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RESEARCH PAPER

Peabody's legacy: the Moenkopi Formation (Middle Triassic, Anisian) tetrapod ichnofauna—updates from an extensive new tracksite in NE Arizona, USA

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Abstract

The Lower-Middle Triassic Moenkopi Group/Formation in the southwestern USA has yielded a famous tetrapod skeletal and ichnofossil fauna. A new locality in the Holbrook Member of the Moenkopi Formation (Anisian) of northeastern Arizona appears to be the most extensive Middle Triassic tetrapod tracksite in North America. The ichnofossil-bearing level is close to the base of the Holbrook Member and several meters below the overlying Shinarump Formation (Upper Triassic, Carnian) of the Chinle Group. The track-bearing bed is a mudstone layer overlain by a massive-to-laminar, tabular sandstone body that represents sheet-like non-channelized flow deposited by flooding and preserves the collected natural casts of the tracks. A low diversity invertebrate ichnoassemblage dominated by *Scoyenia* on the track-bearing surface represents the *Scoyenia* ichnofacies. The paleoenvironment can be characterized as an intermittently subaerial/subaqueous setting on a nonmarine riverine floodplain. The tetrapod ichnoassemblage is dominated by archosaur tracks with the chirotheriids *Chirotherium barthii*, *C. rex*, *Isochirotherium marshalli*, *Synaptichnium diabloens*e, *S. pseudosuchoides*, and small *Rotodactylus cursorius*. *Synaptichnium* and *Rotodactylus* are the most abundant tetrapod ichnogenera at this location. Chirotheres occur with different size classes, possibly suggesting a mixed archosaur community with individuals of different growth stages and ages. Biostratigraphically, the composition of the assemblage and the presence of the ichnospecies *Chirotherium barthii* in the Holbrook Member indicate the *Chirotherium barthii* biochron for this unit. The lack of *Chirotherium sickleri* supports former conclusions about paleobiogeographic peculiarities of the North American assemblage, if compared to early Anisian ichnoassociations of Europe, where *Chirotherium barthii* is commonly associated with *C. sickleri*. Interestingly, the new tracksite lacks archosauromorph/lepidosauromorph tracks such as *Rhynchosauroides* or therapsid tracks such as *Dicynodontipus* that co-occur at other localities.

Keywords Holbrook member · Archosaur footprints · Chirotheres · *Rotodactylus* · *Scoyenia* ichnofacies

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Introduction

In North America, footprint-bearing continental Triassic strata are present in two regions: (1) the great Triassic–Jurassic rift valley deposits along the East Coast, and (2) the red beds of the Southwest, in particular in northern Arizona, Nevada, Utah, Wyoming, Colorado, and New Mexico. In the eastern part, fluvio-lacustrine deposits of the Newark Supergroup yielded diverse Upper Triassic (Carnian–Rhaetian) tetrapod ichnoassemblages with the ichnogenera *Brachychirotherium*, “*Chirotherium*”, *Apatopus*, *Evazoum*, *Atreipus*, *Grallator*, *Rhynchosauroides*, *Gwyneddichnium,* and *Procolophonichnium* (e.g., Olsen and Baird 1986; Weems 1987; Olsen 1988; Szajna and Silvestri 1996; Olsen and Huber 1998; Szajna and Hartline 2003). In this area, older, Lower-Middle Triassic strata are mostly documented from drilling cores, so they are not exposed at the surface. In the western and southwestern part of North America, the Moenkopi Group/Formation and the Red Peak Formation (Olenekian-Anisian) have provided diverse tetrapod-footprint ichnoassemblages with *Chirotherium*, *Synaptichnium*, *Isochirotherium*, *Protochirotherium*, *Rotodactylus*, *Rhynchosauroides*, *Chelonipus*, *Procolophonichnium*, *Therapsipus, Batrachichnus*, indeterminate ichnotaxa, and swim traces that have been extensively studied by F. E. Peabody (1948, 1956) and other researchers (e.g., Hunt and Lucas 1993; Hunt et al. 1993; Lockley and Hunt 1995; Schultz et al. 1995; Lockley et al. 1998, 2021; Nesbitt 1999; Mickelson et al. 2000, 2001, 2005, 2006a, 2006b; Zeilstra and Lohrengel 2001; Lucas et al. 2003; Mickelson 2003; Mickelson and Huntoon 2008; Klein and Lucas 2010b; Lovelace 2011; Lovelace and Lovelace 2012; Thomson 2014; Thomson and Lovelace 2014; Thomson et al. 2014; Thomson and Droser 2015; Lichtig et al. 2018), together with a famous vertebrate body fossil fauna (see Heckert et al. 2005; Nesbitt 2005a, b, c; Schoch et al. 2010). The occurrences of *Protochirotherium* are the only records known from North America. In particular, the partial trackway from the Red Peak Formation (Olenekian) of Wyoming figured in Lovelace and Lovelace (2012), figs. 10A, 11 assigned by these authors to *Chirotherium barthii*, appears to be *Protochirotherium* (Fichter and Kunz 2004; Klein et al. 2013) based on the relatively broad overall shape and compact digit group I–IV compared to the functionally tridactyl *C. barthii* that has a posteriorly shifted pedal digit I. Furthermore, the inferred low pace angulation of 145° (Lovelace and Lovelace 2012) rather points to *Protochirotherium* than to *C. barthii*. The Moenkopi Formation underlies the Chinle Group, which, like the Newark Supergroup in eastern North America, has yielded a diverse Upper Triassic (Carnian-Rhaetian) tetrapod-footprint ichnofauna. The Moenkopi ichnossemblages have been studied and documented in numerous papers (see Hunt and Lucas 2007; Lucas et al. 2010; Klein and Lucas 2021 for reviews). Since their discovery, the classic tetrapod-footprint localities of Peabody (1948) have been considered the most extensive Moenkopi footprint sites, with abundant material being stored in different collections, for example in the University of California Museum of Paleontology (UCMP) at Berkeley, California and the Museum of Northern Arizona (MNA) at Flagstaff, Arizona. It took more than 70 years to discover another extensive ichnosite, near the town of Snowflake in northeastern Arizona (Fig. 1). It was in 2021 when James Lang discovered several sandstone slabs

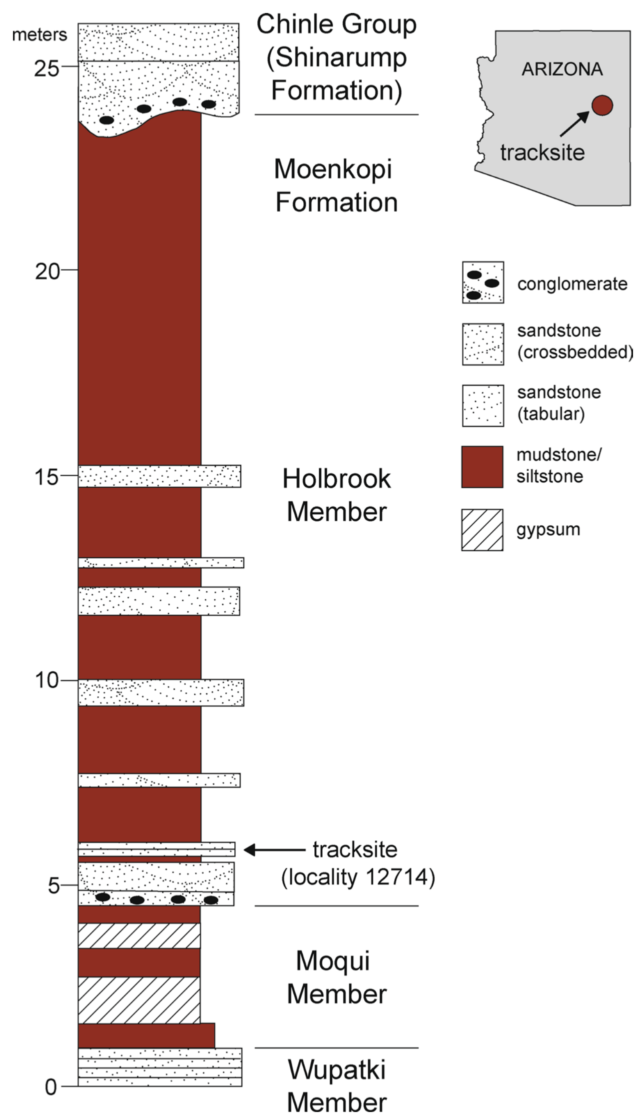


Fig. 1 Stratigraphic section with Triassic strata at the Snowflake tracksite with position of the track-bearing horizon near the base of the Holbrook Member of the Moenkopi Formation

with chirothere and other footprints in a dry creek and outcrops on his land east of Snowflake. Immediately, he recognized that these were part of an extensive trampled surface belonging to the Moenkopi Formation, and during months of collecting and puzzling found hundreds of large slabs with footprints that he stored carefully near his house. He sent pictures to Spencer Lucas, from the New Mexico Museum of Natural History in Albuquerque, New Mexico, who invited an international team of ichnologists to study the site in Fall of 2021. A short overview of the ichnoassemblage was given in an abstract for the meeting of the European Association of Vertebrate Palaeontology in 2022 (Klein et al. 2022). Here, we present a first description, documentation, and analysis of selected footprint-bearing slabs; further studies will follow.

Institutional and ichnological abbreviations

NMMNH = New Mexico Museum of Natural History and Science, Albuquerque; pl = pes length; pw = pes width; ml = manus length; mw = manus width; PL = pace length; SL = stride length; TW = trackway width of pes = distance between digit III bases perpendicular to midline; PA = pace angulation; δ = rotation of pes from midline; γ = rotation of manus from midline.

Geological setting

Rocks termed Moenkopi Group or Formation are siliciclastic red beds that were deposited in the Moenkopi back-bulge basin that formed along part of the western margin of Pangea during the Early and Middle Triassic. During the late Early Triassic (Olenekian = Smithian-Spathian) and earliest Middle Triassic (early Anisian), more than 700 m of siliciclastic red beds (Moenkopi strata) were shed to the north and northwest into this basin and interfinger with marine carbonates deposited on the Pangean marine shelf and in the arc-trench system to the west (e.g., Dickinson 1976; Blakey et al. 1993; Lawton 1994).

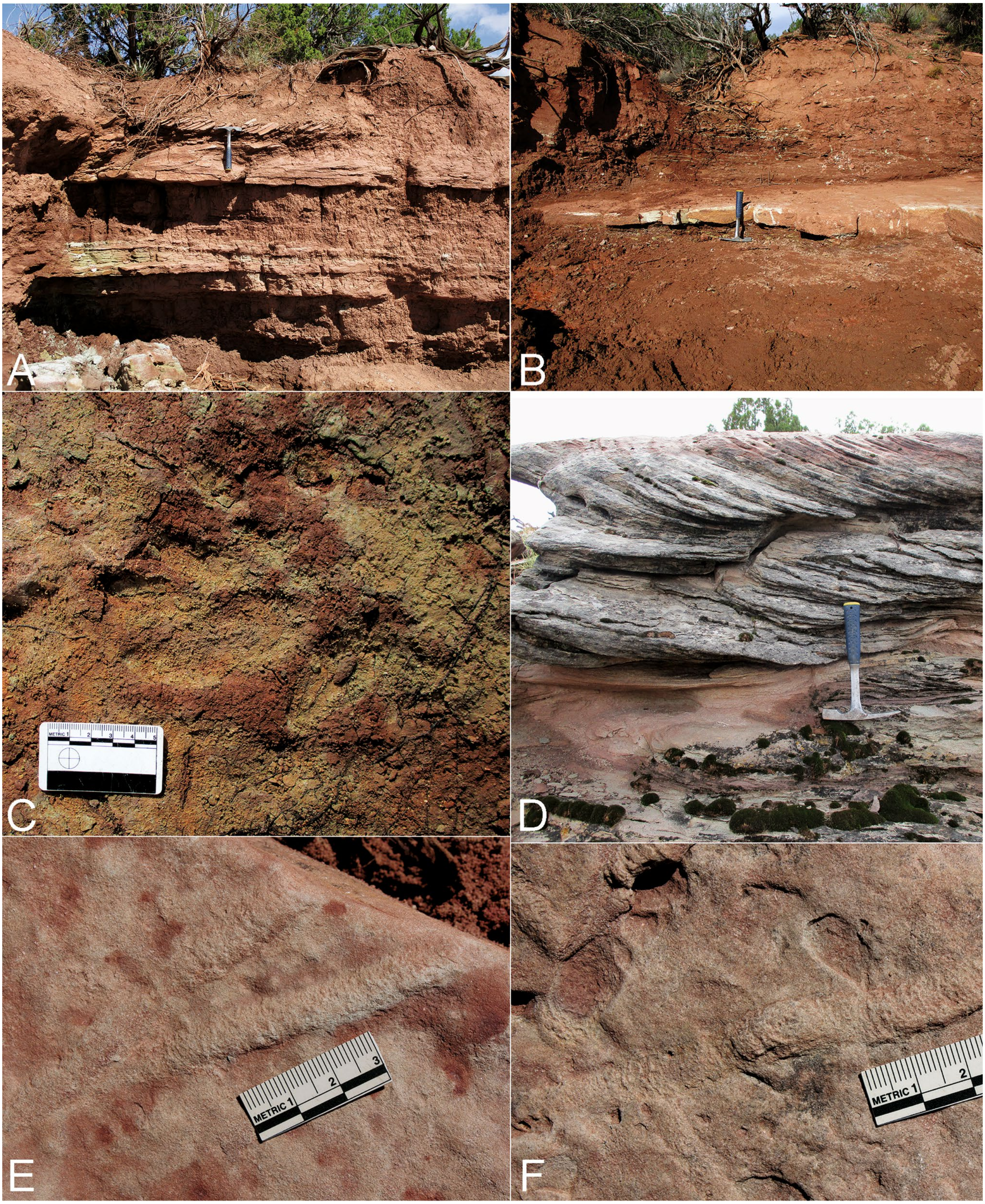
In northern Arizona (from the Little Colorado River near Cameron southward), the Moenkopi section is relatively thin (less than about 122 m thick: McKee 1954; Stewart et al. 1972). Here, we refer to the section as Moenkopi Formation, divided into the three members recognized by McKee (1954): Wupatki (lowest), Moqui and Holbrook (highest) (Figs. 1, 2). The Wupatki Member (up to 37 m thick) consists of a lower sandstone interval overlain by pale-reddish-brown micaceous siltstone. The lower sandstone is laterally persistent and is the entirety of the Wupatki Member at the Snowflake tracksite. The Moqui Member (up to 50 m thick) consists of variegated pale-reddish-brown, greenish-gray, and dusky-yellow, massive-to-horizontally laminated and locally ripple laminated siltstone intercalated with beds of white gypsum that constitute 10% or less of the member. The Holbrook Member (up to 42 m thick) consists of pale-brown, dark-yellowish-brown, or pale-red micaceous sandstone intercalated with grayish-red and pale-reddish-brown siltstone. Sandstone beds are typically trough crossbedded, and there are some intraformational conglomerate beds.

The Snowflake tracksite is in one of the southernmost exposures of the Moenkopi Formation in Arizona (McKee 1954). To the north, at Holbrook, Moenkopi thicknesses are 23, 15, and 14 m for the Wupatki, Moqui, and Holbrook members, respectively. At the Snowflake tracksite, the Wupatki Member is at least 5 m thick (base not exposed), the Moqui Member is ~ 4 m thick, and the Holbrook Member is ~ 20 m thick. The documented track surface comes from the Holbrook Member, 1 m above its base, and about 18 m below the overlying Shinarump Formation (Upper Triassic, Carnian) of the Chinle Group.

We measured a stratigraphic section of the Moenkopi strata at the Snowflake tracksite (Figs. 1, 2). The strata exposed are: (1) the uppermost sandstone beds of the Wupatki Member; (2) a thin (~ 4 m thick) section of the Moqui Member that consists of thinly laminated siltstone and fine-grained sandstone, some mudstone, and beds of massive or laminar gypsum (Fig. 2A); and (3) the overlying Holbrook Member. The base of the Holbrook Member is a thin (~ 10 cm thick) bed of conglomerate consisting of intraformational sandstone and siltstone pebbles up to 2 cm in diameter. Above is a laterally accreting set of crossbedded sandstone with a scoured base that ranges in thickness from 0.3 to 0.8 m (Fig. 2A). The track-bearing sandstone overlies that bed and is a tabular sandstone body 0.1–0.4 m thick (Fig. 2B).

