BRILL

Amphibia-Reptilia 44 (2023): 313-323

brill.com/amre

The gator grapnel: pedal anchoring in the American alligator (*Alligator mississippiensis*)

Collin Walter, Michael Cramberg, Bruce A. Young*

Department of Anatomy, Kirksville College of Osteopathic Medicine, Kirksville, MO 63501, USA
*Corresponding author; e-mail: byoung@atsu.edu
ORCID iD: Young: 0000-0002-0988-7731

Received 17 November 2022; final revision received 4 May 2023; accepted 5 May 2023;
published online 23 May 2023; published in print 8 August 2023
Associate Editor: Sergio A. Balaguera-Reina

Abstract. To resist forward displacement of their body during non-locomotor behaviors such as feeding, American alligators (*Alligator mississippiensis*) hold their hindfeet vertical, then push the foot into the substrate so that the dorsum of the foot forms a contact area with the substrate. Herein this form of bracing is termed pedal anchoring. The purpose of the present study was to describe pedal anchoring and to demonstrate whether it entailed interaction between the hindfoot (pes) of *Alligator* and the substrate that differed from the interactions seen during locomotion. *Alligator* tracks were studied in the wild, during controlled field trials, and on a mud trackway in the laboratory; in each setting locomotor and pedal anchoring tracks were photographed, cast in Plaster of Paris, then features of the casts quantified. Statistical analysis demonstrated greater variation in the wild tracks, presumably reflecting the larger size and velocity ranges of the alligators involved, and suggested that the mud trackway used during the locomotor trials did not create significant artifact. Tracks produced during locomotion and pedal anchoring by the same alligators, on the same substrate, yielded significantly different quantitative features, different matrices of Pearson correlation coefficients, and different patterns of character distribution following Principal Component Analysis. These results all support the conclusion that pedal anchoring involves fundamentally different interaction between the pes and the substrate than occurs during locomotion.

Keywords: Archosaur, locomotion, Reptilia, trace fossils, trackways.

Introduction

Crocodylian trackways have long been studied as a means of gaining understanding for the interpretation of trackways left by other Archosaurs, particularly dinosaurs (Milàn and Falkingham, 2016). The American alligator (*Alligator mississippiensis*) is particularly useful for exploring the evolution of locomotor diversity in Archosaurs. Alligators have three different cursorial "gaits," the high walk, the low walk, and the gallop (e.g., Hutchinson et al., 2019) and can switch between gaits during locomotor sequences (Reilly and Elias, 1998). The different gaits influence the forces acting between the feet and the substrate (Kubo and Benton, 2009), and thus the tracks left by the crocodylian (Carpenter, 2009; Kubo, 2010). The tracks of *A. mississippiensis*, and other crocodylians, offer insight into the limb mechanics responsible for trackways of extinct Archosaurs (e.g., Falkingham et al., 2020), including the evolution of bipedalism in Crocodyliformes and other Archosaurs (Kim et al., 2020).

Crocodylian trackways are studied by measuring and casting trackways found in nature (Farlow and Elsey, 2010) or by having captive animals locomote over substrate beds in the laboratory (e.g., Milàn and Hedegaard, 2010). To better understand the diversity of limb mechanics in crocodylians, specimens have been trained to locomote over force plates (e.g., Willey et al., 2004; Iijima et al., 2021) or analyzed with cineradiography

Published with license by Koninklijke Brill NV | DOI: 10.1163/15685381-bja10141
 | ISSN: 0173-5373 (print) 1568-5381 (online)

(Gatesy, 1991). Increases in imaging technology now enable exploration of the functional interaction between the digits and the substrate during unrestrained locomotion (Turner and Gatesy, 2021).

Crocodylian limbs are not used solely for cursorial locomotion. American alligators, and other crocodylians, climb using their appendages (Dinets et al., 2014). *Alligator mississippiensis* scratches and digs with the limbs during nest building and the excavation of gator holes (McIlHenny, 1935; Kley and Kearney, 2007). There have been reports of crocodylians using their hindfeet as ovipositors (e.g., Brazaitis and Watanabe, 2011). The limbs are also used to help the animal maintain a purchase on the substrate, the behavior herein termed "pedal anchoring."

Pedal anchoring is distinct from braking. Braking is a normal consequence of locomotor footfall, and occurs primarily with the forefeet in *Alligator* (Willey et al., 2004). Pedal anchoring is not a locomotor behavior. During pedal anchoring the limbs are held relatively rigid, the tips of the digits are depressed into the substrate, then the dorsum of the hindfoot is used to apply force against the substrate in order to resist forward displacement of the alligator. While we have observed similar anchoring performed with the forefeet (manus), it is more commonly done with the hindfeet (pes). Pedal anchoring is commonly observed when an alligator has been noosed, but crocodylians also use the behavior in more natural contexts including; prey capture of large terrestrial animals out of the water (Pienaar, 1969; Shoop and Ruckdeschel, 1990); as an adjunct to "death rolling" during foraging or intraspecific conflict over a food item (Drumheller et al., 2019); and during inertial feeding of large objects (Cleuren and De Vree, 2000). The importance of axial or locomotor systems to feeding has been increasingly recognized (Higham, 2007; Montuelle and Kane, 2019); pedal anchoring may represent an appendicular contribution to feeding in *Alligator*.

The purpose of the present study is to describe pedal anchoring in *Alligator mississippiensis*, and to document that it involves different interactions with the substrate than are seen during locomotion.

Materials and methods

Wild tracks

During the end of June 2022, alligator tracks were located in the Rockefeller National Wildlife Refuge with the assistance of the Louisiana Department of Wildlife and Fisheries. Clean prints were photographed with a numbered scale, then casted using Plaster of Paris. To decrease the setting time of the Plaster of Paris, Potassium Sulfate (2% v/v) was added to the Plaster of Paris (Taqa et al., 2015), and the powders dissolved using water heated to 35°C (Clifton, 1973). Only a single cast was taken from each identified alligator trackway. A total of 20 pes and 11 manus casts were made in the wild; judging by their size, these wild prints were all from sub-adult (150-200 cm total length) and adult (>200 cm total length) alligators, though the smallest may have been from a juvenile (<150 cm) animal (for different age/size classes in *Alligator* see Lance, 1989 and Milnes et al., 2002). All of the tracks that were cast were known to be fresh (we benefitted from the scouting service of the game wardens) and were all gathered from the muddy edges of ponds under light rain.

