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Late Cretaceous Mammal Tracks from North America

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Mammal tracks from the latest Cretaceous (Campanian-Maastrichtian) of Colorado are described as *Schadipes crypticus* ichnogen. et ichnosp. nov., on the basis of material from the Laramie Formation in Golden, eastern Colorado. This ichnospecies, and a closely related form (*Schadipes* sp.) from the Mesaverde Group of western Colorado, represent the only mammal tracks so far identified from the Upper Cretaceous. A possible mammal track from North Africa *(Agadirichnus elegans)* was originally attributed to a lizard/lacertilian. Other purported Lower Cretaceous mammal tracks are based on isolated specimens of materials that are dubious or as yet undescribed in detail. Morphologically, Late Cretaceous mammal tracks resemble those of some modern rodents. However, based on the dominant mammalian elements of faunas at that time they are probably of marsupial or multituberculate affinity.

Keywords Mammal tracks, Upper Cretaceous, Laramie Formation, Mesaverde Group

INTRODUCTION

Mammal tracks are rare in the Cretaceous of North America and may be completely unknown on any other continent in rocks of this age. Possible examples include tracks from Canada reported by Sarjeant and Thulborn (1986) and a track from Maryland reported by Stanford and Lockley (2002). As noted elsewhere in this volume throughout the entire Mesozoic there are only a handful of reports of true mammal tracks, from South America (Casamiquela, 1964; Leonardi, 1994 and Rainforth and Lockley, 1996), from southern Africa (Ellenberger, 1972, 1974, 1975) and from North America (Olsen, 1980; Lockley et al., 1996; Lockley 1999). Many of these reports are dubious due to the limited amount of material, quality of preservation, and the possibility that the track makers were non-mammalian vertebrates. Many of the Late Triassic to Early or Middle Jurassic reports could represent various non-mammalian synapsids rather than true mammals.

Such equivocal interpretation of early Mesozoic trackmakers (mammal v. non-mammalian synapsids) is not a problem in the Cretaceous, and we herein report two sites from the latest Cretaceous of Colorado where mammalian tracks have been discovered. The first site, which provides the largest sample, is a single specimen from the Campanian Mesaverde Group of western Colorado (Roehler, 1990). The second site, from the Maastrichtian Laramie Formation of the Golden area in eastern Colorado, has yielded two specimens. The specimens have been cataloged in the Museum of Western Colorado (MWC) and joint University of Colorado at Denver—Museum of Western Colorado (CU-MWC) collections (see abbreviations below).

GENERAL DESCRIPTION OF SPECIMENS

Specimen MWC 2226 (Fig. 1), which is currently on display at the Museum of Western Colorado, from the Mesaverde Group of western Colorado, consists of a single slab of brownish sandstone about 60 x 50 cm (maximum dimensions). The specimen was found by Dan Chaney and donated to the Museum of Western Colorado. A replica of this slab (CU-MWC 222.2) is also available in the University of Colorado at Denver collections. About 40 partial, separate or overlapping tracks are preserved as natural casts on the underside. These are all attributed to mammals, with one exception.

There is one track that appears to represent a small bird (Fig. 1) with a foot length and width of 3.5 x 3.0 cm, including hallux. Digits III and IV show faint traces of pad impressions. Digit divarication (between II and IV) is about 100°. The hallux is directed posteriorly but slightly to one side: assuming this to be the medial side, because birds rarely, if ever, have a hallux rotated laterally beyond the posterior position, the track appears to be a right footprint. The toe impressions are rather thick. However, this may be an extramorphological (preservational) rather than an original morphological feature.

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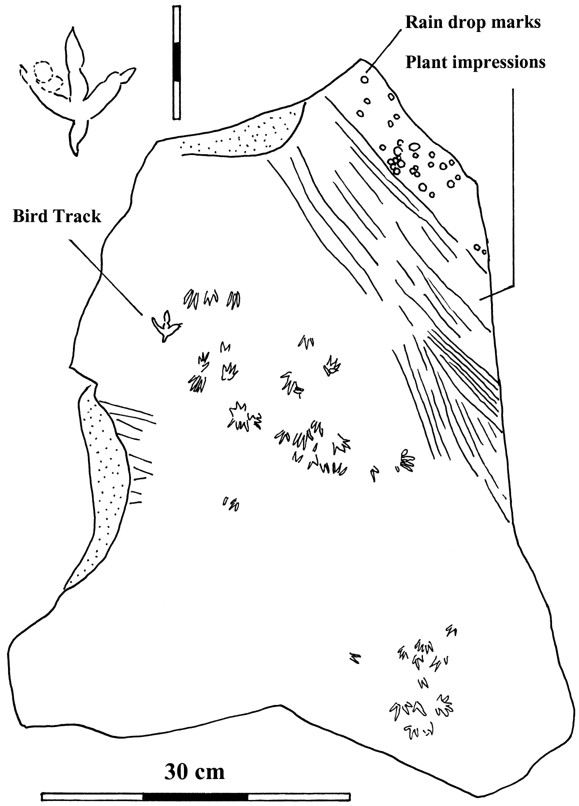

FIG. 1. Mammal tracks from the Mesaverde Group (MWC 2226). Note bird track (with enlargement, top left: scale bar 3 cm) and separation of zones with rain drop marks, plant impressions and mammal tracks.

