Crouching theropod and *Navahopus* sauropodomorph tracks from the Early Jurassic Navajo Sandstone of USA

JESPER MILÀN, DAVID B. LOOPE, and RICHARD G. BROMLEY

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Numerous tracks and trackways are preserved in the a cross-strata of the Lower Jurassic Navajo Sandstone of northern Arizona and southern Utah, USA. Tracks and trackways of small theropod dinosaurs are particularly abundant within one 10-m-thick interval. This paper describes a crouching trace from a theropod dinosaur that shows impressions of all four limbs, the ischial callosity, the tail, and tracks leading to and away from the crouching site, and revises the interpretation of a well preserved trackway hitherto referred to the synapsid ichnogenus *Brasilichnium* and here considered to be from a sauropodomorph dinosaur. It is named *Navahopus coyoteensis* isp. nov. on the basis of morphological differences from the type ichnospecies *N. falcipollex*. The ichnofamily Navahopodidae is revised to include *Tetrasauropous unguiferus*, *Navahopus falcipollex*, and *N. coyoteensis*.

Key words: *Navahopus*, Navahopodidae, Sauropodomorpha, Theropoda, ichnology, locomotory habits, crouching trace.

Jesper Milàn [Milan@geol.ku.dk] and Richard G. Bromley [rullard@geol.ku.dk], Department of Geography and Geology, University of Copenhagen, Øster Voldgade 10, DK-1350 Copenhagen K, Denmark;
David B. Loope [dloope1@unl.edu], Department of Geosciences, University of Nebraska, Lincoln, NE 68588-0340, Lincoln, Nebraska, USA.

Introduction

The Early Jurassic Navajo Sandstone is the remains of an erg considered to have covered as much as 350.000 km^2 at the time of deposition, and to have reached thicknesses in excess of 700 m. Tracks and trackways of dinosaurs are common in the Navajo Sandstone Formation, with more than 60 sites reported in the unit and its correlative strata (Lockley 1998). The sparse but diverse tetrapod body-fossil record known comprises tritylodonts, crocodylomorphs, and dinosaurs (Irmis 2005).

The outcrops of Navajo Sandstone in southern Utah and northern Arizona are composed of large-scale, southeast-dipping a cross-strata (Loope and Rowe 2003). The full height of the bedforms that created the distinct, large-scale cross-strata is estimated, from studies of a nearby outcrop of similarly sized cross-strata (Hunter and Rubin 1983), to have represented a typical dune height of about 30 m. The present day weathering profile of the Navajo Sandstone is such that individual, potentially track-bearing surfaces are rarely exposed (DeBlieux et al. 2006), but at the Coyote Buttes site located on the Utah-Arizona border, tracks of vertebrates occur in a single, distinct stratigraphic interval up to 10 m thick (Fig. 1). In this area, Loope and Rowe (2003) described evidence for three pluvial intervals during Navajo deposition that lasted tens of thousands of years. During these wet periods, animal and plant life flourished, but dune migration continued at about the same rate as during the drier intervals. Three trace-fossil-rich intevals are recognized at the Coyotes buttes locality, each comprising a rich invertebrate ichnofauna (Ekdale et al. 2007). The tracks described herein are from the middle of these trace fossil-rich intervals (Fig. 1).

The focus of this study is to describe a new theropod trackway that shows the animal to crouch down on the sand and then continue up the dune slope, and further to describe a new sauropodomorph trackway and to revise the ichnofamily Navahopodidae (Olsen and Galton 1984) to include a new ichnospecies of *Navahopus* from Coyote Buttes.

Theropod tracks

The vertebrate track assemblage at Coyote Buttes comprises predominantly tridactyl tracks of small theropod dinosaurs with foot-lengths from 5–15 cm. Morphologically and size-wise the tracks fall into the ubiquitous theropod ichnogenus *Grallator*, and in many instances, the tracks form long, narrow-gauge trackways that can be followed for several metres on exposed surfaces (Fig. 2). Some of the surfaces are so trampled that it becomes impossible to distinguish individual trackways. All the theropod tracks are preserved as true tracks that are filled with sand of a different color which makes them stand out against the color of the ambient surface. This mode of preservation prevents identification of anatomical details such as number and configuration of digital pads, and also does not preserve skin impressions, but traces of long, sharp claws are visible in many cases.

