FOOTPRINTS AND TRACKWAYS OF THE AMERICAN ALLIGATOR, ROCKEFELLER WILDLIFE REFUGE, LOUISIANA

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Abstract—Trails made by American alligators at Rockefeller Wildlife Refuge, Louisiana, are most often observed during droughts, when water levels in this wetland complex are lower. Most observed trails are made by animals moving to or from water; traces are made in muddy substrates, and are commonly associated with mud cracks. Alligator trails are made by animals walking, with their bellies off the substrate, or sliding along the substrate. There is usually a distinct tail drag mark. Left and right manus-pes sets are well separated. Pes prints are placed close behind manus prints in trails of walking alligators. Manus prints rotate outward with respect to the direction of travel of a walking alligator, while pes prints are parallel to the direction of travel. There are five digit impressions in well-preserved manus prints, the inner three of which show claw marks, and the impressions of digits I and V are almost aligned. Pes prints have a long heel impression and four digit impressions, the outermost of which lacks a claw mark; interdigital webbing can readily be seen in well-preserved pes prints. The impressions of digits I and IV form an acute angle. In both manus and pes prints digit impressions may extend further forward beneath the substrate than the surface expressions of the prints.

INTRODUCTION

Although vertebrate palichnologists have described several fossil traces possibly made by crocodylians or their relatives (e.g., Olsen and Padian, 1986; McAllister, 1989a, b; Bennett, 1992; Demathieu and Sciаu, 1992; Foster and Lockley, 1997; Fuentes Vidarte and Mejide Calvo, 1999; Mazin et al., 2003; Esquerra and Pérez-Lorente, 2003; Pérez-Lorente and Ortega, 2003; Lockley and Meyer, 2004; McCrea et al., 2004; Erickson, 2005; Kukihara, 2006; Lockley et al., 2006; Avanzini et al., 2007; Foster, 2007; Pérez-Lorente and Gascón, 2007), there have been few published descriptions of tracks and traces known to have been made by modern crocodylians in the wild (Reineck and Howard, 1978; Frey and Pemberton, 1986). Over the years we (particularly RME) have observed numerous trails made by the American alligator (Alligator mississippiensis) at Rockefeller Wildlife Refuge in Louisiana. Although these observations have been casual rather than systematic, collectively they constitute a record of alligator traces in a natural setting that may be of use to palichnologists seeking to interpret fossil crocodylian traces.

STUDY AREA

Rockefeller Wildlife Refuge (RWR) is located along the U.S. Gulf Coast in eastern Cameron and western Vermilion Parishes, Louisiana, off Highway 82 (latitude 29.661’ N, longitude 92.688’ W). The refuge was created by a gift from the Rockefeller Foundation to the state in 1920. Initially the refuge had an area of about 86,000 acres, but subsequent enlargement created by a gift from the Rockefeller Foundation to the state in 1920.

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RWR alligators range in size from hatchlings to large males with total lengths of 3.5 m or more (Farlow and Britton, 2000; Farlow et al. 2005). The manus has five fingers, with well-developed claws on digits I-III. Webbing connects digits I-IV; digit V attaches to the manus more proximally than the other four digits (Fig. 1C). The pes has four digits, with claws on digits I-III (Fig. 1D). Digits I through III project progressively further away from the heel of the foot. The distal extent of webbing connecting the toes increases from the inside to the outside of the foot, such that the proportion of digit IV that extends beyond the webbing is less than that of the other toes.

