Louis H.Taylor, Robert G. Raynolds, and Spencer G. Lucas, eds., 2024, Vertebrate Paleoichnology: A Tribute to Martin Lockley. New Mexico Museum of Natural History and Science Bulletin 95.

FOLLOWING IN THE FOOTSTEPS OF DR. MARTIN G. LOCKLEY: ANOTHER 10 YEARS OF PALEONTOLOGICAL INVESTIGATIONS IN GLEN CANYON NATIONAL RECREATION AREA, UTAH AND ARIZONA

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Abstract—Dr. Martin G. Lockley explored and published extensively on vertebrate ichnological resources at Glen Canyon National Recreation Area (GLCA), primarily from the shores of Lake Powell in Utah and Arizona. Since 2010, a team from the St. George Dinosaur Discovery Site, working in conjunction with GLCA and National Park Service paleontologists, has focused research primarily on specific vertebrate tracksites in the Lower Jurassic Glen Canyon Group, especially in the Kayenta Formation and Navajo Sandstone. In the process, several significant body fossil sites have been discovered in the Upper Triassic Chinle Formation that have produced plants, fishes, and archosaurian reptiles. Additionally, two tritylodont bonebeds have been discovered, one each in the uppermost Kayenta Formation and lower Navajo Sandstone. As recognized by Lockley, GLCA, and NPS, the paleontological resources within GLCA park boundaries are extensive, ranging from the Pennsylvanian to Late Cretaceous, and the Pleistocene.

Here, we summarize the major fossil localities studied at GLCA in the last decade and also report on the first occurrences of these trace fossils from GLCA (in geologic order): cf. *Psammichnites* from the lower Cutler beds; cf. *Oravaichnium*, *Scoyenia*, and cf. *Gwyneddichnium* from the Shinarump Member of the Chinle Formation; *Evazoum gatewayensis*, cf. *Evazoum*, and *Brachychirotherium* from the lower Wingate Sandstone; *Undichna*, cf. *Ameghinichnus*, and cf. *Rhynchosauroides* from the Kayenta Formation; a large *Eubrontes* crouching trace with possible manus prints from the Kayenta–Navajo transition, the ninth known example worldwide and second from GLCA; and *Navahopus* tracks from the Navajo Sandstone. We also report on locally abundant *Grallator* tracks in the upper part of the Navajo Sandstone.

INTRODUCTION

Glen Canyon National Recreation Area (GLCA) was established October 27, 1972 "to provide for public use and enjoyment and to preserve the area's scientific, historic, and scenic features," and is administered by the U.S. National Park Service (NPS). Glen Canyon was formed by the downcutting of the Colorado River and its tributaries, creating a beautiful desert landscape on the Colorado Plateau. The construction of the Glen Canyon Dam, completed in 1966, resulted in the flooding of Glen Canyon, creating Lake Powell. The recreation area extends across five counties in two states: Garfield, Kane, San Juan, and Wayne Counties in Utah, and Coconino County in Arizona. GLCA largely follows the Colorado River, from the southwest boundary of Canyonlands National Park south to Page, Arizona, where the river is dammed by Glen Canyon Dam forming Lake Powell, and below the dam to Lee's Ferry. The recreation area also includes lands along tributary rivers, including the San Juan River in the southeast and the Escalante River in the northwest. GLCA in its entirety encompasses 507,649.45 ha (1,254,401.79 acres or 5,076.38 km^2) (Kirkland et al., 2010). Both the Escalante and San Juan rivers intersect the Colorado River in the south-central area of GLCA in the vicinity of Navajo Mountain.

The expansive and picturesque landscape of deep canyons and towering cliffs exposes Upper Paleozoic and Mesozoic strata rich in paleontological resources, and fossil-bearing localities having been recorded over most of its area (Fig. 1A). GLCA preserves an incredible abundance of vertebrate trace fossils, especially those of dinosaurs, because of extensive exposures of Upper Triassic–Lower Jurassic Chinle Formation and Glen Canyon Group strata (Lockley et al., 1998, 2014).

The first report of fossils from within GLCA originated long before the recreation area was established. Riggs (1904) described a small slab of tracks (FMNH P 25123) from the area of Lee's Ferry (Fig. 2A; Fig. 1A #12; locality # GLCA_PalLoc_0741). The late Dr. Martin G. Lockley, who truly pioneered research on dinosaur and many other vertebrate tracks and traces (Fig. 2B), was the first to discuss the Riggs specimen in any detail after its initial description (Lockley et al., 1998). Riggs generally has been credited with collecting the specimen, but it was actually collected by T. V. Keam and purchased from him by the Field Museum of Natural History (FMNH) in 1904 according to their database records.

Prior to St. George Dinosaur Discovery Site (SGDS) field crews starting their work in GLCA in 2010, Martin Lockley and his team documented hundreds of vertebrate tracksites within

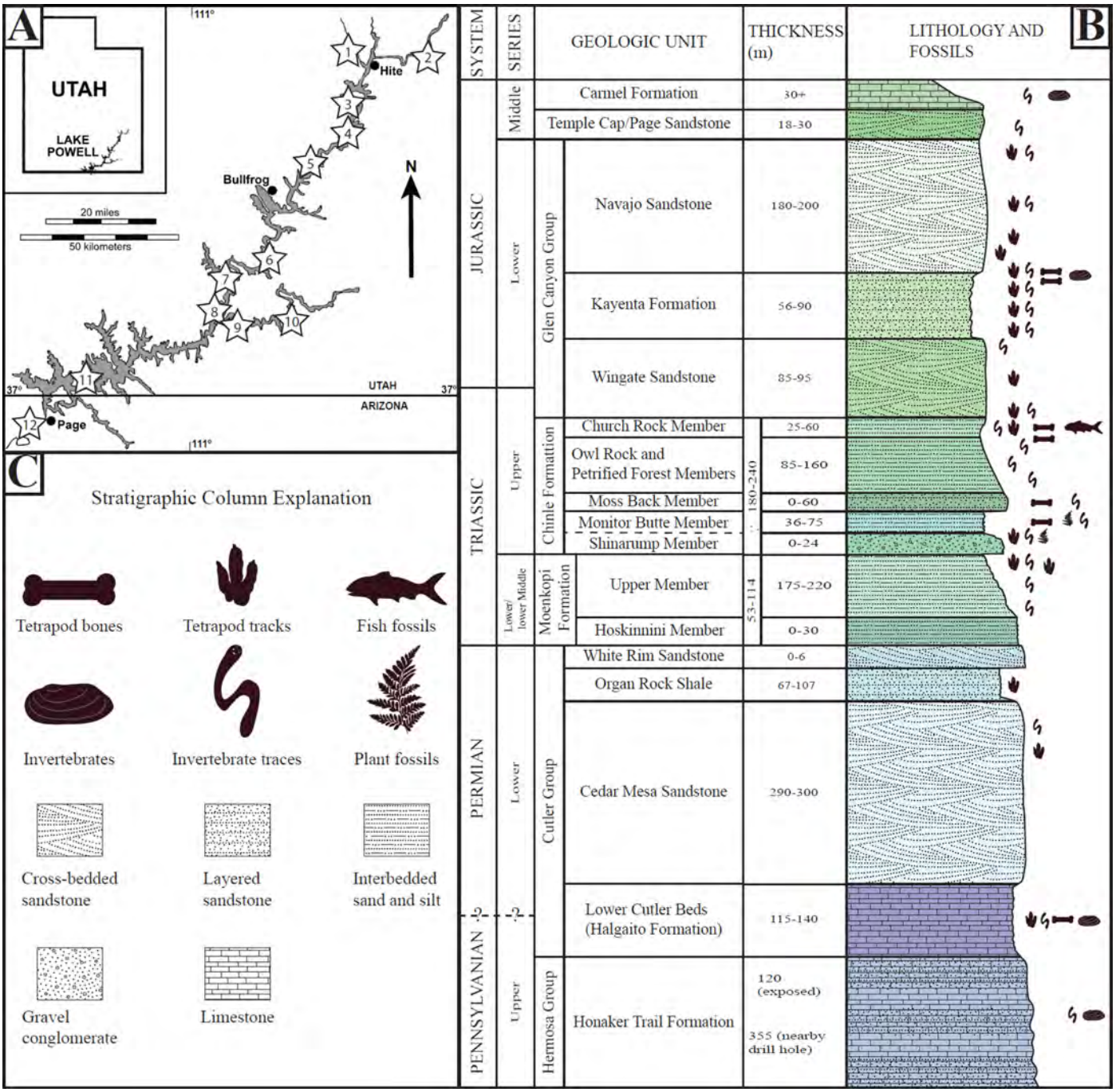


FIGURE 1. Generalized locality map and stratigraphic section of Glen Canyon National Recreation Area (GLCA), Utah and Arizona. **A,** Map of Lake Powell with numbered stars indicating generalized fossil localities (refer to text for associated locality numbers); **B,** Generalized and partial stratigraphic section of GLCA indicating approximate levels at which various fossil types occurrence. Section shortened based on range of sites focused on in this paper; **C,** Legend for symbols used in stratigraphic section (**B**).

GLCA from 1992–1999. Many of these specimens were housed at the University of Colorado at Denver and later transported to the collection facility at University of Colorado at Boulder (UCM), where they now reside.

Although the main focus of this paper deals with the Upper Triassic–Lower Jurassic Glen Canyon Group, we also report on new localities from the lower Cutler beds and the Chinle Formation for the first time. Most of the localities and specimens documented in this manuscript are only briefly covered here; the more important sites and fossils will be described in depth elsewhere. Some of the localities examined herein were previously published by Martin Lockley and company elsewhere, but we add new information about these localities based on new observations and photogrammetry.

HISTORY OF PALEONTOLOGICAL MANAGEMENT

A variety of pre-dam construction surveys and mapping projects were undertaken in GLCA by the U.S. Geological Survey, other agencies, academic scientists, and private organizations to document the geological, paleontological, archaeological, and other resources of Glen Canyon before the canyon would be flooded during the mid-1960s (P. Robinson,

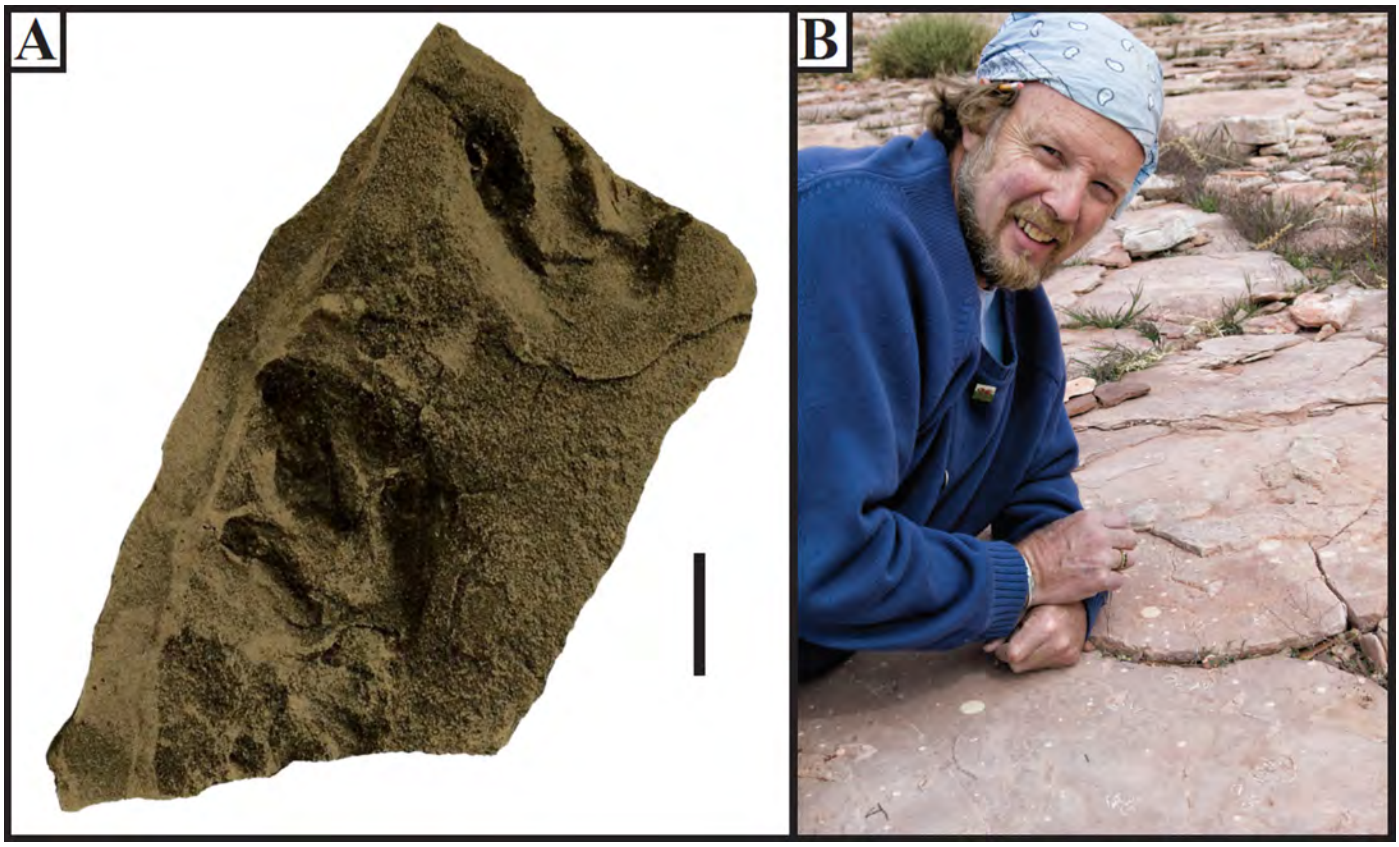


FIGURE 2. **A,** *Grallator* tracks (FMNH P 25123) reported by Riggs (1904) are the first record of a fossil collected within GLCA boundaries. Specimen may have originated from the Wingate Sandstone at Lee's Ferry, Arizona (locality # GLCA_PalLoc_0741). Scale = 5 cm; **B,** Photo of Martin Lockley at the "Killer Bees Site" (locality # GLCA_PalLoc_0072) mapping small quadruped tracks on May 4, 2005 (photo credit, A. Delgalvis).

personal commun., 2018). During the early 1990s, GLCA Chief of Resources Management John Ritenour recognized the need to better document and manage the rich fossil resources at the recreation area. John contacted one of us (V. L. Santucci), at the time the Park Paleontologist at Petrified Forest National Park to seek guidance and support with the paleontological resource needs identified at GLCA. Santucci contacted paleontologists Martin Lockley and Adrian Hunt, who were specialists in vertebrate ichnofossils. Martin Lockley was invited to join in field work at GLCA to initiate an inventory and study of the fossil footprints preserved within the recreation area and along the shorelines of Lake Powell. This was the beginning of a lifelong interest in the fossil tracks of Lake Powell by Lockley (Lockley et al., 1992, 1998, 2005, 2014).

In November 2000, NPS Senior Paleontologist V. L. Santucci coordinated a paleontological resource scoping meeting and field trip at GLCA. More than a dozen paleontologists who had undertaken research in or near GLCA were invited to this scoping meeting and field trip to help develop a strategy for future research involving and resource management of the rich paleontological resources at GLCA. In addition to the planning meeting, a number of important fossil localities were visited by the team using "houseboat paleontology" on Lake Powell (Fig. 3). The unanimous conclusion and recommendation by the paleontology team was that previous work has "only scratched the surface" for the potential fossil record at GLCA and the park would benefit from focused paleontological resource inventory and monitoring.

A few important outcomes resulted from the GLCA paleontological resource scoping meeting including: (1) the plan to hire paleontology interns to provide some day-to-day support for the wide range of paleontological resource needs and potential projects tied to the paleontological resources of the park and (2) development of a formal partnership and cooperative agreement between the NPS Paleontology Program and the Utah Geological Survey (UGS) to collaborate on a variety of paleontological resource inventory and monitoring projects in the State of Utah (Swanson et al., 2005; DeBlieux et al., 2005 (unpubl. Report for NPS), 2006, 2021, 2023a, b; Kirkland et al., 2010, 2011; Madsen et al., 2012; Martz et al., 2015, 2017; Santucci and Kirkland, 2010).

Between 2002 and 2012, the NPS Paleontology Program completed paleontological resource inventories for the 32 Inventory and Monitoring Networks established by the NPS. These networks are regional clusters of parks that are in geographic proximity and are tied together as ecoregions with similar biotas, climates, and other natural factors. The paleontological resources for GLCA were described within the Southern Colorado Plateau Inventory and Monitoring Network Paleontological Resource Inventory Report (Tweet et al., 2009). This report represented the first comprehensive summary of all of the paleontological resources documented at GLCA. The NPS Paleontology Program defines paleontological resource inventories as the "compilation of baseline paleontological resource data in order to determine the scope, significance, distribution (both geospatially and temporally), and the management issues related to NPS fossils."

Fluctuations in water levels of Lake Powell were identified as a potential resource management concern for fossils located along the shorelines of the lake. Many fossil localities were observed to intermittently become exposed above water during periods of low lake-water levels and become submerged



FIGURE 3. Glen Canyon NRA Paleontological Resource Scoping Field Trip in November 2000 (from left to right): Jim Kirkland, Dave Gillette, Ken Cole, Vincent L. Santucci, Greg McDonald, Norm Henderson, Pat Monaco, Ron Blakey, Kris Thompson, Steve Hasiotis, Debra Mickelson, Alan Titus, and Larry Agenbroad (NPS photo).

below water during periods of high lake-water levels. The paleontologists and park staff were interested in how this periodic emergence/submergence cycling may impact fossil localities along the shores of Lake Powell.

Paleontologists in the NPS Geologic Resources Division began to evaluate and define the concept of "Paleontological Resources Monitoring" around 2001. The general lack of previous literature and the limited guidance available concerning monitoring *in situ* fossils became quickly apparent. The topic of paleontological resources monitoring has not traditionally been an area of interest to academic and research paleontologists. Rather, it was a topic of greater relevancy to resource managers working for land management agencies. Because paleontological resources are recognized as non-renewable resources, the management activities and planning for fossils is distinct from the methods and practices employed for renewable resources such as modern wildlife and vegetation.

After wide communication and consultation with the paleontology and natural resource management communities, the NPS published an introduction to the concept of paleontological resources monitoring in 2003 (Santucci and Koch, 2003). This initial article led to a more in-depth planning effort to develop comprehensive guidance, methods, and considerations for paleontological resources monitoring. A chapter dedicated to paleontological resources monitoring was published in a Geological Society of America Special Publication on geologic monitoring (Santucci et al., 2009). This included a basic definition for paleontological resources monitoring undertaken by the NPS as an assessment of the condition and stability of *in situ* paleontological resources (Santucci et al., 2009).

In association with the development of the paleontological resource management publication and guidance for the NPS, plans were advanced to identify a prototype paleontological resources monitoring park to begin to test and implement the guidance in the 2009 publication. After an assessment of the various issues related to monitoring in situ paleontological resources across the NPS, GLCA was selected as the NPS prototype paleontological resources monitoring park. The factors considered with the decision to establish the pilot project at GLCA include: (1) the rich fossil records preserved at GLCA as determined through baseline paleontological resource inventories and research (Tweet et al., 2009); (2) NPS awareness and observations related to the natural and anthropogenic threats to GLCA fossils; (3) the dramatic fluctuations of the lake water levels of Lake Powell (including historically low water levels associated with drought and climate change); and, (4) the opportunity to partner with the professional paleontology and geology staff at the UGS.

A cooperative agreement was established between the NPS Geologic Resources Division and the UGS to support the pilot paleontological resources monitoring project at GLCA starting in September 2009. Field work complemented the guidance presented in Santucci et al. (2009) and resulted in the development of site-specific paleontological resources monitoring prescriptions and procedures to gather data over time (Kirkland et al., 2010, 2011). The paleontology staff/interns

followed up with the initial planning and recommendations from 2009 to undertake periodic monitoring of several fossil localities. Several important new fossil discoveries were made during paleontological resources monitoring at GLCA, demonstrating the value of this resource management tool.

Photogrammetry, a tool for generating 3D images and models, has become an important component of paleontological resources management, and monitoring at GLCA. The implementation of paleontological resource photogrammetry at GLCA supports scientific research, inventory and monitoring of in situ fossils, and presents opportunities for education and interpretation. NPS Geologist Jack Wood has supported several photogrammetry projects at GLCA (Wood and Santucci, 2014; Santucci and Wood, 2015; Wood et al., 2021; Milner et al., 2023b).

During 2023, the NPS Paleontology Program worked with GLCA to coordinate paleontological resource inventory and monitoring during the periods of historically low water levels at Lake Powell. This work involved revisiting some of the fossil sites established for paleontological resources monitoring originally in 2009. The sites showed significant changes in the stability and condition of the fossils—they were heavily eroded and degraded from their conditions established during the original documentation of the localities (Fig. 4). New sites were also recorded. One of the most important discoveries made during field work at GLCA in March 2023 was the discovery of the aforementioned tritylodont bonebeds in areas normally submerged below water of Lake Powell. The NPS supported a permit to allow excavation of the tritylodont bonebeds; specimens from the collected blocks are currently being prepared and studied.

GEOLOGY AND PALEONTOLOGICAL RESOURCES WITHIN GLCA

The geological record at GLCA is one of the most geographically and temporally expansive for any NPS area, spanning from the Pennsylvanian through most of the Mesozoic (Fig. 1B; Willis, 2004). The Triassic Period and Jurassic Period are especially well represented within GLCA and are the focus of recent paleontological resource inventories and discoveries (Milner et al., 2023a, b). The general geology and paleontology of GLCA have been the focus of a number of publications and internal NPS reports (Peterson and Pipiringos, 1979; Lockley et al., 1992, 1998, 2014; Sansom, 1992; Santucci, 2000; Sprinkel et al., 2000; Chidsey et al., 2000; Tweet et al., 2009; Anderson et al., 2010; Kirkland et al., 2010, 2011; Santucci and Kirkland, 2010; Martz et al., 2017; Henderson et al., 2022; Bennett et al., 2023; DeBlieux et al., 2023a, b; Milner et al. 2023a, b).

The fossiliferous geologic formations mapped in GLCA include, from oldest to youngest: the Paradox Formation and Honaker Trail Formation of the Hermosa Group; the Halgaito/"Rico" Formation, Cedar Mesa Sandstone, Organ Rock Formation, and White Rim Sandstone of the Cutler Group; the Moenkopi Formation; the Chinle Formation; the Wingate Sandstone, Kayenta Formation, and Navajo Sandstone of the Glen Canyon Group; the Carmel Formation, Entrada Sandstone, and Summerville Formation/Romana Sandstone of the San Rafael Group; the Morrison Formation; the Naturita Formation; the Tropic Shale; and the Straight Cliffs Formation, plus a variety of unconsolidated Quaternary deposits (Ehler et al., 2011; Willis, 2004). Although there are limited areas mapped for the Coconino Sandstone, Toroweap Formation, Hermit Shale, Kaibab Formation, and the Dinosaur Canyon Member of the Moenave Formation in the southern areas of GLCA—all known to be fossiliferous at localities outside of GLCA—no fossils have been reported yet from any of these units in the recreation area.

The fossil record of GLCA and the history of paleontological work in the recreation area was derived primarily through comprehensive literature reviews of published research, internal NPS reports, and gray literature. Additional information on GLCA fossils was obtained through museum collection inventories, review of U.S. Geological Survey internal memos (Examine and Report on Referred fossils [E&R reports]), historic park records, and GLCA records maintained by the NPS Paleontology Archives (Santucci et al., 2018). In 2023, a geospatial paleontological locality database was developed for



FIGURE 4. Prototype paleontological resource monitoring locality at Glen Canyon National Recreation Area (GLCA_PalLoc_0054) established in September 2009, selected based on occurrence of more than 145 individual dinosaur tracks preserved in the Lower Jurassic Navajo Sandstone. The locality was periodically submerged. **A,** Photo shows dinosaur tracks in situ (red circle); highwater mark (red arrow); water level at time of locality documentation in September 2009 (blue arrow); down-dropped sandstone blocks impacting track-bearing unit (yellow arrow); undercutting of a more rapidly eroding mudstone beneath the track-bearing unit (green arrow); and section of track-bearing sandstone showing evidence of where the dinosaur tracks were chiseled out and removed by park visitors (yellow oval) (NPS Photo). **B**, Close-up view of illegally removed slab in **A** (NPS Photo).

GLCA that compiled more than 30 years of fossil locality data, resulting in a list of more than 740 fossil localities within the recreation area. A primary focus of paleontological research at GLCA has been on the rich vertebrate ichnofossil assemblages preserved in Permian, Triassic, and Jurassic strata (Riggs, 1904; Longwell et al., 1923; Hunt et al., 1953; Edwards, 1967; Stokes, 1978; Barnes, 1986; Kelsey, 1989; Davies, 1992; Lockley et al., 1992, 1998, 2005, 2014; Lockley and Madsen, 1993; Lockley and Hunt, 1995; Schultz et al., 1995; Santucci et al., 1998; Mickelson et al., 2001, 2005, 2006; Milner et al., 2016, 2023a, b).

