**, Desmoinesian stage; **Fm.**, formation; **lst.**, limestone; **Mis.**, Missourian stage; **Virg.**, Virgilian stage; **Wolfcamp.**, Wolfcampian stage.

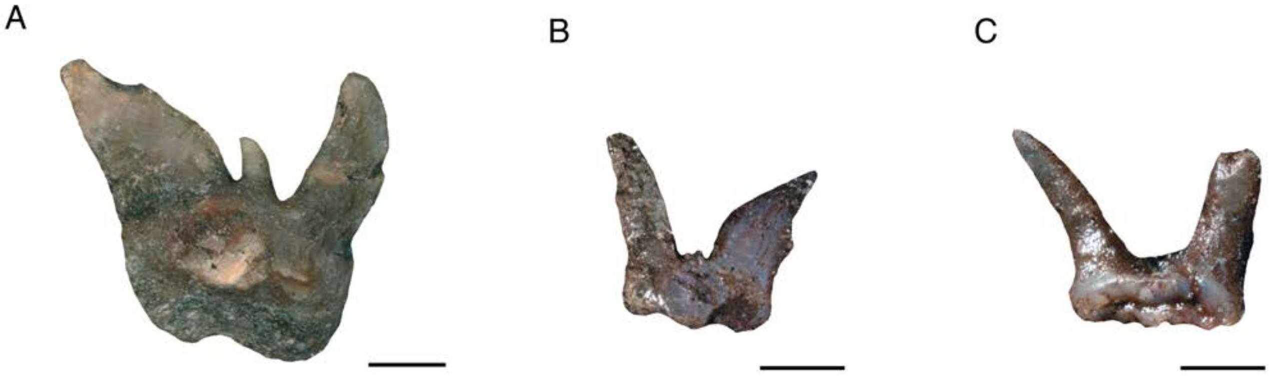

Fig. 2.—Xenacanthimorpha from the Maroon Formation. **A**, Morphotype 1 "*Orthacanthus*" type (UMNH VP 36368). **B**, Morphotype 1 "*Orthacanthus*" type (UMNH VP 35493). **C**, Morphotype 2 (UMNH VP 35494). Scale bars for A–C = 1 mm.

Emmons et al. (1894) for Paleozoic coarse clastic redbeds in the Crested Butte area, and later mapped by Brill (1944, 1952) who attempted to define its stratigraphic relationships throughout western Colorado. The Maroon Formation varies in thickness, ranging from 200 m to an estimated 4,600 m, with abrupt thickness variations due to uplifted fault blocks, causing rapid facies changes (Freeman and Bryant 1977; De Voto et al. 1986). Its lower contact with the shallow marine Minturn Formation is a likely time-transgressive sequence of mudstones and carbonates that gives way to sheet-like sandstones and conglomeratic channels interbedded with red siltstone beds interpreted as loessites (Johnson 1987a, b; Soreghan et al. 2014). In some areas of the basin, where the Minturn-Maroon formational contact is present, the boundary may be defined by a gradational color change from the predominantly brown and gray rocks of the Minturn Formation to the overlying redbeds of the Maroon Formation (Langenheim 1954; Bartleson 1972; De Voto 1980). In the Derby Junction area, the Minturn-Maroon transition is also defined by a gradational "color change" in the middle of this sequence from "underlying brown and gray rocks [to] overlying redbeds" (Johnson 1987a:2). There are no absolute ages for the base of the Maroon Formation in the Derby Junction sequence. Biostratigraphically informative conodont elements from the middle portion of the Minturn Formation near Meeker, Colorado, suggest a Desmoinesian (late Carboniferous) age for at least part of the Minturn Formation (Murray and Chronic 1965), while tetrapod tracks and geochronological evidence (e.g., U-Pb ages of detrital zircons; Soreghan et al. 2014) suggest a Wolfcampian (early Permian) age for the terrestrial redbeds that form most of the upper Maroon Formation in the Frying Pan and Aspen sub-basins (Voigt et al. 2005, 2021). Together, these data provide upper and lower age constraints that place the C–P geologic boundary imprecisely in either the upper Minturn or lower Maroon formations (Fig. 1).

Marine carbonate facies in the Maroon Formation are rare and typically occur only in the lower half of the formation when present (Johnson 1987a, 1987b; Voigt et al. 2005). Johnson (1987b) documented only a thin "marine limestone" in the upper Maroon Formation in proximity to the Schoolhouse Tongue near Ripple Creek, Garfield County. At Derby Junction, thin (< 1 m) carbonate beds occur at regular intervals starting at approximately 8 m above the base of the Maroon Formation and repeating up to 85 m (Fig. 1). The fossil-bearing carbonates at Derby Junction were formed as microbial laminated bindstone containing a mix of fine-grained quartz clasts and bioclasts. The fossils occur in extremely thin (millimeter scale) seams that follow a slightly wavy laminated texture. Invertebrate fossils are sparse, but occasional small bivalves (1–2 cm) and microconchids were observed both in hand-sample and upon preparation in the laboratory. Microconchid worms have been shown to have widespread distributions, including in fluvial and lacustrine settings, and likely indicated brackish or freshwater conditions in many Paleozoic shallow carbonate environments (Zatoń et al. 2012). Microconchid fossils occur elsewhere in the southwestern U.S. in equivalent strata of the lower Cutler beds (Paradox Basin), Utah (Huttenlocker et al. 2018, 2020). We interpret the fossiliferous carbonates of the Maroon Formation as similarly representing relatively shallow water coastal habitats formed under fluctuating brackish to freshwater conditions.

SYSTEMATIC PALEONTOLOGY

CHONDRICHTHYES Huxley, 1880
XENACANTHIMORPHA Nelson, 1976
(Fig. 2)

Material.—All materials are represented by isolated marginal teeth: UMNH VP 35493; UMNH VP 35494; UMNH VP 36368; CM 96040; CM 96041.

Brief Description.—Chondrichthyan teeth attributed to xenacanths occur rarely in the fossil-bearing limestones and make up less than 10% of sampled vertebrate material at the site. The teeth are very small (2–3 mm) but are generally well preserved with two divergent main cusps and a wide, robust base.

At least two xenacanth tooth morphotypes are identified in the assemblage. Morphotype 1 bears resemblance to the C–P taxon *Orthacanthus* (Figs. 2A–B). The principal cusps are broad and lightly compressed, and strongly curved, with a small intermediate cusp in between. The basal 'button' is wide and deep and is especially deep in UMNH VP 36368 where it makes up 50% of the tooth height (Fig. 2A). There is a small, apically positioned tubercle on the button. The small size of the teeth, as well as the size and shape of the button and the position of the tubercle is most reminiscent of *O. platypternus*, differing from *O. compressus* and *O. texensis* where the tubercle is low and oriented basally. The teeth also differ from *O. texensis* in that they show no evidence of serrations, although this could be due to weathering and imperfect preservation. The teeth might belong to *O. donnelljohnsi*, known from the Early Pennsylvanian (late Bashkirian) of the Black Prince Limestone of southeastern Arizona, the teeth of which are small and lack serrations (Johnson and Thayer 2009).

Mophotype 2 bears similarities to non-*Orthacanthus* xenacanths, particularly bransonelliforms (*Barbclabornia*) or xenacanthiforms (*Triodus*). These tooth types have a more conserved morphology with simple (non-recurved) principal cusps, a shallower base, and may or may not bear an intermediate cusp. The principal cusps in UMNH VP 35494 are relatively straight and slender and bear no obvious carinae, serrations, or fluting.

Remarks.—Xenacanths are very common components of Paleozoic shallow water coastal assemblages in North America, making their rarity in the Maroon assemblage peculiar. Multiple xenacanth morphotypes co-occurred elsewhere in the North American late Carboniferous, including in the Mattoon Formation, Illinois Basin (Carpenter et al. 2011). These included *Triodus*, *Xenacanthus* cf. *X. ossiani*, *Orthacanthus* cf. *O. compressus*, and *Dicentrodus* cf. *D. alatus*, which the authors determined to represent brackish to freshwater forms based on Sr isotopic analysis (Carpenter et al. 2011). In the southwestern U.S., *Orthacanthus* is known to have occurred in the C–P Cutler Group, Paradox Basin (southeastern Utah), in the form of the large *Orthacanthus* aff. *O. texensis*, which has also been interpreted as a nonmarine form (Huttenlocker et al. 2018). The *O. texensis* lineage likely spans the C–P boundary (Johnson 1999; Huttenlocker et al. 2018). The paucity of well-preserved material diagnostic to species limits the biostratigraphic utility of the Maroon Formation records for now. *Orthacanthus* teeth ranged from the Carboniferous through the early Permian, and xenacanths more broadly ranged through the late Triassic.

HYBODONTIFORMES Maisey, 1975
Hamiltonichthys Maisey, 1989
(Figs. 3B–C)

Material.—UMNH VP 35489, lateral marginal tooth; UMNH VP 35490, lateral marginal tooth.

Brief Description.—In general, hybodont elements are relatively more abundant in the assemblage than the xenacanths, dominating among chondrichthyans. Numerous hybodont marginal teeth are present in the sample, the most complete and diagnostic of these belonging to the genus *Hamiltonichthys* (known previously only from the Virgilian of Kansas; Maisey 1989). The presumed lateral oral teeth are characteristically low-crowned and transversely elongated (2–3 mm long) with a single asymmetrical peak and bear strong apico-basal cristae that extend to the occlusal ridge (Figs. 3B–C). The lateral teeth differ from other hybodonts in which complete oral dentitions are known, such as *Lissodus* lateral teeth, which may be slightly higher crowned, have fewer cristae, and may have additional cusps or cusplets (Cross et al. 2018: figs. 7d–e).

