INTRODUCTION

Experiments on the transport of skeletal remains in controlled fluvial systems have been of significant use in deciphering relative hydrodynamic properties and behaviors of remains in vertebrate taphonomic studies (e.g. Voorhies, 1969; Behrensmeyer, 1975; Boaz and Behrensmeyer, 1976; Hanson, 1980; Blob, 1997; Nasti, 2005; Peterson and Bigalke, 2013). A majority of previous flume experiments have been conducted on a variety of macrovertebrate taxonomic groups, such as mammals and dinosaurs (e.g. Voorhies, 1969; Behrensmeyer, 1975; Boaz and Behrensmeyer, 1976; Coard and Dennell, 1995; Coard, 1999; Nasti, 2005; Peterson and Bigalke, 2013). ~~While~~ Although microvertebrate remains are commonly collected and utilized for paleoecological and taphonomic reconstructions, few studies have employed flume experiments to explore the role of differing relative hydrodynamic properties in the development of microvertebrate assemblages or “microsites” (e.g. Dodson, 1973; Blob, 1997; Trapani, 1998).

“Microsites” are accumulations of small, fragmentary, moderately to well-sorted ~~small~~ fossil material, including largely disarticulated vertebrate remains, typically dominated by fish scales, bone fragments, and shed teeth (Wood et al., 1988). ~~While~~ Although scales and bone fragments are of interest for their potential uses in taphonomic reconstructions (e.g. Blob and Fiorillo, 1996; Wilson 2008; Peterson et al, 2011), the abundance of shed dinosaur teeth in Mesozoic deposits is of particular interest in attempts to infer dental physiology (Sereno and Wilson, 2005; D’Emic et al., 2013), feeding behaviors (Jennings and Hasiotis, 2006), paleoecology (Bakker and Bir, 2004), and their potential for population studies (Erickson, 1996).

Comment [t1]: ‘While’ implies time.

However, interpretations regarding feeding behaviors, paleoecology, and population dynamics based on shed teeth may be biased by taphonomic processes such as fluvial sorting influenced by tooth shape: shed teeth (removed from the skull ~~*en*~~ *in vivo*) and teeth possessing roots (removed from the skull *post-mortem*) may behave differently in fluvial settings due to their shape differences ~~in shape~~. In order to determine the role of fluvial processes on the preservation and distribution of shed and root-bearing dinosaur teeth, an experiment was conducted to ascertain the hydrodynamic properties of two morphologically distinct sets of dinosaur teeth from Late Jurassic theropods and sauropods. Presented here are the results of this experiment and a discussion on the potential biases of shed teeth in the fossil record.

Institutional Abbreviations

UWO-VPC – University of Wisconsin Oshkosh Vertebrate Paleontology Cast Collection, Oshkosh, WI, USA.

MATERIALS AND METHODS

To test for variation in relative transport distances in theropod and sauropod teeth in fluvial settings, casts were made of four different dinosaur teeth using a urethane resin and placed in a recirculating flume at increasing stages of flow velocity. Casts were chosen ~~over~~ instead of ~~utilizing~~ fossil teeth in order to avoid damage to delicate fossil specimens, and to maintain a consistent specific gravity among specimens. Tooth casts were produced using Replicator 400^{TM} (Alumilite), which has a cured specific gravity of approximately 1.5 g/cm^3. Enamel and dentine have specific gravities of 2.8 g/cm^3 and 2.3 g/cm^3~~,~~ respectively (Brekhus and Armstrong, 1935). While the specific gravity of the casting resin is different than that of teeth, relative comparisons can be conducted among cast elements of different shapes with the use of this standardized specific gravity.

Comment [t2]: Surely this can't be a serious problem, given the availability of such fossils.

