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Ratite Footprints and the Stance and Gait of Mesozoic Theropods

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Abstract

Footprints of the rhea *(Rhea americana)* are identical in several diagnostic features to tridactyl footprints of the Mesozoic Era attributed to theropod dinosaurs. Of particular interest, (i) the rhea's feet are placed very close to its body midline as it walks, so that it virtually places one foot in front of the other; (ii) its middle toe (digit III), the central weight–bearing axis, is directed slightly inward under normal conditions; and (iii) the feet are very deliberately placed on the substrate, and the toes and claws leave no drag marks. These are all characteristic of Mesozoic theropod (and ornithopod) trackways, and invite extended comparison of fossil and recent theropods. Modern ratites and Mesozoic theropods are essentially identical in bone morphology and in joint structure and articulations. Their trackways are similar because the structure and function of the hindlimbs of the two groups are also essentially identical. These similarities are to be regarded as homologies because birds are descended from Mesozoic theropods, and the ratites merely retain characters plesiomorphic for the group since the Late Triassic. Mesozoic theropods had fully erect stance and parasagittal posture, as both bone structure and articulation, and footprints reveal. Hypotheses of semi–erect posture based on hypothetical muscle reconstructions are not supported by the available evidence.

Introduction

Dinosaurs were unknown as a group when Edward Hitchcock described gigantic three–toed trackways from the redbeds of the Connecticut River Valley in the early 1830s. Hitchcock (1836) noted that they were first regarded as prints made by giant birds, including "Noah's raven." He named the prints "*Ornithichnites*" to reflect their origin and thereby differentiate them from the tracks of reptiles, or "*Saurichnites,*" found in the same beds. Sir Richard Owen named the Dinosauria in 1842, but on such fragmentary material that the Connecticut Valley tracks could not be associated with the osseous remains of dinosaurs until the late 1800s (Colbert 1968, Desmond 1975), when relatively complete skeletons of carnivorous and herbivorous dinosaurs became known from places as diverse as Belgium and the western United States. By the time Lull published the first edition of *Triassic Life of the Connecticut Valley* (1915), footprints could be referred not only to dinosaurs but to other archosaurian groups, often at the family or even genus levels. The parataxonomy of fossil footprints is still preserved, but in specific cases the inference that certain bones and trackways may have been left by the same animals has been of great use in reconstructing stance, gait, and functional morphology of extinct tetrapods, particularly reptiles (Haubold 1971).

Experimental studies (e.g., Schaeffer 1941, Peabody 1959, Padian and Olsen 1984a,b) of the trackways of living tetrapods have been able to shed light on the process of trackmaking and how it relates to the structure of the foot, the kinematics of the limb, and the competence of the substrata (Baird 1954, 1957; Padian and Olsen 1984a). In many cases, the form of a footprint can reveal not only the identity of the trackmaker and the condition of the surface, but also the animal's stance and gait, which may vary with behavioral and environmental circumstances. The experimental approach is especially powerful when comparing fossil and living members of a single phylogenetically restricted group. For example, the earliest known crocodilian trackways *(Batrachopus,* reviewed in Olsen and Padian 1986) differ in no appreciable way from those of living crocodiles (Padian and Olsen 1984a), which suggests that crocodilian locomotory trends have remained conservative over nearly 200 million years.

The present study is an attempt to test alternative hypotheses of the stance and gait of Mesozoic theropod dinosaurs, using the evidence of fossil and recent footprints. No living vertebrates have precisely the same pelvic structure as Mesozoic ornithischian and saurischian dinosaurs. Some lines of evidence, such as the shapes of pelvic and hindlimb joints and the inferred angles of articulation of

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their bones, have led paleontologists to conclude that Mesozoic dinosaurs walked in fully upright position (e.g., Ostrom 1970, Charig 1972). However, certain problems associated with reconstruction of muscles on these dinosaurs have suggested to others (e.g., Tarsitano 1983) that fully erect posture was impossible, and a more crocodilian, semi-erect stance was more likely.

