

Earliest Evidence of Marine Habitat Use by Mammals

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Abstract

Evidence for the earliest invasion of the marine realm by mammals was previously restricted to Eocene (48.6-37.8 Ma) skeletal remains. We report incontrovertible ichnofossil evidence for brackish-water habitat use by at least two mammalian species in southern Wyoming during the late Paleocene (58 Ma). These are the first Paleocene mammal trackways recorded in the United States and only the fourth documented in the world. Multiple tracks preserved in restricted marine deposits represent animals repeatedly walking across submerged to partially emergent tidal flats. Hundreds of tracks are preserved in planform and cross-sectional exposure within five horizons along a 1,032 m tracksite. Four prints exhibit five clear toe imprints, while two others distinctly display four toes. Some tracks penetrate beds populated by dwelling traces of marine bivalves and polychaetes in the upper layers and sea anemones at the base. Candidates for the five-toed tracemakers are pantodonts such as *Titanoides*, *Barylambda*, and *Coryphodon*, which have been recovered from late Paleocene strata throughout western North America. The four-toed tracks provide the earliest evidence of previously-undescribed large artiodactyls and/or tapiroids, mutually supporting recent molecular phylogenetic studies that place the origin of Cetartiodactyla near the Cretaceous-Paleogene boundary (~67.7 Ma). Collectively, these trackways irrefutably demonstrate the utility of ichnological data in reconstructing the evolutionary history and adaptive behaviors of extinct taxa beyond the evidence provided by body fossils alone.

Introduction

Despite intense interest in and field studies of early Cenozoic mammalian radiation and dispersal patterns, Paleocene mammal trackways are exceedingly rare with only three previously reported worldwide. The early Paleocene *Sarjeantipes*¹ from Alberta, Canada is a medium-sized, five-toed ichnotaxon that superficially resembles prints made by modern raccoons (*Procyon lotor*). A heavily-eroded 11.2 m long trackway, also from Alberta, Canada, was laid down by large mammals in the late Paleocene. Although the prints are reported to be wide-gauge², they might represent a parallel pair of narrow-gauge tracks. A narrow-gauged trackway from the late Paleocene of Spitsbergen, Norway is the ichnotype of *Thulitheripus svalbardii* and has been attributed to large pantodonts traversing a continental coastal mire³.

Here we report a newly discovered, aerially-extensive series of late Tiffanian (58 Ma) mammalian trackways, dispersed across multiple stratigraphic intervals and traceable for 1,032 m along a belt of well-exposed siltstone and very fine-grained sandstone outcrops. Uniquely preserved in brackish-water delta complexes within a restricted marine embayment or lagoon, these trackways attest to the recurrent use of marine habitats by medium- to large-bodied mammals during the late Paleocene. A minimum of two mammalian taxa are identifiable: one associated with relatively large, narrow-gauge, five-toed tracks, and the other with medium-sized, four-toed tracks. This direct evidence of marine habitat utilization by early Paleocene mammals predates the earliest mammalian skeletal remains preserved in marine

sediments⁴ by 9.4–20 million years and highlights the potential for ichnological data to identify previously unknown taxa and their ecological adaptations.

Geological Context

The Paleocene-Eocene (63 – 53 Ma) Hanna Formation in the Hanna Basin (Wyoming, U.S.A.) contains a mosaic of fluvial, lacustrine, and brackish-water paleoenvironments^{5,6}. The track-bearing interval occurs in the lower portion of a newly recognized, 216 m thick, brackish-water member of the formation (Fig. 1). Fossil plants and pollen collected from surrounding deposits indicate a late Paleocene age (upper P5-P6 palynostratigraphic zone: 58 Ma) for the tracksite⁶. The bulk of the formation below the brackish-water unit consists of siltstone, fine-grained sandstone, and pebble to cobble conglomerate weathering into badlands topography. Crayfish burrows preserved within siltstones demonstrate seasonally low paleo-water tables and the development of well-drained soils⁷. Transition to the unnamed, brackish-water member is marked by a lithological shift to carbonaceous shales, coals, and prominent, rusty-orange sandstone and siltstone ridges. This unit is further differentiated by the presence of definitively marine ichnofossils, including *Thalassinoides*, *Siphonichnus*, *Bergaueria*, *Arenicolites*, *Gyrochorte*, *Ophiomorpha*, *Skolithos*, *Cylindrichnus*, *Palaeophycus*, and *Rhizocorallium*, preserved in silty and very fine-grained sandy delta front, tidal flats, and lagoonal deposits.

Hundreds of prints are preserved in at least five discrete horizons within two separate, silty to very fine-grained sandy delta lobes (Fig. 2). The delta complex is 12 m thick, with individual lobes composed of 1–2 m thick packages of coarsening-upward clay, silt, and very fine-grained sand. A 1.5-2 m thick and 113 m wide distributary channel separates the northwestern portion of the trackway from the southeastern. Wavy and lenticular bedding dominate prodelta and delta front successions with current ripples, climbing ripples, and small-scale trough and planar cross-bedding more common towards the proximal delta front. In addition to the mammal footprints, heavily-burrowed, contorted siltstone beds are marked by an abundance of polychaete and bivalve traces, supporting their interpretation as tidal flat environments. The presence of *Bergaueria* (sea anemone burrows), *Rhizocorallium* (polychaete burrows), *Gyrochorte* (polychaete trails), *Siphonichnus* (marine bivalve burrows), and other marine-derived ichnofossil suites throughout the silty beds is definitive evidence of marine or brackish-water influence during deposition of these strata^{8,9,10,11,12,13,14,15}.