Most of the mammal tracks are the same size and type consisting of three, four or occasionally five, straight, narrow digits up to 1.5 cm long. Several tracks appear to show three slightly divergent central digits of near-equal length with one (or two) shorter more divergent lateral digits (Fig. 2A). Such pentadactyl patterns are fairly typical of the pes of ancient eutherians, multituberculates, and triconodonts as well as the tracks of modern rodents such as mice, rats and squirrels (Figs. 2B, 2C), and some marsupials. However, placental (eutherian) mammals were less common in the Late Cretaceous than marsupials and multituberculates (Gingerich and Badgley, 1984; Carroll, 1988), and it is likely that there was significant convergence in foot structure between these various groups. In cases where the tracks appear tetradactyl (i.e., with only one shorter divergent digit), it is possible that the tracks represent a manus, or a partial pes imprint. Several of the tracks show faint traces of pad impressions. Digit impressions taper distally, but only slightly.

Specimens from the Laramie Formation (designated CU-MWC 220.28 and 220.33) are similar to the Mesaverde tracks though slightly larger (length about 2 cm). However, they are less abundant. Specimen CU-MWC 220.28, an original, preserved as a natural cast on gray sandstone, appears to be a partial trackway of six footprints (Figs. 3 and 4). When first discovered, it was tentatively interpreted as the trackway of a lizard (Lockley et al., 2001). The second specimen (CU-MWC 220.33) preserved as a rubber mold and replicas of natural casts that remain *in situ*, consist of five partial tracks that may also form part of a trackway, in which tracks are regularly spaced about 12 cm apart (Fig. 3). This second specimen reveals digit pad impressions, and helps create a better picture of the morphology of individual tracks (Lockley et al., 2002, Lockley 2003). This allows us to define an ichnotaxon (*Schadipes crypticus*) more precisely, as done in the systematic section below. The former specimen (220.28) designated as *Schadipes* ichnosp. indet., was discovered by Dr. Joanna Wright (University of Colorado at Denver). The latter specimen (220.33) was discovered by the senior author.

SYSTEMATIC ICHNOLOGY

Class Mammalia
Schadipes ichnogen **nov.**
Figs. 3 and 4

Diagnosis: Small, slender toed tetradactyl and pentadactyl tracks with central digits (II–IV) subequal in length and only

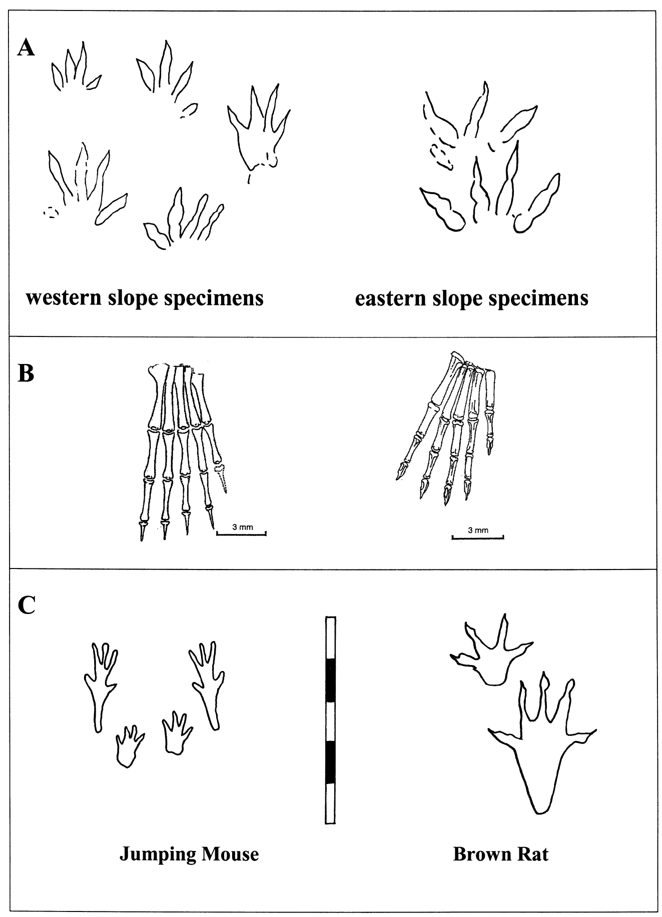

FIG. 2. **A.** detail of mammal tracks from the Mesa Verde and Laramie Formations, **B.** hind feet of Mesozoic mammals (*Eomaia*, left and *Jeholodens*, right) after Ji et al., (2002 and 1999) **C.** modern rodent tracks (after Murie, 1974, and Bang and Dahlstrom, 2001). All drawn to same scale (bar = 5 cm). Foot skeletons enlarged x 4 for clarity. After Lockley et al. (2002).

