Tracy Thomson attended the College of Eastern Utah and then received his B.Sc. in geology from the University of Utah. He is currently attending the University of California-Riverside and Dr. Mary Droser is his advisor.

BEHAVIORAL AND PALEOENVIRONMENTAL IMPLICATIONS OF REPTILE “SWIM TRACKS” FROM THE EARLY TRIASSIC OF WESTERN NORTH AMERICA

The Permian/Triassic mass extinction was the largest in earth history and resulted in the restructuring of the marine and terrestrial realms. The nature of this biotic recovery is critical to our understanding of how ecosystems recover from and are restructured after such events. Recovery in the marine realm is considerably better understood than that in the terrestrial realm largely because of the nature of the fossil record. The Lower Triassic Red Peak and Moenkopi formations are the oldest stratigraphic record of terrestrial rocks from the post-extinction time interval cropping out throughout Wyoming and the Colorado Plateau (UT, NV, AZ, and NM) (**Figure 1**). These units thus form a well-exposed and widespread natural laboratory for investigating the aftermath of this extinction in the terrestrial realm. They also provide the first window in time for studying the Early Triassic radiation of reptiles and their behaviors.

Figure 1: Map of western North America showing the general outcrop distribution of the Lower Triassic Moenkopi and Red Peak formations and currently known swim track localities.

In the Moenkopi Formation very few reptile genera, mostly large archosauriforms, are known from actual skeletal remains (Morales, 1987) and no tetrapod remains of any kind have been reported from the Red Peak Formation. However, diverse vertebrate tracks attributed to various types reptiles are ubiquitous throughout these Lower Triassic deposits (Klein & Lucas, 2010; Lovelace & Lovelace, 2012) indicating that reptiles undoubtedly comprised a diverse and ecologically important part of the fauna at that time. Preliminary work has shown that a rather unusual but common and geographically widespread component of these track assemblages are swim tracks produced under subaqueous conditions by buoyant or partially buoyant animals (Thomson & Lovelace, in review) (**Figure 2**). The purpose of this research is to 1) document and describe these swim tracks and test the hypothesis that they are formed by multiple different types of reptiles "swimming" in shallow water and 2) place these trackways into the context of known Triassic reptiles and their possible paleoenvironmental affinities.

Figure 2: Swim tracks comprising an offset trackway in Capitol Reef National Park, Utah.

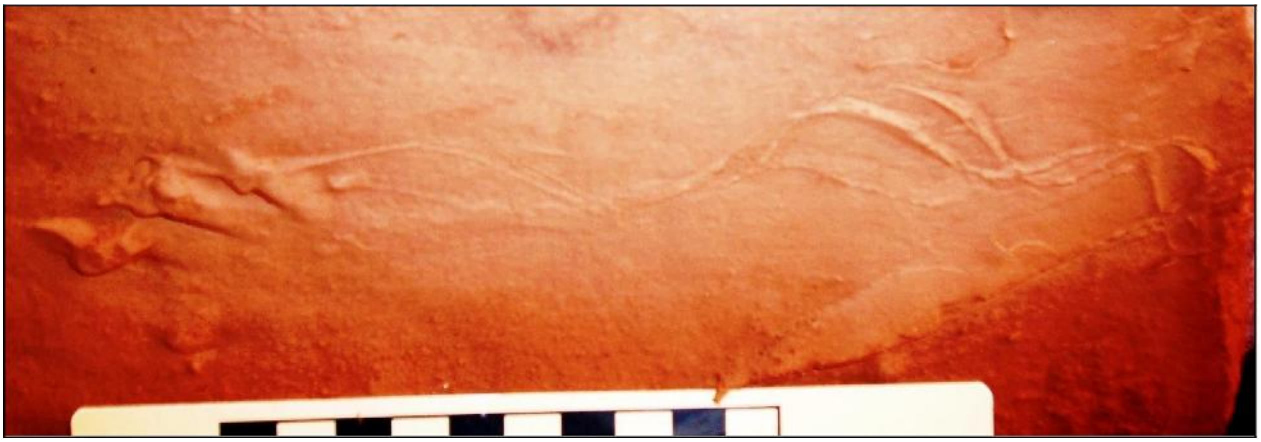

Figure 3: Long, sinuous swim track leading up to a *Rotodactylus* footprint.