Remarks.—Prior records of *Hamiltonichthys* have come exclusively from the upper Carboniferous (Virgilian) Hamilton Quarry, Greenwood County, Kansas (Maisey 1989). A single, isolated cephalic spine from the Surprise Canyon Formation of Arizona was also compared to *Hamiltonichthys*—identified as cf. *Hamiltonichthys* (Hodnett and Elliott 2018)—but this was only a tentative assignment. A partial neurocranium and associated materials of an indeterminate hybodont was also reported from the Kasimovian-aged Kinney Brick Quarry (Atrasado Formation) of New Mexico, but was excluded from *Hamiltonichthys* based on dental differences (Hodnett and Lucas 2021). Personal examination of the New Mexico material by one of us (A.K.H. 2018) corroborates this given the oral teeth are more symmetrical and the occlusal surface is smoothly rounded without cristae (unlike *Hamiltonichthys*). The Hamilton Quarry represents an incised valley cut into the Hartford Limestone (Shawnee Group) of the Forest City Basin. In addition to well-preserved invertebrate and plant remains, the quarry has similarly produced a variety of aquatic vertebrate taxa, primarily fishes, with occasional terrestrial vertebrate elements mixed in (Mapes and Mapes 1988). Thus, the Derby Junction locality provides the first diagnostic dental remains of *Hamiltonichthys* outside Kansas and has the potential to produce other shared faunal elements with the Hamilton Quarry. The well-constrained biostratigraphy of the assemblage within the cyclothemic sequence of the Shawnee Group makes *Hamiltonichthys* a potentially important Virgilian (late Carboniferous) index taxon for the western region.

HYBODONTIFORMES indet.
(Figs. 3A, D–F)

Material.—UMNH VP 36367, small anterior oral tooth associated with an actinopterygian maxilla; CM 96037,

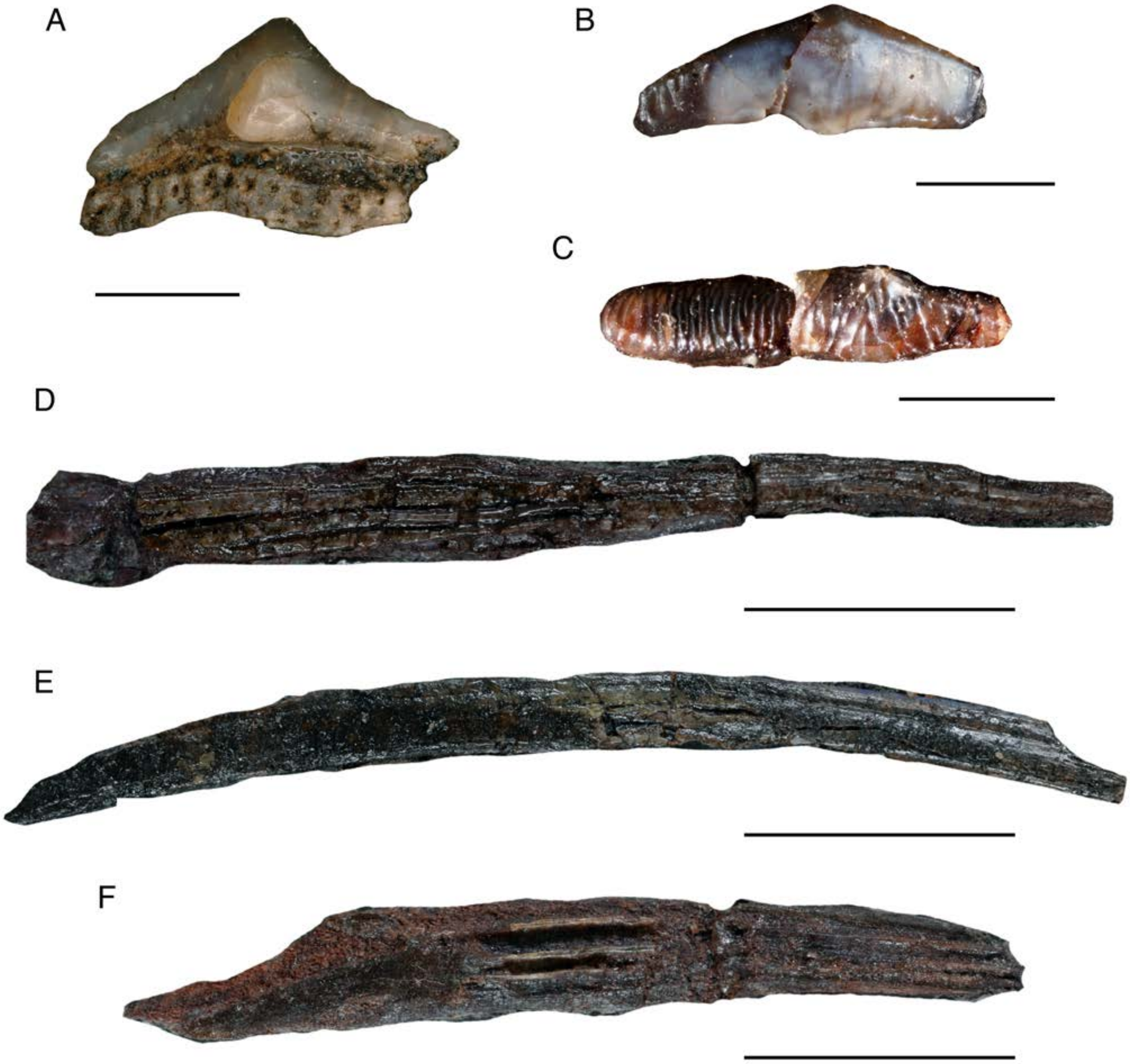

Fig. 3.—Hybodontiformes from the Maroon Formation. **A**, Indeterminate hybodont tooth (UMNH VP 36367), possibly *Hamiltonichthys*. **B**, *Hamiltonichthys* lateral tooth **(**UMNH VP 35489). **C**, *Hamiltonichthys* lateral tooth **(**UMNH VP 35490). **D–F**, Indeterminate hybodont spines: **D**, CM 96049; **E**, CM 96037; **F**, CM 96050. Scale bars for A and B = 1 mm; C = 2 mm; D–F = 10 mm.

fin spine; CM 96039, fin spine; CM 96048, fin spine; CM 96049, fin spine; CM 96050, fin spine; UMNH VP 35512, fin spine; CM 96051, fin spine; CM 69057, fin spine.

Brief Description.—Isolated teeth and spines of hybodonts were frequently encountered in the assemblage, but their disassociated nature, poor preservation, and conservative morphology make genus-level identifications difficult in some cases. A tiny anterior tooth from a hybodont (UMNH VP 36367) was found in a slab associated with an actinopterygian maxilla (UMNH VP 35508). The hybodont tooth surface texture is smooth and simple (Fig. 3A), lacking cristae unlike on the diagnostic lateral teeth of *Hamiltonichthys*. However, the shape and texture varies with tooth position (Maisey 1989). Parsimoniously, the isolated anterior tooth most likely belongs to *Hamiltonichthys* as reported above, but the smooth anterior teeth of both *Hamiltonichthys* and *Lissodus* are morphologically identical (Maisey 1989; Cross et al. 2018: fig. 7c).

In addition to isolated teeth, several hybodont fin spines were also collected (Figs. 3D–F). The hybodont spines are diagnosed by their elongated and gently curved shaft with lateral ornaments frequently consisting of longitudinal costae and shallow costal grooves (Maisey 1978). In well-preserved specimens, the lateral sides and grooves may preserve a series of neurovascular pits arranged in longitudinal rows. Although their anterior edge may bear a smooth, sharp crest, none of the fin spines in our sample preserve any denticles.

Remarks.—Although hybodont elements are abundant at the Derby Junction site, it is difficult to determine whether they represent a single taxon (*Hamiltonichthys*) or if multiple hybodont taxa are represented. Little is mentioned of the spine structure of *Hamiltonichthys*, but they are figured as slender, recurved spines bearing a small number of coarse costae as lateral ornaments (three or four costae; Maisey 1989: figs. 22–23). Most of the sampled Maroon Formation spines are similarly small and slender and show up to four costae, suggesting these hybodont spines could potentially also belong to *Hamiltonichthys*. However, the lack of any articulated specimens with spines and oral skeletons with teeth makes this presumption tenuous. Moreover, *Hamiltonichthys* fin spines are shown to bear denticles (Maisey 1989: figs. 18, 22–23), which are lacking in the Maroon Formation spines. We reserve the possibility that multiple hybodont taxa could be represented in the assemblage, but more and better-preserved material is needed to make a more confident determination.

OSTEICHTHYES Huxley, 1880
ACTINOPTERYGII sensu Goodrich, 1930
PLATYSOMIDAE Young, 1866
(Fig. 4)

Material.—UMNH VP 35491, denticle plate.

Brief Description.— A platysomid actinopterygian is represented by a single concave, lozenge-shaped (‘phyllodont’) denticle plate. The individual denticles are small, rounded, and are of irregular-sizes. This type of denticle plate is traditionally identified as “*Sphaerolepis*” in Carboniferous–Permian sedimentary deposits, but represent platysomids, likely *Platysomus* (Johnson and Zidek 1981).

Remarks.—*Platysomus* is well documented in marine to onshore cyclothems in the Forest City Basin (Kansas–Nebraska) where it spans the C–P geologic boundary (Wabaunsee and Council Grove groups) (Schultze 1985), but it is known from C–P sedimentary deposits throughout western North America (Schultze and Chorn 1986), including the Kasimovian-aged Kinney Brick Quarry of New Mexico where it is one of the most common vertebrate taxa (Huber 1992). Johnson and Zidek (1981) attempted to classify platysomids according to the shape and curvature of the phyllodont denticle plates, but cautioned that morphologic variation is not well understood in the absence of articulated material, and such variation could represent differences in upper and lower occluding plates or other intraspecific variation. As a clade, platysomids ranged at least from the early Carboniferous to the Triassic (Wilson et al. 2021).

Fig. 4.—Platysomidae from the Maroon Formation. Concave ‘phyllodont’ denticle plate (UMNH VP 35491) in occlusal view. Scale bar = 2 mm.

