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Article

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Trackways of the American Crocodile (*Crocodylus acutus*), Northwestern Costa Rica: Implications for Crocodylian Ichnology

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INTRODUCTION

As noted by Kubo (2010a: 187), “lack of knowledge about extant reptile tracks and trackmakers is one of the main reasons for misidentification of extinct trackmakers.” Leonardi (1975:308) stated that it would be “a useful practice to examine recent trackways and compare them with the body and skeleton of their makers.”

Like the footprints of dinosaurs, fossil tracks and traces attributed to crocodylians and their close relatives have received considerable attention, particularly in recent years (Bennett, 1992; Moratalla et al., 1995; Fuentes Vidarte and Meijide Calvo, 2001; Mazin et al., 2003; Lockley and Meyer, 2004; McCrea et al., 2004; Erickson, 2005; Pascual Arribas et al., 2005; Avanzini et al., 2007; Mateus and Milàn, 2010; Milàn et al., 2010; Contessi and Fanti, 2012; Abbassi et al., 2015; Hadri et al., 2015; Rajkumar et al., 2015; Segura et al., 2016). Unlike nonavian dinosaurs, which are so inconveniently extinct, about thirty crocodylian species remain (at least for now) extant (Grigg and Kirshner, 2015), permitting both laboratory and field observations of footprint creation by these animals (von Huene, 1913; Reineck and Howard, 1978; Padian and Olsen, 1984b; Kubo, 2008, 2010b; Carpenter, 2009; Farlow and Elsey, 2010; Kumagai and Farlow, 2010; Milàn and Hedegaard, 2010). Tracks and traces of modern crocodylians are of considerable use in field research into ecology, conservation biology, and management of these big reptiles (cf. Riley and Huchzermeyer, 1999; Platt et al., 1990, 2006, 2009; Wilkinson and Rice, 2000; Oliveros et al., 2006; Simpson, 2006; Buden and Haglelgam, 2010; Chang et al., 2012, 2015; Gómez Velasco, F. 2012; Bezuijen et al., 2013; Stuart and Stuart, 2013; Sam et al., 2015). Comparisons of fossil trackways of quadrupedal archosaurs besides crocodylians (e.g. Haubold and Klein, 2000, 2002; Lockley and Meyer, 2000; Rainforth, 2003; Gand et al., 2007; Porchetti and Nicosia, 2007; Romano et al., 2007; Avanzini and Petti, 2008; Lockley et al., 2009; Marty et al., 2010; Petti et al., 2010; Klein et al., 2011; Li et al., 2012; Contessi, 2013; Boutakiout et al., 2014; Masrour and Pérez-Lorente, 2014; McCrea et al., 2014; Xing et al., 2015) with modern crocodylian trackways may allow inferences about terrestrial locomotion of the extinct trackmakers (Carpenter, 2009). Consequently we believe that detailed information about traces made by extant crocodylian species will be of considerable value for interpreting traces attributed to living crocodylians as well as those of ancient crocodylomorphs and other quadrupedal archosaurs.

The American crocodile (*Crocodylus acutus*) is a large-bodied crocodylian, distributed across southern North America, Central America, Hispaniola, Jamaica, Cuba, and northern South America (Moore, 1953; Hernández Hurtado et al., 2006; Thorbjarnarson, 2010; Balaguera-Reina et al., 2015; Grigg and Kirshner, 2015; Venegas-Anaya et al., 2015). Like the Australian estuarine crocodile (*Crocodylus porosus*), *C. acutus* is highly tolerant of salt water (Leslie and Taplin, 2000; Grigg and Kirshner, 2015).

For obvious reasons (mostly involving teeth and tails), most studies of track-making by extant crocodylians have been based on small to medium-sized individuals, carried out with captive animals. We opportunistically encountered several trackways made by medium-sized to large American crocodiles in Guanacaste Province of northwestern Costa Rica, animals that were not immediately influenced by the presence of humans. Some of these trackways displayed exquisitely registered footprints. Because of the size and condition of these traces, we made detailed observations and measurements of the trackways. Our results provide some notion of the minimum range of variation that one could expect to encounter in trackways known to have been made by conspecific crocodiles. We also made tentative comparisons of our American crocodile trackways with those of other living and extinct crocodylomorphs, and with body measurements made on intact crocodiles and alligators.

Crocodylians use different gaits during terrestrial locomotion, and may travel considerable distances overland (von Huene, 1913; Cott, 1961; Zug, 1974; Bustard and Singh, 1977; Parrish, 1987; Frey, 1988, Whitaker and Andrews, 1988; Gatesy, 1991; Richardson et al., 2002; Renous et al., 2002; Campos et al., 2003; Baier and Gatesy, 2013; Grigg and Kirshner, 2015). In this study we will be concerned mainly with the high walk of crocodiles on land, but will offer brief comments about aquatic locomotion as related to possible underwater traces.

SITE DESCRIPTIONS

The trackways in this study were observed at the mouths of two estuaries, Estero Tamarindo (10.309' N, -85.837 W) and Estero Ventanas (10.347' N, -85.860 W) (Fig. 1A). The estuaries about 4.5 km apart, and both are encompassed by Parque Nacional Marino Las Baulas, on the Pacific Coast of Costa Rica.

Estero Tamarindo is a tidal estuary bordered by a mangrove forest, which is replaced at the mouth of the estuary by two sandy beaches: Playa Grande to the North and Playa Tamarindo to the South. All trackways near the estuary were observed on the Playa Grande side at the seaward limit of the mangrove forest. Trackways usually extended 4 – 5 meters landward from the water’s edge, at which point the crocodile turned around and returned to the water (Fig. 2). Because there is strong tidal flow of the estuary close to its mouth, we hypothesize that crocodiles are leaving the water to reduce energy expenditure in swimming against the current.

Estero Ventanas is only connected to the ocean during the rainy season (July – November). After the rains, the estuary mouth quickly dries up, and the estuary becomes a lagoon. The dry estuary mouth then constitutes a continuation of the sandy Playa Ventanas that extends southward from the estuary. Most trackways here are made by crocodiles crossing the dry river mouth of the lagoon, both to and from the ocean. There are multiple instances where it appears that a single crocodile left the lagoon during the night, returning to the lagoon by early morning. We hypothesize that crocodiles are venturing out of the lagoon to feed on fishes or crustaceans in the shallow waters of the rocky coastline just north of the estuary mouth. We have observed crocodiles occasionally swimming between the Ventanas and Tamarindo Estuaries.

METHODS

Trackway Documentation

Keeping in mind our goal of maximizing the usefulness of our study for comparison with trackways of other living and extinct crocodylians and non-crocodylian crocodylomorphs, we present detailed qualitative and quantitative observations, with explicit measurement protocols (Fig. 3), in our description of *Crocodylus acutus* trackways.

Trackways were serendipitously discovered during routine patrols along the beaches of Playa Grande and Playa Ventanas in search of trackways made by nesting sea turtles. Because the crocodile trackways were made in unconsolidated sand, it was not possible to make measurements directly on the individual prints or the trackways without disrupting them. Measurements were instead made from digital photographs (taken with a Nikon COOLPIX AW100 camera with 16 MP definition) shot from as nearly directly above the trackways as possible, with a numerical scale or other object of known size in the images. Because it is unlikely that our photographs were taken perfectly perpendicular to the ground surface, our measurements made from them are likely a bit off. Furthermore, because conditions of lighting at the time the photographs were made could not be controlled, the accuracy of measurement was likely affected by how clearly visible the defining reference points are in the images.

We tried to ensure as much consistency in measurements as possible by having all of them made by the same person (Farlow). Measurements were made on 8 inch by 10 inch printouts of digital photographs, using digital calipers, metric rulers, and protractor, with linear dimensions converted to their true size using rulers or other objects of known size in the printed photographs. For data analyses, linear dimensions were converted from measurements on the printouts to true size calculated to the nearest millimeter, but given the abovementioned issues of accuracy and precision, summary trackway measurements are reported (Table 1) more conservatively, to the nearest centimeter, with averages (means, medians) calculated to the nearest 0.1 cm. Comparisons among different images showing the same features suggest that these are reasonable levels of precision for most measurements of our trackways (cf. Webb and Messel [1978] for measurements of crocodiles themselves). Because of the possibility of image distortion at the periphery of the camera lens, where such a distinction could be made in our photographs we report measurements made when a footprint or trackway feature was near the center of the image, as well as all measurements made on that feature.

Where possible, overlapping digital images were stitched together in Photoshop to create composite images of longer portions of trackways. In some cases it was also possible to use software to generate three-dimensional models of trackways (cf. Falkingham et al., 2014).

Because claw-bearing fingers and toes generally dug into the substrate (cf. Kubo, 2008; Kubo, 2010b), the distal ends of the impressions of manus digits I-III, and pes digits I-III, are not the anatomical toetips. Thus measurement of true digit lengths is impossible, and so we do not report the lengths of individual digit impressions in footprints. This also means that measurements of footprint lengths are likely to be slight underestimates of the lengths of the manus and pes that would be made on the autopodia of the crocodile itself, with the digits extended in a straight line.

We measured several footprint and trackway parameters using the distalmost ends of the digit impressions, as seen in surface expression, as the reference points. We designate this distalmost end of the surface expression of the digit impression the toetip or terminus, but do not identify this feature with any specific anatomical landmark. Due to variations in the

Commented [PF1]: Would be nice to also cite Falkingham 2012, as it's more pure methods:

Falkingham, P. L. (2012). "Acquisition of high resolution three-dimensional models using free, open-source, photogrammetric software." Palaeontologia Electronica **15**(1): 1T:15p.

Commented [PF2]: Great!

footsubstrate interaction, the toetip / terminus will not necessarily correspond to the same anatomical feature of the foot from one print to the next; this extramorphological variability introduces an unavoidable but minor element of subjectivity in footprint and trackway measurements, forcing ad hoc decisions about exactly where a toe mark ended. Difficulties in ascertaining where an impression starts and ends are not unique to the tracks described herein, and can have more significant effects when interpreting tracks made by an uncertain track maker (Falkingham 2016).

Commented [PF3]: If I'm being a bit cheeky, feel free to leave this out, but it seemed like a good place to bring it up!

Falkingham, P. L. (2016). Applying Objective Methods to Subjective Track Outlines. Dinosur Tracks: The Next Steps. P. L. Falkingham, D. Marty and A. Richter. Bloomington, Indiana University Press**:** 72-81.

To facilitate comparison of our trackways with those of other crocodylomorph ichnites, both modern and fossil, we will describe the way our measurements were made as explicitly as possible, and how they are similar to or different from other measurement protocols.

Manus Print Length: measured in a straight-line distance from the terminus of the digit III impression in a best-fit manner through the long axis of digit III to the proximal edge (here defined as the wrist) of the handprint. Manus print length was measured this way to make it as closely comparable to the length of the manus as measured on live crocodylians as possible (Farlow and Britton 2000; Kumagai 2010; Kumagai and Farlow 2010). Simpson (2006: 40) measured manus lengths of *Crocodylus siamensis* in a similar fashion, except that he excluded the mark of the claw, while our digit III terminus would include at least the basal part of the claw. Individual digit lengths were not measured because of the inability to determine their true lengths.

Manus Print Width: measured in a straight-line distance from the terminus ends of the impressions of digits I and V. Manus print width is not constrained to be perpendicular to manus print length, unlike the protocol for measuring manus width of Leonardi (1987: item 37 and plate V panel F). Simpson (2006: 40) measured manus print width of Siamese crocodiles in a protocol like ours, except that he excluded the claw marks in taking his measurements.

Manus Print Interdigital (Divarication) Angle I-V: angle formed by the intersection of best-fit line segments drawn through the long axes of digits I and V. If the digit impression is curved, greatest emphasis is placed on the more proximal portion of the imprint, unless there is a sharp bend (dog-leg) in the digital impression; should that be the case, the best-fit line is drawn through the distal portion of the impression. The best-fit line is not constrained to pass through either the terminus of a digit mark or the wrist of the handprint. These measurement protocols appear to be consistent with those of Leonardi (1987: item 56 and plate V panel G, plate VI panels B-D) and Milàn and Hedegaard (2010).

Pes Print Length: measured from the most posterior point on the heel impression to the terminus of the impression of digit III (sometimes including displacement rims of sand). Footprint length is likely an underestimate of the length of the foot because claws dig into the substrate, but serves as a proxy for foot length as measured on live crocodylians. Platt et al. (1990: 297) measured pes print length of *Alligator mississippiensis* “from the impression formed by the base of the heel to the tip of the longest toe [digit III] (just inside the claw impression).” Wilkinson and Rice (2000: 338) measured alligator pes length “from the first single extended scute posterior to the heel to the anterior end of the longest toe (3rd digit), not including the nail.” Simpson (2006: 40) measured pes print width as we did, except that he excluded the mark of the claw. Our pes length measurement appears similar to that of Leonardi (1987: items 33

Commented [PF4]: Why were displacement rims sometimes included?

and 37, plate V panel F), and possibly that of Milàn and Hedegaard (2010). Individual digit lengths were not measured because of the inability to determine their true lengths.

Pes Print Width: measured across the terminal ends of the impressions of digits I and IV (ignoring laterally directed claw marks presumably made when the foot was lifted off the substrate; see below). As with manus width, and unlike Leonardi (1987: item 37 and plate V panel F), pes print width is not constrained to be perpendicular to pes length, but in practice is close to it. Our measurement of pes print width appears similar to that of Milàn and Hedegaard (2010).

Pes Print I-III Width: measured across the terminal ends of the impressions of digits I and III; (ignoring laterally directed claw marks presumably made when the foot was lifted off the substrate). Simpson (2006), in contrast, measured pes width across the tips of digits II-IV.

Pes Print Interdigital Angle I-IV: angle formed by the intersection of best-fit line segments drawn through the long axes of digits I and IV. If the digit impression curves distally away from the midline of the footprint, greater emphasis is placed on the proximal than on the distal end of the impression in fitting a line segment to the digit long axis. Best-fit lines are therefore not constrained to pass through the terminal end of the digit impression; neither are they constrained to meet at the heel of the footprint.

Manus (Oblique) Pace: Distance from the terminus of the digit III impression of one handprint to the same point on the next handprint of the opposite side. For some analyses, a distinction is made between paces that end in a particular handprint, and paces that begin with that handprint.

(Opposite) Manus Stride: Distance from the terminus of digit III of one handprint to that of the next handprint of the same side. The stride is here characterized as “opposite” because in comparisons of manus stride against manus length (a proxy for crocodile size), a given stride measurement is compared with the handprint of the crocodile’s contralateral side; that is, the opposite stride for a handprint was made as the forelimb opposite that handprint was being protracted. Boyd (2006) appears to have measured manus (and also pes) stride as we did.

Manus Pace Angulation (Step Angle): Angle defined by the juncture of two successive paces.

Manus-Pes Distance: straight-line distance between the terminal ends of the impressions of digit III of the manus and the pes in a manus-pes set. Unlike Leonardi (1987: item 19 and plate I), we did not measure this distance as projected against the trackway midline, but in practice the distance would nearly parallel the midline. We considered measuring the manus-pes distance using the bases of the impressions of digit III of both autopodia as the reference points, but decided against this for two reasons. First, in some trackways the pes print overlapped its associated manus imprint enough that the base of digit III on the manus print could not be seen. Second, the base of the digit III impression was often not clearly seen in manus and/or pes sets of a set, but the terminus of digit III of both was usually clear.

Commented [PF5]: Is this right? Doesn’t make sense to me.

Pes (Oblique) Pace: Distance from one footprint to the next footprint of the opposite side. For some analyses, a distinction is made between paces that end in a particular footprint, and paces that begin with that footprint. Because of variations in the quality of impression of footprints, two measurements of pes paces are reported. One of these is measured from the tips of the terminal ends of the digit III impression of successive contralateral footprints, and the other from the heels of successive contralateral footprints. We considered measuring pedal paces and strides from the proximal ends of the digit III impression, but this point is often not clearly defined in our crocodile trackways. Kubo (2008) used the midpoint of a line segment connecting the tips of digits II and III as the reference point for measuring pedal paces and strides, while Milàn and Hedegaard (2010) apparently used a point near the center of the sole (Leonardi 1987: item 41 and plate V panel F) of the pes print as the reference point for measuring paces and strides.

(Opposite) Pes Stride: Distance from one footprint to the next footprint of the same side. The stride is here described as “opposite” for the same reason that manus stride was so characterized. As with the pace, strides are measured both from the terminus of the digit III impression, and also from the heel, of successive ipsilateral pedal prints.

Pes Pace Angulation (Step Angle): Angle defined by the juncture of two successive paces; measured for paces defined from the terminal end of the digit III impression, and also for paces defined from the heel of the footprint.

Trackway Midline: defined on the basis of pes prints. The midpoint of each (oblique) pace over a series of successive paces (defined on the basis of the terminus of the digit III impression) of the pedal trackway is determined. The trackway midline then is defined as a series of line segments connecting the midpoints of the successive paces. Because of the way the midline is defined, the positions of the first and the final footprint in a trackway relative to the midline are, strictly speaking, not measurable. However, if the crocodile moved nearly in a straight-line manner between the position of the first or final footprint, and the portion of the trackway downtrail from the first print, or uptrail from the final footprint, the midline could be projected uptrail or downtrail from the defined midline so that the position or rotation of the footprint relative to the projected midline was measurable.

Manus Digit III Distance to Midline: Perpendicular distance from the terminus of the manus digit III impression to the trackway midline.

Manus Wrist Distance to Midline: Perpendicular distance from the wrist of the manus impression to the trackway midline.

Commented [PF6]: Should this be in quote marks: ‘wrist’, as the manus impression doesn’t have a wrist as such, it has an impression of a wrist.

(maybe this is just Steve’s influence rubbing off on me!)

Pes Digit III Distance to Midline: Perpendicular distance from the terminal end of the pedal digit III impression to the trackway midline.

Pes Heel Distance to Midline: Perpendicular distance from the rear of the heel of the pes impression to the trackway midline.

Commented [PF7]: I assume, rather than say the centre of the heel?

Midpoint Manus Midline Distance – Midpoint Pes Midline Distance: The overall distance of an individual manus print from the trackway midline was calculated as the midpoint between the distance from the tip of digit III to the midline and the distance from the wrist to the midline. Similarly, the overall individual pes print midline distance was calculated as the midpoint between the distance from the tip of digit III to the midline and the distance from the heel to the midline. The midpint pes midline distance was then subtracted from the midpoint manus midline distance to provide a measure of whether overall the manus or the pes print in a manus-pes set was closer to the midline. A positive number indicates that the manus is farther from the midline than the manus, and a negative number that the manus is closer to the midline than the pes.

Manus Trackway Inner (Internal) Width: A series of line segments connects the most medial part of handprints (typically the terminal end of the digit I impression) along both the left and right sides of the trackway. Trackway inner width is the distance between the left and right segments, measured from each manus print to the line segment of the opposite side. This parameter is equivalent to the intermanus width of Leonardi (1987: item 23, plate I) except for details of the way it is measured. Leonardi (1987:45) measured it "between the internal (medial) parallel tangents to two consecutive left-right footprints."

Manus Trackway Outer (External) Width: A series of line segments connects the most lateral part of handprints (typically the terminal end of the digit IV or V impression) along both the left and right sides of the trackway. Trackway outer width is the distance between the left and right segments, measured from each manus print to the line segment of the opposite side. This measurement is equivalent to the external trackway width as measured by Leonardi (1987: item 21 and plate I).

Pes Trackway Inner Width: A series of line segments connects the most medial part of pes prints (typically the terminal end of the digit I impression) along both the left and right sides of the trackway. Trackway inner width is the distance between the left and right segments, measured from each pes print to the line segment of the opposite side. The measurement is equivalent to that of Leonardi (1987).

Pes Trackway Outer Width: A series of line segments connects the most lateral part of pes prints (typically the terminal end of the digit IV impression) along both the left and right sides of the trackway. Trackway outer width is the distance between the left and right segments, measured from each pes print to the line segment of the opposite side. Leonardi (1987), Simpson (2006), Kubo (2008), and Milàn and Hedegaard (2010) measured trackway width in the same or a nearly similar way.

Manus Print Rotation: Angle formed by the intersection of the best-fit line segment drawn through the long axis of digit III of the handprint and the midline or projected midline of the trackway. Crocodile manus prints nearly always angle outward (positive rotation) with respect to the trackway midline. Leonardi's (1987: item 28 and plate I) divarication of foot from midline is similar, except that he recognizes that the divarication of the footprint's longitudinal axis may differ from that of digit III.

Manus Calculated Print Divarication: An alternative way of measuring manus print rotation. The distance of the wrist from the midline is subtracted from the distance of the tip of digit III from the midline. This value is then divided by manus length, which quotient is the sine of an angle between the trackway midline and the long axis of digit III (the latter forming the hypotenuse of a right triangle). The calculated print divarication is then the arcsine of the calculated sine. We designate the calculated angle the divarication, as opposed to the rotation measured from photographs, to distinguish between the two ways of measuring the angle between the long axis of the handprint and the trackway midline.