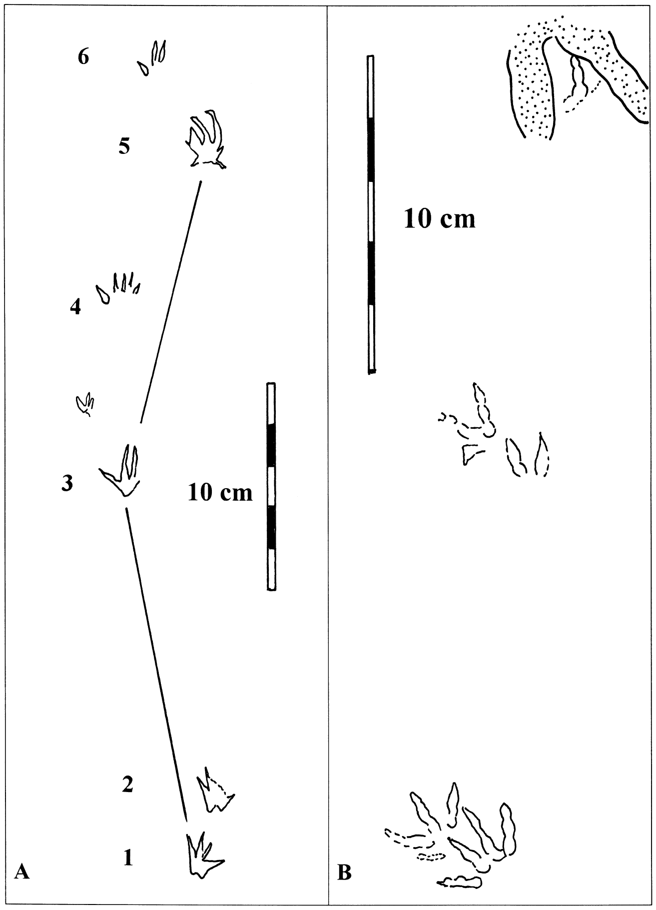

FIG. 3. Mammal tracks (*Schadipes*) from the Laramie Formation of the Golden area. **A.** *Schadipes* sp. CU-MWC 220. 28 (left), with lines to show inferred steps between pes 1, 3 and 5. Note small partial track between tracks 3 and 4. **B.** 220.33 (right) shows holotype of *Schadipes crypticus* with clear digital pad impressions. Uppermost (distal) track is overprinted by a larger vertebrate footprint.

slightly divergent. Lateral digits (I and V) shorter and more divergent when preserved at all. Trackway pattern variable. Differs from lacertilian tracks in being more symmetrical with more equi-dimensional digits.

Type specimen: CU MWC 220.33. Rubber mold and replica of original specimen, preserved in field.

Type horizon and locality: Maastrichtian (latest Cretaceous), Laramie Formation, Fossil Trace Golf Course, Golden, Colorado.

Etymology: *Schad*: named in honor of Dr. Wolfgang Schad (Institute for Evolutionary Biology and Morphology, Witten-Herdecke University, Germany) for his pioneering work on mammals: pes meaning footprint.

Schadipes crypticus ichnosp. nov.

Figs. 3 and 4

***Description*:** Pes probably pentadactyl with straight subequal central digits (i.e., digits II–IV), which are only slightly divergent (typically 20–30°). Length of digits II–IV between 1.5 and 2 cm. Lateral digits shorter and more highly divergent. Outer digit (V) may be longer (about 1 cm) than inner digit (I) but is shorter than digits II–IV and diverges from digit IV at a high angle (up to 50–60°). Inner digit (I) shortest. Digits II–V sometimes revealing up to 3 clear pad impressions. Manus smaller and shorter and probably tetradactyl. Trackway variable, with inter footprint distances (?steps) up to 12 cms.

Type specimen: CU-MWC 220.33 (as for ichnogenus).

Holotype Horizon and Locality: As for ichnogenus.

Etymology: *Schadipes* (see above): *crypticus*, referring to hidden location.

Other related material: CU MWC 200.28 (Figs. 3 and 4) comes from the same geographical locality but from a horizon that is about 20 meters stratigraphically below the type locality. We refer to it tentatively as *Schadipes* ichnosp. indet.

Systematic Discussion: On the basis of specimen CU-MWC 220.28, which has one track with what appears to be curved digit impressions, these tracks were initially attributed to a lizard track maker (Lockley et al., 2001). The subsequent discovery of additional material (CU-MWC-220.33), here designated the holotype of *Schadipes crypticus*, with straight digits and three phalanageal pad impressions in well-preserved impressions of digits II–V confirms the mammalian origin of these tracks (Lockley et al., 2002: Lockley, 2003) and is consistent with a 2-3-3-3-3, mammalian phalangeal formula rather than the 2-3-4-5-3(4) formula of lizards/lacertilians: *sensu* Leonardi, 1987). It is for this reason that 220.33 is selected as the holotype rather than 200.28. Indeed, we cannot be sure that this latter specimen (200.28) represents the same morphology, so we herein refer to it as *Schadipes* ichnosp. indet. The phalangeal formula evidence appear to be confirmed by examination of the specimen from western Colorado (MWC 2226), which appears to show the same morphology and is, therefore, also designated as *Schadipes* sp., though in this specimen no trackways can be resolved. In most cases there seems little ambiguity about identifying inferred pes digits II–IV, and in some cases (e.g., trackway 220.28) digit V is easily identified also. However, additional material, comprising well-preserved manus pes sets may be necessary to confirm the exact configuration and relative proportions of all digits on both manus and pes.