PYGOPTERIDAE Aldinger, 1937
aff. *Progyrolepis* Fritsch, 1893
(Figs. 5–7)

Material.—UMNH VP 35503, disarticulated skeleton with scales on two slabs (part and counterpart); UMNH VP 35508, isolated dentary.

Brief Description.—A large ‘palaeoniscoid’ actinopterygian is represented by multiple specimens, including a disarticulated but associated skull and partial skeleton, an isolated maxilla, and abundant scales scattered throughout the fossil site. The partial skeleton, UMNH VP 35503, preserves partial maxillae and other dermal elements, palatal elements, gular and branchial elements, scales, and other assorted elements (Figs. 5–6). The marginal dentition consists of a series of large, widely-spaced fang-like teeth, with smaller conical teeth in between the marginal fangs. An intermittent row of fine denticles is present labial to the marginal tooth row. Scales and dermal bones exhibit vermiform sculpturing on their surface (Figs. 7A–C). A second partial jaw, a left dentary (UMNH VP 35508; Fig. 7D), preserves the same dermal sculpturing which becomes more tubercular rostrally and along the oral margins, and fang-like marginal dentition with small but well-preserved acrodin caps.

Remarks.—So-called “large-toothed” palaeoniscoids have been documented throughout the Carboniferous–Permian of western North America, including in the late Carboniferous (Ghzelian) of the midcontinent (Kansas), C–P beds

Fig. 5.—aff. *Progyrolepis* from the Maroon Formation. Photograph of aff. *Progyrolepis* (UMNH VP 35503) disarticulated skeleton with scales on slab. Dashed boxes correspond to detailed close-ups in Figure 7. Scale bar = 10 mm.

in the Four Corners region (New Mexico), and the early Permian (Asselian-Sakmarian) of Texas. The Maroon form compares most closely with the large, predatory palaeoniscoid *Progyrolepis* based on several features. The teeth on the dentary are organized in two distinct rows: an outer row of very fine teeth and an inner row of large, widely spaced teeth. Teeth on the inner row have a broad base and a wide pulp cavity, and lack the sinusoidal flexure seen in other early actinopterygians. The dermal sculpture is also consistent with *Progyrolepis*; the dermal bones are covered in densely organized fine anastomosing (vermiform) ridges of ganoine which become tubercular closer to the oral margin (Štamberg 1991: figs. 17–18). Scales show diverse surface texture, from coarse parallel ridges to finer anastomosing ridges, with a serrate posterior edge on flank scales.

Progyrolepis was originally described from the Carboniferous of the Czech Republic (Fritsch 1875, 1893), but

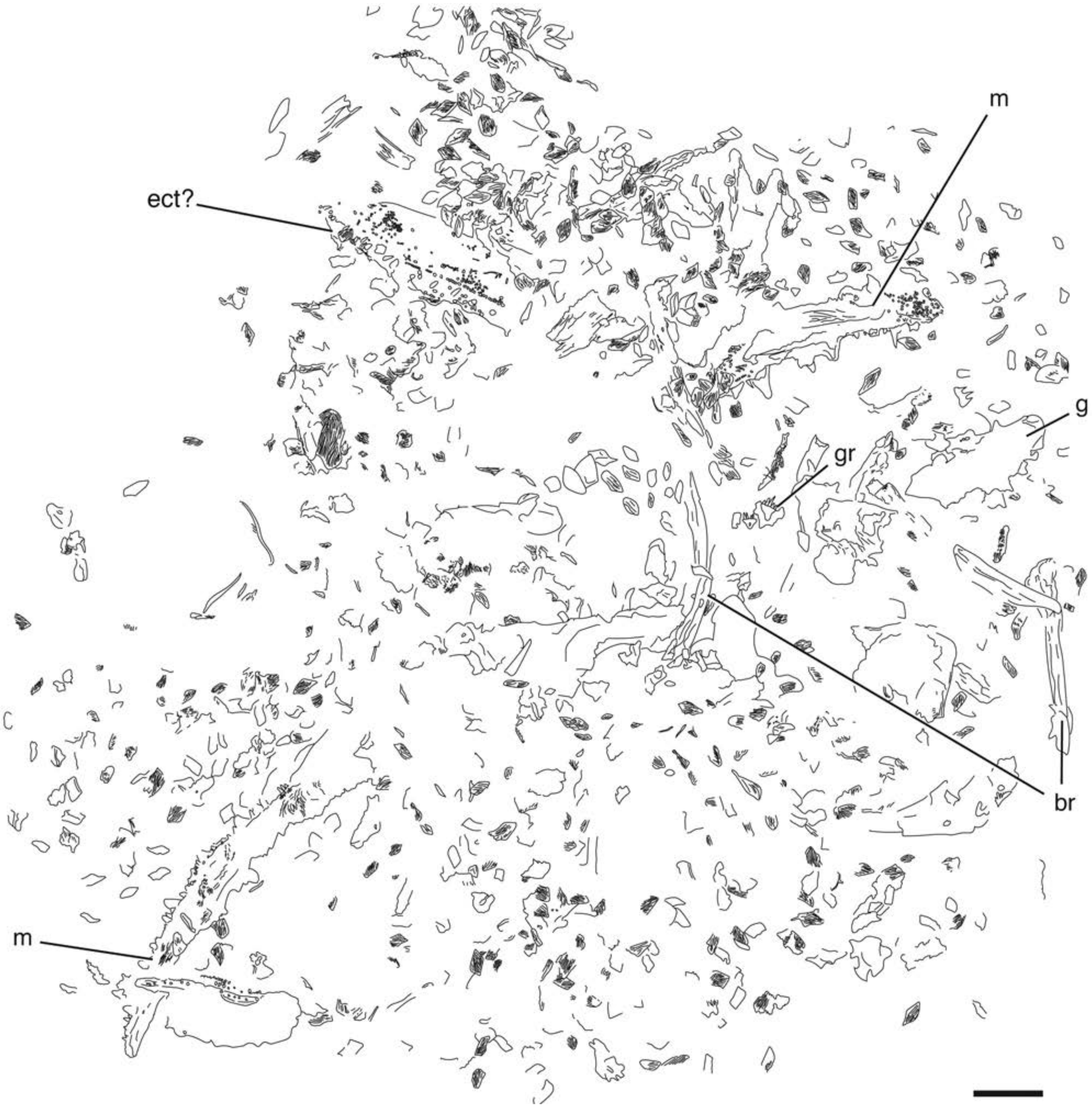

Fig. 6.—aff. *Progyrolepis* from the Maroon Formation (continued). Line drawing of aff. *Progyrolepis* (UMNH VP 35503). Scale bar = 10 mm. **Abbreviations: br**, branchial elements; **g**, gular; **m**, maxilla; **ect?**, ectopterygoid.

additional material has been reported from North America, France, and the United Kingdom, suggesting the genus was widespread during the Carboniferous–Permian transition. As with other members of the genus, the Maroon form was a relatively large palaeoniscoid with a mandibular ramus length of 6–8 cm and an estimated total length of approximately 50–60 cm. Three species have been named: *P. speciosus*, *P. tricessimalaris*, and *P. heyleri*. Most material has been assigned to *P. speciosus* Fritsch (1875), first described from the Stephanian B (Kasimovian-Ghzelian) of the Czech Republic (Štamberg 1991). *Progyrolepis speciosus* material has also been reported from the Stephanian C (Ghzelian) of Puertollano Basin, Spain (Soler-Gijón and Moratalla 2001; Štamberg 2018). A second species, *P. tricessimalaris*, was described by Dunkle (1946) based on a largely complete skull from the Archer City Formation of Texas (Asselian-Sakmarian). The Texas form differs from *P. speciosus* in having a more tubercular cranial