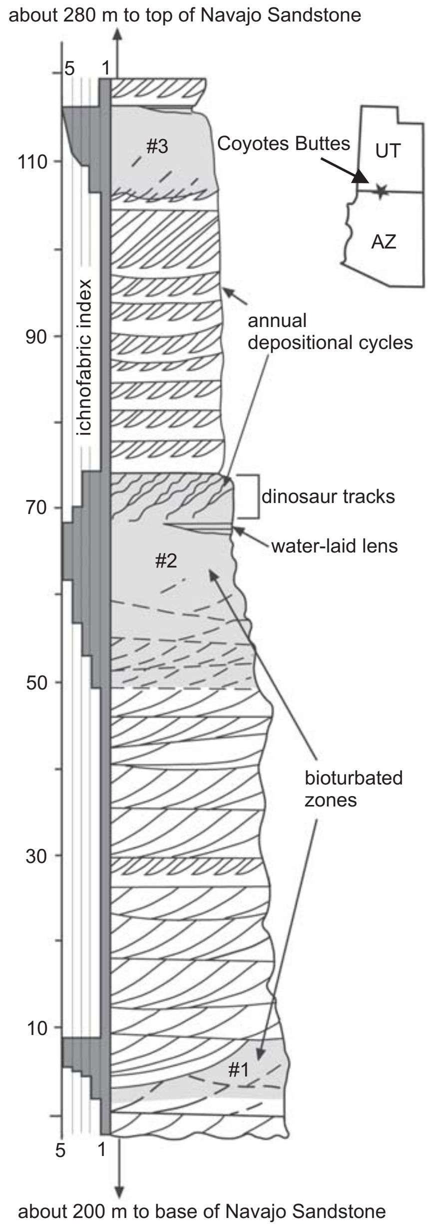

Fig. 1. Stratigraphic column of the Navajo Sandstone outcrop at Coyote Buttes. The studied tracks are all found at the top of the middle zone of bioturbation. The Coyote Buttes locality is located on Bureau of Land Management property (accessible by permit only) at the border between Utah and Arizona at 36°59'58''N, 112°00'35''W. Ichnofabric index 1–5 is zero to total bioturbation.

Among the abundant theropod tracks and trackways, an association of tracks constituting the resting trace of a small individual facing upslope was found on the steeply sloping lee face of a dune (Fig. 3). The angle of the slope today (after correction for tectonic tilting) is around 25° due to compaction of the sandstone, but the original angle of slope when the animal made the trace is estimated to have been around 32°, which is the residual angle of dry sand after shearing (Allen 1984). Most prominent in the resting trace are the two elongate, parallel metatarsus impressions. In front of these are two small, rounded, amorphous manus impressions. The subcircular impression of the ischial callosity is located behind the metatarsus impressions and approximately in the midline of the track constellation. Farther behind the pubic impression is the curved, partial impression of the dinosaur's tail. In connection to the resting track, a single track leads to and four tracks lead away from the resting place (Fig. 3).

Sauropodomorph tracks

Less common than the theropod tracks are bi- and quadrupedal trackways from sauropodomorph dinosaurs together with other tracks of reptilian affinities (Loope and Rowe 2003; Loope 2006). A well-preserved quadrupedal trackway (Fig. 4) preliminarily identified as *Brasilichnium*, an ichnotaxon usually attributed to a synapsid, typically a tritylodont or bona fide mammal (Loope and Rowe 2003), shows close similarity to the sauropodomorph trackway *Navahopus falcipollex* Baird, 1980 from the Navajo Sandstone of Arizona, and the trackway *Tetrasauropus unguiferus* from the Stormberg group of South Africa (Ellenberger 1972).

Systematic palaeontology

Ichnofamily Navahopodidae Olsen and Galton, 1984

Emended diagnosis.—Quadrupedal trackways with strong heteropody. The pes is tetradactyl with impressions of slender, clawed digits. Digit I shortest, and digits III or IV the longest. Pedal digits can be orientated either inward or outward. Manus trace tri- or tetradactyl, having impressions of short, clawed digits II and III directed forward, and a horizontally recumbent, falciform medially directed trace of a pollex claw.

Ichnogenus *Navahopus* Baird, 1980

Type ichnospecies: *N. falcipollex* Baird, 1980.

Emended diagnosis.—Quadrupedal trackway with strong heteropody. Pes tetradactyl, clawed, having impression of digit I shortest and either digit III or IV the longest. Manus trace tridactyl, having impressions of short, clawed digits II and III directed forward, and a horizontally recumbent, falciform medially directed trace of a pollex claw.

Navahopus falcipollex Baird, 1980

Emended diagnosis.—*Navahopus* having pedal digit traces in order of increasing length I–II–VI–III; pedal hypices between digits I–II, II–III, and III–IV similar.

Navahopus coyoteensis isp. nov.

Derivation of name: After type locality.

Holotype: Trackway shown in Fig. 4; a cast will be prepared (permit pending) and stored in the collection of Museum of Northern Arizona.

Type locality: Coyotes Buttes locality at the border between Utah and Arizona, USA (36°59'57.6''N, 112°00'34.6''W) (Figs. 4, 5).

Type horizon: Early Jurassic Navaho Sandstone (Fig. 1).