Pes Calculated Print Divarication: Pes print rotation was not directly measured from trackway photographs because footprints are nearly parallel to the trackway midline. However, we did calculate an alternative version of print divarication in the same way that we calculated manus print divarication, using the difference between the distances of the tip of digit III, and the heel, from the midline, and the length of the pes print.

Glenoactebular Length: When possible, measured using the bases of the impressions of digit III of the manus and pes (or their inferred near vicinity, if not clearly marked on prints) as reference points. Otherwise the glenoacetabular length was measured using the terminal ends of digit III of the manus and pes. The glenoacetabular length was measured following the protocol of Leonardi (1987: Plate VIII panel C). Measurements of the glenoacetabular length were associated with the manus-pes set opposite the backward-positioned pes print and the forward-positioned manus print of the contralateral side.

Commented [PF8]: (random thoughts follow):

I need to do some measurements on extant quadrupeds, but I'm surprised this measurement works. It requires the gait to have a point where all four limbs are in contact with the ground. The horse (D) in Leonardi's plate VIII has G-A distance measured differently.

I guess if the croc is moving quickly, G-A estimation from tracks will be more inaccurate?

Data Analyses

Summary Measures of Overall Footprint and Trackway Proportion Variability. Because our trackmakers showed modest variability in overall size, we calculated simple measures of variability in footprint and trackway proportions in such a way as to remove absolute size. Autopodial widths and trackway linear dimensions were scaled by dividing them by the appropriate autopodial length. We then calculated two measures of ratio variability. One of these was itself also a ratio, that of the maximum/minimum value of the ratio-scaled parameter. In addition, we calculated the standard deviation of the ratio-scaled parameter.

Two versions of each of these measures were calculated. The “single cases” treatment employed each measurement of a parameter in a trackway as a data case, with no attempt to take into account that the number of measurements of that parameter varied among trackways. The “trackway means” treatment used mean values of each parameter across trackways as the data cases.

Statisticians may blanch at our use of ratios, but we made no attempt to use ratios in any parametric tests. Furthermore, all of our trackmakers were bigger than very young crocodiles, and so any effects of allometry on footprint or trackway proportions are likely reduced. We therefore think that way we used ratio measurements of trackway proportions to create “quick and dirty” measures of minimum intraspecific shape variability is justified.

Interactions among Footprint and Trackway Dimensions. In addition to summary measures of intraspecific variability, we analyzed interactions among trackway dimensions using more sophisticated statistical tools. Bivariate interactions in trackway dimensions that were presumed not to be affected by trackmaker size were examined using simple correlation analyses. Interactions in which absolute size were deemed likely to have an impact were examined in two ways: 1) by partial correlation analyses, with autopodium size as the control variable, and 2) by analyzing correlations between ratio parameters using nonparametric methods.

Trackmaker Sizes

Footprint and Trackway Dimensions and Crocodile Size. Kumagai (2010) measured wild individuals of *C. acutus* captured at night in Parque Nacional Marino Las Baulas (Estero Tamarindo) and Parque Nacional Palo Verde (Río Tempisque). In addition, some large captives from Río Tempisque were measured at a local zoo near Palo Verde. Crocodiles were measured using the protocols established by Farlow and Britton (2000) for American alligators. Four size measurements were used in the present study.

Crocodile Total Length: Measured along the ventral surface of the animal, from the tip of the snout to the tip of the tail. If the length couldn't easily be measured along the ventral surface, it was measured along the dorsal surface, but this will be a little longer than length measured along the ventral surface.

Shoulder-Hip Length: Measured from the midpoint between the bases of the forelimbs to the midpoint between the bases of the hindlimbs, along the midline of the animal.

Commented [PF9]: Not sure 'bases' is the best word: Does it mean mid point between feet/tracks, or betwee shoulders and acetabluae?

Manus Print Length Proxy: Manus length of crocodiles was measured from the midpoint of a line connecting the proximal ends of digits I and V to the tip of the claw of digit III, with digit III held straight out. The proxy for manus print length was then calculated by subtracting the length of the claw on digit III from overall manus length.

Pes Print Length Proxy: The “palm” of the foot was measured as the distance from the heel of the foot (identified as the most convex part of the back of the foot when it was dorsoflexed) to a line cutting across the bases of digits I and IV in ventral view. To this palm length was then added the length of digit III, excluding the claw, to create the pes print length proxy.

Relationships between total length or shoulder-hip length, with manus or pes print proxy length, could then be examined, and used to estimate the total lengths and shoulder-hip lengths of our crocodylian trackmakers.

Direct Observation. We observed one of our crocodiles in the act of making footprints (Trackway 4: 20141117), and estimated the animal’s total length at 1 m. We shot video of a possible trackmaker from a drone (Fig. 1D, E). This crocodile was seen in the ocean just offshore of Estero Ventanas, in water 4.5-6 m deep. During most of our observations the crocodile swam slowly, with its limbs against its body, propelled in the usual manner by undulations of the tail (Fig. 1E). However, the animal repeatedly interrupted axial swimming, and engaged in bottomwalking (cf. Grigg and Kirshner, 2015: Figs. 4.21, 4.24, 9.2) for a few to several steps. The crocodile passed near reef cornetfishes (*Fistularia commersonii*; typical total length 120 cm: Fig. 1D) and a yellow-bellied sea snake (*Pelamia platurus*; typical total length 75-80 cm); these animals provided scales that allowed us to estimate a total length of about 3 m for the crocodile.

RESULTS

Trackway Descriptions

We will first provide information about the individual trackways we observed, after which we will make more general observations.

Trackway 1: 20130419, Playa Ventanas, 19 April 2013 (Fig. 4). Noteworthy features of the trail include the markedly sinuous tail drag mark, and overprinting of the rear margins of some manus prints by pes prints of the same manus-pes set.

Trackway 2: 20140313, Playa Ventanas, 13 March 2014 (Fig. 5). The crocodile (thought to be a female) came out of the water about an hour before the trackway was observed, just before dawn. The footprints were beautifully impressed, the wet sand recording scale impressions from the sole of the foot, including those of large scutes along the outer edge of the foot (a typical feature of crocodylids and gharials, but not alligatorids: Grigg and Kirshner, 2015). The tail drag mark was much less sinuous than that of trackway 20130419, and situated close to prints of the left side.

Trackway 3: 20140323, Playa Ventanas, 23 March 2014 (Fig. 6). The trackway shows a faint, not very sinuous tail drag mark that is symmetrically placed close to the trackway midline.

Trackway 4: 20141117A, Playa Ventanas, 17 November 2014 (Fig. 7). The crocodile was seen making the trackway at 0612 hours local time. The trackmaker’s total length was estimated at 1

m. The animal’s trackway extended about 4 m away from the estuary, after which the crocodile turned around and headed back to the water. The trackway was made in very firm sand at the mouth of the estuary, a spot that is seldom covered at high tide, but is wetted by rain. Because the substrate was so firm, and the crocodile rather small, footprints in the trackway are very faint. Only the tail drag mark is clearly visible.

Commented [PF10]: I find it interesting that Track 3 has deep prints and a shallow tail drag, but Track 4 has shallow prints and a deep cutting tail drag

Trackway 5: 20141117B, Estero Tamarindo, 17 November 2014 (Fig. 8). The trackway was found at 0647 hours. The crocodile exited the estuary and moved about 5 m up the beach. Footprints were reasonably clear in the sand of the intertidal zone, but became indistinct above the hightide line. The trackway was probably made by a large crocodile that had repeatedly been observed in the estuary, and reported to have eaten two local dogs. A distinctive feature of the trackway is that the not-particularly-sinuous tail drag mark is not symmetrically positioned near the trackway midline, but rather hugs the left margin of the trail, cutting across left-side manus prints. Another distinctive feature is that the centers of manus prints of the left, but not the right, side of the trackway are closer to the trackway midline than their associated pes prints. Most of the individual footprints are not particularly well-formed.

Trackway 6: 20141120, Estero Tamarindo, 20 November 2014 (Fig. 9). This trackway was probably made by the same individual as Trackway 5. It was discovered at 0525 hours. The crocodile moved out of the estuary to about 7 m above the high tide line. Footprints in the beach below the high tide line had been washed away, indicating that the trackmaker made its excursion onto the beach before the high tide of the previous night (0045 hours). Unlike Trackway 5, this trackway showed several clear footprints. When the crocodile walked across

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firm, moist sand, its tail drag mark again was close to the left side of the trackway, cutting across manus prints and the inner edges of pes prints; the tail sometimes flopped over and slid on its side. The tail mark was closer to the trackway midline when the animal walked on softer, drier sand.

Trackway 7: 20141130, Estero Tamarindo, 30 November 2014 (Fig. 10). Another trackway probably made by the same crocodile as the maker of trackways 5 and 6. The trackway was discovered at low tide at 0605 hours, and had probably been made sometime before the previous high tide. Over part of the trackway the tail was once again dragged across footprints of the left side, but in another portion of the trackway the tail mark was more symmetrically placed.

Trackway 8: 20141209, Estero Ventanas, 9 December 2014 (Fig. 11). The trackway was probably at least a day old when it was noticed at 0605 hours. The trackway headed across dry sand from the ocean to the estuary in soft, dry sand. Consequently the individual footprints were not very clear, but the low-amplitude tail drag mark was clearly visible near the trackway midline. Several arthropod traces cut across the trackway.

Trackway 9: 20150119, Estero Tamarindo, 19 January 2015 (Fig. 12). The trackway was found at low tide, 0610 hours. The only preserved portion of the trackway was the part where the crocodile returned to the water, and so the animal probably emerged from the water before high tide (0115 hours). The trackway has conspicuous claw drag marks made by both manus and pes. The tail mark varies from being symmetrically placed near the trackway midline to cutting across prints of the right side. Some pes prints clearly show impressions of webbing between the toes.

Trackway 10: 20150129, Estero Tamarindo, 29 January 2015 (Fig. 13). The trackway as encountered at 0720 hours, at low tide. Only tracks recording the animal's return to the water were preserved, indicating that the crocodile probably came out of the water before high tide at 2133 hours the previous night. The tail mark cuts across left-side footprints, suggesting that this is could be yet another trackway made by the makers of trackways 5-7, although its autopodial dimensions are larger (Table 1). The trackway has a relatively long manus-pes distance in manus-pes sets.

Trackway 11: 20150311, Estero Ventanas, 11 March 2015 (Fig. 14). The tracks were seen at 0700 hours. They led from the ocean across the sand at the estuary mouth to the lagoon on the shoreward side of the sand. This trackway has some beautiful footprints, and a low-sinuosity, medially-positioned tail mark.

Trackway 12: 20160116, Estero Ventanas, 16 January 2016 (Fig. 15). The trackway was found at 0900 hours. The tail drag mark is moderately sinuous. The most noteworthy feature of the trackway, however, is that prints of the left pes are atypically shaped: the digit III impression is rather short, and the distance separating the impressions of digits II and III, and thus also the corresponding interdigital angle, look especially large, as though the crocodile's left foot had been injured or otherwise malformed. Consequently measurements of trackway dimensions related to the pes were made only on right footprints (except for paces, strides, pace angulations, and measurements of glenoacetabular length, which used data from both left and right footprints).

Trackway 13: 20160202, Estero Ventanas, 2 February 2016 (Fig. 16). Found at 0630 hours, this is another lovely trackway. The only photograph taken was shot obliquely down the trackway. The tail mark looks to be closer to the right than the left side of the trackway.

Qualitative Features of American Crocodile Trackways

Like other crocodylians, *Crocodylus acutus* has five fingers on the manus, and four toes on the pes, with digits I-III of both autopodia bearing claws (Richardson et al., 2002; Farlow and Elsey, 2010; Kumagai and Farlow, 2010; Milàn and Hedegaard, 2010; Grigg and Kirshner, 2015). The impressions of digit I of both autopodia are a bit shorter than those of the more lateral digits within the same autopodia; the four outer digits of the manus, and the three outer digits of the pes, leave impressions of subequal length (cf. Kumagai and Farlow, 2010: Fig. 5). The plantigrade hindfoot digits are conspicuously webbed, especially between digits IV and V. All of these morphological features may register in wellformed trackways (Figs. 17, 18). In addition, crocodylian trackways more generally are wide-gauge, with prints of the left side well separated from those of the right, with a distinct tail drag mark (Reineck and Howard, 1978; Padian and Olsen, 1984b; Mazin et al., 2003; Boyd, 2006; Kubo, 2008; Carpenter, 2009; Farlow and Elsey, 2010; Milàn and Hedegaard, 2010; Gómez Velasco, 2011; Stuart and Stuart, 2013; cf. Romano et al., 2007; Marty et al., 2010).

Our Costa Rican American crocodile trackways show these and other features with unusual clarity. Although made in sand, and so unlikely to survive drying out, our trackways show characters likely to register in firm, moist, fine-grained substrates of a kind with higher preservation potential.

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Pes prints are roughly twice as long as manus prints, and pes prints can be placed either some distance behind, or overlapping, manus prints of the same set. There is some variability among, and sometimes even within, trackways with respect to whether the centers of manus prints are closer to, the same distance as, or farther away from, the trackway midline than pes prints in the same sets (see below). The position of the wrist on a handprint is located at about the same level along a trackway as the position of the heel in the next following pes print of the opposite side.

Relative to a line segment between digits I and V, manus prints rotate distinctly outward (positive) with respect to the crocodile’s direction of travel, although this rotation is less marked if expressed in terms of the long axis of the impression of digit III (see below). Pes prints give the appearance of being nearly parallel to the direction of travel (but see below).

Digit claws dig deeply into the sediment (Fig. 17E, 18), and so lengths of the finger and toe impressions are less than the lengths of their respective digits. If the substrate is quite firm, claw marks may be among the most visible features of the trackway (Fig. 10A). Pes prints are usually more deeply impressed than manus prints (Fig. 18), and the inside of pes prints, and the heel, are (aside from claw marks) the deepest parts of hindfoot prints (cf. some sauropod trackways: Farlow et al., 2015). Webbing between digits II-III, and III-IV, of the pes may register as a shallow region of the print (Figs. 17B, 18D, E).

As the hindfoot is lifted from the substrate, clawtips may drag laterally across the print, making outward-pointed marks (Figs. 17B, C). During protraction the manus and/or the pes may create linear or curved, concave-inward drag marks (Figs. 4A, 9, 10B, 12C, D, 13-17A) similar to those seen in some lizard trackways (cf. Leonardi, 1975; Padian and Olsen, 1984a; Farlow and Pianka, 2000; Kubo, 2010b; Gómez Velasco, 2011).

The tail mark may be fairly sinuous (Figs. 4, 5A, 15B, 17A), or only slightly sinuous to nearly linear (Figs. 5B, 8, 9B, 11, 12A, 14, 15A, 16). It may be positioned along the midline of the trackway (Figs. 4A, 5B, 9B, 10B, 11, 14, 15, 17A) or hug the left (Figs. 5A, 8, 9A, 10A, 13) or right (Figs. 12C, D, 16) side, cutting across prints. The shape and position of the tail mark vary even within the same trackway. The tail mark may be faint (Figs. 6, 10A, 12A, B, 13, 17E), or a conspicuous trackway feature (Figs. 7, 10B, 11).

The tail may flop over and slide across the substrate (Fig. 9A).

Quantitative Comparisons

Trackway Proportions. Trackway measurements made only from images close to the center of photographs did not differ appreciably from those made using all images in a shot (Table 1), and so we will employ the later in our analyses. Our trackmakers spanned a modest size range (mean measured pes print length ranging 15 to 24 cm), but did not include any very small/young individuals. Variability of trackway dimensions expressed as ratios against manus or pes length (Table 2) was, unsurprisingly, generally greater for parameters related to locomotion, and thus under control by the crocodiles (stride length, manus-pes distance, trackway widths, distance of prints from trackway midline: maximum/minimum ratio of scaled parameters up to 3.55; standard deviation of scaled parameters up to 0.828) than for parameters related to autopodial proportions (print width/length ratio, manus/pes length ratio: maximum/minimum ratio of scaled parameters 1.74 or less; standard deviation of scaled parameters 0.179 or less). Interestingly, mean values of trackway dimension ratios, and the standard deviations of such ratios, were often about the same when calculated for individual measurements without regard to which crocodile had made them, and also when calculated using mean values for trackways. Maximum/minimum ratios of the trackway dimension ratios obviously were greater when calculated for individual measurements than when calculated for trackway means, because the former treatment included more extreme values.

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Several trackway parameters were geometrically interrelated. The various measures of manus and pes relative stride length were, unsurprisingly, positively correlated (Table 3; Fig. 19A, B). Relative stride length (presumably related to trackmaker speed; cf. Reilly and Elias, 1998) may be negatively correlated with the manus-pes distance (Table 3), but it should be noted that much of the negative correlation seems to be due to data from a single trackway (Fig. 19C). A more surprising result is that relative trackway width was positively correlated with relative stride length (Table 3), but this result is somewhat suspect, because it is strongly influenced by a single measurement (Fig. 19D). Pace angulation is positively correlated with relative stride length, and negatively correlated with relative trackway width (Table 4; Fig. 20; cf. Kubo and Ozaki, 2009).

Although there is some variability among trackways (Fig. 21), particularly in the manus portion of trackways, pace angulations of both the manus and pes portions of trackways are roughly the same, averaging about 90 degrees when measured with respect to the terminal ends of digit III of manus and pes. Pace angulation measured using the heel of the pes results in higher values than when measured from the tip of digit III, due to the slight outward rotation of pes prints. (A similar result would probably also have been the case if we had measured pace angulation with respect to both the wrist and the terminus of digit III of the manus). These values are in the range of those reported for trackways of other crocodylian species (Kubo, 2008; Milàn and Hedegaard, 2010).

Interdigital angle I-V of manus prints is typically about 140-160 degrees, and interdigital angle IIV of pes prints is typically about 35-45 degrees (Fig. 22). The proximo-distal midpoints of manus prints, on average, are about the same distance from the trackway midline as the proximo-distal midpoints of pes prints (Fig. 23), unlike many lizard trackways, in which pes prints are farther from the trackway midline than manus prints (Fichter, 1982; Kubo, 2010; but see Leonardi [1975] for a trackway of a walking *Tupinambis* similar to our crocodile trackways in the relative distance of manus and pes prints from the midline).

Both manus and pes prints usually angle slightly outward with respect to the trackway midline (Fig. 24). Although the nearly linear arrangements of digits I and V of the manus prints cause them to appear to be more sharply rotated outward than are pes prints, when manus rotation or calculated divarication based on the long axis of digit III is compared with calculated pes divarication, the difference between manus and pes rotation is much less.

Trackmaker Size. Most extant crocodylians follow a similar relationship between total length or shoulder-hip length and manus or pes length (Fig. 25)--*Crocodylus siamensis* being a possible exception, with relatively long autopodia for its body size. Despite some unexplained outliers (Fig. 25B, D), our *C. acutus* data mostly follow the trends defined by *Alligator mississippiensis* and other species. Most of our crocodiles had estimated total lengths of at least 2 m (Tables 5, 6), and the largest crocodile may have been more than 3 m long. Our observation of a swimming crocodile with an estimated length of 3 m (Fig. 1.D, E) is consistent with the size of our bigger trackmakers, but it isn't certain that any of these crocodiles was the very animal seen in the ocean.

Pes lengths predicted slightly larger crocodiles than manus lengths. Shoulder-hip lengths estimated from manus and pes lengths were substantially larger than glenoacetabular lengths measured from trackways. While this may in part be due to the reference points we used in measuring glenoacetabular lengths, Leonardi (1975) also found that the glenoacetabular length measured from a trackway made by the teiid *Tupinambis teguixin* slightly underestimated the same distance measured on the skeleton of the trackmaker itself. Conceivably this discrepancy between trackway glenoacetabular length and anatomical shoulder-hip length relates to the role of lateral body bending during crocodylian high-walking (cf. Reilly and Elias, 1998; Carpenter, 2009; Baier and Gatesy, 2013).

Irregular Gait. Left pes prints of trackway 12: 20160116 (Figs. 15, 17A) consistently showed an atypical morphology, with a wide splay between the impressions of digits II and III, and a rather short digit III impression, suggesting a malformation due to injury or other malady. Unlike another of our trackways, which like trackway 12 was represented by several pace measurements, trackway 12 showed a significant difference between pes—but not manus--pace lengths between paces that began with a left print, and paces that began with a right print (Table 7). Trackway 12 therefore is a good candidate for a trackway showing a "limping gait" as defined by McCrea et al. (2015).

DISCUSSION

Comparisons Across Crocodylian and Crocodylomorph Species

Because the terminal ends of the claw-bearing digits of the autopodia dig into the sediment during high-walking, it seems rather pointless to measure individual digit lengths in crocodylian footprints. Consequently our comparisons of *Crocodylus acutus* with those of other extant crocodylian species and with fossil crocodylomorph trackways will focus on overall print and trackway proportions. Our discussion will be somewhat limited by the scarcity of available data, but the data that do exist nonetheless reveal some interesting patterns worth further exploration.