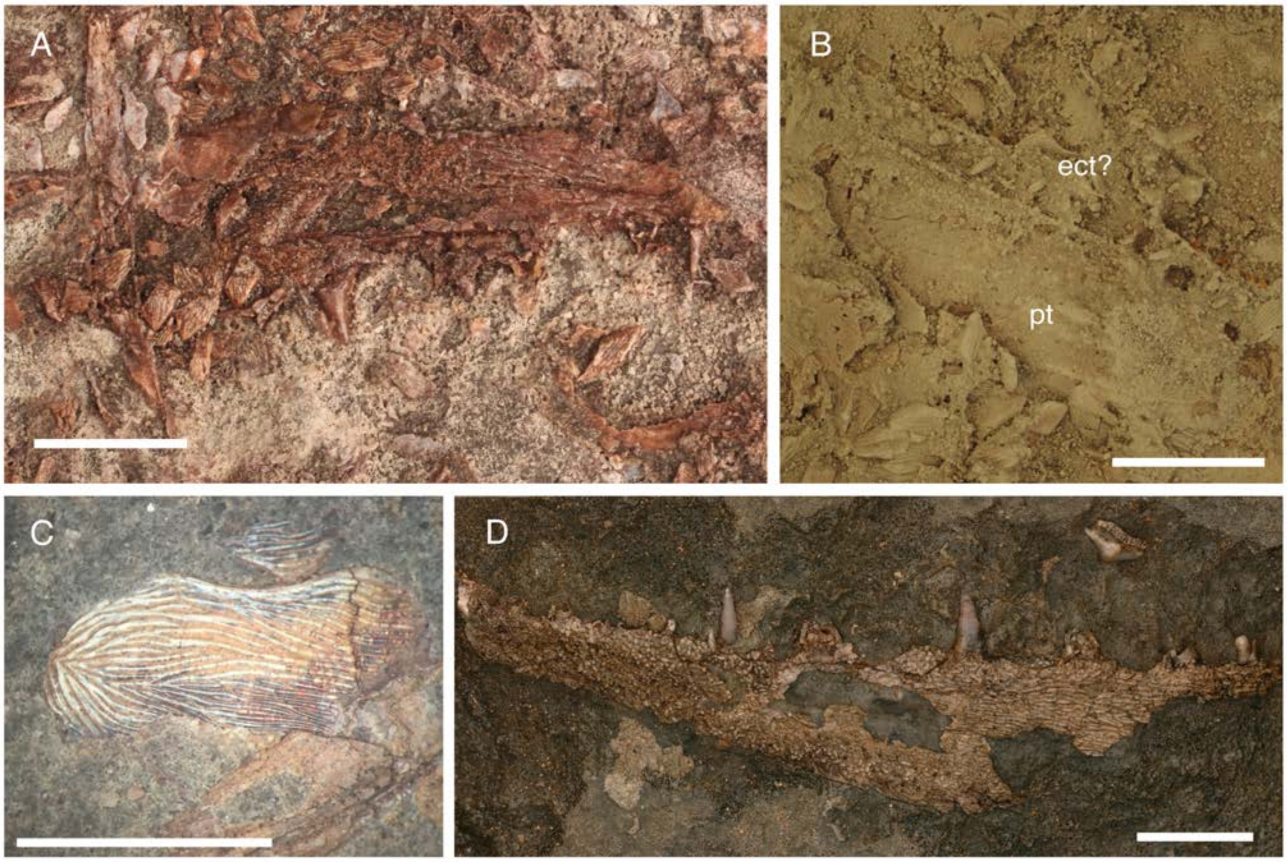

Fig. 7.—aff. *Progyrolepis* from the Maroon Formation (continued). **A–C**, Close-up photographs of disarticulated skeleton UMNH VP 35503: **A**, right maxilla of UMNH VP 35503 showing detail on teeth, dermal sculpture, and associated scales (anterior direction toward right). **B**, palatal elements bearing dentition (**ect**, ectopterygoid; **pt**, palatoquadrate) in UMNH VP 35503 (anterior direction toward right). **C**, large ridge scale of UMNH VP 35503 showing detail of ornamentation pattern. **D**, UMNH VP 35508, aff. *Progyrolepis* isolated left dentary (anterior direction toward left) (with hybodont tooth UMNH VP 36367 seen on upper right). All scale bars = 5 mm.

ornamentation and slightly coarser scale ornamentation. Poplin (1999) erected a third species, *P. heyleri*, for specimens from the C–P Buxières-les-Mines fauna, which exhibited slightly different dentine sculpturing in the tooth bases as well as an anteroposteriorly compressed postorbital bone bearing distinct vertical linear sculpturing. The Maroon form is definitively not the Permian *P. tricessimalaris*, based on the dermal sculpturing, but it is difficult to exclude a relationship to the Carboniferous *P. speciosus* or *P. heyleri* based on the anatomy preserved here.

Elsewhere in the southwestern U.S., Langston (1953) reported co-occurrences of a *Progyrolepis*-like actinopterygian and *Orthacanthus* in the C–P Camp Quarry assemblage (Cutler Group, Rio Arriba County, New Mexico). The Camp Quarry assemblage is assigned to the Coyotean land vertebrate faunachron, which spans approximately the C–P boundary (Lucas et al. 2005). Similar large-toothed palaeoniscoids with vermiform bone sculpturing have also been described from the Ghzelian-aged Hamilton Quarry, Kansas (Gottfried 1988: figs. 1–3), and the Kasimovian-aged Kinney Brick Quarry, New Mexico (Bardack 1992: fig. 7).

ACTINOPTERYGII indet.
(Fig. 8)

Material.—UMNH VP 35511, isolated braincase; UMNH VP 36364, teeth; UMNH VP 35513, scales; UMNH VP 36366, jaw fragment; UMNH VP 35497, tooth; UMNH VP 35504, cleithrum; UMNH VP 36370, scale; UMNH VP 36371, bromalites with scales and teeth; UMNH VP 36372, bromalites with scales and teeth; CM 96038, rib; CM 96053, cleithrum; CM 96054, cleithrum; CM 96056, scale; CM 96060, scales and associated bones; CM 96059, scales; CM 96047, scale.

Brief Description.—Compared to other taxa, actinopterygian scales, teeth, and miscellaneous bones represent the largest proportion of specimen ‘lots’ collected at the Derby Junction site, comprising about 20–25% of specimens collected. Miscellaneous actinopterygian elements included abundant palaeoniscoid scales and isolated teeth recognizable by their translucent acrodin caps, poorly preserved girdle elements including multiple cleithra, and an isolated and poorly preserved indeterminate braincase.

The isolated cleithra (Figs. 8A–B) are dorsoventrally elongated, delicate L-shaped elements with light sculpturing preserved on the ventral portion and thus may represent a single morphotype. The ventral portion arches in the oral direction as in many palaeoniscoids and is slightly more robust. The dorsal lamina is thin and only the posterior margin is preserved, extending dorsally toward the supracleithrum contact where it tapers. The overall shape vaguely resembles palaeoniscoids like *Watsonichthys* or *Progyrolepis* (Štamberg 1991), suggesting that some of the isolated cleithra could belong to one of these taxa (the latter was already documented at this site based on cranial remains), but they are too poorly preserved to assign with confidence. The dermal sculpture is fine and irregular on the ventral portion, but forms thin, vertical striations more dorsally where preserved, similar to the sculpture described in *Watsonichthys* (Štamberg 1991).

Also of note, an isolated braincase, UMNH VP 35511, was collected from the site, showing the potential for more diagnostic cranial remains to be found. Unfortunately, the braincases of most North American C–P actinopterygians are not well characterized, thus preventing detailed comparisons. The present specimen consists of a posterior occipital region that was well ossified, showing posteriorly the notochordal pit, anteroventrally the parabasisphenoid rostrum, and dorsally the bases of paired pillar-like processes that would have bounded the lateral walls of the foramen magnum in life (Figs. 8C–D).

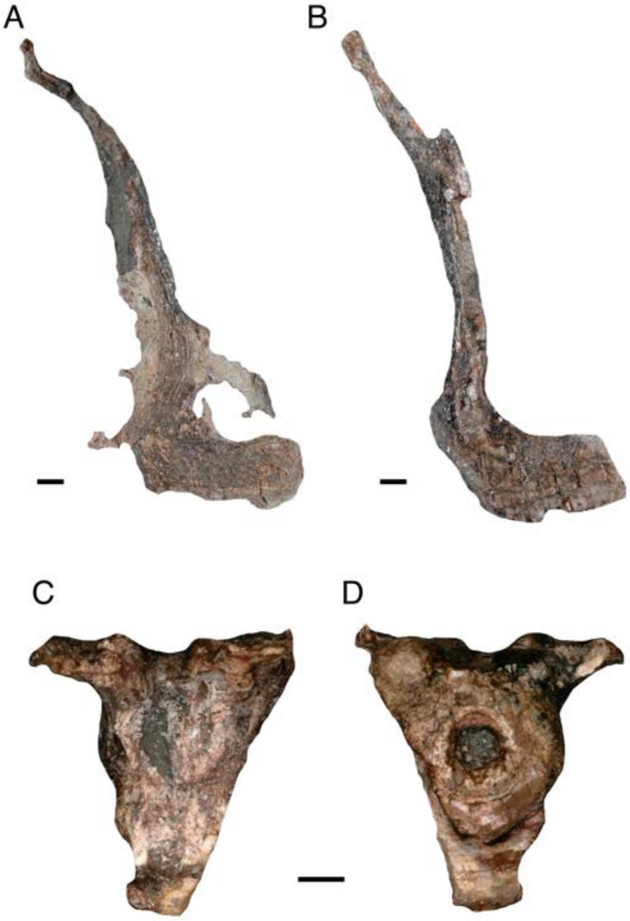

Fig. 8.—Actinopterygii indet. from the Maroon Formation. **A**, isolated cleithrum (CM 96053) (anterior direction toward right). **B**, isolated cleithrum (UMNH VP 35504) (anterior direction toward right). **C–D**, isolated posterior braincase (UMNH VP 35511) in anterior (C) and occipital (D) views. All scale bars = 1 mm.

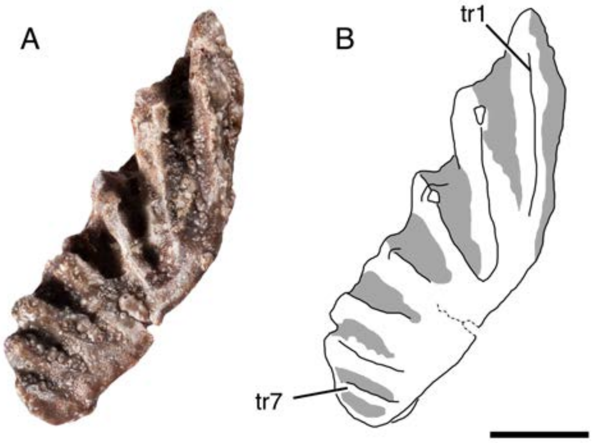

Fig. 9.—Dipnomorpha from the Maroon Formation. *Sagenodus* left prearticular toothplate (UMNH VP 35499). **A**, Photograph of toothplate in occlusal view. **B**, Line drawing of the specimen in same view. Anterior direction toward top of page. Scale bar = 10 mm. **Abbreviations: tr#**, tooth ridge.

Remarks.—The fragmentary nature of the majority of actinopterygian specimens makes precise taxonomic determinations difficult. Nonetheless, it documents an aquatic assemblage with abundant actinopterygian elements and the potential to reveal additional aquatic diversity with the discovery of more specimens. Actinopterygians constitute the bulk of fossils collected from the site and their abundance likely reflects their dominance in the environment during the time of deposition.

SARCOPTERYGII Romer, 1955
DIPNOMORPHA Ahlberg, 1991
SAGENODONTIDAE Jaekel, 1911
Sagenodus Owen, 1867
(Fig. 9)

Material.—UMNH VP 35499, isolated left prearticular toothplate.