ALLIGATOR TRACES

Context

Alligator trails at RWR (Fig. 2) are most often seen during droughts, probably because the reptiles have to move further to get from drier patches to the water, from one pond to another, or from shallower parts of a marsh to deeper water channels (cf. McIlhenny, 1976). However, some traces may be made when there is still water covering the substrate, to become exposed (and thus visible) later in the drought. The traces are made in muddy substrates, and so are commonly associated with mud cracks (in some cases mud cracks propagate from the ends of toe marks). Because these aquatic reptiles orient so strongly toward the water, many trails are perpendicular to the water’s edge. Sometimes, however, alligator trackways are oriented parallel to a remaining water trail that connects perpendicularly to a larger pool/pond of water (Fig. 2E; cf. McAllister [1989b] and Bennett [1992] for fossil examples of parallel trackways possibly made by crocodylians [although McAllister doubted the crocodilian trackmaker interpretation]). Were such traces to become fossils, the occurrence of multiple trackways headed in the same direction might be mistaken as evidence for herding behavior. Furthermore, because alligators concentrate in the remaining water holes during prolonged droughts, large concentrations of tracks will be created in and around such holes, which again might incorrectly be interpreted as indicative of gregarious habits.

Trace Morphology

Alligator traces are illustrated and described in Figs. 3-6 and their captions. Our sample includes trails made by animals that were walking and supporting their weight off the ground, and also trails made by...
alligators sliding on their bellies (“sprawl” of Reilly and Elias [1998]). Walking alligators (Fig. 3) make wide-gauge trackways, with footprints of the left and right sides well separated from each other and the trackway midline; the centers of manus prints appear to be closer to the trackway midline than the centers of pes prints, as in Osteolaemus (von Huene, 1913) and Caiman (Padian and Olsen, 1984; Carpenter, 2009), but possibly not Crocodylus (Mazin et al., 2003). Pes prints are placed close behind manus prints of the same side of the animal. Manus prints rotate outward with respect to the animal’s direction of travel (as in Crocodylus, Osteolaemus and Caiman [von Huene, 1913; Mazin et al., 2003; Carpenter, 2009]), but pes prints are parallel with the direction of travel (cf. Schaeffer, 1941; Brinkman, 1980). There is usually a distinct, slightly to strongly sinusoidal tail drag mark (cf. Farlow and Pianka [2000] for varanid lizards, von Huene [1913] for Osteolaemus, and Carpenter [2009] for Caiman). When the degree of sinuosity is slight, the tail mark is positioned close to the midpoint between prints of the left and right feet (Fig. 3A; cf. Padian and Olsen [1984] for Caiman and Mazin et al. [2003] for Crocodylus), but when the sinuosity is exaggerated (Fig. 3B) the tail mark nearly touches the inner margins of footprints (Fig. 3B). Trackways made by walking alligators can grade into those

FIGURE 1. Alligators at or near the Rockefeller Wildlife Refuge. A. Alligator observed outside the refuge on private property during a drought in 2000. B. A large alligator (2.4 m+ total length) responsible for some of the trackways in our sample. C-D. Right manus and pes, respectively, of RWR 26, a 2.4-m wild male.
FIGURE 2. Alligator traces in environmental context. A, Aerial view of alligator trails at a nesting study site, June 1996. The trails are belly slides, with footprints at the lateral edges of each slide. The alligators were leaving a drying pool (bottom of photograph) in search of another water body. B, Scratch marks made by alligator claws, probably as the animals hauled up onto the little shelf of mud. Tape scale is about 1 foot (305 mm). C-F, Alligator trackways near refuge headquarters. C, Alligator tracks made as the reptiles walked toward a retreating slough. D, Close-up of the tracks in C. E-F, Two views showing still closer views of some of the alligator tracks; tape = 20 inches (508 mm). Note faint tail drag mark associated with the trackway adjacent to the tape. D-F show trails of more than one animal traveling toward the water. Note the association of alligator traces with mud cracks.

made by belly-sliders (Fig. 4B). Belly sliding is probably usually done when the substrate is wetter (Reilly and Elias, 1998), or the alligator is larger/heavier. The alligator’s body leaves a smooth surface as it slides along the mud, or a deep impression if the mud is soft enough, and footprints are often distorted from the actual shape of the autopodia.