We proceed from the premises that (i) similarities of bone shapes and joint articulations between two tetrapods suggest similar gaits: that is, if no functionally significant difference is demonstrated, none can be assumed; and (ii) functional similarity between animals is correlated with degree of phylogenetic relationship, given the caveat listed in (i). If the bones and articulations of two animals show no significant functional differences, and if their footprints match in all respects related to kinematics of the limbs, then the inference that those kinematics are fundamentally similar is a strong one. We realize that, except in certain cases, fossil tracks cannot be assigned to a trackmaker at a generic or specific level, and we will content ourselves with similarities and differences pertinent to the "family" level or above. In the case of Mesozoic theropods, as Olsen (1980) has demonstrated, differences that characterize ichnogenera can often reduce to a single allometric transformation series; that is, *Grallator, Anchisauripus,* and other theropodan footprint taxa intergrade statistically according to size alone, and it is impossible to know whether a given footprint was made by an adult of a small species or a juvenile of a large species.

Previous Work

For 150 years, the resemblance of footprints of living ratite birds to those of Mesozoic dinosaur tracks has been noted — even before the latter were recognized as dinosaurian. Hitchcock (1858, Plate LV, Fig. 1) figured what he described as a track of a "South American Ostrich" (i.e., a rhea) to compare with fossil tracks of the Connecticut Valley. Ratites are the largest of living birds as well as the most primitive, and so they were natural models for comparison with the large petrified tracks that were being found in New England, Europe, and elsewhere.

Because living ratites are confined to the Southern Hemisphere, most records of ratite footprints, both living and fossil, come from southern continents. Dr. Donald Baird has kindly provided us with his file of some references to these records, most of which are likely to be overlooked. They include records of footprints of the extinct moa *(Dinornis)* in New Zealand (Gillies 1872, Williams 1872, Owen 1879, Voy 1880, Benham 1913, Wilson 1913, Lambrecht 1933 p. 174–175, Archey 1941) and a Tertiary record of a "kiwi-like bird" from New Zealand (Hutton 1899). Heilmann, who was extremely thorough in his paleo-ornithological investigations, figured cassowary tracks in *The Origin of Birds* (1926 p. 180–181) along with tridactyl dinosaur tracks from the Connecticut Valley; the latter photos were taken from the work of Beebe (1906 p. 396–397). Dr. Baird notes two other treatments of ratite tracks, this time of the emu, in Jaeger (1948 p. 215–218) and Mountford (1946). Finally, Rich and Green (1974) compared the footprints of living cassowaries and emus with those of fossil dromornithine footprints from Tasmania.

The footprints of ratites should be of special interest to dinosaurian paleontologists because birds are living dinosaurs. Their origin from Mesozoic coelurosaurian theropods is now beyond reasonable dispute (Ostrom 1985; Gauthier and Padian 1985; Gauthier 1984, 1986). By cladistic convention, birds must be classified as theropod dinosaurs because they evolved from theropod dinosaurs. Because Mesozoic theropods are so closely related to living birds, it ought to prove interesting to compare their tracks. Differences in limb proportions (especially the general elongation of the metatarsus), changes in pelvic structure, and the loss of the tail have been salient features in the evolution of birds from non-avian theropods. Trackways, as indicators of stance and gait, ought to shed light on whether any changes in these functional features have occurred as a result of the morphological evolution mentioned above. Yet we know of no study in the published literature that has compared trackways of living and extinct dinosaurs in an effort to address these questions.