Overlying Holbrook Member strata (Fig. 1) can be divided into two units: (1) lower ~ 9 m of interbedded grayish-red mudstone and trough crossbedded, medium–coarse-grained litharenitic sandstone; and (2) upper ~ 8 m of grayish-red mudstone. Some of the sandstone beds in the lower unit preserve sparse, poorly preserved chirothere footprints, and there are local concentrations of the invertebrate burrow *Palaeophycus*.

Near the Snowflake tracksite, the Holbrook Member is overlain by the Upper Triassic Shinarump Formation of the Chinle Group. The lowermost bed of the Shinarump Formation is a 1.0–1.5 m-thick bed of trough crossbedded quartzose sandstone with lenses of siliceous (chert, quartzite and jasper) pebbles. Total thickness of the Shinarump locally is ~ 6 m, and the unit is a multistoried stack of trough crossbedded sandstone (Fig. 2D). Overlying mudrock and interbedded sandstones and conglomerates are the Cameron Formation of Lucas (1993), and the conglomerates contain



coprolites and bones, bone fragments and teeth of metoposaurs and phytosaurs indicative of a Late Triassic age.

Deposition of the Holbrook Member took place by fluvial processes, mostly by ephemeral streams (e.g., McKee 1954; Stewart et al. 1972; Baldwin 1973; Blakey et al. 1993). At

◂**Fig. 2** Outcrop photos at and near the Snowflake tracksite. **A** Moqui Member siltstone, sandstone, mudstone, and gypsum beds overlain by basal conglomerate and overlying lateral accretion sandstone body of the Holbrook Member. Moqui-Holbrook contact at approximate base of hammer handle. **B** View of the track-bearing sandstone. Note that the top surface of the sandstone is nearly flat, and the irregularities of the base were produced by large tetrapod footprints preserved at the base in convex hyporelief. **C** Chirothere footprint in mudrock beneath the track-bearing sandstone. This is the original surface in which the tracks were registered. **D** Multistoried trough crossbedded quartzose sandstone, and siliceous conglomerate of Upper Triassic Shinarump Formation. **E**, **F** *Scoyenia* specimens on track surface. For scale, the hammer is 28 cm long, and the scale bars in **E** and **F** are in mm and cm

the Snowflake tracksite, the track-bearing sandstone is a tabular bed in which the tracks are preserved on the bottom surface in convex hyporelief.

The actual footprints were registered in the very thin mudstone immediately below the sandstone (Fig. 2C). This mudstone is color mottled, flakey, and heavily invested with rootlets. The track layer has some localized mudcracks and a low diversity invertebrate ichnoassemblage briefly described below. The mudstone in which the tracks were registered is readily interpreted as an overbank deposit on a riverine floodplain.

The sandstone bearing the natural casts of the tracks is massive-to-horizontally laminated and fine- to coarse-grained (it coarsens upward). This kind of sandstone represents sheet-like non-channelized flow and can be described also as a sheet splay deposited by flooding (e.g., Williams 1971; Picard and High 1973; Tunbridge 1981; Miall 1996). In the terminology of Miall (1996), its architectural element is a minor sandstone sheet.

The tetrapod footprints were registered as concave epireliefs in the mudstone beneath the track-bearing sandstone. Some desiccation followed, as indicated by localized mudcracks. That desiccation likely solidified and indurated the mudrock, so that the deposition of the overlying sand sheet, likely by a short lived flood event, filled the track molds, and did not substantially damage or obliterate the tracks and other traces.

Materials and methods

All footprints are preserved as convex hyporelief on the underside of an extensive sandstone bed. The documented material comprises about 50 trackways and 5000 imprints on a surface of 75 square meters. In total, 36 slabs were collected and catalogued as NMMNH P-89570–89605. They are listed and described in detail below.

Photographs have been taken under both natural and artificial light conditions using a Nikon D5200 camera with AF-S Nikkor 18–70 mm lens. A total of 1.100 photographs have been taken to generate 16 photogrammetric 3D models.

The photogrammetric models were generated with Agisoft Metashape (v. 1.8.4) using high-quality settings and visualized following the methodology presented by Lallensack et al. (2022). In Agisoft Metashape, meshes were generated based on depth maps rather than dense clouds. Models were exported in the .ply format along with separate texture files that contain photo-realistic color information. Post-processing (cleaning, cropping, orientation, and automatic fitting to the horizontal plane) of the models was done in Meshlab (v. 2022.02). Four types of visualizations were exported in orthographic projection: orthophotos (top view of the model with photo-realistic color), height maps (highlighting elevation), shaded reliefs (shading with low-angled artificial light), and inclination plots (where steep slopes appear dark and horizontal surfaces white), each highlighting different aspects of the 3D surface (see Lallensack et al. 2022 for detailed methodology). Orthophotos and shaded reliefs were generated using Meshlab, while height maps and inclination plots were generated with ParaView (v. 5.10). In the shaded reliefs, the artificial light source is always located on the top left. The color scale of the height maps was restricted to the relevant part of the vertical topography; i.e., very high or low parts of the model, as often found in the slab edges, were filled with a single color and excluded from the color scale legends.

Interpretive outline drawings were made on transparency film and digitalized using Adobe Illustrator CS5 software. Measurements of best preserved specimens were taken based on standard procedures proposed by Haubold (1971a, b) and Leonardi (1987) (Table 1). The quality of preservation of specimens has been determined based on the scale established by Marchetti et al. (2019), and tracks and trackways used for systematics have been sorted accordingly to base the analysis on anatomy-consistent morphological characters.

Systematic ichnology

Invertebrate traces

The tetrapod footprints described here are directly associated in the track-bearing sandstone with moderately abundant and lowly diverse invertebrate trace fossils that we briefly describe here. Most common (about 90% of the invertebrate trace fossils) is the ichnogenus *Taenidium*, horizontal burrows of slightly varying diameter with meniscate backfill (Fig. 2E, F). These burrows are 12–25 mm in diameter and have courses as long as 780 mm. Where they are eroded to expose the interior of the burrows, these can be seen

Table 1 Measurements of tetrapod footprints and trackways from the Snowflake site in centimeters and degrees. * =estimated values and measurements after different incomplete imprints

Ichno-taxon	*Chirotherium barthii*											*C. rex*	*Isochirotherium marshalli*									
Specimen NMMNH	P-89594					P-89592		P-89591		P-89589	P-89590	P-89576	P-89595-1							P-89595-2		P-89571
pl	16	16	15	15	–	13	16	14	15	12.5	13.5	25	16	16.5	17	19	14	–	16	22	18	18
pw	9	12	9	9	–	9.0	9.0	8.0	8.5	7.3	8.0	23	9.0	10	10	10	10	–	9.0	13	12	12
pl/pw	3.2	1.3	1.7	1.7	–	1.4	1.8	1.8	1.8	1.7	1.7	1.1	1.8	1.7	1.7	1.9	1.4	–	1.8	1.7	1.5	1.5
ml	5.5	–	6.0	5.0	–	–	–	6.5	–	–	7.0	12	5.0	–	–	–	–	–	–	–	5.0*	–
mw	5.0	–	6.0	5.0	–	–	–	5.5	–	–	5.0	13	5.0	–	–	–	–	–	–	–	6.0*	–
ml/mw	1.1	–	1.0	1.0	–	–	–	1.2	–	–	1.4	0.9	1.0	–	–	–	–	–	–	–	0.8	–
βp	0-17	–	–	–	–	–	–	0-14	–	–	–	–	27.2	19.3	24.2	25.8	–	–	–	–	–	–
βm	8-45	–	–	–	–	–	–	15	–	–	–	–		–	–	–	–	–	–	–	–	–
PL	44	44	46	–	–	42.5	45	40	40	43	41	–	40	40	40	37	40	30	–	37	35	47
SL	88	–	–	–	–	87	–	79	–	–	–	–	73	76	66	–	–	–	–	66	77	–
TW	12	–	–	–	–	–	–	10.5	–	–	–	–	12.5	–	–	–	–	–	–	–	–	–
PA	149	160	177	170	162	167	165	149	–	–	–	–	143	147	132	–	–	–	–	141	120	–

Ichno-taxon	*Synaptichnium pseudosuchoides*										*S. diabloense*			*Rotodactylus cursorius*				
Specimen NMMNH	P-89588–1			P-89588–2					P-89597		P-89588			P-89588				P-89570
pl	11	12	11	8.0	8.5	8.0	–	–	9.5	8.0	5.3	4.0	4.3	3.5	4.5	5.0	3.0	4.3
pw	7.5	7.0	7.0	6.0	6.0	5.0	5.5	–	4.5	4.5	2.5	2.0	2.5	2.5	3.3	2.3	2.7	2.7
pl/pw	1.5	1.7	1.6	1.3	1.4	1.6	–	–	2.1	1.8	2.1	2.0	1.7	1.4	1.4	2.2	1.1	1.6
ml	6.5	6.0	5.5	4.5	4.5	5.5	4.5	–	–	–	–	–	–	–	–	–	–	–
mw	5.5	6.0	6.0	4.5	4.5	4.5	5.0	–	–	–	–	–	–	–	–	–	–	–
ml/mw	1.2	1.0	0.9	1.0	1.0	1.2	0.9	–	–	–	–	–	–	–	–	–	–	–
βp	–	–	–	16.6	14.4	–	–	–	–	–	–	–	–	–	–	–	–	–
βm	–	–	–	0	–	–	–		–	–	–	–	–	–	–	–	–	–
PL	29	25	23	25	25	25	25	26	–	–	–	–	–	–	–	–	–	–
SL	44	42	–	45	44.5	46	46	46	45.5	–	–	–	–	–	–	–	–	–
TW	–	–	–	11.6	–	–	–	–	–	–	–	–	–	–	–	–	–	–
PA	–	–	–	130	138	128	–	–	–	–	–	–	–	–	–	–	–	–

to contain canted meniscae. Other invertebrate traces are rare, only represented by a handful of specimens: (1) *Cochlichnus*, smooth and regularly spaced meandering surface burrows and trails that resemble a sine wave; (2) *Gordia*, overlapping, non-branching loops and meandering trails with 2 mm diameters; (3) *Arenicolites*, paired cylindrical burrows 1 cm in diameter with 2–4 cm spacing that crosscut bedding and have a massive fill; and 4) a single, unusual, ladder-shaped trail that somewhat resembles *Climactichnites*. Tracemakers of these invertebrate traces were likely arthropods, worms or worm-like organisms and gastropods (cf. Buatois and Mangano 2011).

The invertebrate ichnoassemblage from the Snowflake site is an impoverished example of the *Scoyenia* ichnofacies (e.g., Frey et al. 1984; Buatois and Mángano 2004). It is characterized by small, horizontal, backfilled feeding burrows, other kinds of small burrows with structureless fill and trails. The co-occurrence with tetrapod footprints is consistent with this ichnofacies. The *Scoyenia* ichnofacies characterizes low energy, periodically submerged/emergent paleoenvironments. Floodplain ichnoassemblages of the *Scoyenia* ichnofacies are common at many locales across Triassic Pangea (Lucas et al. 2010, Table 7).

Tetrapod footprints

Ichnogenus ***Chirotherium*** Kaup, 1835a, b
Chirotherium barthii Kaup, 1835a, b

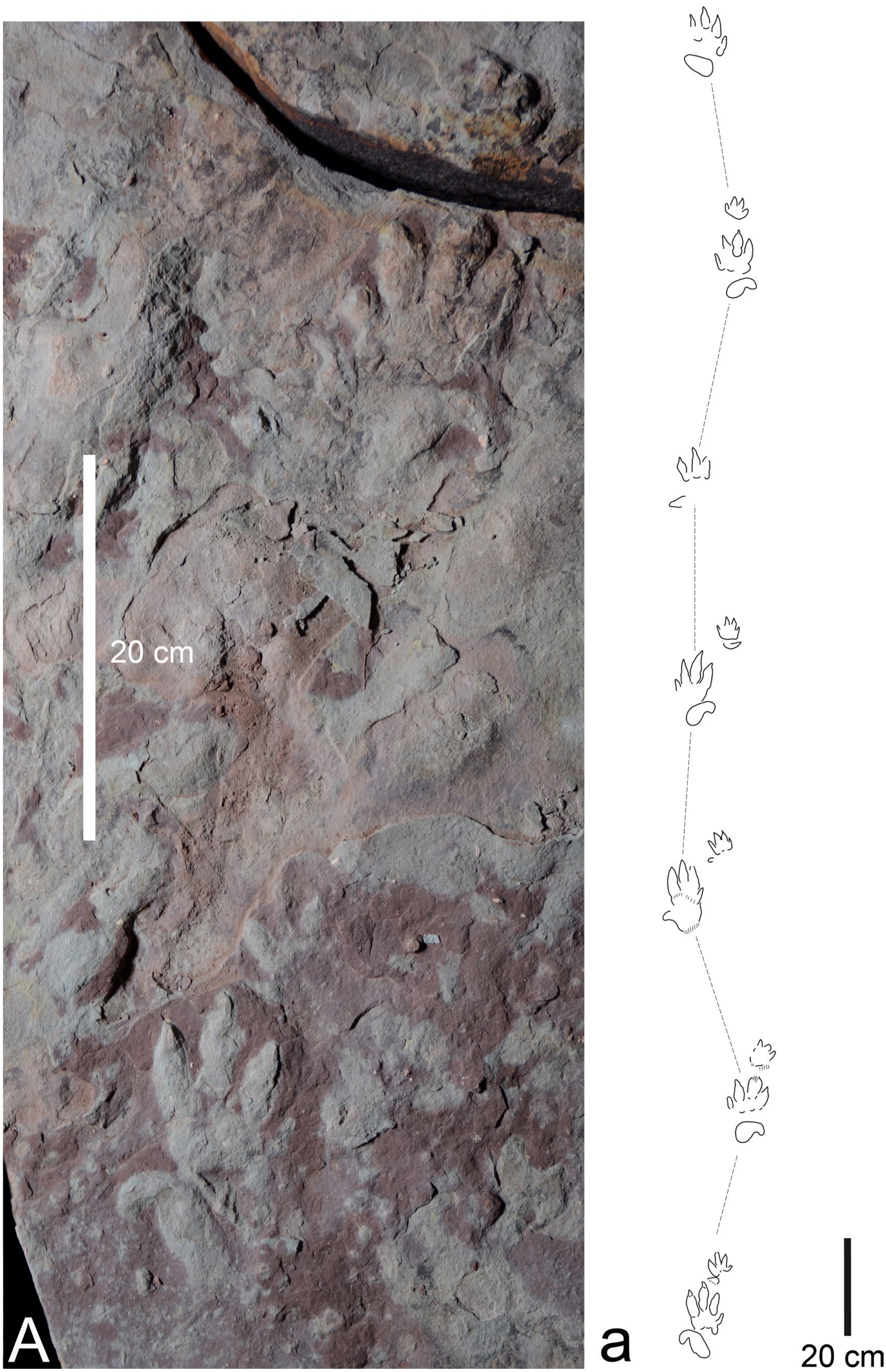
Figures 3, 4, 5 and 6

Referred material. NMMNH P-89573, 3 successive pes imprints; P-89578, isolated pes-manus set; P-89579, trackway with 4 successive pes-manus imprints; P-89581, 1 step with 2 pes and 1 associated manus imprint;? P-89588, indistinct trackway with 3 pes imprints; P-89589, 1 step with 2 pes and ?associated manus imprints; P- 89,590, 1 step with 2 pes-manus sets; P-89591, trackway with 3 successive pes-manus sets; P-89592, trackway with 4 successive pes-manus sets, 1 step with 2 successive pes-manus sets, isolated tracks; P-89594, trackway with 7 successive pes imprints, 5 with associated manus imprint; P-89596, isolated pes-manus set; P-89599, trackway with 3 successive pes-manus sets; P-89605, trackway with 3 successive pes imprints, 2 with associated manus imprint.