When prints of the manus and pes are distinct, they can readily be related to the morphology of the hand and foot (Figs. 1, 6). Distinct claw marks can register in the impressions of manus digits I-III. The marks of digits I and V are almost aligned (interdigital angle I-V approaching 180°). Pes prints have a long heel mark that can be rounded or pointed. Claw marks are often seen in the impressions of digits I-III, and the extreme distal extent of the webbing between digits III-IV commonly registers. Digits I and IV form an acute angle of about 45-55°. In both manus and pes prints the toe marks may plunge downward into the mud, such that the surface expression of the prints is smaller than their true sizes.

Reineck and Howard (1978) described traces made by a small (1.25-m total length) alligator high-walking across moist sand on the beach of Sapelo Island, Georgia. Although this animal’s trackway resembled our trails of walking alligators in showing a distinct tail drag mark, and the placement of the tail mark with respect to pes impressions, it also showed
FIGURE 3. Two of the better trackway segments in our sample, probably from the same trackway and made by the same alligator, observed near refuge headquarters. In both panels about 19 inches (483 mm) of tape provide the scale. Pes prints are about 200 mm long, suggesting an alligator with a total length of about 3 m (Farlow and Britton, 2000). From the depth of the footprints, the animal was supporting its weight at the time these prints were made; the tail drag mark is well-defined but shallow. In both trackway segments the tail drag mark is sinuous, more so in B than A. In A the tail drag mark is nearly symmetrically placed between left and right prints, but in B the tail drag mark swings closer to the footprints in the top two manus-pes sets. Manus prints are smaller than pes prints, and the manus prints in the right half of the trackway segment shown in B are rotated outward with respect to the alligator’s direction of travel, with the impressions of digits I and V almost forming a straight line. Pes prints are placed close behind manus prints. The pes pace angulation (B) is about 105°, and the stride length between the two right pes prints is about 610 mm.
FIGURE 4. Numerous examples of alligator trackways. B-C, show two views of the same trackway segment, and panels K and L show two views of a different trackway. In G and possibly H the alligators were moving toward the viewer, but in the other panels the alligators were moving away from the viewer. Where the picture has a tape for a scale, about 19 inches (483 mm) of tape is exposed. In F, J, K, L and possibly H, as well as the top portions of B and I, the smooth, broad surface of the midline of the trackway (between the footprints) indicates that the alligator’s belly was likely dragging across the substrate. In other panels the alligator may have carried its body off the ground. Note that the tail drag mark can be relatively broad (A-D), very narrow (bottom of H), very faint (bottom part of I) or even absent (K, L and the top of H).
some interesting differences from our alligator trackways. Instead of being placed behind manus prints, pes prints in the Georgia trackway were partly superimposed on manus prints, somewhat disrupting them. During protraction an autopodium (identified by Padian and Olsen [1984] as the manus) made curved, convex-outward drag marks of a kind we have not observed in trails of RWR alligators, but similar to those seen in trackways of large Australian desert varanids (Farlow and Pianka, 2000). Finally, the interdigital webbing of the pes did not register in the Georgian footprints. Whether these differences between traces of the Georgian alligator and those of our RWR animals are due to differences in size, gait, or substrate is unknown, and suggests that systematic study of the effects of all of these variables on alligator trace morphology would be profitable.

Although they were made by much bigger animals, the walking trackways in our RWR sample show some similarities to the ichnogenus *Crocodylopodus* from the Early Cretaceous of Spain (Fuentes Vidarte and Meijide Calvo, 1999; Lockley and Meyer, 2004). There are five manual digit impressions in *Crocodylopodus*, and manus prints rotate outward with respect to the trackmaker’s direction of travel. Pes prints of *Crocodylopodus* have four digital impressions and a long heel impression. The relative sizes of manus and pes impressions in *Crocodylopodus* are fairly similar to our alligator trackways, and the placement of manus and pes prints in the two kinds of trackway are much the same. However, *Crocodylopodus* shows a much greater pace angulation and a relatively narrower trackway (compared with the size of the prints themselves) than do our walking alligator trackways, and *Crocodylopodus* seems not to show a tail drag mark. Interdigital angle I-IV of the pes of *Crocodylopodus* may be greater than in our alligator pes prints, but that may merely reflect differences in the way the divarications were measured. All told, were we to find trackways of walking alligators as ichnofossils, we would probably refer them to a new ichnospecies of *Crocodylopodus*.