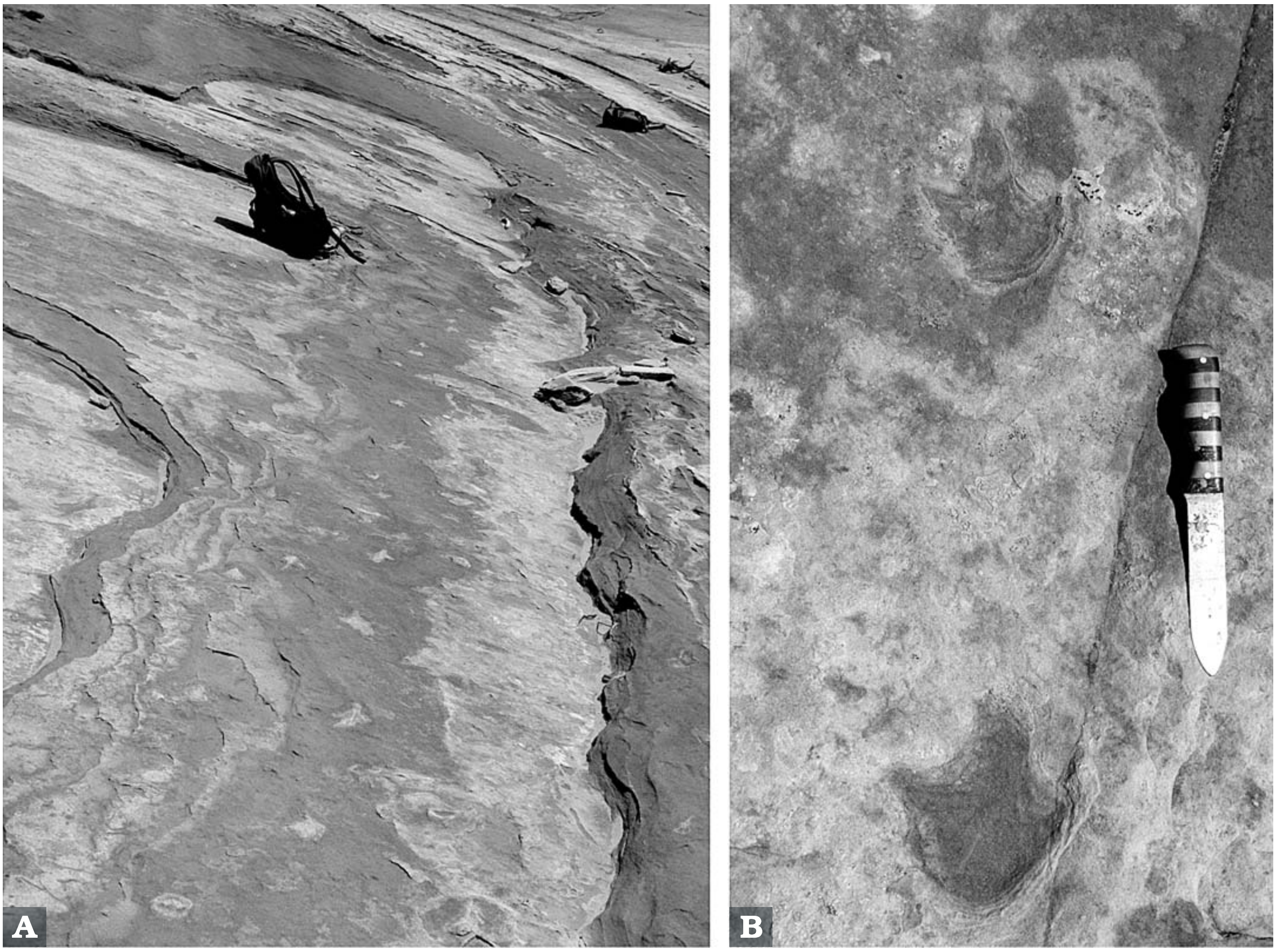

Fig. 2. Theropod trackways from the Early Jurassic Navajo Sandstone, Coyote Buttes locality, USA (both left in the field). **A**. Long, narrow-gauge trackway from a small theropod. Backpack is 50 cm high. **B**. Close-up of two consecutive footprints that are preserved as true tracks infilled with darker colored, lithified sand. Knivehandle is 10 cm long.

Diagnosis.—*Navahopus* having pedal digit impression IV of equal or greater length than digit III. Pedal hypex III–IV markedly greater than hypeces I–II and II–III.

Description.—An approximately 2.5 m long segment of a trackway from a larger, quadrupedal track maker is found on a steeply-sloping surface representing the lee face of a dune (Fig. 4). As in the case with the theropod resting trace, the present-day slope of the surface is around 25°, compacted from an original 32°. The tracks exhibit distinct heteropody. The pes impressions are around 0.2 m long, but the exact lengths of the original tracks are difficult to estimate because of the elongated drag traces from the claws being dragged forward through the substrate, elongating the apparent lengths of the digit impressions. The pes impressions are tetradactyl, and the impressions of digits IV and III are of approximately equal length, followed by the progressively shorter digits II and I. A deep hypex separates the two outer digits. The manus is tridactyl, consisting of two short, forward-oriented, clawed digit impressions and a prominent, inwardly directed impression of a large pollex claw. Like the pes, the manus impressions also bear evidence of the manual claws being dragged forward through the sand as the animal walked.

The trackway pattern changes along the exposed trackway segment. The first part of the trackway shows the orientation of the feet to be angled up the slope, while the direction of the trackway is at an angle to the slope (Fig. 5). Midway through the exposed trackway segment, the trackway changes direction to directly upslope and the orientation of the foot axis corresponds to the axis of the trackway.