Holotype trackway 220.33 is intriguing because it appears to represent three equally spaced sets of tracks, each 12 cm apart. The first set is the best preserved, revealing a pair of tracks that appear to be aligned obliquely to the series. The second set shows a similar, but less complete configuration, and the third (a partial track) is obscured by part of a larger footprint. It is possible that this configuration represents a hopping animal. In combination with the other evidence this suggest that the *Schadipes* trackmaker could alter its gait between walking, running and hopping. This inference is not surprising for a rodent-like animal.

Trackway 220.28 reveals what appears to be a normal walking gait with all central digits (II–IV) oriented forward. It also conveniently appears to provide us with the classic sequence of three pes-manus sets that helps define all the essential trackway

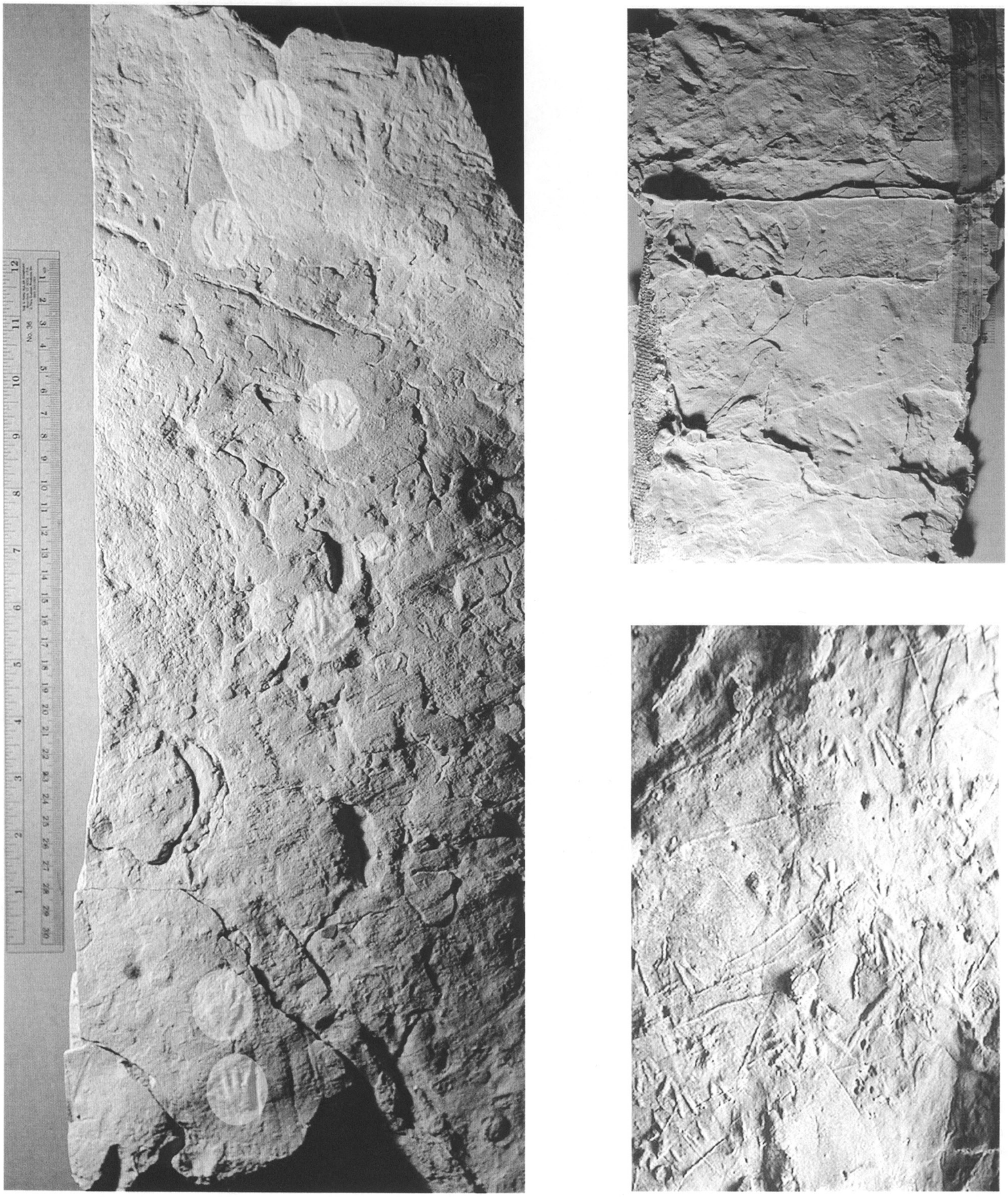

FIG. 4. Left, photo of trackway 220.28, *Schadipes* ichnosp indet., with individual tracks highlighted, (compare with Fig. 3A, reversed), and, **top right,** latex mold of holotype of *Schadipes crypticus* (compare with Fig. 3B, same orientation) from the Laramie Formation of the Golden area. **Bottom right,** concentration of mammal tracks, *Schadipes* ichnosp indet., from the Mesa Verde Group of western Colorado (compare with Fig. 1).