The oldest exposed rocks documented in GLCA belong to the Middle–Late Pennsylvanian Hermosa Group, which measures approximately 355 m thick, based on drill cores (Fig. 1B; Chidsey et al., 2000). Two formations are identified within the Hermosa Group in GLCA: the Paradox Formation and the overlying Honaker Trail Formation (Wengerd and Strickland, 1954). Both are exposed primarily in the northeastern part of GLCA (Dubiel et al., 1989; Schoderbek and Kottlowski, 1997; Anderson et al., 2010). The Paradox Formation comprises limestone, shale, and gypsum, and a marine invertebrate fauna from the Paradox Formation within GLCA includes bryozoans, brachiopods, crinoids, and fusulinids (Lewis and Campbell, 1965; Williams, 2009; Nail, 1996). The Honaker Trail Formation comprises fossiliferous marine sandstone, shale, and limestone, and preserves various microfossils, invertebrates and plants, including dasycladacean algae, foraminiferans, corals, bryozoans, brachiopods, bivalves, gastropods, phillipsiid trilobites, crinoids, echinoids, conodonts, and invertebrate trace fossils in GLCA (Lewis and Campbell, 1965; Doelling, 1975; Loope and Kuntz, 1987; Ritter et al., 2002; Williams, 2009).

The overlying Cutler Group (~550 m at maximum thickness; Fig. 1B) consists of a sequence of sedimentary units spanning from Late Pennsylvanian to Early Permian in GLCA, representing a complex interplay of marine and terrestrial deposition that became increasingly eolian over time. The primary subdivisions of the Cutler Group include the lower Cutler beds (formerly the Halgaito Formation), Cedar Mesa Sandstone, Organ Rock Shale, and White Rim Sandstone (De Chelly Sandstone in Arizona is equivalent in part). Vertebrae and some fragmentary bones of the temnospondyl amphibian *Platyhystrix* were collected from fluvial deposits in the lower Cutler beds in GLCA (Santucci and Kirkland, 2010). Five vertebrate ichnofossil localities that preserve synapsid and reptile tracks were reported in the Early Permian Cedar Mesa Sandstone in GLCA (Lockley et al., 1992, 1998).

During the Early Triassic and early Middle Triassic, the GLCA area was a nearshore and coastal plain that was periodically flooded by the sea to the northwest (Blakey, 1974). The Moenkopi Formation (~53–114 m thick; Fig. 1B) is a widespread geologic unit across the southern Colorado Plateau and is exposed in GLCA, where it preserves a variety of invertebrate and vertebrate ichnofossils including invertebrate burrows, horseshoe crab trackways and possible resting traces, and reptile tracks and swim traces (Mickelson et al., 2001, 2006; Mickelson, 2010; Lockley et al., 1998; Thomson, 2014).

The Late Triassic paleoecosystem in southern Utah and northern Arizona was dominated by braided and meandering river systems flowing generally southeast to northwest across lowland floodplains (Martz et al., 2017), swamps, coniferous forests, and lakes (Gottesfeld, 1972). The Chinle Formation within GLCA measures 180–240 m in thickness (Fig. 1B) and is divided into the following members, from oldest to youngest: the Shinarump Member (which is, in part, laterally interbedded with the lower part of the Monitor Butte Member); the Moss Back Member; the Petrified Forest Member; the Owl Rock Member; and the Church Rock Member. The Chinle Formation is capped by the Wingate Sandstone, the lowermost formation of the Glen Canyon Group.

The Chinle Formation was deposited throughout most of the Late Triassic and preserves a significant taxonomic turnover in plant (Berry, 1930; Ash, 1986), invertebrate (McRoberts and Good, 1993), and vertebrate assemblages (Colbert, 1972; Long and Ballew, 1985; Heckert and Lucas, 1996). The swamps and lowlands were dominated by freshwater fishes, large metoposaurid amphibians, and crocodile-like phytosaurs. The upland deposits preserve early predatory dinosaurs, bipedal reptiles related to the ancestors of crocodiles, armored herbivorous aetosaurs, and large synapsids (Colbert, 1972). The remains of petrified logs, plants, freshwater bivalves, gastropods, conchostracans, fishes, metoposaurs, and archosaurs, along with invertebrate burrows and vertebrate tracks, have been documented in the Chinle Formation in GLCA (Hasiotis, 1992; Kirkland et al., 2010).

During the Late Triassic–Early Jurassic transition in southern Utah, increasing aridity led to the onset of the first of several giant Mesozoic ergs (Blakey, 2000; Blakey and Ranney, 2008). The Wingate Sandstone, which measures 75–95 m thick at GLCA (Fig. 1B), preserves an eolian paleoenvironment along with stromatolites and vertebrate and invertebrate ichnofossils. Wingate tracksites are abundant in many areas within GLCA, but the majority of localities are represented by fallen blocks, so identifying their exact stratigraphic positions is problematic. The blocks at the majority of sites are from low in the unit and preserve typical Upper Triassic ichnofaunas, but at some sites, blocks originating from higher up in the formation preserve typical Lower Jurassic ichnofaunas.

Above the Wingate Sandstone is the thin ‘sandy facies’ (or ‘typical facies’) of the Kayenta Formation that measures only about 56–90 m thick within GLCA—this contrasts with the ‘silty facies’ in north-central Arizona, which can measure up to 140 m thick, and the thicker ‘main body’ of the Kayenta in southwestern Utah, which is ~320 m thick. The braided fluvial systems and playas of the Kayenta Formation brought in massive accumulations of sand that, with increasing aridity later into the Early Jurassic, led to the formation of the Navajo erg (Blakey, 1994, 1996; Peterson, 1994; Graham, 2007; Bryant and Miall, 2010).

The Kayenta Formation is rich in invertebrate and vertebrate ichnofossils, especially within GLCA. Vertebrate ichnofaunas include those of theropods, sauropodomorphs, ornithischians, crocodylomorphs, and synapsids (Lockley et al., 1992, 1998, 2014; Kirkland et al., 2010). *National Geographic Magazine* featured an article on Lake Powell during the 1960s that included reference to a Kayenta Formation vertebrate tracksite from the Explorer Canyon area (Edwards, 1967; Barnes, 1986; Lockley et al., 1998).

Fluvial and eolian strata in the upper part of the Kayenta Formation and lower Navajo Sandstone are gradational and intertonguing substantially with one another over large areas, and we observed this phenomenon in many areas of GLCA (Lockley et al., 2014; Milner et al., 2023b). We follow other authors by referring to this sequence as the Kayenta–Navajo transition (Harshbarger et al., 1957; Middleton and Blakey, 1983; Sansom, 1992; Herries, 1993, Blakey, 1996; Lockley et al., 2014; Milner et al., 2023a, b).

The Kayenta–Navajo transition zone, as well as interdunal lacustrine/playa facies in the Navajo Sandstone itself, preserve a diverse vertebrate ichnofauna. Documented ichnogenera include: *Undichna* (fishes), *Grallator*, *Eubrontes*, and *Kayentapus* (theropod), *Otozoum* and *Navahopus* (sauropodomorph), *Anomoepus* (small ornithischian), *Moyenisauropus* (large ornithischian), *Batrachopus* (crocodylomorph), *Brasilichnium* (synapsid), other synapsid track morphotypes (discussed below), and *Characichnos* (tridactyl swim traces), along with arthropod tracks, termite mounds, and vertebrate and invertebrate burrows

(Sanabria, 2001; Hasiotis, 2004; Kirkland et al., 2010; Santucci et al., 2011, 2012; Lockley et al., 2014; Milner et al., 2023b).

Additionally, body fossils have been recorded from the Kayenta–Navajo transition within GLCA. Lockley et al. (2014, fig. 7) reported coquinas of unionid bivalves from the Slick Rock Canyon region (Fig. 1A #5), which were the first body fossils reported from these units in GLCA. However, in March 2023, the lead author stumbled upon a tritylodontid bonebed in interdune deposits of the lowermost Navajo Sandstone. The bonebed was exposed during historically low-water levels due to drought conditions in Lake Powell in 2022 (Milner et al., 2023a). On a return visit in April 2023 to excavate the Navajo bonebed before snowmelt from the mountains submerged the site once again, Adam Marsh came across a second, older tritylodontid bonebed located nearby in the uppermost Kayenta Formation while measuring a stratigraphic section (Milner et al., 2023a). The Navajo bonebed is associated with vertebrate burrows and tracks.

Later in the Early Jurassic (Pliensbachian–Toarcian; Loope et al., 2004), large portions of the Colorado Plateau were dominated by the expansive Navajo Erg, the largest sand sea known from North America, and possibly the largest to have existed on Earth. This low-latitude erg was situated on the western margin of Pangaea and is today preserved as the Navajo Sandstone (Harshbarger et al., 1957; Chronic and Chronic, 2004; Graham, 2007; Blakey and Ranney, 2008). Although uncommon, interdunal carbonate beds (playa/lacustrine) are documented in the Navajo Sandstone, especially in south-central and southeastern Utah, are more prominent in the lower half of the formation (Marzolf, 1983). These beds rarely measure more than 1 m thick, but in a few cases they can be quite extensive, spanning areas of more than a kilometer (Doelling et al., 1989; Stokes, 1991; Bryant et al., 2016). Generally, these beds are composed of dolostone and cherty limestone deposited between dune sets along interdunal surfaces.

Vertebrate tracks and invertebrate traces can be locally abundant on and within these interdunal carbonates. Track types observed on interdunes surfaces include *Grallator*, *Eubrontes*, *Otozoum*, *Navahopus*, *Batrachopus*, *Brasilichnium*, and other synapsid morphotypes requiring formal description. Additionally, stromatolites and microbial mat surfaces are quite common in some areas, including many localities within GLCA. Tracks, dominated by *Brasilichnium* but also including arthropod trackways, are also present on dune faces at many localities. Vertebrate burrows are well known in the Navajo Sandstone outside GLCA (Hasiotis et al., 2004, 2019, 2023; Lucas et al., 2006), and are also recorded within GLCA, but they have not received much attention within the park.

We documented rare vertebrate track localities within GLCA in March 2023 (Fig. 1A #12), and one of these localities preserve dozens of tridactyl tracks ranging in size from 2.5–10 cm. Some invertebrate traces were also documented near the main fossil track localities, but these will require further study.

The Carmel Formation caps the Middle Jurassic Temple Cap Formation/"Page Sandstone," followed by the last large erg event in southern Utah represented by the Middle Jurassic Entrada Sandstone. This unit in GLCA preserves some theropod dinosaur tracks previously attributed the Navajo Sandstone (Lockley et al., 2005).

By the Late Jurassic, aridity in the GLCA area decreased as the North American continent continued to move north. The Morrison Formation paleoecosystem is interpreted as a semiarid savannah. Fossils from the Morrison Formation documented in GLCA include dinosaur bones, a sauropod manus track, and termite nests (Lockley et al., 1998; Engelmann, 1999; Engelmann et al., 2004; Hasiotis, 2004).

The Morrison Formation is capped by a more than 40 million year-long disconformity. Deposition did not resume until about 100 Ma, when the shallow Western Interior Seaway (a.k.a. the Cretaceous Interior Seaway) began to transgress into the central United States. The Naturita Formation (previously the Dakota Formation in Utah and western Colorado, although the Dakota Formation is still a distinct unit in central Colorado) signals the onset of several Cretaceous transgressive and regressive cycles (Gustason, 1989; Aubrey, 1991; Ulicny, 1999). The Seaway extended from the Arctic to the Gulf of Mexico in a general northwest–southeast direction (Kirkland, 1990, 1996; Aubrey, 1991; Miller et al., 1991; Elder and Kirkland, 1993, 1994; Graham, 2006), bisecting North America into Appalachia to the east and Laramidia to the west (Lemon, 1993).

The Naturita Formation is an Upper Cretaceous geologic unit within GLCA and across much of the southern Colorado Plateau. The lower portion of the Naturita Formation is characterized by river channels and floodplain deposits. The upper portion consists of coastal plain deposits, representing estuarine, lagoonal, and swamp paleoenvironments. Fossils from the Naturita Formation within GLCA include chlorophyte algae, fern spores, and pollen from conifers and angiosperms, petrified wood, bivalves, ammonites, gastropods, shark teeth, actinopterygian fish teeth, and turtles (Peterson, 1969).

After depositing the Naturita Formation, the Western Interior Seaway transgressed at GLCA only once more during the Cretaceous, so it consequently has only one dominant Upper Cretaceous marine unit, the Tropic Shale, deposited during the greatest transgression of the Seaway (Albright et al., 2007a), about 94 Ma. A wide variety of fossils have been reported from the Tropic Shale in GLCA, although only the marine vertebrates have received detailed study. Invertebrates and microfossils include foraminiferans, corals, brachiopods, bivalves, ammonites, belemnites, gastropods, scaphopods, and serpulids (Peterson, 1969, 1973; Peterson and Barnum, 1973; Elder, 1987). Vertebrates include sharks, rays, actinopterygian fishes, marine turtles, plesiosaurs, and mosasaurs (Albright et al., 2001, 2006, 2007a, b, 2013; Polcyn et al., 2023). Three marine reptile species have been named from the Tropic Shale of GLCA: the plesiosaurs *Eopolycotylus rankini* (Albright et al. 2007a, b) and *Dolichorhynchops tropicensis* (McKean, 2012; now *Scalamagnus tropicensis* (Clark et al., 2023)) and the mosasaur *Sarabosaurus dahli* (Polcyn et al., 2023).

Following deposition of the Tropic Shale, the shallow sea regressed, and marine shales were replaced in GLCA by beach and coastal plain deposits of the Straight Cliffs Formation (Peterson, 1969; Anderson et al., 2010). The Seaway fully retreated from the GLCA area during the last phases of the Sevier Orogeny about 71 Ma, prior to the regional unconformity that developed between the Sevier and Laramide orogenies (Cather, 2003; Roberts, 2005; Roberts et al., 2005). The Upper Cretaceous Straight Cliffs Formation marks the end of the Mesozoic at GLCA. Fossils from the Straight Cliffs Formation in GLCA include palm leaves, bivalves, ammonites, gastropods, shark teeth, and invertebrate burrows (Peterson, 1969).

Upper Cretaceous strata in GLCA are overlain unconformably by Pleistocene deposits. An important Quaternary fossil record is present in GLCA, often preserved in caves, rock shelters, and alcoves, and includes a variety of fossil vertebrates, invertebrates, plants, trace fossils, and packrat middens (Martin and Sharrock, 1964; Haynes et al., 1966; Davis et al., 1984, 1985; Mead et al., 1984, 1986, 1992; Davis, 1987, 1990, 2003; Betancourt, 1990; Agenbroad and Mead, 1988, 1989, 1990a, 1990b; Mead and Agenbroad, 1988, 1989, 1992; Agenbroad et al., 1989; Elias et al., 1992; Santucci et al., 2001; Davis and Shafer, 2006; Kropf et al., 2007; Tweet et al., 2009; Santucci and Kirkland, 2010).

PHOTOGRAMMETRY

Three-dimensional, high-quality photogrammetric models

were created for many tracksites and individual specimens from GLCA to enhance mapping and to improve ichnomorphological assessments of tracks and other traces. Structure-from-motion (SfM) photogrammetry was used following Matthews (2008), Mallison and Wings (2011), Matthews et al. (2016), and Wood et al. (2021).

Images were processed with the photogrammetry package PhotoScan (now known as MetaShape) v. 1.2.6 build 2834 by AGIsoft, LLC. Raw Nikon (.nef) images were pre-processed for color, exposure, vignetting, and spherical aberration in Adobe Bridge as a batch process. Lens distortion was corrected as part of the photograph alignment and sparse-cloud processing with PhotoScan. Models were internally scaled using a variety of control stick lengths calibrated to ± 0.1 mm. Calibration for these scales was completed by comparing the distances between the printed targets with an ASTM certified ruler.

Both high-definition digital cinematography and high-resolution digital photography are essential elements to the future of monitoring paleontological sites. Digital documentation provides data for historical side-by-side and overlay comparisons of high-quality images and real-time footage (Wood et al., 2021). The collected images and footage can be used to monitor natural or man-made changes to new and existing paleontological localities, including vandalism, theft, and erosion. Implementing digital technology is a vital and essential component for raising public awareness, minimizing resource impacts, and preserving paleontological resources.

GLCA PALEONTOLOGICAL GEODATABASE

The March 2023 field work was also part of a pilot test for field data collection as part of the development of a regional geospatial paleontological locality database by the NPS Intermountain Region (IMR). This ongoing project aims to build a new authoritative dataset for the management and provision of data, as appropriate, to support park staff, researchers, and to better provide an interpretive experience for visitors.

Currently, no standardization for paleontological resources information exists between park units, resulting in the collection of different types and amounts of information at varying levels of detail in multiple formats. Integrating and standardizing the existing data would provide a solid scientific foundation for park project compliance through predictive modelling and new insights into the distribution of paleontological resources, institutionalizing paleontological protection and management in the future.

The new relational, geospatial database is designed with both park management and future academic research in mind. Over three decades of GLCA park paleontological resource field documentation, research, and collection were compiled for more than 740 localities. Geodatabase layers include sites, surveys, and photo-points. Related tables hold information for site monitoring, collected specimens, and photo identification. The IMR envisions data will be amassed through collaborative collection between park units and will limit viewability by park unit and to those with permission to access the data.

INSTITUTIONAL ABBREVIATIONS

ACH-ICH, "Appleton Cabinet," Beneski Museum of Natural History (formerly Pratt Museum of Amherst College), Amherst, Massachusetts; **AMNH,** American Museum of Natural History, New York, New York; **CEUM**, Utah State University Eastern Prehistoric Museum, Price, Utah; **FMNH**, Field Museum of Natural History, Chicago, Illinois; **GLCA,** Glen Canyon National Recreation Area, Page, Arizona; **GSENM,** Grand Staircase-Escalante National Monument, Kanab, Utah; **MNA,** Museum of Northern Arizona, Flagstaff, Arizona; **SGDS**, St. George Dinosaur Discovery Site at Johnson Farm, St. George, Utah; **UCM,** University of Colorado at Boulder, Boulder, Colorado; **UMNH**, Natural History Museum of Utah, Salt Lake City, Utah.

PALEONTOLOGY

The sections below do not cover all of the geologic formations and their corresponding fossils discussed above. Instead, we only focus on the formations and localities (Table 1) we have examined since 2010 and that add to the known records.

Cutler Group

A single locality occurs in the Cutler Group at the northern end of Lake Powell near Hite, in Dark Canyon. This locality (Fig. 1A #2; GLCA_PalLoc_0098) has been known by the NPS for many years (since circa 1980), yet it never received much attention. It was referred to as a snake, but it is interpreted here as a mollusc grazing trace (Fig. 5).

Meniscate traces with a medial ridge within the lower Cutler beds of Utah have been referred to as *Scolicia* (Terrell, 1972). These trace fossils are known from tidal bar–tidal flat, mouth-bar, and shallow marine carbonate deposits of lower parts of the Cutler Group in which continental and marine strata intertongue (Jordan and Mountney, 2010; Oliver et al., 2023). This mollusc grazing trace (Fig. 5) would morphologically be classified as *Laminites*, but *Laminites* is a preservational variant of the ichnogenus *Scolicia* (Uchman, 1995). *Scolicia* traces are linked to spatangoid echinoids starting in the Mesozoic (Smith and Crimes, 1983), but prior to the Mesozoic, they were likely produced by molluscs with an extending siphon; such traces have been referred to as *Psammichnites* (Mángano et al., 2002). More recent workers have suggested that these post-Cambrian/pre-Mesozoic morphologies are more appropriately distinguished as *Olivellites* (Pazos and Gutiérrez, 2022).

Although our team has not yet visited this locality, the block containing the specimen likely fell from a unit within the undifferentiated lower Cutler beds, which are Late Pennsylvanian to Early Permian in age. Photogrammetry, replication, and/or recovery of this unique trace fossil should be considered.

Chinle Formation

Several new paleontological localities have been identified in the under-explored Chinle Formation exposures within the areas of the San Juan Arm, Good Hope Bay, and away from Lake Powell within the northwestern portion of GLCA. Below are some of the results from our preliminary explorations.

Neskahi Wash area

The basal member of the Chinle Formation, the Shinarump Conglomerate, preserves a diverse flora several miles up the San Juan River in the Neskahi Wash area (Fig. 1A #10; GLCA # pending). Similar to other plant localities in the lower Chinle Formation around the Colorado Plateau (e.g., Holt, 1947; Stewart et al., 1972; Ash, 1975, 2001, 2014), most of the plant fossils here are represented by bennettitalean leaf morphotypes, such as cf. *Zamites* (Fig. 6A–B), a second morphotype with much narrower leaflets (Fig. 6C–D), equisetalean stems segments and shoots (cf. *Neocalamites*; Fig. 6E–H), and silicified conifer logs (Fig. 6I). The plant specimens were found in close proximity to invertebrate and vertebrate trace fossils.

The invertebrate trace fossils from the Shinarump Member resemble *Oravaichnium* and *Scoyenia*, although suboptimal preservation prevents more accurate diagnosis. These trace fossils, the first reported from the Shinarump Member, comprise smooth, continuous ridges (Fig. 7A) similar to *Oravaichnium*, an ichnogenus that is produced by wedge-foot bivalves (Uchman et al., 2011; Naimi and Cherif, 2021). The second trace fossil morphology has faint meniscate textures (upper left of Fig. 7B), which resemble the outer toponomy of thick, regularly spaced backfills of *Taenidium*, but the right side (Fig. 7B) appears to have faint, offset, meniscate backfills that would suggest that

TABLE 1. List of taxa and ichnotaxa known from GLCA ordered by rock formations. We have only included geologic formations discussed within the paleontology section of this paper, greatly reducing the list.

Cutler Group
cf. *Psammichnites* (this paper)

Stenichnus isp. (Lockley and Madsen, 1993; Lockley et al., 1998)
cf. *Anomalopus* or *Chelichnus* (Lockley and Madsen, 1993; Lockley et al., 1998)

Platyhystrix sp. (Santucci and Kirkland, 2010)

Moenkopi Formation
cf. *Kouphichnium* (Lockley et al., 1998)
cf. *Rhynchosauroides* isp. (Lockley et al., 1998)

Chinle Formation
cf. *Scoyenia* (this paper)
cf. *Oravaichnium* sp. (this paper)
Camborygma isp. (Hasiotis, 1992)

Atreipus isp. (Lockley et al., 1998)
Rhynchosauroides isp. (Lockley et al., 1998)
cf. *Gwyneddichnium* (this paper)
Grallator isp. (Lockley et al., 1998)
Brachychirotherium isp. (this paper)
Batrachopus isp.

Unionidae
Gastropoda
Conchostraca

Lophionotus sanjuanensis (this paper)
Lophionotus sp. (this paper)
Semionotidae (this paper)
Lasalichthys stewarti (this paper)
Lasalichthys sp. (this paper)
Redfieldiidae (this paper)
Mawsoniidae (this paper)

Metoposauridae
Phytosauria (this paper)
Indet. Pseudosuchia (this paper)

cf. *Neocalamites* sp. (this paper)
Equisetales (this paper)
Bennettitales morphotypes A and B (this paper)

Wingate Sandstone
Brachychirotherium isp. (this paper)
Evazoum gatewayensis (this paper)
cf. *Evazoum* (this paper)
Grallator isp. (Lockley et al., 1998)
Eubrontes isp. (Wood et al., 2021; this paper)
cf. *Kayentapus* isp. (Wood et al., 2021; this paper)

Kayenta Formation
Undichna cf. *simplicitas* (this paper)
Grallator isp. (Lockley et al., 1998, 2014; this paper)
Eubrontes isp. (Lockley et al., 1998, 2014; this paper)
Anomoepus isp. (Lockley et al., 1998, 2014; this paper)
Moyenisauropus isp. (Lockley et al., 1998, 2014; this paper)
cf. *Kayentapus* (this paper)
cf. *Otozoum* (Lockley et al., 2014)
Batrachopus isp. (Lockley et al., 1998, 2014; this paper)
cf. *Rhynchosauroides* (this paper)
cf. *Brasilichnium* (Lockley et al., 2014; this paper)
cf. *Ameghinichnus* (this paper)
Characichnos tridactylus (Lockley et al., 2014; this paper)
Characichnos isp. (Lockley et al., 2014; this paper)
Synapsid tracks indet. (Lockley et al., 2014; this paper)

cf. *Kayentatherium* (Milner et al., 2023a; this paper)

Navajo Sandstone
Taenidium cf. *barretti* (Milner et al., 2023b)
Palaeophycus isp. (this paper)
cf. *Octopodichnus* (this paper)
?*Paleohelcura* isp. (this paper)

Eubrontes isp. (Lockley et al., 1998, 2014; Xing and Lockley, 2015; Milner et al., 2023b; Bennett et al., 2023; this paper)
Kayentapus isp. (Milner et al., 2023a)
Grallator isp. (Lockley et al., 1998, 2014; Milner et al., 2023a; this paper)
Anomoepus isp. (Lockley et al., 1998, 2014; this paper)
Moyenisauropus isp. (this paper)
Navahopus isp. (this paper)
Otozoum isp. (Lockley et al., 1998, 2014; this paper)
Batrachopus isp. (Milner et al., 2023a; this paper)
Brasilichnium isp. (Lockley et al., 1998, 2014; this paper)
Synapsid tracks indet. (Lockley et al., 2014; this paper)

Unionidae (Lockley et al., 2014)

this trace is more attributable to *Scoyenia* (Smith et al., 2008).