Brief Description.—A left prearticular toothplate is attributable to a large lungfish. There are seven weakly diverging denticle rows present, with the anterior three denticle rows noticeably larger than the posterior four and well spaced. Denticle rows are heavily remodeled and worn, with denticulation preserved only at the labial margins of the toothplate. The tooth rows do not fully converge medially. With its high aspect ratio, short ridges, and relatively low number of ridges, the toothplate is most similar to the form *Sagenodus inaequalis* (Carboniferous of Europe; Kemp 1996; Beeby et al. 2020) but also compares well with *Sagenodus serratus* (Carboniferous–Permian of North America; Schultze and Chorn 1997). It differs from *Sagenodus hlavini* from the Carboniferous of New Mexico (Zidek 1975) in its greater mediolateral breadth and in the greater height of the ridges (A.K.H. pers. obsv.).

Remarks.—The genus *Sagenodus* has a long temporal range from the earliest Mississippian to at least the end of the Cisuralian (early Permian) (Schultze and Chorn 1997; Olive et al. 2012). Five valid species are known from the Carboniferous and Permian of North America: *S. ohioensis* from the Moscovian of Ohio, *S. hlavini* from the Kasimovian of New Mexico, *S. copeanus* from the Kasimovian-Gzhelian throughout the southwest and Midcontinental U.S., and *S. serratus* and *S. periprion* both known from the C-P sequences of the Eastern U.S. (Illinois and Dunkard basins) and the Cisuralian of the Midcontinental U.S. (Texas-Oklahoma) (Lund 1970; Zidek 1975; Schultze and Chorn 1997).

Additional taxa are known from Europe, most notably the morphologically similar *S. inaequalis* from the late Pennsylvanian of the United Kingdom and *S. quinquecostatus* from the Mississippian of Scotland (Beeby et al. 2020) and an unnamed species from the late Pennsylvanian of France (Olive et al. 2012). Delineation of *Sagenodus* species has always been challenging as most species-level differences consist of differences in number of denticle rows in the toothplate and aspect ratio of toothplates (Schultze and Chorn 1997), with considerable overlap between species. Thus, although UMNH VP 35499 appears most similar to *S. serratus* and *S. inaequalis*, it is not possible to assign it with confidence to one form or the other. If the Maroon form represents a related species, it would suggest a wider range for some Carboniferous *Sagenodus* species, consistent with our working hypothesis that environmentally sensitive aquatic taxa ranged widely in Euramerica prior to Permian aridification and subsequent fragmentation (Pardo et al. 2019).

TETRAPODOMORPHA Ahlberg, 1991
TEMNOSPONDYLI Zittel, 1888
DISSOROPHOIDEA Bolt, 1969
AMPHIBAMIFORMES sensu Schoch, 2022
AMPHIBIOMORPHA sensu Schoch, 2022
(Fig. 10)

Material.—CM 92155, incomplete cranium and articulated lower jaw with associated elements.

Brief Description.—A small temnospondyl (skull length approximately 15 mm)—preserving much of the cranium, lower jaws in articulation, and associated appendicular elements—is one of few tetrapods recovered from the Derby Junction site. The skull is exposed only in ventral view and is missing much of the posterior portions of the palate and braincase, making it difficult to precisely identify or diagnose this specimen. Nonetheless, the skull preserves combinations of apomorphic features that make it possible to narrow its approximate phylogenetic position to the Amphibamiformes, a group of small dissorophoids noteworthy for their evolutionary proximity to batrachians (frogs and salamanders). Among amphibamiforms, the Derby Junction form may occupy a position close to the Amphibiomorpha of Schoch (2022), an inclusive clade that encompasses branchiosaurids, batrachians, and amphibamid-grade (i.e., non-micropholid) amphibamiforms. Among amphibamid-grade species, as in the present specimen, there is no lateral lappet of the frontal bordering on the orbit, and instead the prefrontal and postfrontal are joined on the orbital rim (shared with *Milnererpeton*, *Platyrhinops*, *Amphibamus*; Werneburg et al. 2021). However, unlike the amphibamids *Platyrhinops*, *Doleserpeton*, and *Amphibamus*, the marginal teeth are tiny, simple cones, lacking multiple cusps, and are non-pedicellate. A pair of vomerine tusks is found anterior to the choana preserved on both sides of the skull. A second pair of tusks is found more posteriorly on the palatines. Though the posterior skull table is imperfectly preserved, the skull appears to have been relatively short and wide as in other amphibiomorphs (Schoch 2022), although comparably longer than that of *Amphibamus*, *Milnererpeton,* or *Platyrhinops*.

Remarks.—This is the first definitive documentation of an amphibamiform from Colorado and a rare record of the group from the southwestern U.S. Although Vaughn (1972) listed an *Amphibamus*-like temnospondyl dentary from the Sangre de Cristo Formation of Badger Creek, Colorado, no voucher specimen was figured. The small temnospondyls from Vaughn's Badger Creek collection have been recently interpreted as either small eryopoids or zatrachydids and are currently under study (A.C. Milner and A.C. Henrici, pers. comm. 2015), although we are aware of fragmentary amphibamiform material from the Badger Creek locality made by the DMNH in the 1990s (Small, Huttenlocker, and Pardo pers. obs.). Hunt et al. (1996) described the small dissorophoid *Milnererpeton* (= *Milneria*) *huberi* from the Kasimovian-aged (Missourian) Kinney Brick Quarry, New Mexico. Although *Milnererpeton* has been variably assigned to either a branchiosaurid or an amphibamid, it has been most recently interpreted as an amphibamid-grade amphibamiform, but this is based on the description of a specimen which remains in anonymous private ownership and whose provenance cannot therefore be independently verified (but see Werneburg et al. 2021). Although we cannot rule out a close relationship with *Milnererpeton*, the evidence presented above suggests the Derby Junction form conservatively occupies a phylogenetic position among the Amphibiomorpha. The

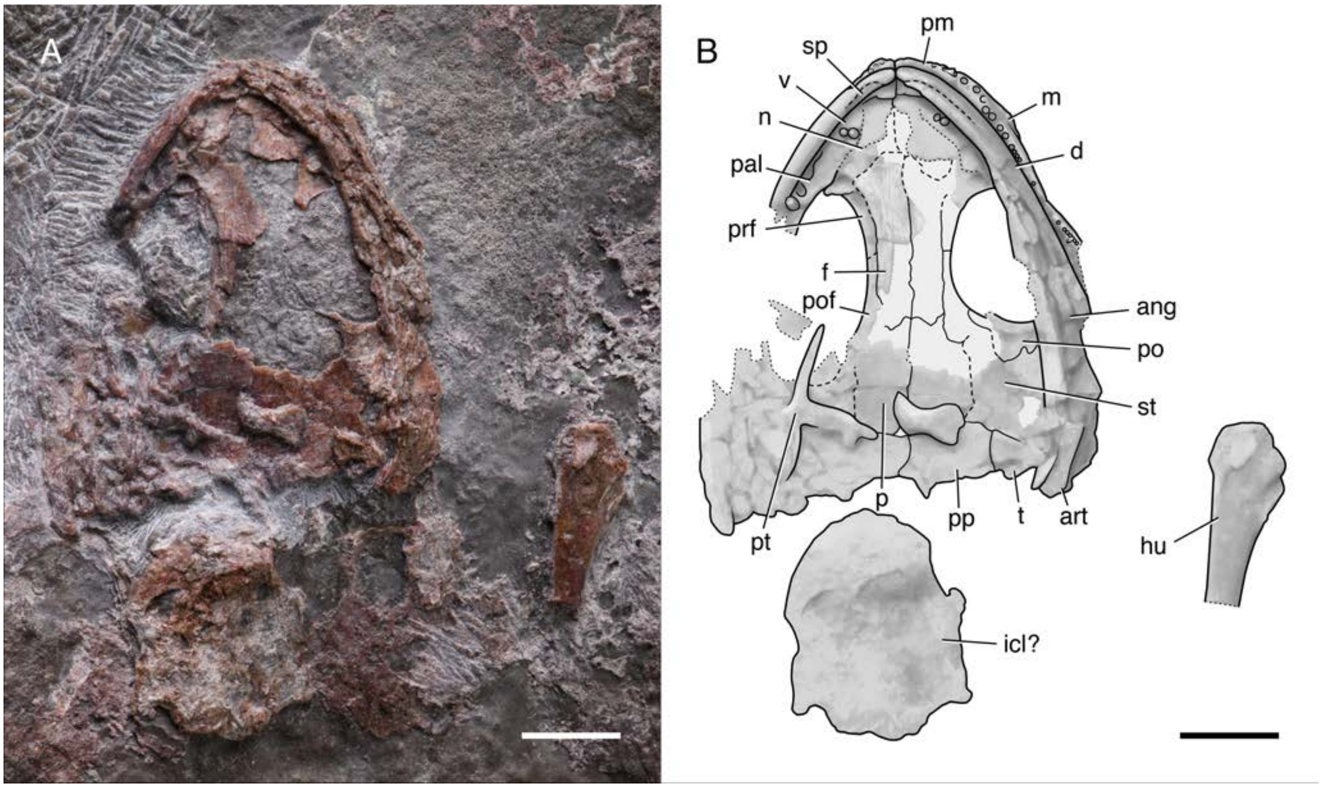

Fig. 10.—Amphibamidae indet. from the Maroon Formation. Amphibamid partial cranium, mandible, and associated elements (CM 92155). **A**, Photograph of specimen in ventral view. **B**, Interpretive drawing of the specimen in same view. Solid light gray areas in 'B' represent bone impression. Scale bar = 5 mm. **Abbreviations: ang**, angular; **art**, articular; **d**, dentary; **f**, frontal; **hu**, humerus; **icl**, interclavicle; **m**, maxilla; **n**, nasal; **p**, parietal; **pal**, palatine; **pm**, premaxilla; **po**, postorbital; **pof**, postfrontal; **pp**, postparietal; **prf**, prefrontal; **pt**, pterygoid; **sp**, splenial; **st**, supratemporal; **t**, tabular; **v**, vomer.

clade Amphibiomorpha has a long temporal range from the early late Carboniferous (Desmoinesian North American stage / Moscovian global stage) to present-day.