Description Of Tracks And Trackways

Along the 1,032 m transect of track-bearing strata, four footprint morphotypes can be recognized: 1) round, amorphous depressions on bedding surfaces, 2) moderately- to well-preserved, five-toed prints preserved on bedding surfaces, 3) well-preserved, four-toed prints preserved on bedding surfaces, and 4) natural load casts penetrating underlying, heterolithic strata and exposed in cross-sectional view. Siltstone beds contain prints preserved with clearer outlines and toe impressions than those in fine-

grained sandstone beds. The lower surface area to volume ratio of individual sand grains compared to silt results in lower grain-to-grain adhesion and a decreased ability for the substrate to retain an imprint, causing prints to be poorly preserved in sandstone compared to those in siltstone beds.

Individual five-toed imprints are mostly poorly-defined, but measure on average between 15–20 cm long and 15–22 cm wide with specimens ranging up to 24.5 cm long and 25 cm wide, approximating the upper size range of the North American Brown Bear (*Ursus arctos*)¹⁶ (Fig. 3). Four larger toes are directed forward, while a smaller, fifth toe is angled nearly 90° to the others. Two of the four clearest bedding plane prints are broader than long (21.5 x 15 cm and 19 x 14 cm), one is equally broad and long (18 x 18 cm), and a fourth appears longer than broad (37 x 15 cm), but exact measurements of the latter are hampered by the incomplete register of the foot along its posterior margin and possible slide-in mark (Fig. 3A, B). A particularly deep track preserves possible evidence of a direct register gait in which the apparently narrow-clawed manus impression is partially or completely obliterated by the pes (Fig. 3F, G). Alternatively, the imprint may be an artifact of the deep penetration and withdrawal of a blunt-toed foot triggering inward collapse of more saturated, deeper sediment, giving the impression of narrower digits towards the bottom of the print.

Clearly distinguishable from the larger, five-toed tracks are prints bearing four distinct, equal-sized digits. One 11 cm-wide x 11.5 cm-long print with four toe imprints exhibits a drag mark representing forward and downward movement of the foot (Fig. 3D, E). A possible partial imprint of another, forward-facing toe is visible but is obscured by the third toe from the left, a pattern consistent with a direct register gait. The print is situated within a trackway consisting of six amorphous prints with a bearing of 94°. A roughly parallel trackway (bearing 97°) of four prints 58 cm to the north of these tracks also includes a four-toed imprint (Fig. 3J, K). The two middle toes in this 13 cm-wide x 12 cm-long track are tightly appressed and initially appear to be a single digit. Both four-toed prints were likely made by the same mammalian taxon, and differences in the spread between the median toes of the prints in each trackway resulted from varying toe placement, probably reflecting differences in substrate moisture.

Where exposed in cross-section, the larger, five-toed prints display characteristics of footprints made by heavy vertebrates in water-saturated, weakly-consolidated sediment^{20,21,22}(Fig. 4). Although poor preservation precludes detailed analysis of print morphology in the cross-sectional examples, evidence for the direction of travel is afforded by the downward rotation of the anterior portion of the foot as the toes press deeper into the substrate during forward propulsion³. Distinct toe imprints are rare in deeply-penetrating footprints and natural casts, but five blunt toe marks can be recognized in a single 17.25 cm long track (Fig. 4A, B).

The stratigraphically-lowest trackway is located to the northwest of the distributary channel (Fig. 2). A broadly lenticular, silty sandstone bed hosts thousands of *Bergaueria* at its base (Fig. 4H). Polychaete and bivalve burrows (*Skolithos* and *Siphonichnus*, respectively) are distributed across the surface of this bed, indicating continuation of marine conditions after deposition of the sediment (Fig. 4I). Mammalian footprints originate in a siltstone horizon 25–30 cm above the base of the bed and penetrate as deep as

39 cm into the underlying silty claystone (Fig. 4D). Tracks are exposed in plan-view as well as in cross-section with several preserved in both views, confirming that surface-only tracks are not simply anomalous depressions.

Southeast of the distributary channel, a continuous, 356 m-long exposure of several trackways exhibits planform (Fig. 5A, B) and cross-sectional imprints that penetrate and deform underlying strata. Four separate horizons are identifiable, each representing flood-delivery of siltstone and very fine-grained sand onto the brackish-water delta front, mouth bars, and tidal flats. The uppermost horizon is traceable for 230 m and contains hundreds of individual prints arranged into more than 20 distinct trackways, although portions are obscured by vegetation cover or damaged by weathering. The majority of prints with discernable toe impressions are located in this horizon, their enhanced preservation attributable to the rheology of the very fine siltstone in which these tracks were imprinted. Evidence of social behavior exists in some of the clearer trackways. For instance, a pair of tracks consisting of a large (average = 17.5 cm wide x 14.8 cm long) and a 70% smaller (average = 12 cm wide x 11 cm long) set of prints, walking in tandem to the southeast (105° bearing) may represent an adult and juvenile or a sexually-dimorphic pair traversing together for approximately 3 m (Fig. 5B).

A well-exposed, 7 m-long, planform trackway composed of amorphous and five-toed morphotypes is located proximal to the northwestern side of the distributary channel and includes parallel tracks of at least three individuals preserved in very fine-grained sandstone (Fig. 5C). This trackway appears to be the highest stratigraphically, but the distributary channel forms a stratigraphic barrier that impedes its direct correlation to any of the trackways to the southeast (Fig. 2).