The Shinarump Member more broadly preserves few trace fossils. The only previously recorded trace fossils from the unit were vertebrate tracks from two sites in southwestern Utah (Lockley and Milner, 2006). One of these, in Washington County, preserves large swim tracks, probably produced by phytosaurs. The other report is of purported tridactyl traces on a pebble conglomerate surface, but the veracity of this report is dubious.

A single, small track slab preserves the first vertebrate tracks from the Shinarump Member at GLCA (Fig. 8A; GLCA 25204/UCM 98261). They may pertain to the ichnogenus *Gwyneddichnium* based on its larger plantar surface and a posterolateral digit V trace (H. Klein, personal commun., 2024). *Gwyneddichnium* is thought to have been made by tanystropheid archosauromorphs (Lockley, 2006; Lucas et al., 2014; Klein and Lucas, 2021). *Gwyneddichnium* is better known from the Upper Triassic Newark Supergroup in eastern North America, from the post-Shinarump Chinle Formation of Utah, Colorado, and New Mexico, and from the Middle Triassic of Germany (Klein and Lucas, 2021).



FIGURE 5. Mollusc trace from the lower Cutler beds of Glen Canyon National Recreation Area (locality # GLCA_PalLoc_0098). Scale = 5 cm.

North Wash area

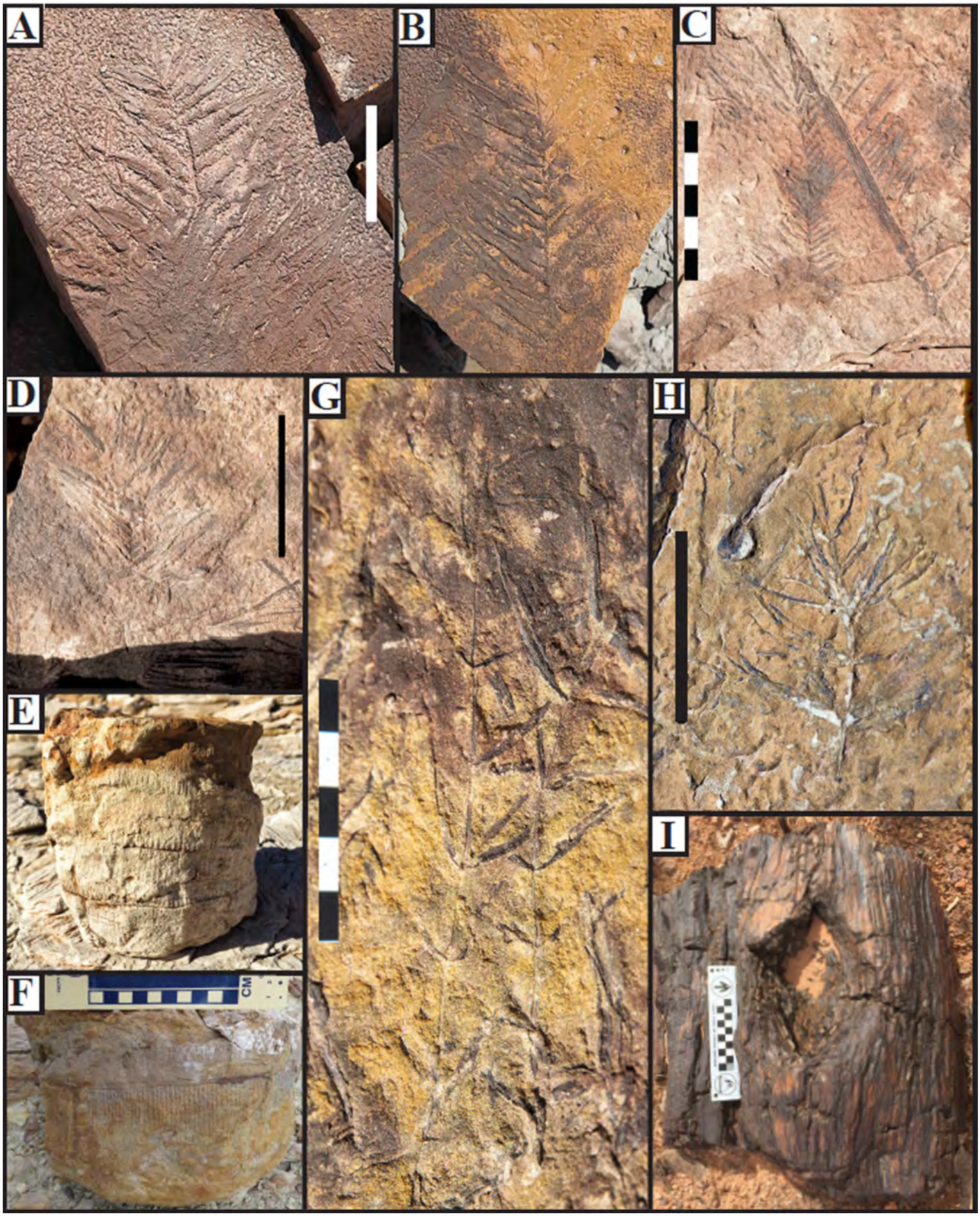
A single specimen of the semionotiform fish *Lophionotus sanjuanensis* (Fig. 9A; GLCA 26055/CEUM 83850; Gibson, 2013a) was found in 2021 by park visitor Kirk Warner in the Church Rock Member of the Chinle Formation. The locality is along North Wash, northwest of Hite (Fig. 1A #1; GLCA_PalLoc_0097). The specimen preserves the fish in right lateral view, but the majority of elements are covered by an iron-rich mineralization that makes observing diagnostic features difficult. However, the specimen has the prominent 'postcranial hump' unique to *L. sanjuanensis*, as opposed to *L. chinleana* and *L. kanabensis* (Gibson, 2013b).

Good Hope Bay area

The Church Rock Member of the Chinle Formation in the area surrounding Good Hope Bay is quite fossiliferous, preserving vertebrate trace fossils and body fossils (Fig. 1A #4). The trace fossils include a manus-pes set of *Brachychirotherium* tracks preserved as natural casts on a surface of mudcracks (Fig. 8C; not collected), and a second slab of cross-cutting *Batrachopus* trackways (Fig. 8D–E; GLCA 26061/UMNH VP 29838). All of the fossils from the area are ex situ and associated in float with archosauromorph bones (see below). Viewing fossils in situ would be extremely challenging and dangerous because of the steep, slippery surfaces presented by outcrops in this region, and rockfalls of the upper Church Rock Member are not uncommon. However, further exploration, mostly on talus slopes and in rockfalls, will doubtlessly yield many important specimens.

Brachychirotherium is only known from Upper Triassic units globally, and *Batrachopus* is more common in Lower Jurassic strata, especially in the Glen Canyon Group of the southwestern United States (Klein and Lucas, 2021). Both ichnogenera are thought to have been made by pseudosuchian archosaurs, but *Batrachopus* is generally much smaller and was likely made by crocodylomorphs (Olsen and Padian, 1986; Klein and Lucas, 2010). Two tridactyl tracks that may have been produced by a theropod were found in the same region by one of us (A. Delgalvis; Fig. 8B; not collected). These footprints differ

FIGURE 6 (facing page). Late Triassic fossil plants from Glen Canyon National Recreation Area, Utah. All are from the Shinarump Conglomerate Member of the Chinle Formation. **A**–**B,** Bennettitales (cf. *Zamites*) morphotype A; **C**–**D,** Bennettitales morphotype B; **E**–**F,** cf. *Neocalamites*, horsetail stem section. **E** is approximately 20 cm in diameter (locality # GLCA_PalLoc_0066); **G,** Equisetalean stalks with leaves preserved; **H,** Equisetalean terminal shoot; **I,** Petrified log section with knot preserved. GLCA locality numbers pending for **A–D** and **G–I**. Scales: **A–D**, **G–H** = 5 cm.


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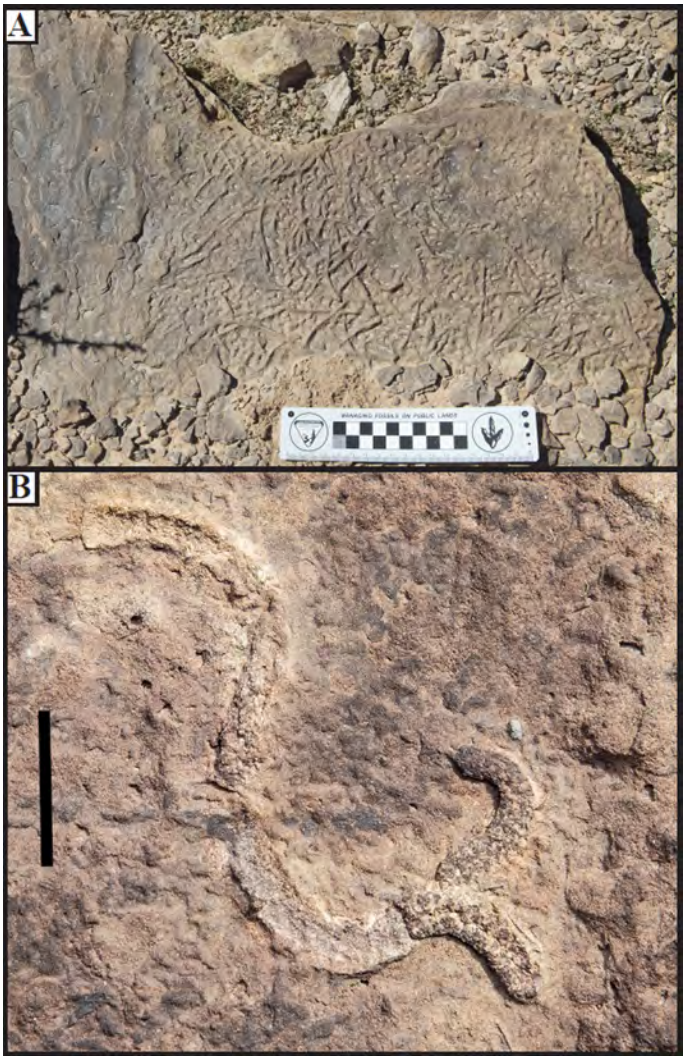


FIGURE 7. Invertebrate traces associated with fossil plants from the Shinarump Member of the Chinle Formation in Glen Canyon National Recreation Area (GLCA locality # pending). **A,** cf. *Oravaichnium* isp.; **B,** cf. *Scoyenia*. Scale = 2 cm.

markedly from other tridactyl tracks, such as *Grallator* and *Atreipus*, both of which are known from the Chinle Formation in GLCA (Lockley et al., 1998). These footprints could be extramorphological variants of one of these ichnotaxa, but they require a closer look.

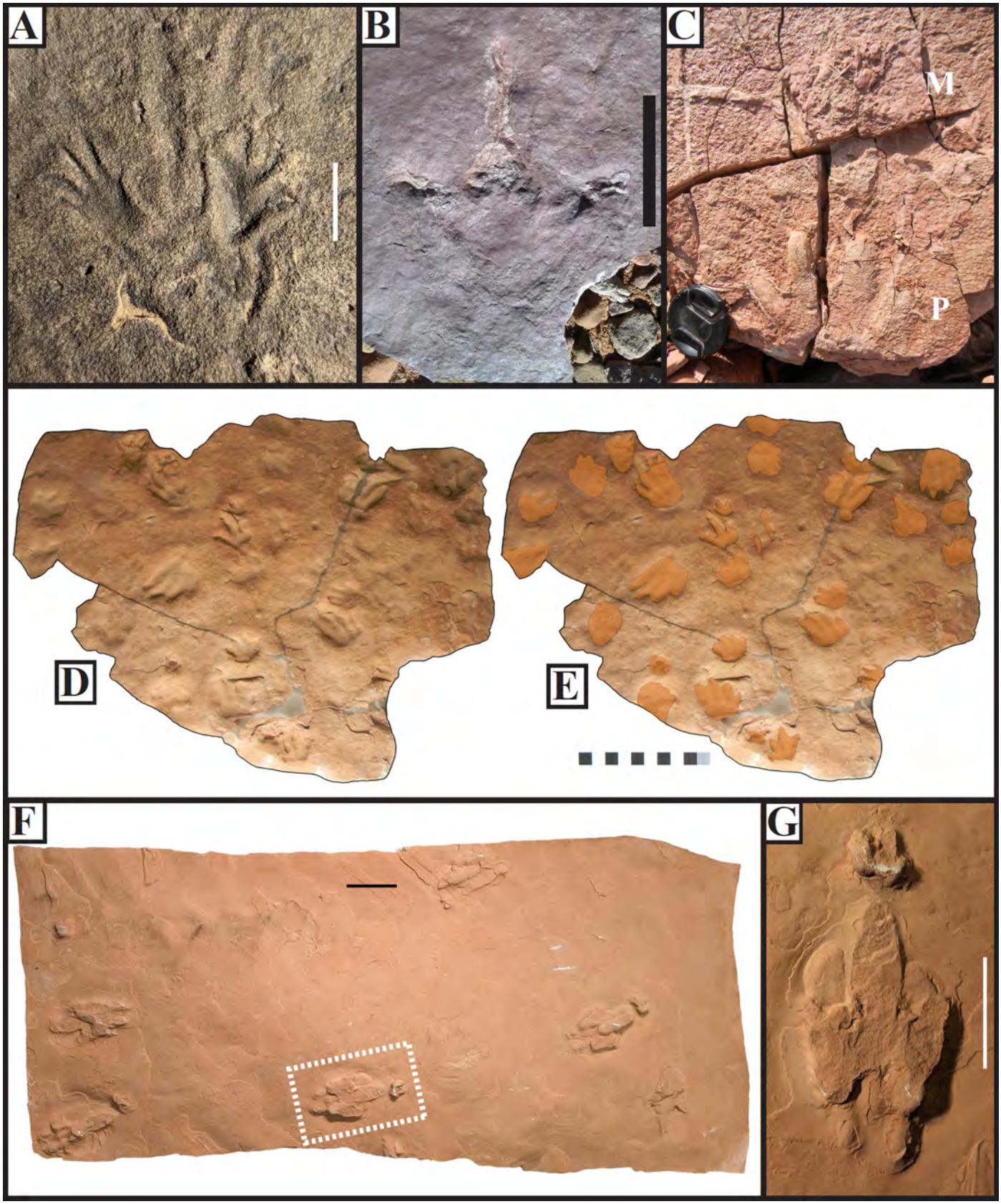
Vertebrate body fossils associated with the aforementioned tracks at Good Hope Bay likely are all phytosaur remains because phytosaurs seem to be particularly common in the Church Rock Member (Martz et al., 2014, 2017). The most diagnostic bone is a right scapulocoracoid found at locality # GLCA_PalLoc_0074, which is preserved in lateral view, partially obscured by sandstone matrix (Fig. 10A; not collected). This can be positively identified as being from a phytosaur by its laterally-projecting glenoid, the straight ventral margin of the scapular blade, and the anterior hook of the coracoid (Sereno, 1991; Nesbitt, 2011). Other potential phytosaur elements include a left partial hemipelvis preserving the proximal portion of a pubis and some of the ischium (Fig. 8B; GLCA 26060/UMNH VP 28687), a partial caudal vertebra (Fig. 10C; GLCA 26062/UMNH VP 29839), and many isolated teeth that were observed but not collected (Fig.10D).

One large slab from the Church Rock Member at Good Hope Bay preserves at least three taxa of fishes (Fig. 9B; GLCA 26057/UMNH VP 28684), including the semionotiform *Lophionotus*, the redfieldiiform *Lasalichthys*, and a ?mawsoniid coelacanth. Two specimens of *Lophionotus* cf. *L. sanjuanensis* (Fig. 9C–D) preserve the "postcranial hump" characteristic of that species (Gibson, 2013b). One preserves a partial skull, which may be important to better identify that individual. The two redfieldiiform individuals (Fig. 9E–F) lie immediately adjacent to one another on the slab and may pertain to the genus *Lasalichthys*, a taxon found in the Upper Triassic of western Texas and Utah (Schaeffer, 1967; Gibson, 2018). The coelacanth fossils in the slab include fin rays associated with one of the redfieldiiforms (Fig. 9E). An isolated coelacanth pelvic bone found in the area (Fig. 9G; GLCA 26059/UMNH VP 28686) has two anterior apophyses connected by a thin web of bone, a broad posterior lobe, and the broken base of a dorsal prong, closely resembling that of the mawsoniid genus *Diplurus* from both Upper Triassic–Lower Jurassic of the Newark Supergroup (Schaeffer, 1948, 1952). Also found nearby was an isolated specimen of *Lasalichthys* cf. *L. stewarti* (Fig. 7H; not collected) found on a float block. *Lasalichthys stewarti* as a new combination was first proposed and described from specimens in the upper part of the Chinle Formation at Lisbon Valley, San Juan County, Utah (Gibson, 2018).

Four Mile Canyon area

Lockley et al. (1992, fig. 2) first documented manus and pes tracks and trackways attributed to the ichnogenus *Atreipus* (Fig. 8F–G; GLCA 23068, UCM 167.15) from the Church Rock Member of the Chinle Formation in Four Mile Canyon (Fig. 1A #3; GLCA_PalLoc_0152). Several slabs were collected in 1992 along with closely associated *Rhynchosauroides* tracks (Lockley et al., 1998). These *Atreipus* tracks were the first of the ichnogenus to be reported from the southwestern United States (Lockley et al., 1992, 1998, 2014; Lockley and Hunt, 1995). This ichnogenus has now also been reported in the American Southwest from the Rock Point Member of the Chinle Formation near Moab, Utah (Lucas et al., 2006; Foster and Lockley, 2019). (Note that the latter authors referred to the uppermost unit in the Chinle Formation of the Moab area as the Rock Point Member, but the UGS and others such as Martz et al., (2014, 2017) prefer to refer to these correlative strata as the Church Rock Member.) *Atreipus* was first thought to have been made by ornithischian dinosaurs (Olsen and Baird, 1986), an attribution rendered problematic by the absence of unambiguous body fossils of Triassic ornithischians in North America (Parker et al., 2005; Irmis et al., 2007; Nesbitt et al., 2007), depending on whether or not silesaurids are considered early-diverging ornithischians (*sensu* Norman et al., 2022; q.v., Klein and Lucas, 2021). These tracks generally are thought to have been made by early diverging dinosaurs and/or non-dinosaurian dinosauromorphs (see discussion in Klein and Lucas, 2021).

FIGURE 8 (facing page). Tetrapod tracks from the Chinle Formation within Glen Canyon National Recreation Area, Utah. **A,** Close-up of cf. *Gwyneddichnium* from the Shinarump Member (GLCA 25204, UCM 98261; locality # GLCA_PalLoc_0066); **B,** Indeterminate tridactyl tracks from the Good Hope Bay area (not collected; GLCA locality # pending); **C,** *Brachychirotherium* from the Church Rock Member (M = manus; P = pes) (not collected; locality # GLCA_PalLoc_0075); **D–E,** *Batrachopus*, float slab from uppermost Church Rock Member (GLCA 26061, UMNH VP 29838; locality # GLCA_PalLoc_0075); (**D**) photo, and (**E**) map of slab with dark orange outlined tracks; **F–G,** *Atreipus* slab (GLCA 23068-1b, UCM 167.16; locality # GLCA_PalLoc_0152); **F,** Photo of entire slab with white dash box shown in **G**. Scale: **A** = 1 cm; **B, G** = 5 cm; **D–F** = 10 cm.


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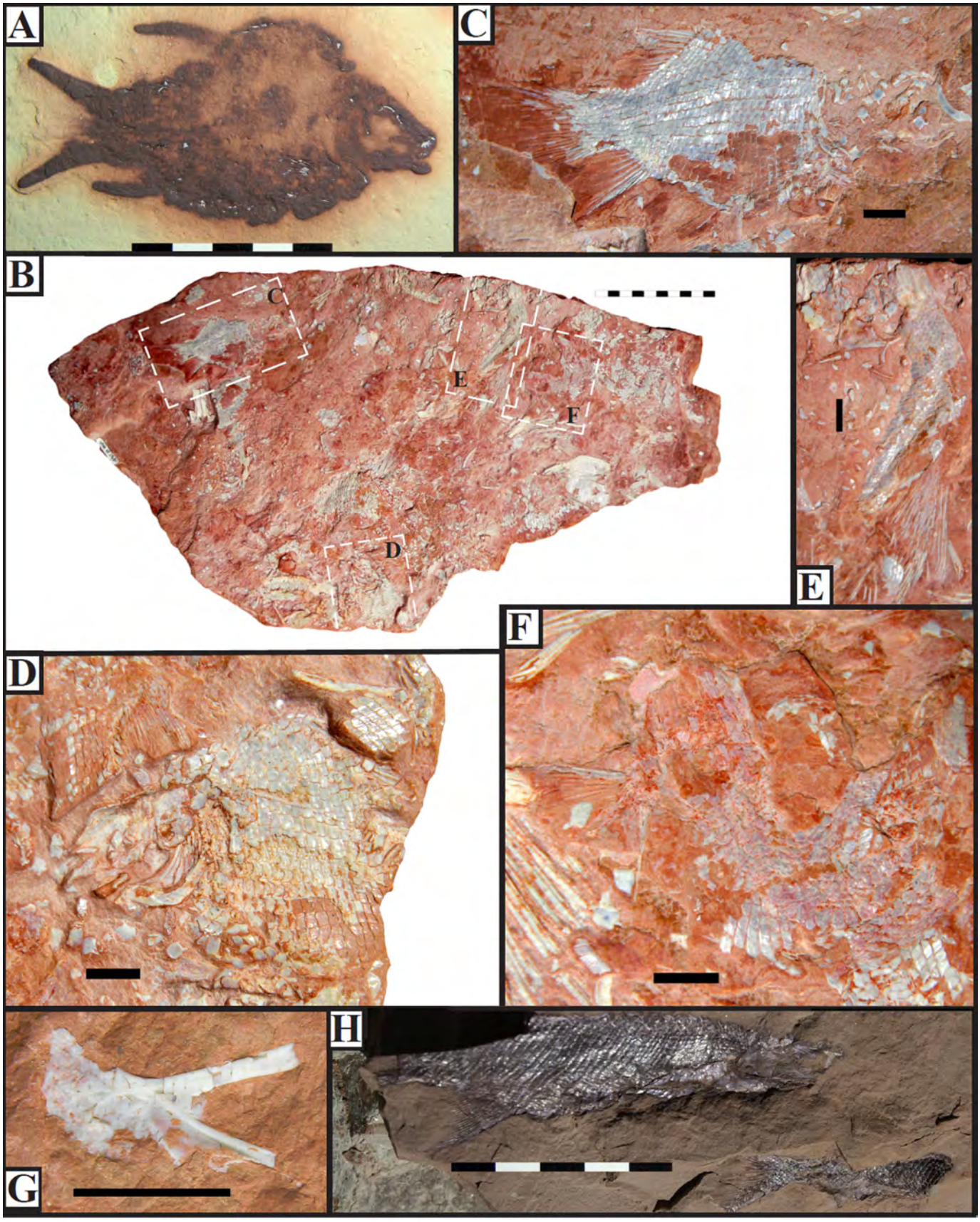

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FIGURE 9 (facing page). Fish fossils from the Church Rock Member, Chinle Formation in Glen Canyon National Recreation Area. **A,** *Lophionotus sanjuanensis* (GLCA 26055, CEUM 83850; locality # GLCA_PalLoc_0097), Grand County, Utah. Discovered by Kirk Warner in 2021; **B,** Large fish slab containing *Lophionotus*, cf. *Lasalichthys*, unidentified redfieldiids, and ?mawsoniid coelacanths (GLCA 26057, UMNH VP 28684). White dash boxes indicate enlarged photos (**C–F**); **C,** *Lophionotus* cf. *sanjuanensis* nearly complete with disarticulated skull; **D,** Articulated, partial *Lophionotus* cf. *sanjuanensis*; **E,** Nearly complete cf. *Lasalichthys* in dorsal view. Larger, elongate bones near the caudal region are coelacanth fin rays; **F,** cf. *Lasalichthys* skeleton in dorsal view and curved toward the right. Coelacanth fin rays to bottom left; **G,** Coelacanth (Mawsoniidae) pelvic bone (GLCA 26059, UMNH VP 28686). **H,** *Lasalichthys stewarti* (not collected). **B-H** comes from locality # GLCA_PalLoc_0073. Scales: **A, H** = 5 cm; **B** = 10 cm; **C–G** = 1 = 1 cm.