Description. Pentadactyl, functionally tridactyl pes imprints of long and slender overall shape. Digit III projects farthest beyond digits II and IV, digit I short and slightly posteriorly shifted, digit V with elongate oval basal pad and recurved phalangeal part. Manus imprints pentadactyl, short and round, digit III longest, followed by II and IV, digit V shorter, digit I shortest. Phalangeal and metatarsophalangeal pads rounded, the latter in digits I–IV arranged in a posteriorly concave arch. Claw traces elongate triangular in shape. NMMNH P-89594 (Fig. 3) has a 15–16 cm pes length and shows a very narrow trackway pattern with a varying pace angulation of 149°–177°. Pes slightly outwardly rotated by 0°–17°, manus with stronger outward rotation by 8°–45° and position relative to the pes varying between anteriorly, antero-medially and antero-laterally. Pace lengths range from 44 to 46 cm, and the stride length is 88 cm. The highest estimated degree of preservation of imprints from the long trackway NMMNH P-89594 is 2.5 for the pes and 2.0 for the manus, of NMMNH P-89589 (Fig. 4A) is 2.0 for the pes and 1.0 for the manus, of NMMNH P-89581 (Fig. 4B, C) is 2.0 for the pes and 1.5 for the manus and of NMMNH P-89579 (Fig. 4D) is 1.5 for the pes.

Discussion. There is no doubt that this material belongs to the classical ichnospecies *Chirotherium barthii* that was originally described by Kaup (1835a, b) from Buntsandstein deposits (Middle Triassic, Anisian) of the Germanic Basin and is widely distributed in Europe (Rühle v. Lilienstern 1939; Haubold 1971a, 1971b; Demathieu 1984; King et al. 2005; Díaz-Martínez et al. 2015; Klein et al. 2016; De Jaime-Soguero et al. 2021; Marchetti et al. 2021), North America (Klein and Lucas 2010b), South America (Rusconi 1951; Peabody 1955; Melchor and De Valais 2006), North Africa (Klein et al. 2011), and East Asia (Xing and Klein 2021; Xing et al. 2013) (see Klein and Lucas 2021 for overview).

Chirotherium barthii footprints are similar to the specimens described here (Peabody 1948; Nesbitt 1999; Klein and Lucas 2010b). Their morphology with the slender pentadactyl, functionally tridactyl pes imprint showing a mesaxonic anterior digit group I–IV and a slightly posteriorly shifted, short digit I, is diagnostic for this ichnospecies (Klein and Lucas 2021). Furthermore, the manus imprint with the relatively short digit IV is typical. Therefore, we assign the material from the Snowflake site to *C. barthii.* A significant feature of this new material is the slender appearance of most specimens (Figs. 4, 5), which might be due to the optimal substrate conditions permitting a nearly undeformed preservation of the foot anatomy with clear pad impressions and slender digit traces. We do not consider this an ichnotaxonomically relevant character justifying a new ichnospecies. Other slender *Chirotherium* ichnospecies such as *C. ferox* and *C. postchirotherioides* (Klein and Lucas


20 cm
A
a
20 cm

◂**Fig. 3** NMMNH P-89594, part of large surface from Snowflake locality with *Chirotherium barthii* trackway. **A** Detail as photograph. a. Interpretive outline drawing of the trackway

2021) show pedal digit I in a much more posterior position when compared to the specimens described here.

cf. ***Chirotherium rex*** Peabody, 1948
Figure 7

Referred material. NMMNH P-89576, 2 right pes-manus sets with partial polygonal skin texture; P-89580, digit impressions with sliding marks and polygonal skin texture.

Description. NMMNH P-89576 (Fig. 7) shows 2 overlapping tetradactyl-pentadactyl plantigrade pes imprints of ~ 25 cm length and 23 cm width. Digits are preserved with a triangular shape, which is probably an extramorphological feature. Manus imprint anterior to the pes, ~ 12 cm in length and ~ 13 cm in width, with incomplete, tri- to pentadactyl preservation. All deeply impressed and showing lateral striation. Skin impressions with polygonal texture mainly are observed in the posterior portion of the pes imprints (Fig. 7B). NMMNH P-89580 consists of 3 or 4 digit impressions that have extensive horizontal sliding marks. Some exhibit transition of slide marks to polygonal skin texture in the posterior digit portion. One digit has a sharp claw mark distally. The degree of preservation of NMMNH P-89576 is 1.0.

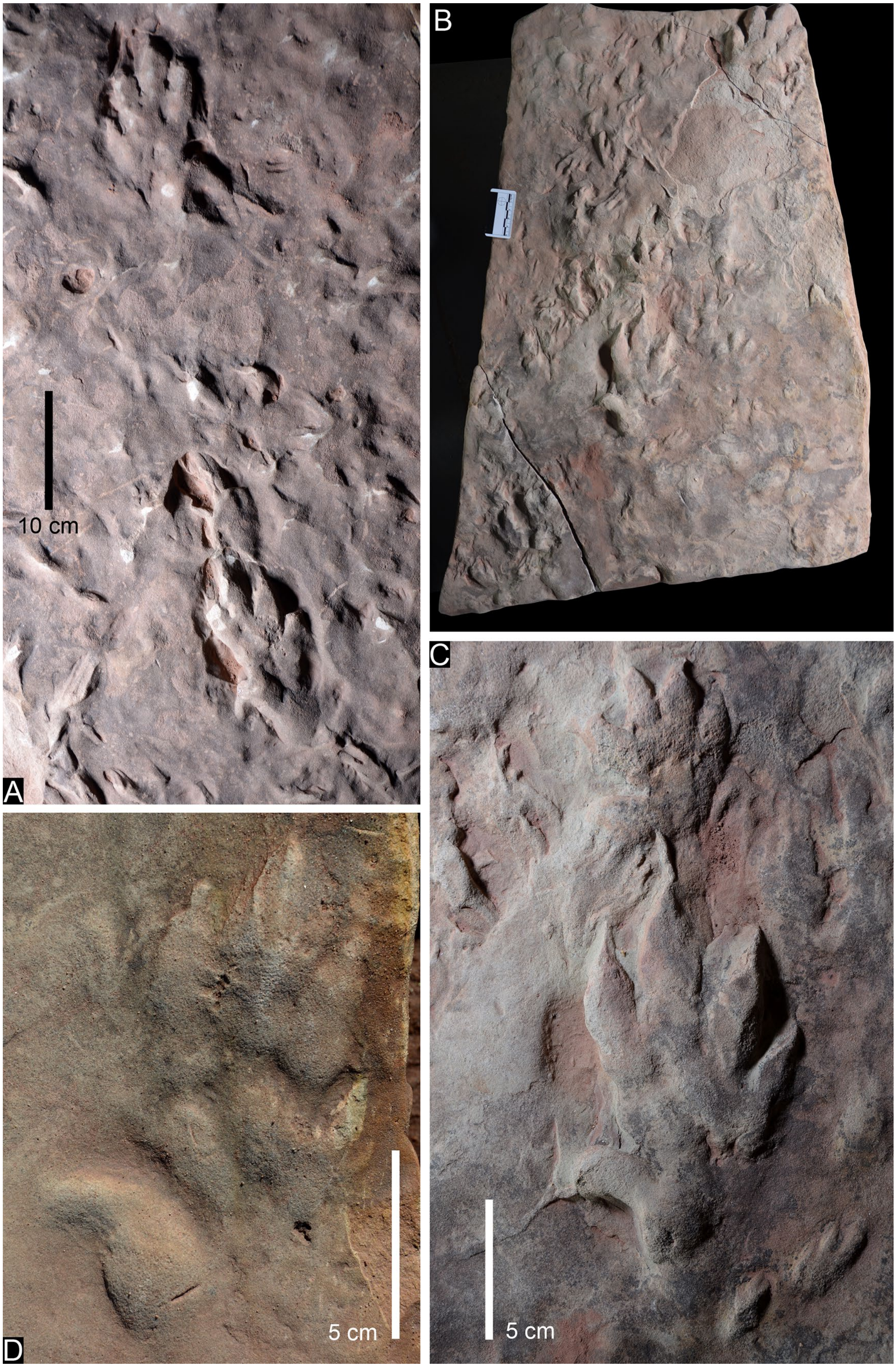
Discussion. Unfortunately, this is isolated material only, as no trackways have been discovered at the Snowflake site. Also, the preservation of the overall shape and the digit traces is poor, even though some patches with skin texture are visible (Fig. 7B). The large semiplantigrade-to-plantigrade pes imprints with the robust digit traces and the massive posterior "heel" portion suggest the presence of *Chirotherium rex.* This ichnospecies is well known from the Moenkopi Group/Formation of North America and was originally described from this unit by Peabody (1948). In their revision of the Moenkopi ichnofauna with Peabody's material, Klein and Lucas (2010b) suggested that *C. rex* could possibly be a junior synonym of *Isochirotherium herculis* (Egerton 1838; see also King et al. 2005). The similarity, in particular with the pes morphology of the latter, is striking. However, *C. rex* has a relatively larger manus imprint if compared to the latter. Furthermore, the assignment of *C. rex* to the ichnogenus is considered doubtful after the revision of *Chirotherium* by Klein and Lucas (2021). Some diagnostic features of the ichnogenus, such as the functionally tridactyl pes imprint, cannot be identified in the Moenkopi material of *C. rex*. The poorly preserved imprints in our new material do not permit a decision, and better specimens have to be discovered at the locality in the future.

Ichnogenus ***Isochirotherium*** Haubold, 1971b

Isochirotherium marshalli (Peabody, 1948)
Figures 8, 9, 10 and 11

Referred material. NMMNH P-89571, 2 steps from different trackways, including 4 pes and 1 manus imprint, 1 isolated pes-manus set; P-89572, 1 step with 2 pes and 1 manus imprint, 1 isolated pes-manus set, 1 pes imprint, 1 manus imprint; P-89573, 1 step with pes and manus imprints, 1 isolated pes imprint; P-89574, 2 isolated complete pes imprints, 2 fragmentary pes imprints, 2 isolated manus imprints; P-89578, 1 step with 2 pes-manus sets; P-89579, trackway with 3 pes and 2 manus imprints; P-89586, isolated pes and isolated manus imprint; P-89595, 4 trackways with 4, 5, 6 and 10 pes imprints, mostly with associated manus imprints; P-89597, one step with 2 pes-manus sets; P-89600, 1 step with 2 pes-manus sets, 2 isolated pes-manus sets; P-89601, one step (2 pes and 1 manus imprint); P-89602, one step (2 pes imprints, 1 manus imprint); P-89603, isolated pes imprint; P-89604, one step with 2 pes imprints.

Description. Medium-sized to large (14–22 cm in length and 9–13 cm in width) pentadactyl, plantigrade pes imprints with associated small pentadactyl manus imprints being 5 cm in length and width. In the pes, digits II and III are longest, with digit III being slightly longer than II. Digits I and IV are much shorter; digit V shows a large oval basal pad that is elongated into a massive "heel", and a thin recurved phalangeal portion with a blunt distal end. Phalangeal and metatarsophalangeal pads are rounded. Phalangeal pads are often amalgamated with two or three pads per digit only. Claw impressions have a spatule-like shape with rounded distal ends. Trackways are narrow but show a relatively low pace angulation ranging from 132° to 147° in NMMNH P-89595–1 and 120° to 141° in P-89595–2 (Figs. 8, 9). The pace length of P-89595–1 ranges from 37 to 40 cm and in P-89595–2 ranges from 35 to 37 cm. The stride length ranges from 66 to 73 cm in the two trackways with pes imprints having a maximum length of 19 cm and 22 cm. The pes imprint shows a stronger outward rotation (up to 27.2°) relative to the midline if compared to the manus imprint. The highest estimated degree of preservation of trackway NMMNH P-89595–1 is 2.5 for the pes and 2.0 for the manus, of trackway NMMNH P-89595–2 is 2.5 for the pes and 1.5 for the manus, that of NMMNH P-89,571 (Fig. 10) is 2.5 for the pes and 2.0 for the manus and that


A
B
C
D
10 cm
5 cm
5 cm

◂**Fig. 4** Slabs with *Chirotherium barthii* tracks and trackways. **A** NMMNH P-89589 showing one step. B. NMMNH P-89581 showing one step with associated *Rotodactylus* and *Synaptichnium* footprints. **C**. Detail of **B**. **D**. NMMNH P-89579, detail of trackway in Figs. 16, 17. Note slender shape of *C. barthii* pes imprints

of NMMNH P-89572 (Fig. 11) is 2.5 for the pes and 1.5 for the manus.

Discussion. Isochirotherium was introduced by Haubold (1971b) with the type ichnospecies *I. soergeli* based on material from the German Buntsandstein (Middle Triassic, Anisian). It is diagnosed by the dominance in length of pedal digits II and III, with digits I and IV being short, and by the relatively small manus imprint when compared to the pes imprint (Haubold 1971b). The Moenkopi Formation in Arizona yielded two *Isochirotherium* ichnospecies: *I. marshalli* and *I. coltoni*. The former is from the upper Moenkopi Formation (Holbrook Member), whereas the latter comes from the lower part of the unit (Wupatki Member). Both were originally introduced by Peabody (1948). *I. marshalli* has a more robust appearance of the pes imprint with a massive, large basal pad on digit V when compared to *I. coltoni* in which it is less developed. Our new material shows a large robust digit V basal pad, so it is assigned to *I. marshalli*.

Only seven *Isochirotherium* ichnospecies are considered here as valid. *I. soergeli* is distinguished by the smaller metatarsophalangeal pad V and by the overall shape of the pes similar to that of *Chirotherium barthii* but with a short digit IV (Haubold 1971a, 1971b). *I. coureli* is distinguished by the triangular shape of the basal pad V lacking a separate phalangeal portion of the digit (Demathieu 1970). *I. felenci* is differentiated by the elongate triangular shape of the basal pad V (Courel and Demathieu 1976), *I. herculis* by the broader pes and more robust digits (Egerton 1838; Haubold 1971a, 1971b), *I. delicatum* by the more slender pes and proportionally longer pedal digits II and IV (Courel and Demathieu 1976) and *I. lomasi* by the relative longer pedal digit II when compared to digit III (Baird 1954). The fine preservation and several longer trackways of the Snowflake material permit the addition of detailed trackway data for this ichnospecies that adds to the background of the incomplete type material (Peabody 1948).

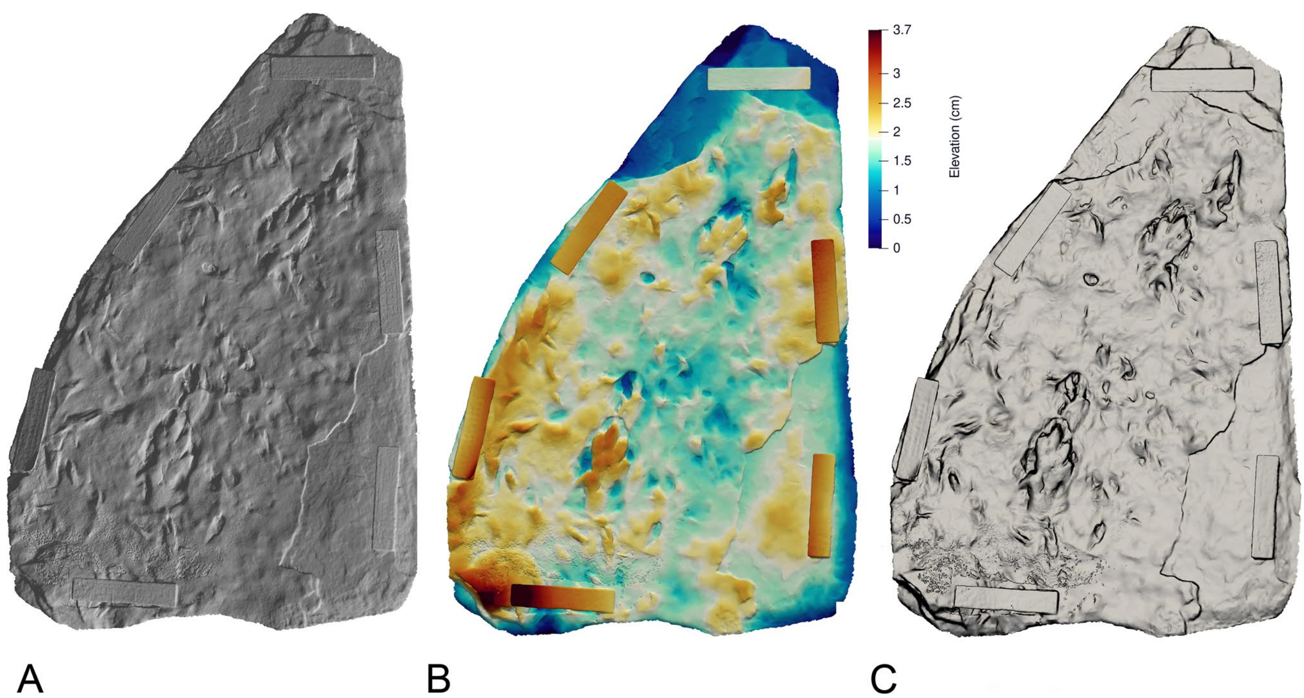


Fig. 5 3D photogrammetric images of NMMNH P-89589 slab with *Chirotherium barthii* partial trackway as shaded relief (**A**), height map (**B**), and inclination plot (**C**)