Trackways of other extant crocodylian species (Figs. 26, 27; also see von Huene, 1913; Reineck and Howard, 1978; Padian and Olsen, 1984b; Simpson, 2006; Kubo, 2008, 2010b; Carpenter, 2009; Farlow and Elsey, 2010; Kumagai and Farlow, 2010; Milàn and Hedegaard, 2010; Gómez Velasco, 2012) are qualitatively similar to those of the American crocodile. For this reason, and because there can also be dramatic differences in trackway pattern among conspecifics (e.g. the degree of tail mark sinuosity/amplitude of alligator trackways in Fig. 26), differences in trackway pattern across species, to the extent that they exist, are likely to be subtle and revealed mainly by quantitative comparisons (Figs. 25, 28). (The likely absence of scute marks in pes prints of alligatorids, and their presence in pes prints of other crocodylians, however, is an obvious example of a qualitative difference that should distinguish well-registered alligatorid trackways from those of some other crocodylians.)

As already noted (Fig. 25A, B) the available data suggest that most crocodylians (except, perhaps, *C. siamensis*) show much the same relationship between animal total length and autopodium length. Consequently we hypothesize that print lengths will likely permit reasonable estimates of the total lengths of the makers of most fossil crocodylian trackways made by walking animals, and perhaps the lengths of the makers of many non-crocodylian crocodylomorph trackways.

The relationship between manus length and pes length also looks rather uniform across trackways of extant crocodylians and extinct crocodylomorphs (Fig. 28A), although *C. acutus* and the Early Cretaceous trackmaker from the Oncala Group of Spain (Pascual Arribas et al., 2005) may have a slightly longer pes length for a given manus length, while *C. siamensis* does the opposite. The relationship looks curvilinear, such that among larger individuals the ratio of pes length to manus length becomes less, reducing the degree of manus-pes size heteropody in big crocodylomorphs. The relationship between pes print width and length also looks rather uniform, although the Oncala Group trackmaker is an outlier, with a rather broad pes print width for its length.

The relationship between stride length and pes print length is also very uniform (Fig. 28C), except for one conspicuous outlier, another trackway from the Early Cretaceous of Spain, this one from the famous Las Hoyas site (Moratalla et al., 1995). The Mesozoic trackmaker took unusually long stride for its size, a possible explanation for which will be presented below.

The relationship between trackway external width and pes length (Fig. 28D) shows increasing scatter with increasing size. *Crocodylus siamensis* may have a relatively broad trackway, while *C. acutus* seems to have a relatively narrow trackway.

Crocodylian Locomotion and Trackway Pattern

Terrestrial High-Walking. The functional morphology and kinematics of crocodylian terrestrial locomotion have received considerable attention (von Huene, 1913; Schaeffer, 1941; Zug, 1974; Brinkman, 1980; Parrish, 1987; Frey, 1988; Gatesy, 1991; Reilly and Elias, 1998; Blob and Biewener, 1999, 2001; Salisbury and Frey, 2000; Renous et al., 2002; Richardson et al., 2002; Meers, 2003; Reilly and Blob, 2003; Willey et al., 2004; Reilly et al., 2005; Hutchinson, 2006; Carpenter, 2009; Allen et al., 2010; Kubo and Ozaki, 2009; Kubo, 2010b; Hutson and Hutson, 2012, 2013, 2014; Baier and Gatesy, 2013; Grigg and Kirshner, 2015). Several features of our American crocodile trackways clearly are consistent with the results of kinematic analyses of high-walking. It should be noted, however, that studies of crocodylian limb kinematics using live animals have, as with studies of track-making, generally been limited to much smaller individuals (most often *Alligator mississippiensis*) than most of the trackmakers in our study. They have also primarily employed animals walking on firm "substrates" (e.g. treadmills and force plates) rather than across soft sediment.

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Early in hindlimb protraction, the distal end of the femur undergoes slight abduction, relative to its position at the end of the stance phase, as it swings forward, the extent of abduction varying among individuals in *Alligator* (Gatesy, 1991; Reilly and Elias, 1998). The pes may not consistently be elevated completely off the ground, "with the toes of a protracting foot dragging forward more frequently in hindlimbs than forelimbs" (Willey et al., 2004: 562). Such motions during the swing phase undoubtedly are responsible for the curvilinear toe claw marks of the pes, and sometimes also the manus, observed in our trackways (e.g. Fig. 17A), as well as for laterally directed pedal claw mark impressions created in the first stage of lift-off (Fig. 17B, C).

Peak vertical forces exerted by the autopodial of crocodilians are greater for the pes than the manus (Willey et al., 2004; cf. Allen et al., 2010). This does not necessarily imply that tracks left by the pes will be deeper; pes and manus surface areas will act to convert such forces into pressures, and smaller forces may produce deeper tracks if applied through smaller feet (Falkingham et al. 2011; 2012; 2014). Dynamic autopodia may change that surface area throughout the step cycle, creating variable pressures under a single pes or manus, and previous studies have shown that there may only be a tenuous link between underfoot pressures and localized track depth (Bates et al. 2013; Hatala et al. 2013).Neverthless, we generally observe a greater depth of pes than manus prints of our crocodile trackways (Fig. 18). Alligators have a pronounced mediolateral component to the ground reaction force of the limbs (Willey et al., 2004), which is directed medially (i.e. the foot is pushing laterally)and might

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(2014 can be omitted if you want to keep references down)

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be expressed in the greater depth of the medial than the lateral sides of prints (Fig. 18), and conceivably might also be related to the evolutionary loss of claws on the outermost digit(s) of the autopodia.

The crocodylian tail plays the major role in swimming, and so is quite large and muscular, but constitutes a source of drag when the animal walks on land (Willey et al., 2004). This is consistent with the prominent tail drag marks seen in most of our trackways (Figs. 4-16). The amplitude of lateral bending of the animal's body during walking is greatest in the caudal region (Reilly and Elias, 1998), consistent with the marked sinuosity of some—but interestingly not all—of the drag marks of our trackways.

Underwater Locomotion. Crocodylians exert considerable control over their buoyancy, allowing them to maintain themselves at a desired position in the water column with little effort (Kirshner, 1985; Grigg and Kirshner, 2015). We observed one American crocodile (Fig. 1D) engaged in bottom walking at the ocean floor, and this mode of progression occurs in other crocodylian species as well (Kirshner, 1985; Davenport and Sayer, 1989; Frey and Salisbury, 2000; Seebacher et al., 2003). Whitaker and Andrews (1988: 621), for example, reported that "submerged gharial were frequently observed to propel themselves quickly along through shallow water by pushing their feet along the bottom with a gait reminiscent of the varanid gait."

David Kirschner (personal communication) noted that during bottom walking "the tail drags behind but so lightly that I'd be surprised if it left anything beyond a very vague track if anything at all. The key thing you'd be looking for in recognizing bottom-walking is the engagement of only the clawed toes in the footprints…You'd see sets of claw marks and little else…[but] the animals I was studying were small (~1 m and less) and for the most part undisturbed, so a larger animal (and/or one in a hurry) could leave deeper tracks. The other thing to be considered is that crocs will mix and match movement styles, so a croc doing a hybrid bottom-walking/swimming movement would leave different tracks than one strictly bottom walking."

We suspect that many Recent and fossil traces attributed to "swimming" crocodylians (e.g. McCrea et al., 2004; Houk et al., 2010; Kumagai and Farlow, 2010) were made by reptiles that were either bottom walking or combining bottom walking with slow swimming. The absence of tail marks in many crocodylomorph trackways might be explained if their makers had been moving underwater (although we concede that the tail mark is faint in some of our trackways of high-walking crocodiles). Our observations of an American crocodile in the ocean indicate that such locomotion is not restricted to very shallow (such that the animal would be forced to touch bottom) water. Video clips of Nile crocodiles moving close to the bottom (e.g. those of wildlife photographer Daniel Botelho [www.youtube.com/watch?v=t51MQaQL9Zc]) show the animals touching the bottom with their feet in a manner that occasionally could produce manus-pes sets with their autopodial prints positioned in a manner like that of high-walking individuals, but with long spaces between touch-downs generated as the crocodile pushed off the bottom with its hindfeet and glided through the water. Such progression might account for crocodylomorph trackways with anomalously long stride / pes length ratios, like the Las Hoyas trackway described above.

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Conclusions

Our study documents minimum variability in size and shape of trackway features created during the high walk, both within and among individuals of one crocodylian species. The degree of size variability would clearly increase, and the degree of shape variability would probably increase (cf. Dodson, 1975; Farlow and Britton, 2000; Allen et al., 2010), if we were to add trackway data for very small individuals of the American crocodile to our sample. As it is, however, our observations and data should provide some useful “canons” for assessing whether trackways of fossil crocodylian (and possibly non-crocodylian crocodylomorphs, and perhaps even other quadrupedal archosaurs) are similar enough to be considered likely to have been made by the same species of trackmaker. In so doing, our results identify variations in trackway features that would not necessarily indicate that trackmakers were members of different species.

Comparison of trackway data for *Crocodylus acutus* with the limited available data for other crocodylian species suggest that most differences among species are likely to be quantitative rather than qualitative in nature. That being the case, we recommend that future studies of crocodylian ichnology make as many trackway measurements as preservation and circumstances allow. In this study we have provided what we hope is a thorough set of measurements that will be useful for comparative purposes.

It is gratifying that several features of American crocodile trackways can be correlated with kinematic features of crocodylian locomotion during the high walk. It is equally satisfying to note that it may be possible to interpret features of fossil trackways of “swimming” crocodylomorphs—which are far more common than trackways attributed to high walking animals (Milàn et al., 2010)—in terms of the actual kinematics of crocodylians moving underwater. It seems, then, that there is considerable potential for future comparative studies relating crocodylian locomotion to ichnology.

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FIGURE CAPTIONS

Fig. 1. Study area and possible subjects. **A.** Locations of places where crocodiles or their tracks were examined. **B-E**. Crocodile(s) observed at or near the places where our trackways were made. It is possible, but not certain, that this/these crocodile(s) were responsible for some of the trackways we studied. **B**. Large crocodile high-walking on land. **C-E**. Crocodile(s) seen in the ocean. **C**. Crocodile swimming in the surf. **D-E**. Crocodile moving along the bottom. **D**. Crocodile bottom-walking. Note the straight tail and extended limbs, and the clouds of sediment suspended by the animal's autopodia on either side of its body. The cornetfish (*Fistularia commersonii*) to the right of the crocodile allowed estimation of the reptile's size. **E**. Crocodile swimming slowly.

Fig. 2. Patterns of two trackways at Estero Tamarindo. **A**. Trackway 6: 20141120, 20 November 2014. The crocodile left the water, crossing the beach and entering the exposure from the center bottom, then made a tight hairpin turn (upper left) and returned to the water (right). **B**. Trackway 10: 20150129, 29 January 2015. The crocodile emerged onto the beach (top of exposure), made a hairpin turn (bottom), and returned to the water near the spot whence it came. Note impressions of the animal's belly at the closed end of the trackway loop.

Fig. 3. Measurements of crocodile footprints and trackways. Manus length = A – A^1. Manus width = B – B^1. Pes length = C – C^1. Pes width (toetip I-IV) = D – D^1; pes width (toetip I-III) = C^1 - D. Manus-pes distance = A^1 – C^1. Manus pace = A^1 – A^1 (right to left hand or left to right hand). Manus stride = A^1 – A^1 (left hand to left hand, or right hand to right hand). Manus pace angulation (step angle) = ϴ. Pes pace (digit III) = C^1 – C^1 (left to right foot, or right to left foot); pes pace (heel) = C – C (left to right foot, or right to left foot). Pes stride (digit III) = C^1 – C^1 (left foot to left foot, or right foot to right foot); pes stride (heel) = C – C (left foot to left foot, or right foot to right foot). Pes pace angulation (digit III) = ϕ; pes pace angulation (heel) = β. The trackway midline is defined by a series of line segments connecting the midpoints (M) of successive pes paces. Distance of manus wrist to midline = A - G. Distance of manus digit III to midline = A^1 – H. Distance of pes heel to midline = C - E. Distance of pes digit III to midline = C^1 - F. Manus inner trackway width = distance from tip of digit I (B) of one hand to a line segment connecting two successive digit I tips (B – B) of the opposite hand. Manus outer trackway width = distance from tip of digit IV or V (B^1) of one hand (whichever is farther from the trackway midline) to a line segment connecting two successive digit IV and/or V tips of the opposite hand. Pes inner trackway width = distance from tip of digit I (D) of one foot to a line segment connecting two successive digit I tips of the opposite foot. Pes outer trackway width = distance from tip of digit IV of one foot (D^1) to a line segment connecting two successive digit IV tips of the opposite foot. Manus rotation = angle between a best-fit line segment through the long axis of digit III, roughly between wrist (A) with tip of digit III (A^1)—but not necessarily passing through both points A and A^1--and the adjacent midline. Where possible, glenoacetabular

length = length of line segment between midpoint (K) of a line segment connecting base of digit III of two successive contralateral pes prints (J – J), and midpoint (L) of a line segment connecting base of digit III of two successive contralateral manus prints (I –I), where one of the manus and one of the pes prints are members of the same manus-pes set. If the base of digit III of the manus and/or pes are not clearly defined in prints, the glenoacetabular length is alternatively measured as a line connecting the midpoint of a pes pace (digit III; C^1 – C^1) and the midpoint of a manus pace (A^1 – A^1), where one of the manus and one of the pes prints are members of the same manus-pes set.

Fig. 4. Trackway 1: 20130419, Playa Ventanas. **A.** Oblique view of the trackway, with the crocodile moving away from the viewer. Note the conspicuous, sinuous trail drag mark. **B**. Overhead view of part of the trackway; the photographer’s foot is about 28 cm long. **C**. Left manus-pes set.

Fig. 5. Trackway 2: 20140313, Playa Ventanas. **A**. Oblique view of the trackway (the crocodile moving away from the viewer), moving from wet onto dry sand. Note that the tail mark is positioned along footprints of the animal’s left side. **B**. Overhead view of part of the trackway, featuring beautifully registered prints. The larger scale is marked off in 20 1-cm increments.

Fig. 6. Overhead view of trackway 3: 20140323, Playa Ventanas. The scale is just over 15 cm long.

Fig. 7. Overhead view of trackway 4: 20141117A, Playa Ventanas. The prints are quite faint, but the tail drag mark is distinct. The scale is just over 15 cm long.

Fig. 8. Slightly oblique overhead view of Trackway 5: 20141117B, Estero Tamarindo. The tail drag mark hugs the left side of the trackway. Manus prints of left (but not right) side are positioned closer to the trackway midline than associated pes prints. The scale is just over 15 cm long.

Fig. 9. Trackway 6: 20141120, Estero Tamarindo. **A**. Overhead view of portion of the trackway with clearly registered prints. The larger scale is just over 30 cm long, and the smaller scale just over 15 cm long. Note curvilinear drag marks made by fingertips of the manus during protraction. The tail mark stays close to the left side of the trackway, sometimes flopping over and sliding sideways. **B**. Less distinctly impressed part of the trackway, made in drier sand. The tail mark is more symmetrically positioned here.

Fig. 10. Trackway 7: 20141130, Estero Tamarindo. **A**. Portion of the trackway with reasonably distinct prints and a tail mark along the left side of the trackway. **B**. Portion of the trackway

made in softer sand, with the tail mark running along the trackway midline. The scale is just over 15 cm long.

Fig. 11. Trackway 8: 20141209, Estero Ventanas. Trackway made in soft sand. **A**. Oblique view showing much of the trackway; the crocodile was moving away from the viewer. **B**. Overhead view of portion of the trackway. The larger scale is just over 30 cm long, and the smaller scale just over 15 cm long. Note arthropod trails crossing the crocodile trackway.

Fig. 12. Trackway 9: 20150119, Estero Tamarindo. Panels **A – D** show four segments of the trackway. The small scale is just over 15 cm long. Note variable position of the nearly linear tail mark, from symmetrically located near the midline (panels **A** and **B**) to cutting across footprints of the right side of the trackway (panels **C** and **D**). Drag marks made by claws of digits I-III of the pes are clearly seen in panels **C** and **D**), cutting across manus prints. Drag marks of manus claws are seen in panel **C**.

Fig. 13. Trackway 10: 20150129, Estero Tamarindo. The small scale is just over 15 cm long. The low-sinuosity tail mark cuts across footprints of the left side. The manus-pes distance is particularly long.

Fig. 14. Trackway 11: 20150311, Estero Ventanas, a trackway with beautifully registered prints. The larger scale is just over 30 cm long, and the smaller scale just over 15 cm long. **A**. Overhead view of trackway. **B**. Oblique view.

Fig. 15. Trackway 12: 20160116, Estero Ventanas. **A**. Overhead view of a portion of the trackway; the larger scale is just over 30 cm long, and the smaller scale just over 15 cm long. Note the unusual configuration of digits II-III of the left pes. **B**. Oblique view of trackway; note sinuous tail mark.

Fig. 16. Trackway 13: 20160202, Estero Ventanas. The small scale is just over 15 cm long.

Fig. 17. Details of footprint and trackway morphology. **A**. Trackway 12: 20160116 (Fig. 15). Note atypical morphology of left pes, and curvilinear toe drag marks of both manus and pes, with pes marks cutting across manus marks (especially clear on left side of trackway). **B**. Particularly good right manus-pes set from trackway 2: 20140313 (Fig. 5). Note distinct scale marks on sole of manus and pes, impressions of large scutes along the outer margin of the rear of the pes print, and laterally directed claw marks on digits I and II of pes. **C**. Right manus-pes set from trackway 10: 20150129 (Fig. 13). Note longitudinal sediment pull-ups in digits IV and V of the manus print, and laterally directed claw marks of the pes print. **D**. Right manus-pes set of trackway 7: 20141130 (Fig. 10A). Note conspicuous protraction drag marks of manus claws II

and III. **E**. Left manus-pes set of trackway 11: 20150311 (Fig. 14). Note great depth of claw marks compared with other parts of the prints, and rather faint tail drag mark.

Fig. 18. Digital models of trackways. Warmer (red) colors indicate deeper parts of the trackway in panel **A**, and cooler (blue) colors indicate deeper parts of the trackway in panels **B - F**. **A**. Trackway 2: 20140313. **B**. Trackway 5: 20141117B. **C**. Trackway 6: 20141120. **D - E**. Trackway 9: 20150119. **D**. Left manus-pes set. **E**. Right manus-pes set. **F**. Left manus-pes set of trackway 11: 20150311 (cf. Fig. 17**E**). Note deeply impressed claw marks, deeply impressed medial side of hindfoot prints, and shallowly impressed webbing connecting digits II-III-IV of the pes.

Fig. 19. Interactions involving different measures of relative stride length (expressed as a ratio against autopodium length) in the crocodile trackways (Table 3). Data cases are individual measurements within a trackway, and thus provide a minimum indication of within-animal variability in the comparison. The key to trackways in panel **C** also applies to other panels. **A.** The two measures of pes relative stride length are, unsurprisingly, closely correlated. **B**. Relative manus and pes stride length are likewise closely correlated. **C**. Relative manus-pes distance and relative stride length may be negatively correlated, but the relationship is strongly affected by points for a single, possibly atypical, trackway (12: 20160116). **D**. Relative pes trackway inner width may be positively correlated with relative stride length, but the strength of the relationship is strongly affected by a single measurement.

Fig. 20. Interactions between pace angulation and other trackway parameters. The key to trackways in panel **C** also applies to other panels. **A**. Manus pace angulation and manus relative stride length are positively correlated. **B**. Manus pace angulation and manus trackway relative inner width are negatively correlated. **C**. Pes pace angulation and pes relative stride length are positively correlated. **D**. Pes pace angulation and pes trackway relative inner width are negatively correlated.

Fig. 21. Distribution of values of pace angulations of the manus and pes portions of crocodile trackways. In panels **A** and **C**, data are broken down by individual trackways (see text for key to trackway number); in panels **B** and **D**, data are pooled across trackways, without considering the number of measurements in each trackway. **A** and **B**. Manus portion of trackway. **C** and **D**. Pes portion of trackway.

Fig. 22. Interdigital angles. In panels **A** and **C**, data are broken down by individual trackways (see text for key to trackway number); in panels **B** and **D**, data are pooled across trackways, without considering the number of measurements in each trackway. **A** and **B**. Manus prints. **C** and **D**. Pes prints.

Fig. 23. Distribution of values of the quantity (midpoint manus midline distance – midpoint pes midline distance). **A**. Data broken down by individual trackways. **B**. Pooled data across trackways, without considering the number of measurements in each trackway. Values are centered on zero, indicating that the midpoints of manus prints are generally about the same distance from the trackway midline as the midpoints of pes prints.