Discussion

Theropod tracks.—Direct traces of theropods in full crouching posture with impressions of the metatarsi, ischial callosity, and manus are uncommon: so far, only three specimens have been described in the literature. Two are from the Early

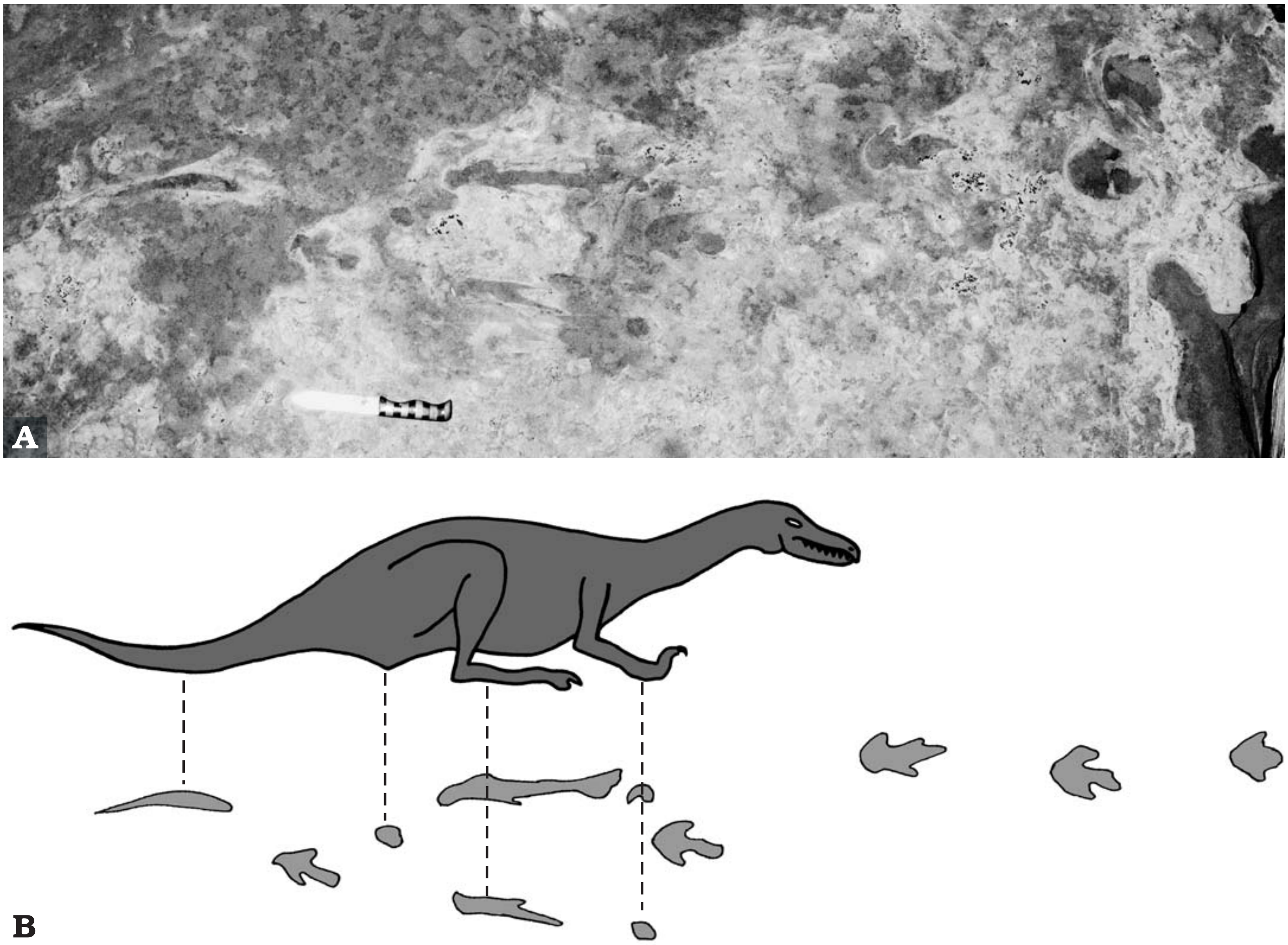

Fig. 3. Trace of a crouching theropod (left in the field). **A**. The crouching track comprises subparallel impressions of the metatarsus, two small, undetailed manus imprints, the imprints of the ischial callosity, the impression of the tail, and tracks from the dinosaur walking toward and away from the resting site. Upslope direction is to the right. Knivehandle is 10 cm long. **B**. Interpretative drawing of an unspecified small theropod dinosaur crouching down to produce the configuration of tracks seen in A. The manus posture during resting, where only the metacarpals are in contact with the ground producing an amorphous rounded depression is based on Weems (2006). The animal was progressing directly up the slope and was crouching facing upslope before it continued directly up the dune face.

Jurassic of the Connecticut Valley and another is from the Early Jurassic of Sichuan, China (Lockley et al. 2003). The Connecticut Valley specimens were originally described by Hitchcock (1848) as *Sauropus barratti*. The ichnotaxonomic status of these specimens has subsequently changed numerous times, but at present they are assigned to *Grallator* (for a detailed ichnotaxonomic account of the Connecticut Valley specimens, see Lockley et al. 2003). The Chinese specimen was found at the Wu Ma Cun site, Sichuan, China (Yang and Yang 1987). A fourth, as-yet undescribed trace of a crouching theropod was recently discovered in the Early Jurassic Moenave Formation at the St. George Dinosaur Discovery Site at Johnson Farm, St. George, Utah (Milner et al. 2006), and a fifth site is known from the Lower Jurassic Kayenta Formation of Southern Utah (Martin Lockley, personal communication 2007). Furthermore, a few trackway segments where a theropod had slowed down to full stop and dropped down on all fours have been described from the Culpeper Crushed Stone Quarry, Virginia (Weems 2006).

The Connecticut Valley material comprises subparallel metatarsus impressions and a rounded impression of the ischial callosity (Lockley et al. 2003). One specimen includes the elongate impression of the dinosaur's belly as well; the other specimen shows small manus impressions. The Chinese specimen comprises subparallel metatarsus impressions, a sub-spherical ischial impression, and an elongate belly impression (Lockley et al. 2003).

