In quest of the *Pteraichnus* trackmaker: Comparisons to modern crocodilians

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The *Pteraichnus* trackmaker is usually hypothesized to be either a pterosaur or a crocodilian. Though the latter interpretation is recently not widely accepted, more experimental work on trackways of extant crocodilians is necessary to settle the debate. Here, the trackways of three species of modern crocodiles (*Paleosuchus trigonatus*, *Crocodylus porosus*, and *Tomistoma schlegelii*) in all major gaits and postures, namely sprawling, walking and running, were compared with *Pteraichnus* trackways. In all experimentally generated crocodilian trackways pentadactyl manus tracks are recognized, the external width between pes tracks is wider than the corresponding internal width between manus tracks, and tail marks are usually present. All crocodilian trackways collected in the present study revealed significant differences from *Pteraichnus*, which strongly suggests a non-crocodilian origin of *Pteraichnus*.

Key words: Crocodilia, *Pteraichnus*, trackway, gait, posture, kinematics, neoichnology.

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Introduction

In 1957, Stokes described a fossilized trackway from the Morrison Formation of Apache County, Arizona. While describing the quadrupedal trackway *Pteraichnus*, Stokes (1957) assumed that the trackmaker was a pterosaur. This interpretation was widely accepted until the neoichnological experiment with the crocodilian *Caiman sclerops* by Padian and Olsen (1984). These authors pointed out the similarity of crocodilian tracks to *Pteraichnus* and as a consequence, during the late 1980s and early 1990s, many researchers supported a crocodilian origin of *Pteraichnus*. However, findings of additional *Pteraichnus* trackways in the mid-1990s stimulated further discussion about the trackmaker identity. Currently, many researchers assume pterosaurs as a good candidate for the trackmaker (Lockley et al. 1995; Unwin 1996; Bennett 1997; Mazin et al. 2003) while Padian (2003) supports a crocodilian origin of all *Pteraichnus* trackways, except the *Pteraichnus* trackways from Crayssac, France where the width between the manus tracks is far wider than that of the pes tracks and length of pes tracks is approximately four times greater than its width at the metatarso-phalangeal joint.

In previous studies, two methods were mainly used to test the trackmaker of *Pteraichnus*: (i) reconstruction of pterosaur locomotion, pes morphology and manus morphology (e.g., Bennett 1997; Padian 2003), or (ii) comparison between a modern crocodilian trackway and *Pteraichnus* trackways (e.g., Padian and Olsen 1984; Mazin et al. 2003). However, the reconstruction of pterosaur terrestrial locomotion is itself debated, varying from digitigrade bipedal (Padian 1983) to plantigrade quadrupedal with sprawling posture (Wellnhofer 1988) or with erect outward angling limbs (Unwin 1996; Bennett 1997).

Some pterosaur researchers argue that their reconstructions are consistent with *Pteraichnus* trackways (Lockley et al. 1995; Unwin 1996), while others do not agree with these reconstructions (Padian 2003). The reconstruction of the pterosaur pes is also a matter of debate. Padian (2003) claimed that all pterosaurs are basically digitigrade and their metatarsals are closely appressed. In turn, Lockley et al. (1995), Unwin (1996) and Bennett (1997) assume a plantigrady of pterosaurs with splayed metatarsals.

Conclusions drawn from comparisons with experimental crocodilian trackways require further justification because only a few trackways of modern crocodilians have been described (Huene 1913; Reinech and Howard 1978; Padian and Olsen 1984; Mazin et al. 2003), among which, only Padian and Olsen (1984) analyzed modern crocodilian trackways in detail while discussing the producer of *Pteraichnus*. This situation is surprising when taking into account that even the account of only the *Caiman* trackway has prompted a hot debate about the identity of the *Pteraichnus* trackmaker. The majority of previous authors emphasized the similarity or dissimilarity between *Pteraichnus* and the *Caiman* trackways. In the studies suggesting a pterosaurian origin of *Pteraichnus*, dissimilarities are regarded as hard evidence of non-crocodilian origin of *Pteraichnus* (Lockley et al. 1995; Unwin 1996; Bennett 1997). On the other hand, the researchers who interpreted crocodilians as trackmakers of *Pteraichnus* regarded that these differences can be attributed to substrate conditions and kinematics of the trackmaker (Padian and Olsen 1984, Padian 2003).