Dr. W. A. S. Sarjeant has kindly drawn our attention to two studies of tridactyl footprints from the Triassic conglomerate of Wales, a set of five theropod prints that Sollas (1879) and artist T. H. Thomas (1879) compared to footprints of the living emu and to the feet of stuffed cassowary and rhea. Sollas' study, of which we will repeat some details below, concludes with the following passage:

> So complete is the agreement in all essential points between the footprints in the Triassic conglomerate and those of the living Emu, that, leaving all other considerations out of the question, one would not feel much hesitation in declaring for the Avian and, indeed, Ratitous character of the animal which produced the former. But the other considerations are too important to be overlooked. Although the remains of fossil vertebrates have in several instances been discovered in the Triassic deposits of S.W. England, yet none have hitherto been referred or referable to Birds; on the other hand many of them are true Reptiles, though with extraordinarily strong ornithic affinities. The existence of Dinosaurs during the Trias gives, indeed, a strong *prima facie* probability to the supposition that these associated bird-like footprints were really produced by some form of Ornithic Reptile.
>
> The occurrence of *Thecodontosaurus* and *Palaeosaurus* in the magnesian conglomerate of Durdham Down, Bristol, which is on the same parallel of latitude as Newton Nottage, and only 45 miles distant, is very suggestive; and I cannot help thinking that one or other of the animals which possessed the bones must have been a near relation to that which has left its footprints in the magnesian conglomerate of S. Wales.

The Discussion at the end of Sollas' paper records: "Professor Hull pointed out that Prof. Marsh had suggested that the supposed footprints of birds in the Connecticut Valley may probably have been made by Dinosaurs." From these discussions it is clear that the similarities of bird and dinosaur tracks were being considered, but in the absence at that time of a viable hypothesis of ancestry of birds from dinosaurs (apart from Huxley's [1868, 1870] studies, which had by no means received full acceptance), there was no indication that the resemblances of ratite tracks to those of the presumed "Ornithic Reptiles" was anything more than coincidental.

Materials and Methods

We decided to record the footprints of the rhea *(Rhea americana)* because (unlike the ostrich) it conserves all three pedal digits primitive to theropods, it is relatively docile, and it was readily available at the Oakland Zoo. The rhea that we used was subadult and weighed about 25 kg. These birds are not known for their intelligence, but this one was relatively accustomed to human contact.

Our methods were similar to those we used in taking the footprints of the Komodo monitor (Padian and Olsen 1984b). On a base of plywood 120 cm by 240 cm we laid slabs of potters' clay 2 cm thick, smoothed the surface, and sprayed it occasionally with water to prevent drying. The rhea was placed at the end of the trackbed and encouraged to walk across it. At first it avoided the clay but eventually accepted it. Because its first trail was uncertain, we had the rhea walk across the clay a second time. We examined and photographed the trackbed and then took molds of the entire clay slab with ordinary casting plaster. All measurements and observations used in the study were taken from the plaster molds.