TETRAPODOMORPHA indet.
(Fig. 11)

Material.—UMNH VP 35507, vertebral centrum; CM 96052, partial intercentrum.

Brief Description.—Indeterminate tetrapod remains are extremely rare in the assemblage, represented here by two isolated vertebra fragments. The most complete of these, UMNH VP 35507, is a tiny, vertebral body (1.5 mm width, 2 mm anteroposterior length) that is completely ossified around the notochord as in the small holospondylous vertebrae of various Carboniferous tetrapods classically referred to 'Lepospondyli' (Baird 1965a). It is a solid, cylindrical centrum element having relatively flat, vertical anterior and posterior faces (non-sloping) with a shallow notochordal pit, but is missing most of the overlying neural arch (Figs. 11A–C). Ridges for the neural arch attachments are preserved, but no sockets, ruling out similar-sized actinopterygian vertebrae (Vaughn 1967; Schultze and Chorn 1986). The dorsolateral corners of the centrum bear longitudinal laminae, whereas, the ventrolateral faces bear broad fossae that make up most of the lateral sides of the centrum. The ventral margin of the centrum is strongly arched in lateral view (Fig. 11A). Parapophyses are not well developed. A second vertebra, CM 96052, is represented by a partial intercentrum from a larger animal (1 cm width). Although it is too incomplete for a detailed taxonomic assignment, it differs from the other specimen in that it is an anteroposteriorly short, disk-like element pierced by a complete notochordal canal, and therefore suggests additional tetrapod diversity at the site.

Remarks.—The rarity of tetrapod remains is consistent with the largely aquatic and fish-dominated nature of the assemblage. Although the isolated tetrapod vertebral remains cannot be referred to specific taxa, the smaller holospondylous vertebra, UMNH VP 35507, resembles most closely a recumbirostran similar to the molgophid *Brachydectes*. Both have a single large, solid pleurocentrum that is anteroposteriorly elongated rather than short and stout, and bear concave lateral fossae on the centrum bordered dorsally by a transverse lamina. The neural arches are also disassociated, suggesting a loose connection (unfused) as in molgophids which have a persistent neurocentral suture throughout ontogeny. Despite these broad similarities to well-known North American Carboniferous clades, more and better-preserved tetrapod material is needed to clarify the affinities of the tetrapod fossils found at the Derby Junction site.

DISCUSSION

Paleoenvironment and Taphonomy

During the late Paleozoic, the Derby Junction area of Eagle Basin was located at paleotropical latitudes, in a cool, semi-arid to monsoonal climate zone based on paleogeographic reconstructions (Scotese 1997). Basin margin facies of the lower Maroon Formation included shallow marine limestones which we have shown to contain vertebrate body fossils, differing in their taxonomic composition from the previously reported tetrapod ichnoassemblage (Voigt et al. 2005; Small and Sanders 2007). Unlike the assemblages that the Derby Junction fauna most closely resembles (e.g., Hamilton, Forest City Basin, Kansas; Friendsville, Illinois Basin), the fossil-bearing beds are not incised-valley fills (Carpenter et al. 2011). Instead, the beds formed along a broad, flat, coastal plain based on the geometry and laterally continuous nature of the carbonate beds. The assemblage is dominated by chondrichthyans and actinopterygians (together comprising more than 69% of specimens collected) with additional lungfishes, tetrapods, and indeterminate vertebrate materials and bromalites. Autochthonous remains of 'fishes' were associated with wetter cycles, represented by the thin carbonate beds (< 1 m), but accompanying tetrapod remains were also likely deposited in situ during these wet cycles rather than reworked from terrestrial paleosols due to similar preservation within the limestones and semi-articulation in some cases (e.g., amphibamid, Fig. 10). Tetrapods were therefore a component of the fauna during both wetter transgressive intervals and drier lowstands (despite low bone preservation potential in the terrestrial redbeds where only their footprints and trackways are observed).

The assemblage likely represents only a limited sample of the original community composition due to taphonomic bias. Nevertheless, the taxa identified to date show broad similarities to other well-known C–P assemblages in the northern midcontinent and southwestern U.S.A. For example, the Robinson locality in Kansas (Forest City Basin), which was also formed along a coastal environment with carbonate facies and bioherms, was dominated by acanthodians, xenacanths, palaeoniscoids, and the lungfish *Sagenodus* and gnathorhizids (Foreman and Martin 1988; Schultze and Chorn 1997), as well as rare temnospondyl amphibians (Chorn 1984). Likewise, the Hamilton assemblage of Kansas has a similar representation of mainly aquatic chondrichthyans and actinopterygians, *Sagenodus*, some small temnospondyls (e.g., the amphibamiform *Eoscopus*), and other rare terrestrial or semi-terrestrial taxa.

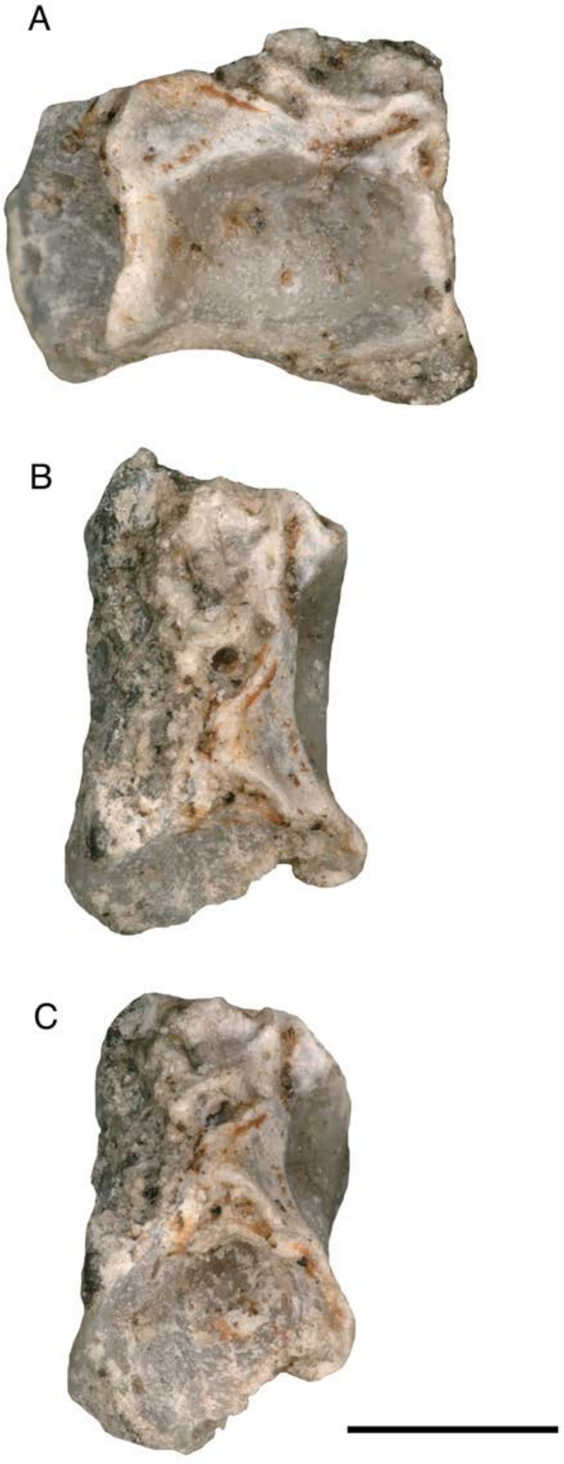

Fig. 11.—Tetrapodomorpha indet. from the Maroon Formation. Tetrapodomorph 'lepospondylous' vertebra (UMNH VP 35507). **A**, Lateral view. **B**, Dorsal view. **C**, Dorsal and slightly oblique view showing notochordal pit. Scale bar = 1 mm.