The four specimens of dinosaur teeth were chosen based on their differences in shape, size, and representation in the fossil record (Blob and Fiorillo, 1996) (Table 1). To model theropod and sauropod teeth associated with *post-mortem* cranial disarticulation, a single set of casts were was produced of root-bearing maxillary tooth specimens of *Camarasaurus* (UWO-VPC-2013.003) and *Allosaurus* (UWO-VPC-2013.001) (Figure 1A, B). The *Camarasaurus* tooth cast UWO-VPC-2013.003 was cast made from a shed crown and attached to a sculpted root. Similarly, to model shed theropod and sauropod teeth associated with tooth regeneration *in vivo*, a second set of casts were was produced (UWO-VPC-2013.002 and UWO-VPC-2013.004) with the root portions of the casts removed (Figure 1 C, D). The casts used in this study are housed at the University of Wisconsin Oshkosh Department of Geology, and were based on specimens in private collections. Casts were also digitized into 3D models using a NextEngine Desktop 3D Scanner and processed with ScanStudio HD Pro (NextEngine) (Figures S1-S4, Text S1).

Comment [t3]: 'set' is singular

Comment [t4]: Why wasn't a real tooth used?

Comment [t5]: Great idea!

Transport experiments were conducted at the re-circulating flume maintained at the University of Wisconsin-Oshkosh Department of Geology. The flume measures 0.45 m deep x 0.15 m wide and 3.5 m in length (Figure 2), and was filled to maintain a depth of 10 cm during trials. To determine relative transport distances associated with flow velocity, tests were conducted on a planar glass surface in 10 cm water depth. Each tooth cast was repeatedly placed in the flume perpendicular and parallel to flow (Figure 3A-F) at three different velocity settings; 10.0–19.9 cm/sec, 20.0–29.9 cm/sec, and 30.0–39.9 cm/sec. The apex of the tooth crown was pointed in the upstream direction for trials where the teeth were placed parallel to flow (Figure 3B, D). Additionally, trials ran in the perpendicular direction involved placing the apex of the tooth crown perpendicular to flow (Figure 3A, C). Each test consisted of 10 trials per tooth cast in each orientation and at each velocity stage. To avoid interactions between tooth casts during transport, casts were placed in the flume alone during for the duration of the experiment. Total

Comment [t6]: I wonder how these compare to estimated fluvial flow rates during the Jurassic.

transport distance and flow velocity at the location of settling were collected for each trial. Relative transport distance serves as a ~~relative~~ proxy for relative time of transport ~~duration~~ and offers insight into time averaging (Aslan and Behrensmeyer, 1996). Relative transport distance data also serve as ~~relative~~ comparisons of the relative transportability among tooth casts. Entrainment velocity, the velocity required to move the casts, was determined by recording the fluvial velocity (HACH FH950 Portable Velocity System) at the location of settling.

Statistical Methods

Analysis of variance (ANOVA) was employed to compare the mean transport distances of the four tooth casts under different flow velocities. An initial one-way ANOVA found no significant difference between the transport distances of parallel- and perpendicular-oriented datasets (Figure 4); each dataset is therefore analyzed independently. A two-factor ANOVA followed by a Bonferroni multiple comparisons test was run for each dataset. The Bonferroni test compares the simple effects of tooth cast shape within each velocity range, utilizing a conservative single-family grouping for all comparisons. A nominal significance level of 0.05 was used in all ANOVA tests to reject the null hypothesis that the mean transport distances are the same for all tooth shapes and at all flow velocities. All analyses were carried out using Prism version 6.0c for Macintosh (GraphPad Software, La Jolla California USA, www.graphpad.com).

Comment [t7]: Were samples normal, as assumed by ANOVA?

RESULTS

During flume tests, teeth commonly initiated transport by sliding on the bottom of the flume~~,~~; however, in a few instances, teeth rolled for a short distance and then slid to their final ~~de~~position. Two-factor ANOVA tests produced multiple significant results. Perpendicular-oriented tooth casts were found to vary significantly in transport distance due to tooth morphology (F=17.00, df=3, p<0.0001) and flow velocity (F=33.80, df=2, p<0.0001), with a strong interaction effect (F=10.56, df=6, p<0.0001) (Table 2A). The Bonferroni test indicates that significant differences occur between the shed *Camarasaurus* tooth and all other tooth cast specimens (p<0.0001), but only at high velocities (30–39.9 cm/s) (Table 2B). The strong interaction effect in the two-factor ANOVA is likely due to the unusual behavior of the shed *Camarasaurus* tooth cast at high velocities. All other comparisons were not significant in the other flow velocity ranges.