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As reviewed above, most researchers have a consensus on the reconstruction of pterosaurs in quadrupedal locomotion. Nevertheless, conflicting opinions about reconstruction of pterosaur locomotion makes it difficult to settle the discussion about the producers of *Pteraichnus* at present. On the other hand, comparisons with crocodilians are readily assessable by investigating a variety of modern crocodilian trackways. Crocodilians adopt various gaits (walking and running) and locomotory postures (sprawling and semi-erect) on land. When sprawling, movement is always slow and the belly is dragged (Reilly and Elias 1998). In semi-erect posture, both walking and running are used. These are the three ways of movement that are typically adopted by crocodilians. The kinematics of locomotion are a factor that influences the trackways (Padian 2003); however, the only crocodilian trackways that have been described previously were produced by a walking gait. Thus, it is important to examine crocodilian trackways of various gaits for comparison with *Pteraichnus* trackways. If the features of the *Caiman* trackways, which are different from *Pteraichnus*, can be commonly observed in crocodilian trackways of various kinematics, *Pteraichnus* is unlikely to have been produced by crocodilians (Lockley et al. 1995; Unwin 1996; Bennett 1997). The purpose of this paper is to investigate various modern crocodilian tracks and compare them with *Pteraichnus* in order to discuss the origin of *Pteraichnus*.

Material and methods

Three species of crocodilians, reared in Ueno Zoo, Tokyo, Japan, were used in these experiments: a juvenile *Paleosuchus trigonatus*, two juvenile *Crocodylus porosus*, and two juvenile *Tomistoma schlegelii*. Their body weight, body length and snout-vent length are given in Table 1. These individuals are the maximum size suitable for the experiments due to safety reasons.

To collect trackways, a bed of potter's clay was made for about 1 square meter and its surface was smoothed by trowel. A water spray was occasionally used to keep the clay wet. A crocodile was set in front of the clay bed, where its nostrils touched the clay. As described by Padian and Olsen (1984), threatening or pinching did not make the crocodiles move forward. Crocodiles usually do not start moving for several hours. In particular, *T. schlegelii* did not move when humans were in their sight. Thus only one or two trackways could be collected in a day. After the trackways were impressed on the

Table 1. Measurements of crocodilian specimens used in this study.

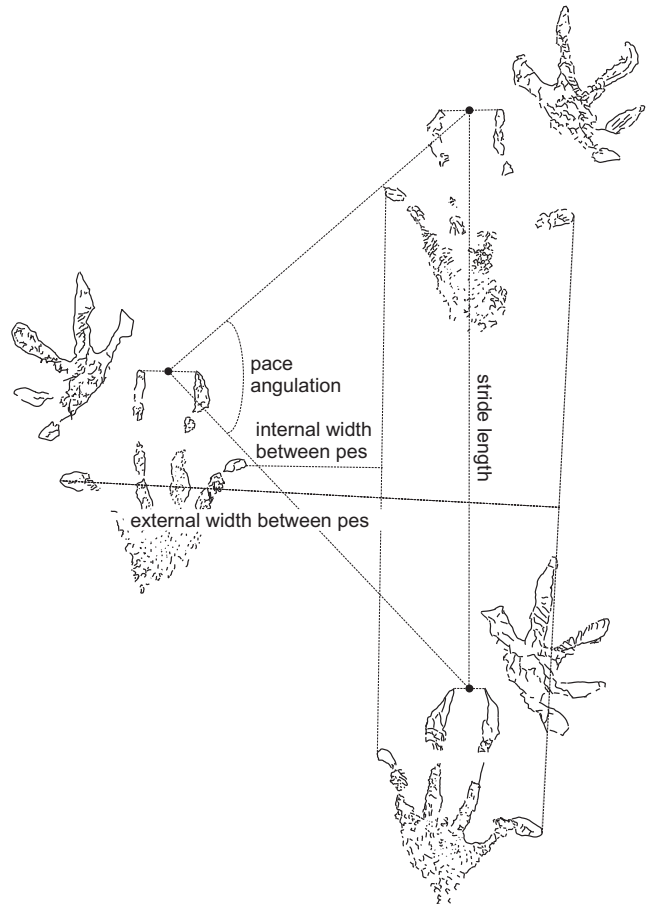| Taxon	Body weight [g]	Body length [cm]	Snout-Vent length [cm]
Paleosuchus trigonatus	230	38	19
Crocodylus porosus	2100	96	45.5
Crocodylus porosus	735	73	36
Tomistoma schlegelii	765	72	36
Tomistoma schlegelii	765	71	38

Fig. 1. Trackway measurements. Schematic diagram of pace angulation, stride length, external and internal width between opposing pes.

clay, a mold of the trackway was made by plaster of Paris. These molds were photographed using a digital camera. Lens barrel distortion of the photographs were corrected using computer software, PTLens. Measurements were taken from these digital images. The midpoints between two middle toes (II and III) of consequent pes imprints were connected to measure stride length and pace angulation. Internal and external trackway widths between both the pes and manus tracks were measured (Fig. 1). When possible, angles of axes of pes and manus digit imprints, and lengths of pes and manus tracks were measured (Table 2).