Discussion

Identity of Track Makers

The late Paleocene age of the Hanna Formation trackways limits the known mammalian taxa sizeable enough to produce the five-digitated prints to the Pantodonta^{3,19}. One or more species, such as *Titanoides primaevus*, *Barylambda faberi*, or *Coryphodon proterus*, were likely responsible for the tracks deposited in this Paleocene lagoon (Fig. 6). *Titanoides* was identified as the originator of Late Paleocene *Thulitheripus svalbardii* from Norway³. The five clear toe impressions of *T. svalbardii*, with those on the manus appearing to be claw-like and strongly curved, bear some resemblance to the deeper print from the possible direct register track described above (Fig. 3F). However, we cannot definitively attribute any of the tracks to *Thulitheripus* nor to its associated *Titanoides* maker since the apparently narrow-clawed manus imprint from the Hanna Formation may be an artifact of substrate collapse in the deeper portion of the track.

The brackish-water setting of the trackways and their recurrence of deposition suggests that their five-toed mammalian originators routinely exploited aquatic habitats. The morphology and stable isotope chemistry of *Coryphodon* indicate that this pantodont exhibited semiaquatic habits analogous to those

of extant common hippopotamus (*Hippopotamus amphibius*)²³. At an estimated weight of 700 kg, the only known Paleocene species of *Coryphodon*, *C. proterus*, was larger than later species and has only been documented from western North America²⁴. The combination of mass and hypothesized natural history of these pantodonts renders them the most plausible candidates for our track makers. Since the Hanna Formation trackways are approximately 1.0-1.5 m.y. older than the earliest skeletal record of *Coryphodon*, confirmed attribution of these tracks to this genus would extend its origin farther into the Paleocene than indicated by the body fossil record alone.

The four-toed prints do not correspond to the skeletal elements of any mammals described from the late Paleocene but bear remarkable resemblance to tracks made by medium- to large-bodied artiodactyls and forefoot imprints of modern tapirs (Perissodactyla). Trace fossil evidence for the origination of animal taxa prior to their sampling in the body fossil record has been well documented for various invertebrate lineages, though not without controversy^{22,25,26}. The earliest osteological record of tapiroids is from early Eocene strata of Ellesmere Island, Canada, fueling the hypothesis that the lineage had an earlier origin within North America²⁷. Although the phylogeny of Paleocene mammals remains poorly constrained²⁸, recent time-calibrated molecular investigations have proposed a late Cretaceous or early Paleocene (74.4–64.1 Ma, mean 67.7 Ma) origin for Cetartiodactyla and its sister taxon the Perissodactyla²⁹. Consequently, attribution of the Hanna Formation four-toed tracks to either tapiroid or artiodactyl tracemakers is consistent with molecular phylogenetic studies and substantiates these hypotheses with tangible, physical evidence. Therefore, we contend that these four-toed Paleocene prints are attributable to as-of-yet undiscovered North American tapiroids or large-bodied artiodactyls.

Paleoecological Implications

The restricted marine setting of the Hanna Formation tracks has intriguing paleoenvironmental and behavioral implications. The trackways demonstrate shallow, tidally-influenced, brackish-water habitat use by at least two mammalian species during the late Paleocene (58 Ma), an interaction with marine environments previously unknown prior to the Eocene (48.6–37.8 Ma) on the basis of body fossils. Although the presence of sea anemone traces is typically associated with offshore or nearshore marine settings³⁰, anemones can tolerate a wide range of physicochemical extremes, including subaerial exposure during low tide³¹. Therefore, the sea anemone traces abundantly preserved in beds bearing mammalian prints are consistent with shallow subtidal to intertidal settings (Fig. 4H).

The use of brackish-water habitats by modern large-bodied, terrestrial to semiaquatic mammals is relatively common. Mammals weighing ≥ 28 kg exploit estuarine and marine habitats temporarily to permanently, exhibiting a variety of non-exclusive behavioral strategies. Saltwater environments serve as dispersal routes between offshore islands or between mainland and island habitats for Asian elephants (*Elephas maximus*), Baird's tapirs (*Tapirus bairdii*), caribou (*Rangifer tarandus*), chamois (*Rupicapra* spp.), Sumatran serow (*Capricornis sumatraensis*), and various species of deer^{32,33,34,35,36,37,38}. The use of brackish-water environments may also reflect seasonally-expressed migratory responses to climatic stimuli, as demonstrated by the movement of polar bears (*Ursus maritimus*) with sea ice patterns and the

rainy season dispersal of riverine hippopotamus to coastal regions^{39,40}. Regular and year-round residence in estuarine and marine locales are generally associated with unique foraging opportunities provided in the form of saltwater-tolerant vegetation, invertebrates, vertebrates, and scavenge-able carcasses transported downstream by flooding events or landward by tidal action^{41,42}. Aquatic habitats are also important for mammals seeking refuge from biting insects and/or potential predators^{36,43}. CAMELS

In subtropical to tropical regions, similar to the climatic and environmental conditions in which the Paleocene tracks were deposited, extant megafauna use brackish water environments for thermoregulation^{36,43,44}. Hippopotamus submerge in South Africa's St. Lucia Estuary to minimize sun exposure, regulate body temperatures, and reduce energy expenditure⁴⁴. Estuarine areas shallow enough to stand in, but deep enough to remain partially to fully submerged (*i.e.* water depths of 1.0-1.49 m for animals with a shoulder height of 1.5 m), are preferred. Locations adjacent to river mouths support greater hippopotamus densities due to the opportunity for more efficient thermoregulation provided by bathymetric changes associated with sandy mouth bars⁴⁴. Notably, the trackways we describe occur in sediments analogous to these microenvironments favored by thermoregulating hippopotamus. Specifically, the greatest density of tracks is situated proximal to the Paleocene distributary mouth (Fig. 2). Abundance of tracks decreases 412 m to the southeast of the channel, where exposure becomes limited, and disappears completely 300 m to the northwest of the channel despite good exposure.