Two-factor ANOVA results of tooth casts oriented parallel to flow indicated significant differences in mean transport distance due to tooth morphology (F=12.38, df=3, p<0.0001) and flow velocity (F= 27.95, df=2, p<0.0001) (Table 2C), with no significant interaction effect. The Bonferroni test shows that the most significant differences occur between the shed *Camarasaurus* tooth and rooted *Allosaurus* tooth casts (p<0.01) at high velocities (30–39.9 cm/s), and shed *Camarasaurus* tooth and rooted *Camarasaurus* tooth casts at both intermediate (20.0–29.9 cm/s) and high velocities (p<0.001) (Table 2D).

DISCUSSION

These results demonstrate a close link between shape differences in vertebrate teeth and their potential representation in a fossil assemblage due to the influence of shape on hydrodynamic behavior (Behrensmeyer, 1975; Coard and Dennell, 1995; Peterson and Bigalke, 2013). The initial orientation of the tooth (parallel vs. perpendicular) had no significant effect on relative transport distance (Figure 4). The most notable difference in hydrodynamic behavior is observed between shed and rooted teeth, where shed teeth travelled further than rooted teeth under most conditions (Figure 5A, B). However, the interaction effect noted in the two-way ANOVA results show that the hydrodynamic behavior of each tooth shape varies with flow velocity. At lower flow velocity, the teeth may behave more similarly with the differences in hydrodynamic behavior becoming more apparent at higher flow velocities. This has been previously noted for other skeletal elements during fluvial transport (e.g. Voorhies, 1969).

Comment [t8]: This should be moved to Results.

Shed and root-bearing teeth differ significantly in hydrodynamic behavior and thus have an increased likelihood of contributing preservational biases; elongate~~-shaped~~ teeth (i.e. root-bearing) and teeth approaching a conical shape (i.e. shed theropod teeth) do not transport as far with increasing flow velocities as compact~~-shaped~~ teeth (i.e. shed *Camarasaurus* teeth). This suggests that compact~~-shaped~~ teeth~~, such as shed *Camarasaurus* teeth,~~ have a higher transport potential~~ for continued transport,~~ while elongate~~-~~ and conical~~-shaped~~ teeth~~, such as the root-bearing teeth of *Camarasaurus* and the shed and root-bearing teeth of *Allosaurus*,~~ are more likely to remain as lag, thus increasing their potential for preservation in the fossil record.

Comment [t9]: Redundant

Comment [t10]: In my experience with microsites, teeth are most often preserved without roots.

This may be tested by comparing the abundance, taphonomic signatures (i.e., quartz-grain equivalence, sorting, weathering, etc.), and distal proximity of root-bearing teeth to their original cranial elements. Indeed, root-bearing teeth are typically discovered relatively close to other skeletal remains, as they were removed during *post-mortem* cranial disarticulation and show relatively little transport (e.g. Breithaupt, 2001; Lehman and Coulson, 2002; Derstler and Myers, 2008). This is also supported by the high frequency of shed theropod teeth associated with proposed feeding sites (e.g. Argast et al., 1987; Bakker, 1997; Jennings and Hasiotis, 2006; Roach and Brinkman, 2007).

Comment [t11]: What?

Comment [t12]: I'm not sure how important this observation is as it relates to the relative transportability of root-bearing vs. shed teeth. Shed teeth aren't likely to occur near associated skeletons anyway because they are shed in life, as the animal is on the move, not after death.

Comment [t13]: Ditto. How does the association of shed teeth with feeding sites relate to transportability?