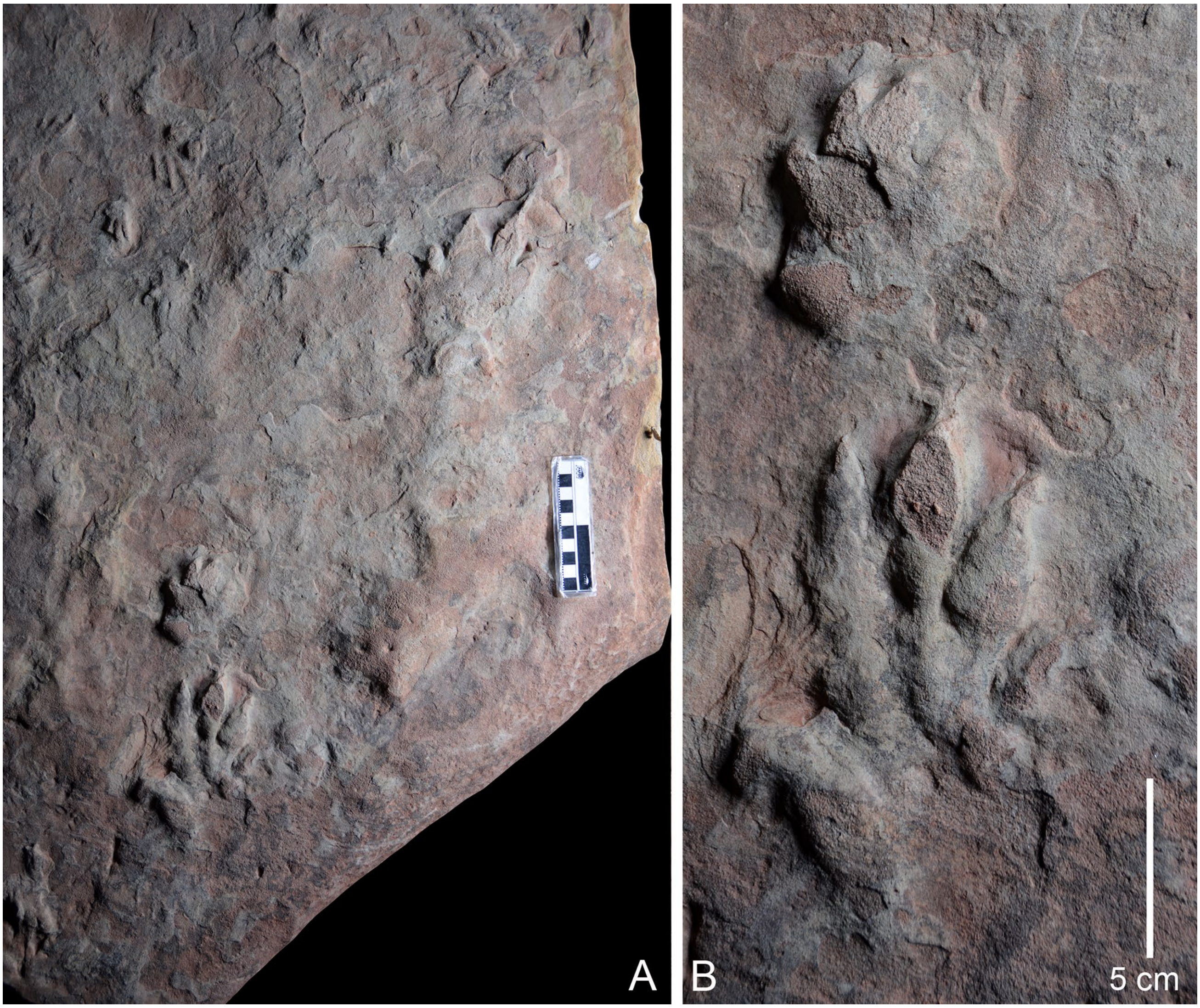


Fig. 6 NMMNH P-89590, *Chirotherium barthii* partial trackway from Snowflake locality. **A** Overview of slab. **B** Detail. Note *Rotodactylus cursorius* pes-manus set on top left of A

Ichnogenus ***Synaptichnium*** Nopcsa, 1923

Synaptichnium pseudosuchoides Nopcsa, 1923
Figures 12, 13, 14A, B, 15, 16 and 17

Referred material. NMMNH P-89571, trackway with 3 successive pes and indistinct manus imprints; P-89572, 1 step with 2 pes-manus sets; P-89573, trackway with 3 pes and 5 manus imprints; P-89575, isolated pes-manus set; P-89577, indistinct trackway; P-89578; P-89579, trackway with 4 successive pes-manus sets; P-89582, trackway with 4 successive pes-manus sets; P-89583, several indistinct trackways with pes and manus imprints; P-89584, trackway with 3 successive pes-manus sets; P-89585, trackway with 3 successive pes-manus sets; P-89586, 1 step with 2 successive pes-manus sets; P-89587, indistinct trackway consisting of several pes and manus imprints; P-89588, 2 trackways comprising 9 pes tracks and 5 pes tracks with associated manus imprints; P-89593, trackway with 7 pes-manus sets; P-89595, trackway with 5 successive pes-manus sets; P-89597, trackway with 3 successive pes-manus sets; P-89598, trackway with 4 successive pes-manus sets; P-89602, isolated tracks; P-89604, trackway with 3 successive pes-manus sets, isolated tracks.

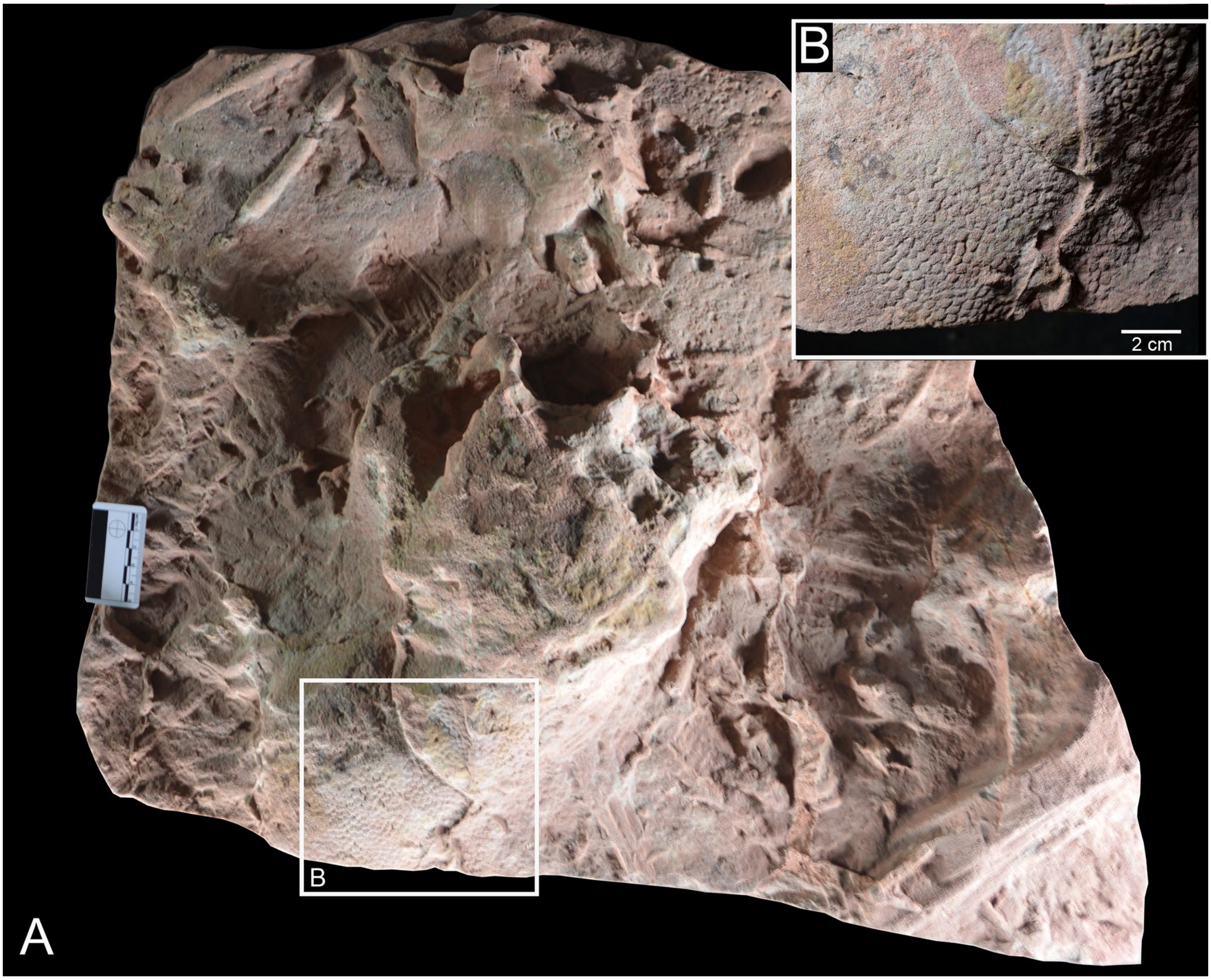


Fig. 7 NMMNH P-89576, *Chirotherium rex* two overprinted pes and associated manus imprints. **A** Overview of slab. **B** Detail with skin impressions at heel areas

Description. These are medium-sized pentadactyl and semiplantigrade-to-plantigrade pes and manus imprints with robust digit traces. In the pes digit lengths increase from digit I to digit IV, with IV being longest or III and IV being subequal, whereas in the manus, digit III is longest, followed by II and IV that are shorter and subequal in length and digit I that is shortest. The anterior digit group positioned posterolateral to digit V consists of a massive oval basal pad and a thinner and straight phalangeal part. Rounded phalangeal and metatarsophalangeal pads are also preserved in digits I–IV. Digits are mostly straight; in some cases, anterior digits I–IV are slightly curved outward or inward, distally ending in sharp claw traces, sometimes being dragged and elongated anteriorly. Trackways show relatively short steps. The pace length (PL) ranges from 23 to 29 cm in NMMNH P-89588–1 and 25 to 26 cm in P-89588–2, associated with pes lengths ranging from 11 to 12 cm and 8 to 8.5 cm, respectively (Figs. 12, 13). The pace angulation (PA) is low and ranges from 128° to138° in P-89588–2. The pes shows a strong outward rotation if compared to the manus (max. 16.6° vs. 0°), the latter being antero-medially or anteriorly positioned to the former. P-89588–1 is more deeply impressed with lateral striations shown along digit traces (Fig. 12B). While most imprints from this slab are very clear and detailed in anatomical features, some are obscured by extensive dragging or slipping marks (Fig. 12A, a). Expulsion rims can also be observed in some imprints. The highest estimated degree of preservation of NMMNH P-89588–1 is 2.5 for the pes and 2.0 for the manus, that of NMMNH P-89588–2 is 2.0 for the pes and 1.5 for the manus (Figs. 12, 13), that of


NMMNH P-89595-1
NMMNH P-89595-2
Missing
Missing
20 cm
N
S 78° E
Missing
A
a

◂**Fig. 8** NMMNH P-89595, portion of large surface from Snowflake locality showing four *Isochirotherium marshalli* trackways, one going in the opposite direction. **A** Photograph. **B** Interpretive outline drawing. Note small *Synaptichnium pseudosuchoides* trackway associated (**a**, left)

NMMNH P-89575 is 2.0 (Fig. 14A), and that of NMMNH P-89576 is 2.5 (Fig. 14B).

Discussion. Synaptichnium is diagnosed by ectaxonic pes imprints with digit IV being longest or subequal to digit III. Manus imprints are relatively large in this ichnogenus and the trackways have relatively low pace angulation and strong outward rotation of the pes imprints. Nopcsa (1923) introduced the ichnogenus based on footprints from the Middle Triassic of Great Britain (see also King et al. 2005). Subsequently numerous ichnospecies have been described by different authors (Klein and Lucas 2018, 2021 for overview). From the Moenkopi Formation of northern Arizona, Peabody (1948) described two (originally *Chirotherium*) ichnospecies that were later referred to *Synaptichnium* as new combinations (Haubold 1971b): *S. diabloense* and *S. cameronense*. The former is originally from the Wupatki Member, the latter from the Holbrook Member (Peabody 1948; Klein and Lucas 2010b; see below). The revision of the Moenkopi ichnofauna by Klein and Lucas (2010b) revealed a third, larger and more robust morphotype that was tentatively assigned by these authors to *Synaptichnium* isp. There is a distinct similarity of *Synaptichnium* isp. with the large form from the Snowflake site and with the type ichnospecies *S. pseudosuchoides* by the continuous increase of digits I–IV and the overall shape with the robust elongated and straight, anteriorly oriented pedal digit V. Therefore, we re-assign these tracks here to *S. pseudosuchoides,* including the material from the Snowflake site.

Synaptichnium diabloense (Peabody, 1948)
Figures 14C–G

Referred material. NMMNH P-89571, isolated set; P-89573, trackway with 2 pes tracks and 2 manus tracks; P-89588, several isolated sets; P-89591, isolated pes-manus set.

Description. Small (4.0–5.3 cm in length, 2.0–2.5 cm in width) slender pes imprints. Digits are narrow and straight, occasionally curved inward along their distal portions. Digit proportions with III and IV long and subequal in length, II much shorter and I shortest. Digit V is elongate with a subtriangular basal pad and a thin phalangeal portion, straight or slightly outward curved. The manus imprint is short, rounded with digit III longest, II and IV shorter and I shortest. The outward rotation of the pes imprint is stronger than that of the manus imprint. All digits have rounded phalangeal pads and small, sharp claw traces. In our sample, no complete trackways can be observed. The highest estimated

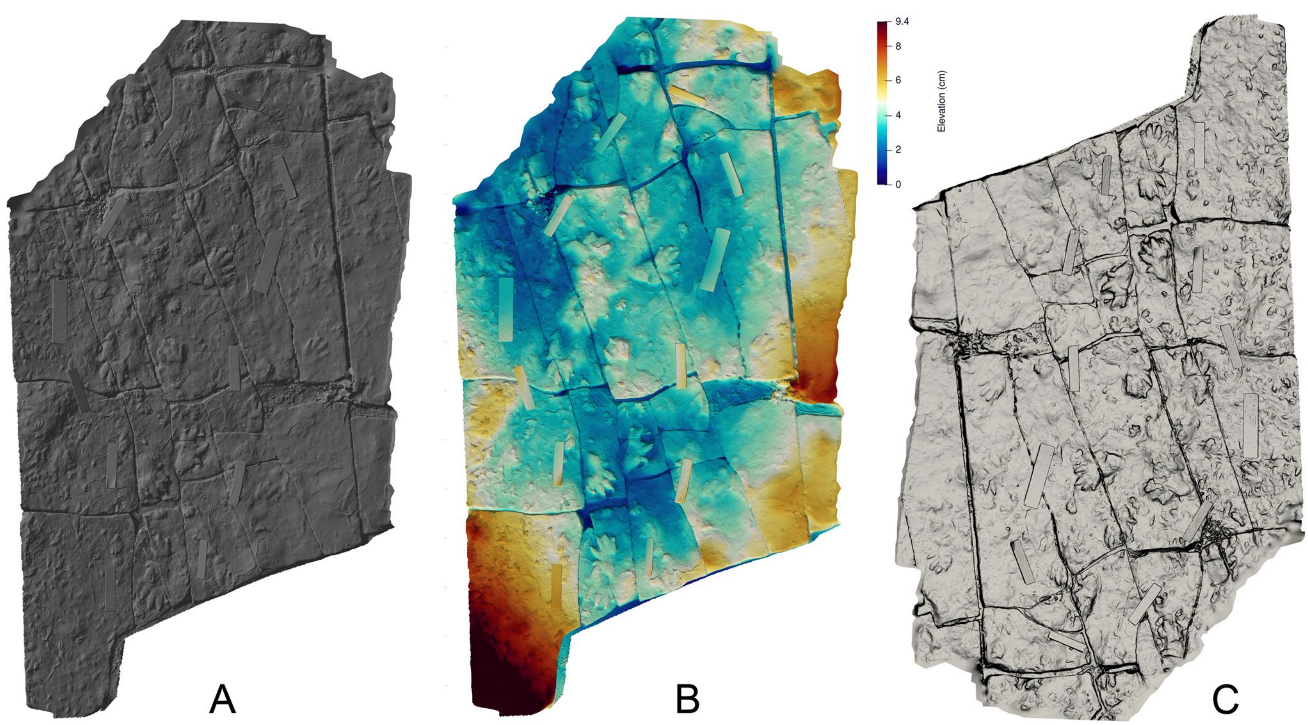


Fig. 9 3D photogrammetric images of NMMNH P-89595 from seen at bottom of Fig. 8A and B. **A** Shaded relief. **B** Height map. **C** Inclination plot