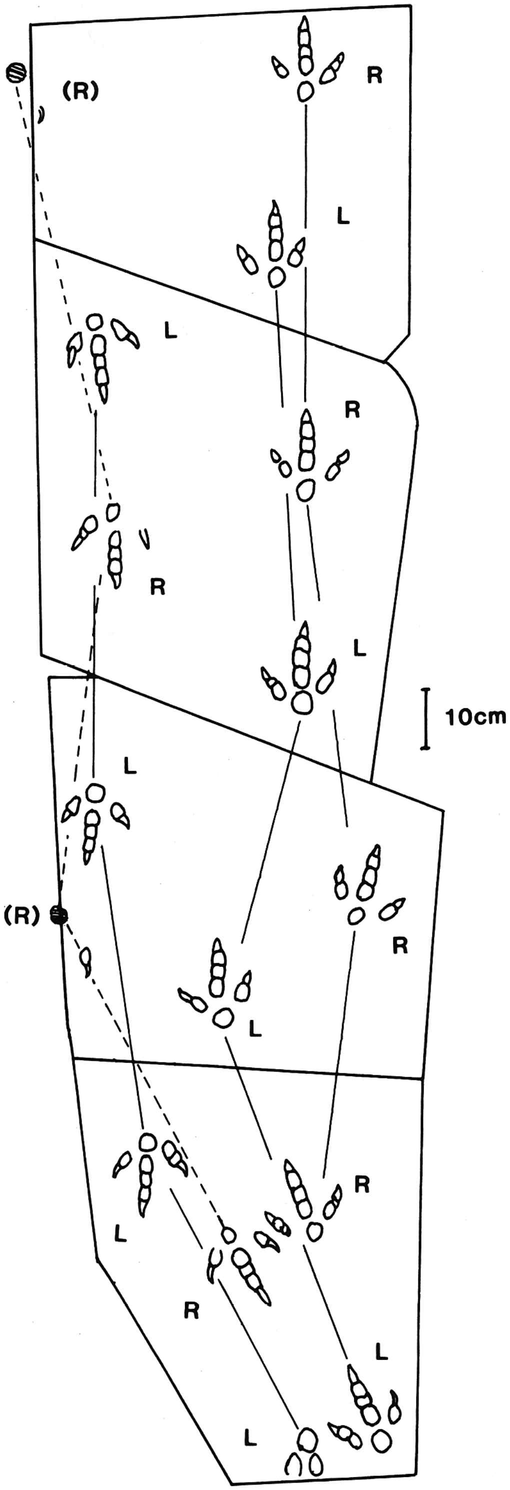
Results

Figure 24.1 is a diagram of the rhea's trackways; it represents the plaster mold of the clay trackbed. It should be remembered that the topographic "left" foot of the plaster mold was really made by the rhea's right foot; however, for the sake of clarity we will refer to the topographic left foot of the plaster mold as the track of the left foot.

In Figure 24.1 the first trackway made by the rhea proceeds down the page, and the second trackway proceeds up the page. The impressions of the digits II–IV measure 8, 13, and 7.5 cm respectively. Of particular interest are the following features.

1. The rhea's phalangeal formula is 3–4–5 for digits II–IV. In general, the proximal phalanx of the second digit and the proximal two phalanges of the fourth digit were not impressed. All four phalanges of the third toe are visible except the proximal part of the first phalanx, which is separated by a slight gap from the round central metatarsal pad. Similar spaces separate the other toes from this pad. (Thomas [1879] noted that this feature in the rhea resulted from the thick horny boss at the end of the metatarsal, but that the separation was not complete in the first digit of the emu.) It should be remembered that the pads of sauropsids (including birds) cover the interphalangeal joints, not the phalanges themselves as in the grasping hands of mammals. A reconstruction of the rhea's skeletal

Figure 24.1. Diagram of *Rhea americana* trackways (UCMP 131683), plaster mold of clay trackbed.



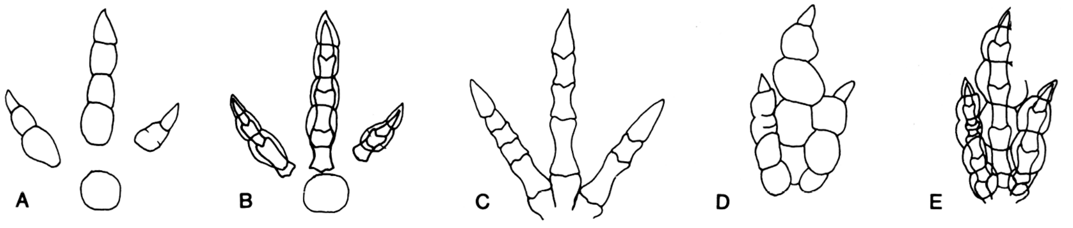


Figure 24.2. **A.** Footprint of *Rhea americana* (UCMP 131683). **B.** Reconstruction of foot skeleton based on preserved phalangeal impressions. Note how this differs from **C,** The foot skeleton of a real rhea, by virtue of the functional pattern of the rhea's gait (see Fig. 24.3 and discussion in Padian and Olsen, 1984a). **D,** *Anchisauripus* sp. (A.C. 49/1) from slab diagrammed in Figure 24.4. **E,** Reconstruction of the theropod foot skeleton that made this footprint. All drawings of left foot; not to scale.

foot, based on its footprints, is given in Figure 24.2.