Field trials

Eight sub-adult (150-187 cm total length) *Alligator mississippiensis* were wild caught at the Rockefeller National Wildlife Refuge. The mouth of each alligator was bound shut with vinyl tape, then it was placed in a large field cage. The field cages were transported to a trial site at the edge of a pond in the refuge. The trial site was selected due to the presence of a clean mud substrate which extended with little slope to the edge of the pond. A wooden palette was placed at the edge of the pond to serve as a stable platform for one researcher. Each alligator was removed from the field cage, fitted with a large fabric collar, then placed on the substrate approximately 4 m from the edge of the pond. A soft rope was attached to the collar and held by the researcher standing on the palette; a second researcher stood several meters away filming the alligator. The rope was kept slack and free of the alligator's limbs; the alligator, sensing an opportunity to escape, would locomote over the substrate then start swimming in the pond. Using the rope the researcher would pull the alligator from the pond, onto the substrate on the opposite side of the palette from the locomotor trial; when the alligator reached the shallows of the pond it would perform pedal anchoring. Locomotor and pedal anchoring prints were photographed and casted as described above. The field trials yielded 8 pes locomotor casts, and 10 pedal anchoring casts.

Lab trials

The eight sub-adult alligators were transported to Kirksville, MO and housed communally in a 29 m^2 facility that featured three submerging ponds, natural light, and artificial lights on a 12:12 cycle. The facility was maintained at 30-33°C, warm water rain showers were provided every 20 minutes, which helped maintain the facility at >75% relative humidity. The alligators were maintained on a diet of previously frozen adult rats. The husbandry and use of the live alligators followed all applicable federal guidelines, and were approved by the IACUC of A.T. Still University (Protocol #226, approved April 2022).

A trackway was constructed 235 cm long, 90 cm wide and 50 cm tall. The trackway was lined with a vinyl liner, then filled to a depth of 20 cm (approximately 0.42 m^3) with sifted fine topsoil. When wetted, this produced a soft clay-like mud. Before each trial the substrate was wetted and mixed by hand, then smoothed. To ensure consistency the substrate was tested using a 450 g probe with a blunt 1.2 cm diameter end; trials were only performed if the probe sunk 3-4 cm into the substrate at multiple testing points.

An individual alligator was noosed, its jaws taped shut with vinyl tape, then it was strapped to a 30 × 155 cm transport board. The transport board was placed at one end of the trackway. At the other end of the trackway, camouflage material and black light screens were used to create a dark "nest" visible to the alligator. In every trial, as soon as the animal was unstrapped from the transport board, it walked straight down the trackway and into the "nest." An overhead video camera (Action camera, YI Technology) was used to record each trial (see supplementary video S1 for an example of these videos). Video records were exported into Kinovea (kinovea.com), which was used to determine the instantaneous velocity of each footstep. Individual footprints were photographed and casted as detailed above.

One or two days following the walking trial, the same animal was again placed on the (freshly prepared) substrate for the "anchoring" trial. A soft rope handling noose was placed on the animal, then it was positioned in the middle of the trackway. A researcher would squat down facing the alligator and apply tension to the handling noose, pulling the animal toward the researcher. In this scenario the alligators never voluntarily advanced toward the researcher, instead they would pedal anchor with their pes and resist the tension being applied by the handling noose. Once the pedal anchoring behavior was observed the alligator was quickly lifted vertically off the trackway in order to preserve the pedal anchoring prints. Individual pedal anchoring prints were photographed and casted as detailed above. The laboratory trials yielded 15 manus locomotor casts, 25 pes locomotor casts, and 13 pedal anchoring casts.

Statistical analysis

All of the casted prints were soaked overnight in tap water, then cleaned in running water using a soft toothbrush. Once cleaned, the cast was dried for 24 h in a 37°C oven (Gallenkamp). The dried casts were photographed from multiple angles using a digital camera (D3100, Nikon) then the images imported into Image J (NIH) for quantification. Quantified features of the cast are listed in table 1 and illustrated in supplementary fig. S1. Additional representations of the casts were made using Metascan (Abound Labs). The initial analysis compared three different sets of locomotor pes casts (wild, field, and laboratory); these casts came from different alligators, moving at different speeds, over different substrates. For this analysis, Multivariate analysis of variance (MANOVA) was used to test for significant differences among the quantified features of the casts. Post-Hoc Tukey's tests were used to identify which sets of features were significantly different; the cut-off value for the Tukey's test was Bonferroni-adjusted down (to 0.0026) to account for the number of features tested. The two data sets (wild and laboratory) for the locomotor manus casts were from the same group of alligators moving at the same velocity range. These data were normalized using a Z-transformation, then each feature of the manus casts was compared using a two-tailed t-test with a Bonferroni-adjusted (down to 0.0022) threshold p value to account for the number of features tested. The pedal anchoring and locomotor pes data sets obtained from the trackway trials involved the same alligators. These data were normalized using a Z-transformation, then each feature of the pes casts was compared using a two-tailed t-test with a Bonferroni-adjusted (down to 0.0026) threshold p value to account for the number of features tested. To look for relationships among the quantified features of the casts, the Z-transformed data sets (which were all obtained from the same group of alligators) were used to create Pearson Correlation Coefficient matrixes and to perform Principle Component Analyses using Q Research Software (DisplayR, Chicago, USA).

Table 1. Quantified characters from the hindfoot (pes) casts; three additional characters were taken from the casts of the forefoot (manus).