The newly discovered resting trace from Coyote Buttes resembles the Chinese and Connecticut Valley specimens in comprising sub-parallel metatarsus impressions, small manus impressions, and a sub-circular ischial impression. In addition to these features, however, the Coyote Buttes specimen exhibits a partial impression of the tail plus tracks leading toward and away from the place at which the theropod crouched down. These features are also present in the St. George specimen except for the tail impression (Milner et al. 2006).

The manus impressions appear as amorphous, rounded impressions without evidence of digits or other anatomical details. Early Mesozoic, well-preserved theropod tracks assigned to the ichnotaxon *Kayentapus* are described as having manus impressions consisting only of rounded amorphous depressions. This suggests that the trackmakers rested their hands on the metacarpals only, with the digits flexed upward (Weems 2006). The manus impressions of the herein described specimen consist likewise of a similar small amorphous depression, suggesting a similar resting posture for the trackmaker (Fig. 3).

No fine anatomical details like skin texture, number and arrangement of digital pads, etc. are preserved in the Coyote Buttes specimen; this is due to the consistency of the substrate at the time of, and subsequent to, track manufacture. Sand is a poor medium for the preservation of anatomical details because it has poor cohesive properties and tends to flow together when the sand is dry, obliterating all but the gross overall shape of the footprint (Milàn 2006).

The configuration of the tracks constituting the resting trace allows reconstruction of the timing and succession in which the tracks were emplaced and the possible movements exercised by the dinosaur both when it lay down and got up again. The first track to be emplaced was the track leading toward the resting trace. Assuming the bipedal theropod dinosaur settled down to rest in a way similar to modern flightless birds, like the emu (Milàn 2006), the theropod dropped down on its elongate metatarsi, and the hands and ischial callosity came into contact with the ground. When an emu rises up from resting position, it tilts the front part of its body forward and upward—thus simultaneously tilting the hindquarters downward—before rising up on its feet (J.M. unpublished data). When a theropod, with its plesiomorphically long tail, rose up in a similar way, the tail would have necessarily pressed down into the substrate. This would, in this case account for the curved tail impressions located behind the paired impressions of the metatarsus and the ischial impression.

Sauropodomorph tracks.—The apparent sideways walking pattern on the first part of the sauropodomorph trackway, made by an animal trudging up the steep slope of the dune, is similar to the patterns found in Permian tetrapod trackways from the a Coconino Sandstone (Brand and Tang 1991). The sideways walking pattern of these tracks was interpreted as evidence for an underwater origin of the tracks, but that interpretation is highly controversial (Lockley 1992; Loope 1992), and a similar sideways walking pattern has been described from goat traces in Pleistocene aite from Mallorca (Fornós et al. 2002).

The trackway was preliminarily identified as *Brasilichnium* by Loope and Rowe (2003). However, a closer examination shows that this attribution to be incorrect. The morphology of both the manus and pes impressions, and especially the manus tracks with their prominent impressions of a large, in-

Fig. 4. Trackway of *Navahopus coyoteensis* isp. nov., as shown by Loope and Rowe (2003) and here reinterpreted as a sauropodomorph dinosaur walking up the lee slope of a dune. Note the elongate traces from the claws being dragged through the sediment. The present day slope is approximately 25°, due to compaction of the sediments. The original angle of slope was around 32° which is the residual angle of slope of dry sand after shearing (Allen 1984). Hammer is 30 cm long.

wardly directed pollex claws, suggests a sauropodomorph rather than a synapsid trackmaker. The trackway *Navahopus falcipollex* Baird, 1980, described from the Navajo Sandstone of Arizona, was likewise identified as a prosauropod trackway, on the basis of morphological comparisons between tracks and the pedal skeleton attributed to the prosauropod *Ammosaurus*, which had been excavated in the area near the trackway (Baird, 1980). Recent analysis has cast doubt on the sauropodomorph origin of the *Navahopus falcipollex* holotype (Lockley and Hunt 1995). According to new interpretations of the holotype (Fig. 6), the alleged medially directed pollex impressions in the manus prints were not very well preserved and suggested an extramorphological feature. Without the medially directed pollex impression *Navahopus falcipollex* could as well be an extramorphological variant of a large tritylodont trackway, and not a sauropodomorph trackway (Lockley and Hunt 1995; Lockley 2005; Hunt and Lucas 2006; Shibata et al. 2006). A bipedal trackway from the Antelope Island site in Utah has preserved tetradactyl pes imprints similar to, but significantly larger than *Navahopus*, but no associated manus