parameters (cf. Peabody, 1955). However, there appears to be a smaller, seventh track, (Fig. 3A) between tracks 3 and 4. Given that it is much smaller than the inferred manus pes tracks in the sequence I-6, it is not considered part of the trackway. (No animal should have tracks of three different sizes unless it is a case of pathological disfiguration). Only about 3 cm separates the heel of the first two tracks (1 and 2 respectively) which evidently represent the first pes-manus set. The next pair (3 and 4), reveals a pronounced difference in digit lengths, which seems to confirm a distinctive pes-manus set. The final pair, (5 and 6) also shows this pes-manus size difference (heteropody). The step (for the pes) varies from 16.3–18.3 cm, the stride is 34.5 cm and the pace angulation is about 157° for both the pes and manus. The average step to pes length ratio (17.3/2.5) is about 7.0. This is high and indicates a running animal (speed 12.8 km/hr based on the formula of Alexander, 1976). Pes-manus spacing is short on the right side of the trackway (between 1–2 and 5–6) but long on the left side (between 3 and 4).

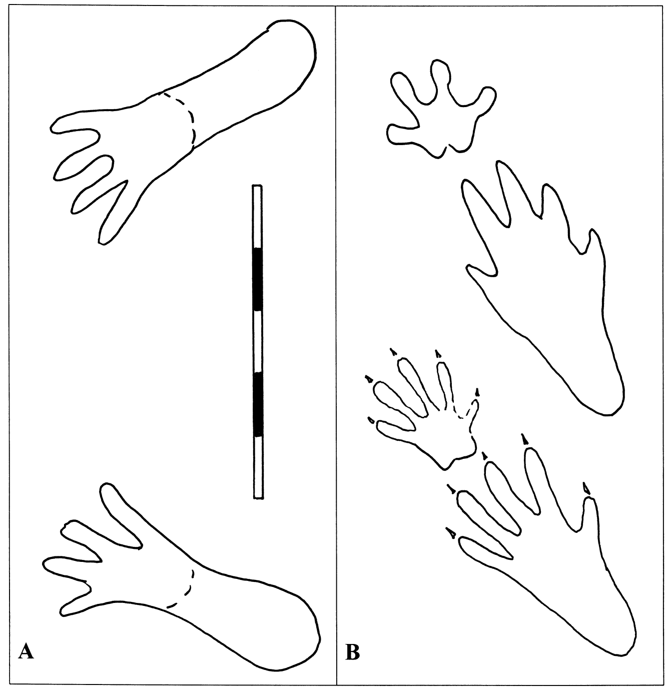

FIG. 5. **A.** *Agadirichnus elegans*: a tetradactyl track from the Maastrichtian of Morocco, (after Ambroggi and Lapparent, 1954), drawn to show original relationship between two footprints. **B.** muskrat pes and manus tracks for comparison. Lower pair after Sheldon (1997), upper pair after Jaeger, (1948, pl. 63). All drawn to same scale (bar = 10 cm).

GENERAL DISCUSSION

Schadipes crypticus is the first ichnospecies name explicitly applied to a Cretaceous mammal track. Based on foot shape and size as well as gait pattern, the attribution of the trackmaker to Class Mammalia seems certain. Until recently few Cretaceous mammal feet have been recorded. However, a complete eutherian mammal (*Eomaia*) was recently described from the famous Yixian Formation of China (Ji et al., 2002). The hind foot of this rodent-like animal is about 1.5 cm long and the front foot only about 1.0 cm. Although the Colorado tracks are some 55–60 million years younger than *Eomaia* (age about 125 ma), the phalangeal formula would have been the same. Other complete, or near-complete mammal skeletons are known from this famous Chinese formation: these include *Jeholodens* (Ji et al., 1999) and *Zhangeotherium* (Hu et al., 1997).

The Colorado tracks lack the elongate impression of the heel of the pes seen in modern rodents (e.g., Fig. 5), but as there are no Cretaceous rodents, the trackmaker probably belonged to some other mammalian group. Also, as indicated in many modern field guides to mammal tracks (e.g., Murie, 1974) the heel is often not impressed. Thus this feature is largely dependent on whether the trackmaker adopts a more or less digitigrade stance. As indicated in Fig. 2, typical modern rodents (e.g., mice, rats and squirrels) have pentadactyl hind feet that are larger than their tetradactyl front feet. Though generally similar to the feet of modern mice, rats and squirrels (Myomorpha and Scuriomorpha *sensu* Schad, 1977; Carroll 1988) these families are not known to have existed with certainty in the Late Cretaceous (Campanian-Maastrichtian). According to McKenna and Bell (1997) the oldest rodent is *Heomys* from the early Paleocene, and Archibald et al. (2001) note that rodents probably share a common ancestor with the Late Cretaceous zalambdalestids. Carroll also cites *Acritoparamys (Paramys) atavus* from the Upper Paleocene as a well-known early representative of the Rodentia. Given the appearance of many eutherian and other mammal groups by the middle of the Early Cretaceous, as shown by the Yixian fauna (Hu et al., 1997; Ji et al., 1999, 2002), many potential trackmakers must be considered before narrowing down the affinity of the Colorado footprints.