Code	Feature
A	angle between digits 1 and 2
B	angle between digits 2 and 3
C	angle between digits 3 and 4
D	angle between the medial and lateral digits
E	horizontal length of digit 1
F	horizontal length of digit 2
G	horizontal length of digit 3
H	horizontal length of digit 4
I	medial to lateral span of digits
J	distance from base of pad to horizontal end of digit 2
K	distance from base of pad to horizontal end of digit 3
L	area of the plantar pad
M	vertical length of digit 1
N	vertical length of digit 2
O	vertical length of digit 3
P	vertical length of digit 4
Q	depth of pad base
R	depth of mid pad
S	depth of pad at base of digit 2

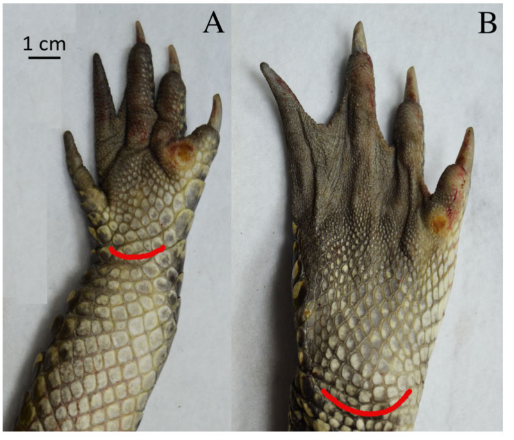


Figure 1. Palmar surface of the (A) manus (forefoot) and (B) pes (hindfoot) of a 178 cm total length *Alligator mississippiensis*. The red line denotes the approximate proximal margin of the palmar surface/pad. Note the marked discrepancy in the shape and size of the palmar surfaces of the manus and pes. The digits of the manus are numbered 1-5 from right to left; the digits of the pes are numbered 1-4 from right to left.

Results

The feet of Alligator mississippiensis

The manus of *A. mississippiensis* supports 5 digits, the fifth (and most lateral) digit, being well proximal to the remaining four (fig. 1A). The pad of the manus is relatively short proximal-distal; the plantar surface of the manus is broader than it is long (the length:width ratio of the manus in fig. 2B is 0.74). The pes supports 4 digits, with the third being the longest (fig. 1B). The pad of the pes is elongate proximal-distal; the plantar surface of the pes is longer than it is broad (the length:width ratio of the pes in fig. 2C is 1.34).

Description of the locomotor casts

The digits of the pes are weakly abducted during locomotion, giving the cast a crudely triangular shape (fig. 2). The phalanges flex during lift-off of the pes, so the distal phalanges typically penetrate further than the proximal phalanges (fig. 2); the third digit typically penetrates furthest. The digits of the pes typically all point in the same general direction. The pad of the pes is broadest at the proximal phalanges, then narrows to a rounded base (fig. 2); the proximal rounded base typically penetrates less into the substrate than the remainder of the foot. Examples of the 3-D scans of the pes locomotor casts are provided in (supplementary scans S1 and S2.

The fifth (most lateral) digit of the manus is often missing from tracks; when present it extends caudolaterally beyond the short plantar pad of the manus. The digits of the manus are typically abducted to a degree that the first and fourth digits are pointing in opposite directions (fig. 2). The pad is often poorly represented proximal to the base of digits 1-4; the footprint often resembles a pentagon with four radiating lines from the apex (fig. 2).

Comparison of the locomotor casts

All of the features quantified during the laboratory and field trials fell within the range of those same features determined from the wild casts. MANOVA, with a Bonferroni-adjusted p of 0.0026, revealed that 9 of the 19 quantified features (47%) of the pes locomotor casts were significantly different among the three data sets (supplementary table S1). Tukey's post-hoc analyses revealed that in all but one of the significantly different features, the difference was between the wild casts and the field trial casts, as well as the wild casts and the laboratory casts; but that the field trial and laboratory casts were not significantly different (supplementary table S1). A t-test, with a Bonferroni-adjusted p of 0.0022, performed on the Z-transformed data revealed that only 1 of the 22 (4.5%) quantified features of the manus locomotor casts were significantly different (supplementary table S2).

Description of the pedal anchoring casts

During pedal anchoring the pes is held more vertically and the digits are abducted (fig. 3A). The digits and dorsum of the pes may displace some of the substrate, often leaving scratches in the substrate and consistently creating a mound