Fig. 24. Footprint rotation / divarication. In panels **A**, **C**, and **E**, data are broken down by individual trackways; in panels **B**, **D**, and **F**, data are pooled across trackways, without considering the number of measurements in each trackway. **A** and **B**. Manus rotation measured directly from photographs. **C** and **D**. Calculated manus divarication. **E** and **F**. Calculated pes divarication. Both manus and pes angle outward (positive rotation / divarication) with respect to the trackway midline.

Fig. 25. Crocodylian size vs. autopodium or print length. Where possible (data for *Alligator mississippiensis* and *Crocodylus acutus*), manus and pes print lengths measured on the animals themselves were converted to their footprint length proxies; otherwise autopodial lengths were used as reported in the data source. The symbol key in panel **B** applies to all other panels as well. **A.** Total length vs. manus or manus print length. **B**. Total length vs. pes or pes print length. **C**. Shoulder-hip length vs. manus or manus print length. **D**. Shoulder-hip length vs. pes or pes print length. Data from Leonardi (1984), Padian et al. (1984a), Farlow and Britton (2000),

Kubo (2008), Carpenter (2009), Kumagai (2010), Milàn and Hedegaard (2010), Rajkumar et al. (2015), and B. Simpson (personal communication).

Fig. 26. Trackways of *Alligator mississippiensis*. Note spacing of manus and pes prints in sets, and relative to the trackway midline. The trackways in panels **A-C** and (some in) **E** show moderate relative amplitude of the tail drag mark, while the trackways in panels **D** and **F** show very little or no tail mark displacement. **A-B**. Trackway of a large alligator, St. Catherines Island, Georgia. Scale marked in centimeter increments. **A**. Alligator moving away from the viewer. **B**. Alligator moving obliquely toward the viewer; inset shows a left manus-pes set. **C-F**. Trackways at Rockefeller Wildlife Refuge, Louisiana. **C**. Trackway of a large alligator (Farlow and Elsey, 2010); 19 inches (483 mm) of tape are exposed. **D-F**. Trackways of young alligators; Sharpie markers (length 137 mm) provide the scale. **D**. Trackway amid numerous bird tracks; note Sharpie scale at far right of panel. Inset shows a detail of the trackway. **E-F**. Digital models of trackways. The scale bar in panel **E** is 137 mm (one Sharpie length).

Fig. 27. Trackways of *Crocodylus porosus*, Northern Territory, Australia. Note the sharply sinuous (high-amplitude) tail drag marks of both trackways, and the overlapping of manus by pes prints. **A**. Crocodile crossing a mudflat; photograph courtesy Gordon Grigg. **B**. Trackway of crocodile crossing the beach into the ocean, West Alligator Head; photograph courtesy Gary Lindner.

Fig. 28. Footprint and trackway proportions in extant crocodylian and fossil crocodylomorph trackways. Footprint data for *Crocodylus acutus* are trackway means from this study. **A**. Manus length (measured on the animals themselves) or manus print proxy length vs. pes print length (measured on the animals themselves) or pes print length proxy. In panels **B**-**D** all measurements are made on footprints and trackways. **B**. Pes print width vs. pes print length. **C**. Pes stride length (digit III) vs. pes length. **E**. Pes trackway external width vs. pes length. Data sources as in Figure 25, as well as Moratalla et al. (1995), Fuentes Vidarte and Meijide Calvo (2001), Mazin et al. (2003), Pascual Arribas et al. (2005), Avanzini et al. (2007), Mateus and Milàn (2010), Stuart and Stuart (2013), and Abbassi et al. (2015).

TABLE 1

Measurements of crocodile trackways. Single values and ranges of linear dimensions reported to nearest cm, with means and medians (the latter reported if the number of measurements is three or more) calculated to nearest 0.1 cm. Single values and ranges of angles reported to nearest degree, with means and medians calculated to nearest 0.1 degree. It was not possible to measure every parameter for every trackway. Where there are two lines of data for a parameter, a distinction was made between all measurements made, from all photographs (first line), and only those measurements made when the print under consideration is near the center of the relevant photograph (second line). If only a single line of data appears, either this distinction was not made, or all measurements were made for prints near the center of the relevant photograph

Trackway	Print	Parameter	Mean (Median)	Range	N
1: 20130419	Manus	Length	8	----	1
		Width	14	-----	1
	Pes	Length	18	-----	1
		Width (Toetip I-IV)	15	-----	1
		Width (Toetip I-III)	10	-----	1
		IDA I-IV	39.0	36-42	2
		Manus-Pes Distance	9	-----	1

		Inner Trackway Width	10	-----	1
		Pace (Heel)	39.3 (39.3)	39-39	3
			39.4	39-39	2
		Stride (Heel)	62.8	61-64	2
		Pace Angulation (Heel)	106.0	103-109	2
		Glenoacetabular Length	45	-----	1
2: 20140313	Manus	Length	11.0 (11.0)	10-12	7
			10.4	10-11	2
		Width	14.0 (14.1)	13-15	7
			14.2	14-14	2
		IDA I-V	143.7 (145.0)	134-153	7
			147.5	145-150	2
		Distance Wrist to Midline	18.5 (18.6)	14-22	6
			15.8	15-17	2
		Distance Fingertip III to Midline	15.5 (15.8)	12-19	6
			18.6	18-19	2
		Inner Trackway Width	22.5 (22.6)	22-23	3
			23	-----	1
		Outer Trackway Width	46.7	47-47	2
			47	-----	1
		Pace	49.7 (50.0)	47-51	4
			50.0	49-51	2
		Stride	61.1	61-61	2
		Pace Angulation	73.5	73-74	2
		Rotation	17.3 (16.5)	12-26	6
			13.0	12-14	2
		Calculated Divarication	16.3 (15.2)	10-27	6
	Pes	Length	22.7 (22.3)	21-25	7
			22.5	22-23	2
		Width (Toetip I-IV)	14.9 (14.8)	13-17	7
			14.3	14-14	2
		Width (Toetip I-III)	9.7 (9.6)	9-11	7

			10.1	10-11	2
		IDA I-IV	40.6 (42.0)	33-46	7
			44.5	43-46	2
		Manus-Pes Distance	18.0 (18.2)	17-20	5
			17.5	17-18	2
		Distance Heel to Midline	14.4 (14.3)	11-17	7
			13.2	13-14	2
		Distance Toetip III to Midline	17.3 (17.3)	17-18	6
			17.3	17-17	2
		Inner Trackway Width	15.0	14-15	2
		Outer Trackway Width	45.7	45-47	2
		Pace (Toetip III)	45.9 (45.9)	45-46	4
			45.7	45-46	2
		Pace (Heel)	41.6 (42.2)	38-44	5
			42.7	42-43	2
		Stride (Toetip III)	60.2	59-61	2
		Stride (Heel)	60.8 (61.3)	58-63	3
			62.3	61-63	2
		Pace Angulation (Toetip III)	82.5	82-83	3
			82.5	82-83	2
		Pace Angulation (Heel)	92.7 (93.0)	90-95	3
			94.0	93-95	2
		Calculated Divarication	5.7 (5.2)	1-11	6
		Midpoint Manus Distance – Midpoint Pes Distance	2.7 (2.7)	2-4	4
		Glenoacetabular Length	51	-----	1
3: 20140323	Manus	Length	8	-----	1
		Width	8.7 (8.7)	9-9	2
		IDA I-V	149.0	147-151	2
		Inner Trackway Width	12	-----	1
		Outer Trackway Width	28	-----	1
		Pace	30.6	31-31	2
			31	-----	1

		Stride	47	-----	1
		Pace Angulation	99	-----	1
	Pes	Length	14.9 (14.9)	14-16	2
		Width (Toetip I-IV)	9.5 (9.8)	8-10	4
			10	-----	1
		Width (Toetip I-III)	7.3	7-7	2
		IDA I-IV	43.5	39-48	2
			39	-----	1
		Manus-Pes Distance	8.9	9-9	2
		Inner Trackway Width	6.4	6-6	2
			6	-----	1
		Outer Trackway Width	27	-----	1
		Pace (Heel)	28.4 (28.2)	28-29	3
			28	-----	1
		Stride (Toetip III)	47	----	1
		Stride (Heel)	48	-----	1
		Pace Angulation (Heel)	116	-----	1
4: 20141117	Pes	Width (Toetip I-IV)	15	-----	1
		Width (Toetip I-III)	10	-----	1
		Stride (Toetip III)	62	-----	1
6: 20141120	Manus	Length	8.4 (8.5)	8-9	3
			8.3	8-9	2
		Width	10.8 (10.8)	11-11	3
			10.8	11-11	2
		IDA I-V	153.0 (154.0)	142-163	3
			148.0	142-154	2
		Distance Wrist to Midline	8.5 (8.6)	6-11	3
			8.6	6-11	2
		Distance Fingertip III to Midline	8.7 (9.1)	6-11	3
			8.4	6-11	2
		Inner Trackway Width	10	-----	1
		Outer Trackway Width	29	-----	1
		Pace	31.6	31-32	2
		Stride	50	-----	1

		Rotation	2.0 (4.0)	-2-4	3
			1.0	-2-4	2
		Calculated Divarication	2.0 (3.3)	-1-3	3
	Pes	Length	16.2 (16.1)	15-17	3
			16.6	16-17	2
		Width (Toetip I-IV)	11.4 (11.4)	11-12	4
			11.4	11-12	2
		Width (Toetip I-III)	7.9 (7.0)	7-8	4
			7.6	7-8	2
		IDA I-IV	35.7 (33.0)	31-43	3
			38.0	33-43	2
		Manus-Pes Distance	14.3 (14.0)	13-16	3
			14.8	14-16	2
		Distance Heel to Midline	8.4 (7.8)	7-11	3
			9.2	8-11	2
		Distance Toetip III to Midline	11.9 (12.2)	11-12	4
			12.2	12-12	2
		Inner Trackway Width	8.2	8-9	2
		Outer Trackway Width	31.5	31-32	2
		Pace (Toetip III)	32.9 (33.6)	30-35	3
			34.5	34-35	2
		Pace (Heel)	29.6	28-31	2
			31	-----	1
		Stride (Toetip III)	49.0	48-50	2
		Pace Angulation (Toetip III)	91.5	90-93	2
		Calculated Divarication	12.4 (15.9)	5-16	3
		Midpoint Manus Distance – Midpoint Pes Distance	-2.2	-5-1	2
7:20141130	Manus	Length	9.0	8-10	2
		Width	11.0 (10.9)	10-12	5
			10.6	10-11	2
		IDA I-V	140.0 (153.0)	85-158	6

			110.0	85-135	2
		Distance Wrist to Midline	15.4 (16.3)	12-18	3
			17.0	16-18	2
		Distance Fingertip III to Midline	19.6 (20.4)	18-21	3
			20.5	20-21	2
		Inner Trackway Width	21.1 (21.8)	16-25	4
			19	-----	1
		Outer Trackway Width	42.3 (44.1)	38-45	3
			38	-----	1
		Pace	47	-----	1
		Stride	51.4 (53.1)	42-58	3
		Rotation	22.3 (23.0)	21-23	3
			22.0	21-23	2
		Calculated Divarication	23.3	23-24	2
	Pes	Length	16.7 (17.2)	15-18	5
			16.7	15-18	2
		Width (Toetip I-IV)	11.5 (11.0)	10-14	4
			10.8	10-11	2
		Width (Toetip I-III)	6.8 (7.0)	6-7	5
			6.4	6-7	2
		IDA I-IV	33.7 (31.0)	25-45	3
			35.0	25-45	2
		Manus-Pes Distance	17.0 (16.7)	15-19	4
			16.7	16-17	2
		Distance Heel to Midline	10.4 (9.7)	8-14	5
			8.7	8-10	2
		Distance Toetip III to Midline	13.5 (13.3)	13-15	6
			13.3	13-14	2
		Inner Trackway Width	14.2 (14.2)	11-16	5
			12.5	11-14	2
		Outer Trackway Width	36.9 (38.1)	34-38	3
			36.2	34-38	2
		Pace (Toetip III)	37.0 (38.6)	30-41	5

			34.5	30-39	2
		Pace (Heel)	35.4 (35.2)	30-41	4
			35	-----	1
		Stride (Toetip III)	52.7 (54.4)	44-61	5
			49.0	44-54	2
		Stride (Heel)	53.2 (51.0)	51-59	3
			51	-----	1
		Pace Angulation (Toetip III)	83.5 (82.5)	80-89	4
			84.5	80-89	2
		Pace Angulation (Heel)	98.7 (98.0)	96-102	3
			98	-----	1
		Calculated Divarication	11.4 (13.2)	-1-20	5
		Midpoint Manus Distance – Midpoint Pes Distance	7.8	7-9	2
		Glenoacetabular Length	41.8 (42.8)	34-48	4
			39.5	34-45	2
9: 20150119	Manus	Length	9.3 (9.1)	9-11	15
			9.2 (9.3)	9-9	5
		Width	11.4 (11.3)	11-12	16
			11.2 (11.3)	11-11	6
		IDA I-V	147.6 (145.5)	133-168	16
			146.6 (143.0)	143-156	6
		Distance Wrist to Midline	11.7 (11.3)	9-19	14
			10.5 (10.0)	9-12	5
		Distance Fingertip III to Midline	12.8 (12.6)	9-21	16
			11.8 (12.2)	9-13	6
		Inner Trackway Width	14.4 (13.7)	12-18	4
			18	-----	1
		Outer Trackway Width	36.0 (35.4)	34-39	4
			39	-----	1
		Pace	35.8 (35.4)	33-42	11
			36.1 (34.8)	33-42	4

		Stride	49.7 (49.6)	48-51	5
			51	-----	1
		Pace Angulation	88.4 (92.0)	81-93	5
			81	-----	1
		Rotation	8.9 (6.0)	-1-21	15
			4.4 (5.0)	-1-9	5
		Calculated Divarication	10.2 (8.8)	1-23	13
	Pes	Length	16.2 (16.2)	14-18	14
			15.9 (16.1)	14-17	4
		Width (Toetip I-IV)	12.4 (12.4)	11-13	11
			12.5	12-13	2
		Width (Toetip I-III)	8.0 (8.1)	7-9	20
			7.9 (7.9)	7-8	6
		IDA I-IV	39.4 (38.5)	32-50	8
			40.3 (40.0)	36-45	3
		Manus-Pes Distance	17.0 (17.3)	14-20	18
			17.1 (17.6)	15-18	6
		Distance Heel to Midline	11.0 (10.8)	10-12	13
			10.9 (10.8)	10-12	4
		Distance Toetip III to Midline	13.1 (13.4)	12-14	18
			12.9 (13.0)	12-14	6
		Inner Trackway Width	11.6 (11.8)	9-13	6
			11.5 (12.0)	9-13	4
		Outer Trackway Width	37.1	36-39	2
			39	-----	1
		Pace (Digit III)	36.1 (35.9)	33-40	18
			36.2 (35.9)	34-40	6
		Pace (Heel)	33.7 (33.4)	31-38	6
		Stride (Digit III)	49.1 (49.0)	47-51	8
			49.2 (49.0)	47-51	6
		Pace Angulation (Digit III)	86.4 (84.0)	81-95	7
			88.0 (88.0)	83-95	5
		Calculated Divarication	7.7 (7.9)	4-11	13

		Midpoint Manus Distance – Midpoint Pes Distance	-0.6 (-0.9)	-3-2	9

		Glenoacetabular Length	41.7	42-42	2
			42	-----	1
10: 20150129	Manus	Length	9.7 (9.6)	9-10	8
			9.6 (9.5)	9-10	4
		Width	12.6 (12.4)	12-13	6
			12.5 (12.4)	12-13	3
		IDA I-V	143.7 (141.0)	132-156	7
			137.0 (139.0)	132-140	3
		Distance Wrist to Midline	12.3 (12.1)	9-17	6
			13.7 (14.3)	9-17	4
		Distance Fingertip III to Midline	13.4 (13.6)	9-16	7
			14.0 (14.4)	12-15	4
		Inner Trackway Width	16.2 (16.2)	16-17	3
			16	-----	1
		Outer Trackway Width	40.2 (40.4)	40-41	3
			41	-----	1
		Pace	38.4 (38.2)	36-42	9
			37.6 (38.0)	36-39	5
		Stride	49.4 (49.8)	47-51	4
			51	-----	1
		Pace Angulation	80.0 (80.1)	77-82	4
			80	-----	1
		Rotation	6.2 (4.0)	-5-19	6
			4.0 (3.5)	-5-14	4
		Calculated Divarication	4.5 (3.5)	-10-17	6
	Pes	Length	18.7 (18.3)	16-22	9
			17.8 (17.9)	16-19	4
		Width (Toetip I-IV)	13.1 (13.1)	12-14	5
			12.3	12-12	2
		Width (Toetip I-III)	8.9 (8.8)	9-10	8
			8.7 (8.6)	9-9	3

		IDA I-IV	43.3 (41.5)	37-54	8
			44.5 (43.5)	37-54	4
		Manus-Pes Distance	21.6 (21.6)	19-24	9
			21.7 (21.6)	21-23	4
		Distance Heel to Midline	13.7 (12.6)	11-20	8
			13.2 (12.6)	12-16	5
		Distance Toetip III to Midline	16.4 (15.4)	14-20	8
			15.3 (14.0)	14-19	4
		Inner Trackway Width	11.8	11-12	2
		Outer Trackway Width	43	-----	1
		Pace (Digit III)	41.2 (39.0)	37-51	8
			39.0 (38.2)	37-43	4
		Pace (Heel)	37.1 (36.8)	33-40	9
			37.4 (36.9)	36-40	6
		Stride (Digit III)	50.7 (51.9)	45-54	5
			50.9 (52.6)	45-54	4
		Stride (Heel)	52.2 (52.7)	48-55	4
		Pace Angulation (Digit III)	78.2 (86.0)	63-88	5
			82.0 (87.0)	66-88	4
		Pace Angulation (Heel)	91.2 (94.0)	80-95	5
		Calculated Divarication	6.6 (5.5)	-1-16	7
		Midpoint Manus Distance – Midpoint Pes Distance	-2.5 (-1.9)	-11-1	6
		Glenoacetabular Length	49.7 (51.4)	46-52	3
			51.6	51-52	2
11: 20150311	Manus	Length	12.2 (12.4)	11-13	8
			11.9 (12.1)	11-13	5
		Width	16.3 (16.9)	15-18	7
			16.8 (17.0)	15-18	5
		IDA I-V	148.4 (153.0)	124-167	7
			156.8 (155.0)	151-167	5
		Distance Wrist to Midline	14.7 (15.1)	13-15	5

			14.9 (15.1)	15-15	3
		Distance Fingertip III to Midline	17.2 (16.6)	16-20	5
			16.4 (16.3)	16-17	3
		Inner Trackway Width	17.6 (17.6)	16-19	3
			16.9	16-18	2
		Outer Trackway Width	46.8 (46.3)	46-49	4
			46.1 (46.0)	46-47	3
		Pace	50.2 (50.6)	47-52	6
			50.5 (50.6)	47-52	4
		Stride	70.9 (70.2)	69-75	5
			71.5 (70.6)	69-75	3
		Pace Angulation	90.7 (91.0)	87-94	4
			92.0 (94.0)	88-94	3
		Rotation	14.2 (15.0)	4-25	5
			10.3 (9.0)	4-18	3
		Calculated Divarication	11.7 (9.1)	3-22	5
	Pes	Length	23.7 (23.8)	22-24	7
			23.7 (23.8)	22-24	5
		Width (Toetip I-IV)	16.6 (16.1)	15-18	9
			17.0 (17.8)	15-18	5
		Width (Toetip I-III)	10.7 (10.7)	10-11	8
			10.9 (11.1)	10-11	5
		IDA I-IV	42.3 (41.0)	32-57	9
			40.4 (41.0)	38-42	5
		Manus-Pes Distance	19.8 (19.8)	18-21	8
			20.0 (19.9)	18-21	5
		Distance Heel to Midline	14.7 (14.9)	14-15	5
			14.6 (14.8)	14-15	4
		Distance Toetip III to Midline	18.1 (18.2)	18-19	5
			18.3 (18.2)	18-19	3
		Inner Trackway Width	16.2 (16.7)	15-17	7
			16.0 (16.1)	15-17	5

		Outer Trackway Width	49.9 (50.1)	48-52	7
			49.7 (50.1)	48-51	5
		Pace (Digit III)	51.6 (51.5)	49-53	6
			50.8 (51.3)	49-52	4
		Pace (Heel)	46.2 (46.5)	44-48	7
			45.3 (45.3)	44-46	4
		Stride (Digit III)	71.4 (72.7)	69-73	5
			71.5 (72.7)	69-73	3
		Stride (Heel)	70.9 (70.6)	69-74	6
			70.4 (70.2)	69-72	4
		Pace Angulation (Digit III)	88.3 (89.0)	84-91	4
			88.3 (90.0)	84-91	3
		Pace Angulation (Heel)	102.7 (102.5)	99-109	6
			102.7 (101.5)	99-109	4
		Calculated Divarication	8.6 (8.6)	8-10	4
		Midpoint Manus Distance – Midpoint Pes Distance	-0.3 (-0.4)	-1-1	4
		Glenoacetabular Length	59.0 (59.0)	59-59	3
			59.2	59-59	2
12: 20160116 Crocodile 1	Manus	Length	9.6 (9.7)	9-10	18
			9.6 (9.6)	9-10	11
		Width	12.1 (12.2)	11-12	20
			12.1 (12.2)	11-12	12
		IDA I-V	160.7 (162.0)	145-179	20
			164.1 (163.5)	153-179	12
		Distance Wrist to Midline	12.0 (12.8)	7-17	13
			12.3 (14.5)	7-16	7
		Distance Fingertip III to Midline	13.7 (14.5)	7-18	14
			13.5 (14.5)	8-18	8
		Inner Trackway Width	13.9 (13.9)	12-16	8
		Outer Trackway Width	36.8 (37.0)	35-39	7
		Pace	43.2 (43.3)	40-49	15
			43.6 (43.3)	40-49	11
		Stride	68.8 (69.4)	65-73	7