Glen Canyon Group —Wingate Sandstone

Pinnacle Rock Area

All of the fossils recorded to date from the Wingate Sandstone in GLCA are vertebrate tracks and unpublished invertebrate traces. *Grallator* (Fig. 11A–B) and *Brachychirotherium* (Fig. 11C, E) are known from the lower part of the Wingate Sandstone, but here we report the first occurrence of *Evazoum gatewayensis* from GLCA (Fig. 11D; see Lockley et al., 2006, 2022b for comparison) and a second *Evazoum* form with more robust digit traces (Fig. 11E). All of the ichnotaxa listed here are only known from the Pinnacle Rock area along the San Juan Arm (Fig. 1A #9), except for *Grallator*, which occurs in many areas within GLCA where the Wingate Sandstone is exposed (Lockley et al., 1998).

The majority of tracks from the cliff-forming Wingate Sandstone occur ex situ on fallen blocks. Observations of in situ tracks usually take place in the lowermost Wingate Sandstone, close to or at the contact with the underlying Chinle Formation, usually on the undersides of overhanging ledges. Tracks from the lower Wingate Sandstone are typical Upper Triassic ichnotaxa, including *Brachychirotherium*, *Evazoum*, *Atreipus*, and *Eosauropus* (Lockley et al., 2011, 2022b; Hunt-Foster et al., 2016). *Grallator* and *Batrachopus* have also been reported from the lower Wingate, although both ichnotaxa also occur in the Lower Jurassic (Lockley et al., 2018, 2022a).

Little Cave Cove Tracksite

Sites have also been recorded from near the top of the Wingate Sandstone outside of GLCA, all of which preserve typical Lower Jurassic ichnotaxa such as *Eubrontes*, *Anomoepus*, and *Otozoum* (Lockley et al., 2004, 2022b; Lockley and Gierliński, 2006). This indicates that the Triassic–Jurassic transition and end-Triassic extinction boundaries occur within the Wingate Sandstone, but pinning down their exact positions has been practically impossible because the unit crops out in sheer, vertical cliffs lacking good exposures of in situ track-bearing surfaces. However, a discovery in March 2017 by one of us (A. Delgalvis) of a giant fallen block in the Good Hope Bay area called the Little Cave Cove Tracksite (LCCT; Fig. 12; Fig. 1A #4; locality # GLCA_PalLoc_0078; Wood et al., 2021, fig. 4) may be helpful. This 11 m tall block potentially can be correlated with similar microbially laminated horizons near the middle of the Wingate Sandstone as seen in the in situ cliff adjacent to a massive, slumped section from the cliff face (Fig. 12A). As with many other Wingate localities, accessing

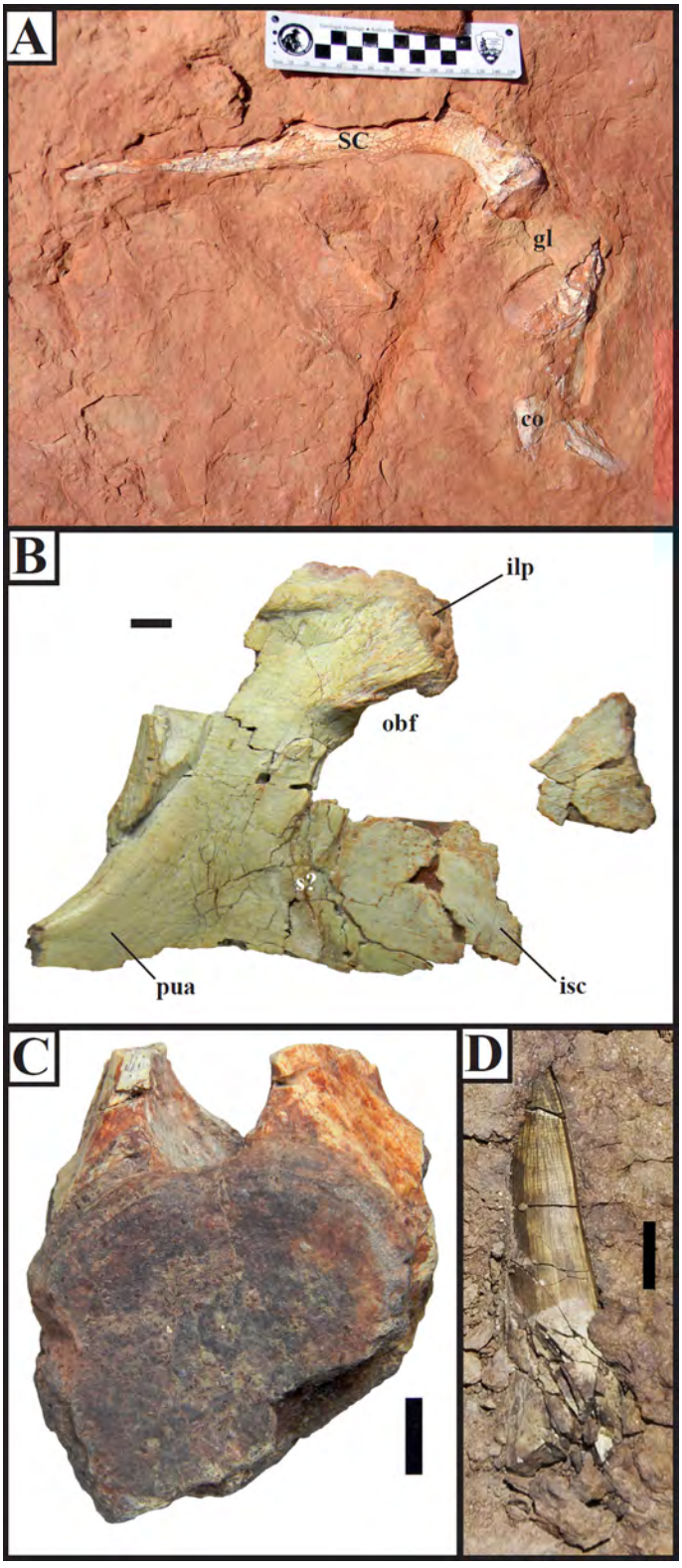


FIGURE 10. Tetrapods from the Church Rock Member, Chinle Formation in the Good Hope Bay area, Glen Canyon National Recreation Area. **A,** Large phytosaur scapulocoracoid (not collected; locality # GLCA_PalLoc_0074); **B,** Pseudosuchian pelvic bones (GLCA 26060, UMNH VP 28687; locality # GLCA_PalLoc_0075); **C,** Phytosaur partial centrum (GLCA 26062, UMNH VP 29839; locality # GLCA_PalLoc_0077); **D,** Large phytosaur tooth (not collected; GLCA_PalLoc_0073). Scales for **B–D** = 1 cm. Abbreviations: co, coracoid; gl, glenoid; ilp, iliac pedicle of pubis; isc, ischium; obf, obturator foramen; pua, pubic apron; s?, possible suture between pubis and ischium; sc, scapula.

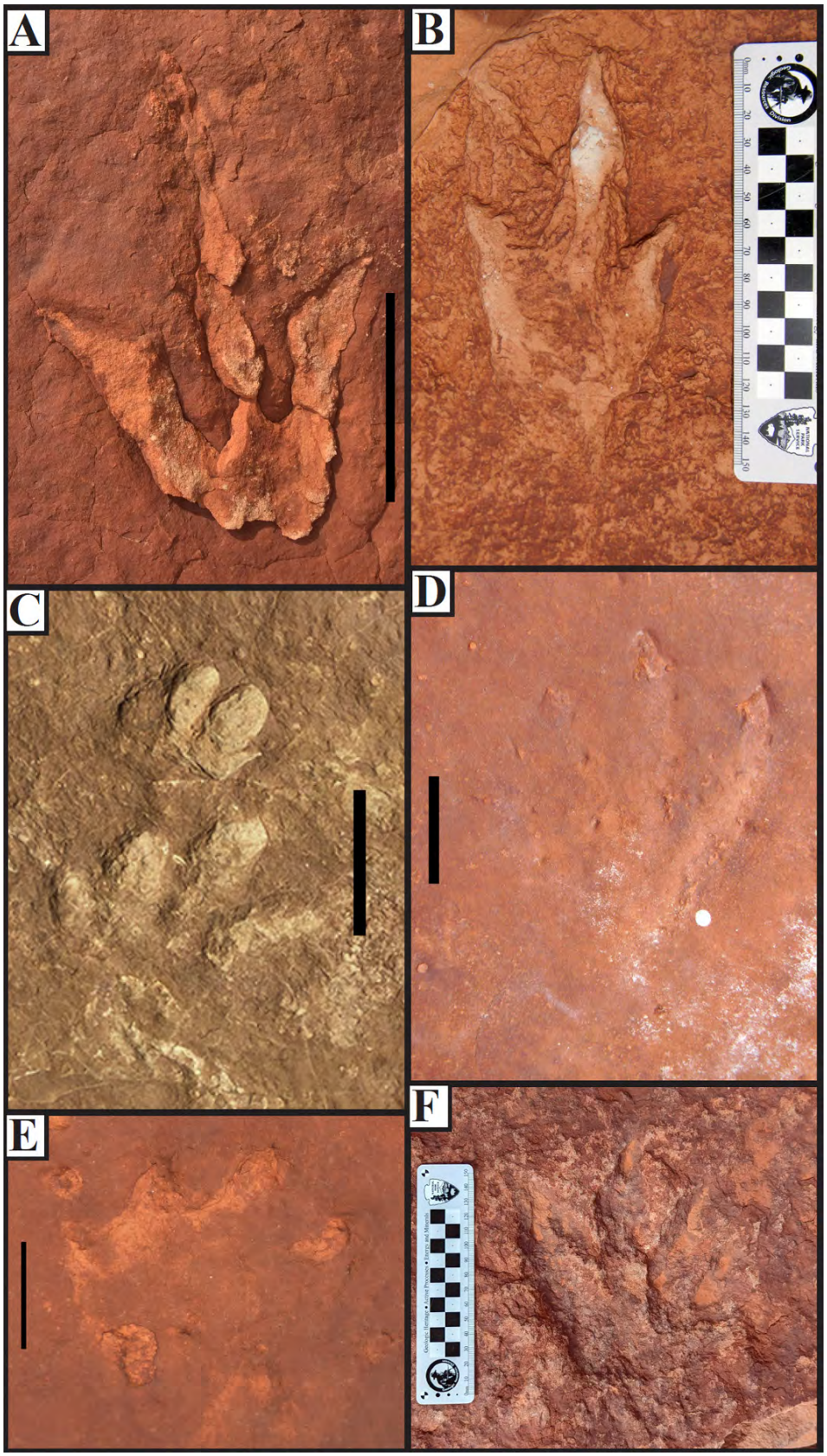


FIGURE 11. Typical vertebrate tracks from the Upper Triassic of the lower Wingate Sandstone, Glen Canyon National Recreation Area. All tracks except for **C** come from the Pinnacle Rock area along the San Juan Arm, San Juan County, Utah (locality # GLCA_PalLoc_0067). **A,** *Grallator* right track mold; **B,** *Grallator* left track natural cast; **C,** *Brachychirotherium* left manus-pes set preserved as natural casts from Good Hope Bay region (photo by A. Delgalvis; locality # GLCA_PalLoc_0234); **D,** *Evazoum gatewayensis* right track mold; **E,** cf. *Brachychirotherium* right pes track mold; **F,** cf. *Evazoum* right track natural cast. Scale: **A, D, E** = 5 cm; **C** = 2 cm.

this locality is extremely dangerous. Very large blocks can move underfoot on and around this rockfall/slump.

The LCCT part and counterpart blocks preserve numerous tracks, all attributed to theropod dinosaurs, including *Eubrontes*, *Kayentapus*, *Grallator*, and cf. *Characichnos* (Fig. 12; Wood et al., 2021). Wood et al. (2021) reported the track surfaces to contain 102 natural cast tracks in 13 identifiable trackways, but our recent reexamination of the photogrammetric data reveals the presence of 111 tracks in 15 trackways. Several of the LCCT trackways preserve interesting and different behavioral traits. *Eubrontes* trackways T1 and T2 appear to preserve elongate heel (metatarsal) imprints, and all tracks in the trackway toe inward, with foot-falls being more than 1 m apart. Trackways T3 and T4 are similar in all aspects, except the metatarsal traces are shorter. Two *Kayentapus* trackways, T6 and T7, also toe inward dramatically and have steps just over 1 m apart. Trackways T14 and T15 do not possess heel traces, nor did they toe inward, and their steps are separated by slightly more than 1 m. Trackways T8 and T9 are similar to T6 and T7 in pace and stride and by toeing inward, but are morphologically unusual, almost reminiscent of theropod swim traces (cf. *Characichnos*; for discussions on swim traces see Whyte and Romano, 2001; Milner et al., 2006b; Milner and Lockley, 2016) except that all tracks in T8 and all but one in T9 possess only digit III traces (the sixth track in T9 preserves two digit traces). Finally, a long *Grallator* trackway (T10) preserves 23 footprints in a somewhat meandering trackway. This spectacular tracksite will be described in greater detail elsewhere.

Based on the presence of the characteristically Early Jurassic ichnotaxa *Eubrontes* and *Kayentapus* on the LCCT, the Triassic–Jurassic boundary can be estimated to lie within the lower half of the Wingate Sandstone (Fig. 12A).

"Sandy Facies" of the Kayenta Formation and the Kayenta–Navajo Transition'

Resting on the Wingate Sandstone in GLCA is the 'sandy facies' of the Kayenta Formation, in which tracks are extremely abundant and have been recorded at many localities (Lockley et al., 1998, 2014). The Kayenta Formation and Kayenta–Navajo transition sequence comprises fluvial sandstones, siltstones, minor conglomerates, laminated carbonate beds made up of microbial mats, and thin chert beds deposited in small lakes and playas. Across the American Southwest, theropod tracks dominate the Early Jurassic landscape, greatly outnumbering ornithischian, sauropodomorph, and other vertebrate tracks at most sites. The sheer abundance of tracks preserved within this thin Kayenta/Kayenta–Navajo transition sequence is striking, especially in areas #5–8 (Fig. 1A). Clearly, this region was rich with life during the Early Jurassic.

Associated with this diverse vertebrate ichnofauna is an equally amazing diversity of invertebrate traces, mostly burrows and grazing trails. Very little attention has been paid to the invertebrate ichnofaunas from GLCA, but future fieldwork will include a greater effort to identify and interpret these traces and the paleoenvironments on a more localized scale. To date, we have identified *Palaeophycus* (Fig. 13A, C), *Skolithos* (Fig. 13B), and a variety of unidentified invertebrate burrows (Fig. 13D) from lacustrine/playa facies. *Palaeophycus* and *Skolithos* more broadly occur in a wide variety of environments, from lacustrine to floodplain to wet interdune (Buatois and Mángano, 1995). *Palaeophycus* in the Dinosaur Canyon Member of the Moenave Formation, which underlies the Kayenta Formation in southwestern Utah and northwestern Arizona, have been attributed to insect (wasp, cricket) tracemakers (Tanner et al., 2006). *Palaeophycus* and *Skolithos* in the overlying Navajo Sandstone have similarly been attributed to arthropod tracemakers (Riese et al., 2011). These shallow-burrowing insect tracemakers were abundant in the interdune environments of the Navajo Sandstone (Loope and Rowe, 2003) or associated with pluvial intervals (Ekdale et al., 2007). *Skolithos* has been previously reported from floodplain settings in the Kayenta Formation (Difley and Ekdale, 2006).

Theropod tracks dominate the Kayenta Formation, Kayenta–Navajo transition, and Navajo Sandstone at GLCA. By far the most common footprints are those of *Grallator* (Fig. 14A–F), followed by *Eubrontes* (Fig. 14G–M), and *Kayentapus* (Fig. 14N).

Lockley's Cove

One area of GLCA that Lockley et al. (2014) studied extensively is now referred to as Lockley's Cove (Fig. 1A #6). Many localities exist here around the Kayenta–Navajo transition and in the lowermost Navajo Sandstone. Several in situ tracksites have been documented, one of which (the Slick George Tracksite, locality # GLCA_PalLoc_0054) was chosen as the prototype paleontological monitoring locality at GLCA (discussed above, Fig. 4). Theropod tracks, dominated by *Grallator*, occur in abundance in the Lockley's Cove area; *Eubrontes* is less common (Fig. 12M), and many ornithischian tracks (*Anomoepus* and cf. *Moyenisauropus*) also occur (discussed briefly below). Additionally, Lockley et al. (2014) reported poorly preserved *Otozoum*, but we have not observed any sauropodomorph footprints to date in either the Kayenta Formation or the Kayenta–Navajo transition. Surely sauropodomorph tracks should exist from GLCA within these units (Galton, 1971; Sertich and Loewen, 2010), but none have been adequately documented at this time. Sauropodomorph tracks are well-documented from GLCA in the Navajo Sandstone on both interdune and dune faces (see Navajo Sandstone section below for further discussion). Additionally, Lockley et al. (2014, fig. 7) reported and figured the first occurrence of body fossils from these strata within GLCA in the form of unionid bivalve coquinas preserved as steinkerns (also photographed by Delgalvis, 2015, p. 147).

An impressive natural cast track slab from the Lockley's Cove area (Fig. 15) preserves large *Eubrontes*, *Grallator*, and a single, intermediate-sized *Kayentapus*-like theropod track at a site to the north of Slick Rock Canyon (Fig. 1A #6; locality # GLCA_PalLoc_0266). This near-vertical block was originally published by Lockley et al. (2014, fig. 4A–C), who attributed the footprints to *Grallator* and *Eubrontes*. We note here that one of the tracks (Fig. 15F) resembles *Kayentapus*.

Since Lake Powell was filled, this track slab has been at or close to the waterline most of the time for the past 50+ years (Fig. 15A–B). However, in March 2023, following the 2022 drought, the NPS-SGDS team visited the site when it was high above the lake level (Fig. 15C). Martin Lockley mapped this block by hand during one of his many expeditions to GLCA in the 1990s (Fig. 15B; photo date uncertain), creating the map published in Lockley et al. (2014, fig. 4C), which is modified herein (Fig. 15D).

In 2023, one of us (J. Wood) collected photogrammetric data from this track slab (Fig. 15C), producing an accurate, high-resolution model (Fig. 15E). Here we compare our photogrammetric model and new block map (Fig. 15F) with the hand-drawn map produced by Lockley et al. (2014). Comparisons between the two maps reveal that two theropod tracks Lockley had figured are not visible in the photogrammetry (indicated by blue dashed circles in Fig. 15D, F). Possibly the smaller of the two tracks have eroded away over time, while the larger track could also have been partially eroded, or potentially misinterpreted. At this latter location in the photogrammetry, we observed an elongate structure that may represent digit III on the Lockley et al. map, but we cannot discern a clear footprint. Likewise, our photogrammetry reveals four additional tracks that were overlooked in Lockley et al. (2014) (identified by red

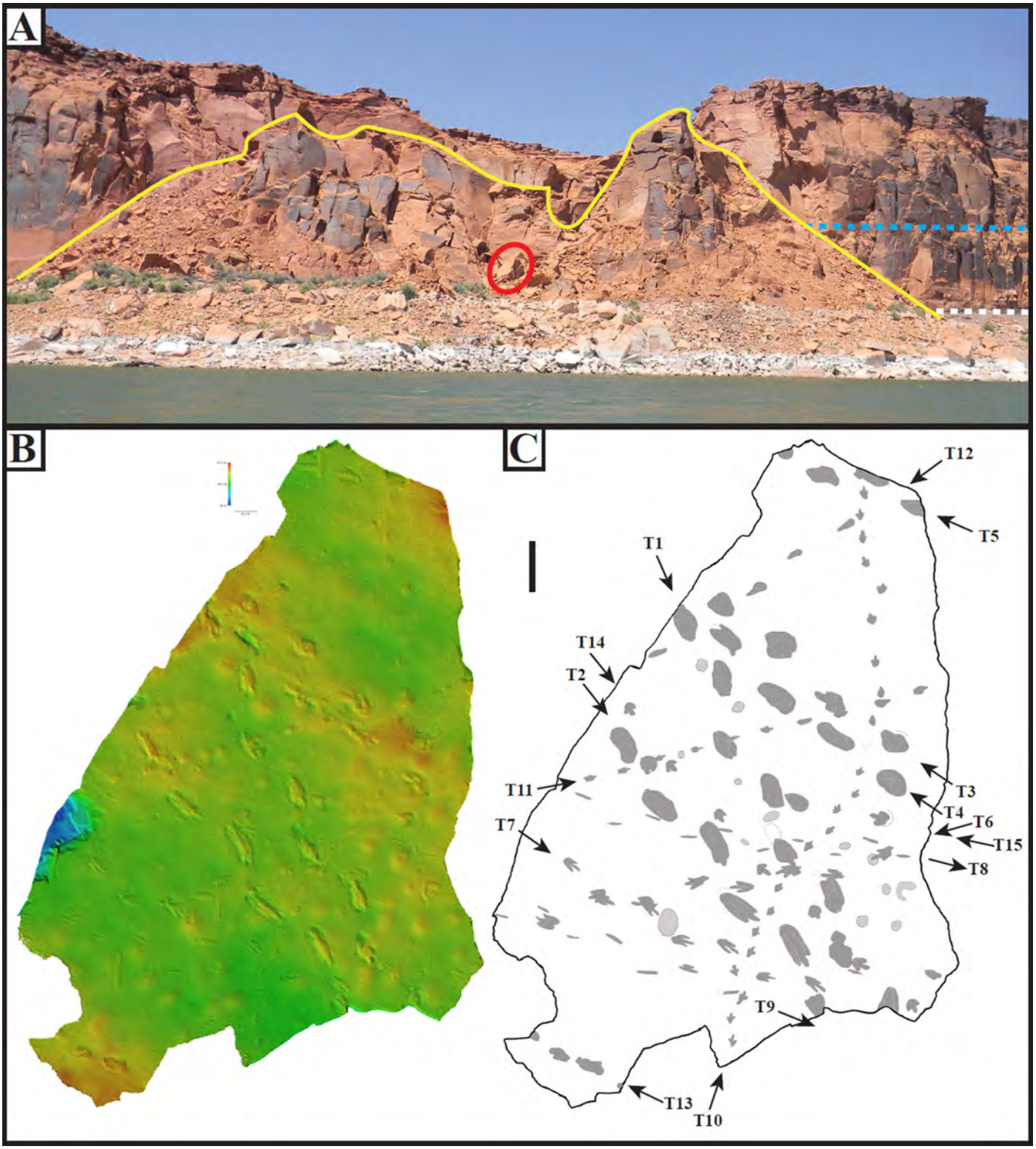


FIGURE 12. The Little Cave Cove Tracksite (LCCT) discovered by A. Delgalvis in March 2017 in Glen Canyon National Recreation Area (GLCA_PalLoc_0078). Track types are typical of an Early Jurassic ichnofauna. **A,** Slumped cliff face can be correlated with the cliff behind. Microbial laminations on the side of the part and counterpart blocks may correlate with similar facies preserved *in situ* in cliff, placing the possible tracks origin in the middle part of the Wingate Sandstone. This indicates that the Triassic–Jurassic boundary is within the lower half of the Wingate Sandstone. Red circle = LCCT; blue dash line = approximate location of block origin within in situ cliff; yellow line = top of slumped cliff and associated debris; white dash line = Chinle Formation–Wingate Sandstone contact; **B,** Photogrammetric contour image of LCCT block; **C**, Map of tracks and trackways showing orientations of all 15 identified trackways. **B–C** scale = 1 m.