These results provide further support for an interaction between conditions in the depositional environment and transported elements. Despite finding no statistically significant difference in average transport distance between perpendicular and parallel orientations, a great degree of variability occurred within and between the different velocity ranges. Hydrodynamic behavior (as measured by relative transport distance) depended on the flow velocity. If flow conditions were not interacting with the hydrodynamic properties of each tooth, one would expect to see a linear response and relatively fixed differences among the tooth morphologies. The non-linear responses were found across velocity ranges and tooth morphologies. This variability is most apparent in perpendicular-oriented trials. Environment of deposition plays a role in assembly of lags and microsites (Rogers and Brady, 2010). More kinds of teeth of varying shapes may indicate shorter transport distance, whereas many similar kinds of teeth may be more affected by transport (either carried in or winnowed). It is important to consider that differences in substrate could have implications not addressed in this preliminary study of hydrodynamic tooth behavior. Further work exploring these questions, including interactions with different substrate types, will be necessary.

Comment [t14]: This appears to be the the case with the shed Allosaurus teeth.

The variable transportability of shed and root-bearing teeth has important implications for taphonomic reconstructions. The results shown here indicate that, not only does tooth morphology matter in transport potential, but the interaction between hydrodynamic properties of tooth shape and conditions in the depositional environment that contribute to microfossil accumulations. ~~While~~ Although this study focused on just two common Jurassic taxa, further experimental studies on the taphonomy of shed teeth of varying morphologies have the potential to indicate preservation biases in a microfossil assemblage that may influence interpretations of dinosaur population dynamics, paleoecology, and feeding behaviors.

Comment [t15]: It is necessary to go into further detail, here, with practical examples.

Comment [t16]: Awkward.

Comment [t17]: How?

ACKNOWLEDGEMENTS

We thank Collin Dischler (UWO) for assistance in producing tooth casts, Patty Ralrick, Mike Newbry (TMP), and James Farlow (IPFW), stimulating discussion and experimental design, Tom Suszek and Ben Sanderfoot (UWO) and Roy Plotnick (UIC) for assistance in running the flume systems. We also thank Heinrich Mallison (MfN) for encouragement and assistance at PeerJ.

References

ARGAST, S., FARLOW, J.O., GABET, R.M., AND BRINKMAN, D.L., 1987, Transport-induced abrasion of fossil reptilian teeth: implications for the existence of Tertiary dinosaurs in the Hell Creek Formation, Montana. Geology 15: 927-930.

ASLAN, A., AND BEHRENSMEYER, A.K., 1975, Taphonomy and a time resolution of bone assemblages in a contemporary fluvial system: the East Fork River, Wyoming. PALAIOS, v. 11, p. 411–421.

BAKKER, R.T., 1997, Raptor family values: allosaur parents brought giant carcasses in to their lair to feed their young. D.L. Wolberg, E. Stump, G.D. Rosenberg (Eds.), Dinofest International, Academy of Natural Sciences, Philadelphia: 1997. pp. 51–63

BAKKER, R.T., AND BIR, G., 2004, Dinosaur crime scene investigations: theropod behavior at Como Bluff, Wyoming, and the evolution of birdness. In: Currie P.J, Koppelhus E.B, Shugar M.A, Wright J.L, editors. Feathered dragons. Indiana University Press; Bloomington, IN: 2004. pp. 301–342.

BEHRENSMEYER, A.K., 1975, The taphonomy and paleoecology of Plio-Pleistocene vertebrate assemblages east of Lake Rudolf, Kenya: Bulletin of the Museum of Comparative Zoology, v. 145, p. 473–574.

BLOB, R.W. AND FIORILLO, A.R., 1996, The significance of vertebrate microfossil size and shape distributions for faunal abundance reconstructions: a Late Cretaceous example. *Paleobiology*, 22:422-435.