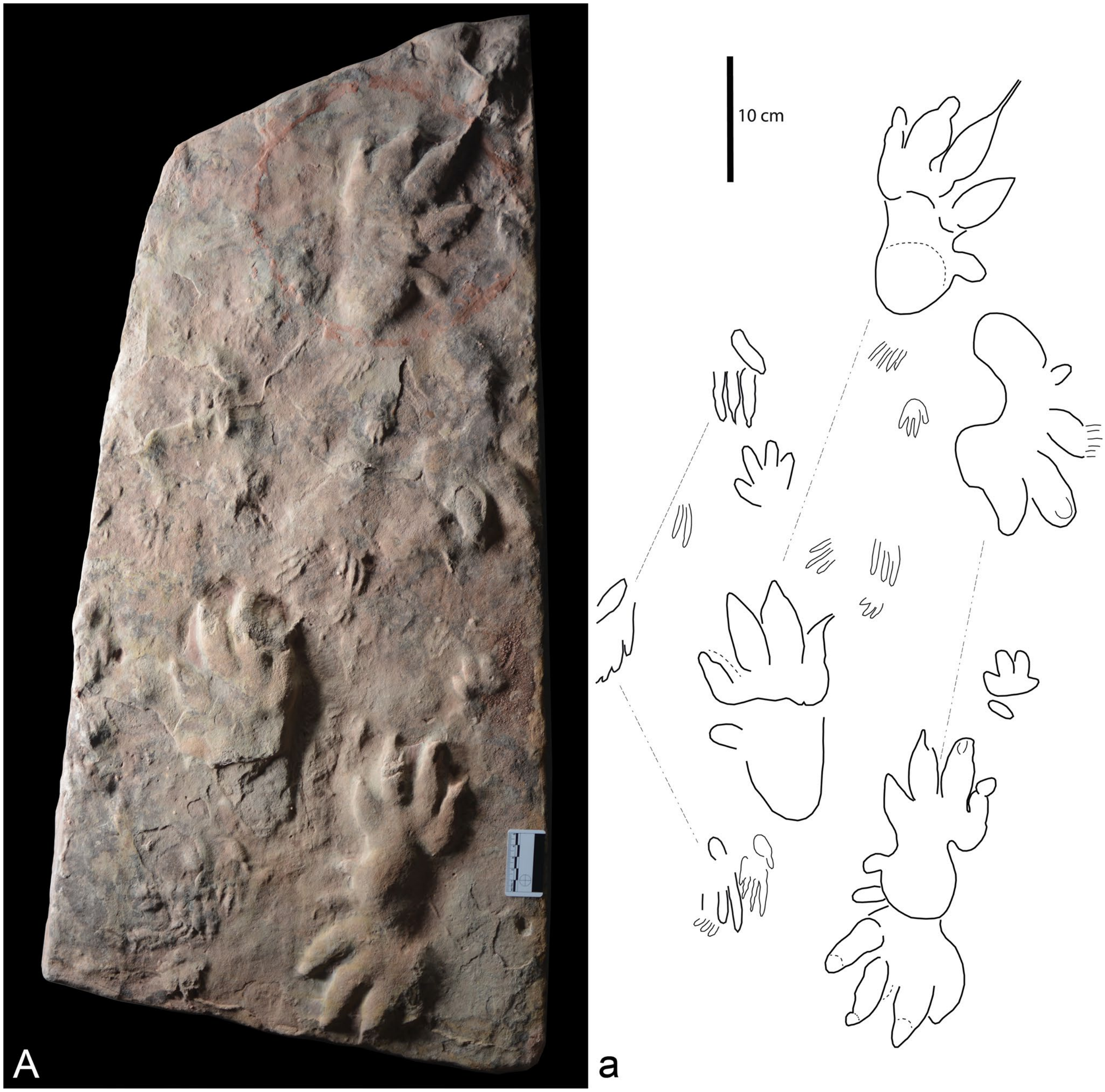


Fig. 10 NMMNH P-89571, slab with two *Isochirotherium marshalli* partial trackways and isolated tracks. **A** Photograph. **B** Interpretive outline drawing. Note *Synaptichnium pseudosuchoides* trackway at left and isolated smaller *Synaptichnium* and *Rotodactylus* imprints associated

degree of preservation of NMMNH P-89573 (Fig. 14D, E) is 2.0 for the pes and 1.5 for the manus.

Discussion. Peabody (1948) introduced two new chirotheriid ichnospecies from the lower and upper part of the Moenkopi Formation in Arizona that he assigned to the ichnogenus *Chirotherium*: *C. diabloense* and *C. cameronense*. These have later been re-assigned to the ichnogenus *Synaptichnium* as *S. diabloense* and *S. cameronense* (Haubold 1971b). Both are small (~ 5 cm length) pentadactyl pes imprints and associated relatively large pentadactyl manus imprints, the former showing a strong tendency toward relatively short pedal digits I and II, that are often medially spread, whereas digits III and IV are much longer and subparallel and adjacent to each other (Klein and Lucas 2010b). The difference between *S. cameronense* and *S. diabloense* essentially concerns the trackway pattern with the former showing longer strides, larger pace angulation, minor outward rotation of the pes and manus and lacking lateral overstep of the manus by the

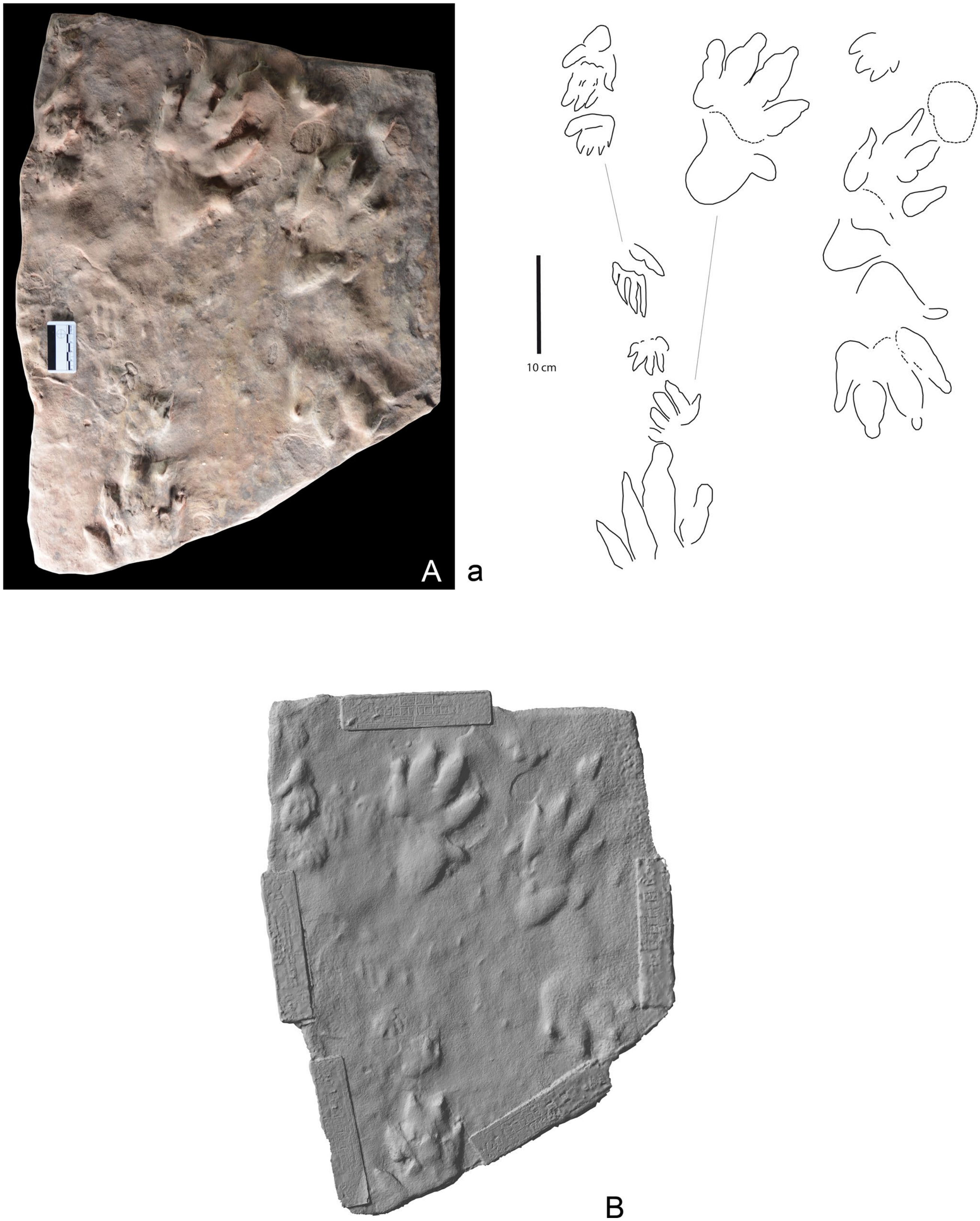
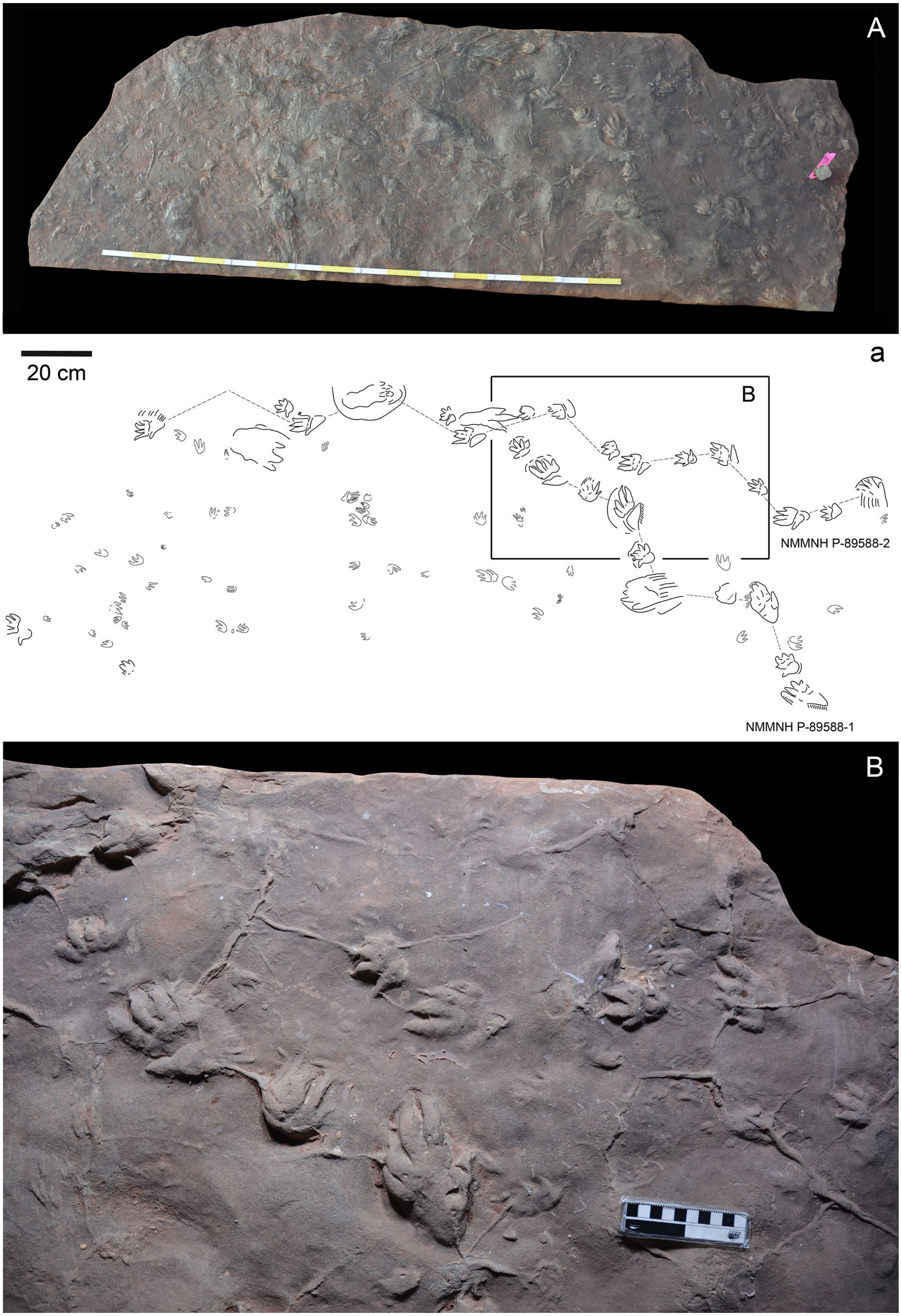


Fig. 11 NMMNH P- 89,572, slab with partial trackway and isolated tracks of *Isochirotherium marshalli* associated with *Synaptichnium pseudosuchoides* partial trackway at left. **A** Photograph. **B** Interpretive outline drawing. **C** Shaded relief photogrammetric image


A
20 cm
a
B
NMMNH P-89588-2
NMMNH P-89588-1
B

◂**Fig. 12** NMMNH P-89588. Large slab with two longer *Synaptichnium pseudosuchoides* trackways, a possible *Chirotherium barthii* trackway on top and abundant isolated tracks, including *Synaptichnium diabloense* and *Rotodactylus cursorius*. **A** Overview as photograph. **a** Interpretive outline drawing. **B** Detail as photograph

pes, even in running trackways. In contrast, *S. diabloense* has shorter strides, lower pace angulation, and a strongly outwardly rotated pes and manus that show overstep in running trackways. Minor differentiating features are the shorter pedal digit V and the longer and more slender manual digits in *S. cameronense* if considering the holotype (Klein and Lucas 2010b). However, this cannot be observed constantly in all trackways and could be extramorphological. The material from the Snowflake site described here has no complete trackways preserved but occasionally shows lateral overstep of the manus by the pes (Fig. 14F, G). We therefore assign these tracks to the ichnospecies *S. diabloense*.

Ichnogenus ***Rotodactylus*** Peabody, 1948

Rotodactylus cursorius Peabody, 1948
Figures 18, 19

Referred material. NMMNH P-89570, P-89573, P-89577, P-89579, slabs with numerous isolated and well-preserved pes and manus tracks; P-89588, slab with high density of well-preserved tracks; P-89590, a few isolated tracks, 1 distinct pes-manus set; additional less well-preserved tracks are present on most other slabs from the locality.