Modern mammals are also drawn to brackish and marine environments to satisfy physiological requirements related to sodium deficiencies^{36,43}. Forest elephants (*Loxodonta cyclotis*) in Gabon are attracted to salt-laden coastal vegetation, while Asian elephants in Malaysian rainforests frequent the coast to drink saline and hypersaline water^{43,45}. Similar to their modern large, terrestrial mammal analogs, the Paleocene trackmakers were likely prone to mineral deficiencies due to excessive mineral-leaching from the adjacent tropical forest soil and the resulting decreased availability of sodium in the tropical and subtropical vegetation, driving them to take advantage of coastal mineral resources.

Conclusions

We report the world's largest assemblage of Paleocene mammal tracks preserved in Wyoming's late Paleocene Hanna Formation. Not only are these trackways the first such reported for the United States, but they are only the fourth mammalian trackways described in the world. Hundreds of individual prints, representing at least two large mammalian taxa, are exposed in varying preservation in a minimum of five discrete horizons, which can be traced laterally for up to 1,032 m.

Pantodonts are likely responsible for the larger (15-24.5 cm long x 15–25 cm wide), five-toed prints, with paleoecological data supporting the semi-aquatic *Coryphodon* as a probable candidate. Clear four-toed prints (11.5–12 cm long x 11–13 cm-wide) are also evidenced within the trackways, possibly left by as-of-yet undescribed artiodactyls and/or tapiroids. Molecular phylogenetic hypotheses for a late Cretaceous to early Paleocene origin of these taxa is thus significantly augmented by these ichnological data, despite the absence of osteological remains.

The trackways were deposited in a restricted marine embayment or lagoon, on silty and sandy tidal flats near an active fluvial distributary channel. This interpretation is supported by the presence of mammal tracks in beds hosting low-diversity, marine ichnofauna. Fossilized skeletal remains previously established the Eocene as the earliest marine habitat use by mammalian taxa, whereas the Hanna Formation trackways extend the origin for mammals' expansion into brackish-water environments to at least 58 Ma. Late Paleocene mammalian megafauna were likely drawn to these ecosystems to fulfill similar needs as their modern analogues: migration, thermoregulation, protection from predators and biting insects, and access to sodium and other minerals, which would have been limiting in the North American Western Interior's tropical forests. As such, the Hanna Formation trackways offer compelling insight into early Cenozoic mammalian evolution and paleoecology, providing us with a glimpse into the lives of megafauna mucking through the brackish-water tidal flats of the late Paleocene and preserving behavior that couldn't be predicted from analysis of body fossils alone.

Methods

Ichneological, stratigraphic, and sedimentological reconnaissance was undertaken for late Paleocene strata within the Hanna Formation, north of Medicine Bow Wyoming, U.S.A. from 2016-2020. Previously unidentified brackish-water strata and tracksites were subsequently identified, examined, measured, and photographed in the field. All-purpose baking flour was used to highlight the prints for photographic purposes, such that marking would not inflict any significant adverse impact on the natural environment. Sedimentary sections were logged through the stratigraphic interval comprising the deltaic complex in which the trackways are preserved. Grain size, sedimentary structures, bedding contact, lateral continuity, and associated trace fossils were recorded in detail. Individual beds were walked out to establish correlations and relationships to surrounding horizons. A variety of modern and historic animal footprints and tracksites were examined to critically evaluate the morphology, taxonomic affinity, and locomotory behavior of the trace-making taxa. Avian, reptilian, amphibian, and invertebrate animals were excluded as potential footprint-making candidates based on the morphology of the prints and the gait pattern preserved in many of the tracks. Black and brown bear (*Ursus arctos* and *U. americanus*) footprints were photographed and cast in dental plaster in Alaska and Colorado, USA, and Alberta, Canada for comparison with the Paleocene tracks.

Declarations

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AUTHOR CONTRIBUTIONS

AF-JW was responsible for all the fieldwork, photography, and drafting of figures. BEG-W was responsible for all analog and modern ecological investigations. Both AF-JW and BEG-W prepared and edited the manuscript.

COMPETING INTERESTS

The authors declare they have no competing interests.