Results

Collected trackways.—Ten trackways were collected from individuals of three species (Fig. 2). Three trackways were made by *Paleosuchus trigonatus*, two by the smaller *Crocodylus porosus*, three by the larger *Crocodylus porosus* and one for each *Tomistoma schlegelii*. Modern crocodilians are known to use two locomotory postures, namely semi-erect (high-walk) and sprawling (belly dragging) (Reilly and Ellias 1998). Among the ten collected trackways, only one trackway of the larger *C. porosus* was made by sprawling

Table 2. Measurements of modern crocodilian trackways obtained in this study. Pes and manus track length were measured when possible. Values in parenthesis are average.

Taxon	Gait	Number of manus-pes set	Stride length [cm]	Pes external width [cm]	Pes internal width [cm]	Manus external width [cm]	Manus internal width [cm]	Pace angulation (degree)	Pes length [cm]	Manus length [cm]
Paleosuchus trigonatus	walking	15	10.3–17.3 (12.6)	8.1–10.0 (9.0)	2.4–4.4 (3.4)	4.0–9.0 (7.4)	1.2–6.0 (4.3)	62–115 (94)	3.0–3.9 (3.6)	2.0–3.0 (2.4)
Paleosuchus trigonatus	running	5	20.5–29.9 (25.1)	12.1–15.2 (13.4)	5.9–9.5 (7.1)	6.1–7.5 (6.8)	2.0–3.9 (2.9)	85–114 (97)	4.5	3.6
Paleosuchus trigonatus	running	5	23.6–28.7 (26.7)	11.6–13.3 (12.2)	5.9–7.4 (6.5)	6.5–7.4 (7.0)	2.6–3.4 (3.0)	85–114 (97)	2.6–-4.0 (3.3)	2.1–2.8 (2.4)
Crocodylus porosus	walking	8	17.4–20.6 (18.7)	9.5–12.3 (11.4)	5.0–6.5 (5.6)	11.1–15.5 (12.9)	5.8–11.1 (7.8)	92–101 (96)	5.6–6.1 (5.8)	2.4–3.6 (3.0)
Crocodylus porosus	walking	9	16.7–20.0 (18.8)	10.3–13.4 (11.5)	3.2–4.8 (3.8)	11.4–13.6 (12.4)	5.2–7.9 (6.6)	92–120 (109)	5.8–6.5 (6.0)	2.6–3.4 (3.0)
Crocodylus porosus	sprawling to walking	4	35.0–35.4 (35.2)	21.1–22.4 (21.8)	11.6–12.9 (12.3)	15.8–17.2 (16.5)	8.5–10.3 (9.4)	89–91 (90)	7.2 –8.8 (8.1)	3.8–4.3 (4.1)
Crocodylus porosus	sprawling	4	26.6–26.9 (26.8)	21.3–22.0 (21.6)	11.6–12.9 (12.3)	18.4–19.5 (19.0)	10.6–12.1 (11.4)	73–76 (75)	7.1–8.0 (7.6)	3.3–3.6 (3.5)
Crocodylus porosus	walking	6	29.8–32.8 (31.9)	15.8–16.6 (16.2)	5.5–7.0 (6.4)	12.5–13.4 (13.0)	3.4–4.1 (3.8)	105–115 (112)	8.7–9.8 (9.2)	4.0–4.9 (4.6)
Tomistoma schlegelii	walking	5	25.2–28.2 (26.8)	18.3–19.9 (19.1)	9.7–12.4 (11.1)	9.6–11.9 (10.7)	2.7–6.5 (4.6)	71–82 (76)	5.7–6.0 (5.8)	3.3–4.6 (3.8)
Tomistoma schlegelii	walking	7	20.5–25.1 (22.4)	13.7–15.0 (14.2)	6.2–8.1 (7.0)	12.9–15.3 (13.8)	7.6–10.2 (8.5)	82–97 (89)	5.6–6.2 (6.0)	3.5–3.9 (3.7)

(Fig. 2C), and another trackway of the same individual was impressed during the transition from sprawling to semi-erect walking—all the others were impressed while the crocodiles was in a semi-erect posture. Within these eight semi-erect trackways, two trackways of *P. trigonatus* were made by running (Fig. 2B), and the other six trackways were made by walking. Measurements are shown in Table 2.