Although terrestrial reptile tracks have been thoroughly described and are well known from the Moenkopi Formation (Klein & Lucas, 2010), swim tracks from this rock unit have not been given similar consideration. They have been previously misidentified as tool marks (Boyd, 1975) and even when recognized as tetrapod traces the identity of the trackmaker has remained somewhat controversial, with most workers ascribing them to either amphibians or reptiles (Kirby, 1987; Peabody, 1956). However, certain characteristics of the swim tracks such as scale striations and nail/claw marks indicate reptilian producers. In some instances these swim tracks have been found in association with reptilian ichnotaxa such as *Chirotherium* and *Synaptichnium* (medium- to large-sized rauisuchian archosauriforms), *Rotodactylus* (small- to medium-sized lepidosauromorph) (**Figure 3**), and *Rhynchosauroides* (small lepidosauromorph) (Thomson & Lovelace, in review).

The presence of scale striations and claw marks is due to the fact that these swim tracks and the surfaces on which they were originally produced have been extremely well-preserved. High-fidelity preservation is a common feature among these Early Triassic localities, whereas well-preserved tetrapod swim tracks from other time periods appear to be localized occurrences (Milner et al., 2006; Romilio et al., 2013). This suggests that the production and preservation of Early Triassic swim track are neither random nor accidental occurrences but actually represent the regionally widespread and repetitious aquatic behaviors of a variety of reptiles coupled with common taphonomic processes and paleoenvironmental conditions at the time of swim track production. Stratigraphic sections from several swim track localities and a detailed study of the swim tracks themselves will provide the sedimentological and trace fossil data necessary to identify and describe the taphonomic and paleoenvironmental

Figure 4: Swim track (upper left) with flow marks and current crescents on a track surface. Scale bar = 2 cm.

controls on track production and preservation operating at regional scales during the Early Triassic in western North America.

Track surfaces throughout the Moenkopi and Red Peak formations preserve several types of current flow indicators, such as current crescents (Peabody, 1947) (**Figure 4**), flow lines, and tool marks. Ripple marks, including interference ripples, and cross-bedded sandstones are also common sedimentary structures preserved in rock units of terrestrial origin within these formations. These and other structures have led to previous interpretations that all reptile tracks, including swim tracks, were originally produced in fluvial or lacustrine paleoenvironments. However, the invertebrate trace fossil assemblages associated with these vertebrate tracks have not been taken into account and these assemblages, which include trace fossils such as *Diplocraterion parallelum* (**Figure 5**), are actually indicative of coastal marine paleoenvironments.

The high-fidelity with which the swim tracks are preserved allows for the identification of track characteristics which indicate the swim direction of the trackmaker. Preliminary investigations indicate that an overwhelmingly number of determinable swim track directions are parallel and nearly opposite current flow, suggesting that track production is favored when the organisms traveled against the current. This hints at the presence of some complex interactions between reptile behavior and paleoenvironment and how these control track production and preservation. These interactions will become clearer as these swim tracks are described in more detail.

Figure 5: *Diplocraterion parallelum* from a swim track site in Glen Canyon National Recreation Area, Utah

Terrestrial tracks of all ages have long been used to approach questions of limb kinematics and behavior (e.g., Milner et al., 2009) yet similar analyses on swim tracks are lacking, especially on those produced by quadrupedal tetrapods. In the Moenkopi Formation individual swim tracks representing the successive interaction of all four limbs of the trackmaker with the substrate can be identified in single trackways. This makes it possible to determine the relative order and timing of the swim stroke of each limb and thus a description of the overall swim kinematics of the trackmaker can be approached (Thomson, 2011). Such descriptions will allow for interpretations on how these reptiles moved through the water and if their propulsion was by the use of limbs (as in dinosaurs), tails (as in crocodylians), or a combination of both.