BLOB, R.W., 1997, Relative hydrodynamic dispersal potentials of soft-shelled turtle elements: implications for interpreting skeletal sorting in assemblages of non-mammalian terrestrial vertebrates. PALAIOS, v. 12, p. 151–164.

BOAZ, N. and BEHRENSMEYER, A.K., 1976, Hominid taphonomy: transport of human skeletal parts in an artificial fluviatile environment; American Journal of Physical Anthropology, v. 45, p. 53–60.

BREITHAUPT, B.H., 2001, The case of "Big Al" the *Allosaurus*: a study in paleodetective partnerships, p. 95-106 In Santucci, V.L. and McClelland, L. (eds.) Proceedings of the 6th Fossil Resource Conference (National Park Service, U.S. Department of the Interior, Geologic Resources Division Technical Report (NPS/NRGRD/GRDTR-01/01) p. 226.

BREKHUS, P.J. AND ARMSTRONG, W.D., 1935, A method for the separation of enamel, dentin, and cementum. Journal of Dental Research 15(1): 23-29.

COARD, R., 1999, One bone, two bones, wet bones, dry bones: Transport potentials under experimental controls: Journal of Archaeological Science, v. 26, p. 1369–1375.

COARD, R. AND DENNELL, R.W., 1995, Taphonomy of some articulated skeletal remains: Transport potential in an artificial environment: Journal of Archaeological Science, v. 22, p. 441–448.

D'EMIC, M.D., WHITLOCK, J.A., SMITH, K.M., FISHER, D.C., AND WILSON, J.A., 2013, Evolution of high tooth replacement rates in sauropod dinosaurs. PLoS ONE 8(7): e69235. doi:10.1371/journal.pone.0069235

DERSTLER, K. AND MYERS, J.M. 2008. Taphonomy of the *Tyrannosaurus rex* Peck's Rex from the Hell Creek Formation of Montana. In Tyrannosaurus rex: The Tyrant King, P Larson and K Carpenter (eds) p. 75-82. Indiana University Press

DODSON, P., 1973, The significance of small bones in paleoecological interpretation: Contributions to Geology, v. 12, p. 15–19.

ERICKSON G.M., 1996, Incremental lines of von Ebner in dinosaurs and the assessment of tooth replacement rates using growth line counts. Proceedings of the National Academy of Sciences 93: 14623–14627.

HANSON, C.B., 1980, Fluvial taphonomic processes: models and experiments, *in* Behrensmeyer, A.K., and Hill, A., eds., Fossils in the Making: University of Chicago Press, Chicago, p. 156–181.

JENNINGS, D.S., AND HASIOTIS S.T., 2006, Taphonomic analysis of a dinosaur feeding site using geographic information systems (GIS), Morrison Formation, southern Bighorn Basin, Wyoming, USA. Palaios 21(5): 480-492.

LEHMAN, T.M. AND COULSON, A.B., 2002, A juvenile specmen of the sauropod dinosaur *Alamosaurus sanjuanensis* from the upper cretaceous of big bend national park, texas. Journal of Paleontology 76(1):156-172.

NASTI, A., 2005, Dragging and scattering of camelid bones by fluvial action in the Real Grande Gorge, Province of Catamarea, Southern Argentinean Puna. Journal of Taphonomy 3(4): 173-183.

PETERSON, J.E. AND BIGALKE, C.L., 2013, Hydrodynamic behaviors of pachycephalosaurid domes in controlled fluvial settings: a case study in experimental dinosaur taphonomy. Palaios 28(5): 285-292.

ROACH, B.T. AND BRINKMAN, D.L., 2007, A reevaluation of cooperative pack hunting and gregariousness in *Deinonychus antirrhopus* and other nonavian theropod dinosaurs. Bulletin of the Peadoby Musuem of Natural History 48(1): 103-138.

ROGERS, R.R., AND BRADY, M.E., 2010, Origins of microfossil bonebeds: insights from the Upper Cretaceous Judith River Formation of north-central Montana. Paleobiology 36(1): 80-112.