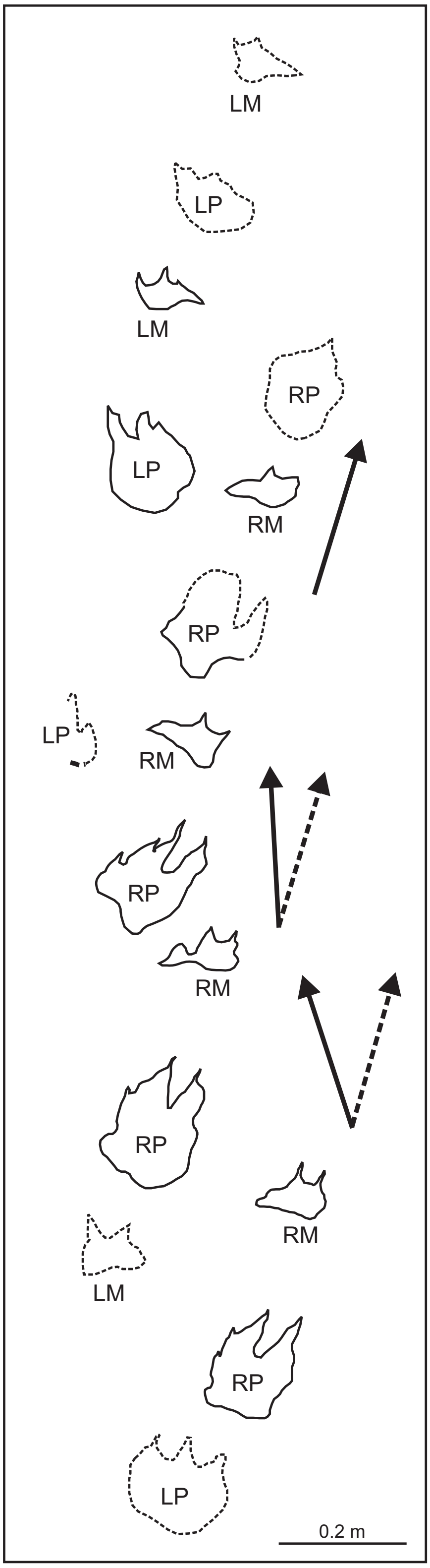

Fig. 5. Sketch of the trackway in figure 4. The sketch is redrawn from high-resolution digital photographs of the trackway. RM, right manus; LM, left manus; RP, right pes; LP, left pes. The solid arrow indicates the direction of progression and the broken-line arrow the orientation of the body during progression. Notice how the animal walked at an oblique angle upslope in the first half of the trackway, and then changed to progress head on, up the slope.

prints, and could represent a bipedal gait from the *Navahopus* trackmaker or similar animal (Lockley 2005). Recent investigations, however, support that *Brasilichnium* and *Navahopus* should be considered as separate ichnotaxa (Reynolds 2006).

The new ichnospecies from Coyote Buttes, *Navahopus coyoteensis*, supports the original sauropodomorph interpretation of *Navahopus falcipollex* (Baird 1980), in that it displays well-preserved manus impressions consisting of two short, clawed, forward-facing digits and a large medially directed falciform pollex claw. The pes is tetradactyl, with subequally long digit I and II impressions followed by successively shorter digits III and IV (Fig. 6). However, the Coyote Buttes trackway differs from *N. falcipollex* in having a 0.1 m deep hypex separating the impressions of digits III and IV, while no apparent gap is present between the impressions of digits I to III. The deep digit III–IV hypex is consistently present in all tracks from both left and right sides of the animal (Figs. 4–7), which excludes the possibility that it is a pathological phenomenon or sedimentary back-filling of the track. Instead, it suggests that it represents peculiar foot morphology, with digit IV being functionally separated from the adjacent digits. Further, *N. coyoteensis* originates from a larger animal than *N. falcipollex* in that the pes impressions of *N. coyoteensis* are around 0.2 m long and the pes impressions of *N. falcipollex* are 0.1–0.12 m long (Baird 1980).

Another ichnogenus supposed to be of sauropodomorph origin is *Otozoum* (Lull 1915, 1953). *Otozoum* is commonly found in the Navajo Sandstone and *N. coyoteensis* falls within the size range of *Otozoum*. However, *Navahopus* differs from *Otozoum* in several important aspects. The pedal digits of *Otozoum* are curved inwards, digit III being the longest. Only two convincing *Otozoum* manus tracks are known, and they are pentadactyl and outward rotated (Lockley et al. 2006). Further, the manus in *Otozoum* is located on the outside of the pes prints (Lull 1915, 1953), while in *Navahopus*, the manus is tetradactyl, not rotated, and located directly in front of the pes. The trackway *Tetrasauropus unguiferus* from the Stormberg group of South Africa shares a similar manus structure with *Navahopus*, while the pedal digits appear to be inward rotated and the pes length is around 0.4 m. Two other species of *Tetrasauropus*: *T. jacquesi*, and *T. seakansis,* shares a similar pedal structure to *T. unguiferus* but the manus prints are not known in *T. jacquesi* and the manus of *T. seakensis* does not appear to have the impression of the falciform pollex claw. A fourth ichnospecies, *T. gigas*, is significantly larger with impressions of five blunt pedal digits and a badly preserved, pentadactyl manus (Ellenberger 1970; Fig. 6 herein). Olsen and Galton (1984), include *Tetrasauropus unguiferus* in Navahopodidae, and synonymize *T. gigas*, *T. jacquesi*, and *T. seakansis* with *Brachychirotherium*, an interpretation we support as these tracks do not posses the prominent pollex impression of the manus. Lockley and Meyer (2000) further propose to include *T. gigas* in *Pentasauropus*, a suggestion confirmed by a recent reexamination of *Tetrasauropus* and related ichnotaxa (Porchetti and Nicosa 2007). *T. seakansis* was excluded from *Tetrasau-*