Additionally, these swim tracks are comprised of several different morphotypes which can be distinguished by characteristics such as size, overall shape, and inferred digit motion through the substrate (Thomson, 2012). One of these morphotypes exhibits a size range comparable to that of foot skeletal elements from a currently undescribed diapsid reptile known from several skeletons recovered from Arizona. Detailed study of this swim track morphotype will augment interpretations on the evolution, behavior, and paleoenvironmental affinities of this new reptile when it is properly described. A swim track morphotype unique to the Early Triassic, called a “z-trace”, is made by a single digit interacting with the substrate in a back and forth motion producing a z-shaped trace (**Figure 6**). The exact aquatic behavior behind this unique trace is still unknown but it is common enough that in some instances it forms nearly 25% of the entire sequence of swim tracks in a single trackway. The widespread geographic distribution of this and the other swim track morphotypes, combined with the ubiquitous nature of their occurrences, indicates that each one potentially represents the aquatic behaviors and paleoenvironmental affinities of many different types of reptiles during the Early Triassic.

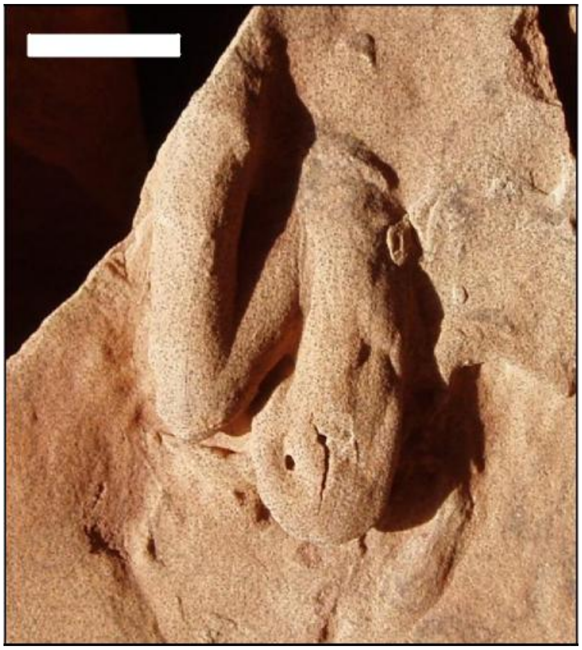

Figure 6: "Z-trace" swim track morphotype. Scale bar = 2 cm.

A part of my study will focus on identifying previously undescribed sedimentary structures from track localities throughout the Moenkopi and Red Peak formations. I will also investigate the taphonomic processes involved in swim track production and preservation. Sedimentary structure and grain size data from measured stratigraphic sections along with the discovery additional invertebrate trace fossils at these localities will aid in confirming whether or not these swim tracks were produced in coastal marine paleoenvironments, possibly tidally-influenced delta systems. Swim tracks and their associated invertebrate fossil assemblages may actually identify regressive systems tracks in the Moenkopi Formation and the multiple transgressive/regressive cycles recorded throughout this rock unit provide an excellent stratigraphic record with which to test this hypothesis.

Due to the paucity of reptile skeletal remains from the Lower Triassic deposits of western North America, reptile trackways are invaluable, as well as integral, to our understanding of Early Triassic reptile diversity, evolution, and paleoecology. As evidence of aquatic behavior, swim tracks give unique insights into reptilian behaviors during this time period which cannot be gained by other means. They also provide an opportunity to study the paleoecology of a well-preserved portion of the terrestrial realm during the Early Triassic, the diversity and aquatic behaviors of reptiles at that time, and the degree to which these ecosystems had recovered from the Permian/Triassic mass extinction in North America. Because a similar diversity of reptile tracks, including swim tracks, is known from coeval strata in Europe (Klein & Niedźwiedzki, 2012) to which trace fossils from western North America can be compared, behavioral and paleoenvironmental interpretations from this study have implications for understanding the global restructuring of ecosystems after the Permian/Triassic mass extinction.

This research will be accomplished through detailed qualitative observations and quantitative measurements of subaqueous swim tracks, their comparison to the already well known and thoroughly described fully terrestrial reptile tracks from the Moenkopi and Red Peak formations, their observed associations with the latter and with invertebrate trace fossils, and analyses of measured stratigraphic sections from several swim track localities throughout western North America. All of the field work needed to acquire the stratigraphic sections and swim track measurements will be accomplished over a time span of about 1-2 months during the summer of 2013. The rest of the work will be done throughout the year in the form of visits to the museums which house many of the known reptile track specimens from the Moenkopi Formation, including the University of California Museum of Paleontology, the Museum of Northern Arizona, and the New Mexico Museum of Natural History and Science.