		Pace Angulation	103.8 (103.5)	101-106	6
		Rotation	5.3 (4.0)	-5-26	12
			7.1 (5.0)	-4-26	7
		Calculated Divarication	7.4 (6.0)	0-22	12
	Pes	Length	17.4 (17.9)	14-20	9
			17.8 (18.6)	14-20	7
		Width (Toetip I-IV)	11.5 (11.3)	11-12	10
			11.7 (11.6)	11-12	8
		Width (Toetip I-III)	6.9 (6.9)	6-8	9
			7.0 (6.9)	6-8	7
		IDA I-IV	33.3 (36.0)	19-43	6
			31.4 (35.0)	19-40	5
		Manus-Pes Distance	10.5 (10.5)	8-14	9
			11.0 (10.8)	9-14	7
		Distance Heel to Midline	11.8 (12.2)	8-16	14
			12.2 (12.8)	8-16	8
		Distance Toetip III to Midline	15.3 (14.8)	13-19	8
			16.3 (16.6)	14-19	5
		Inner Trackway Width	13.6 (13.3)	8-20	8
		Outer Trackway Width	40.7 (40.7)	35-47	6
		Pace (Digit III)	45.7 (44.9)	37-57	15
			46.2 (44.9)	37-57	9
		Pace (Heel)	40.5 (40.8)	33-44	16
			39.4 (40.3)	33-44	9
		Stride (Digit III)	67.8 (66.7)	64-74	9
		Stride (Heel)	65.6 (65.6)	60-70	7
			66.5 (66.8)	62-70	6
		Pace Angulation (Digit III)	95.0 (96.0)	86-104	8
		Pace Angulation (Heel)	107.9 (110.0)	94-119	7
			110.2 (112.0)	101-119	6
		Calculated Divarication	7.9 (7.9)	1-13	7
		Midpoint Manus Distance – Midpoint Pes Distance	2.4 (1.8)	0-5	5
		Glenoacetabular Length	46.6 (46.7)	45-49	6

TABLE 2

Overall variability in trackway proportions. Measurements are expressed as ratios of the parameter of interest to either manus or pes length. Two versions of each comparison are given. In the “single cases” treatment, individual measurements constitute the data cases, without regard to the number of measurements represented by each trackway, such that trackways with a large number of measurements dominate the sample. In the “trackway means” treatment, data cases are mean values (or single cases, if there is only one measurement for the trackway) for trackways, and so each trackway is represented by a single value.

Ratio	Treatment	Minimum	Maximum	Mean	Standard Deviation	Maximum/ Minimum	N
Manus Length/Pes Length	Single Cases	0.42	0.65	0.520	0.051	1.55	41
	Trackway Means	0.44	0.57	0.518	0.038	1.30	9
Manus Width/Manus Length	Single Cases	1.04	1.76	1.282	0.109	1.69	57
	Trackway Means	1.13	1.76	1.311	0.179	1.56	9
Manus Stride/Manus Length	Single Cases	4.82	7.70	5.922	0.828	1.60	20
	Trackway Means	5.09	7.17	5.837	0.624	1.41	8
Manus Inner Trackway Width/Manus Length	Single Cases	1.09	2.55	1.651	0.375	2.34	20
	Trackway Means	1.14	2.34	1.645	0.379	2.05	8
Manus Outer Trackway Width/Manus Length	Single Cases	3.36	5.00	4.030	0.425	1.49	21
	Trackway Means	3.51	4.70	3.977	0.375	1.34	8
Distance Manus Wrist to Trackway Midline/Pes Length	Single Cases	0.35	1.16	0.731	0.178	3.31	34
	Trackway Means	0.52	0.92	0.707	0.130	1.77	7
Distance Manus Digit III Tip to Trackway Midline/Pes Length	Single Cases	0.38	1.35	0.817	0.193	3.55	38
	Trackway Means	0.54	1.17	0.773	0.196	2.17	7
Manus-Pes Distance/Pes Length	Single Cases	0.48	1.39	0.900	0.230	2.90	51
	Trackway Means	0.51	1.16	0.827	0.225	2.27	9
Pes Width (I-IV)/Pes Length	Single Cases	0.58	0.88	0.701	0.068	1.52	47
	Trackway Means	0.64	0.84	0.707	0.063	1.31	9
Pes Width (I-III)/Pes Length	Single Cases	0.34	0.59	0.459	0.056	1.74	56
	Trackway Means	0.40	0.58	0.467	0.055	1.45	9
Pes Stride (Digit III Tip)/Pes Length	Single Cases	2.27	4.43	3.078	0.465	1.95	28
	Trackway Means	2.65	3.90	3.081	0.380	1.47	8
Pes Stride (Heel)/Pes Length	Single Cases	2.55	3.66	3.059	0.303	1.44	18
	Trackway Means	2.68	3.77	3.164	0.384	1.41	7

Distance Pes Digit III Tip to Trackway Midline/Pes Length	Single Cases	0.69	1.08	0.819	0.095	1.57	46
	Trackway Means	0.73	0.88	0.805	0.057	1.21	7
Pes Inner Trackway Width/Pes Length	Single Cases	0.45	1.12	0.724	0.154	2.49	27
	Trackway Means	0.43	0.85	0.645	0.134	1.98	9
Pes Outer Trackway Width/Pes Length	Single Cases	1.78	2.72	2.165	0.210	1.53	20
	Trackway Means	1.80	2.34	2.128	0.197	1.30	8

TABLE 3

Partial or simple correlations between trackway measurements. Data cases are individual measurements (not trackway means), made without regard to the number of footprints per trackway. Significant correlations indicated in **bold**.

Control Variable	Test Variables		r	p	N
Manus Print Length	Manus Stride	Manus Trackway Inner Width	-0.432	0.108	13
	Manus Stride	Manus Trackway Outer Width	-0.150	0.579	14
-----	Manus Rotation	Calculated Manus Divarication	**0.921**	**<0.001**	47
Pes Print Length	Distance Manus Digit III Tip to Midline	Distance Pes Digit III Tip to Midline	0.019	0.912	35
	Distance Manus Wrist to Midline	Distance Pes Heel to Midline	-0.024	0.893	31
	Pes Trackway Inner Width	Manus-Pes Distance	0.061	0.771	23
	Pes Trackway Outer Width	Manus-Pes Distance	-0.019	0.940	16
	Pes Heel Stride	Pes Digit III Stride	**0.909**	**<0.001**	10
	Pes Trackway Inner Width	Pes Digit III Stride	**0.572**	**0.008**	18
	Pes Trackway Outer Width	Pes Digit III Stride	0.437	0.091	14
	Pes Digit III Stride	Manus-Pes Distance	**-0.708**	**<0.001**	24
	Manus Stride	Pes Digit III Stride	**0.981**	**<0.001**	12

TABLE 4

Nonparametric correlations between relative stride length or relative trackway width and pace angulation. Data cases are individual observations rather than trackway means. Significant correlations indicated in **bold**.

Test Variables		Kendall's tau-b (p)	Spearman's rho (p)	N
Manus Stride/Manus Length	Manus Pace Angulation	**0.574 (0.001)**	**0.779 (<0.001)**	19
Manus Trackway Inner Width/Manus Length	Manus Pace Angulation	**-0.683 (<0.001)**	**-0.828 (<0.001)**	15
Pes Digit III Stride/Pes Length	Pes Digit III Pace Angulation	**0.433 (0.002)**	**0.590 (0.001)**	28
Pes Heel Stride/Pes Length	Pes Heel Pace Angulation	**0.537 (0.003)**	**0.677 (0.003)**	17
Pes Inner Trackway Width/Pes Length	Pes Digit III Pace Angulation	**-0.343 (0.033)**	**-0.470 (0.032)**	21
Pes Inner Trackway Width/Pes Length	Pes Heel Pace Angulation	0.029 (0.881)	0.047 (0.869)	15

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TABLE 5

Regression equations for predicting lengths of *Crocodylus acutus* from the manus and pes length proxies; data from Kumagai (2010). Equations based on pes lengths exclude the two most egregious outlier points (Fig. 25B, D).

Total length (cm) = 27.717 manus print length proxy (cm) - 2.386; r = 0.988, p < 0.001, N = 61

Shoulder-hip length (cm) = 6.602 manus print length proxy (cm) – 1.330; r = 0.989, p < 0.001, N = 57

Total length (cm) = 16.249 pes print length proxy (cm) – 4.157; r = 0.986, p < 0.001, N = 58

Shoulder-hip length (cm) = 3.856 pes print length proxy (cm) - 1.831; r = 0.993, p < 0.001, N = 54

TABLE 6

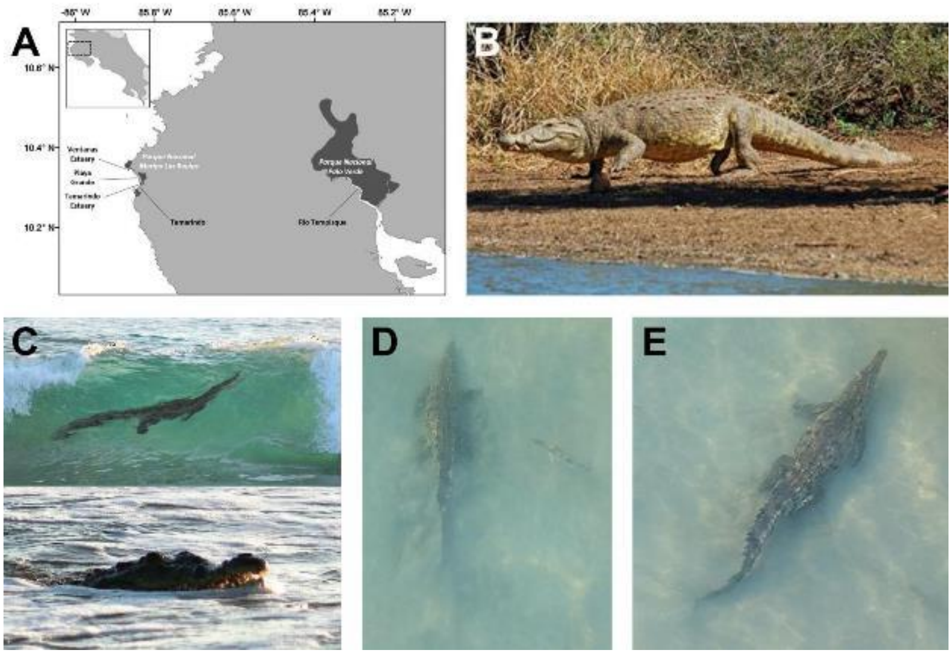
Size estimates of American crocodiles from autopodium lengths and glenoacetabular length. Estimates are based on simple linear regression models of crocodile length vs. autopodium length for *Crocodylus acutus* (Table 5). Trackways 6 and 7 are thought to have been made by the same individual.

Trackway	Autopodium	Mean or Single Autopodium Length (cm)	Estimated Trackmaker Total Length (cm)	Estimated Trackmaker Shoulder-Hip Length (cm)	Mean or Single Trackway Glenoacetabular Length (cm)
1: 20130419	Manus	8	219	51	45
	Pes	18	288	68	
2: 20140313	Manus	11.0	303	71	51
	Pes	22.7	365	86	
3: 20140323	Manus	8	219	51	-----
	Pes	14.9	238	56	
6: 20141120	Manus	8.4	230	54	-----
	Pes	16.2	259	61	
7: 20141130	Manus	9.0	247	58	41.8
	Pes	16.7	267	63	
9: 20150119	Manus	9.3	255	60	41.7
	Pes	16.2	259	61	
10: 20150129	Manus	9.7	266	63	49.7
	Pes	18.7	300	70	
11: 20150311	Manus	12.2	336	79	59.0
	Pes	23.7	381	90	
12: 20160116	Manus	9.6	264	62	46.6
	Pes	17.4	279	65	

TABLE 7

T-tests for left/right irregularity in pace lengths of two Costa Rican crocodile trackways. Tests are performed for comparisons in which there were at least 5 measurements for each left or right beginning pace. Significant test is indicated in **bold**.

Trackway	Pace Parameter	Mean Pace Length Beginning with Print (cm)		t (p)	N (Left: right)
		Left	Right		
Trackway 9: 20150119	Manus	36.2	35.4	0.473 (0.647)	6:5
	Pes Digit III	36.9	35.3	1.785 (0.100)	9:9
Trackway 12: 20160116	Manus	43.3	43.1	0.158 (0.877)	8:7
	Pes Digit III	49.1	42.8	**2.919 (0.012)**	7:8
	Pes Heel	42.1	39.4	1.829 (0.089)	6:10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-86° W
85.8° W
85.6° W
85.4° W
85.2° W
10.6° N
10.4° N
10.2° N
Ventanas Estuary
Playa Grande
Tamarindo Estuary
Parque Nacional Marino Las Baulas
Tamarindo
Parque Nacional Palo Verde
Río Tempisque
B
C
D
E

Figure 1

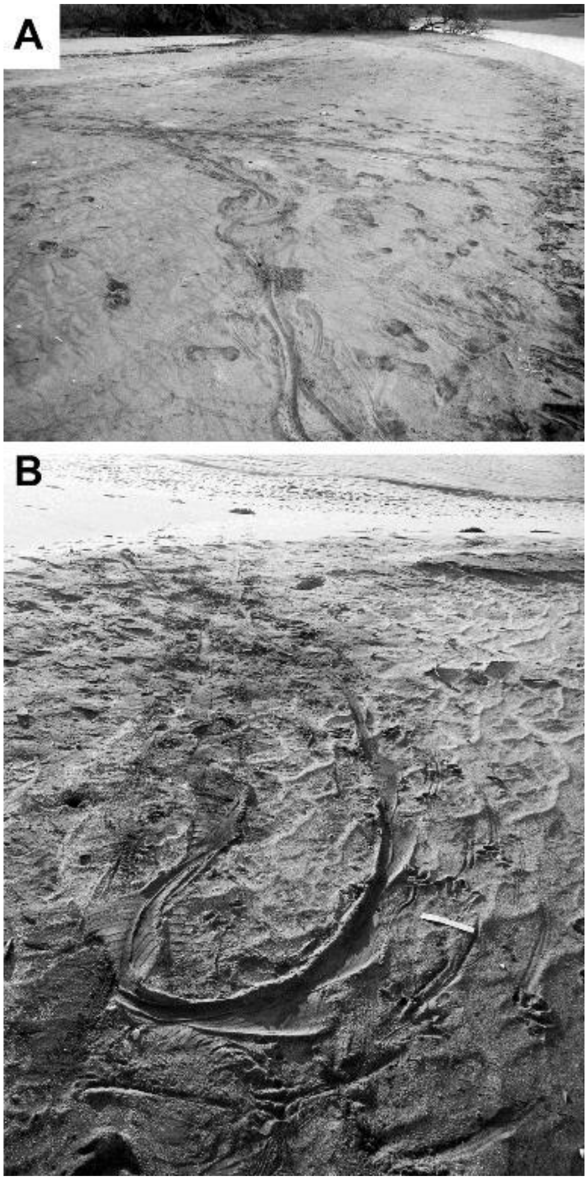

Figure 2

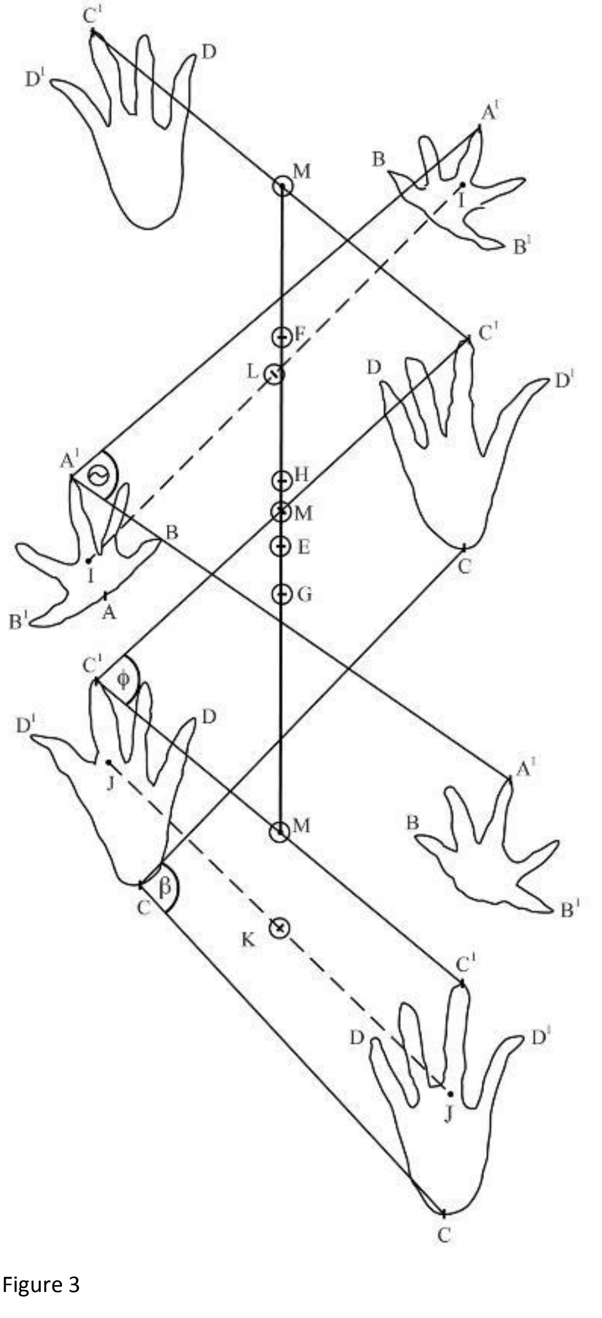
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Figure 3