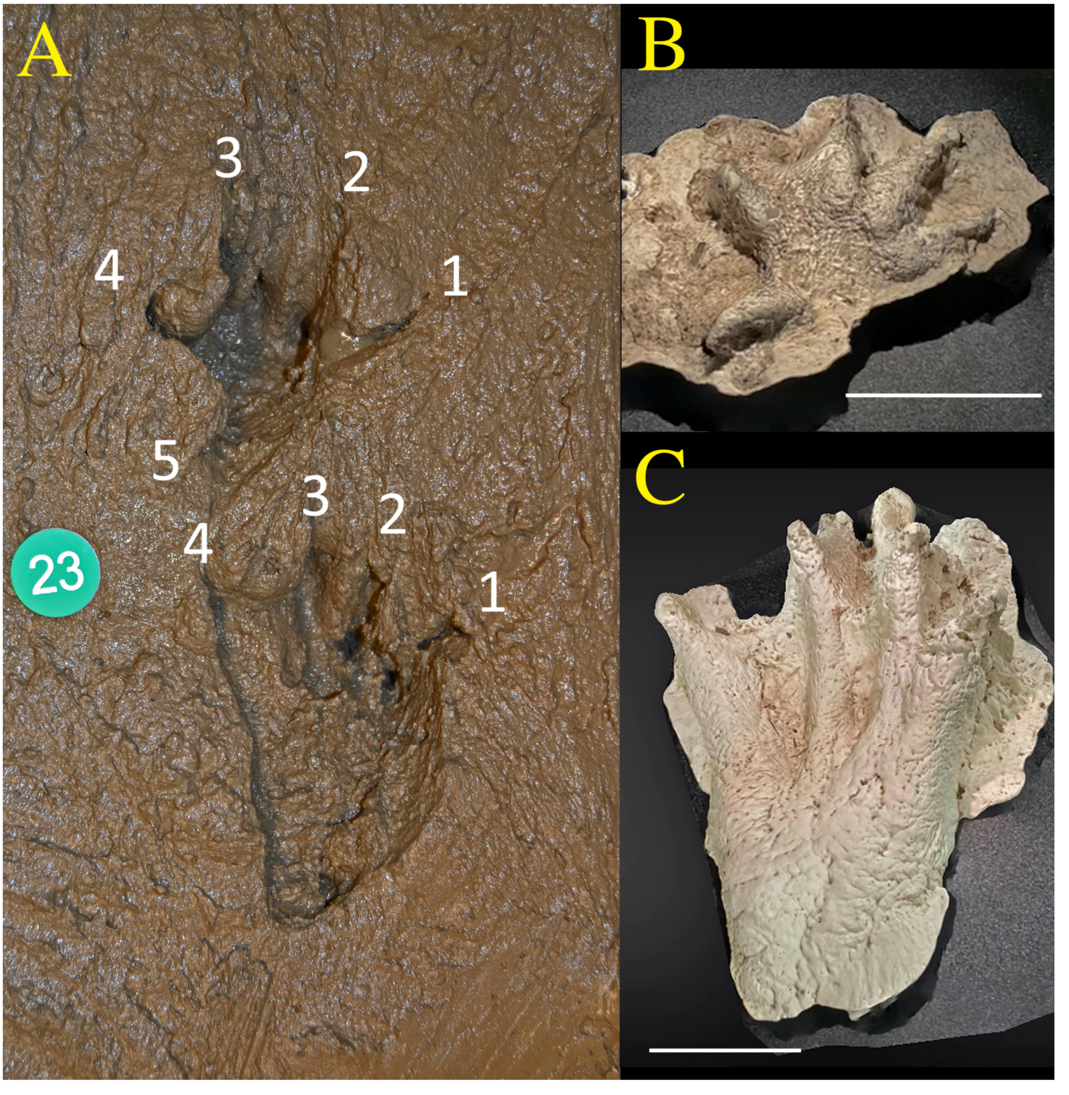


Figure 2. Trackway (A) photographed from above, and photographs of the plantar surface of Plaster of Paris footprints (B, C) from *Alligator mississippiensis*. The five digits of the manus (forefoot) are typically abducted, point in different directions, and little or no palmar pad is evident proximal to the digits (A, B). The four digits of the pes (hindfoot) show less abduction, point in the same general direction, and the palmar pad extends proximally well beyond the digits (A, C). The trackway (A) was formed from the left manus and pes, while the casts (B, C) are from the right manus and pes; because of this, in (B, C) the digits of the manus are numbered 1-5 from right to left, while the digits of the pes are numbered 1-4 from right to left. The numbered disk has a diameter of 1.1 cm; scale bar is 5 cm.

of substrate on the leading edge of the footprint/casts (fig. 3A, B). On the pedal anchoring casts the digits combine to form a leading edge, and there is often an indication of torsion in the pes (fig. 3B, C). Examples of the 3-D scans of pedal anchoring casts are provided in supplementary scans S3 and S4.

Comparison of pedal anchoring and locomotor casts

The casts produced when the eight specimens locomoted over the mud trackway were compared to the casts produced when the same animals performed pedal anchoring on the same substrate (to minimize variability, only

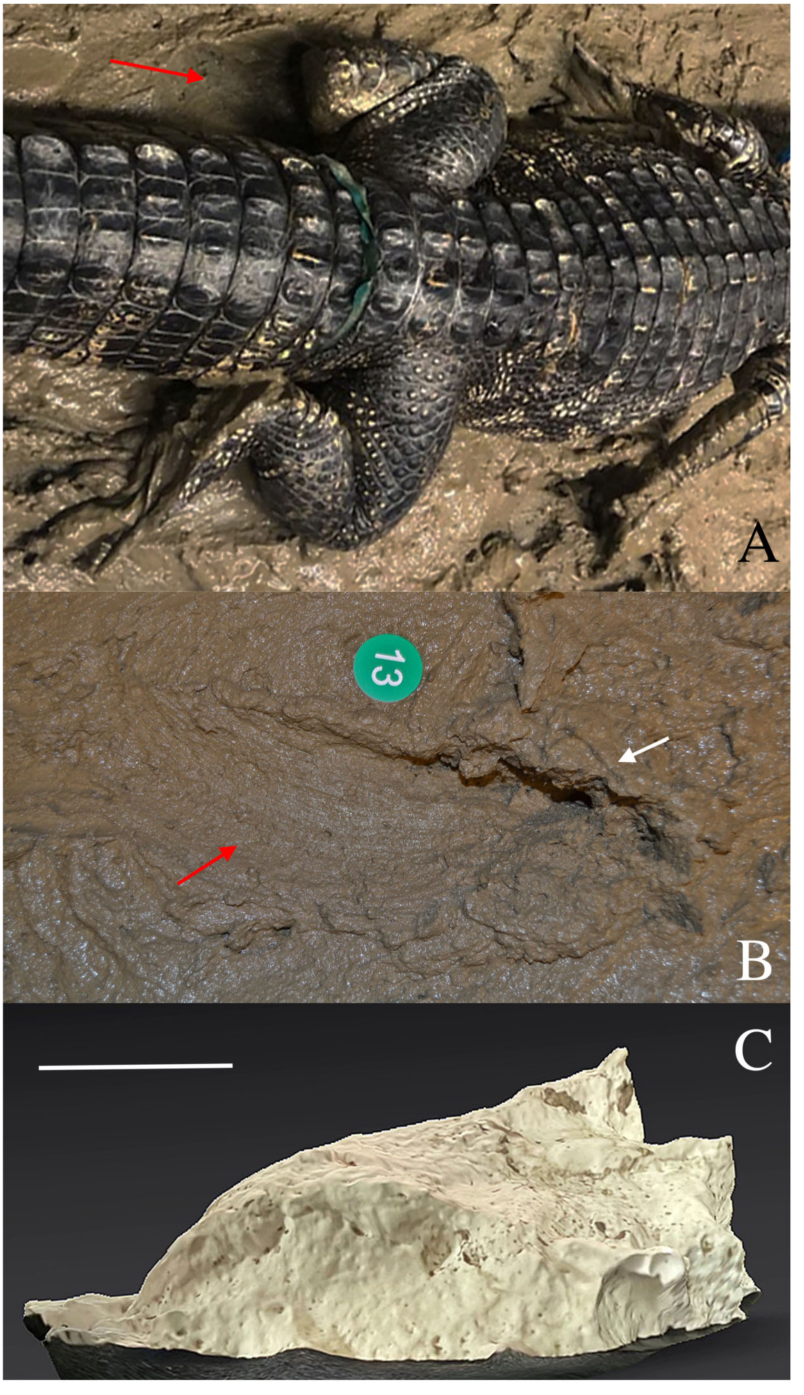
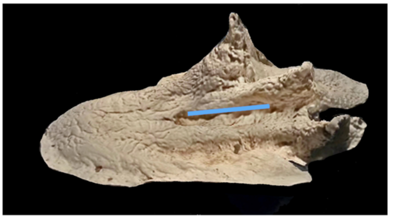