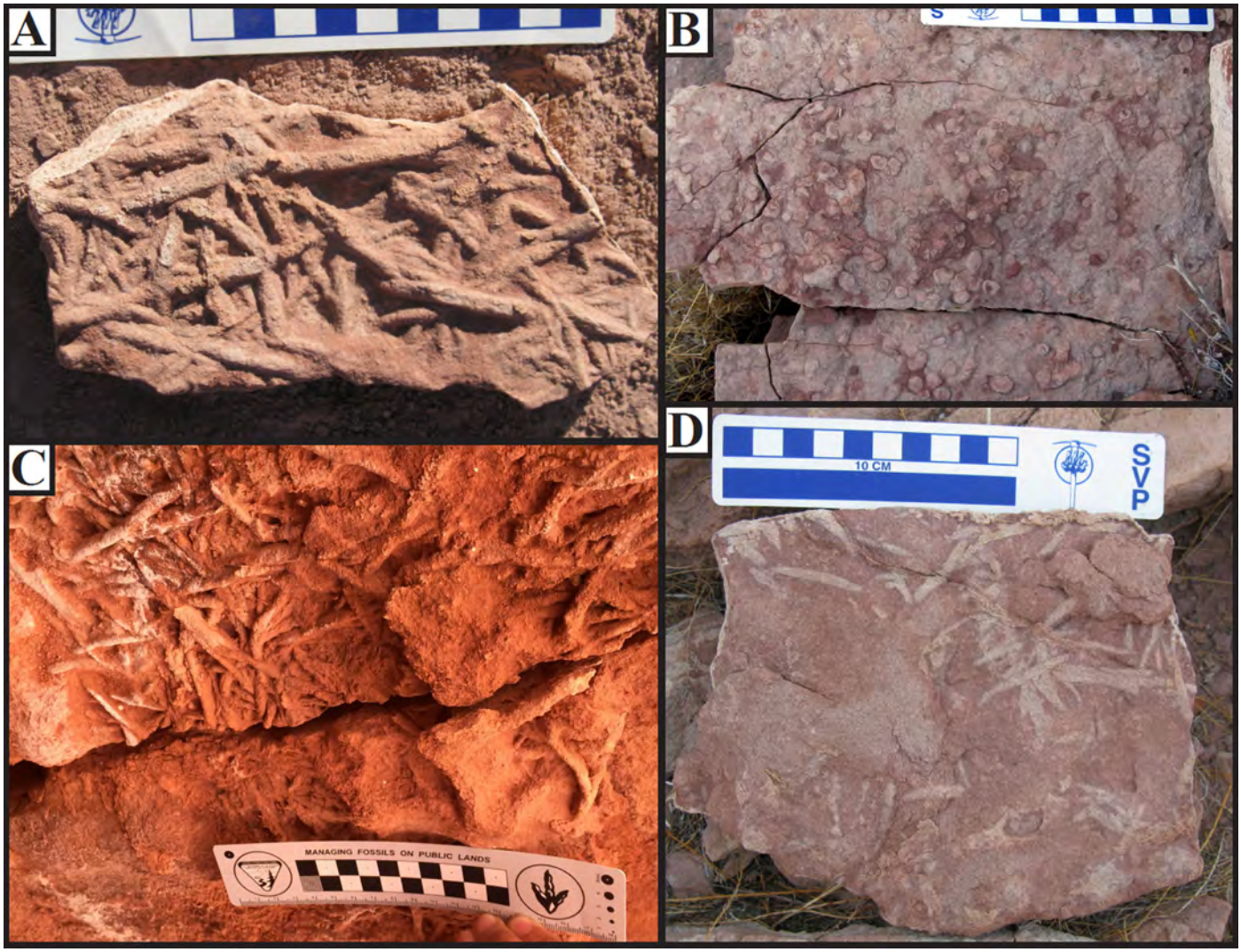


FIGURE 13. Examples of invertebrate traces from the Kayenta Formation and Navajo Sandstone in Glen Canyon National Recreation Area. **A,** *Palaeophycus* from thick sequence of Kayenta facies within the Kayenta–Navajo Transition at Lockley's Cove (locality # GLCA_PalLoc_0054); **B,** *Skolithos* from Kayenta Formation facies at Lockley's Cove area (locality # GLCA_PalLoc_0052); **C,** Example of *Palaeophycus* on the underside of an in situ ledge near Andre's Alcove North site (locality # GLCA_PalLoc_0088) in the lower Navajo Sandstone along the interface of interdune lacustrine and overlying dune series; **D,** Unidentified traces from Kayenta–Navajo Transition in the vicinity of Lockley's Cove (locality # GLCA_PalLoc_0052).

dashed circles in Fig. 15D and F). Two *Eubrontes* tracks were recognized in our photogrammetry, along with a cluster of three *Grallator*-like tracks, where Lockley et al. had only mapped a single track. Finally, one of the larger tracks in the upper right corner is accompanied by an elongate, tapering groove that may represent a claw or tail drag trace (Fig. 15F).

The site discussed above is a fine example of the power of photogrammetry and computerized, 3D models for detailed study away from the field. Not only do these 3D models help identify features that may not be visible in natural light, but they can also be used to take accurate measurements of tracks and other features, and to see how sites change over time (Wood et al., 2021).

Mega Site (aka Killer Bees Site)

Important tracksites in the Kayenta Formation occur in abundance near the mouth of Escalante Canyon and the confluence of the Escalante River with the Colorado River (Lockley et al., 2014). The Mega Site (aka the Killer Bees Site by the SGDS team; Fig. 1A #7, locality # GLCA_PalLoc_0072) preserves a high diversity of vertebrate traces, many of which are preserved in situ on several stratigraphic horizons. Theropod tracks include abundant *Grallator* with less frequent *Eubrontes* (Fig. 14I–K). A fairly large, in situ surface covered in small quadruped trackways is associated with small theropod tracks (cf. *Grallator*). This site was first reported by Lockley et al. (2014, fig. 13) and all of the quadruped tracks were identified as *Batrachopus*. We discuss these quadruped tracks in the synapsid tracks section below.

Another interesting in situ surface has an abundance of dinosaur swim tracks identified as *Characichnos tridactylus* Whyte and Romano 2001 by Lockley et al. (2014, fig. 16A–D). These swim traces were likely produced by *Grallator*-sized theropod dinosaurs. Another swim trace (Fig. 16D) found nearby consists of three digit traces measuring approximately 25 cm in length and was probably produced by the right foot of a theropod. The digit III trace is the longest, arcing to the right, while the digit II trace is short and medial to the nearly parallel digit III trace. The digit IV trace is oriented outward and situated subparallel to the posterior portion of the digit III trace. Sediment mounds occur along the posterior margins of digit traces III and IV. The entire surface is covered in *Skolithos*-

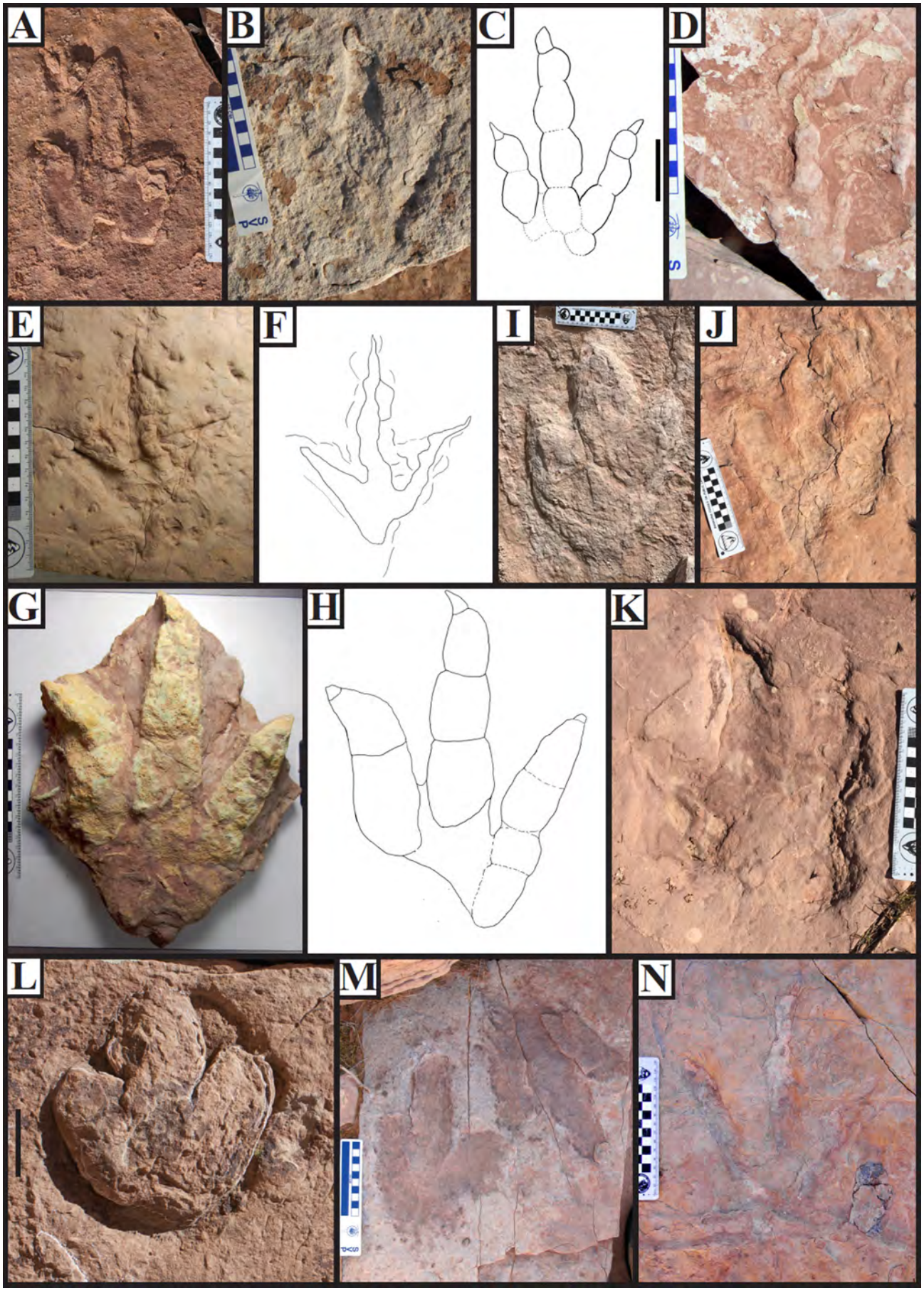

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FIGURE 14 (facing page). Theropod tracks from several localities in the Kayenta Formation, Glen Canyon National Recreation Area. **A,** Left *Grallator* from Tritylodont Cove area (locality # GLCA_PalLoc_0283); **B–C,** Right *Grallator* in situ at Slick George Tracksite at Lockley's Cove (locality # GLCA_PalLoc_0054); (**B**) photo and (**C**) interpretive sketch; **D,** Two natural cast *Grallator* from Anchor Cove (locality #GLCA_PalLoc_0094); **E-H,** *Grallator* mold (**E–F**) on one side of slab with natural cast *Eubrontes* (**G–H**) on the opposite side (GLCA 25456; locality # GLCA_PalLoc_0096); **I,** *Eubrontes* from Lockley's Cove area; **J-K,** Examples of *Eubrontes* extramorphological variation at the Killer Bees Site (locality # GLCA_PalLoc_0072); **L**, *Eubrontes* natural cast track with inflated digits from the John Wesley Powell Fossil Track Block (locality # GLCA_PalLoc_0001; track T1-6 from Milner et al., 2023b, fig. 12C); **M**, pair of shallow, naturally stained *Eubrontes* from Lockley's Cove area (locality # GLCA_PalLoc_0053); **N**, Large *Kayentapus*-like track (locality GLCA_PalLoc_0085). **L** scale = 10 cm.

like invertebrate burrows.

Lockley et al. (2014, fig. 16C) and Delgalvis (2015, p. 23) figured a very large swim trace from a site further to the north of the Killer Bees locality. This trace appears to have been produced by the right foot of a theropod, and only traces of digits III and IV were registered. Swim tracks have not been observed in such abundance anywhere else within the Kayenta and Kayenta–Navajo transition, although a single example was documented in the Lockley's Cove area further to the north (Fig. 16E–F). Dinosaur swim trace occurrences globally are discussed in detail elsewhere (Whyte and Romano, 2001; Milner et al., 2006b; Milner and Lockley, 2016).

The Killer Bees Site also preserves the first record of fish swim traces from the Early Jurassic in GLCA (Fig. 16G). This trace resembles *Undichna simplicitas* as described by Anderson (1976). Lockley et al. (2014) described this site in some detail, but our quick observations indicate that a return visit is in order. As our "Killer Bees Site" name for this locality implies, our only visit to it in September 2017 was cut short by the presence of a large swarm of Africanized honeybees congregated on a nearby bush, and we could not explore the outcrops properly.

Crouching Theropods and a Slipping Trace

Crouching traces (also called sitting or resting traces) of dinosaurs, especially those of theropods (Hitchcock, 1858; Lull, 1904, 1953; Gierliński, 1994, 1996; Lockley et al., 2003, 2014; Milàn et al., 2008; Gierliński et al., 2009; Milner et al., 2006a, 2009), are uncommon worldwide. In comparison, more examples are known of ornithischian crouching traces (*Anomoepus*) are far more common, but they have only been reported from the Newark Supergroup in eastern North America (Hitchcock, 1858; Lull, 1904; Olsen and Rainforth, 2003). To date, no *Anomoepus* crouching traces have been recorded in western North America.

The first crouching trace described from Lake Powell pertains to *Grallator* (Gierliński et al., 2009, fig. 2; Lockley et al., 2014; photos in Delgalvis, 2015, p. 11, 24, 60–63, 67) and was found by one of us (A. Delgalvis) near the confluence of the Escalante and Colorado rivers (Delgalvis Crouching Trace 1 site; Fig. 17A–C; Fig. 1A #7; locality # GLCA_PalLoc_0068). This asymmetrical trace had the right foot and metatarsal placed in advance of the left, and a small, circular ischial callosity is present. Digit I traces are present on both tracks. Our team acquired photogrammetric data of the entire slab for comparison with Gierliński et al. (2009) and Lockley et al. (2014), and we concur with their interpretations.

Here we report for the first time a new theropod crouching trace, the ninth known worldwide and the second from GLCA. This large crouching trace was found by one of us (A. Delgalvis) and is from the Delgalvis Crouching Trace 2 site (Fig. 1A #5; locality # GLCA_PalLoc_0084; Fig. 17D–E; Delgalvis, 2015, p. 64–65). It occurs in the upper part of the Kayenta–Navajo transition on a carbonate surface. This *Eubrontes* crouching trace preserves slightly asymmetrical left and right pes and metatarsal traces, both of which measure ~77 cm in total length. Both are oriented outward, with the left track slightly forward of the right. Anterior and medial to the pedal tracks are what may be manus traces. The left manus trace measures ~27 cm long and appears to be turned anteromedially at an angle of ~45° to the crouching trace midline, with two posteromedially oriented digit traces. The right manus is a poorly preserved, circular depression measuring about 24 cm long. Prior to this, the only positively identified manus traces preserved with a theropod crouching trace are SGDS 18.T1 from the Moenave Formation in southwestern Utah (Milner et al., 2009). Delgalvis Crouching Trace 2 will receive a more detailed description elsewhere. Many other theropod tracks were found near the Delgalvis Crouching Trace 2 site, including a large *Kayentapus* track (Fig. 14N).

Delgalvis (2015, p. 66) discovered what he thought was a third GLCA theropod crouching trace in the Owl Canyon area. However, our visit to the site in 2017 revealed that the photographed structures are actually mudcracks on the underside of a fallen block.

Another interesting trace, discovered by one of us (D. Slauf), is large theropod slip traces on a fallen block in the Lockley's Cove area (Fig. 1A #6; locality # GLCA_PalLoc_0272; Fig. 16H). At least three of these tridactyl traces have nearly parallel, equal-length digit traces; they resemble smaller *Grallator* slipping traces from the Moenave Formation at the SGDS (Milner et al., 2006a, fig. 15A).

Kayenta–Navajo Ornithischian Tracks

Ornithischian tracks are generally uncommon in the Lower Jurassic Glen Canyon Group. As mentioned earlier, theropod tracks greatly outnumber other tetrapod track types at most sites. However, *Anomoepus* tracks (Fig. 18A–H) are locally abundant at some sites in the Lockley's Cove area (Lockley et al., 2014). *Anomoepus* is suggested to have been produced by small, basal, thyreophoran dinosaurs, and *Scutellosaurus* is often used as an example (Colbert, 1981; Breeden and Rowe, 2020; Breeden et al., 2021).

Moyenisauropus tracks (Fig. 18I) are rare in the southwestern United States. The only examples mentioned by Lockley et al. (1998) and noticed by us occur at a couple of localities in the Lockley's Cove area. *Moyenisauropus* tracks are suggested to have been produced by more derived thyreophorans, such as *Scelidosaurus* (Gierliński, 1991).

Tritylodont Cove

One of the most significant recent discoveries at GLCA is a tritylodontid bonebed in the lowermost Navajo Sandstone found during a 2023 tracksite inventory near the confluence of the Colorado and San Juan Rivers (Fig. 1A #8; locality # GLCA_PalLoc_0257; Milner et al., 2023a). A second bonebed was found nearby in the upper Kayenta Formation (locality # GLCA_PalLoc_0718, and a laterally equivalent locality GLCA_PalLoc_0719) was found while measuring a stratigraphic section for the first site. The 6° local dip at the sites suggests that the bonebed in the Navajo Sandstone has likely been submerged since 1968 and was only subaerially exposed for a few months in the spring of 2023, during a historically low water level at Lake Powell. As reviewed above and elsewhere (e.g., Lockley et al., 1998, 2014; Milner et al., 2023b), these two Lower Jurassic formations are well-known in GLCA for their ichnofaunas.

The Navajo Sandstone bonebed is a stacked-sandstone, interdunal deposit less than 1 m in thickness (Fig. 19A). The

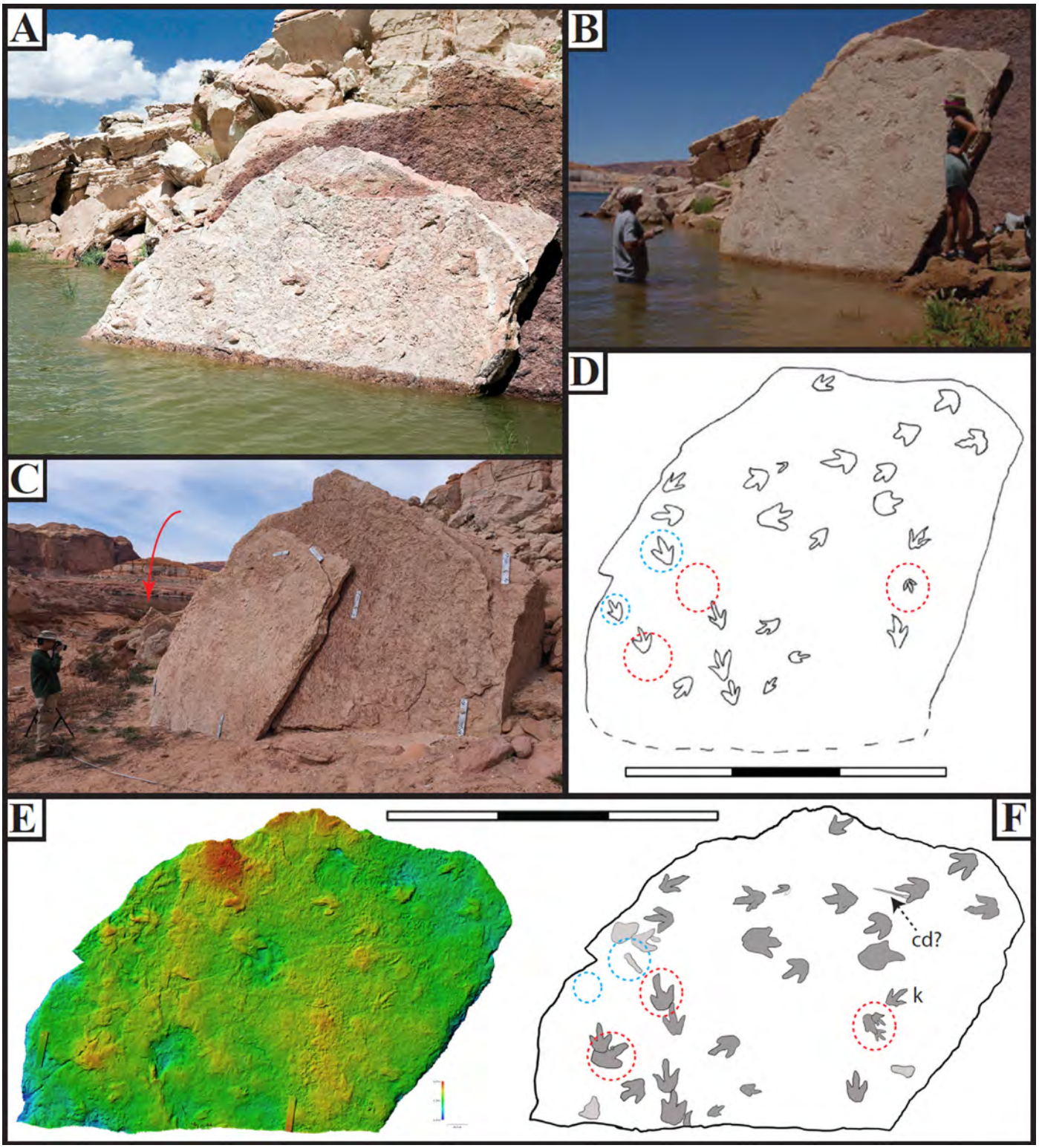


FIGURE 15. Track slab located near buoy 89, Lockley's Cove, north of the mouth of Slick Rock Canyon, Glen Canyon National Recreation Area (locality # GLCA_PalLoc_0266; Lockley et al., 2014, fig. 4A–C). **A,** Photo of slab half submerged on June 6, 2005 (photo credit, A. Delgalvis); **B,** Martin Lockley standing in water hand-mapping slab (unknown photographer and year, courtesy M. Lockley); **C,** Jack Wood taking photogrammetric images of slab in March 2023, Red arrow points to lake in distance due to record low lake levels; **D,** Lockley hand-drawn map with red and blue dash ovals showing discrepancies between it and the map below (modified from Lockley et al., 2014, fig. 4C) (**F**; **E–F,** Photogrammetric contour model (**E**) and map (**F**). Comparisons between **D** and **F**: Blue dash circles = tracks mapped by Lockley, but not recognized in our photogrammetry; and red dash circles = tracks visible in photogrammetry, but not recognized by Lockley. (**D**). Abbreviations: cd? = claw or tail drag trace?; "k" = *Kayentapus*-like track. Scale for **D–F** = 3 m.

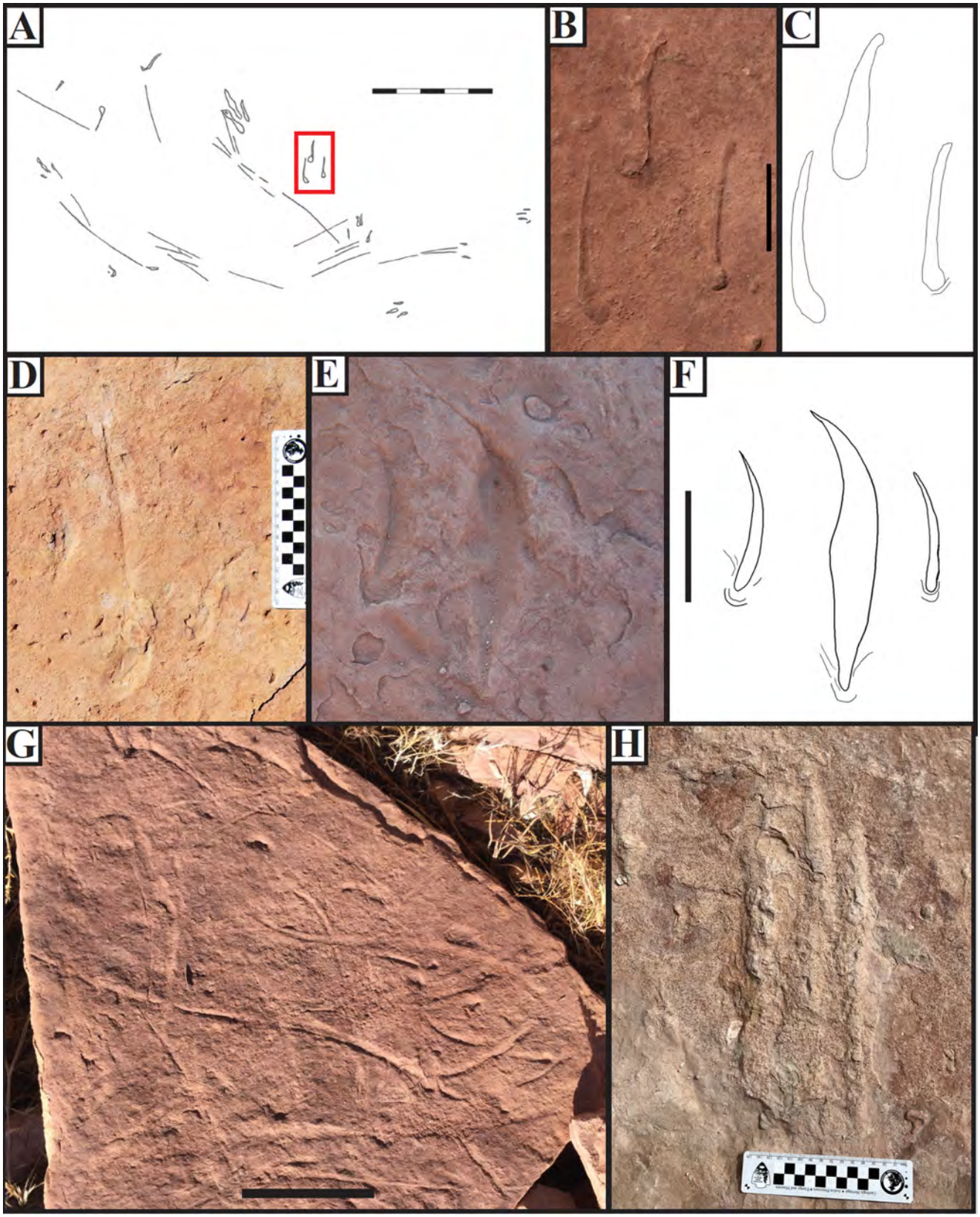


FIGURE 16. A variety of dinosaur swim traces, fish swim trails, and a large theropod "slip" trace from the Kayenta Formation, Glen Canyon National Recreation Area. **A**, Series of grallatorid swim traces identified as *Characichnos tridactylus* by Lockley et al. (1998, fig 14A; modified from this figure). Red rectangle shown in B-C; **B–C**, Close-up photo (**B**) and sketch (**C**) of tridactyl swim trace; **D,** Large tridactyl theropod swim trace with push-up rims along posterior margins (bottom of photo); **E–F,** Photo (**E**) and sketch (**F**) of small, tridactyl swim trace from Lockley's Cove area (locality # GLCA_PalLoc_0052); **G,** *Undichna* fish swim traces with possible dinosaur swim traces associated; and **H,** Large slipping theropod trace (locality # GLCA_PalLoc_0272). **A–D** and **G** all occur at the Killer Bees Site (locality # GLCA_PalLoc_0072). Scale: **A** = 50 cm; **B–C** and **E–G** = 5 cm.