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Figures

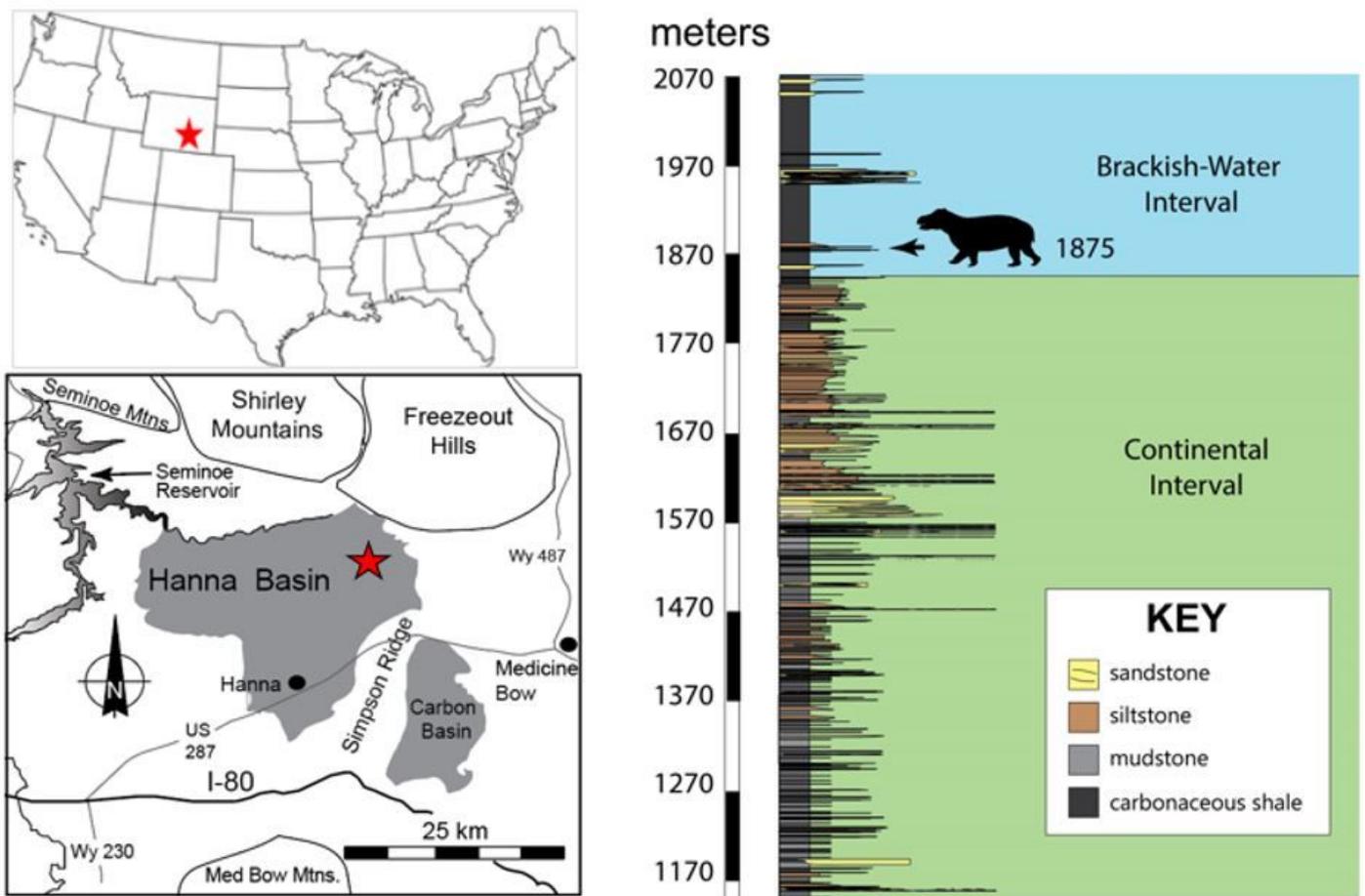


Figure 1

Location and stratigraphic setting of the tracksite. Measured section is stratigraphic elevation above local base of the Hanna Formation. Entire succession falls within P5 palynostratigraphic zone, with tracksite in

uppermost portion of the zone. Note: The designations employed and the presentation of the material on this map do not imply the expression of any opinion whatsoever on the part of Research Square concerning the legal status of any country, territory, city or area or of its authorities, or concerning the delimitation of its frontiers or boundaries. This map has been provided by the authors.

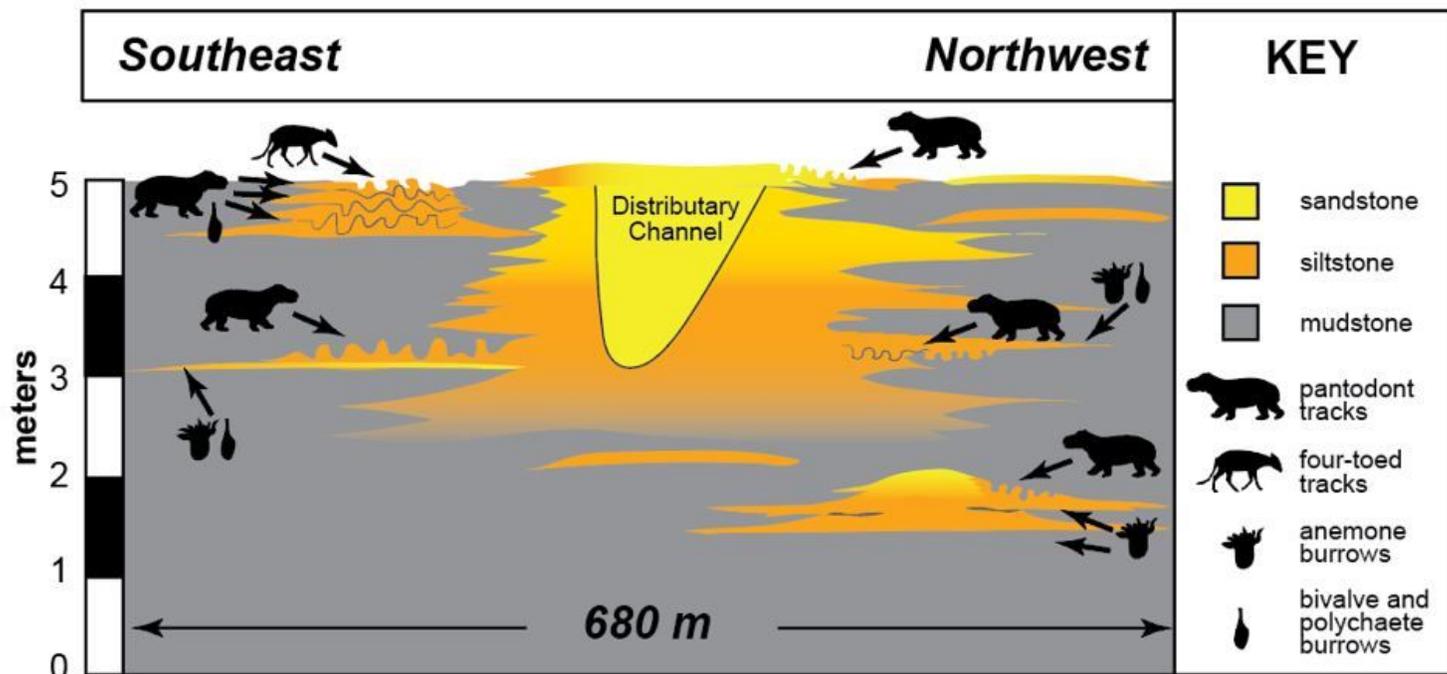


Figure 2

Stratigraphic and aerial distribution of mammal prints and other significant trace fossils within the main section of the tracksite.