Common features of modern crocodilian trackways.— Normally, crocodilian pes tracks are tetradactyl and manus tracks are pentadactyl. Tail dragging impressions are much shallower than manus or pes tracks. Tail marks are usually parallel to the direction of movement and continuous (Fig. 2A, E) or intermittent (Fig. 2D).

In the pes track, the claws are the most deeply impressed and best preserved (Fig. 3C, F). Among the four digit imprints of crocodilian pes, the imprint of digit IV is the shallowest and most rarely preserved, probably due to lack of a claw in digit IV. Usually the imprint of digit IV is curved, the axis is directed anterolaterally and the tip is directed laterally (Fig. 3A, E) in some cases with a sliding mark. Axes of other digit imprints are generally straight. Digit imprints never cross each other. Metapodial phalangeal pads are the second most deeply impressed in the pes tracks and are preserved most often after the claw imprints (Fig. 3A, E). The anterior parts of the digit imprints adjacent to claws are rarely preserved (Fig. 3B). This region may be held up by the claw and therefore does not touch the substrate or, alternatively, may exert very little force on the substrate. Usually, only part of the sole imprints is preserved and as a consequence the rear end of the heel is not clear in most tracks (Fig. 3C). Divergence of digit imprints I–IV is 20° to 55°. Digit imprints II

or III are usually directed most closely to the direction of movement.

In manus tracks, imprints of the claws of digits I, II and III are the most deeply impressed. The imprints of the metapodial phalangeal pads of these three digits are usually the next most deeply impressed, but are rarely deeper than the claw imprints. In some cases, only these three digit imprints are preserved, which makes the track appear tridactyl (Fig. 3B), although other manus tracks within the same trackway are pentadactyl. The other two lateral digits left relatively faint imprints. In many cases, these two digits produced rotary sliding imprints (Fig. 3C–E), which reflect lateral rotation of these two digits at the lift-off of the forelimb. The divergence between digit imprints I–V is 90–160°, the rotary motion of digit imprint V significantly increasing the angle. Digit imprints I, II, and III are directed anterior while the other two digits are directed lateral to posterolaterally.

Pes tracks are usually deeper than the corresponding manus tracks. Imprints of scales are seen in most parts of pes and manus tracks (Fig. 3A–C). The width between opposing manus tracks is similar to the corresponding width between opposing pes tracks. Thus ranges of width (from internal to external) of pes and manus almost always overlap each other (Table 2).