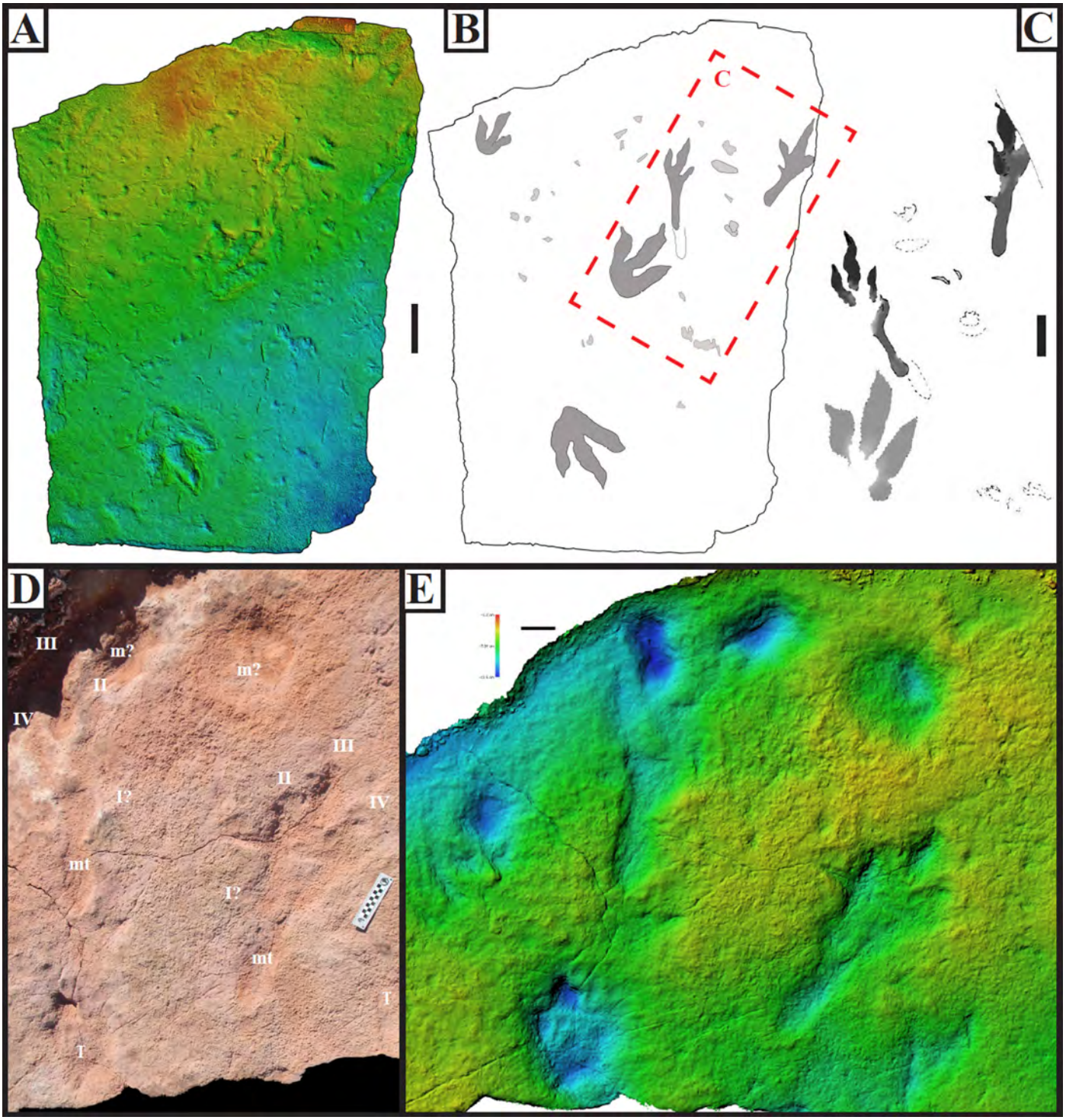


FIGURE 17. Theropod crouching traces from Glen Canyon National Recreation Area. **A–B,** Photogrammetric contour model (**A**) and interpretive sketch (**B**) of the Delgalvis Crouching Trace 1 (locality # GLCA_PalLoc_0068) in Kayenta Formation facies. Red dashed box in **B** shows position of **C**; **C,** Interpretation of *Grallator* crouching trace modified from Gierlinski et al. (2009, fig. 2); **D–E,** Delgalvis Crouching Trace 2 from a lacustrine interdune surface within the lowermost Navajo Sandstone (GLCA_PalLoc_0084). Photo showing positions of possible manus traces, and metatarsal and position of digits I–IV on left and right tracks (**D**), alongside photogrammetric contour model (**E**). Scales: **A–B** = 20 cm; **C, E** = 10 cm. Abbreviations: **I?**, possible digit I traces; **II**, digit II traces; **III**, digit III traces; **IV**, digit IV traces; **m?**, manus traces?; **mt**, metatarsals; **T**, other tracks.

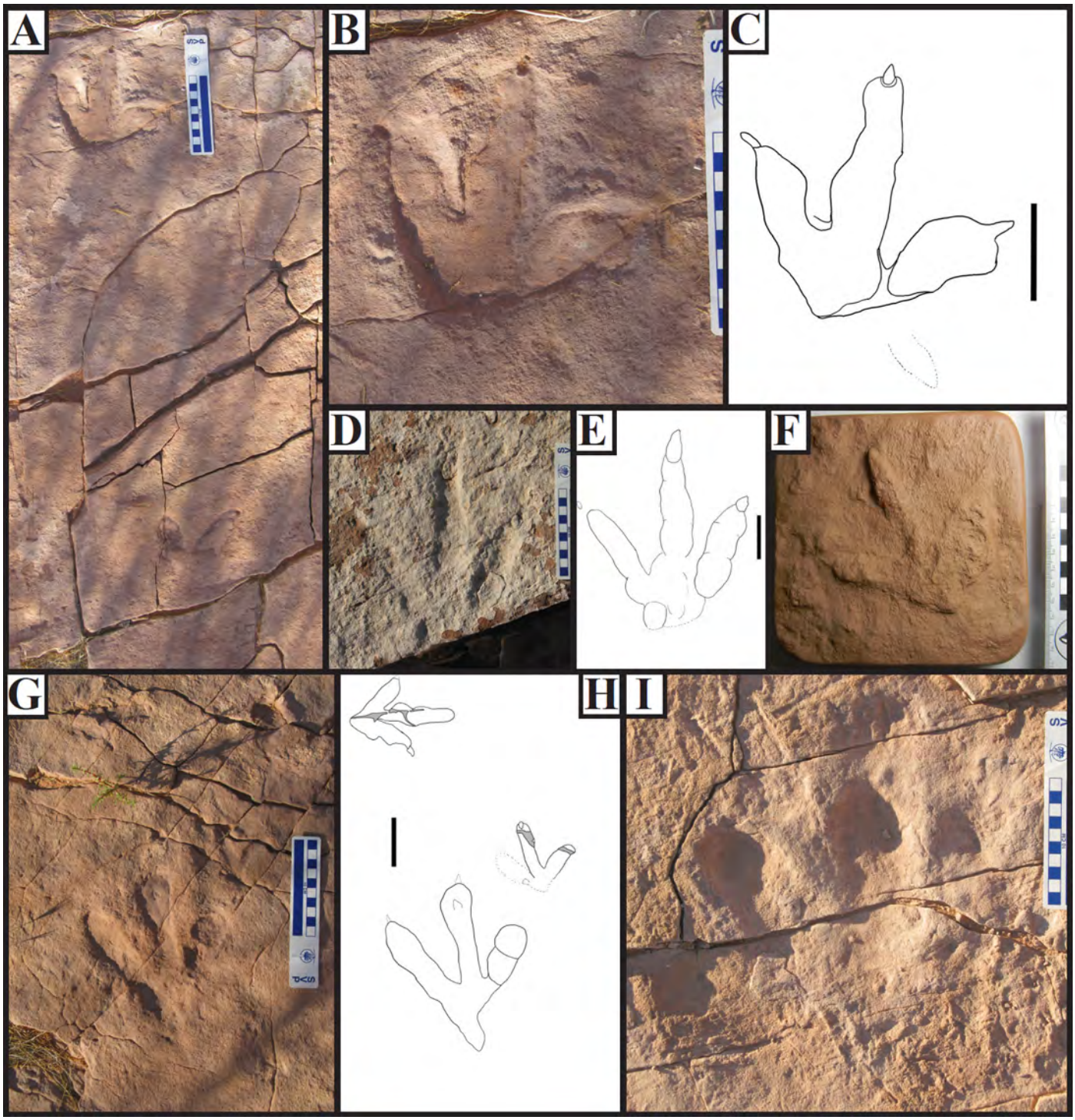


FIGURE 18. Ornithischian tracks from the Kayenta–Navajo Transition within Glen Canyon National Recreation Area. **A,** Two *Anomoepus* tracks in partial trackway at Lockley's Cove (locality # GLCA_PalLoc_0052); **B–C,** Close-up photo (**B**) and sketch (**C**) of second track in A (locality # GLCA_PalLoc_0052); **D–E,** Left *Anomoepus* photo (**D**) and sketch (**E**) from Lockley's Cove (locality # GLCA_PalLoc_0054); **F,** *Anomoepus* (SGDS 1749 replica) from interdunal lacustrine carbonate beds in Navajo Sandstone at Andre's Alcove Tracksite (locality # GLCA _PalLoc_0069). **G–H,** Left *Anomoepus* manus-pes set with *Grallator* associated in upper left corner, photo (**G**) and sketch (**H**). From Lockley's Cove (locality # GLCA_PalLoc_0052); **I,** *Moyenisauropus*-like tracks from Lockley's Cove (locality # GLCA_PalLoc_0052). Scale in **A,** **E**, and **H** = 5 cm.

exposed bones in the lower, friable sandstone were disintegrated and/or dissolved by subaqueous or shoreline conditions, leaving behind natural molds of disarticulated but associated dentaries, vertebrae, and long bones (Fig. 19C). Luckily, bones are abundant and relatively well-preserved within that sandstone unit; numerous blocks were collected, and CT scanning and mechanical preparation are ongoing. The upper part of the bonebed is a thicker sandstone with peculiar, concave-up sedimentary structures in cross-section that, when broken apart, revealed articulated tritylodontid skulls and skeletons (Fig. 19B). Preliminary work suggests that the tritylodontid body fossils from the Kayenta Formation and Navajo Sandstone at GLCA (Fig. 19D) closely resemble *Kayentatherium wellesi*, a taxon known from the Kayenta Formation in northern Arizona (Kermack, 1982; Sues and Jenkins, 2006; Hoffman and Rowe, 2018).

Vertebrate body fossils are rare in the Navajo Sandstone, which only preserves two named taxa, each known from a single specimen: the sauropodomorph *Seitaad ruessi* from southeastern Utah (Sertich and Loewen, 2010) and the coelophysoid *Segisaurus halli* from northern Arizona (Camp, 1936; Carrano et al., 2005). The only other body fossils from the Navajo Sandstone are fragmentary semionotiform fishes from GSENM in southern Utah (Frederickson and Davis, 2017), two indeterminate partial sauropodomorphs (Brady, 1935, 1936; Galton, 1971), three fragmentary protosuchid crocodyliforms (Galton, 1971; Rinehart et al., 2001; Lucas et al., 2005), and a single postcranial skeleton of a tritylodontid (Winkler et al., 1991), the latter six records all from northern Arizona.

The top surface of the same sandstone that preserves the tritylodont bonebed also preserves *Grallator* tracks and *Brasilichnium*-like tracks that may have been made by the tritylodontids themselves; the latter likely pertain to a new ichnotaxon. The same new ichnotaxon (Fig. 20) was observed previously in the Navajo–Kayenta transition upriver at a site found in 2017 called David's Camp 1 (Fig. 1A #6; locality # GLCA_PalLoc_0070) and was partially described and figured even earlier from specimens near the confluence of the Colorado and Escalante rivers (Lockley et al., 2014: fig. 15). *Grallator* and *Brasilichnium* are relatively common in the Navajo Sandstone (e.g., Rainforth, 1997; Irmis, 2005; Lockley et al., 1998, 2014), and the latter has long been hypothesized to have been made by tritylodontid and/or mammaliamorph cynodonts (Lockley, 2011). The associated tracks of the new ichnotaxon will be described and named in a later contribution.

Synapsid Tracks

As just mentioned, the David's Camp 1 locality preserves many tracks of a new ichnotaxon with some similarities to *Brasilichnium* (Fig. 20), but the tracks were registered on lacustrine/playa carbonate sandstones in the upper part of the Kayenta Formation rather than on the eolian dune faces where *Brasilichnium sensu stricto* occur. Lockley et al. (2014, fig. 15; Delgalvis, 2015, p. 58, 59, 109–113) described the tracks as pentadactyl, measuring 5–6 cm long and wide, and with the pes overprinting the manus in a very narrow trackway, steps of 30–35 cm, and track depths of 1–2 cm. They assigned these tracks to *Brasilichnium*. However, we consider these tracks to represent a new ichnotaxon. Lockley et al. (2014) only reported this single site, but our team has now recognized this track morphology at several sites in the Kayenta Formation, Kayenta–Navajo transition, and lowermost interdune carbonate units of the Navajo Sandstone, including examples in close association with tritylodontid bonebeds as mentioned above. Like Lockley et al. (2014), we attribute these tracks to tritylodontids.

We have recognized another synapsid track morphotype from the Kayenta Formation at two localities, the Killer Bees Site discussed above (Fig 21 #7, 21A–B, locality # GLCA_PalLoc_0072), and David's Camp 2 (Fig. 1A #6, 21C–D; locality # GLCA_PalLoc_0071). These tracks bear some resemblance to footprints identified by Olsen (1988, 1995) as *Ameghinichnus* from the upper Towaco Formation (early Hettangian) of the Newark Supergroup at Walter Kidde Dinosaur Park (Riker Hill Quarry), Roseland, New Jersey (Fig. 21E, AMNH 29298). The type *Ameghinichnus* tracks, those of *A. patagonicus* Casamiquela 1961, from the Middle Jurassic La Matilde Formation of Santa Cruz Province, Argentina, have clawless, pentadactyl manus and pes tracks in quadrupedal trackways with manus–pes sets in opposite positions relative to the trackway midline (i.e., the track maker was suggested to be saltatorial). The manus is medial to the trackway and rotated inward, and the pes is rotated outward. Track length/width are subequal, as are digit traces in both length and divarication angles (Casamiquela, 1961; de Valais, 2009). Olsen (1995) stated that the Riker Hill specimens resemble *A. patagonicus* by having paired manus and pes tracks of nearly equal size, however the Riker Hill tracks are larger and have longer and narrower, clawed digits. *Ameghinichnus* tracks have been attributed to either mammaliaforms or derived, non-mammaliaform eucynodonts. The GLCA specimens are similar to those from Riker Hill, but the GLCA examples are generally of larger size. We agree with Olsen (1988, 1995) that this track morphotype does resemble *Ameghinichnus*, but their considerable differences require further investigation elsewhere. The GLCA tracksites need detailed photogrammetric work at the Killer Bees Site, especially the surface where Lockley et al. (2014) mentioned and figured *Batrachopus* trackways with random orientations. We agree that *Batrachopus* occurs abundantly on this surface, but other track types occur including the above mentioned cf. *Ameghinichnus* and other track types, such as cf. *Rhynchosauroides* (Fig. 21C–D). If these tracks are *Rhynchosauroides*, they would be the first occurrence of them in the Lower Jurassic of GLCA and western North America.

Navajo Sandstone

Like the underlying Kayenta Formation and transitional facies of the Kayenta–Navajo, invertebrate and vertebrate tracks and traces are locally abundant in the Navajo Sandstone proper. Our field teams have been focusing on specific sites in detail, including the John Wesley Powell Fossil Track Block (PFTB) (Milner et al., 2023b) and the Andre's Alcove Tracksite (Bennett et al., 2023). Both of these sites are in the lowermost Navajo Sandstone, preserved in interdunal playa and small lake deposits. Additionally, we have been looking at traces on dune surfaces and interdunal non-carbonate sandstones. Tracks and traces are abundant in the southern areas of GLCA around Antelope Island and Labyrinth Canyon, and to the north near Halls Crossing and Bullfrog (not covered in this paper).

Andre's Alcove Tracksite

The Andre's Alcove Tracksite (AAT) locality (Fig. 1A #6; locality # GLCA_PalLoc_0069) comprises an extensive concentration of vertebrate tracks in the lower part of the Navajo Sandstone in GLCA. The tracks are preserved in interdunal lacustrine carbonate beds, with tracks occurring on at least two stratigraphic horizons. This particular interdune set is one of the largest and most laterally extensive we have examined to date in GLCA and extends to an area we call Andre's Alcove North (Fig. 1A #6; locality # GLCA_PalLoc_0086). Both sites were discovered by one of us (A. Delgalvis; Delgalvis, 2015, p. 106) and reported to the NPS. These sites were first visited in 2017 by SGDS and GLCA staff, and on a return visit in 2018 we documented the AAT in detail and collected photogrammetric data. The AAT is by far the largest tracksite yet mapped in the park. The preliminary study of Bennett et al. (2023) documented more than 60 footprints from the AAT, and a more detailed study and description of the site is already underway. Because of the

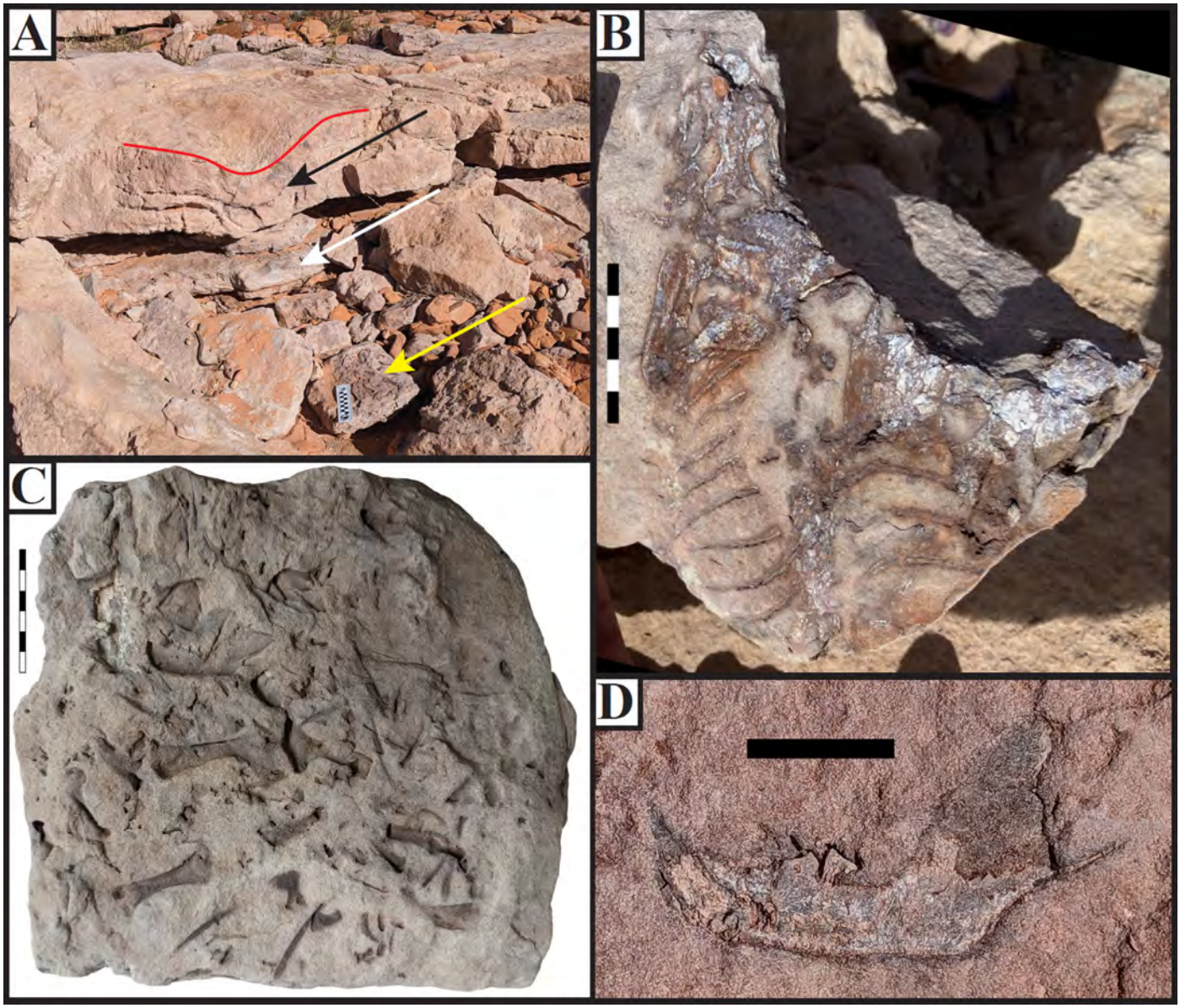


FIGURE 19. Tritylodontid body fossils from Tritylodont Cove, Glen Canyon National Recreation Area. **A,** Discovery Site Navajo Sandstone bonebed with red line showing circular depression (burrow entrance?) on upper bedding surface above articulated tritylodontid skeletons (black arrow; shown in **B**), in turn above beds of mostly disarticulated skeletons (white arrow), and the position of the discovery block (yellow arrow; shown in **C**); **B,** Articulated skeleton with skull towards the top and forelimb to the right; **C,** Discovery block covered in bone impressions and full of bones. This block appears to contain at least three skulls (**A–C** are from locality # GLCA_PalLoc_0257); **D,** Tritylodont mandible from Hunter's Jaw Site (locality # GLCA_PalLoc_0719) in the Kayenta Formation bonebed. Scales: **B–C** = 5 cm; **D** = 2 cm.

way the AAT surfaces are exposed, the locality was divided into three separate sub-sites: Upper Site 1, Lower Site 1, and Lower Site 2.

The vertebrate track types preserved at AAT include those attributed to theropods represented by *Eubrontes* (Fig. 22A) and *Grallator*; small ornithischians represented by *Anomoepus* (Fig. 18F); and protosuchian crocodylomorphs represented by *Batrachopus* (Fig. 22A–C). Theropod tracks are by far the most common track types at this site, and *Eubrontes* tracks greatly outnumber *Grallator*.

To better describe the fossil tracks at the AAT, 3D photogrammetric models of each sub-site were created by one of us (C. Bennett). Due to the ability to remotely study the AAT through these photogrammetric models, research of the AAT continues as remaining fossil tracks are described.

John Wesley Powell Fossil Track Block

The John Wesley Powell Fossil Track Block (PFTB) is yet another spectacular tracksite (Fig. 1A #8; locality # GLCA_PalLoc_0001). The main site is a massive piece of Navajo Sandstone that fell from the adjacent cliff, measuring just over 7 m in height and oriented in a near vertical position. The PFTB preserves 104 natural cast footprints on its main surface (MTL), and several others on a track layer below and another above. This site was described in detail by Milner et al. (2023b); it is the first tracksite within GLCA to receive such an intensive investigation.