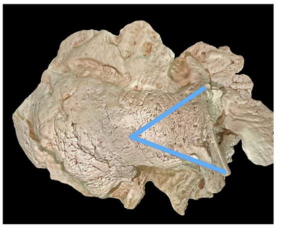
Figure 3. Pedal anchoring in *Alligator mississippiensis*. A) isolated image from a video of a 164 cm total length *Alligator mississippiensis* performing pedal anchoring on a mud trackway; note the vertical posture of the left pes (hindfoot) and the scrapes left in the substrate (red arrow); B) pedal anchoring trackway with the characteristic scraping (red arrow) and the berm of substrate on the leading edge (white arrow), the numbered disk has a diameter of 1.1 cm; C) 3-D image of a Plaster of Paris scan of a pedal anchoring track, note the depth from the surface (bottom of image) and the abrupt leading edge (right side), scale bar is 5 cm.

A



A	1.00																		
B	0.34	1.00																	
C	-0.10	-0.36	1.00																
D	0.83	0.57	0.23	1.00															
E	0.11	0.05	-0.10	0.07	1.00														
F	0.11	0.09	-0.10	0.07	0.86	1.00													
G	0.25	0.12	-0.15	0.16	0.74	0.92	1.00												
H	0.17	0.22	-0.09	0.20	0.69	0.78	0.83	1.00											
I	0.45	0.66	-0.11	0.58	0.14	0.18	0.31	0.41	1.00										
J	0.03	0.42	-0.31	0.03	0.28	0.28	0.22	0.19	0.63	1.00									
K	0.12	0.36	-0.27	0.10	0.25	0.24	0.31	0.24	0.75	0.90	1.00								
L	-0.13	0.21	-0.15	-0.10	-0.52	-0.58	-0.56	-0.49	0.39	0.55	0.52	1.00							
M	0.29	-0.05	0.01	0.23	0.08	-0.22	-0.28	-0.06	-0.05	-0.03	-0.06	0.01	1.00						
N	0.03	-0.05	-0.04	0.02	0.19	-0.06	-0.09	0.02	-0.27	-0.32	-0.29	-0.32	0.63	1.00					
O	0.25	-0.07	0.00	0.19	0.20	0.01	0.00	0.06	-0.19	-0.31	-0.25	-0.35	0.59	0.90	1.00				
P	0.38	0.21	-0.38	0.20	0.35	0.32	0.39	0.36	0.18	0.01	0.11	-0.24	0.11	0.51	0.62	1.00			
Q	0.55	0.44	-0.34	0.48	0.39	0.34	0.35	0.34	0.50	0.29	0.35	-0.10	0.27	0.27	0.37	0.42	1.00		
R	0.38	0.32	-0.25	0.36	0.43	0.32	0.29	0.29	0.43	0.40	0.45	0.01	0.34	0.36	0.48	0.52	0.82	1.00	
S	0.39	0.29	-0.26	0.35	0.39	0.26	0.22	0.25	0.25	0.23	0.26	-0.13	0.51	0.63	0.67	0.64	0.74	0.89	1.00
	A	**B**	**C**	**D**	**E**	**F**	**G**	**H**	**I**	**J**	**K**	**L**	**M**	**N**	**O**	**P**	**Q**	**R**	**S**

B



A	1.00																		
B	0.89	1.00																	
C	0.59	0.50	1.00																
D	0.95	0.90	0.78	1.00															
E	-0.08	-0.02	-0.21	-0.11	1.00														
F	0.06	0.02	0.01	0.04	0.55	1.00													
G	0.00	-0.06	0.17	0.05	0.18	0.62	1.00												
H	0.19	0.09	0.33	0.24	0.49	0.57	0.73	1.00											
I	0.30	0.38	0.41	0.40	0.40	0.27	0.10	0.37	1.00										
J	-0.29	-0.31	-0.31	-0.35	0.08	0.42	0.07	-0.16	-0.23	1.00									
K	-0.10	-0.05	0.11	-0.03	0.14	0.00	0.00	-0.02	0.09	0.40	1.00								
L	-0.44	-0.41	-0.35	-0.48	0.14	0.00	-0.15	-0.15	0.31	0.42	0.52	1.00							
M	-0.06	-0.13	-0.14	-0.13	-0.05	0.03	-0.02	-0.28	0.10	0.22	0.13	0.33	1.00						
N	0.36	0.05	0.35	0.31	-0.45	-0.05	0.07	-0.03	-0.02	-0.13	-0.06	-0.14	0.53	1.00					
O	0.50	0.27	0.68	0.55	-0.52	-0.09	-0.15	-0.09	0.10	-0.15	0.07	-0.13	0.16	0.72	1.00				
P	0.64	0.58	0.80	0.76	-0.46	-0.05	-0.08	0.01	0.19	-0.28	-0.14	-0.45	-0.37	0.30	0.74	1.00			
Q	0.15	0.29	0.00	0.15	-0.38	-0.15	-0.49	-0.60	-0.27	0.37	0.23	0.08	-0.06	-0.17	0.28	0.33	1.00		
R	0.27	0.33	0.01	0.22	-0.42	-0.18	-0.57	-0.66	-0.22	0.39	0.25	0.14	0.17	0.10	0.42	0.32	0.94	1.00	
S	0.31	0.36	-0.05	0.23	-0.37	-0.10	-0.49	-0.60	-0.19	0.48	0.20	0.14	0.26	0.11	0.33	0.23	0.88	0.97	1.00
	A	**B**	**C**	**D**	**E**	**F**	**G**	**H**	**I**	**J**	**K**	**L**	**M**	**N**	**O**	**P**	**Q**	**R**	**S**