Gait- and posture-specific trackway patterns.—Trackway pattern differs significantly depending on the kinematics of the trackmaker. In running trackways, both stride length and trackway width of pes tracks increase compared to those in walking trackways (Table 2), whereas width of the manus tracks did not change considerably. Accordingly, pes tracks were always lateral to manus tracks when running. Pes tracks
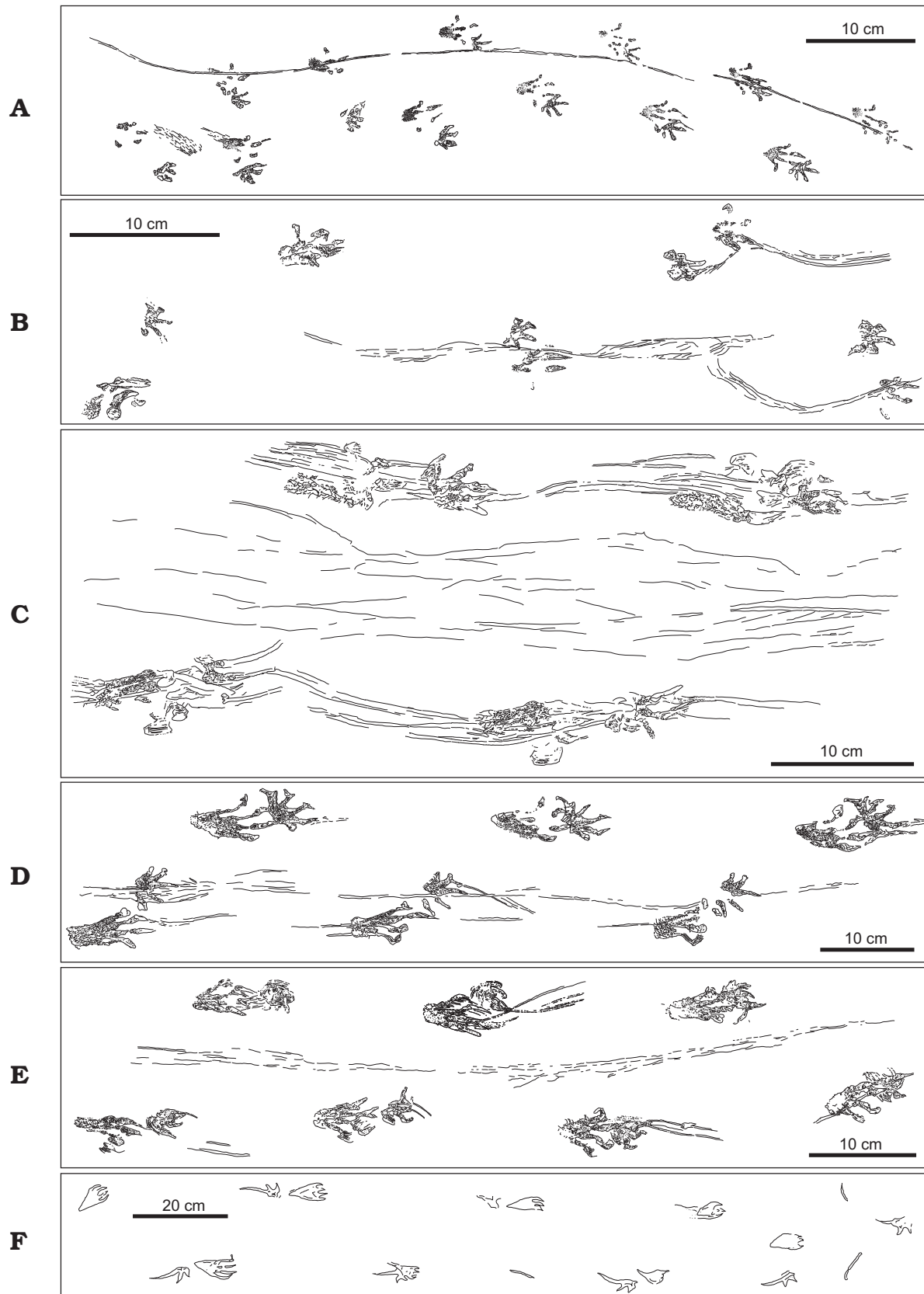
Fig. 2. Modern crocodilian trackways (**A–E**) compared to *Pteraichnus saltwashensis* Stokes, 1957 (**F**). **A**, **B**. *Paleosuchus trigonatus* Schneider, 1801, walking (**A**) and running (**B**). **C**, **D**. *Crocodylus porosus* Schneider, 1801, sprawling (**C**) and walking (**D**). **E**. *Tomistoma schlegelii* Müller, 1838, walking. **F**. *Pteraichnus saltwashensis* type specimen from the Upper Jurassic Morrison Formation of Arizona, USA (modified from Padian and Olsen 1984). Direction of the movement is from left to right.
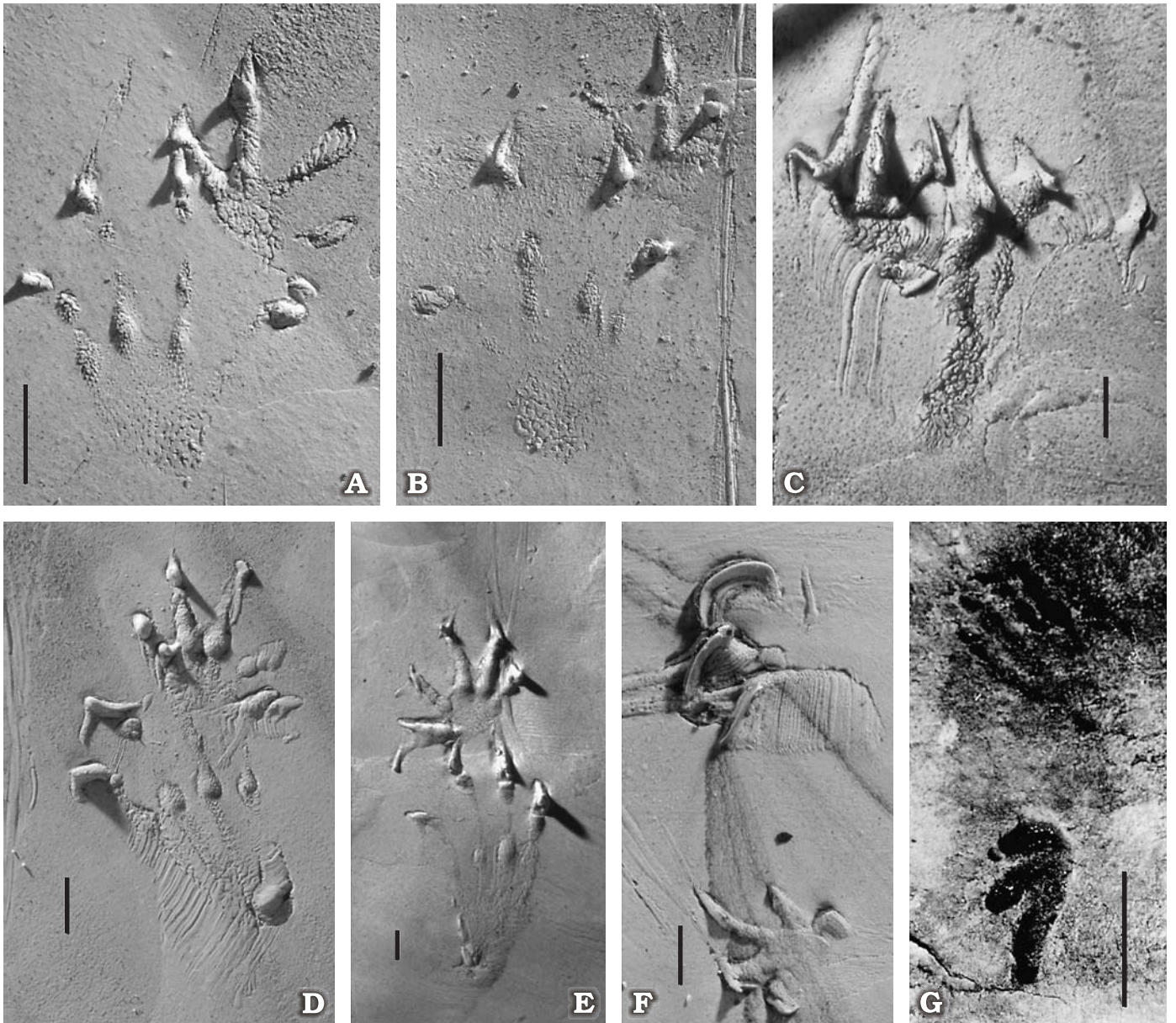
Fig. 3. Plaster molds of pes and manus tracks of modern crocodilians (**A–F**) and *Pteraichnus stokesi* Lockley, Logue, Moratalla, Hunt, Schultz, and Robinson, 1995 (**G**). Direction of the movement is leftward for (**F**) and upward for the others. **A**, **B**. Tracks of *Paleosuchus trigonatus* Schneider, 1801. The pes track preserves imprints of all four digits, whereas the manus track shows only the imprints of digits I to III. **C**. Track of *Tomistoma schlegelii* Müller, 1838. Only claw marks are pressed for the digits III and IV of the pes. Imprints of digit IV and V of the manus show rotational movement and are hard to distinguish from each other. Claw drag marks are seen anterior to the tracks. **D**, **E**. Tracks of *Crocodylus porosus* Schneider, 1801. **D**. The pes track shows a sliding imprint and it overprinted on the manus track, although the general anatomy of the pes and manus are well preserved. Relatively deep claw and metapodial phalangeal pad imprints can be recognized as a convex part of the mold. **E**. Shallow imprint of pes digit IV compared to other digit imprints and the rotary motion of manus digit V can be seen. **F**. Track of running *Paleosuchus trigonatus* Schneider, 1801. The kinematics of trackmaker disrupts shape of tracks. The manus track reflects its anatomical configuration. In contrast, digit imprint number can be counted from the pes track but its general anatomical features are not preserved. **G**. Pes and manus sets of *Pteraichnus stokesi* from the Middle Jurassic Sundance Formation of Wyoming, USA. The photographs are taken from Bennett (1997) with the permission of the author. Scale bars 10 mm, except G, for which is 50 mm.