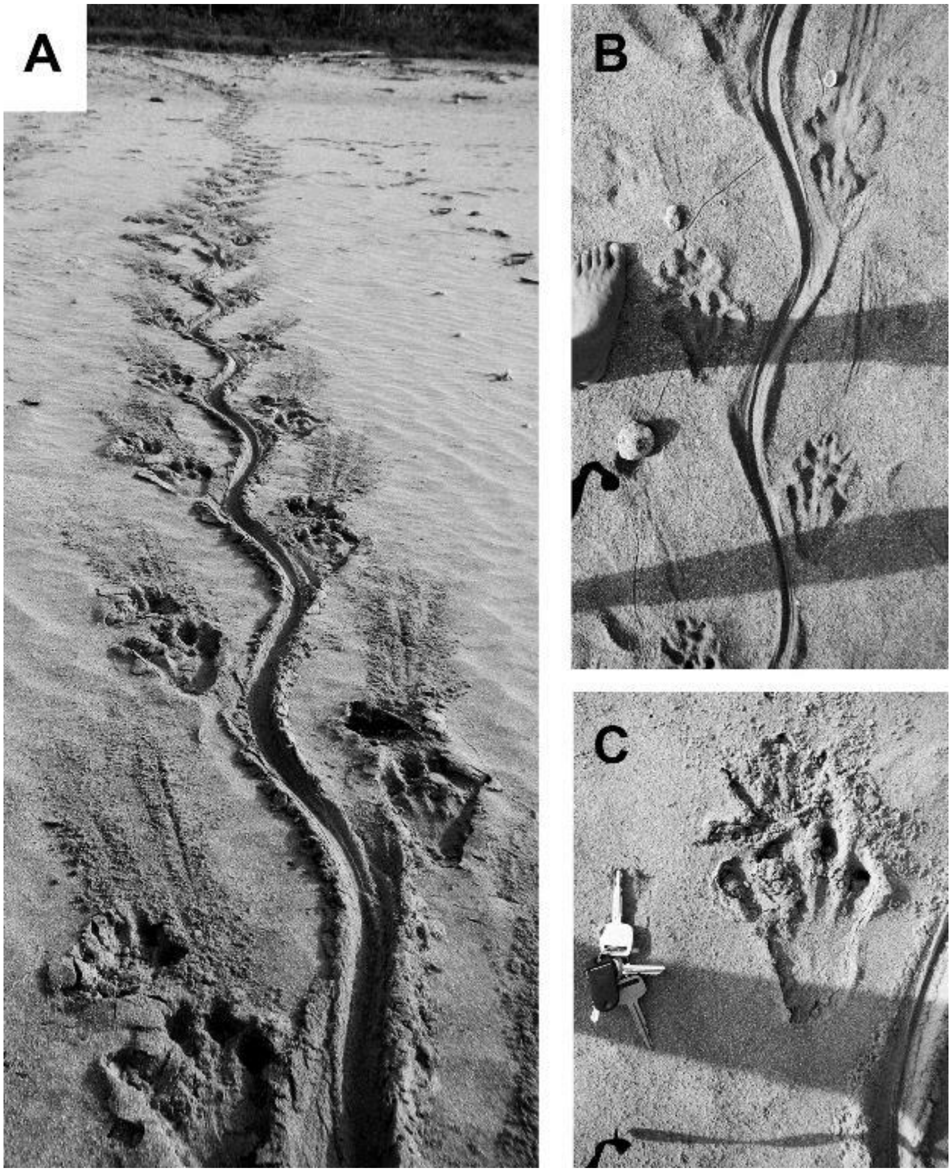

Figure 4

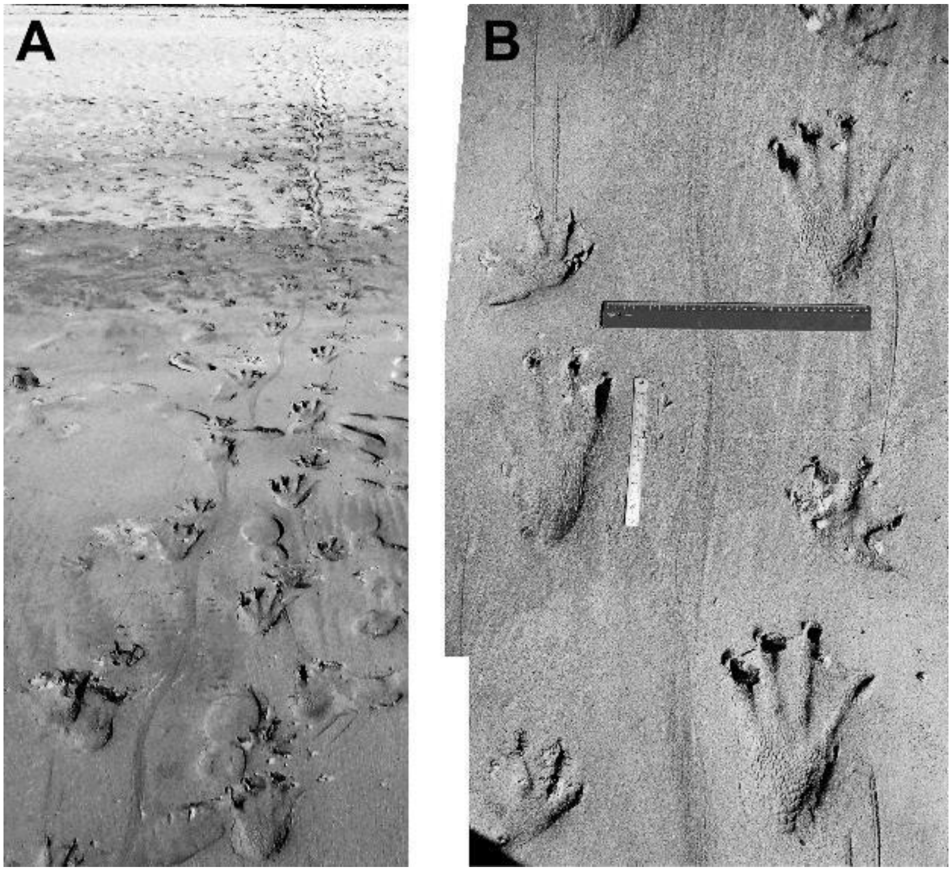

Figure 5

Figure 6

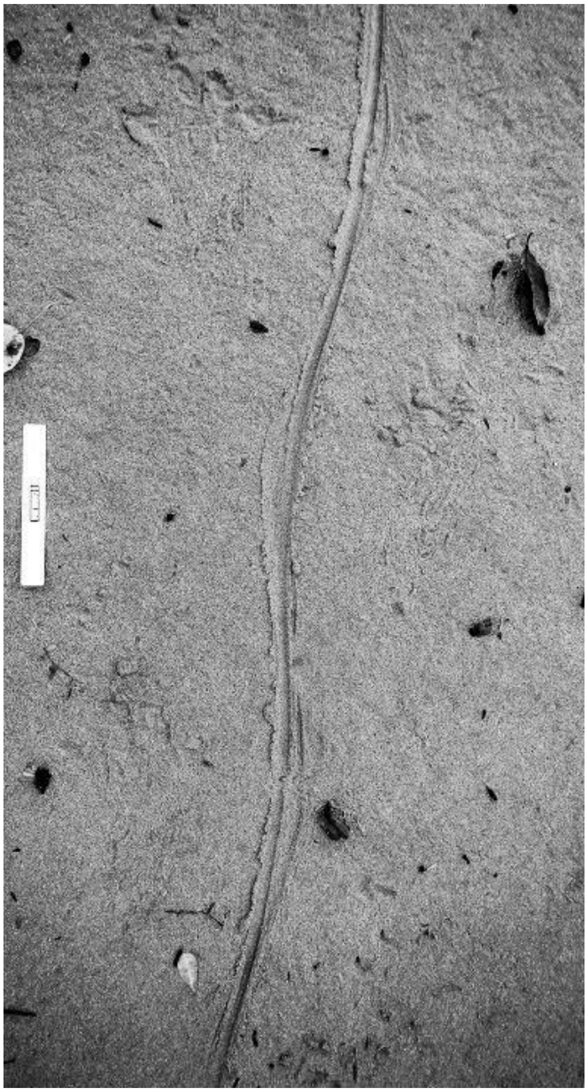

Figure 7

Figure 8

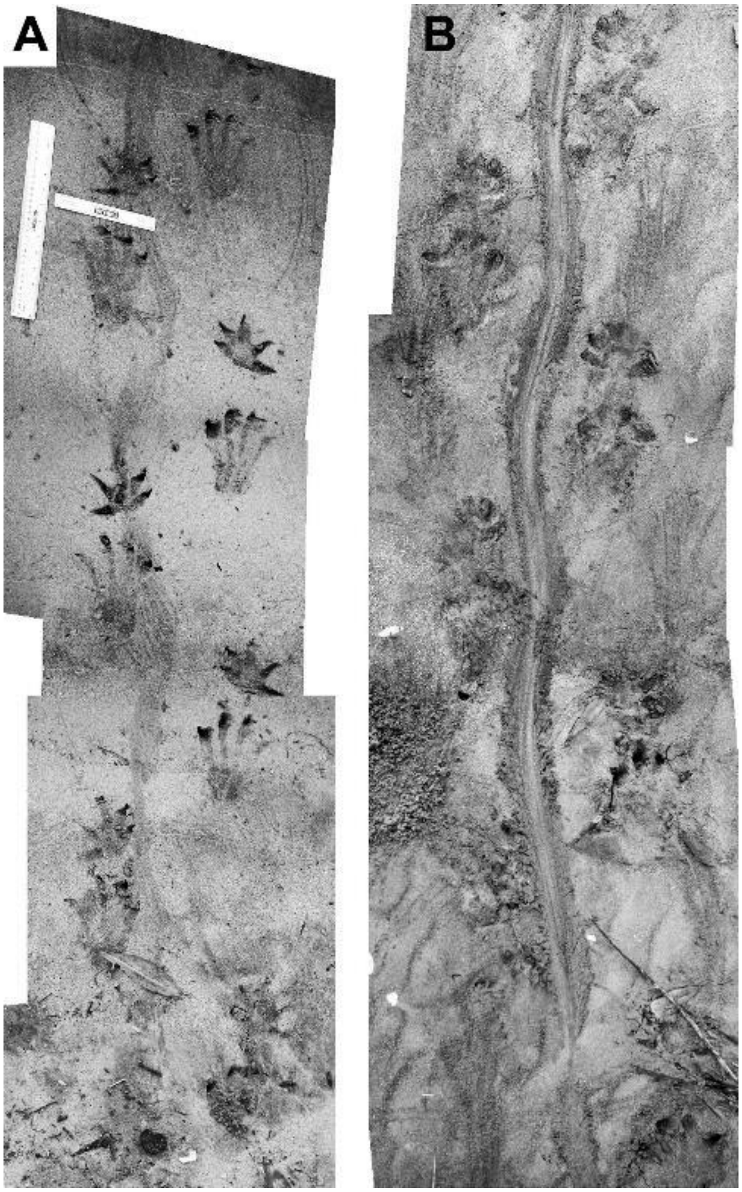

Figure 9

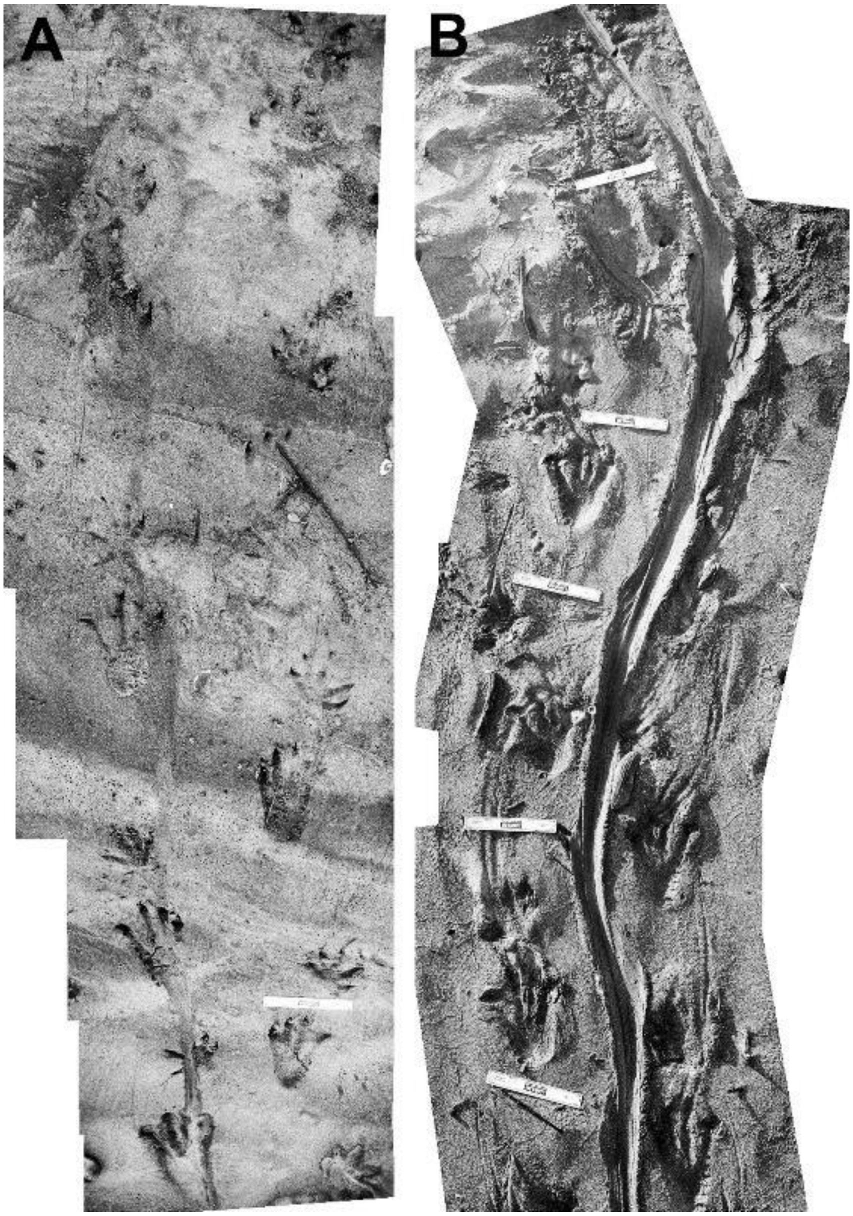

Figure 10

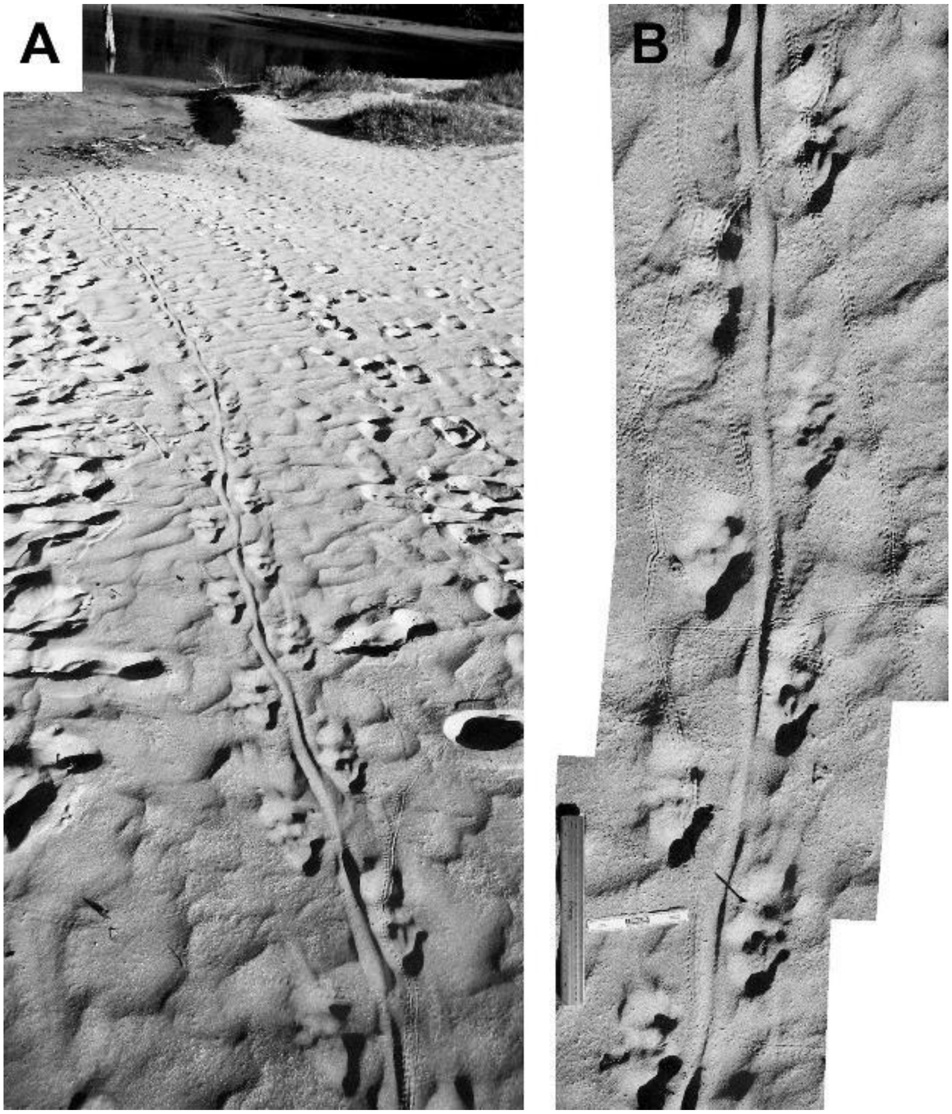

Figure 11

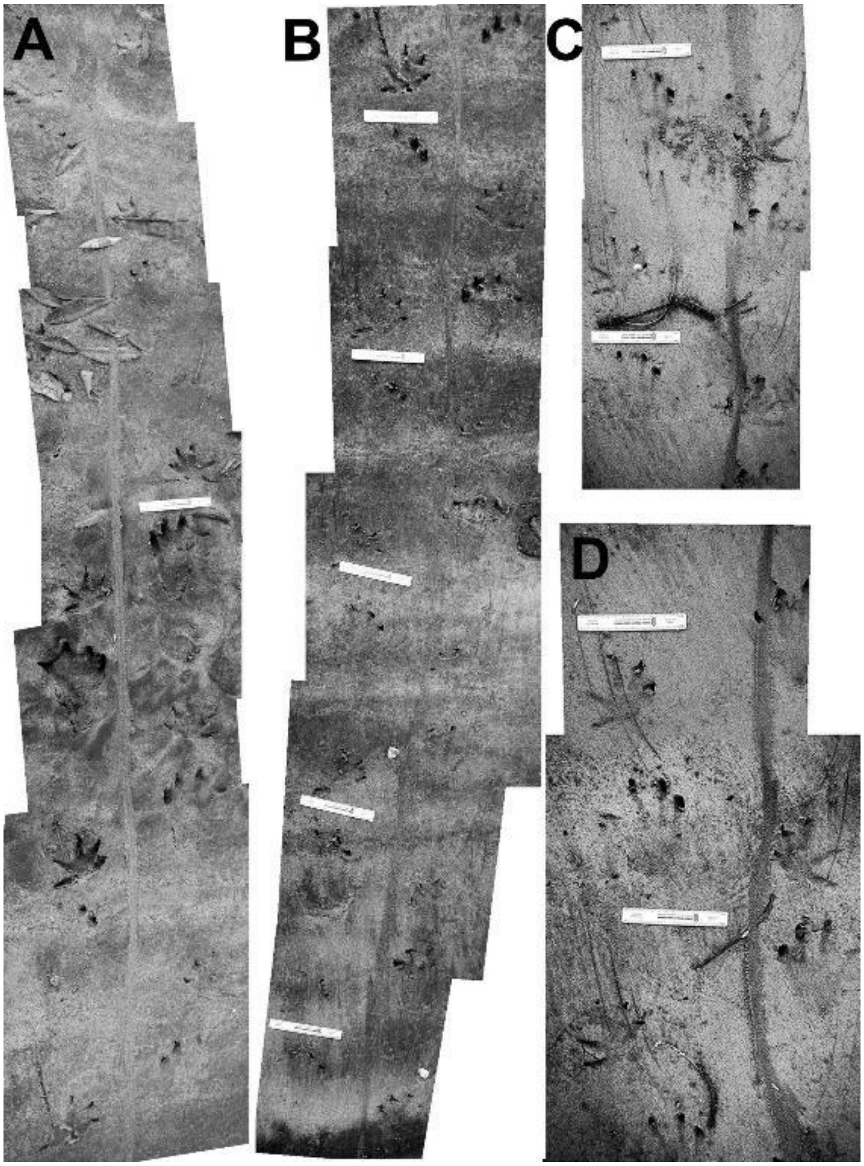

Figure 12

Figure 13

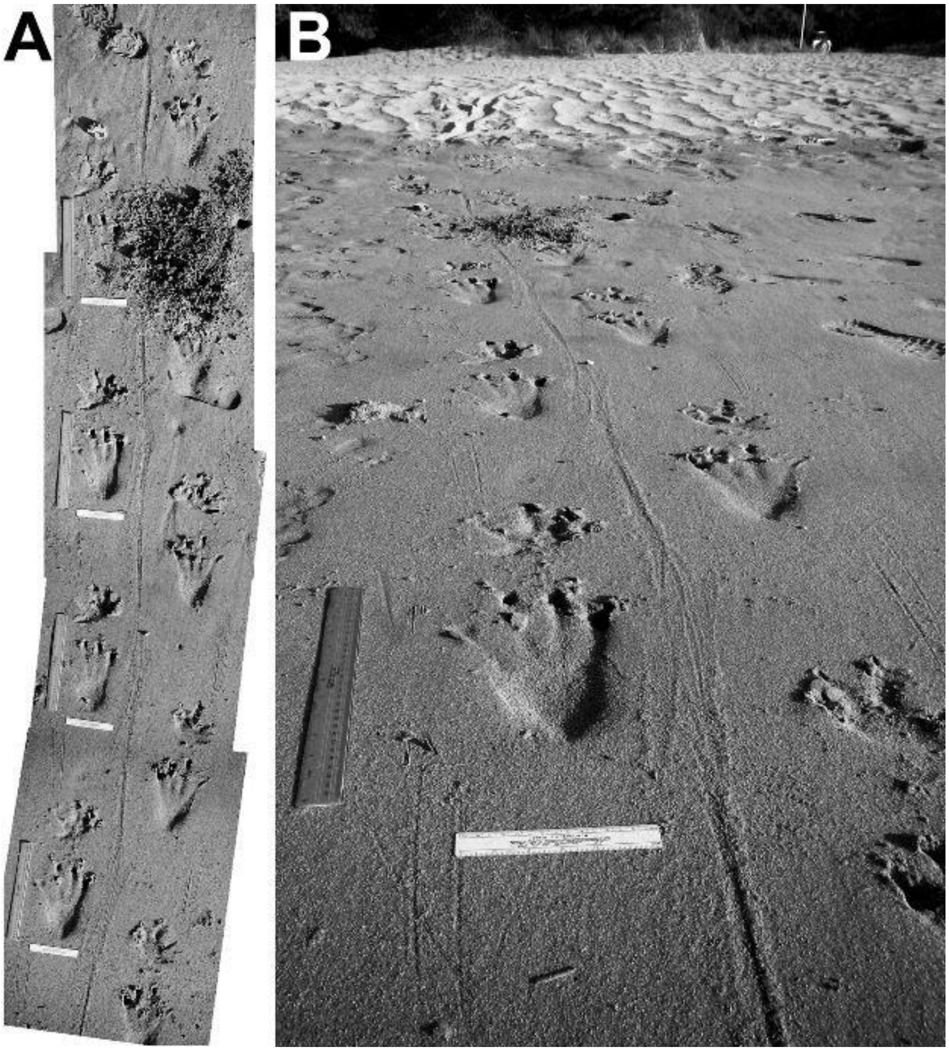

Figure 14

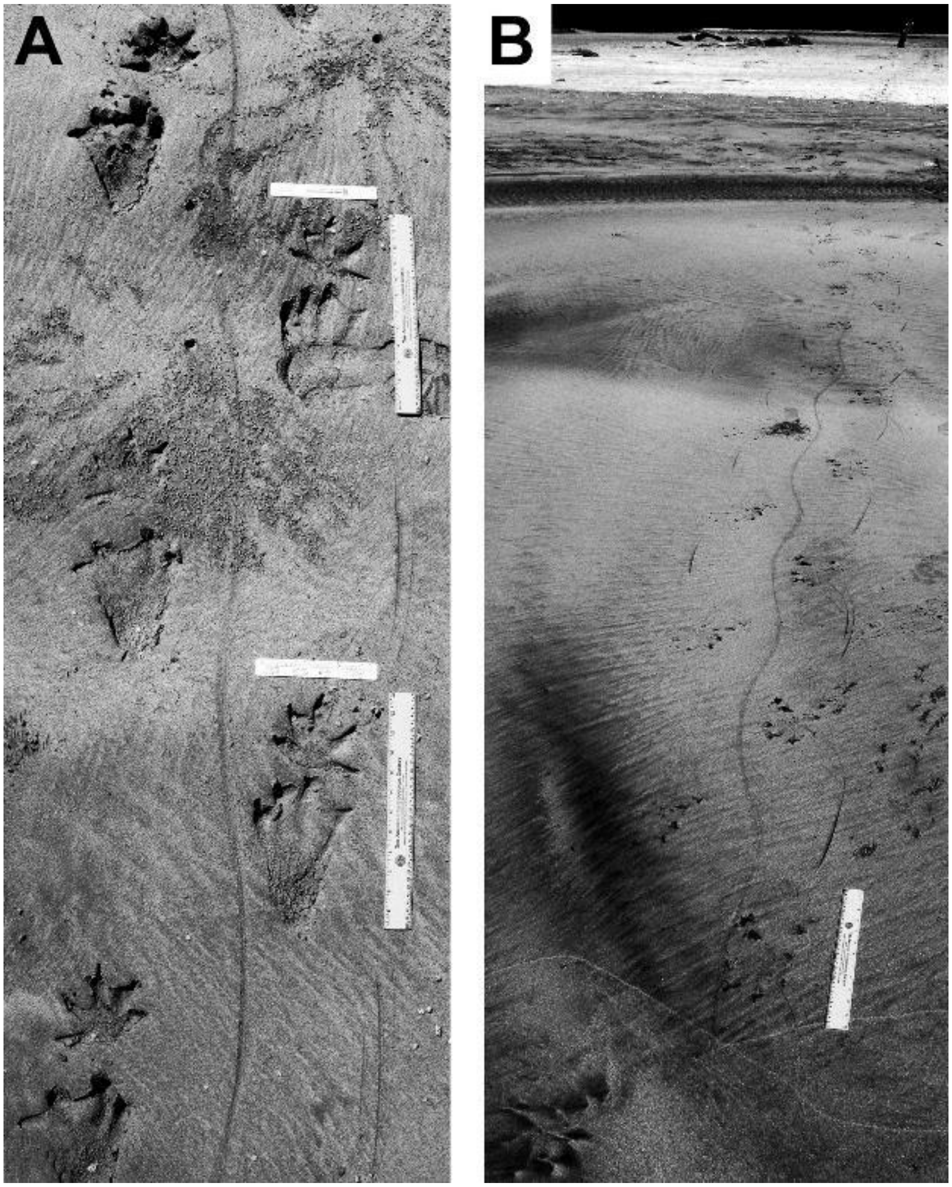

Figure 15

Figure 16

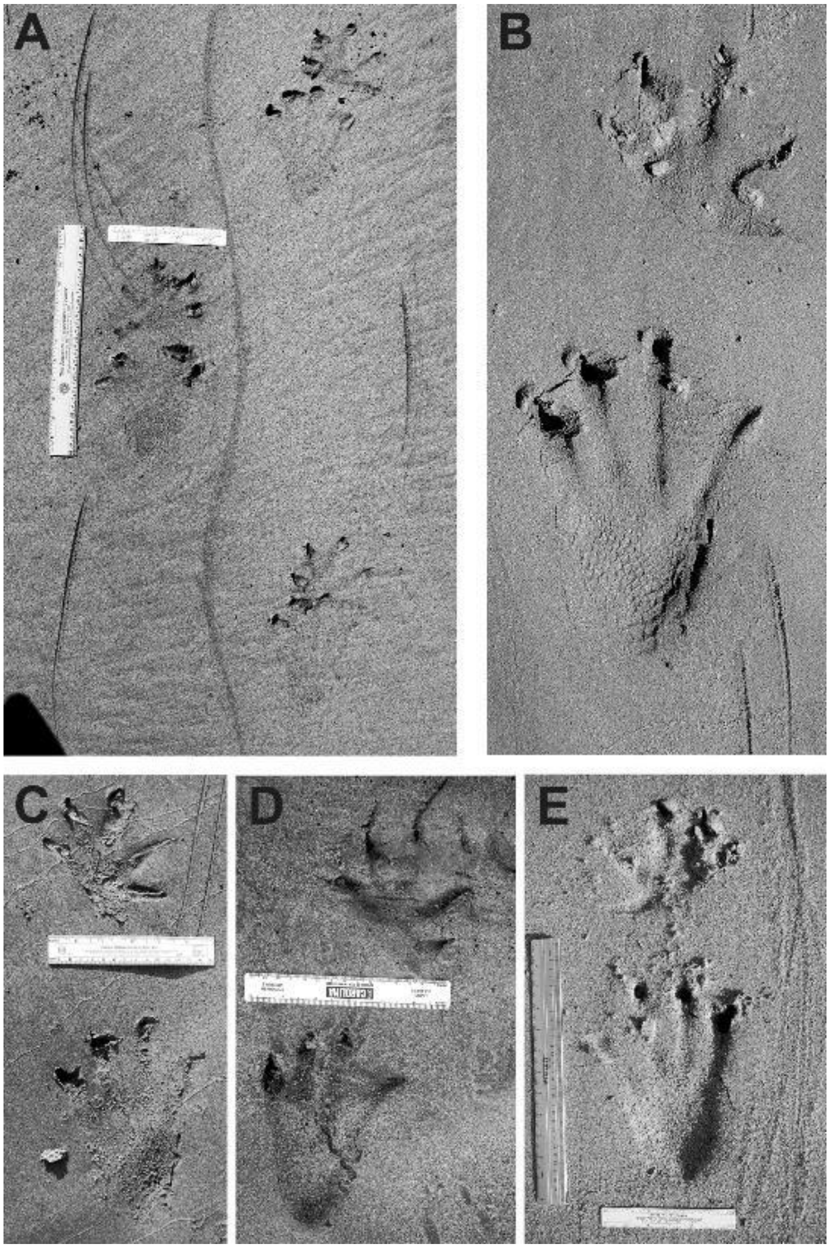

Figure 17

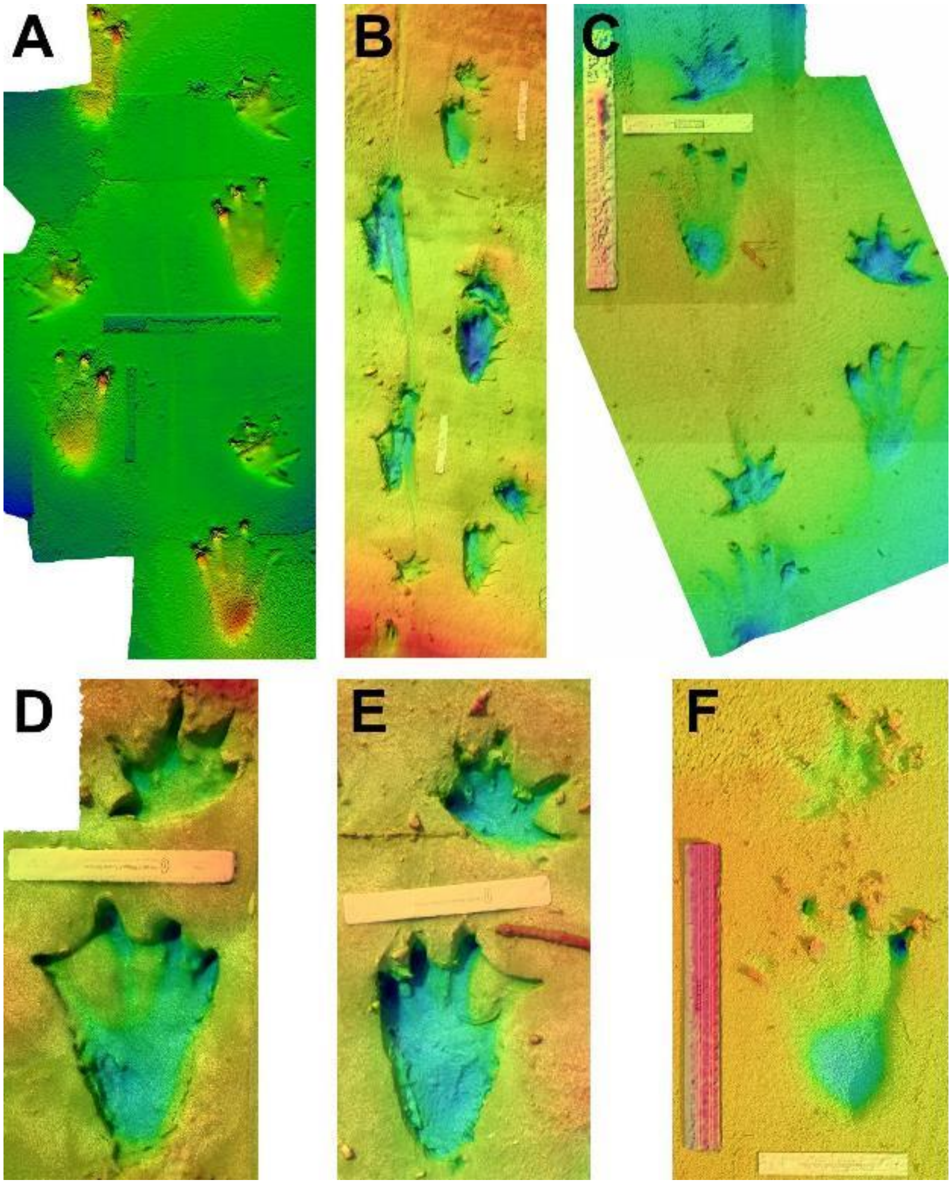

Figure 18

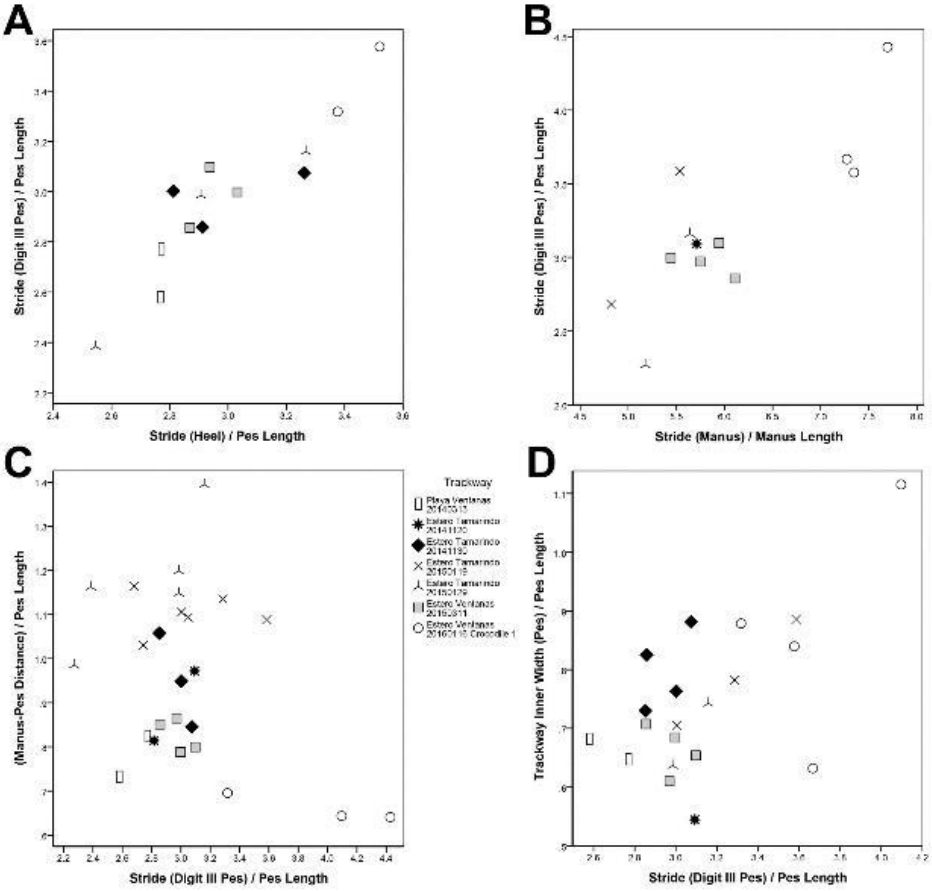
A
Stride (Digit III Pes) / Pes Length
Stride (Heel) / Pes Length
2.2
2.4
2.6
2.8
3.0
3.2
3.4
3.6
B
Stride (Digit III Pes) / Pes Length
Stride (Manus) / Manus Length
2.0
2.5
3.0
3.5
4.0
4.5
5.0
5.5
6.0
6.5
7.0
7.5
8.0
C
(Manus-Pes Distance) / Pes Length
Stride (Digit III Pes) / Pes Length
.6
.7
.8
.9
1.0
1.1
1.2
1.3
1.4
2.2
2.4
2.6
2.8
3.0
3.2
3.4
3.6
3.8
4.0
4.2
4.4
Trackway
Playa Ventanas 20140313
Estero Tamarindo 20141120
Estero Tamarindo 20141130
Estero Tamarindo 20160119
Estero Tamarindo 20150129
Estero Ventanas 20160311