Figure 4. Pearson correlation coefficient matrices from quantified features of the tracks due to locomotion (A) and pedal anchoring (B). Correlation coefficients greater than 0.75 have been highlighted in light blue. The distribution of negative and positive correlation values, as well as the highlighted correlation values differs between the two groups. The inset images illustrate the feature that had the highest overall correlations; for locomotion this was the horizontal length of the 2nd digit, while for the pedal anchoring it was the angle between the 1st and 4th digits.

laboratory-collected casts were used for this analysis). A t-test, with a Bonferroni-adjusted p of 0.0026, performed on the Z-transformed data revealed that 6 of the 19 (32%) quantified features of the pes were significantly different between the two behaviors (supplementary table S3). Pearson Correlation Coefficient matrices calculated from the two Z-transformed data sets (as well as the wild walking data sets) showed similar patterns of character correlations in the two locomotor data sets, but a different suite of correlations within the pedal anchoring features (fig. 4). Pes casts made during walking had the strongest correlations with the horizontal length of the second digit, while casts made during pedal anchoring had the strongest correlations with the total angle of the digits (fig. 4).

Principal Component Analysis (PCA) was performed on the z-transformed data from the laboratory locomotion and pedal anchoring trials. The locomotor analysis yielded a first component that was represented by the area and

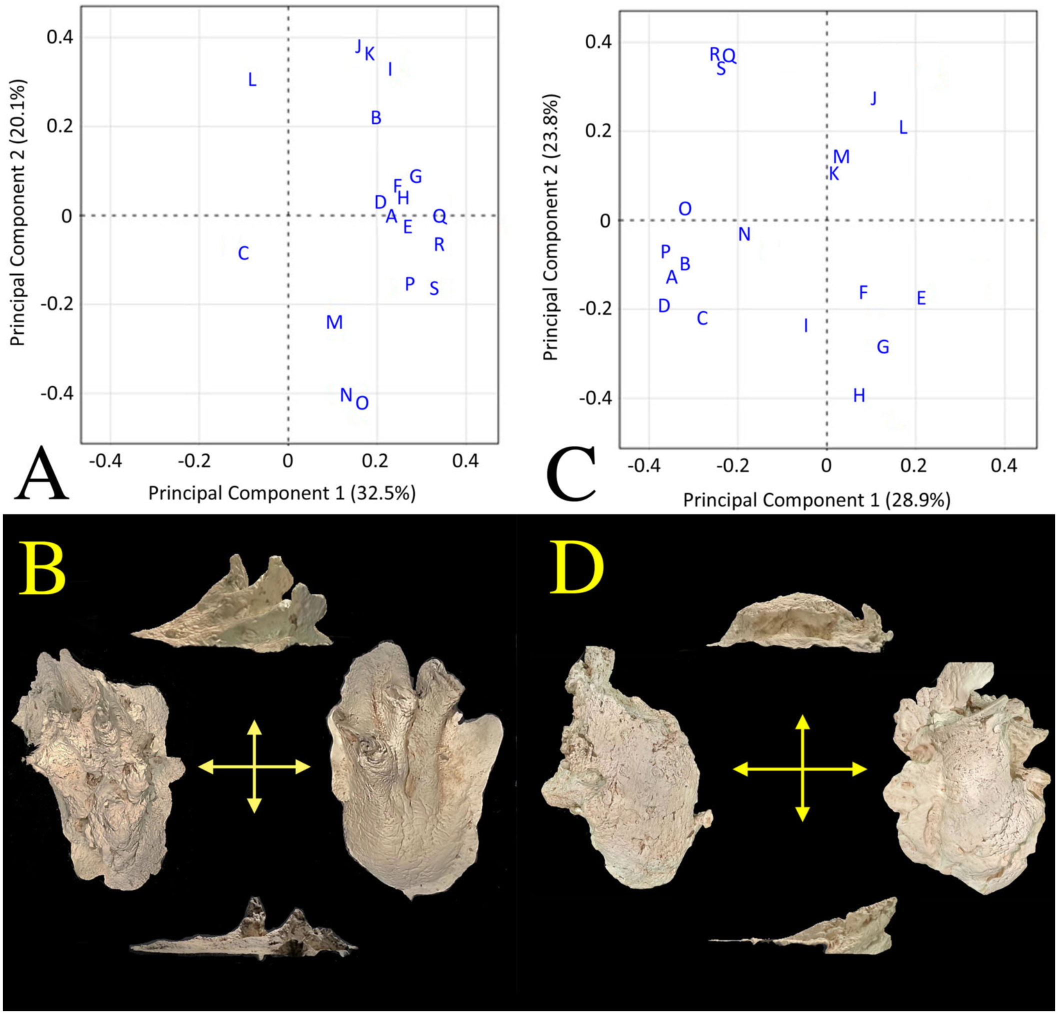


Figure 5. Principal Component Analysis of the quantitative features from locomotion (A) and pedal anchoring (C) tracks. Note the different distribution of the quantified characters. The first two Principle Components are illustrated using 3-D scans showing the range of the character with the highest component score. For locomotion (B) the first component was dominated by the area and depth of the foot pad, the second component was comprised of the length and depth of the digits. For pedal anchoring (D) the first component was dominated by the angle of the digits, the second component was comprised of the vertical depth of the foot pad.

vertical depth of the foot pad, and a second component that was represented by horizontal and vertical length of the digits (fig. 5A, C). The PCA character distributions for pedal anchoring and locomotion were distinct (fig. 5A, B). The pedal anchoring PCA produced a first component represented by the angle of the digits, and a second component represented by vertical depth of the foot pad (fig. 5B, D).