Grallator dominates the MTL, with approximately 50

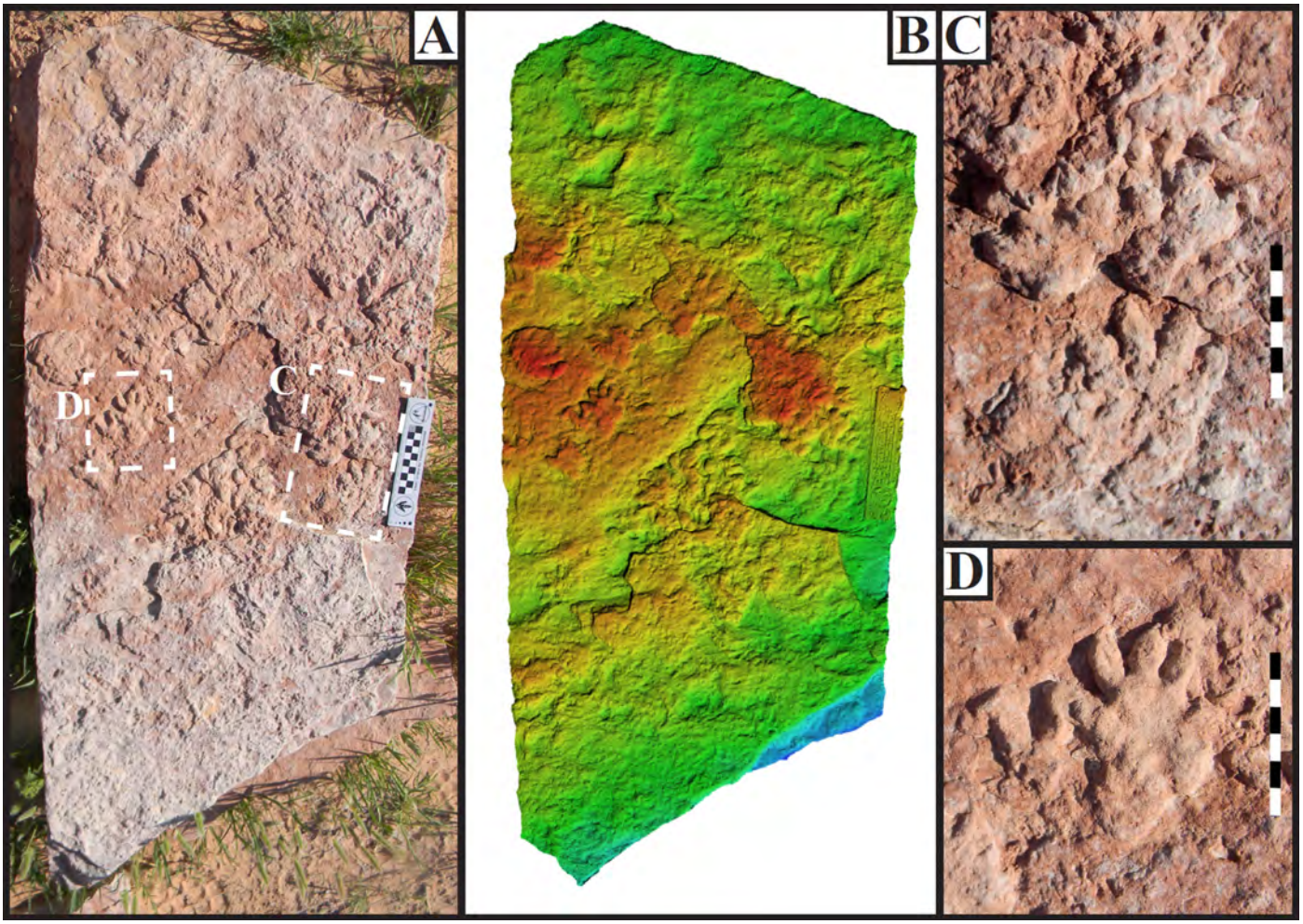


FIGURE 20. Tritylodontid tracks and trackways at David's Camp block 1 Site (locality #GLCA_PalLoc_0070), one of the Slick Ice sites of Lockley et al. (2014) from the uppermost Kayenta Formation, Glen Canyon National Recreation Area. This is a natural cast surface. **A,** Photo of entire slab showing the positions of **C** and **D** close-ups in white dash boxes; **B,** Color contour image of entire track slab; **C,** At least three manus–pes sets of tracks; **D,** Pentadactyl pes track partially overprinting manus track. **C** and **D** scale = 5 cm.

footprints preserved, followed by cf. *Kayentapus* (12 footprints in three trackways). However, the most striking features are two large, superficially ornithopod-like trackways that are, in fact, *Eubrontes* footprints (Lockley and Xing, 2015; Milner et al., 2016, 2023b; Fig. 14L). In total, 15 *Eubrontes* tracks are preserved in three trackways (Milner et al., 2023b).

The 'inflation' of *Eubrontes* tracks on the PFTB that lends them an ornithopod-like appearance has been attributed to lithic compaction of sediment due to load (Lockley and Xing, 2015) and to a combination of sediment load deformation and the fact that the MTL tracks represent undertracks on thick microbial mat interdune carbonate beds that would have been exaggerated at depth due to the spongy nature of the microbial mats (Milner at al., 2023b). The PFTB also has associated, small quadruped tracks, including *Batrachopus* (Fig. 22D–G) found on a nearby block, and cf. *Brasilichnium* on the MTL itself.

Invertebrate traces have been found associated with the PFTB in the form of the back-filled burrow attributed to cf. *Taenidium barretti* (Milner et al., 2023b, fig. 16A; for ichnotaxon description see Nascimento et al., 2023). Some have called similar burrows *Beaconites barretti* (Smith et al., 2008), and Ekdale et al. (2007) called burrows like this from the Navajo Sandstone *Taenidium serpentinum*. These burrow forms have similar architectures to back-filled burrows produced by modern beetle larvae (Nascimento et al., 2023).

Navahopus in GLCA

A rare ichnotaxon called *Navahopus* that is endemic to the Navajo Sandstone in the southwestern United States was produced by sauropodomorphs (Baird, 1980; Hunt and Lucas, 2006; Milàn et al., 2008). The type ichnospecies is *Navahopus falcipollex* Baird 1980, and the holotype (MNA V 3430) is a trackway replica with five manus/pes sets preserved in negative hyporelief. The holotype site (MNA Loc. 226) is near Copper Mine Trading Post on Kaibito Plateau, Navajo Nation, Coconino County, northeastern Arizona, and it is preserved on a dune face (Baird, 1980). This ichnospecies is diagnosed by quadrupedal trackways with a clawed, tetradactyl pes. The pedal digits increase in length order from I, II, IV, and III. The manus is functionally tridactyl with short, clawed digit traces II and III directed forward, and has a falciform pollex claw directed medially (Baird, 1980).

A second valid ichnospecies is *Navahopus coyoteensis*, which comes from the Navajo Sandstone in the northern part of Vermillion Cliffs National Monument, near "The Wave," but in Utah (Milàn et al., 2008; Breithaupt et al., 2021). The holotype is a 2.5 m long trackway on the lee face of a dune preserving nine pes and seven manus tracks (Milàn et al., 2008). No holotype was collected for this ichnospecies, but Breithaupt et al. (2021, fig. 3) created a photogrammetric model of this

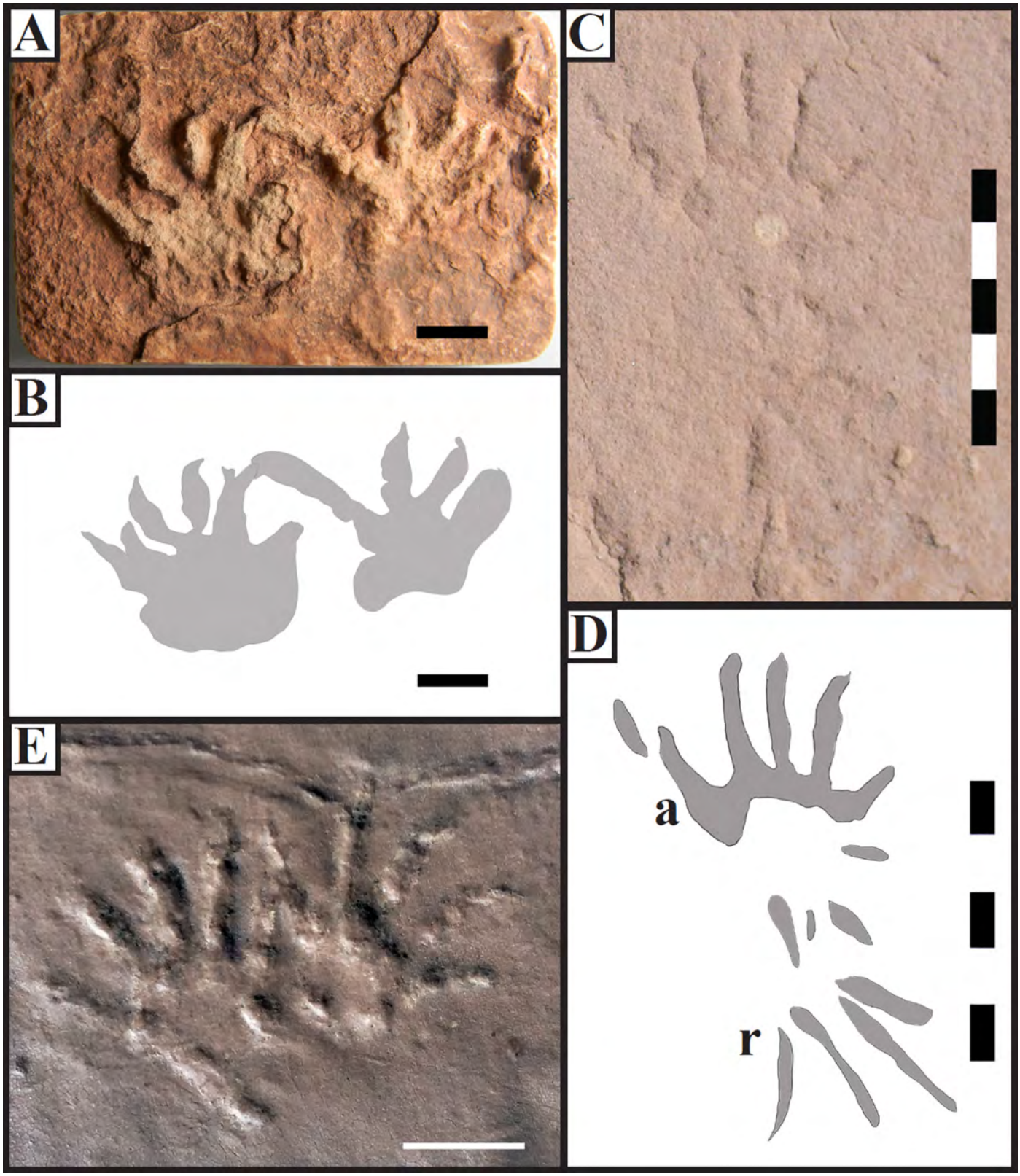


FIGURE 21. Other possible synapsid tracks, cf. *Ameghinichnus*, from Glen Canyon National Recreation Area. **A–B,** cf. *Ameghinichnus* (SGDS 1683, plaster replica) photo (**A**) and rough sketch (**B**) from David's Camp block 2 Site east of Owl Canyon, upper Kayenta Formation (locality # GLCA_PalLoc_0071); **C–D,** photo (**C**) and sketch (**D**) of in situ cf. *Ameghinichnus* at top (a) and cf. *Rhynchosauroides* in bottom right (r) from Killer Bees Site, Kayenta Formation (locality # GLCA_PalLoc_0072).; **E,** cf. *Ameghinichnus* (AMNH 29298, latex peel) from early Hettangian upper Towaco Formation, Riker Hill, Roseland, New Jersey (photo credit, P.E. Olsen). Scales: **A–B** = 2 cm; **C–D** = 5 cm; **E** = 1 cm.

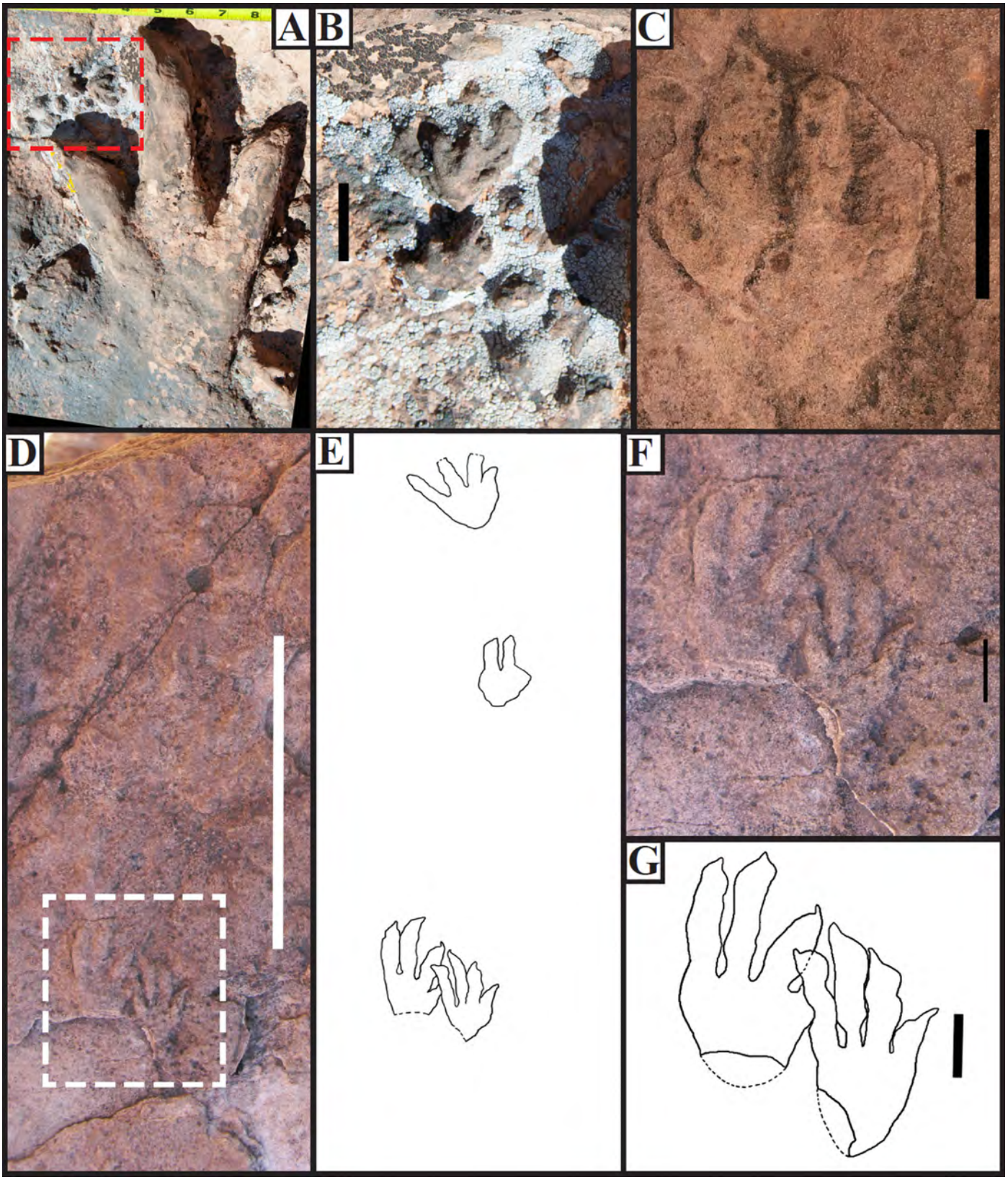


FIGURE 22. *Batrachopus* tracks from the Navajo Sandstone, Glen Canyon National Recreation Area. **A–B**, Fallen block containing natural cast left *Eubrontes* track (**A**) and several *Batrachopus* tracks (**B**) from the Andre's Alcove Tracksite; **C,** *Batrachopus* left pes undertrack from Andre's Alcove Tracksite (locality # GLCA_PalLoc_0069), interdunal carbonate sandstone beds in the lower Navajo Sandstone; **D–G,** *Batrachopus* tracks found next to the John Wesley Powell Fossil Track Block (from Milner et al., 2023a, fig. 16D–F; locality # GLCA_PalLoc_0463), photo (**D**) and interpretive sketch (**E**). White dashed box in **D** shows the position of close-up photo (**F**) and sketch (**G**). Scales: **A**, tape measure at top in inches; **B** = 2 cm; **C** = 5 cm; **D–E** = 10 cm; **F–G** = 1 cm.

trackway. *Navahopus coyoteensis* has digit IV trace of equal or greater length than the digit III trace, and the pedal hypex of III–IV is much greater than hypices I–II and II–III (Milàn et al., 2008).

Here we report the first recorded occurrences of *Navahopus* isp. from GLCA documented at three different locations in the Navajo Sandstone. The best example is on a fallen boulder in the Owl Canyon area (Fig. 1A #6; locality # GLCA_PalLoc_0593), preserving two natural cast tracks with different morphologies in the same trackway (Fig. 23A–C). The first track in the sequence is a left manus trace with three clawed digits turned medially (Fig. 23C). The second is a right pes track that is slightly longer than wide with digits I–IV of nearly equal length (Fig. 23B).

The second occurrence is at the Andre's Alcove North Site (Fig. 1A #6; locality # GLCA_PalLoc_0086). It is a poorly preserved, isolated pes track, but it does show a circular outline with four claw traces and an expulsion rim along the lateral, medial, and posterior margins (Fig. 23D). The third site comes from the Navajo Sandstone along the San Juan Arm (Fig. 1A #10; GLCA locality # pending). This site has a well-preserved left pes track that is also somewhat circular in shape with sharp claws on digit I–IV and of similar lengths (Fig. 23E). Posterior and slightly to the right is a possible right manus trace. This site needs closer examination.

Labyrinth Island Area

Labyrinth Island, or Labyrinth Peninsula during low-water levels, is situated in the southern part of GLCA and there are several recorded localities in the vicinity (Figs. 1A #11, 22). The island and surrounding area display a series of overlapping Navajo Sandstone dune sequences with thin, non-lacustrine interdune surfaces. There are localized abundances of tracks on at least three interdune surfaces dominated by *Otozoum* with uncommon small theropod tracks. On dune facies *Brasilichnium* trackways are the only tetrapod tracks observed so far, along with a possible beetle trackway that was collected near the top of the island.

The possible beetle trackway (Fig. 24A–B; GLCA 24895, UCM 98262; locality # GLCA_PalLoc_0284) somewhat resembles modern darkling beetle (Tenebrionidae) trackways on dune surfaces in Morocco (Peixoto et al., 2020, fig. 11). Tenebrionidae has a body fossil record back to the late Middle Jurassic (Nabozhenko, 2019). However, a different kind of beetle with a similar body plan could have produced trackways on these Early Jurassic sand dune surfaces.

The GLCA specimen has some similarities to *Paleohelcura araraquarensis* trackways from the Upper Jurassic–Lower Cretaceous eolian Botucatu Formation of Brazil (Peixoto et al., 2020), but in our opinion the Labyrinth Island trackway does not represent *Paleohelcura*. Arthropod trackways in eolian paleoenvironments attributed to *Paleohelcura* and *Octopodichnus* (i.e., *Octopodichnus* ichnofacies of Hunt and Lucas, 2007) of the American Southwest have received much attention (e.g., Ekdale and Bromley, 2012; Good and Ekdale, 2014), but overall, other forms of arthropod trackways are understudied; therefore, the ichnotaxonomy is beyond the scope of this paper.

Brasilichnium trackways are locally abundant on many dune surfaces in the Labyrinth Island area (Fig. 24D), and poorly preserved *Otozoum* were recorded prior to 2023; however, our investigation of Labyrinth Peninsula during low water levels in March 2023 resulted in the discovery of at least six *Otozoum* trackways on two closely-spaced interdune surfaces (Fig. 24E–F) along with a single *Grallator*-like theropod track (Fig. 24C). The *Otozoum* trackways at this site are oriented parallel to one another and traveled in a north or south direction. The different trackways also show various size ranges, with the smallest being 15–20 cm in length. Further investigation of the localities in this area is warranted during low water levels.

Antelope Island vicinity

Tracksites in the Antelope Island area of GLCA (Fig. 1A #11) were described by Lockleyet al. (1998, 2014). The Crossing of the Fathers Tracksite (a.k.a. Kammenetsky site; locality # GLCA_PalLoc_0058) was discovered in 1988 in the Warm Creek–West Bay area and preserves relatively small in situ *Otozoum* and *Grallator* trackways on a manganese-stained interdune surface. This locality was the largest site mapped at GLCA (Lockley and Hunt, 1995; Lockley et al., 1998, 2014) until our work at AAT described above (Bennett et al., 2023). The Crossing of the Fathers locality preserves at least 28 *Otozoum* and *Grallator* trackways, and these trackways appear to coincide with the strike of the underlying eolian crossbeds (Lockley et al., 1998). We have not observed a similar trend with *Otozoum* trackways mentioned above from Labyrinth Island, but we have observed a trend in the majority of *Grallator* trackways preserved in the uppermost Navajo Sandstone sites near Page, Arizona described below.

On our return to the boat from the Crossing of the Fathers Tracksite in September 2014, one of us (V. Santucci) recognized an impressive tracksite at the waterline close to where the boat was docked, now called the Santucci Cove Locality (Fig. 25A–B; locality # GLCA_PalLoc_0583). Abundant *Brasilichnium* trackways, including hundreds of individual tracks, along with a well-preserved down-slope *Grallator* trackway (Fig. 25B), are preserved here on a dune foreset. This site was recently studied by one of us for her graduate research at the University of Alberta (Rodriguez, 2023), and she will publish a detailed description elsewhere.

Another site of interest called the Gunsight Bay *Otozoum* Site (Fig. 1A #11; locality # GLCA_PalLoc_0060) preserves a beautiful *Otozoum* trackway consisting of nine footprints, and a second poorly preserved trackway of three footprints occurs together on the same interdune surface (Fig. 25C–F). Footprints in both trackways are of similar size, averaging 33 cm in length and 21 cm wide.

Page Area

Here we report dinosaur tracksites from the uppermost Navajo Sandstone found near Page, Arizona (Fig. 1A #12, 24). The larger site that we investigated a tracksite reported to the GLCA that is call the Mower Tracksite (a.k.a., the Vermilion View Trail Tracksite; locality # GLCA_PalLoc_0293; Fig. 26; Santucci et al., 2023). This tracksite preserves more than 100 footprints, all identified as *Grallator*, on a thin interdune surface. The majority of trackways are oriented parallel to the strike of the dune set below. Several of the *Grallator* tracks at this site preserve digit I traces. A second, smaller site preserving four footprints, with three in a single trackway, was found nearby (locality # GLCA_PalLoc_0256). This site is most likely on the same interdune surface as the Mower Tracksite. A third site was reported to us near the Horseshoe Bend Overlook, but we have yet to examine this locality.

Invertebrate traces found close to the Mower Tracksite (locality # GLCA_PalLoc_0279) resemble *Arenicolites* (Ekdale et al., 2007), but they require further study. A full description of these tracksites will be published elsewhere.

CURRENT PALEONTOLOGICAL RESOURCE MANAGEMENT

The management of non-renewable paleontological resources at GLCA, and throughout the NPS, is based on scientific principles, best practices in resources management, and through the authorities and guidance defined within laws, regulations, and policies. The primary legislation pertaining to fossils from NPS, and other federal lands is the Paleontological Resources Preservation Act of 2009 (PRPA) (16 U.S.C. §

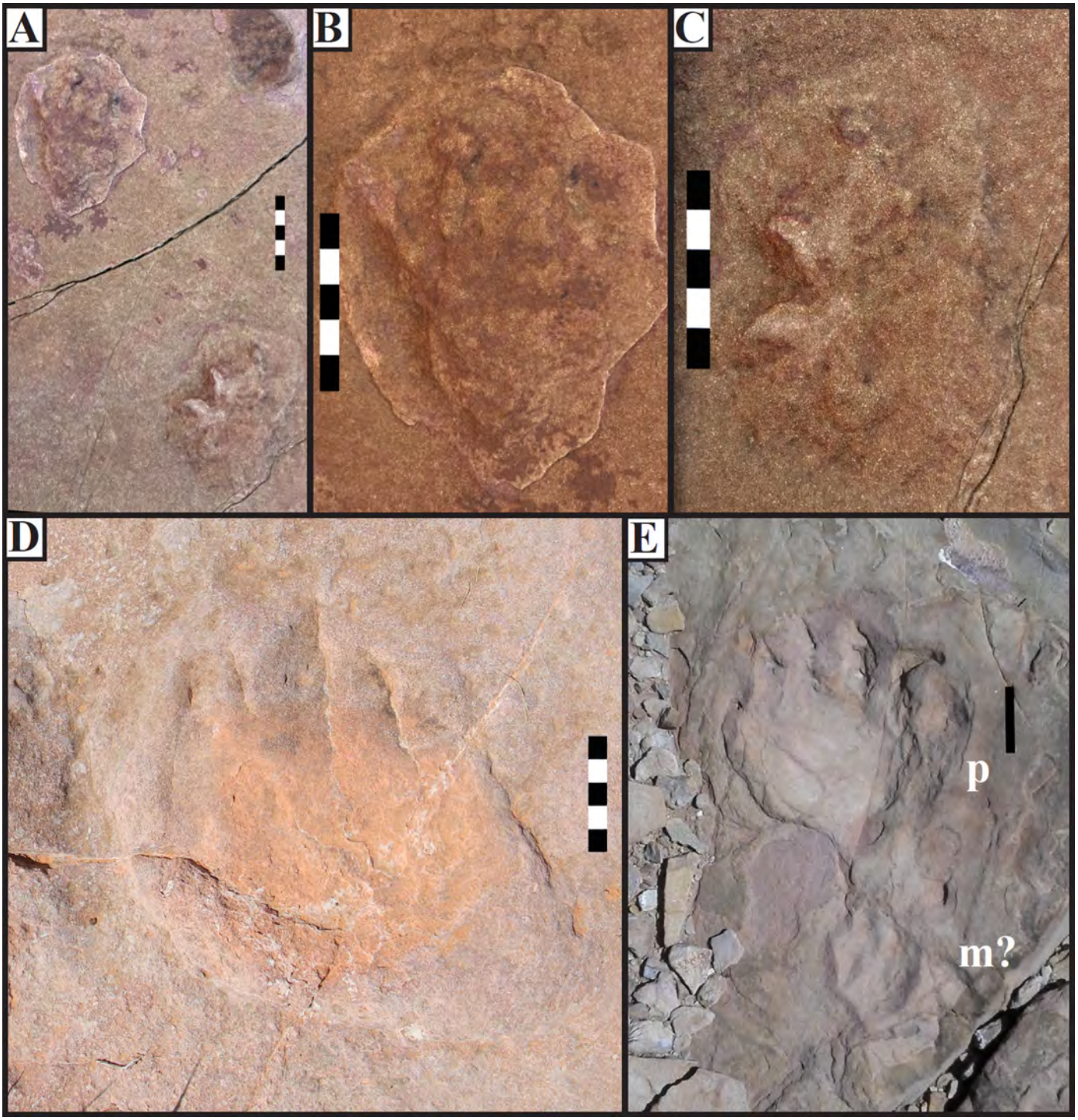


FIGURE 23. Rare *Navahopus* tracks from the Navajo Sandstone at Glen Canyon National Recreation Area. **A–C,** Partial trackway (**A**) made up of left (**B**) and right (**C**) pes tracks from a fallen Navajo Sandstone block (locality # GLCA_PalLoc_0593); **D,** Isolated pes print from Andre's Alcove North locality in the lower Navajo Sandstone (locality # GLCA_PalLoc_0086); **E,** San Juan Arm pes track (p) anterior to possible manus (m?) from previous print in sequence (GLCA locality # pending). Scale for all is 5 cm.