Many Late Cretaceous mammals were marsupials or the extinct multituberculates (Gingerich and Badgley, 1984; Carroll, 1988). In fact, the Williams Fork Formation of the Mesaverde Group in northwestern Colorado yields marsupials and multituberculates in equal proportions (i.e., eight species of each: Archibald, 1987; see also Diem 1999). Eutherians are known from many Late Cretaceous deposits in North America, but in most faunas they are less common than the multituberculates and marsupials and are often smaller. However, complete feet of mammals remain essentially unknown in the Late Cretaceous of North America, as preservation does not compare with the aforementioned specimens from the Lower Cretaceous of China (e.g., Ji et al., 2002). The possibility of marsupial affinity was suggested in the case of an isolated track from the Lower Cretaceous of Canada (Sarjeant and Thulborn, 1986). They supported their case by suggesting that the track showed evidence of syndactyly, which is common among marsupials (e.g., Morrison, 1981, pp. 98–99). However, the track is not well preserved, and we are cautious in assigning it with any confidence to a specific vertebrate group. There are one or two tracks in the western Colorado sample that reveal digit impressions that might conceivably be interpreted as syndactylous. However, the preservation is not good enough to confirm such interpretations, and so we err on the side of caution in concluding that no compelling evidence of this characteristic marsupial morphology is discernable.

It is beyond the scope of this paper to mention all the species that might be potential trackmakers that would fit the Colorado tracks. Despite the important new Lower Cretaceous finds from Asia (e.g., Ji et al., 2002) which add to valuable Late Cretaceous material from that continent (especially Mongolia) which also includes incomplete skeletal remains of feet of several genera (Kielan-Jaworowska, 1977, 1998; Carroll 1988), the record from North America remains sparse before the Maastrichtian. However at this time the North American record of placental mammals is relatively diverse, though they are still much less abundant and diverse than either the marsupials or multituberculates. Since most of these "remains are almost entirely limited to jaws and teeth" (Carroll, 1988, p. 449) the possibility of matching tracks and trackmakers is severely limited. The skeletal evidence only indicates that there were many possible trackmakers in the Maastrichtian, and presumably a significant number in the Campanian also.

It is possible that other mammal tracks exist in the Late Cretaceous and that they have either not been found, or they have been misidentified. For example, Ambroggi and Lapparent (1954) described a tetradactyl track from the Maastrichtian of Morocco named *Agadirichnus elegans* (Fig. 5), which they attributed to a lacertilian. This track purportedly reveals only digits II to V with the following respective average length measurements: 3.0, 2.7, 2.6 and 2.0 cm: note that digit V is relatively short. The track also reveals an elongate heel, which increases the total length of the footprint to an average of 11 cm, which is rather too large to correlate any skeletal remains of known Cretaceous mammals. Nonetheless, although attributed to a lacertilian, such a track could conceivably also be mammalian in origin. Lizard tracks do not normally have a long heel, but such a feature is typical of rodents, and a length of 11 cm is not unusual in extant species (for example Jaeger 1948, and Sheldon, 1997 illustrate muskrat pes prints that that are 8–9 cm long, Fig. 5). Lizard tracks also typically reveal much longer, curved digits with digit IV being the longest. Based on the illustrations and measurements presented by Ambroggi and Lapparent (1954) the digits are neither long, or curved or proportioned in such a way as to indicate lacertilian affinity. It is not inconceivable that *Agadirichnus* is mammalian rather than lacertilian. However, these African tracks are not sufficiently well illustrated nor well preserved or to allow further detailed analysis. Thus, our suggestion is very tentative, pointing only to the presence of a small vertebrate Cretaceous tracksite that might benefit from further investigation.

These differences in digit length, curvature and proportion may be subtle at first sight, especially in small feet and footprints. However, from a morphodynamic viewpoint they may provide subtle clues to trackmaker affinity. For example Lockley (1999, 2002) has discussed the morphodynamic correlations and compensations between foot, leg and body length. Thus animals with long bodies and tails (e.g., rodents and lizards) tend to have long feet and short legs while short bodied animals typically have short feet and long legs. It is also well known that lizards, in comparison with mammals, employ lateral (side to side) flexure of the spine during locomotion rather than a parasagittal (up and down) flexure. Thus, it is interesting that lizard digits also show curvature away from the axial-parasggital plane, whereas mammal digits are essentially straight. This in turn may be related to somewhat narrower mammalian trackways, with less rotation of footprints.