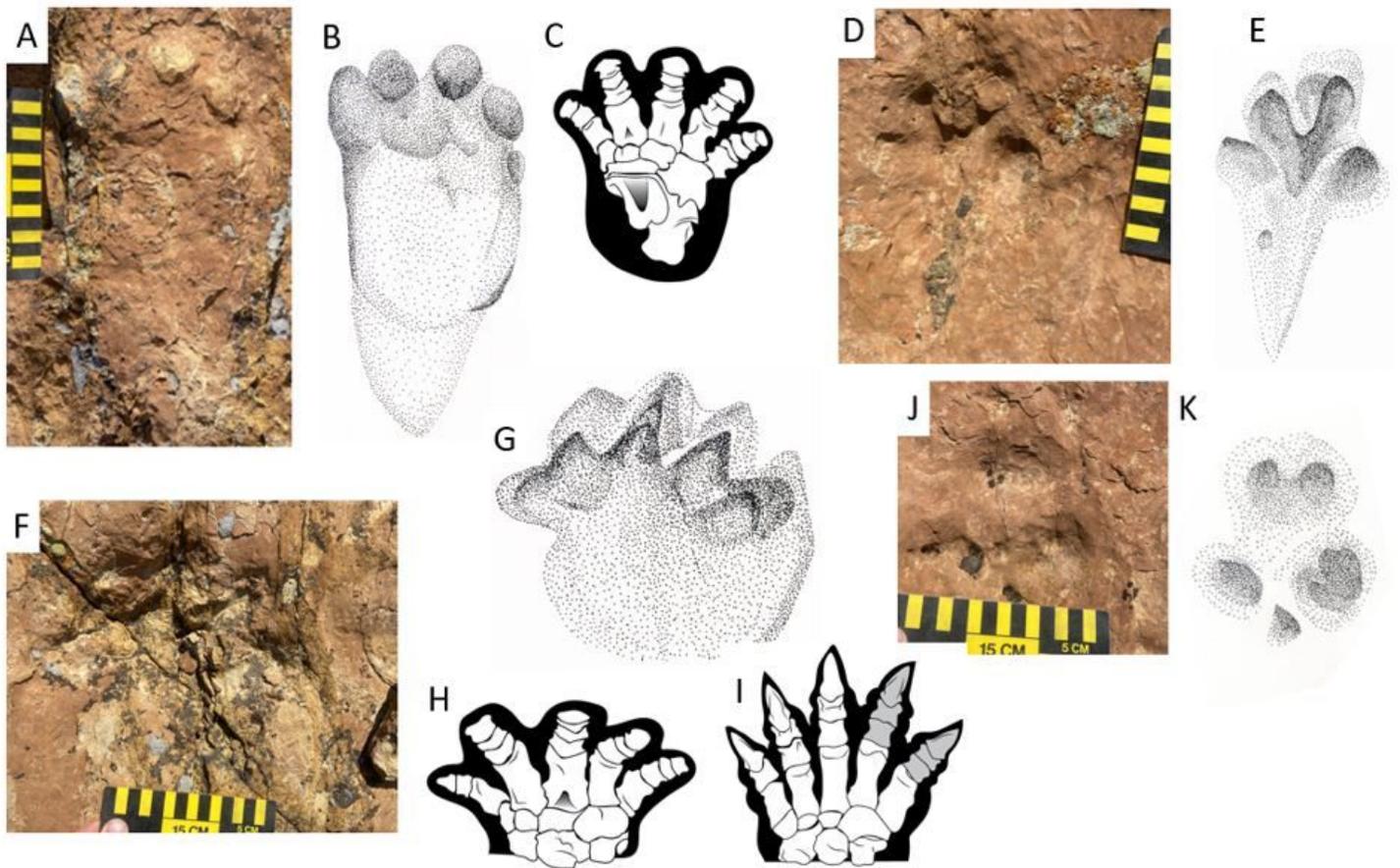


Figure 3

Representative examples of individual footprints with clear toe impressions. (A) Photograph of five-toed footprint; (B) interpretive sketch of A; (C) outline of skeletal elements of *Coryphodon radians* pes (modified from original17); (D) photograph of four-toed footprint showing slide-in; (E) interpretive sketch of D; (F) photograph of five-toed footprint interpreted as a manus or possible direct register imprint; (G) interpretive sketch of F; (H) outline of skeletal elements of *C. radians* manus (modified from original18); (I) outline of skeletal elements of *Titanoides primaevus* manus (modified from original19) with missing bones in grey (modified from original19); (J) photograph of four-toed footprint with middle toes closely appressed, creating the appearance of three toes; (K) interpretive sketch of J.