sometimes overstepped manus tracks in running trackways (Fig. 2B), which are never observed in sprawling and walking trackways. Among ten manus-pes sets collected from two running trackways of *Paleosuchus trigonatus*, four pes tracks overstepped manus tracks, two pes tracks are overprinted on manus tracks and in other manus-pes sets pes tracks are lateral to manus tracks. Positional relationship between manus and pes tracks in running trackways are not stable. Weak impressions of the abdomen were often left as a result of bouncing movements. Manus tracks in running trackways are always well preserved. If not overprinted by the pes tracks, then all five digits of the manus tracks are visible (Fig. 3F). In many cases, the whole manus track is sliding forward, without any rotary motion.

The sprawling trackway is wider than the semi-erect trackway (Table 2). This differs from the observation of Reilly and Elias (1998) who stated that trackway widths of *Alligator mississippiensis* did not differ significantly between semi-erect and sprawling at the same speed. This difference probably resulted from the relatively slow speed of the sprawling posture compared to semi-erect posture in present study. The wide body dragging impression and parallel claw drag marks observed in the trackway reflect belly dragging and shuffling gait of the sprawling crocodile (Fig. 2C).

Discussion

Effect of substrate condition.—Although the influence of substrate was not tested directly in the present study, this topic has been investigated previously with modern western newts, *Taricha torosa* (Brand 1996) and the emu, *Dromaius novaeholandiae* (Milan et al. 2006). Both studies used mud and sand in various wet conditions as the substrate. The shape of emu pes tracks differs depending on the substrate condition. Nevertheless, in most cases all three digit imprints were easily recognized. On damp sand, digit II sometimes left only a faint imprint as it is held higher than the other digits (Milan et al. 2006). Modern newt trackways usually did not preserve imprints of all digits. The numbers of recognizable digit imprints always shows some variation in the same trackway, so that a large sample is needed to know the real digit number of the trackmaker (Brand 1996). In view of these results, whether *Pteraichnus* individual footprints reflect the real anatomy of the trackmaker or not can be judged by assessing the substrate and morphological consistency of the tracks. Of particular relevance is the number of digit imprints in the manus tracks because it appears to differ between *Pteraichnus* and modern crocodilian tracks.

Pteraichnus trackways are preserved on various substrates ranging from mud (Mazin et al. 2003; Pieńkowski and Niedźwiedzki 2005), to fine (Mickelson et al. 2004; Kim et al. 2006) or medium grained sand (Stokes 1957) under wet conditions, often with ripple marks. Occasionally, it is preserved on firmer sand (Bennett 1997). Manus tracks of *Pteraichnus* are always tridactyl, regardless of grain size.

Usually five digit imprints are clearly visible in manus tracks of crocodilians (Fig. 3). When preservation is poor, as is the case in the newt, the number of observable digit imprints is not stable throughout the trackway. However, five digit imprints can be counted from at least one manus track within each trackway. Nevertheless, focusing on a single poorly preserved manus track, the imprints of digits I to III are relatively better preserved than the other two digit imprints. Thus, sometimes a manus track appears to be tridactyl (Fig. 3B). However, these three digit imprints are pointing anteromedially (digit I) to anterolaterally (digit III) and are not similar to *Pteraichnus*, whose digit imprints spread out widely from anterior to posterior (Fig. 3G). In crocodilians, these three digit imprints are always separated from one another and have different preferred orientations (Fig. 3B). The interpretation of the *Pteraichnus* manus track by Padian and Olsen (1984: fig. 3D), whereby digit imprints II and III make a fused imprint by attaching to each other and pointing in the same direction, was not supported by our experiments.

Pteraichnus was found from various substrates and unlike modern newt trackways or poorly preserved crocodilian trackways, *Pteraichnus* manus tracks are consistently tridactyl throughout the trackway (Fig. 2F), which indicates that the shape of the track was not affected by substrate but reflects the anatomy of the producer.

Effect of kinematics.—Trackways of all typical postures and gaits of crocodilians, namely sprawling, walking, and running, were collected. The influence of kinematics on trackway morphology can therefore be examined. If some aspects of the kinematics of crocodilian locomotion can result in crocodilian trackways that resemble *Pteraichnus*, then the differences between *Pteraichnus* and crocodilian trackways should disappear in some gaits. Examples of these differences that will be examined in a following section are the number of manus digit imprints, the posteriorly directed hindmost manus digit imprint, tail mark, overstepping pes tracks, and relatively large distance between opposing manus tracks compared to pes tracks (Lockley et al. 1995; Unwin 1996; Bennett 1997).

Only three digit imprints are recognizable in *Pteraichnus* manus tracks, among which the hindmost digit imprint is directed posteriorly (Fig. 3G). As mentioned above, five manus digit imprints are seen in all trackways of crocodilians regardless of gait or posture. Digit imprint V of the crocodilian manus track is directed posterolaterally, up to 120° from the direction of travel. When digit imprint V shows rotary sliding motion, the angle can reach 160° (Fig. 3C, E). In *Pteraichnus* manus tracks, the long and robust hindmost digit imprint is almost always oriented posteriorly without any evidence of rotational slipping (Fig. 3G). Padian (2003) attributed this long digit imprint to toe dragging. However, in present study, toe dragging marks of crocodilians are always very thin and usually form a few parallel lines produced by several claws either or both posterior and anterior to track (Fig. 2C–E).

No tail marks occur in *Pteraichnus*. In contrast, tail or body impressions are left by all gaits in crocodilians. Running *Paleosuchus trigonatus* left a trunk impression by the bouncing movement and the tail mark occurs occasionally. As expected, the sprawling gait left a wide drag mark of the body along the mid-line of the trackway.