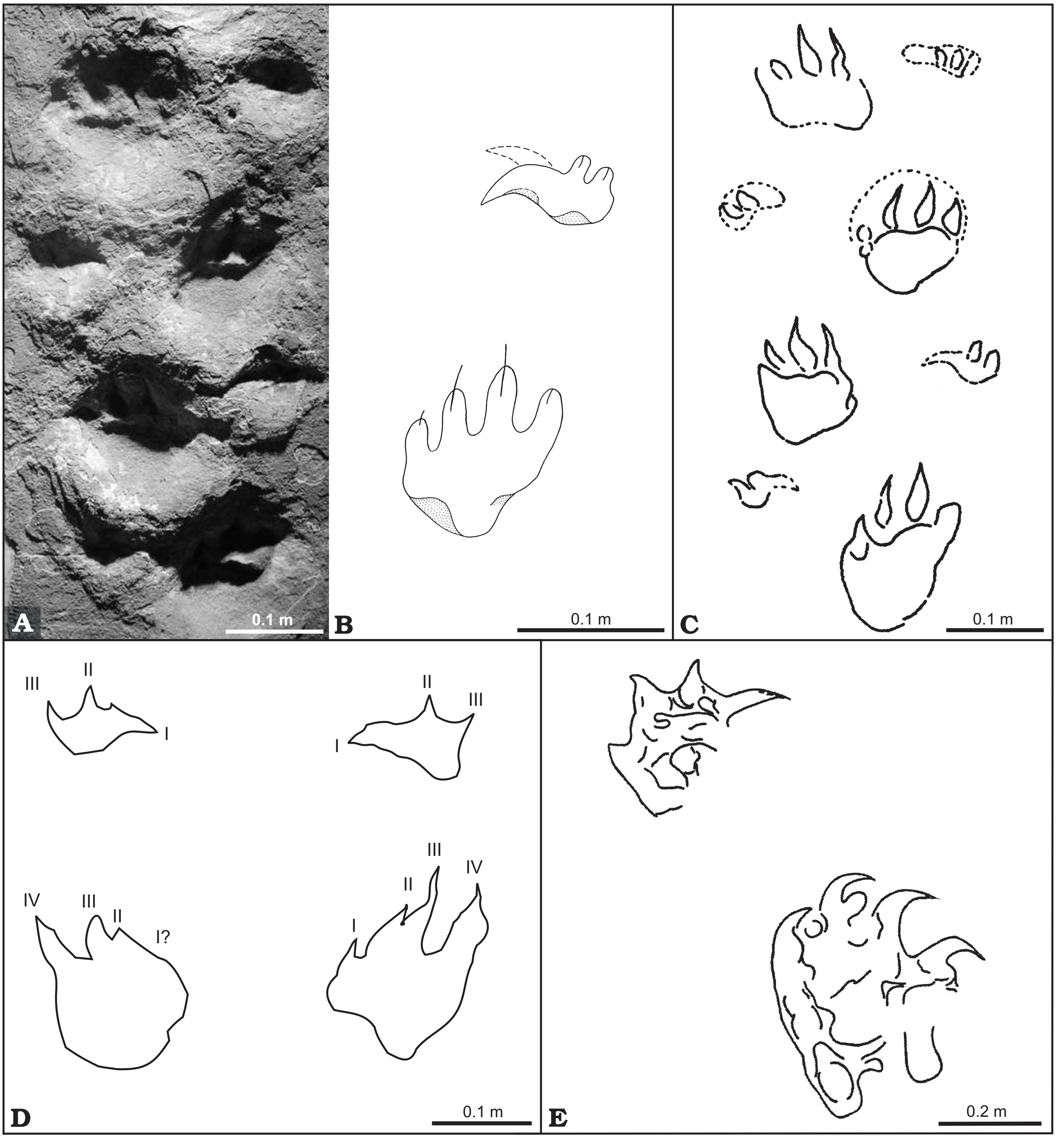

Fig. 6. The ichnofamily Navahopodidae, characterized by the tridactyl manus impression with the prominent inward directed pollex trace. **A**. *Navahopus falcipollex* Baird, 1980, the holotype MNA P3.339 from the collection of the Museum of Northern Arizona, Flagstaff. **B**. Baird's (1980) interpretation of *Navahopus falcipollex* as a sauropodomorph trackway, with an enlarged medially directed pollex claw. **C**. New interpretative drawing of *Navahopus falcipollex*, with less pronounced pollex impressions, and suggested mammal affinities. From Lockley and Hunt (1995). **D**. Sketch of *Navahopus coyoteensis* isp. nov. manus and pes couplets from left and right side of the trackway. In the pes prints, digits III and IV are separated by a deep hypex, recognizable in all well-preserved tracks in the trackway. All manus prints in the new trackway show consistent impressions of a large, medially directed pollex claw, supporting the original interpretation of Baird (1980), that *Navahopus* was made by a sauropodomorph dinosaur. Compare with Fig. 7. **E**. New interpretation of *Tetrasauropus unguiferus* Ellenberger, 1972 from the Lower Stormberg assemblage of Southern Africa (Porchetti and Nicosa 2007).