Results from this study will bear directly on our understanding of early Triassic ecosystems and dissemination of these results will be accomplished through their publication in scientific journals such as PLoS ONE, and PALAIOS. Abstract submissions describing the results from portions of this study are planned for the upcoming 2013 annual meetings of the Geological Society of America and the Society of Vertebrate Paleontology.

Swim tracks are unique to the Mesozoic and provide an insight into post-extinction reptile taxa, the ecology of the terrestrial realm and the behavior of these reptiles. Mesozoic reptiles hold the fascination of young and old alike and are therefore excellent gateways to educating the public about scientific concepts. Fossil footprints, especially swim tracks, are even more engaging because they represent moments in time where an ancient living organism interacted with its environment, as opposed to fossil bones which most of the public perceive as just a dead animal. These aspects of Early Triassic reptilian tracks make them invaluable for engaging the public in science education about how terrestrial ecosystems have recovered from past extinction events. Outreach programs at the University of California, Riverside, such as the Geoscience Education Outreach Program and science fair mentoring for elementary school children, as well as outreach programs elsewhere, have and will benefit greatly as the science of past ecosystems becomes more accessible through fossil tracks and trackways.

BIBLIOGRAPHY

Boyd, D.W., 1975. False or misleading traces, *in* Frey, R.W., ed., The Study of Trace Fossils, p. 65-83.

Kirby, R.E., 1987. Orientation and origin of sole traces from the Moenkopi Formation (Early Triassic), northeastern Arizona: Journal of the Arizona-Nevada Academy of Science, v. 22 (Supplement), p. 42-43.

Klein, H., & Lucas, S.G., 2010. Review of the tetrapod ichnofauna of the Moenkopi Formation/Group (Early-Middle Triassic) of the American Southwest: *New Mexico Museum of Natural History and Science Bulletin 50*, 67 p.

Klein, H., & Niedźwiedzki, G., 2012. Revision of the Lower Triassic tetrapod ichnofauna from Wióry, Holy Cross Mountains, Poland: *New Mexico Museum of Natural History and Science Bulletin 56*, 62 p.

Lovelace, D.M., & Lovelace, S.D., 2012. Paleoenvironments and paleoecology of a Lower Triassic invertebrate and vertebrate ichnoassemblage from the Red Peak Formation (Chugwater Group), central Wyoming: *PALAIOS*, v. 27, n. 9, p. 636-657.

Milner, A.R.C., Lockley, M.G., & Kirkland, J.I., 2006. A large collection of well-preserved theropod dinosaur swim tracks from the Lower Jurassic Moenave Formation, St. George, Utah: *New Mexico Museum of Natural History and Science Bulletin 37*, p. 315-328.

Milner, A.R.C., Harris, J.D., Lockley, M.G., Kirkland, J.I., & Matthews, N.A., 2009. Bird-like anatomy, posture, and behavior revealed by an Early Jurassic theropod dinosaur resting trace: *PLos ONE*, v. 4, n. 3, e4591.

Morales, M., 1987. Terrestrial fauna and flora from the Triassic Moenkopi Formation of the southwestern United States: *Journal of the Arizona-Nevada Academy of Science*, v. 22, p. 1-20.

Peabody, F.E., 1947. Current crescents in the Triassic Moenkopi Formation: *Journal of*

Sedimentary Petrology, v. 17, n. 2, p. 73-76.

Peabody, F.E., 1956. Ichnites from the Triassic Moenkopi Formation of Arizona and Utah: Journal of Paleontology, v. 30, n. 3, p. 731-740.

Romilio, A., Tucker, R.T., & Salisbury, S.W., 2013. Reevaluation of the Lark Quarry dinosaur Tracksite (late Albian-Cenomanian Winton Formation, central-western Queensland, Australia): no longer a stampede?: *Journal of Vertebrate Paleontology*, v. 33, n. 1., p. 102-120.

Thomson, 2011. Aquatic behavior and locomotion of archosauriform reptiles interpreted from Early-Middle Triassic swim tracks of the western United States: *Journal of Vertebrate Paleontology, Abstracts of Papers*, v. 31, n. 3, p. 204.

Thomson, 2012. Regionally conserved swim track morphotypes from the Early Triassic of western North America: *Geological Society of America, Abstracts with Programs*, v. 44, n. 7, p. 500.