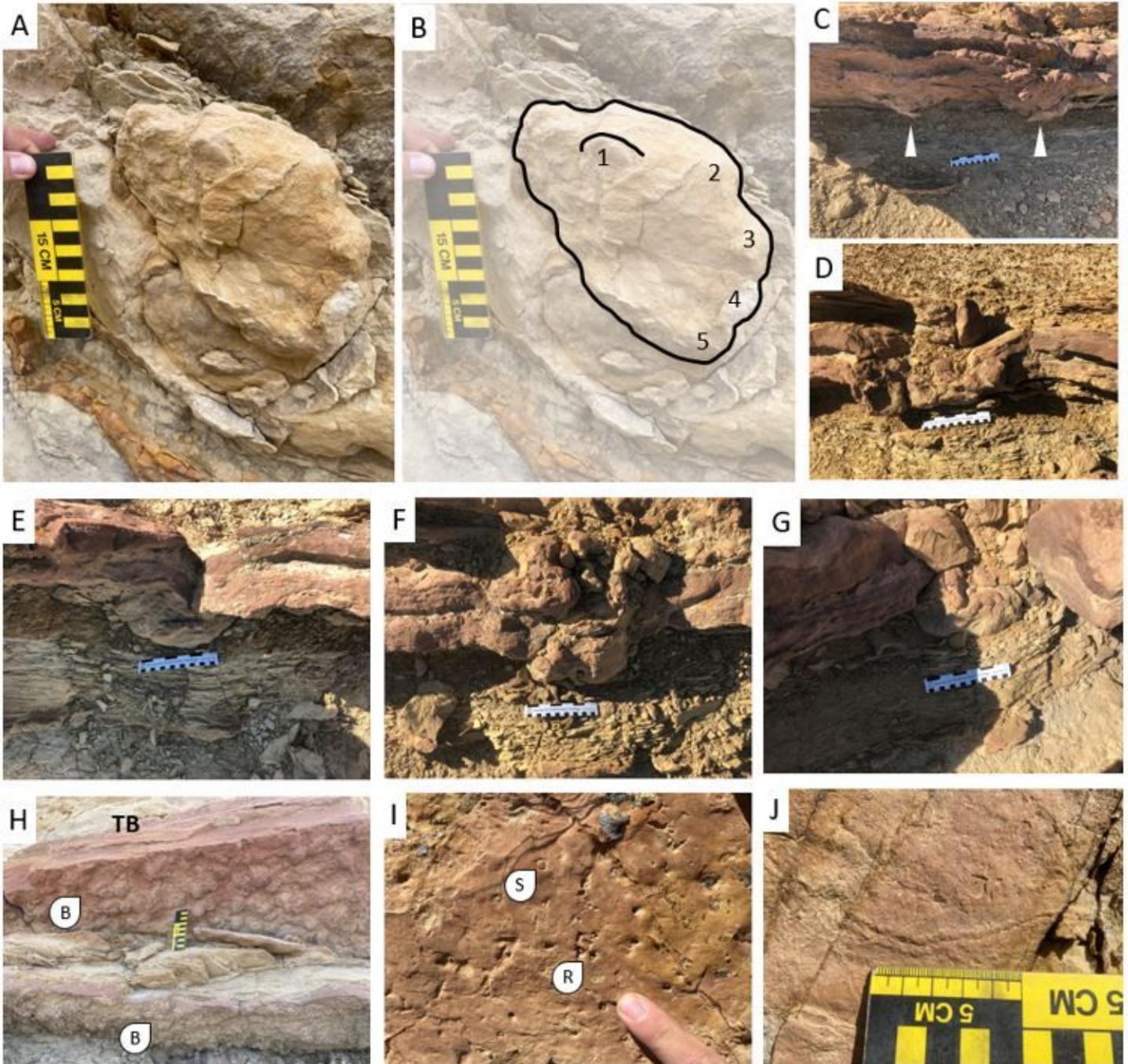


Figure 4

Photographs of representative examples of penetrative footprints and associated brackish-water ichnofossils. Scale bars in A-H, J are 15 cm. (A) Natural cast of blunt-toed print left by animal walking left to right (southeast to northwest); (B) Interpretive outline of A; (C) consecutive footsteps of an animal waking left to right (southeast to northwest), arrows indicate penetration of footprints; (D) large footprint made by animal walking right to left (northwest to southeast); (E) underprint in silty claystone 20 cm below sandstone bed; (F) penetrative footprint with underprint in silty claystone and deformation in track-bearing sand; (G) natural sandstone cast and penetrative print; (H) underside of a track-bearing silty sandstone bed (TB) with abundant *Bergaueria* (B) at the base, overlying a siltstone bed with additional

Bergaueria at the base; (I) upper surface of silty sandstone bed with abundant, small Rhizocorallium (R) and Siphonichnus (S) among other marine ichnofossils. Index finger of AFJW for scale; (J) Gyrochorte in very fine-grained sandstone bed underlying track-bearing siltstone.