Because alligators spend most of their time in and around water, their traces are generally made in muddy settings close to water level. The tracks we observed were made during droughts, and so their long-term survival would depend on multiple factors, including: how long they are exposed before being covered by water; how quickly tracks exposed above water level degrade; how the dried sediment in which the tracks were made responds to eventual submergence; the processes by which tracks are buried once they are submerged. Intuitively we would
FIGURE 6. Alligator manus and pes prints; tape scale in inches. A-E. Manus-pes sets. The long axes of pes prints are parallel to the alligators’ direction of travel, but the manus prints show distinct outward rotation. A, Left manus-set; length of the two prints together about 255 mm. Note distinct claw marks on digits I-III of the manus print. The distal end of the digit IV impression is covered by the tape. B, Left manus-pes set; length of the two prints together about 410 mm. These prints were made by the alligator shown in Fig. 1B. C, Right manus-pes set from the trackway shown in Fig. 3B; length of the two prints together about 265 mm. D, Right manus-pes set; length of the two prints together about 370 mm. E, Right manus-pes set (note tail drag mark to the left of the two prints) with poorly preserved manus; length of pes print about 220 mm. F, Right manus print; width across the impressions of digits I-V (in surface expression of the print) about 80 mm. Digits I-III and V penetrate deeply into the mud, such that the toe impression lengths beneath the mud surface would have been longer than they are in surface expression of the manus print. G-J, Pes prints. Note the acute interdigital angle (ca. 45-55°) formed by the impressions of digits I and IV. G, Probable right pes print; length about 210 mm. The digit IV impression appears to be offset from the other three toe marks due to failure of the webbing between digits III and IV to leave a clear impression (cf. Fig. 1D). H, Right pes print; length about 155 mm in surface expression (excluding the mud push-ups in front of the print), but the toe marks penetrate deeply beneath the surface of the mud, so the true length of the print would be longer. I-J, Two pes prints of the alligator shown in Fig. 1B. I, Right pes print; length in surface expression about 190 mm, but this is still another print in which the toe marks projected forward into the mud well beneath the surface. J, The same left pes print shown in B; length about 220 mm.
suspect that alligator traces have a higher potential for fossilization than those of more dryland large vertebrates. We would expect alligator trace fossils generally to occur in fine-grained sedimentary rocks, and often to be associated with mud cracks.

The trackways of walking and belly sliding alligators that we have described are very conspicuous features, and so were easily noticed by us. In contrast, most trace fossils attributed to crocodylians and their close relatives seem to have been made by swimming animals, as described in several contributions to this volume. Such traces are likely to be more subtle. Whether we would have seen them had we deliberately looked for them is unknown; the closest equivalents to “swim tracks” in our sample are the scratch marks made by alligators hauling out onto a mud bank (Fig. 2B). Conceivably swimming traces are generally made in deeper water than in the situations where we saw our alligator trackways. In any case, systematic surveys of the range and relative abundance of traces made by extant crocodylians in natural settings would be of considerable use to paleontologists seeking to interpret fossil examples.

ACKNOWLEDGMENTS

This research was partly supported by an NSF grant to Farlow. We thank M. Avanzini, K. Carpenter, D. Marty, J. Milan, and M. Lockley for helpful comments.

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Rene Hedegaard from the KrokodilleZoo in Denmark poses with a Chinese Alligator before the experiments. Photo by Jesper Milàn.