Description. Isolated small pentadactyl pes and manus imprints in which the pes oversteps the manus laterally. Pes imprints are 3.5 to 5.0 cm in length and 2.3 to 3.3 cm in width. Manus traces are smaller, but due to incomplete preservation were not measured. Digit traces long and slender, straight or curved inward, increasing in length from I to IV. Digit traces I and V punctiform, isolated from II–IV; digit

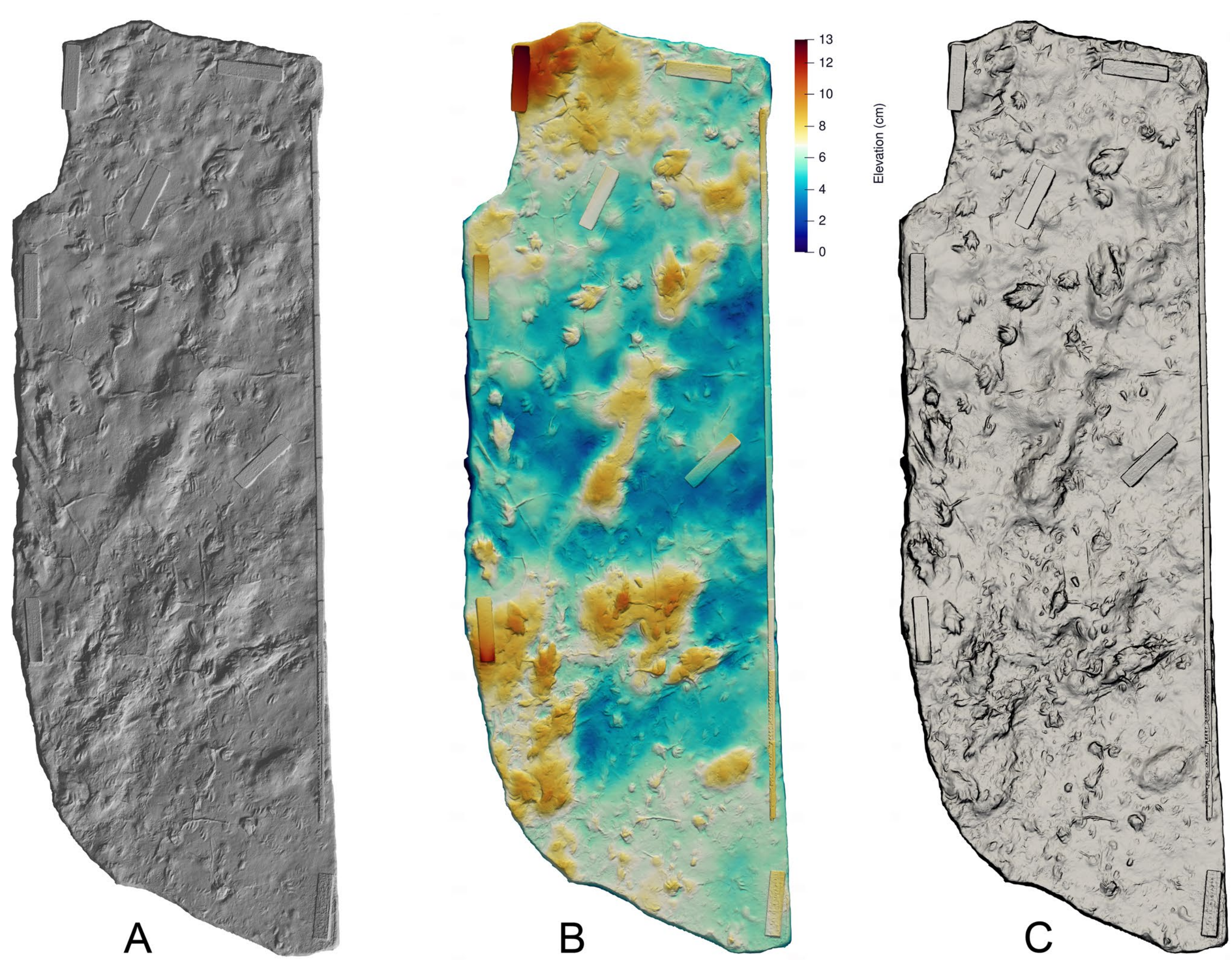


Fig. 13 3D photogrammetric images of NMMNH P-89588. **A** Shaded relief. **B** Height map. **C** Inclination plot

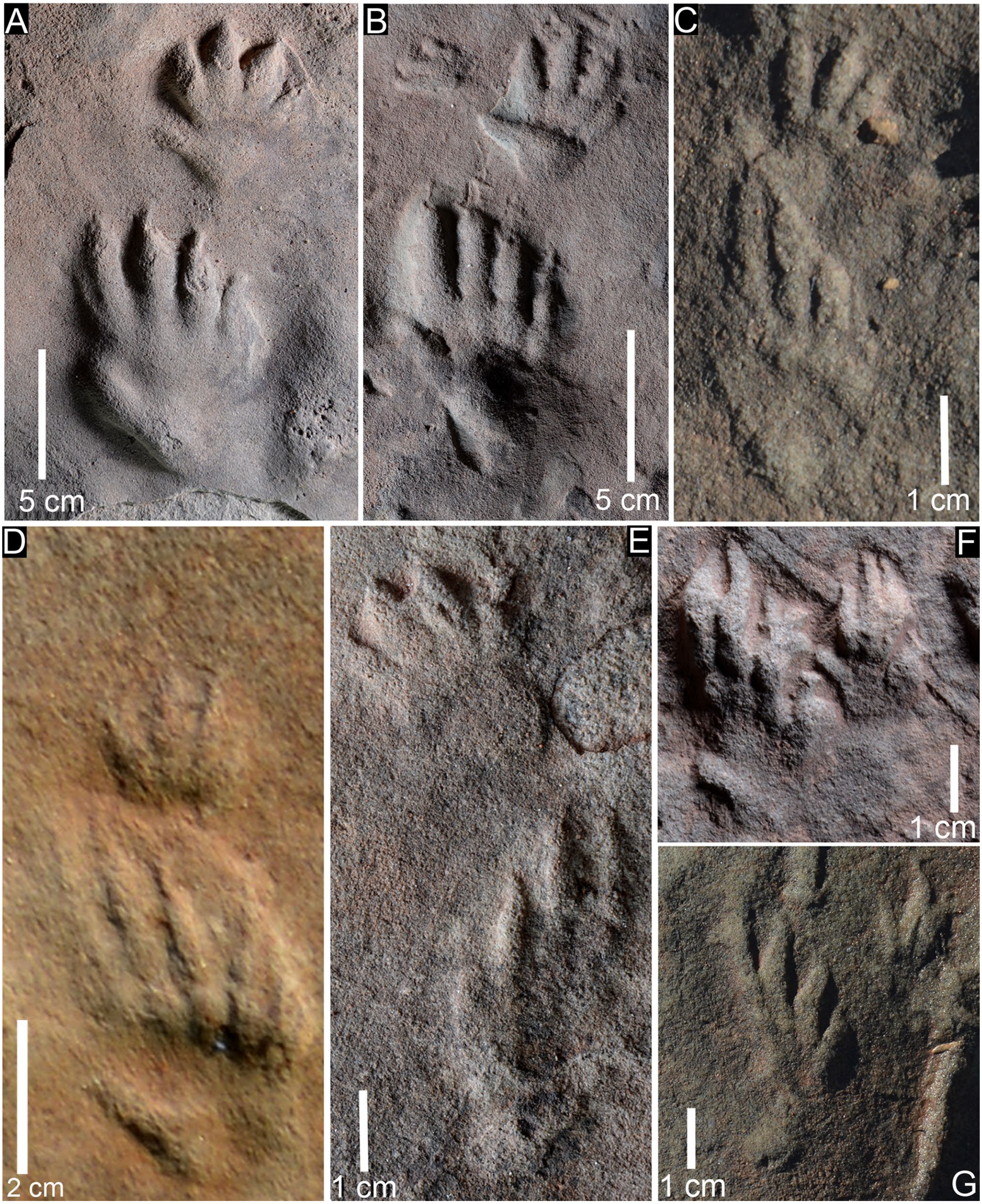


Fig. 14 *Synaptichnium* pes and manus imprints from Snowflake locality. **A**, **B**. *Synaptichnium pseudosuchoides*. **C–G**. *S. diabloense*. **A**. NMMNH P-89575. **B**. NMMNH P-89586. **C**, **F**, **G**. NMMNH P-89588. **D**, **E**. NMMNH P-89573

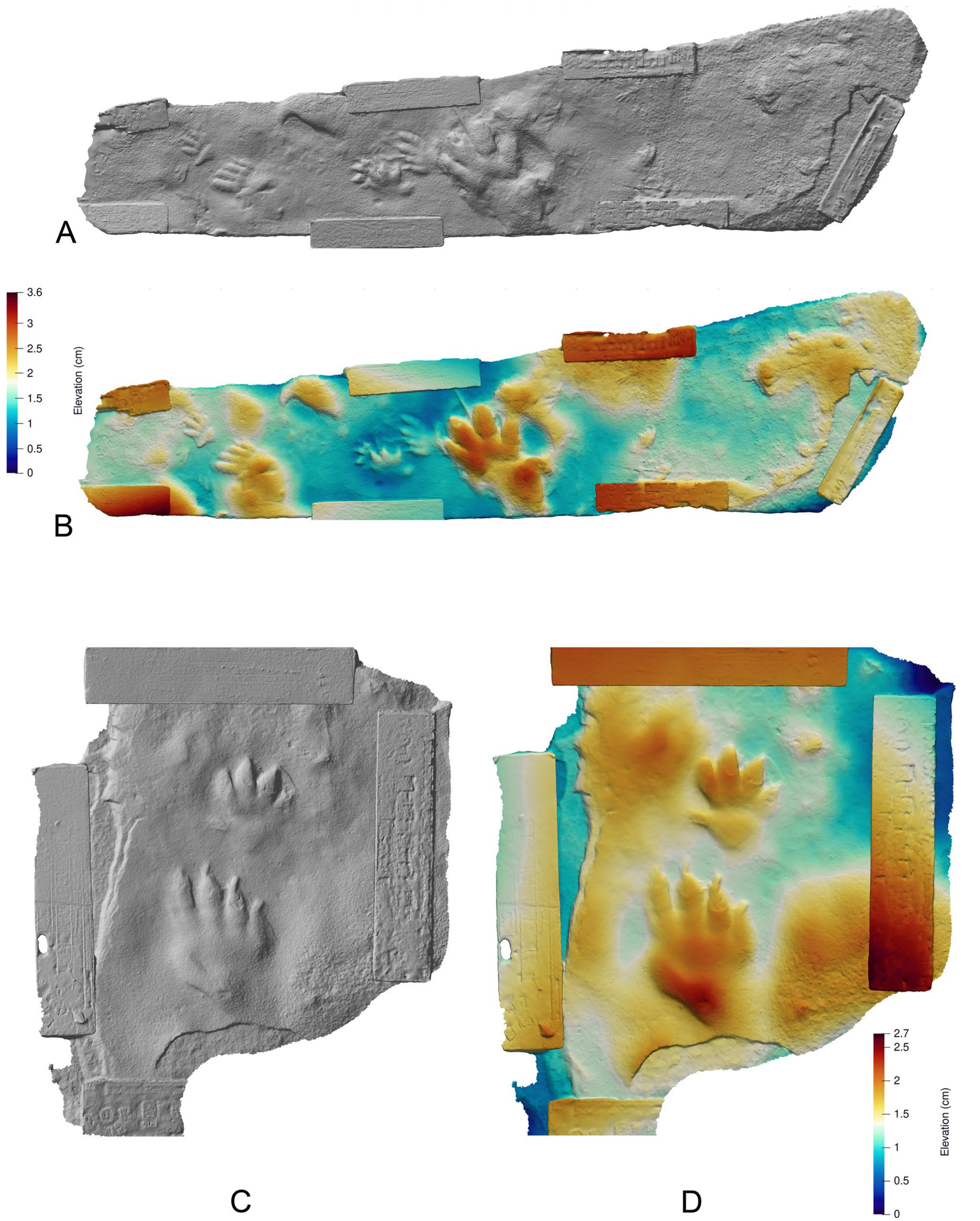


Fig. 15 3D Photogrammetric images of NMMNH P-89586 (**A**, **B**) and NMMNH P-89575 (**C**, **D**) showing slabs with *Synaptichnium pseudosuchoides* partial trackway and isolated pes-manus set. **A**, **C**. Shaded relief. **B**, **D**, Height map. Note *Isochirotherium marshalli* partial trackway in **A**, **B**

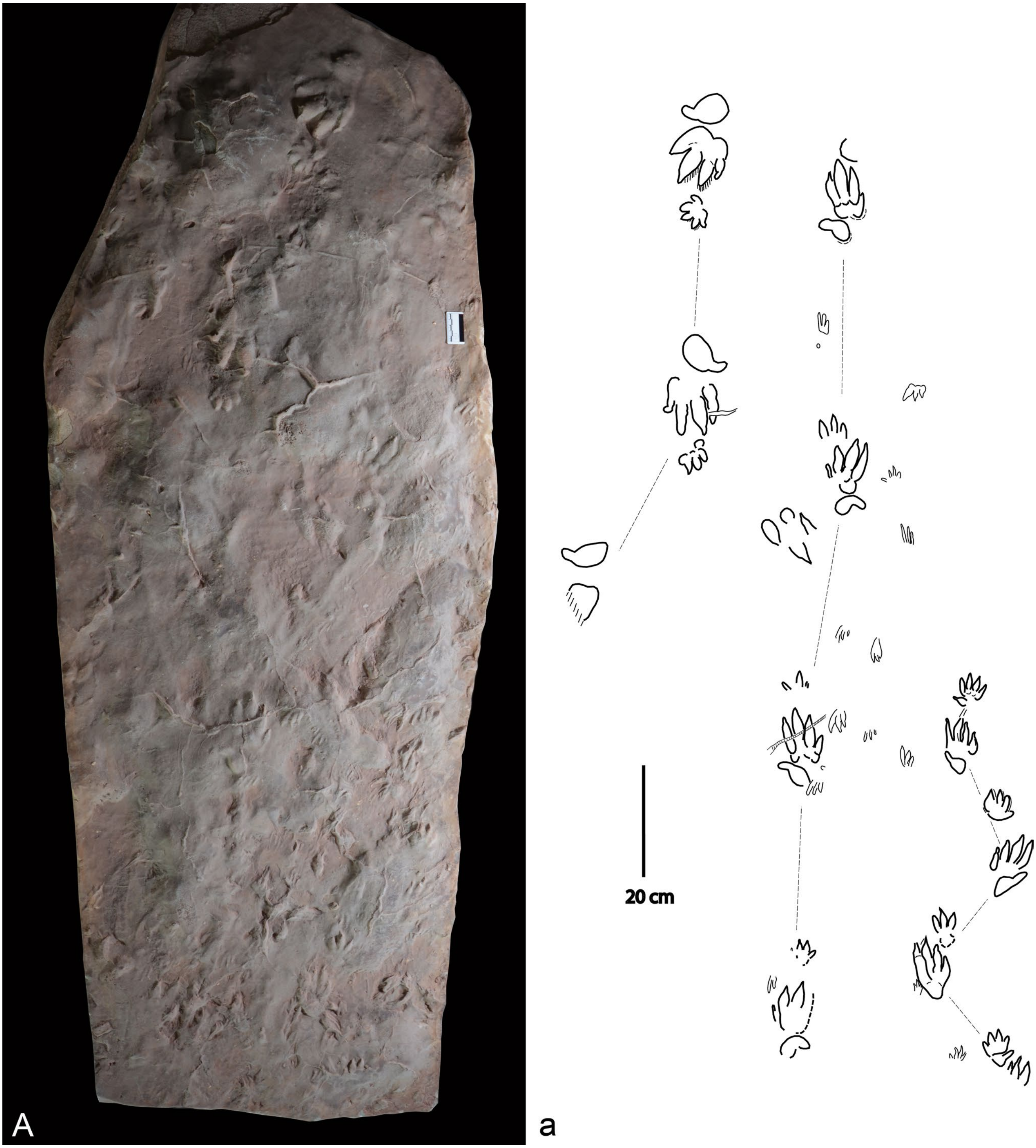


Fig. 16 NMMNH P-89579, slab with trackways of *Isochirotherium marshalli* (left), *Chirotherium barthii* (center) and *Synaptichnium pseudosuchoides* (bottom right). Note associated isolated *Rotodactylus cursorius* tracks

V positioned far posteriorly. Small triangular claws are visible on digit traces II, III, and IV in well-preserved imprints, while in others, distal ends of digit traces can be blunt or transversely elongated. The highest estimated degree of preservation of one of the best imprint sets NMMNH P-89588 (Fig. 18A) is 1.5.