The surface of specimen MWC 2226 is undulating and also preserves raindrop impression casts on one margin beside plant impressions (Fig. 1). The distribution of tracks and rain drop impressions appears rather patchy. It is interesting that there do not appear to be tracks in the area of rain drop impressions nor rain drop impressions in the area where there are tracks. This leads to the speculation that perhaps the tracks were preserved in a sheltered area, possibly beneath the type of vegetation that is preserved as impressions in the intervening area (Fig. 1). It is unlikely that a bird and mammal(s) would be making tracks in such a small area at the same time. It is therefore possible that the bird and mammal tracks represent two different phases of trackmaking activity. Given that the bird track looks somewhat weathered or "rounded out" while the mammal tracks are well-preserved, it is possible that the bird track was made sometime before the mammal tracks.

Both the Mesaverde Group and Laramie Formations represent well-vegetated and fertile lowland, coastal plain settings (Roehler et al., 1990). Both have produced relatively rich vertebrate ichnofaunas dominated by dinosaur tracks. However, small vertebrate tracks have also been reported from a number of localities. These include tracks attributed to birds, frogs and pterosaurs, but until now no mammals (see Lockley and Hunt, 1995 and citations therein for summary). The presence of mammal tracks is not a surprise in such facies. However, tracks preserve evidence of foot morphology that is severely lacking in most body fossils of mammals (dominated by dental remains). Thus Mesozoic mammal tracks provide welcome evidence on the morphology of feet and challenge us to infer the significance of rodent-like, marsupial or multituberculate footprints prior to the known record of rodent body fossils.

CONCLUSIONS

1. *Schadipes crypticus* represents a small mammal track with a superficial resemblance to modern rodent footprints. However, based on the body fossil record a multituberculate or marsupial origin is likely, though corresponding foot skeletons are unknown in deposits of the same age. It is known from three stratigraphic horizons at two different geographical locations in the Upper Cretaceous (Campanian-Maastrichtian) of Colorado.

2. Trackway evidence suggests that the *Schadipes* trackmaker was a small fast moving animal that may have taken refuge in sheltered areas among ground litter and fallen vegetation. Such behavior is typical of small mammals such as rodents.
3. *Agadirichnus elegans*, from the Maastrichtian of North Africa, although first described as a lacertilian trackmaker, may be of mammalian origin. This inference is tentative at best.
4. Mammalian tracks from the Cretaceous of North America are still rare, however, those that are known are associated with deposits that represent fertile, well-vegetated paleoenvironments with diverse vertebrate ichnofaunas.

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REFERENCES

Alexander, R. Mc N. 1976. Estimates of Speeds of dinosaurs. *Nature*, 261: 129–130.

Ambroggi, R. and Lapparent, A. F. de 1954. Les empreintes de pas fossiles dans le Maastrichtien d'Agadir. *Notes et Memoires du Service de mines et de carte Geologique du Maroc,* 10–57.

Archibald, J. D. 1987. Late Cretaceous (Judithian and Edmontonian) vertebrates and geology of the Williams Fork Formation, N. W. Colorado. *In* Currie, P. J. and Koester, E. H. (eds.), Fourth Mesozoic Symposium on Terrestrial Ecosystems. Tyrell Museum of Paleontology, Drumheller: 7–11.

Archibald, D. J., Alexander, A. O., and Ekdale, E. G. 2001. Late Cretaceous relatives of rabbits, rodents and other extant eutherian mammals. *Nature*, 414: 62–65.

Bang, P. and Dahlstrom, P. 2001. Animal tracks and sign. Oxford University Press, Oxford: 264 p.

Carroll, R. L. 1988. Vertebrate Paleontology and Evolution. W. H. Freeman and Co., New York: 698 p.

Casamiquela, R. M. 1964. Estudios icnologicos. *Buenos Aires, Colegio Industrial Pio*, 9:229.

Diem, S. 1999. Vertebrate faunal analysis of the Upper Cretaceous Williams Fork Formation, Rio Blanco County, Colorado. Master's Thesis, San Diego State University, San Diego: 187 p.

Ellenberger, P. 1972. Contribution à la classification des pistes de vertébrés du Trias; les types du Stormberg d'Afrique du Sud,(part 1). *Palaevertebrata, Mémoire extraordinaire, Montpellier*: 152 p.

Ellenberger, P. 1974. Contribution à la classification des pistes de vertébrés du Trias; les types du Stormberg d'Afrique du Sud, (part 2). *Palaevertebrata, Mémoire extraordinaire, Montpellier*: 155 p.

Ellenberger, P. 1975. L'explosion demographique des petities quadrupedes a l'alure de mammiferes dans le stormberg Superieur (Trias) d'Afrique du sud apercu sur leur origine au Permien (France et Karoo). *International Colloquim of the National Center for Scientific Research Bulletin*, 218:409–432.

Gingerich, P. D. and Badgley, C. E. 1984. Mammals: notes for a short course. *University of Tennessee, Dept of Geological Sciences. Studies in Geology*, 8:234.

Jaeger, E. 1948. Tracks and Trailcraft. MacMillan Co., New York: 381 p.

Hu, Y., Wang, Y., Luo, Z., and Li, C. 1997. A new Symmetrodont mammal from China and its implications for mammalian evolution. *Nature*, 390:137–142.

Ji, Q., Luo, Z., and Ji, S.-A. 1999. A Chinese triconodont mammal and mosaic evolution of the mammalian skeleton. *Nature*, 398:326–330.