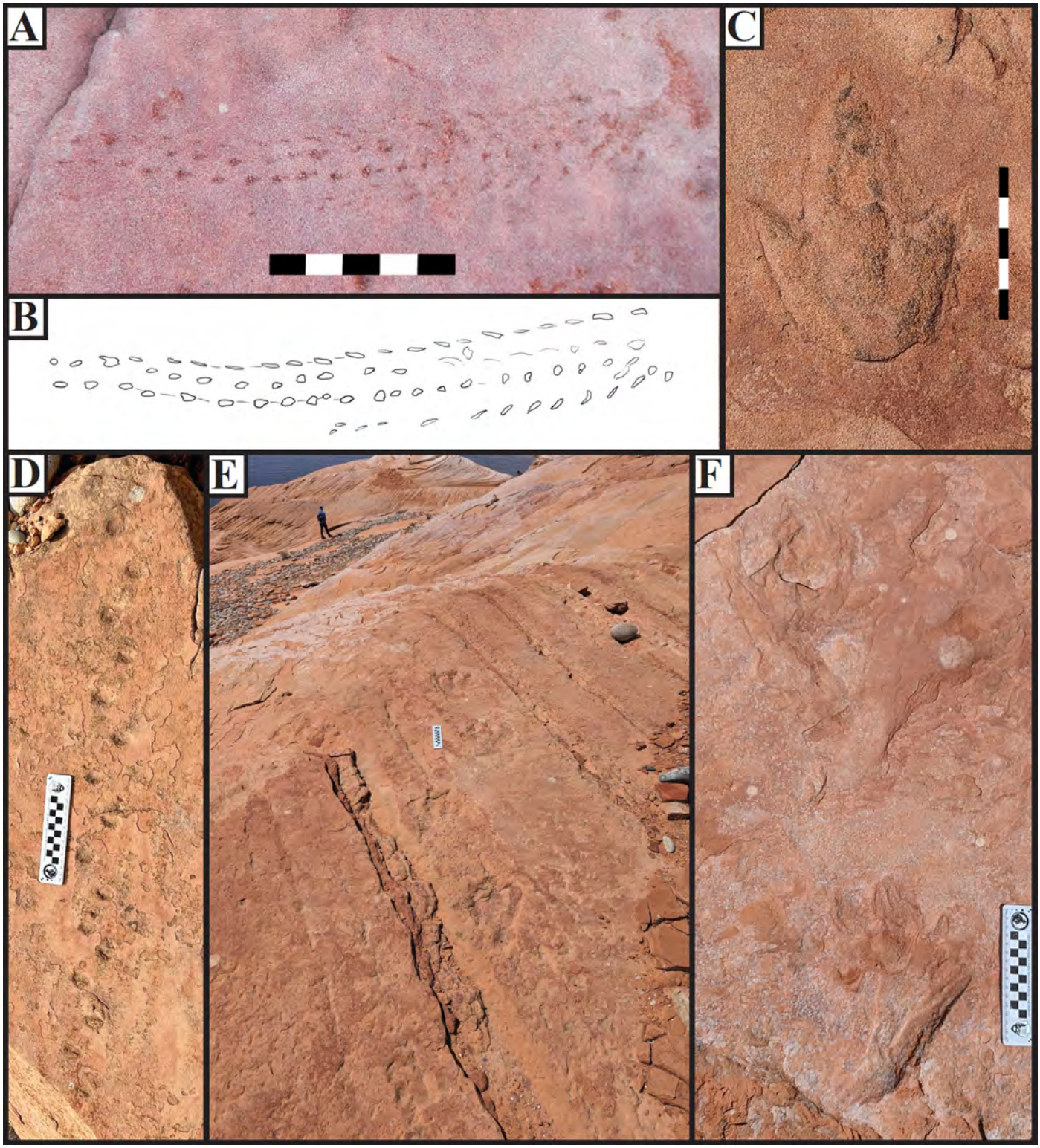


FIGURE 24. Labyrinth Island sites in Navajo Sandstone dunes, Glen Canyon National Recreation Area. **A–B,** photo (**A**) and sketch (**B**) of possible beetle trackway on dune surface (GLCA 24895, UCM 98262; locality # GLCA_PalLoc_0284),; **C,** *Grallator*-like track on interdune surface (locality # GLCA_PalLoc_0242); **D,** *Brasilichnium* trackway on float block now submerged (locality # GLCA GLCA_PalLoc_0231). **E–F,** *Otozoum* trackway on interdune surfaces (**E**), and close-up of the last two tracks in trackway (**F**). Six trackways were noted at this site during the March 2023 drought, but the site was submerged again in May of the same year (locality # GLCA_PalLoc_0295). Scale for **A–C** = 5 cm. Scale for **D**–**E** = 10 cm.

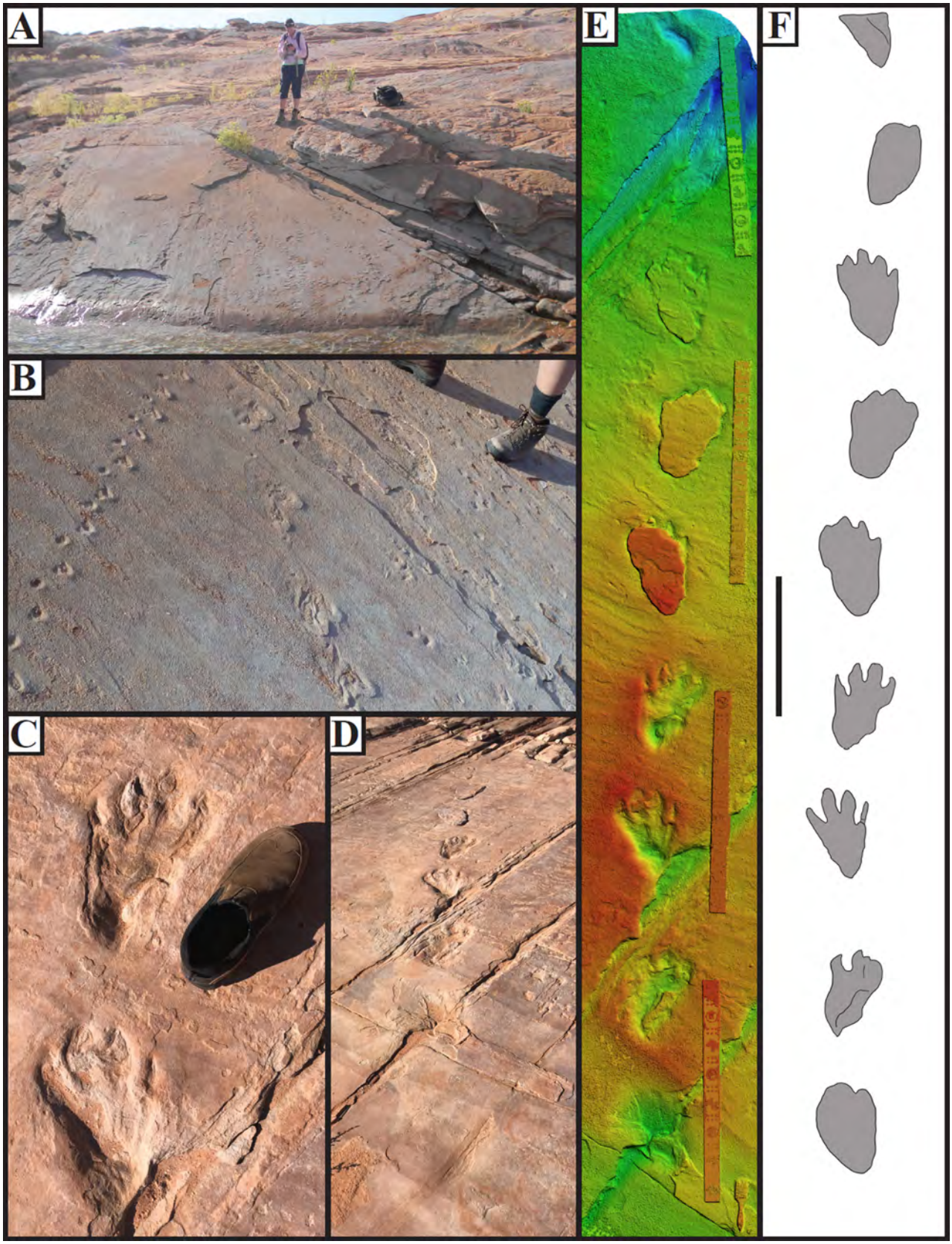


FIGURE 25. New Navajo Sandstone tracksites in the vicinity of Antelope Island, Glen Canyon National Recreation Area. **A,** The Santucci Cove locality photo with Sarah Doyle for scale (locality # GLCA_PalLoc_0583); **B,** Santucci Cove locality showing abundant *Brasilichnium* and a downslope *Grallator* trackway (NPS photo); **C–D**, Photos of the Gunsight Bay *Otozoum* tracksite (locality # GLCA_PalLoc_0060) with a close-up of two of the better preserved footprints next to a men's size 12 shoe (**C**), and an angled view of the entire trackway (**D**) (photo credit, J. Williams); **E–F,** Photogrammetric color contour image (**E**) and map (**F**) of the entire trackway (locality # GLCA_PalLoc_0060). Scale for **E–F** = 50 cm.

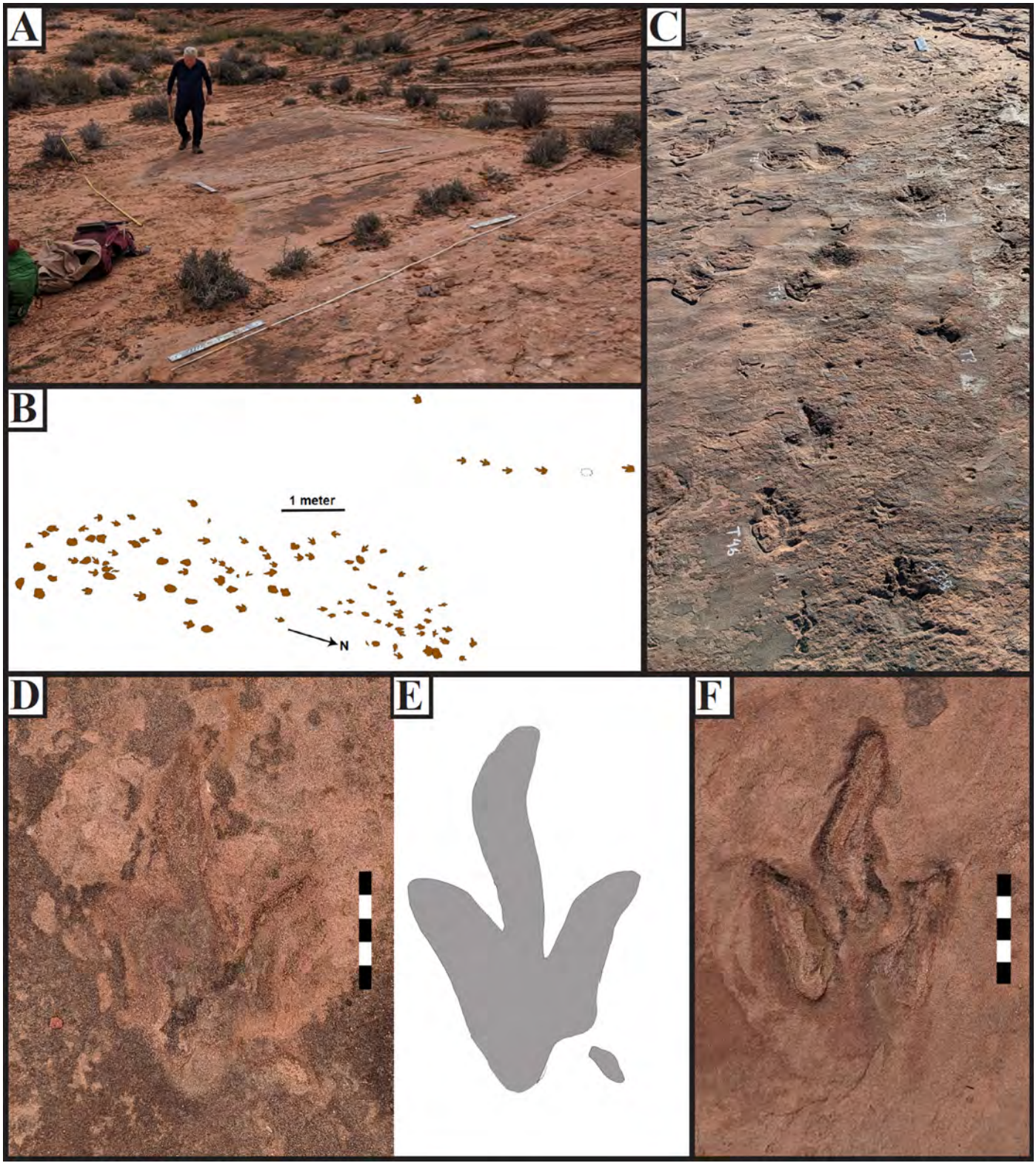


FIGURE 26. The Mower Tracksite (locality # GLCA_PalLoc_00293) in the uppermost Navajo Sandstone near Page, Coconino County, Arizona. **A**, David Slauf on interdune track surface; **B**, Rough map of the tracksite preserving approximately 100 tracks; **C**, Portion of tracksite surface showing multiple *Grallator* trackways; **D–E**, Left *Grallator* track photo (**D**) and sketch (**E**) with digit trace I preserved; **F**, Well preserved right *Grallator* track. Scale for **D–F** = 5 cm.

470aaa 1-11), which was enacted on March 30, 2009, within the Omnibus Public Land Management Act of 2009. PRPA directs the Department of Agriculture (U.S. Forest Service) and the Department of the Interior (National Park Service, Bureau of Land Management, Bureau of Reclamation, and Fish and Wildlife Service) to manage and protect paleontological resources on federal land using scientific principles and expertise.

Additionally, the federal land-managing agencies were directed under PRPA to establish a program to increase public awareness about the significance of paleontological resources. The National Park Service established National Fossil Day to address this provision in the law and to promote the scientific and educational values of fossils (Fig. 27). The National Fossil Day partnership consists of more than 425 partners across the U.S., including museums, science and teacher organizations, universities, libraries, agencies, fossil sites, amateur fossil groups, and others interested in fossils. PRPA provides specific mandates for administering paleontological resource research and collecting permits and the curation of fossil specimens in museum collections. The law also includes provisions for both criminal and civil penalties associated with paleontological resource crimes on federal lands.

CONCLUSIONS

Glen Canyon National Recreation Area is rich in important paleontological resources spanning from the Late Pennsylvanian to the Late Cretaceous, as well as many Pleistocene and Holocene localities. Areas receiving the greatest impact to paleontological resources occur along the shores of Lake Powell, due to the increased impact from erosion, both natural and anthropogenic in nature. The majority of rock formations in proximity to the lake are of Triassic–Jurassic age, especially the Chinle Formation and Glen Canyon Group.

By far the most prominent kinds of fossils within GLCA are invertebrate and vertebrate trace fossils, which dominate the more than 740 paleontological localities recorded within the park. Above we illustrated the growing number of significant fossil sites being discovered as a result of systematic exploration of outcrops not only by professionals, but also by visitors to GLCA. The many miles of shoreline provide access to unexplored areas resulting in important discoveries.

Herein we have reported on several first occurrences within GLCA: (1) a mollusc grazing trail from GLCA from the Late Pennsylvanian–Early Permian lower Cutler beds of the Cutler Group; (2) the first occurrence of plant fossils from the Shinarump Member of the Chinle Formation, including two morphotypes of *Zamites*-like bennettitaleans and large *Neocalamites* with associated leaves; (3) Chinle Formation vertebrate body fossils include the first reports of fishes (*Lophionotus sanjuanensis*, cf. *Lasalichthys stewarti*, and mawsoniid coelacanths); (4) the addition of new phytosaur specimens to GLCA collections from the Church Rock Member of the Chinle Formation; (5) the first identified invertebrate trace fossils in the Chinle Formation including cf. *Oravaichnium* and cf. *Scoyenia* in close association with the above-mentioned plants in the Shinarump Member; (6) the first occurrences of cf. *Gwyneddichnium* and *Brachychirotherium* from the Chinle Formation; (7) the first occurrences of *Evazoum* and *Brachychirotherium* from the Wingate Sandstone; (8) fish swim traces identified as *Undichna* cf. *simplicitas* from the Kayenta Formation; (9) potentially the first example of cf. *Rhynchosauroides* from the Lower Jurassic of western North America associated with possible mammaliaform cf. *Ameghinichnus* tracks from the Kayenta Formation; (10) tracks previously reported by Lockley et al. (2014) as being cf. *Brasilichnium* from the Kayenta Formation, the Kayenta–Navajo transition, and interdunal playas and lacustrine facies in the lower Navajo Sandstone, are here interpreted as a new ichnotaxon produced by tritylodontid synapsids; (11) the discovery of two tritylodontid bonebeds containing cf. *Kayentatherium* from the uppermost Kayenta Formation and lowermost Navajo Sandstone; (12) the ninth crouching theropod trace known worldwide, and the second example from GLCA; (13) the first occurrences of the sauropodomorph track *Navahopus* from GLCA at three different localities in the Navajo Sandstone; (14) the first beetle-like trackway from a sand dune surface in the Navajo Sandstone; and (15) rare identifiable tracks (*Grallator*) from the uppermost Navajo Sandstone.

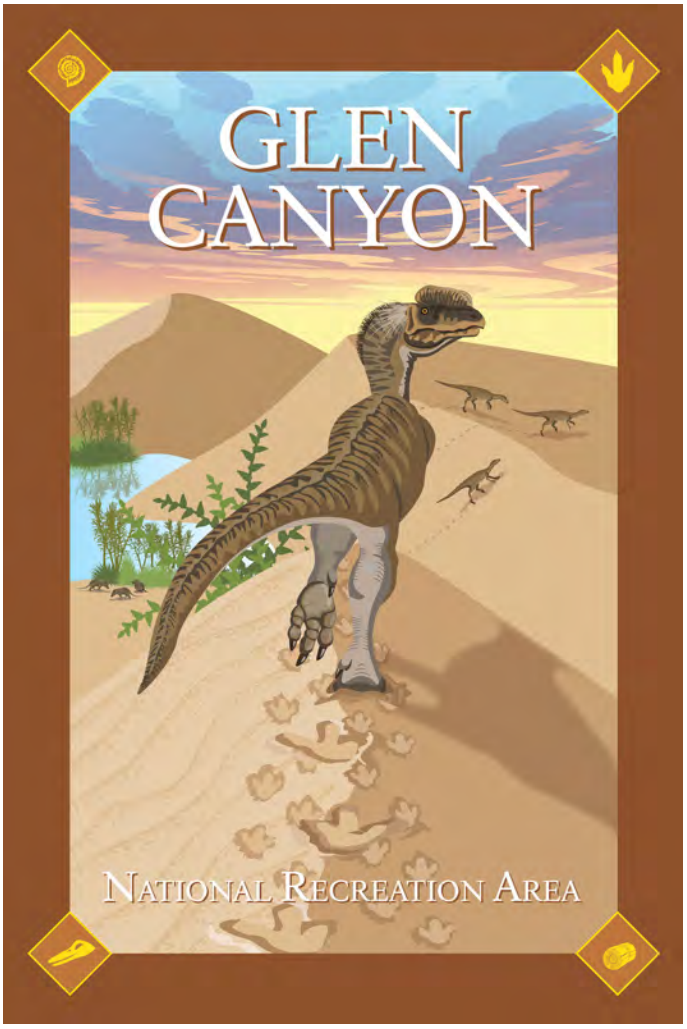


FIGURE 27. 2024 National Fossil Day logo depicting *Dilophosaurus* walking along a dune, producing *Eubrontes* tracks with sauropodomorphs and tritylodontids in the background. (artwork by Studio 105).

ACKNOWLEDGEMENTS

The lands now occupied by GLCA are within the ancestral homelands of the Nuwuvi (Southern Paiute) and Diné (Navajo) peoples. We thank the NPS and SGDS DinosaurAH!Torium Foundation for funding fieldwork and research efforts. Thank you to NPS staff, including Taryn Preston, John Spence, Lisa Reidel, Matthew Miller, Mark Anderson, Ann Miller, Donnie Plassman, Vanessa Glynn-Linaris, and many others for transporting us to localities, assisting with logistics, and for their great hospitality. Special thanks to Sarah Doyle who assisted us in the field with stratigraphy, collection of locality data, photogrammetry, and her boating skills. Thanks to Don DeBlieux, Scott Madsen, and Martha Hayden from the Utah Geological Survey for their input on several of the localities herein. Thanks to Doug Wilder (GIS Coordinator for NPD Intermountain Region) and Rafael

Moreno-Sanchez (University of Colorado, Denver) for their assistance with tablet locality data entries in the field. Thank you to Neffra Matthews (BLM, Denver) for helping with some of our photogrammetry issues. We thank Matt Stimson (New Brunswick Museum, Saint John, New Brunswick, Canada) for assistance with some of the invertebrate trace identifications, and Hendrik Klein for his help identifying tracks from the Chinle Formation. Special thanks to SGDS volunteers Dan W. Whalen, Steve Dzelzgalvis, Mike and Michelle Frielinger, and Mike Callihan for their field assistance. Thank you to Jim Williams (SGDS volunteer) for providing the photos in Figure 23C and D, and Paul E. Olsen (Columbia University) for Figure 19E. Thanks to Jacob Van Veldhulzen and Karen Chin (University of Colorado at Boulder), Carolyn Levitt-Bussian and Randy B. Irmis (Natural History Museum of Utah), and Josh Lively and Katharine Corneli (Utah State University Eastern Prehistoric Museum) for access to collections. Thank you to Bill Simpson (Field Museum of Natural History) for providing photos and specimen data of the Riggs (1904) specimen. Thanks to Rob Gay (Idaho Museum of Natural History) who assisted with early versions of the manuscript, and Brent Breithaupt (BLM, Wyoming) and Don DeBlieux (Utah Geological Survey) for their helpful reviews. Thanks to the editors for the invitation to contribute to this volume, and for the guidance along the way.

The final DOI regulation for PRPA is available on the Federal Register website at: https://www.federalregister.gov/; search for Regulation Identification Number 1093-AA16. Additionally, the NPS governs activities in paleontological parks through the general NPS regulations, found in 36 Code of Federal Regulations (C.F.R.) Chapter I. These regulations apply to federally owned lands and waters administered by the NPS within park boundaries and also to some nonfederal lands and waters within park boundaries (36 C.F.R § 1.2).

We thank a series of Geologist-In-Parks (now Scientists in Parks and formerly GeoCorps America) paleontology staff and interns that from 2005–2020 were tasked with paleontological resource inventory and monitoring and addressed a wide range of fossil-related projects in the recreation area: Sarah Doyle, Anne Miller, Matthew Miller, and Klara Widrig. The positions were funded through a partnership between GLCA and the NPS Geologic Resources Division under the supervision and mentoring of GLCA staff (Norm Henderson, John Spence, and Lex Newcomb) and the NPS Senior Paleontologist.

Finally, we would like to thank Dr. Martin Lockley for his outstanding contributions to the field of vertebrate ichnology and hard work within GLCA and surrounding areas. He was such an amazing researcher, colleague, mentor, and friend to so many of us. You are dearly missed, and we hope this manuscript helps to preserve the paleontological legacy you established at GLCA. May you rest in peace.

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