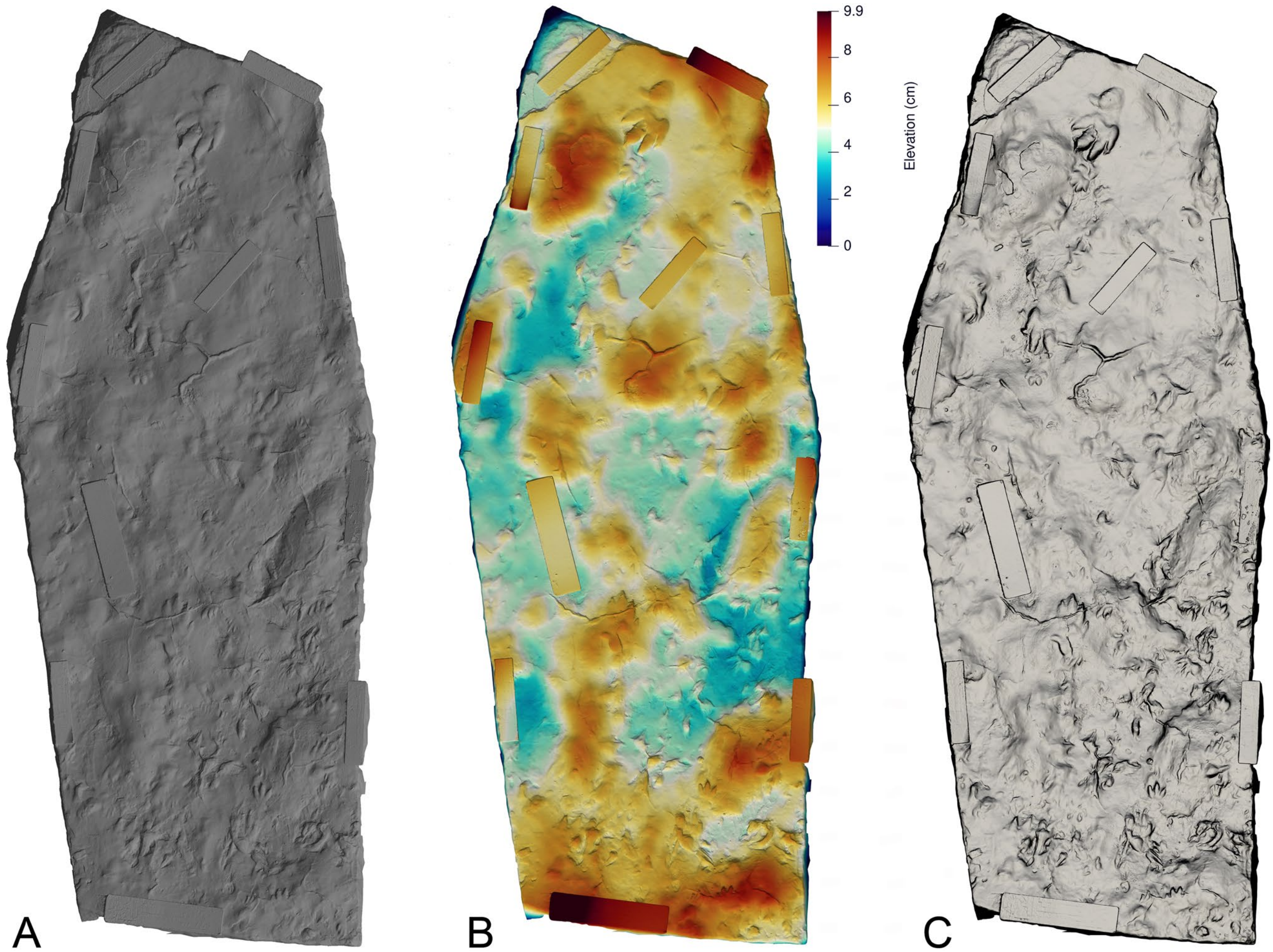


Fig. 17 3D photogrammetric images of NMMNH P-89579. **A** Shaded relief. **B** Height map. **C** Inclination plot

Discussion. Rotodactylus is an ichnogenus introduced for material from the Moenkopi Formation of northern Arizona and Utah by Peabody (1948). It has been documented from Lower–Middle Triassic (Olenekian-Anisian) deposits of North America (Peabody 1948; Klein and Lucas 2010b), North Africa (Klein et al. 2011), and Europe (Klein and Lucas 2021). These small pentadactyl ectaxonic tracks often occur in mass accumulations similar to the lacertoid track *Rhynchosauroides*. However, *Rotodactylus* differs from *Rhynchosauroides* by the narrow and compact proximal digit group I–IV, the far posterior position of a punctiform digit V impression and by the longer strides. There is a continuous lateral overstep of the manus by the pes independent of the velocity of movement of the trackmaker, which might indicate a small dinosauromorph trackmaker similar to *Lagerpeton* from the Triassic of Argentina (Haubold 1999).

From the Moenkopi Formation, three *Rotodactylus* ichnospecies were described by Peabody (1948): *R. cursorius* (type ichnospecies), *R. mckeei*, and *R. bradyi*. *R. mckeei* was synonymized with *R. cursorius,* whereas *R. bradyi* was considered a distinct ichnospecies by Klein and Lucas (2010b). *R. bradyi* differs from *R. cursorius* by pedal digit IV being only slightly longer than digit III, whereas in *R. cursorius* digit IV is distinctly longer. *R. bradyi* is similar to *R. matthesi* from the German Buntsandstein (Solling Formation, Anisian). There are numerous other ichnospecies from the Middle Triassic, in particular from France; however, their validity needs to be confirmed in a comprehensive analysis of *Rotodactylus*. Here, we assign the Snowflake specimens to the type ichnospecies *Rotodactylus cursorius* based on the diagnostic characters observed in the material.

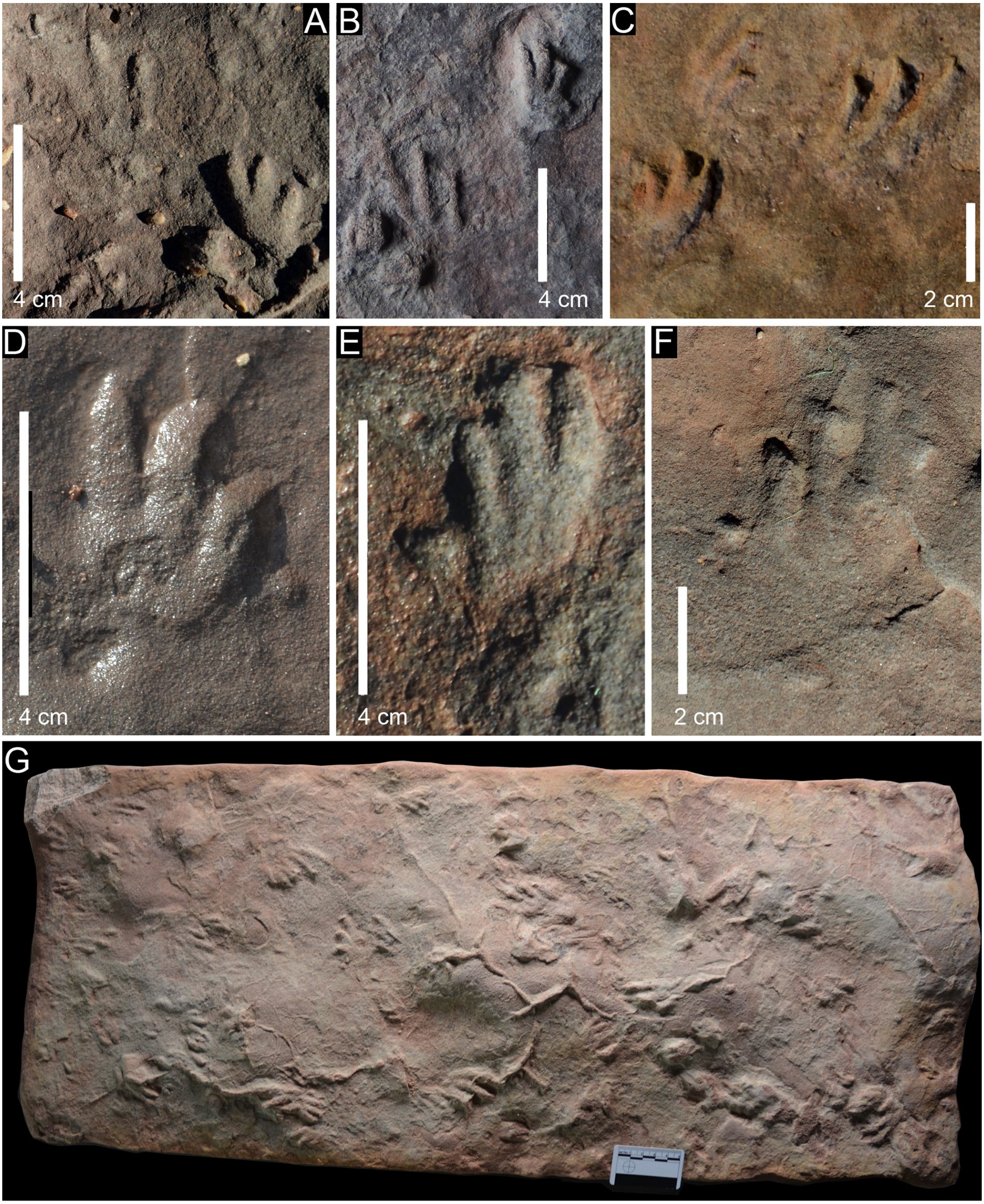


Fig. 18 *Rotodactylus cursorius* pes and manus imprints from different slabs of Snowflake locality. NMMNH P-89588 (**A**, **D**, **E**), NMMNH P-89590 (**B**), NMMNH P-89573 (**C**), NMMNH P-89579 (**F**), NMMNH P-89577 (**G**). Note *Synaptichnium diabloense* trackway associated in **G**

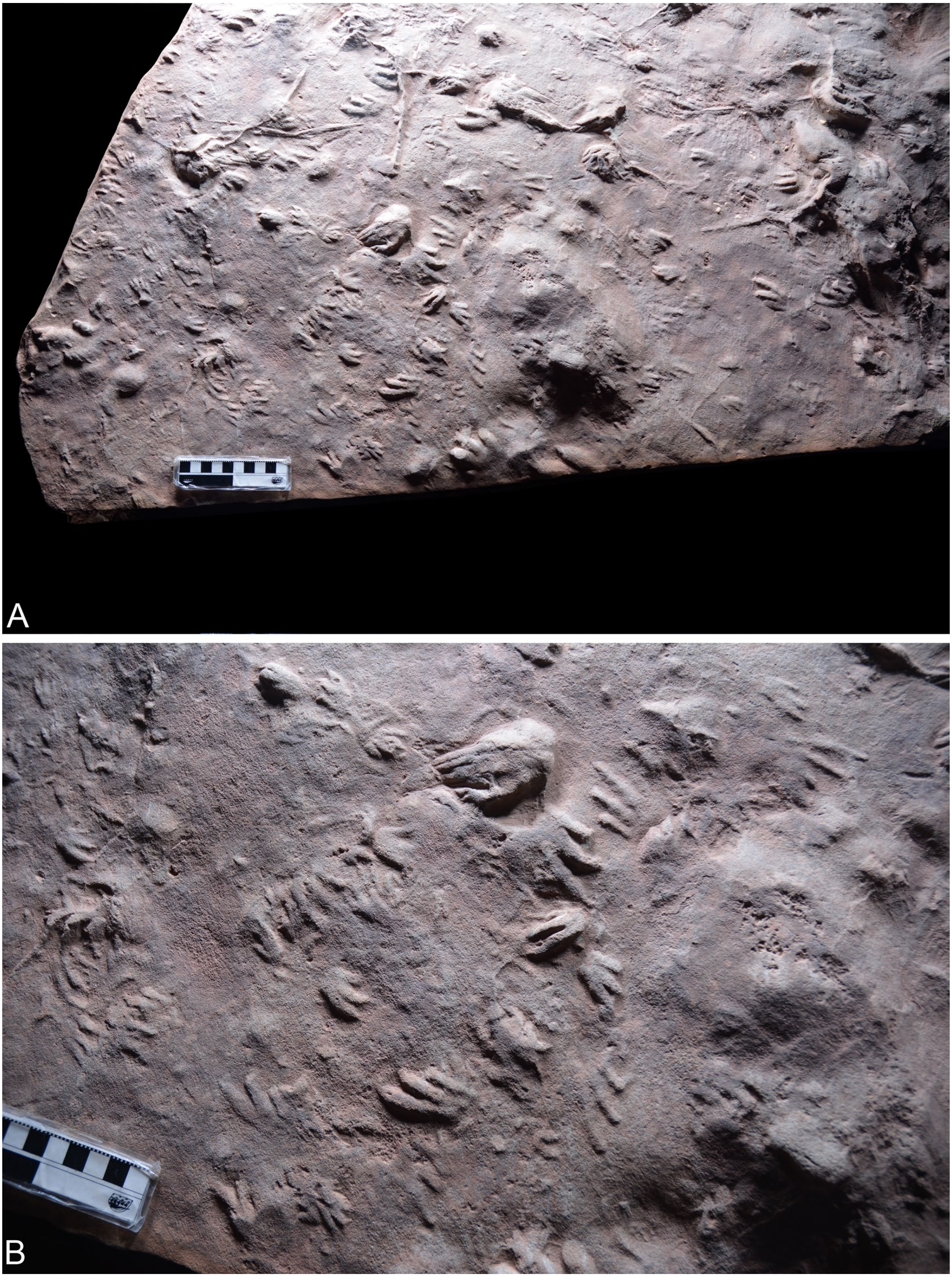


Fig. 19 NMMNH P-89588, portion of slab figured in Fig. 12 with abundant *Rotodactylus cursorius* tracks. **A** Larger section. **B** Detail

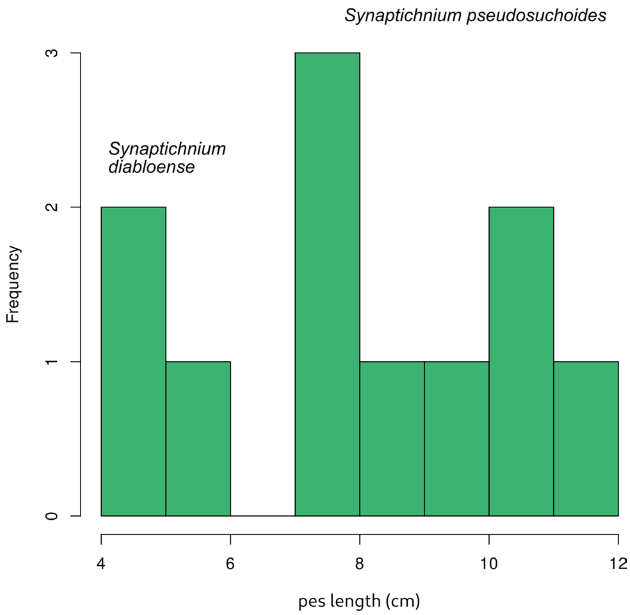


Fig. 20 Diagram showing size distribution in different *Synaptichnium* ichnospecies from Moenkopi Formation of Snowflake locality

Ontogenetic growth or different *Synaptichnium* ichnospecies?