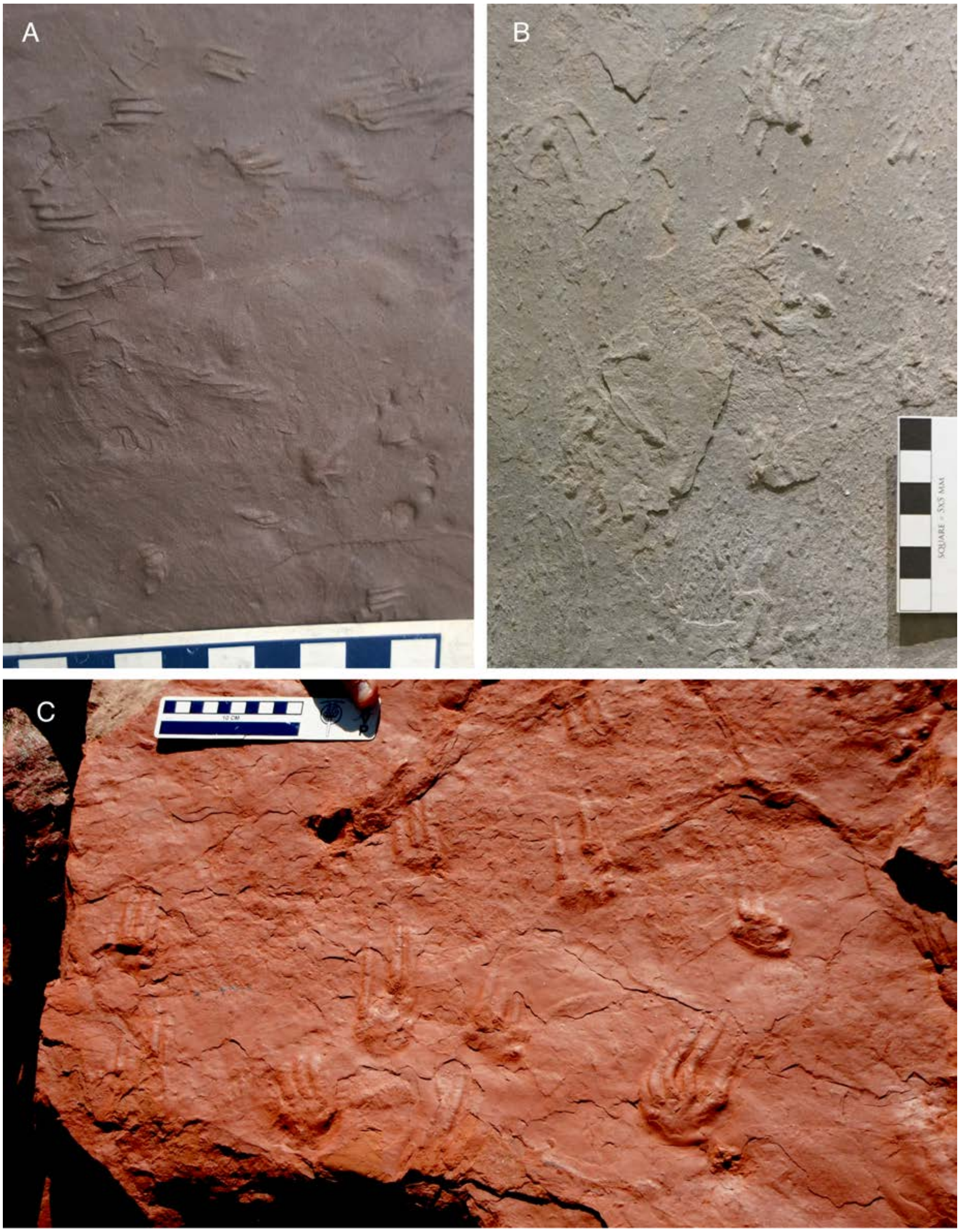

Fig. 12.—New trackway observations in the Maroon Formation, including cf. *Batrachichnus* **(A, B)** and *Amphisauropus* **(C). A**, cf. *Batrachichnus*, field observations of trackways found in float located at the Derby Junction site, Eagle County (B.J.S. 2018). **B**, cf. *Batrachichnus,* tracks collected from near the Derby Junction site, Eagle County, currently housed at the Denver Museum of Nature & Science (DMNH 49302). **C**, *Amphisauropus* with digit trailing marks, field observations of trackways located in the upper Maroon Formation at Red Table Mountain, north of Ruedi Reservoir, Eagle County (B.J.S. 2018).

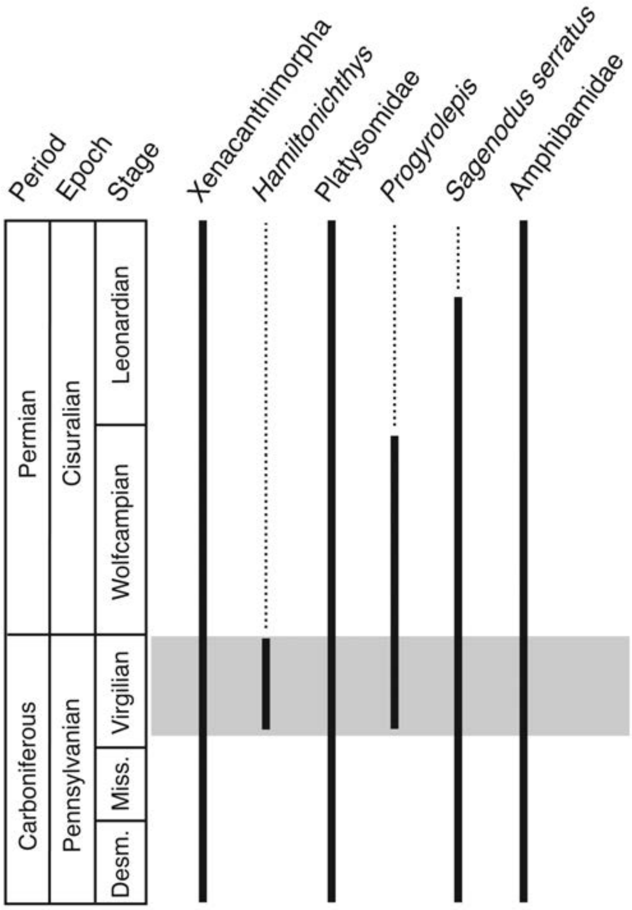

Fig. 13.—Known late Pennsylvanian to early Permian temporal ranges of the representative taxa in the Maroon assemblage. Gray horizontal band highlights overlapping ranges in the Virgilian North American stage (Ghzelian global stage). **Abbreviations: Desm.**, Desmoinesian; **Miss.**, Missourian.

The presence of platysomids in the Maroon assemblage provides no additional stratigraphic information, but adds to the paleoenvironmental interpretation by suggesting intermittent marine or brackish water influence as in an estuary or shallow lagoon setting (Huber 1992). The presence of non-estivating lungfish (*Sagenodus*) is also consistent with permanent water bodies rather than smaller ephemeral ponds (Schultze and Chorn 1997). Moreover, our discovery of the hybodont *Hamiltonichthys* is novel as it is the first occurrence of the genus outside its type locality of Hamilton, Kansas. Thus, the new *Hamiltonichthys* record biogeographically links the Kansas-Nebraska Forest City Basin and Colorado's Eagle Basin during a period in which aquatic and wetland faunas were hypothesized to become progressively more fragmented in Euramerica (Huttenlocker et al. 2008; Pardo et al. 2008, 2019; Dunne et al. 2018).

Comparisons with the Maroon Formation Footprint Fauna

The well-known tetrapod ichnoassemblage in the Maroon Formation 'redbeds' facies shares both similarities and differences with the aquatic-dominated assemblage reported here. Surveys of Maroon Formation trace fossils have produced records of *Batrachichnus* (Figs. 12A–B), *Amphisauropus* (Fig. 12C), *Tambachichnium*, *Varanopus*, *Dimetropus*, *Dromopus*, and especially abundant *Ichniotherium* tracks and trackways (Voigt et al. 2005; Small and Sanders 2007; Small et al. 2020). A single cf. *Batrachichnus* track (DMNH 49302) collected from below the level of the vertebrate site near Derby Junction is consistent with the presence of small temnospondyls (e.g., amphibamiforms) (Small and Sanders 2007). In 2018, more field observations of well-preserved cf. *Batrachichnus* tracks were made near the fossil site (in proximity to the level of the stratigraphic 'color change') (Fig. 12A). Comparison to other C–P ichnoassemblages in Euramerica have suggested important faunal ties to the Tambach Formation of Germany: both regions are interpreted as wet dune systems located in protected intermontane settings (Voigt et al. 2005, 2021; Soreghan et al. 2014) and dominated by large, herbivorous diadectid trackmakers (*Ichnotherium* spp.), as well as reptiles (*Dromopus*, *Tambachichnium*, *Varanopus*), and synapsids (*Dimetropus*). *Ichniotherium* tracks are also known to occur in the C–P Cutler Formation type area at Cutler Creek in Ouray and San Miguel counties, Colorado (Baird 1965b; Small et al. 2020), supporting that diadectids were the earliest abundant vertebrate herbivores in terrestrial ecosystems.

Remarkably, after decades of collecting trackways in the Tambach Formation, some trackmakers have also become represented as body fossils in the classic Bromacker Quarry, including articulated skeletons of diadectids such as *Orobates*, among others (Voigt et al. 2007). In contrast, vertebrate body fossils from the Maroon Formation redbeds have remained elusive. Although it is tempting to assume that the Tambach and Maroon formations record a uniform faunal province, quantitative paleoecological studies have shown that amniote-dominated dryland assemblages often occurred alongside wetland and coastal faunas of very different taxonomic composition (Pardo et al. 2019), so direct evidence of vertebrate diversity in the Maroon Formation is necessary to interpret the Maroon Formation within a regional context. We suggest that differences between the Maroon body fossil assemblage and the tetrapod ichnofossil assemblage were determined by different habitats and facies preferences until the wetland fauna eventually became replaced by a previously marginalized dryland assemblage across the basin.

Age of the Assemblage

In lieu of absolute dating methods, the age of the lower Maroon Formation has largely been constrained through the use of biostratigraphically informative index taxa. Marine index fossils from the Minturn Formation (Chronic and Stevens 1958; Murray and Chronic 1965; Houck 1997) and a combination of detrital zircon ages and tetrapod ichnotaxa from the upper Maroon Formation in the Aspen sub-basin (Voigt et al. 2005, 2021; Soreghan et al. 2014) suggest the transitional carbonate facies near the base of the Maroon Formation could be as old as late Carboniferous (Missourian) or as young as early Permian (Wolfcampian). The vertebrate fauna reported here is limited in its biostratigraphic utility, partly due to the long stratigraphic ranges of the taxa represented. Nevertheless, the broad similarities shared between the Derby Junction assemblage and C–P assemblages of the Forest City Basin (northern U.S. midcontinent), especially the Virgilian-aged Robinson and Hamilton localities of Kansas, support the notion that the lower portion of the Maroon Formation was deposited close to the C–P geologic transition (Fig. 13). Fossils of *Orthacanthus* and closely allied xenacanths, platysomids, and sagenodontids have long temporal ranges spanning the entire C–P transition, a stereotyped pattern in multiple Euramerican C–P basins. However, the pygopterid *Progyrolepis* has a range more restricted in western Pangea, with a rare Wolfcampian record in the Texas Archer City Formation (*P. tricessimalaris*), but it is mainly known from the late Carboniferous of western Europe in Stephanian-aged localities in France, Spain, and the Czech Republic (Virgilian-equivalent). Importantly, the hybodont *Hamiltonichthys*, which is abundantly represented at the Virgilian-aged Hamilton Quarry Lagerstätte, is the only taxon represented in the Maroon assemblage that is limited unambiguously to a late Carboniferous age. However, given the restricted geographic sampling of *Hamiltonichthys* in western North America, previously known only from its type locality, its utility as a stratigraphic index is tentative. Based on congruence of the biostratigraphic data, and in the absence of geochronological evidence to the contrary, we tentatively assign the Derby Junction fossil assemblage to the Virgilian North American stage (Ghzelian global stage). The identification of multiple fossil assemblages that span the Minturn-Maroon transition is a promising result of our study because it suggests a continuous record of deposition across the C–P geologic boundary, mirroring the time-equivalent Cutler Group in nearby Utah and New Mexico, and presents a worthwhile future target for investigating environmental and ecological change during the peak Late Paleozoic Ice Age.