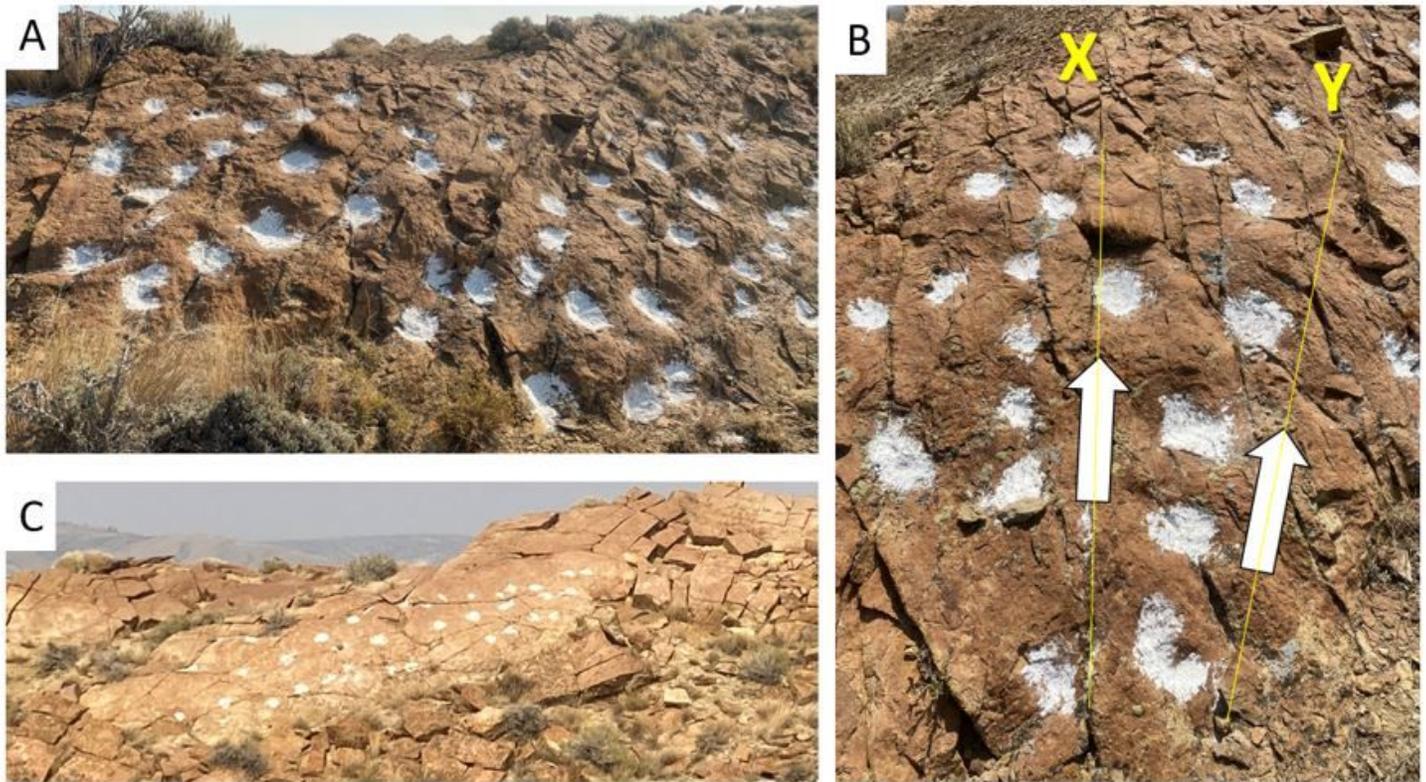


Figure 5

Photographs of the upper surface of the southeastern and northwestern portions of the tracksite. Baking flour used to accentuate individual prints. (A) Heavily trampled surface of the southeastern tracksite; (B) detail of subset of tracks in A. Tracks to the left of line X are from a smaller individual. Tracks to left of line Y are from a larger individual; (C) portion of northwestern section of upper trackway preserved in very fine-grained sandstone.

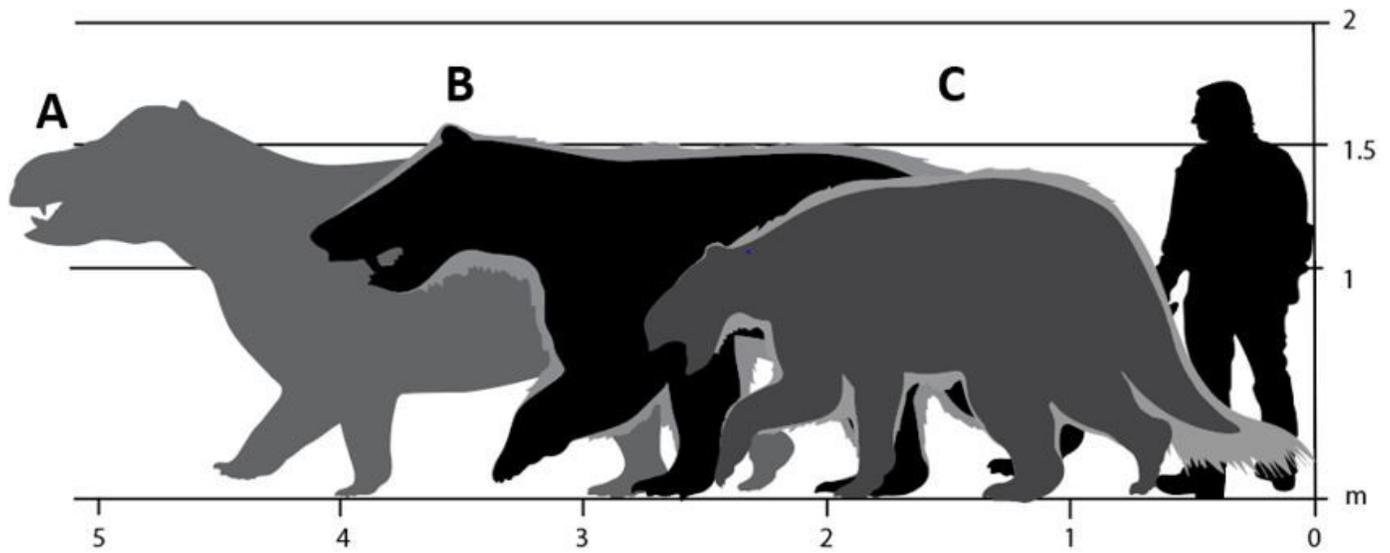


Figure 6

Reconstructed track maker candidates for size comparison. (A) Paleocene *Coryphodon proterus* (Yale Peabody Museum specimen VPOU.016130, with a 62 cm long skull), based on measurements of Eocene *C. radians*¹⁷; (B) *Titanoides primaevus* based on skeletal reconstruction¹⁸ and scaled to holotype specimen (Yale Peabody Museum VPPU.016490); (C) *Barylambda faberi* based on mounted specimen displayed at the Field Museum of Natural History.