Discussion

Simplistically, the nature of the footprint formed by a locomoting alligator will be determined by three features (or sets of features): animal size, nature of the substrate, and the speed/gait of the alligator. When surveying at the Rockefeller National Wildlife Refuge for the "wild" footprints to cast, there was no control over substrate, speed/gait, or size of the alligator. Given that trackways were identified at a distance, there was likely a bias toward larger tracks. This is evident in the range of values for the linear features from the wild data set (supplementary table S1); the means of the laboratory and field data sets are all on the low end of the range determined for the wild data set (supplementary table S1). Of the 9 pes features which differed significantly between the wild and other data sets, 5 (or 56%) directly relate to the size of the animal.

The other two data sets used the same eight alligators, so no size difference exists. During the field and laboratory trials the alligators only employed low-walk locomotion; the mean velocity of the alligators during the field trials (22.3 m/s) was not (t $=$ 1.069, $p = 0.29$, n $=$ 1) significantly different from the mean velocity (30.7 m/s) during the laboratory trials. The mud trackway was designed to promote the alligator walking over a substrate that was specifically mixed to create a soft muddy clay. As noted above, and treated in detail by Melchor (2015), the nature of the substrate will influence the trackways. Having spent several days working with the muddy clay in Louisiana, we sought to approximate it with the trackway constructed in the lab. The fact that only one of the quantified features of the locomotor casts was significantly different between the field and laboratory trials (supplementary table S1) strongly suggests that the mud trackway functioned adequately for the purposes of this study.

Terrestrial locomotor propulsion in *A. mississippiensis* is produced primarily from the hind limb (Willey et al., 2004), though the relative contribution of the fore limb changes during ontogeny (Iijima et al., 2021). The manus of *A. mississippiensis* is smaller than the pes (fig. 1; Farlow and Elsey, 2010) though both follow a similar growth pattern (Livingston et al., 2009); the plantar pad of the manus is much smaller than that of the pes (fig. 1). This differential, and the different functional role, may explain why the manus casts exhibit less significant differences than the pes casts (4.5% vs. 56%; supplementary tables S1 and S2).

When the same eight alligators locomoted, then performed pedal anchoring, on the same substrate, 32% of the quantified features were significantly different (supplementary table S3). This is taken as a strong indication that pedal anchoring is, in fact, a different activity than locomotion. The number of significantly different features between the locomotor and pedal anchoring casts (restricted to the pes of the same animals moving over the same substrate) is an underestimate because the features chosen for quantification were those readily observed on all casts. Other features prominent in the pedal anchoring casts, such as torsion, were not quantified.

The distinctiveness of pedal anchoring is further supported by the matrices of Pearson Correlation Coefficients (fig. 4). The matrices were similar for wild and laboratory walking (this discussion is restricted to correlation coefficient values that exceed 0.75); but a different pattern of correlations was found in the pedal anchoring features (fig. 4). Similarly, PCA found similar clustering of variables between wild and laboratory locomotor casts, but a different pattern emerged from the analysis of pedal anchoring casts (fig. 5).

There are some clear limitations to the pedal anchoring behavior, perhaps the greatest being the penetrability of the substrate. When first noosed in captivity, all of these alligators would attempt to perform pedal anchoring, but the behavior was ineffective on the cement floor of their enclosure. One of the characteristic features of the pedal anchoring tracks is that they are more elongate than the locomotor tracks (figs. 2,3). Elongate tracks have been described from multiple dinosaur taxa; initially the elongation of the tracks were interpreted as the animal crouching (e.g., Lockley et al., 2003; Gierliński et al., 2009). More recently, Lallensack et al. (2022) argued that the elongation of these tracks was due to deeper substrate penetration, not a crouching posture. The summary figure used by Lallensack et al. (2022) to explain elongate tracks is very similar to the limb movements of *Alligator* during pedal anchoring, only with reversed chronology. The tracks produced during pedal anchoring have two fundamental differences from the elongate tracks previously described (e.g., Lockley et al., 2003; Gierliński et al., 2009; Lallensack et al, 2022); the presence of a leading berm or displacement rim, and grooves left by the dorsum of the digits (fig. 3). When sauropods slide against a substrate, they create a forward "berm" of substrate similar to what was produced by *Alligator* (Heredia et al., 2022); other sauropods perform a "bracing" movement, but with their tails, not their feet (Gillette and Thomas, 1985).

Understanding more about pedal anchoring, and the biological significance of pedal anchoring in fossil trackways, will require additional analyses of force transmission between the dorsum of the alligator's pes and the substrate. The biggest limitation of the present study was that it was restricted to the external surface of the pes and manus. Recent work (Turner and Gatesy, 2021) showed that the bones of the alligator pes are re-arranged during locomotion to facilitate interaction with the substrate. We hypothesize that there is another suite of active controls used by alligators during pedal anchoring, which results in both increased flexion of the digits and relative rigidity of the inter-tarsal joints.

Acknowledgements. This work was possible through the kind assistance of the Louisiana Department of Wildlife and Fisheries. Matthew Waite assisted with the field portion of this study; we thank Peter Kondrashov for his continued support.

Supplementary material. Supplementary material is available online at:
https://doi.org/10.6084/m9.figshare.22785203

References

Brazaitis, P., Watanabe, M.E. (2011): Crocodilian behaviour: a window to dinosaur behaviour? Hist. Biol. **23**: 73-90.

Carpenter, K. (2009): Role of lateral body bending in crocodylian track making. Ichnos **16**: 202-207.

Cleuren, J., De Vree, F. (2000): Feeding in crocodilians. In: Feeding: Form, Function, and Evolution in Tetrapod Vertebrates. Schwenk, K., Ed., Academic Press, New York.

Clifton, J.R. (1973): Some aspects of the setting and hardening of gypsum plaster. U.S. Nat. Bureau Stand. **75**: 1-28.

Dinets, V., Britton, A., Shirley, M. (2014): Climbing behaviour in extant crocodilians. Herpet. Notes **7**: 3-7.

Drumheller, S.K., Darlington, J., Vliet, K.A. (2019): Surveying death roll behavior across Crocodylia. Ethol. Ecol. Evol. **31**: 329-347.

Falkingham, P.L., Turner, M.L., Gatesy, S.M. (2020): Constructing and testing hypotheses of dinosaur foot motions from fossil tracks using digitization and simulation. Palaeontology **63**: 865-880.