Ji, Q., Luo, Z.-X., Wible, J. R., Zhang, J.-P., and Georgi, J. A. 2002. The earliest known eutherian mammal. *Nature*, 416:816–822.

Kielan-Jaworowska. Z. 1977. Evolution of the therian mammals in the late Cretaceous of Asia. Part II. Postcranial skeleton in *Kennalestes* and *Asioryctes*. *In* Kielan-Jaworowska, Z. (ed.), Results of the polish Mongolian Paleontological Expeditions. Part VII. *Paleontological Polonica*, 37:65–83.

Kielan-Jaworowska. Z. 1978. Evolution of the therian mammals in the late Cretaceous of Asia. Part III. Postcranial skeleton in Zalambdalestidae. *In* Kielan-Jaworowska, Z. (ed.), Results of the polish Mongolian Paleontological Expeditions. Part VII. *Paleontological Polonica* 38:3–41.

Leonardi, G. 1987. Glossary and manual of Tetrapod footprint ichnology. Ministry of Mines and Energy, Brasilia, Brazil: 75 p.

Lockley, M. G. 1999. The Eternal Trail: a tracker looks at evolution. Perseus Books, Reading: 334 p.

Lockley, M. G. 2002. The relationship between tracks and the whole animal: new morphodynamic approaches. *Journal of Vertebrate Paleontology*, 22:80A.

Lockley, M. G. 2003. A guide to the fossil footprints of the Dinosaur Ridge and Fossil Trace areas. Friends of Dinosaur Ridge, Morrison Colorado, 66 p.

Lockley, M. G., Foster, J., and Manning, M. 2002. Late Cretaceous Mammal tracks from Colorado. Friends of Dinosaur Ridge Annual Report for 2002, Morrison, Colorado: 18–24.

Lockley, M. G. and Hunt, A. P. 1995. Dinosaur Tracks and other Fossil Footprints of the Western United States. Columbia University Press, New York: 338 p.

Lockley, M. G., Hunt, A. P., Gaston, R., and Kirkland, J. 1996. A trackway bonanza with mammal footprints from the late Triassic of Colorado. *Journal of Vertebrate Paleontology*, 16:49A.

Lockley, M. G., Wright, J., Giblin, R., and Manning, M. 2001. "Fossil Trace" trace fossils. New finds of Cretaceous tracks from the Laramie Formation Clay Pits and Golf Course in Golden. Friends of Dinosaur Ridge Annual Report for 2001, Morrison, Colorado: 18–26.

McCrea, R. T. and Sarjeant, W. A. S. 2001. New ichnotaxa of bird and mammal footprints from the Lower Cretaceous, (Albian) Gates Formation of Alberta. *In* Tanke, D. and Carpenter, K. (eds), Mesozoic Vertebrate Life: New Research Inspired by the Paleontology of Philip J. Currie. Indiana University Press, Bloomington: 453–478.

McKenna, M. C. and Bell, S. K. 1997. Classification of Mammals Above the Species Level. Columbia University Press, New York: 631 p.

Morrison, R. G. B. 1981. A field guide to the Tracks and traces of Australian animals. Rigby Publishers Ltd., Sydney: 192 p.

Murie, O. J. 1974. A Field Guide to Animal Tracks. Houghton Miflin Co., New York: 375 p.

Olsen, P. E. 1980. Fossil Great lakes of the Newark Supergroup in New Jersey. *In* Manspeizer, W (ed.), Field Studies of New Jersey Geology and guide to Field trips. 52nd Annual Meeting of the New York State Geological Association: 352–398.

Peabody, F. E. 1955. Taxonomy and the footprints of tetrapods. *Journal of Paleontology*, 29.915–918.

Rainforth, E. C. and Lockley, M. G. 1996. Tracks of diminutive dinosaurs and hopping mammals from the Jurassic of North and South America. *In* Morales, M. (ed.), Continental Jurassic Symposium Volume. Museum of Northern Arizona, Flagstaff: 265–269.

Roehler, H. W. 1990. Stratigraphy of the Mesaverde Group in the central and eastern Greater Green River Basin, Wyoming, Colorado, and Utah. *United States Geological Survey Professional Paper*, 1508:52.

Sarjeant, W. A. S. and Thulborn, R. A. 1986. Probable marsupial footprints from the Cretaceous sediments of British Columbia. *Canadian Journal of Earth Sciences*, 23:1223–1227.

Schad, W. 1997. Man and Mammals: towards a biology of form. Waldorf Press, Garden City, New York: 309 p.

Schultz-Pittman, J., Lockley, M., and Gaston R. 1996. First reports of synapsid tracks from the Wingate and Moenave Formations, Colorado Plateau region. *In* Morales, M. (ed.), Continental Jurassic Symposium Volume. Museum of Northern Arizona: 271–273.

Sheldon, I. 1997. Animal tracks of the Rockies. Lone Pine Publ., Edmonton: 159 p.

Stanford, R. and Lockley, M. G. 2002. Diverse Vertebrate track assemblages from the early Cretaceous of Maryland. *Journal of Vertebrate Paleontology*, 22:111A.