CONCLUSIONS

The Derby Junction locality is the first vertebrate body fossil site discovered in the C–P Maroon Formation of Eagle Basin, Colorado, providing precious information about vertebrate biodiversity and ecological change in western Pangea during an important geologic transition. The fossils are preserved in a series of finely laminated carbonates interbedded with terrestrial sandstones and siltstones near the base of the Maroon Formation. Although most of the fossils are represented by isolated elements, some specimens consist of associated or semiarticulated elements. The assemblage consists of abundant chondrichthyans and actinopterygians, as well as rare lungfish and tetrapods. Notable occurrences include multiple morphotypes of xenacanths, the hybodont *Hamiltonichthys*, an imperfectly preserved pygopterid aff. *Progyrolepis*, a platysomid, the lungfish *Sagenodus*, and an indeterminate amphibamiform temnospondyl. This is also the first occurrence of *Hamiltonichthys* outside the famous Hamilton Quarry Lagerstätte. The assemblage is consistent with the hypothesis that the base of the Maroon Formation was deposited during the late Carboniferous (Virgilian), but independent non-biostratigraphic evidence for the age of the assemblage is wanting. Prior tetrapod trackway evidence from the Maroon Bells and the Permian Tambach vertebrate assemblage of Germany (Voigt et al. 2005, 2021) have suggested a widespread C–P terrestrial amniote fauna across Euramerica, based on abundant herbivorous diadectid tracks and other shared amniote and stem-amniote taxa. Recent studies have shown that C–P amniotes were more cosmopolitan than contemporary amphibians and 'fishes' that depended on more permanent water bodies, the latter being more endemic and therefore more vulnerable to environmental change (Sidor et al. 2005; Huttenlocker et al. 2008; Pardo et al. 2008, 2019; Dunne et al. 2018). The Derby Junction fossil site presents future opportunities to test how Carboniferous wetland environments transitioned to a drier Permian environment along the western edge of Pangea.

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APPENDIX 1. List of specimens and collections.
(*continued on next page*)

Specimen Number	Locality Name	Collection ID
CM 92155	Derby Junction, Marker 150	Amphibamiformes
CM 96037	Derby Junction, Marker 150	Hybodont
CM 96038	Derby Junction, Marker 150	Actinopterygii
CM 96039	Derby Junction, Marker 150	Hybodont
CM 96040	Derby Junction, Marker 150	Xenacanthida
CM 96041	Derby Junction, Marker 150	Xenacanthida
CM 96042	Derby Junction, Marker 150	Actinopterygii
CM 96043	Derby Junction, Marker 150	Osteichthyes
CM 96044	Derby Junction, Marker 150	Osteichthyes
CM 96045	Derby Junction, Marker 150	Osteichthyes
CM 96046	Derby Junction, Marker 150	Vertebrata
CM 96047	Derby Junction, Marker 150	Actinopterygii
CM 96048	Derby Junction, Marker 150	Hybodont
CM 96049	Derby Junction, Marker 150	Hybodont
CM 96050	Derby Junction, Marker 150	Hybodont
CM 96051	Derby Junction, Marker 150	Hybodont
CM 96052	Derby Junction, Marker 150	Tetrapoda
CM 96053	Derby Junction, Marker 150	Actinopterygii
CM 96054	Derby Junction, Marker 150	Actinopterygii
CM 96055	Derby Junction, Marker 150	Vertebrata
CM 96056	Derby Junction, Marker 150	Actinopterygii
CM 96057	Derby Junction, Marker 150	Hybodont
CM 96058	Derby Junction, Marker 150	Vertebrata
CM 96059	Derby Junction, Marker 150	Actinopterygii
CM 96060	Derby Junction, Marker 150	Actinopterygii
UMNH VP 35493	Derby Junction, Marker 150	Xenacanthida
UMNH VP 35494	Derby Junction, Marker 150	Xenacanthida
UMNH VP 35489	Derby Junction, Marker 150	*Hamiltonichthys*
UMNH VP 36364	Derby Junction, Marker 150	Actinopterygii
UMNH VP 35490	Derby Junction, Marker 150	*Hamiltonichthys*
UMNH VP 35487	Derby Junction, Marker 150	Hybodont
UMNH VP 35488	Derby Junction, Marker 150	Hybodont
UMNH VP 35495	Derby Junction, Marker 150	Hybodont
UMNH VP 35502	Derby Junction, Marker 150	Hybodont
UMNH VP 35506	Derby Junction, Marker 150	Chondrichthyes
UMNH VP 36365	Derby Junction, Marker 150	Osteichthyes
UMNH VP 35510	Derby Junction, Marker 150	Chondrichthyes
UMNH VP 35512	Derby Junction, Marker 150	Chondrichthyes
UMNH VP 35491	Derby Junction, Marker 150	Platysomidae
UMNH VP 35503	Derby Junction, Marker 150	aff. *Progyrolepis*
UMNH VP 35513	Derby Junction, Marker 150	Actinopterygii
UMNH VP 36366	Derby Junction, Marker 150	Actinopterygii
UMNH VP 35508	Derby Junction, Marker 150	aff. *Progyrolepis*
UMNH VP 36367	Derby Junction, Marker 150	Hybodont
UMNH VP 36368	Derby Junction, Marker 150	Xenacanthida
UMNH VP 35497	Derby Junction, Marker 150	Actinopterygii
UMNH VP 35504	Derby Junction, Marker 150	Actinopterygii
UMNH VP 35511	Derby Junction, Marker 150	Actinopterygii

CM, Carnegie Museum of Natural History, Pittsburgh; DMNH, Denver Museum of Nature & Science; UMNH, Natural History Museum of Utah, Salt Lake City

APPENDIX 1. List of specimens and collections.
(*continued from previous page*)

Specimen Number	**Locality Name**	**Collection ID**
UMNH VP 36366	Derby Junction, Marker 150	Actinopterygii
UMNH VP 35508	Derby Junction, Marker 150	aff. *Progyrolepis*
UMNH VP 36367	Derby Junction, Marker 150	Hybodont
UMNH VP 36368	Derby Junction, Marker 150	Xenacanthida
UMNH VP 35497	Derby Junction, Marker 150	Actinopterygii
UMNH VP 35504	Derby Junction, Marker 150	Actinopterygii
UMNH VP 35511	Derby Junction, Marker 150	Actinopterygii
UMNH VP 35499	Derby Junction, Marker 150	*Sagenodus*
UMNH VP 35509	Derby Junction, Marker 150	Osteichthyes
UMNH VP 35507	Derby Junction, Marker 150	Tetrapoda
UMNH VP 35492	Derby Junction, Marker 150	Vertebrata
UMNH VP 36369	Derby Junction, Marker 150	Vertebrata
UMNH VP 35496	Derby Junction, Marker 150	Vertebrata
UMNH VP 35498	Derby Junction, Marker 150	Vertebrata
UMNH VP 35501	Derby Junction, Marker 150	Vertebrata
UMNH VP 35505	Derby Junction, Marker 150	Vertebrata
UMNH VP 36370	Derby Junction, Marker 150	Actinopterygii
UMNH VP 36371	Derby Junction, Marker 150	Actinopterygii
UMNH VP 36372	Derby Junction, Marker 150	Actinopterygii
DMNH 49302	Jack Flats Tracks 5	cf. *Batrachichnus*
DMNH 49005	Jack Flats Tracks 2	Vertebrata
DMNH 49005	Jack Flats Tracks 4	Tetrapoda
DMNH 54831	Jack Flats Tracks 2	Tetrapoda
DMNH 48621	Jack Flats Tracks 2	*Ichniotherium*
DMNH 48618	Jack Flats Tracks 2	*Ichniotherium*
DMNH 48619	Jack Flats Tracks 2	*Ichniotherium*
DMNH 49300	Jack Flats Tracks 2	*Ichniotherium*
DMNH 49301	Jack Flats Tracks 2	*Ichniotherium*
DMNH 49007	Jack Flats Tracks 4	*Ichniotherium*
DMNH 48620	Jack Flats Tracks 4	*Ichniotherium*
UMNH VP 35485	Jack Flats Tracks 1	*Ichniotherium*
DMNH 49006	Jack Flats Tracks 1	*Ichniotherium*
DMNH 49874	Gast Footprint Locality	*Ichniotherium cottae*
DMNH 49875	Gast Footprint Locality	*Ichniotherium cottae*
DMNH 49910	Gast Footprint Locality	*Ichniotherium*
DMNH 49910	Gast Footprint Locality	*Ichniotherium cottae*
DMNH 50618	Gast Footprint Locality	*Ichniotherium cottae*
DMNH 50622	Gast Footprint Locality	*Ichniotherium cottae*
UMNH VP 28580	County Road 103	*Dimetropus*
DMNH 49911	Gast Footprint Locality	*Dimetropus*
DMNH 50619	Gast Footprint Locality	*Dimetropus*
DMNH 50621	Gast Footprint Locality	*Dimetropus*
DMNH 49303	Jack Flats Tracks 1	*Varanopus*
DMNH 49876	Gast Footprint Locality	*Varanopus*
DMNH 50620	Gast Footprint Locality	*Tambachichnium*
UMNH VP 35486	Jack Flats Tracks 1	*Dromopus*
DMNH 49304	Jack Flats Tracks 1	*Dromopus*

CM,
Carnegie Museum
of Natural History,
Pittsburgh;
DMNH,
Denver Museum of
Nature & Science;
UMNH,
Natural History
Museum of Utah,
Salt Lake City