Farlow, J.O., Elsey, R. (2010): Footprints and trackways of the American alligator, Rockefeller Wildlife Refuge, Louisiana. New Mexico Mus. Nat. Hist. Sci. Bull. **51**: 31-39.

Gatesy, S.M. (1991): Hind limb movements of the American alligator (*Alligator mississippiensis*) and postural grades. J. Zoology **224**: 577-588.

Gierliński, G.D., Lockley, M.G., Niedźwiedzki, G. (2009): A distinctive crouching theropod trace from the Lower Jurassic of Poland. Geol. Quart. **53**: 471-476.

Gillette, D.D., Thomas, D.A. (1985): Dinosaur tracks in the Dakota formation (Aptian-Albian) at Clayton Lake state park, Union county, New Mexico. In: New Mexico Geological Society 36th Annual Fall Field Conference Guidebook, p. 283-288. Lucas, S.G., Zidek, J., Eds.

Heredia, A.M., Pablo, J.P., Fernandez, D.E. (2022): Unusual sauropod slipping tracks preserved on a biostabilized tidal flat from the Lower Cretaceous of northern Patagonia, Argentina. Geol. Soc. London, Spec. Publ.: 522. DOI:10.1144/SP522-2021-136.

Higham, T.E. (2007): The integration of locomotion and prey capture in vertebrates: morphology, behavior, and performance. Integ. Comp. Biol. **47**: 82-95.

Hutchinson, J.R., Felkler, D., Houston, K., Chang, Y.M., Brueggen, J., Kledzik, D., Vliet, K.A. (2019): Divergent evolution of terrestrial locomotor abilities in extant Crocodylia. Sci. Rep. **9**: 19302.

Iijima, M., Munteanu, V.D., Elsey, R.M., Blob, R.W. (2021): Ontogenetic changes in limb posture, kinematics, forces and joint moments in American alligators (*Alligator mississippiensis*). J. Exp. Biol. **224**: 242990.

Kim, K.S., Lockley, M.G., Lim, J.D., Bae, S.M., Romilio, A. (2020): Trackway evidence for large bipedal crocodylomorphs from the Cretaceous of Korea. Sci. Rep. **10**: 1-13.

Kley, N.J., Kearney, M. (2007): Adaptations for digging and burrowing. In: Fins Into Limbs: Evolution, Development, and Transformation. Hall, B., Ed., University of Chicago Press, Chicago.

Kubo, T. (2010): Variation in modern crocodylian limb kinematics and its effect on trackways. New Mexico Mus. Nat. Hist. Sci. Bull. **51**: 51-53.

Kubo, T., Benton, M.J. (2009): Tetrapod postural shift estimated from Permian and Triassic trackways. Palaeontology **52**: 1029-1037.

Lallensack, J.N., Farlow, J.O., Falkingham, P.L. (2022): A new solution to an old riddle: elongate dinosaur tracks explained as deep penetration of the foot, not plantigrade locomotion. Palaeontology **65**: e12584.

Lance, V.A. (1989): Reproductive cycle of the American alligator. Amer. Zool. **29**: 999-1018.

Livingston, V.J., Bonnan, M.F., Elsey, R.M., Sandrik, J.L., Wilhite, D.R. (2009): Differential limb scaling in the American alligator (*Alligator mississippiensis*) and its implication for Archosaur locomotor evolution. Anat. Rec. **292**: 787-797.

Lockley, M., Matsukawa, M., Jianjun, L. (2003): Crouching theropods in taxonomic jungles: ichnological and ichnotaxonomic investigations of footprints with metatarsal and ischial impressions. Ichnos **10**: 169-177.

McIlhenny, E.A. (1935): The Alligator's Life History. Christopher Publishing House. Boston.

Melchor, R.N. (2015): Application of vertebrate trace fossils to paleoenvironmental analysis. Palaeogeo. Palaeoclim. Palaeoecol. **439**: 79-96.

Milàn, J., Falkingham, P.L. (2016): Experimental and comparative ichnology. In: Dinosaur Tracks: the Next Steps. Falkingham, P.L., Marty, D., Richter, A., Eds, Indiana University Press, Bloomington.

Milàn, J., Hedegaard, R. (2010): Interspecific variation in tracks and trackways from extant crocodylians. New Mexico Mus. Nat. Hist. Sci. Bull. **51**: 15-29.

Milnes, M.R., Woodward, A.R., Rooney, A.A., Guillette Jr, L.J. (2002): Plasma steroid concentrations in relation to size and age in juvenile alligators from two Florida lakes. Comp. Biochem. Physiol. A. **131**: 923-930.

Montuelle, S.J., Kane, E.A. (2019): Food capture in vertebrates: a complex integrative performance of the cranial and postcranial systems. In: Feeding in Vertebrates. Bels, V., Wishaw, I., Eds, Springer, New York.

Pienaar, U.D.V. (1969): Predator-prey relationships amongst the larger mammals of the Kruger National Park. Koedoe. **12**: 108-176.

Reilly, S.M., Elias, J.A. (1998): Locomotion in *Alligator mississippiensis*: kinematic effects of speed and posture and their relevance to the sprawling-to-erect paradigm. J. Exp. Biol. **201**: 2559-2574.

Shoop, C.R., Ruckdeschel, C.A. (1990): Alligators as predators on terrestrial mammals. Amer. Midl. Nat. **124**: 407-412.

Taqa, A.A., Bashi, T.Y.K., Sheet, L.O.A.M. (2015): Evaluation of thermal effect, setting temperature of plaster and its effect on the softening of wax on various gypsum products after adding additives. Internat. J. **3**: 128-136.

Turner, M.L., Gatesy, S.M. (2021): Alligators employ intermetatarsal reconfiguration to modulate plantigrade ground contact. J. Exp. Biol. **224**: 242240.

Willey, J.S., Biknevicius, A.R., Reilly, S.M., Earls, K.D. (2004): The tale of the tail: limb function and locomotor mechanics in *Alligator mississippiensis*. J. Exp. Biol. **207**: 553-563.