Estero Ventanas 20160118 Crocodile 1
D
Trackway Inner Width (Pes) / Pes Length
Stride (Digit III Pes) / Pes Length
.5
.6
.7
.8
.9
1.0
1.1
2.6
2.8
3.0
3.2
3.4
3.6
3.8
4.0
4.2

Figure 19

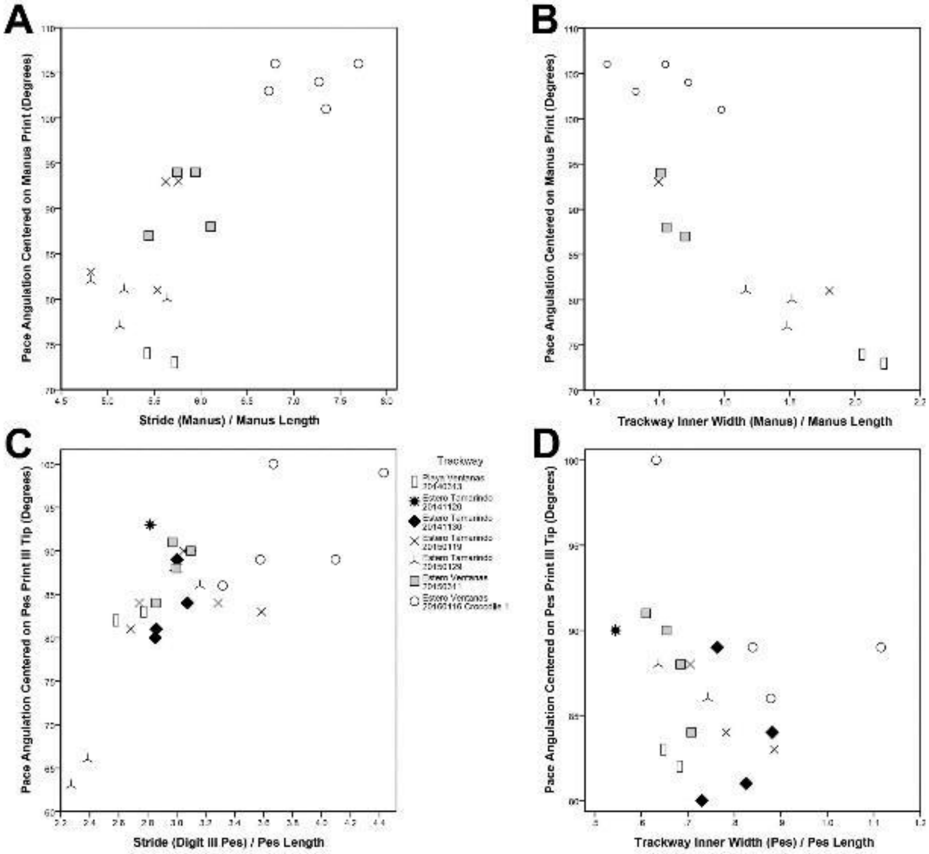
A
Pace Angulation Centered on Manus Print (Degrees)
110
105
100
95
90
85
80
75
70
4.5
5.0
5.5
6.0
6.5
7.0
7.5
8.0
Stride (Manus) / Manus Length
B
Pace Angulation Centered on Manus Print (Degrees)
Trackway Inner Width (Manus) / Manus Length
C
Pace Angulation Centered on Pes Print III Tip (Degrees)
Stride (Digit III Pes) / Pes Length
Trackway
Playa Ventanas 20140213
Estero Tamarindo 20141120
Estero Tamarindo 20141130
Estero Tamarindo 20150119
Estero Tamarindo 20150128
Estero Ventanas 20150211
Estero Ventanas 20160116 Crocodile 1
D
Pace Angulation Centered on Pes Print III Tip (Degrees)
Trackway Inner Width (Pes) / Pes Length

Figure 20

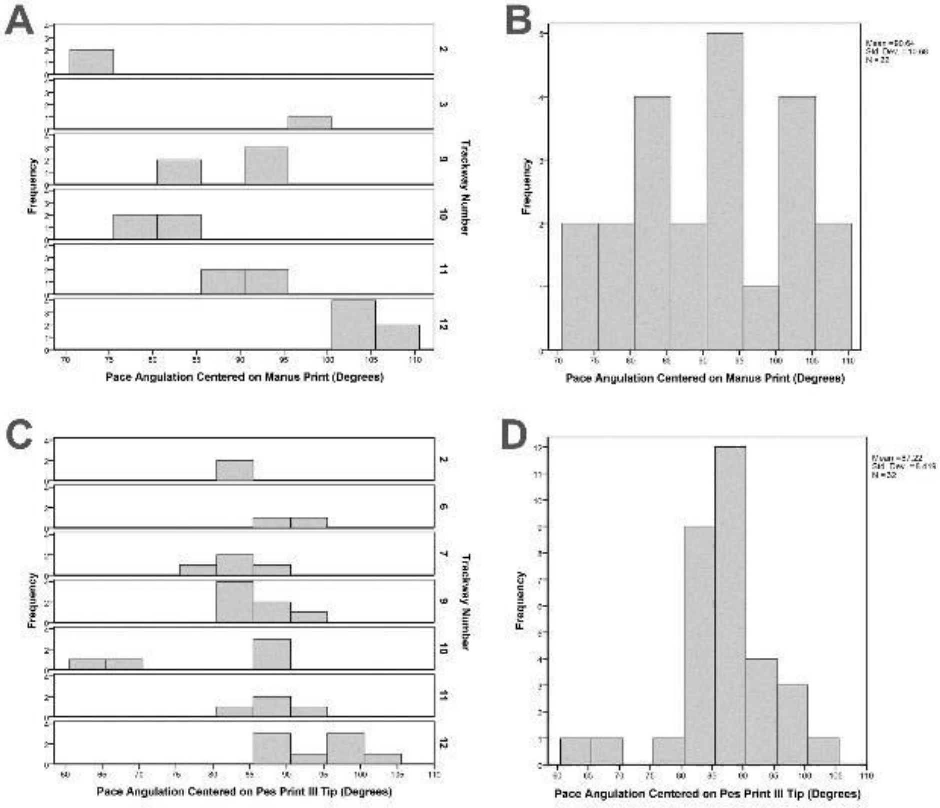
A
B
C
D
Frequency
Trackway Number
2
3
9
10
11
12
6
7
Pace Angulation Centered on Manus Print (Degrees)
Pace Angulation Centered on Pes Print III Tip (Degrees)
Mean =90.64
Std. Dev. =10.66
N = 22
Mean =87.22
Std. Dev. =8.419
N =32
60
65
70
75
80
85
90
95
100
105
110