Pteraichnus pes tracks usually overstep manus tracks (Fig. 2F). When walking, the crocodilian pes never oversteps the manus. Crocodilians move their opposite fore and hind limbs roughly in unison with body undulation. As such, overstepping is impossible unless running. Padian (2003) mentioned that a running crocodilian can overstep, which was reaffirmed in this study (Fig. 2B). The positional relation of the manus and pes tracks in the running crocodilian trackway, however, differs from *Pteraichnus*. The pes track is usually

Table 3. Comparison of *Pteraichnus* and modern crocodilian trackway.

	Manus	Tail drag	Overstepping	Hind-most manus digit	Width between opposing manus tracks
Crocodilians	usually pentadactyl	usually present	occurs in running trackway	directed posterolaterally with rotary sliding mark	roughly same as that of opposing pes tracks
Pteraichnus	tridactyl	absent	always	directied posteriorly, long and robust	often wider than that of opposing pes tracks

positioned medial relative to the manus track in *Pteraichnus* (Fig. 2F). In contrast, the pes track is never medial to the manus track in a running crocodilian trackway (Fig. 2B). When running, crocodilians keep semi-erect posture with their hindlimb swinging over and around the forelimb from the lateral side. The medial side of the hindlimb almost touches the lateral side of the forelimb before the hindfoot contacts the ground. Therefore, hindlimbs of running crocodilians have restricted movement and are unable to place their pes tracks medial to manus tracks.

The width between the manus track in *Pteraichnus* can be up to three times as wide as that observed between the pes tracks and differs markedly from those of crocodilians (Mazin et al. 2003). Padian (2003) acknowledged this feature and admitted that *Pteraichnus* found from Crayssac, France was made by pterosaurs because of this feature. Based on the trackways collected from modern crocodilians, the relationship between the manus and pes trackway widths was further examined. Among 46 manus-pes sets, 19 internal widths between opposing pes are wider than that of manus, 35 external widths between opposing pes are wider than that of manus, only four internal widths between opposing pes are wider than external widths between corresponding manus and internal width between opposing manus never exceeded external width of the corresponding pes (Table 2). These results indicate that distances from the midline to pes and manus are roughly same in crocodilian. Width range (from internal to external) of corresponding pes and manus overlaps each other almost always, moreover, the manus is never located outside of pes. The relatively short forelimbs of crocodilians must be responsible for this configuration. Not only in the case of the Crayssac *Pteraichnus*, but also in many other examples of *Pteraichnus*, the internal manus trackway width is wider than the external pes trackway width (i.e., Lockley et al. 1995: fig. 4; Mickelson et al. 2004: fig. 6). The foregoing indicates that these trackways are unlikely to be made by crocodilians.

Regardless of gait and posture, differences exist between crocodilian trackways and *Pteraichnus* (Table 3). Thus the supposition that a crocodilian with a particular style of kinematics could produce *Pteraichnus* is unlikely.

Conclusions

As a result of analysis of newly collected trackways of various modern crocodilians, features of the trackway of a *Caiman* that are different from *Pteraichnus* are commonly ob-

served in all collected crocodilian trackways. Neither substrate nor kinematical condition is likely to explain the difference between *Pteraichnus* and crocodilian tracks. Only a difference in trackmaker can soundly explain these differences.

Padian (2003) accepted the Crayssac *Pteraichnus* as tracks of pterosaurs, but denied pterosaurs as a trackmaker of most other *Pteraichnus*. The relative width of the manus differs markedly between the Crayssac and other *Pteraichnus* trackways. One possible explanation is that the difference between the Crayssac *Pteraichnus* and other *Pteraichnus* reflects gait difference. For example, the manus trackway of modern chiropterans is much wider than that of pes trackway when they are running unrestrictedly, whereas the widths of manus and pes trackways are more similar in walking or running in restricted space (Brown et al. 1984).

Tracks do not always reflect the anatomy of a trackmaker, as kinematic and substrate conditions may alter it (Padian 2003). Therefore it is very important to present a range of variations caused by kinematics or substrate conditions in neoichnological studies. This study shows how kinematics affects the tracks of crocodilians. It is inferred that when morphologies are similar throughout a trackway with a considerable number of tracks, then it is very likely to reflect real anatomy of a trackmaker (i.e., number of digits). Based on this criterion, many *Pteraichnus* trackways contain enough manus tracks of similar morphology to judge that it is reflecting the anatomy of trackmaker. Thus, dissimilarities between *Pteraichnus* and modern crocodilian trackways produced by various kinematics indicate a different trackmaker.

Acknowledgements

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