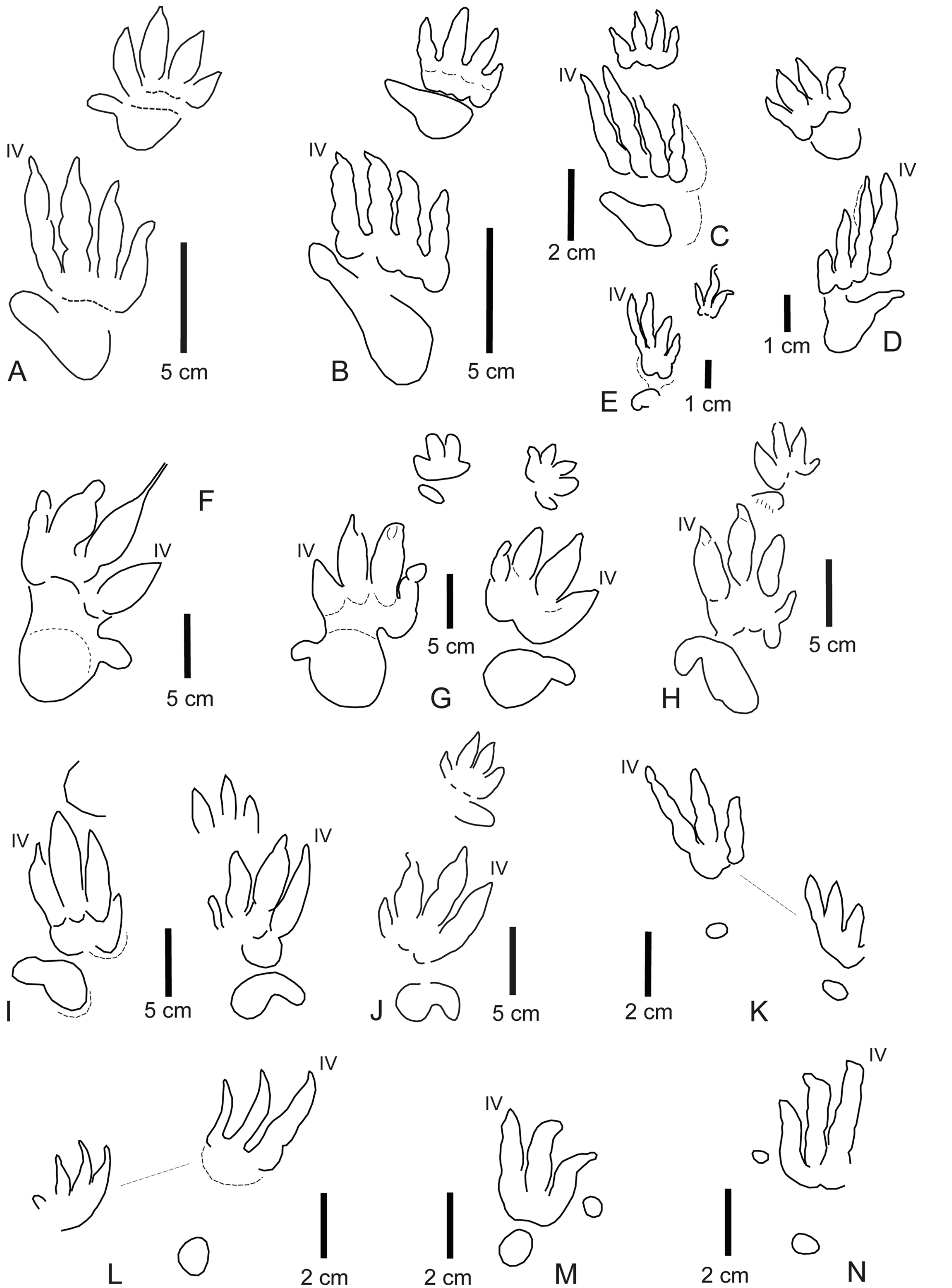
The dominance of *Synaptichnium* tracks and trackways in the chirotheriid assemblage from the Snowflake site is unusual for the upper Moenkopi Formation (Holbrook Member, Anisian) and for coeval tracksites from the global record. Abundant *S. diabloense* trackways have been documented from a classical surface in the lower part of the Moenkopi Formation (Wupatki Member, Olenekian) near Meteor Crater, Arizona (Peabody 1948; Klein and Lucas 2010b). In the Holbrook Member *Synaptichnium* is generally less abundant when compared to other chirotheriid ichnotaxa such as *Chirotherium barthii* or *Isochirotherium*. At the Snowflake site, the co-occurrence of abundant *Synaptichnium* of different sizes suggests the presence of ontogenetic stages of trackmakers or, alternatively, the presence of different trackmaker species. This concerns also the ichnotaxonomy and validity of the above described *Synaptichnium* ichnospecies. Could *Synaptichnium diabloense* be a juvenile representative of the *S. pseudosuchoides* trackmaker and therefore should rather be synonymized with the latter? On one hand, it is tempting to assume that the *S. diabloense* tracks (~5 cm pes length) represent juveniles of *S. pseudosuchoides* (~12 cm pes length), also because there are specimens of intermediate size (~8 cm pes length). From a relatively small sample of trackways, the pes length ranges for the two ichnotaxa are continuous and separated, thus potentially supporting an ontogenetic growth (Fig. 20). Nevertheless, this has to be viewed with caution. Large *Synaptichnium* assigned here to the type ichnospecies *S. pseudosuchoides* shows a continuous increase of pedal digits I–IV, whereas the small specimens (assigned here to *S. diabloense*) show an increase by leaps and bounds in lengths of pedal digits I–IV as in typical *S. diabloense*. Nevertheless, this could reflect allometric ontogenetic growth, which means that digit proportions of adult individuals can differ from those of juveniles, for example, by relatively longer digits I–II.

Fig. 21 Interpretive outline drawings of pes and manus imprints from Snowflake locality. **A**, **B**. *Synaptichnium pseudosuchoides*. **C**–**E**. *S. diabloense*. **F**, **G** *Isochirotherium marshalli*. **H**–**J** *Chirotherium barthii*. **K**–**N** *Rotodactylus cursorius*. **A**. NMMNH P-89575. **B**. NMMNH P-89586. **C**, **D**, **L** NMMNH P-89573. **E**, **K**, **M** NMMNH P-89588. **F** NMMNH P-89571. **G** NMMNH P-89571 and NMMNH P-89579. **H** NMMNH P-89594. **I**, **N** NMMNH P-89579. **J** NMMNH P-89591 ▸

Other differences between these two *Synaptichnium* ichnospecies at the Snowflake site include: slenderer digit imprints, narrower pedal tracks with digits I–IV more overlapping proximally and a pedal digit V more separated from the digit I-IV group in *S. diabloense* (Fig. 14). Quantitative studies of archosaur ontogenetic growth and population structure based on chirotheriid footprints have been performed in an assemblage with *Isochirotherium* from the Middle Triassic of northern Italy (Avanzini and Lockley 2002). These authors documented the presence of different size classes and distinct morphotypes (broad and slender) they interpreted as possible sexual dimorphism. The latter is difficult to prove from footprints and differences in relative length/width of pes imprints could also reflect preservational effects or differences of individual foot anatomy. For Moenkopi *Synaptichnium* a definitive decision can presently not be made, and future comprehensive quantitative studies of the Snowflake and other assemblages are needed to shed light on the community structure of the *Synaptichnium* trackmaker.

Trackmakers

A significant feature of the Moenkopi tetrapod ichno- and body fossil faunas is their very different composition. The ichnofauna is largely dominated by reptile tracks (Peabody 1948; Klein and Lucas 2010b; Fig. 21A–N), whereas those of non-amniotes are extremely rare. The skeletal assemblage, however, comprises abundant temnospondyl non-amniotes and fewer amniotes such as dicynodont synapsids, a procolophonoid parareptile, non-archosauriform archosauromorphs, and poposauroid archosaurs (Welles 1947; Heckert et al. 2005; Nesbitt 2005a, b, c; Nesbitt and Angielczyk 2002; Schoch et al. 2010). The dominance of temnospondyl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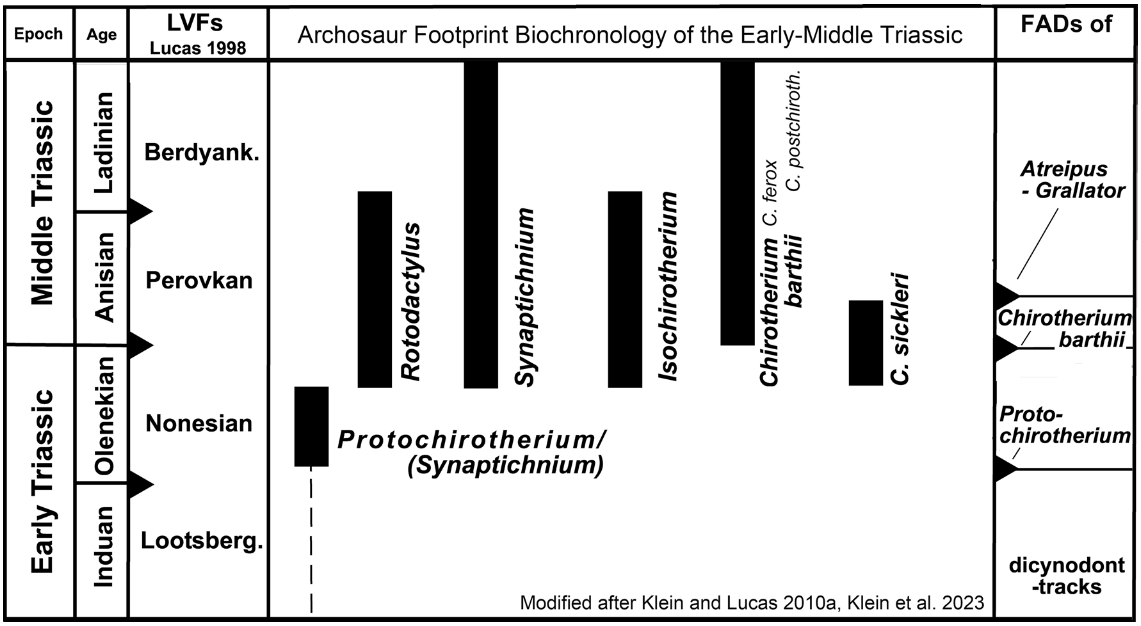

Fig. 22 Archosaur footprint biochronology of the Early-Middle Triassic. The assemblage from the Holbrook Member described in this paper corresponds to the *Chirotherium barthii* biochron. Modified after Klein and Lucas (2010a), Klein et al. (2023)

non-amniotes in the osteological record and reptile tracks in the ichnofauna concerns both the lower Moenkopi Wupatki Member and the upper Moenkopi Holbrook Member. A probable explanation has been given by Klein and Lucas (2010b). After these authors most bone records come from channel lag or bar deposits, whereas the footprints are preserved in unchannelized sand-silt deposits from flow events. Temnospondyl non-amniotes lived in aquatic habitats such as river channels and their bones were preferently preserved in these environments. Similar observations were made by Mujal and Schoch (2020) in coastal or restricted marine deposits of the Lower Keuper (Erfurt Formation, Middle Triassic) in Germany which has abundant temnospondyl skeletons. Here, rare temnospondyl swim tracks have also been found in a subaqueous depositional environment (see also observations by De Jaime-Soguero et al. 2021). A direct correlation of footprints and skeletal taxa from the Moenkopi Formation is not possible because autopodial skeletal elements are scarcely preserved and mostly incomplete. However, studies and attempts for correlations from other assemblages can be used to evaluate the Moenkopi tetrapod faunal composition based on the footprint record.

Chirotherium barthii (Fig. 21H–J) refers to a functionally tridactyl pes with digit III longest and strongly reduced digits I and V and to a manus with a relatively short digit IV. It has been correlated with euparkeriid archosauriforms and with a hypothetical basal avemetatarsalian (Haubold 2006; Haubold and Klein 2002; Klein et al. 2023). *Isochirotherium marshalli* (Fig. 21F–G) can be considered the footprint of a pseudosuchian archosaur and has been hypothetically attributed to the poposauroid *Arizonasaurus,* known from the Holbrook Member of the Moenkopi Formation (Nesbitt 2005b; Diedrich 2015; Klein et al. 2023). *Synaptichnium pseudosuchoides* (Fig. 21A–B) and *S. diabloense* (Fig. 21C–E) refer to a pes with pedal digit IV longest. Similar proportions can be seen in the foot skeletons of the "rauisuchian" archosaurs *Ticinosuchus* and *Batrachotomus* (Krebs 1965; Gower and Schoch 2009; Lautenschlager and Desojo 2011). *Rotodactylus cursorius* (Fig. 21K–N) have been interpreted as the trackways of dinosauromorph or non-crown group archosauromorph archosaurs (Haubold 1999; Klein and Niedźwiedzki 2012).

Biostratigraphy and paleobiogeographic implications

The early Anisian age of the Holbrook Member is established by vertebrate biostratigraphy and magnetostratigraphy (Steiner et al. 1993; Lucas 1998, 2010; Lucas and Schoch 2002; Lucas and Hancox 2022). The footprint ichnotaxa from the Snowflake tracksite support an Anisian age assignment (Fig. 22). Thus, the tetrapod ichnofauna containing the chirotheriid ichnotaxa *Chirotherium barthii* and *Isochirotherium marshalli* indicates a Middle Triassic (early Anisian) age of the Snowflake assemblage. This evaluation corresponds with the mapped lithostratigraphic succession and distribution of the Holbrook Member (upper Moenkopi

Formation, Anisian) in this region. *C. barthii* is the index ichnotaxon of the global *Chirotherium barthii* biochron that can be cross-correlated with the early Anisian (Klein and Lucas 2010a, b, 2021; Schneider et al. 2020). Many classical footprint sites in the Holbrook Member, in particular the localities of Peabody (1948) in northern Arizona, also yielded the chirotheriids *C. barthii* and *I. marshalli*. Characteristic of Anisian assemblages is the co-occurrence of *Synaptichnium* and *Rotodactylus* footprints, even if both have their first appearance in the Olenekian. The *C. barthii* biochron follows the *Protochirotherium* biochron, which can be cross-correlated with the Olenekian and the Nonesian LVF (Klein and Haubold 2007; Klein and Lucas 2010a, 2010b; Klein and Niedźwiedzki 2012; Lucas 1998, 2010). In northern Arizona, the latter is represented by the Wupatki Member of the lower Moenkopi Formation (Klein and Lucas 2010a, 2010b).

The Holbrook Member of the upper Moenkopi Formation in Arizona and Utah yielded a famous vertebrate body fossil fauna including the temnospondyl amphibian *Eocyclotosaurus wellesi,* which is an index taxon of the Perovkan land-vertebrate faunachron (LVF) that can be cross-correlated with parts of the Anisian (Lucas 1998, 2010; Schoch 2000; Lucas and Schoch 2002; Nesbitt 2005b; Schneider et al. 2020; Lucas and Hancox 2022). The Perovkan LVF follows the Nonesian LVF, which can be cross-correlated with the Olenekian (Lucas 1998, 2010; Lucas and Hancox 2022). Remarkable is the lack of the chirotheriid ichnospecies *C. sickleri* in the Anisian Holbrook Member, whereas it is present in the Olenekian Wupatki Member. In European assemblages (and exclusively in this region), *C. sickleri* co-occurs with *C. barthii* (Haubold 1967, 1971a, 1971b), for example at the Anisian type locality of these ichnospecies in Thuringia, Germany. Other Lower Middle Triassic successions in South America, North Africa, and China completely lack *C. sickleri* but have *C. barthii* in their Anisian upper parts (De Jaime-Soguero et al. 2021; Klein and Lucas 2021). In Morocco, asssemblages of the lower Timezgadiouine Formation (Tanamert Member, Olenekian) contain *Protochirotherium* and in the upper part (Aglegal Member, Anisian) have typical *C. barthii* (Klein et al. 2010, 2011). Both units lack *C. sickleri*. Middle Triassic (Anisian) deposits from the Guanling Formation of China yielded abundant *C. barthii,* but lack *C. sickleri* (Xing et al. 2013; Xing and Klein 2019). In North America, *Protochirotherium* is probably present in the Moenkopi and Red Peak formations of the Dinosaur National Monument area in northeastern Utah (Lovelace and Lovelace 2012; Thomson et al. 2014); however, this assemblage also lacks *C. sickleri*. It seems that outside of Europe, *C. sickleri* is only present in the lower Moenkopi Formation (Wupatki Member, Olenekian) of Arizona (Peabody 1948; Klein and Lucas 2010b). This suggests that the trackmaker appeared earlier in North America during the Olenekian, but disappeared and migrated to Europe by begin of the Anisian where it shared habitats with the *C. barthii* producer.

Conclusions

The new tracksite in the Holbrook Member of the Moenkopi Formation (Middle Triassic, Anisian) near Snowflake, northeastern Arizona, shows a diverse vertebrate ichnofauna comprising the archosaur ichnotaxa *Chirotherium barthii*, *C. rex*, *Isochirotherium marshalli*, *Synaptichnium pseudosuchoides*, *S. diabloense*, and *Rotodactylus cursorius.*

Remarkable is the lack of non-archosaurian forms, such as *Rhynchosauroides* or *Dicynodontipus*, in particular the former being more abundant in comparable ichnoassociations from the global record. The occurrence of differently sized *Synaptichnium* with transitional forms between small *S. diabloense* and large *S. pseudosuchoides* may suggest the presence of different ontogenetic stages and allometric growth of the trackmaker that can be considered either a pseudosuchian or a non-crowngroup archosauriform archosaur. These shared the habitat with the basal avemetatarsalian/pseudosuchian *Chirotherium barthii*, the pseudosuchian *Isochirotherium* and other archosaurian, possibly dinosauromorph *Rotodactylus* producers. Invertebrate traces indicate the *Scoyenia* ichnofacies. The depositional environment was a floodplain where larger archosaurs might have fed on smaller members of the group as well as on different subaqueous invertebrates.

The locality represents the most extensive discovery of tetrapod footprints from the Moenkopi Formation since the pioneeering studies of F. E. Peabody and S. P. Welles in the first half of the twentieth century. It offers the further continuation of this research and a re-evaluation of these assemblages from today's perspective.

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Declarations

Conflict of interest We confirm that there is no conflict of interest with any researchers or research and the presented manuscript has not been published in or submitted to any other journal before.

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