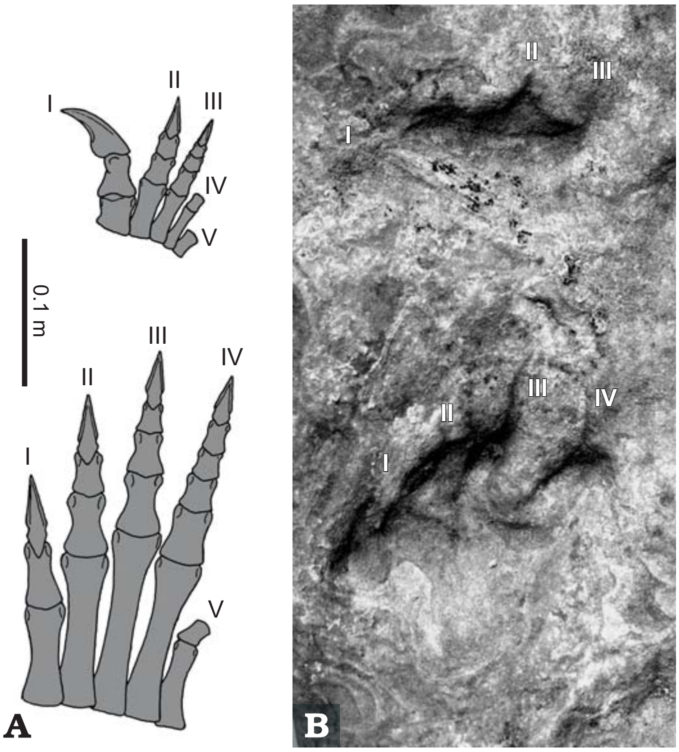

Fig. 7. Comparisons between the manual and pedal skeleton of sauropodomorph material from the Navajo Sandstone of northern Arizona and the *Navahopus coyoteensis* isp. nov. trackway from Coyote Buttes. The skeletal material was originally referred to as *Ammosaurus* (Galton 1971), but has recently been revised and reinterpreted as belonging to an indeterminate sauropodomorph (Yates 2004). **A**. The manus of the sauropodomorph from northern Arizona is tridactyl and consists of two short, forward-facing digits (II and III) and the large pollex claw of digit I directed inward. The pes is tetradactyl with digits III and IV of subequal length, followed by the shorter digits II and I; modified from Baird (1980). **B**. Manus and pes couple from *N. coyoteensis*. Note the close correspondence between the pedal skeleton and the tracks, here shown to the same scale.

ropus by Ellenberger (1972), and included in *Paratetrasauropus*. This leaves *Tetrasauropus* to be monospecific, only including *T. unguiferus*. The subequal pedal digit length of *T. unguiferus* precludes inclusion of the ichnospecies in *Brachychirotherium* or *Chirotherium* (Rainforth 2003). *Tetrasauropus*-like tracks from the Triassic of south Wales have a pes morphology similar to *Navahopus* and *T. unguiferus*, but have an outward rotated manus (Lockley et al. 1996). Based on this, we support the inclusion of *Tetrasauropus* into the ichnofamily Navahopodidae as suggested by Olsen and Galton (1984) and we amend the diagnosis of the ichnofamily Navahopodidae to include quadrupedal trackways with tetradactyl, slender, clawed pes impressions and a tridactyl manus with impression of a prominent, inward-directed, falciform pollex. Navahopodidiae thus include the African genus *Tetrasauropus unguiferus*, and *Navahopus falcipollex* and *N. coyoteensis* from the Navaho sandstone of North America.

Baird (1980) compared the *N. falcipollex* trackway with the pedal skeletal elements of the sauropodomorph dinosaur described as *Ammosaurus* (Galton 1971) from the Navajo Sandstone of northern Arizona, and concluded that the trackmaker responsible for *N. falcipollex* was four-fifths the size of the cf. *Ammosaurus* specimen. The taxonomic status of *Ammosaurus* material from Arizona has since been revised: Yates (2004) revised both *Ammosaurus* and *Anchisaurus* and demonstrated that the two were synonymous. The taxon represents a basal sauropod rather than a prosauropod, and the material referred to *Ammosaurus* by Galton (1971) pertains to an indeterminate, possibly plateosaurid sauropodomorph. When comparing the dimensions of the pedal skeleton of the "*Ammosaurus*" material from Arizona with *N. coyoteensis*, there is an almost perfect agreement in size, even when additional length due to fleshy parts and keratinous claw sheaths are taken into consideration (Fig. 7). *N. coyoteensis* is thus a better match for an "*Ammosaurus*" trackway than is the holotype of *N. falcipollex*. Furthermore, the trackway shows the trackmaker to first have walked somewhat sideways up the slope of the dune before shifting to progression directly upslope.

Conclusion

Tetrapod tracks and trackways are abundant at several horizons in the Lower Jurassic, a Navajo Sandstone of Arizona and Utah. A trace of a small theropod dinosaur crouching down on the sloping face of a dune, with its head orientated upslope, includes both a tail impression and tracks leading toward and away from the resting site. Careful examination of a unique, quadrupedal trackway reveals it to be that of a sauropodomorph dinosaur climbing the front face of a dune, first by progressing sideways up the slope and then changing direction to proceed directly upslope. The trackway is herein granted ichnotaxonomic distinction as *Navahopus coyoteensis* isp. nov., on the basis of morphological differences from the holotype *N. falcipollex*. *N. coyoteensis* is included in the revised ichnofamily Navahopodidae together with *N. falcipollex* and *Tetrasauropus unguiferus.*

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