SERENO, P.C. AND WILSON, J.A., 2005, Structure and evolution of a sauropod tooth battery. In: Curry Rogers KA, Wilson JA, editors. The sauropods: evolution and paleobiology. Berkeley: University of California Press. 157–177.

TRAPANI, J., 1998, Hydrodynamic sorting of avian skeletal remains. Journal of Archaeological Science, v. 25, p. 477–487.

VOORHIES, M.R., 1969, Taphonomy and population dynamics of an early Pliocene vertebrate fauna, Knox County, Nebraska: University of Wyoming Contributions to Geology Special Paper, v. 1, p. 1–69.

WILSON, L.E., 2008, Comparative taphonomy and paleoecological reconstruction of two microvertebrate accumulations from the Late Cretaceous Hell Creek Formation (Maastrichtian), eastern Montana. Palaios 23(5): 289-297.

WOOD, M.W., THOMAS, R.G. and VISSER, J., 1988, Fluvial processes and vertebrate taphonomy: the Upper Cretaceous Judith River Formation, South-Central Dinosaur Provincial Park, Alberta, Canada: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 66, p. 127–143.

FIGURES AND TABLES

FIGURE 1: Photographs and cross-sectional outlines of cast specimens used in the flume experiment. A) Root-bearing *Camarasaurus* tooth (UWO-VPC-2013.003), B) Root-bearing *Allosaurus* tooth (UWO-VPC-2013.001), C) Shed *Camarasaurus* tooth (UWO-VPC-2013.004), and D) Shed *Allosaurus* tooth (UWO-VPC-2013.002). Scale bar = 5cm.

FIGURE 2: Recirculating flume facility at UW Oshkosh where experiments were conducted. Flume dimensions are 45cm tall x 14.5cm wide x 3.5m long.

Comment [t18]: A right-angle shot of the experimental apparatus would be preferable (with dimensions given on figure).

FIGURE 3: Examples of orientations of tooth casts. A) Root-bearing casts oriented perpendicular to flow, B) root-bearing casts oriented parallel to flow, C) shed casts oriented perpendicular to flow, D) shed casts oriented parallel to flow. E) Example of root-bearing *Allosaurus* tooth cast oriented parallel to flow, F) example of shed *Camarasaurus* tooth oriented perpendicular to flow.

FIGURE 4: Bar chart of relative transport distances for tooth casts placed A) perpendicular or B) parallel to flow. Error bars represent standard error.

Comment [t19]: For this and other figures, it would be preferable to write the correct genus name (not simply 'camarasaur' and 'allosaur').

FIGURE 5: A) Average transport distance of cast tooth specimens versus velocity ranges for specimens tested perpendicular to flow and B) parallel to flow. Error bars represent standard error.

TABLE 1: Dimensions and Properties of Cast Tooth Specimens

Comment [t20]: The cells in this table need readjusting.

TABLE 2: Two-factor ANOVA (A) and Bonferroni multiple comparison test (B) results for tooth cast transport distances tested perpendicular to flow; Two-factor ANOVA (C) and Bonferroni multiple comparison test (D) results for tooth cast transport distances tested parallel to flow. Adjusted P value refers to the exact multiplicity-adjusted p-value calculated in Prism version 6.0c.

Comment [t21]: Give abbreviations here.

SUPPORTING DATA

SUPPORTING TEXT 1: Scan data 3D models of tooth cast specimens.
SUPPORTING FIGURE 1: PDF of 3D model of root-bearing *Allosaurs* tooth (UWO-VPC-2013.01).
SUPPORTING FIGURE 2: PDF of 3D model of shed *Allosaurus* tooth (UWO-VPC-2013.02).
SUPPORTING FIGURE 3: PDF of 3D model of root-bearing *Camarasaurus* tooth (UWO-VPC-2013.03).
SUPPORTING FIGURE 4: PDF of 3D model of shed *Camarasaurus* tooth (UWO-VPC-2013.04).