Figure 21

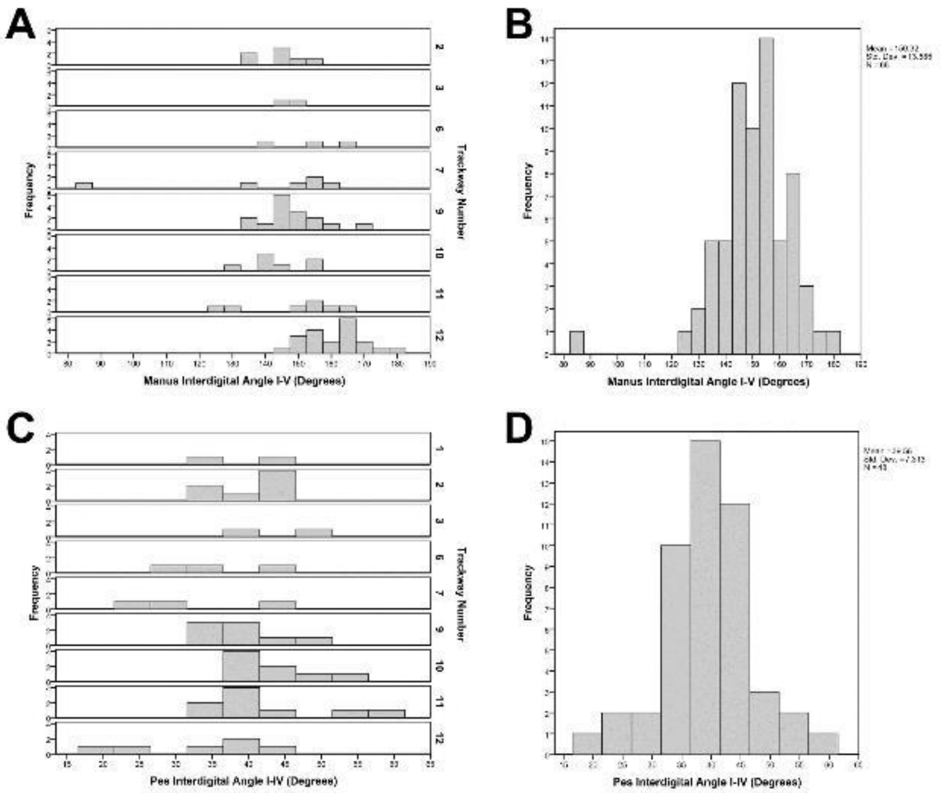
A
Frequency
Trackway Number
2
3
6
7
9
10
11
12
80 90 100 110 120 130 140 150 160 170 180 190
Manus Interdigital Angle I-V (Degrees)
B
Frequency
Mean = 150.32
Std. Dev = 13.595
N = 66
80 90 100 110 120 130 140 150 160 170 180 190
Manus Interdigital Angle I-V (Degrees)
C
Frequency
Trackway Number
1
2
3
6
7
9
10
11
12
15 20 25 30 35 40 45 50 55 60 65
Pes Interdigital Angle I-IV (Degrees)
D
Frequency
Mean = 39.56
Std. Dev. = 7.512
N = 48
15 20 25 30 35 40 45 50 55 60 65
Pes Interdigital Angle I-IV (Degrees)

Figure 22

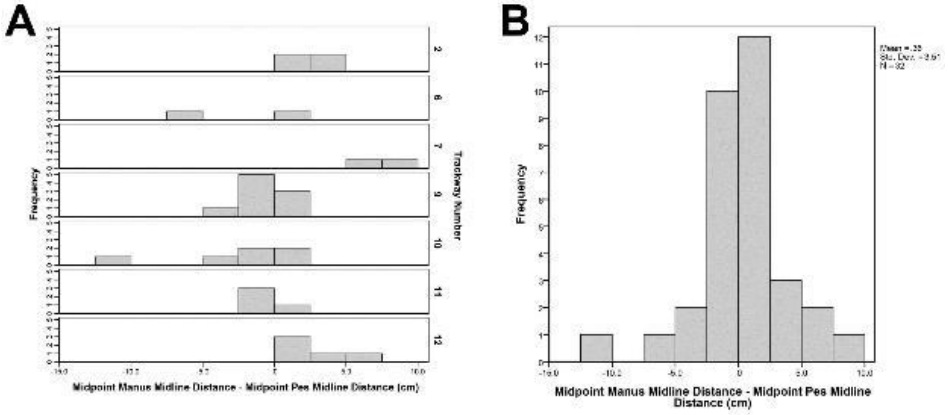
A
Frequency
Trackway Number
2
6
7
9
10
11
12
-15.0
-10.0
-5.0
0
5.0
10.0
Midpoint Manus Midline Distance - Midpoint Pes Midline Distance (cm)
B
Frequency
Mean =.35
Std. Dev. = 3.61
N = 32
-15.0
-10.0
-5.0
0
5.0
10.0
Midpoint Manus Midline Distance - Midpoint Pes Midline Distance (cm)

Figure 23

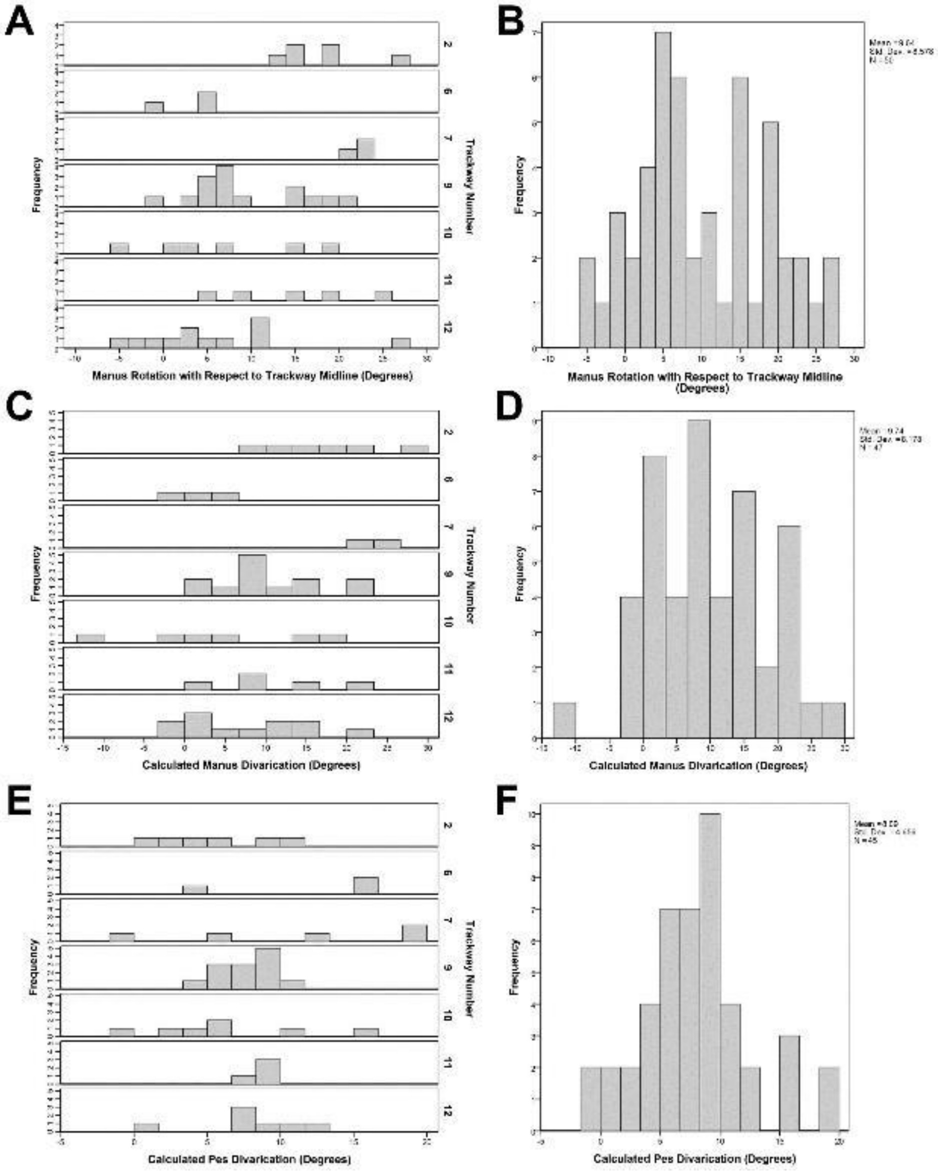
A
Frequency
Trackway Number
2
6
7
9
10
11
12
Manus Rotation with Respect to Trackway Midline (Degrees)
B
Mean =9.64
Std. Dev. =8.578
N =50
Frequency
Manus Rotation with Respect to Trackway Midline (Degrees)
C
Frequency
Trackway Number
Calculated Manus Divarication (Degrees)
D
Mean =9.74
Std. Dev. =8.173
N = 47
Frequency
Calculated Manus Divarication (Degrees)
E
Frequency
Trackway Number
Calculated Pes Divarication (Degrees)
F
Mean =8.09
Std. Dev. =4.656
N =45
Frequency
Calculated Pes Divarication (Degrees)

Figure 24

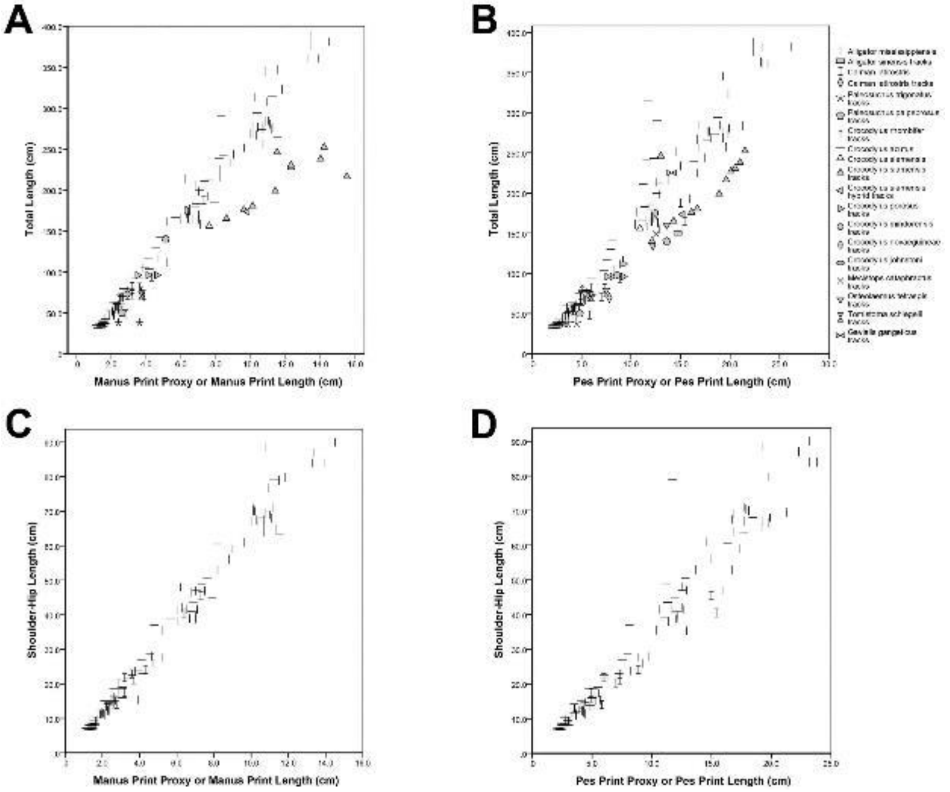
A
Total Length (cm)
Manus Print Proxy or Manus Print Length (cm)
B
Total Length (cm)
Pes Print Proxy or Pes Print Length (cm)
Alligator mississippiensis
Alligator sinensis tracks
Caiman crocodilus
Caiman crocodilus tracks
Paleosuchus trigonatus tracks
Paleosuchus palpebrosus tracks
Crocodylus rhombifer tracks
Crocodylus acutus
Crocodylus siamensis
Crocodylus siamensis tracks
Crocodylus siamensis hybrid tracks
Crocodylus porosus tracks
Crocodylus mindorensis tracks
Crocodylus novaeguineae tracks
Crocodylus johnstoni tracks
Mecistops cataphractus tracks
Osteolaemus tetraspis tracks
Tomistoma schlegelii tracks
Gavialis gangeticus tracks
C
Shoulder-Hip Length (cm)
Manus Print Proxy or Manus Print Length (cm)
D
Shoulder-Hip Length (cm)
Pes Print Proxy or Pes Print Length (cm)

Figure 25

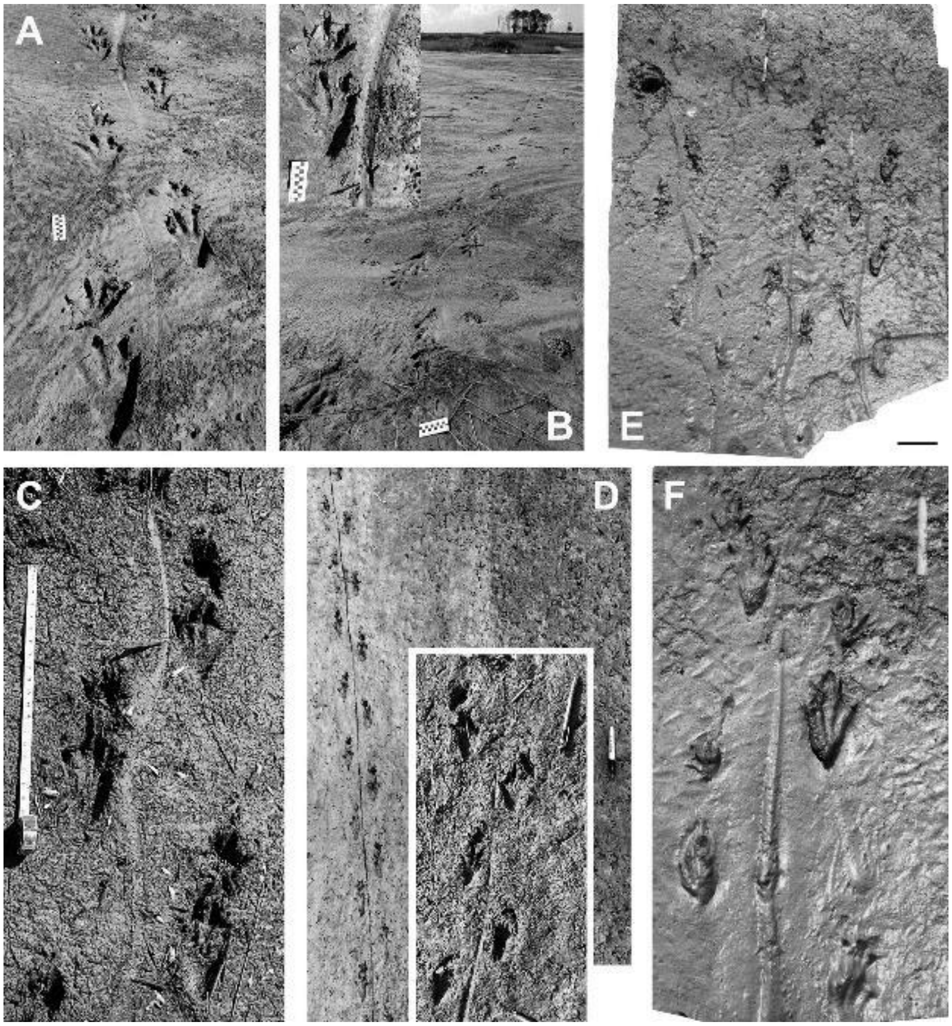

Figure 26

Figure 27

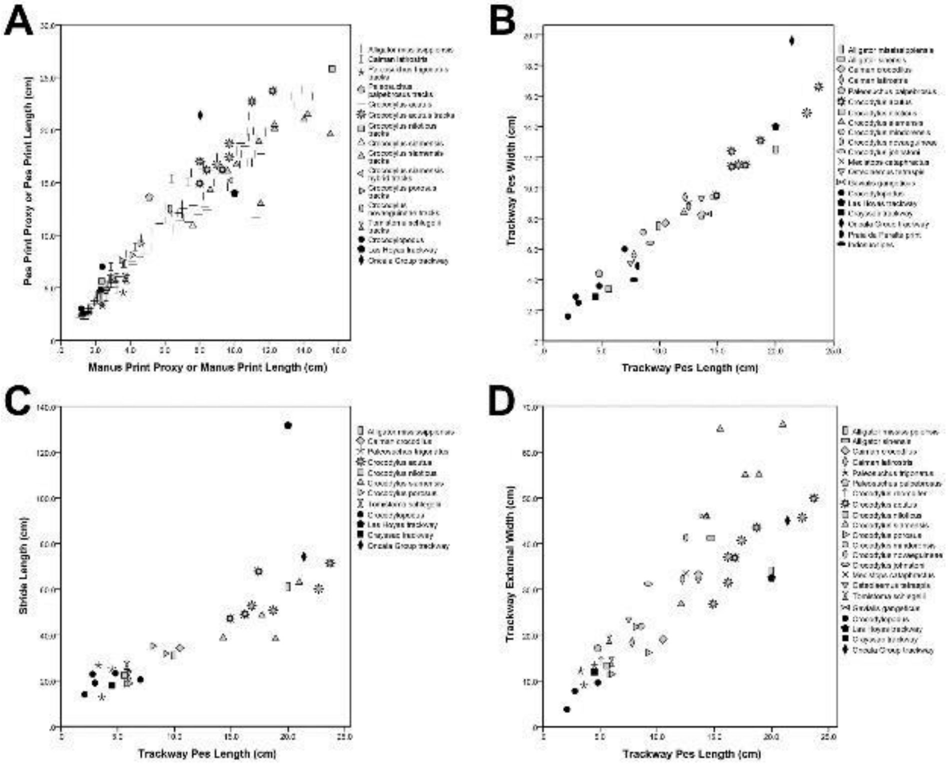
A
Pes Print Proxy or Pes Print Length (cm)
Manus Print Proxy or Manus Print Length (cm)
0
5.0
10.0
15.0
20.0
25.0
30.0
.0
2.0
4.0
6.0
8.0
10.0
12.0
14.0
16.0
Alligator mississippiensis
Caiman latirostris
Paleosuchus trigonatus tracks
Paleosuchus palpebrosus tracks
Crocodylus acutus
Crocodylus acutus tracks
Crocodylus niloticus tracks
Crocodylus siamensis
Crocodylus siamensis tracks
Crocodylus siamensis hybrid tracks
Crocodylus porosus tracks
Crocodylus novaeguineae tracks
Tomistoma schlegelii tracks
Crocodylopodus
Las Hoyas trackway
Oncala Group trackway
B
Trackway Pes Width (cm)
Trackway Pes Length (cm)
0
2.0
4.0
6.0
8.0
10.0
12.0
14.0
16.0
18.0
20.0
5.0
10.0
15.0
20.0
Alligator mississippiensis
Alligator sinensis
Caiman crocodilus
Caiman latirostris
Paleosuchus palpebrosus
Crocodylus acutus
Crocodylus niloticus
Crocodylus siamensis
Crocodylus mindorensis
Crocodylus novaeguineae
Crocodylus johnstoni
Mecistops cataphractus
Osteolaemus tetraspis
Gavialis gangeticus
Crocodylopodus
Las Hoyas trackway
Chayasac trackway
Oncala Group trackway
Praia da Parafita print
Indian print
C
Stride Length (cm)
Trackway Pes Length (cm)
0
20.0
40.0
60.0
80.0
100.0
120.0
140.0
5.0
10.0
15.0
20.0
25.0
Alligator mississippiensis
Caiman crocodilus
Paleosuchus trigonatus
Crocodylus acutus
Crocodylus niloticus
Crocodylus siamensis
Crocodylus porosus
Tomistoma schlegelii
Crocodylopodus
Las Hoyas trackway
Chayasac trackway
Oncala Group trackway
D
Trackway External Width (cm)
Trackway Pes Length (cm)
0
10.0
20.0
30.0
40.0
50.0
60.0
70.0
5.0
10.0
15.0
20.0
25.0
Alligator mississippiensis
Alligator sinensis
Caiman crocodilus
Caiman latirostris
Paleosuchus trigonatus
Paleosuchus palpebrosus
Crocodylus rhombifer
Crocodylus acutus
Crocodylus niloticus
Crocodylus siamensis
Crocodylus porosus
Crocodylus moreletii
Crocodylus novaeguineae
Crocodylus johnstoni
Mecistops cataphractus
Osteolaemus tetraspis
Tomistoma schlegelii
Gavialis gangeticus
Crocodylopodus
Las Hoyas trackway
Chayasac trackway
Oncala Group trackway

Figure 28