Sollas (1879) noted in his study of the emu's footprints:

> On comparing the regions of the sole of the Emu's foot with its skeletal structure, one is struck with their wide divergence in details, which clearly shows the futility of too closely arguing in all cases from the skeletal structure of a foot to the impression it might make on the surface of a sedimentary deposit. Thus, while the feet of most of the Ratitae possess a prominent heel, the end of the tarso–metatarsal bone, on the other hand, does not appear to reach the level of the ground; so too, while the articulations of the phalanges are the most swollen parts of the digital skeleton, on the sole of the foot they are the least so, owing to the excessive development of tissue over the middle of the phalangeal bones; and, finally, while the inner toe possesses three phalanges in all, and the outer toe as many as five, yet the imprints left by these digits on the ground show only two depressions in each case — one a mere pit indicating the nail, the other a long groove representing all the rest of the phalanges. Moreover the number of phalanges indicated varies with the way the foot is set on the ground....

Our observations are in general agreement with those of Sollas, except that he did not recognize that the interphalangeal articulations are the most swollen parts of the sole of the foot, and therefore of the footprint.

Sollas' remark about the incomplete impression of the proximal phalanges, which we have noted in our results, also applies to the footprint figured by Hitchcock (1858 Plate LV, Fig. 1). This seems to be a general characteristic of avian trackways. Although the outline of the posterior part of the foot is visible, the proximal phalangeal impressions are seldom clear. We suspect that this is related to the longer metatarsus and short toes of these birds, and to the angle at which the metatarsus meets the ground. The third metatarsal is the longest, the second and fourth are shorter and laterally divergent. This was true for theropods plesiomorphically, but birds have longer metatarsals than other theropods. Because these bones are longer, in order to maintain the relative position of the center of mass of the body (represented by, but not equivalent to, the position of the acetabulum over the metatarsal–phalangeal joint), they may have been angled more vertically than those of other theropods (Fig. 24.3). Another possibility is that the metatarsals of birds elongated to move the center of support farther forward to compensate for (1) the increased pectoral muscle mass of birds, which make up one–fourth to one–third of their muscle mass, and (2) the loss of the long, fleshy tail of their dinosaurian ancestors.

If this generalization is true, then we would expect a similar pattern in the trackways of ornithomimid theropods, which had exceptionally long metatarsals and foreshortened toes. Unfortunately, it is difficult to verify that particular footprints were made by ornithomimids. Sternberg (1926) named "*Ornithomimipus angustus*" without diagnosis as the footprint of *Ornithomimus*, because the latter was "the only animal which would make tracks similar to those here preserved." Like the rhea tracks, Sternberg's show a gap where the proximal part of the second toe and distal part of its metatarsal would have been expected to have been impressed. Significantly, metatarsal II is shorter than III and IV so Sternberg's inference about the trackmaker may be correct. Avnimelech (1966) assigned some mid–Cretaceous (upper Albian or lower Cenomanian) tracks from Israel to ornithomimids, but most are too poor for diagnosis. A few (his Fig. 2, bottom row; 'Type A') show both the circular impression of the metatarsal 'boss' and gaps where the proximal parts of digits II–IV would have been impressed. Unfortunately Avnimelech gave no measurements and only figured isolated tracks, not trackways, so it is impossible to evaluate the variation.

2. The angle between digits II–III ranged from 33° to 47°, with a mean value of 40°. The angle between digits III–IV ranged from 45° to 54°, with a mean value of 52°. The uniformly wider angle between digits III–IV is characteristic of birds and facilitates assignment of isolated tracks to left or right. The angle between digits II–IV ranged from 84° to 99°, with a mean value of 91°. Most of the variation in this latter measurement was due to the variation in the angle between digits II–III. The average stride length was 67 cm, with a range of 54 to 78 cm, but stride length should not be considered characteristic, because the rhea walked slowly and cautiously as it tested the trackbed.

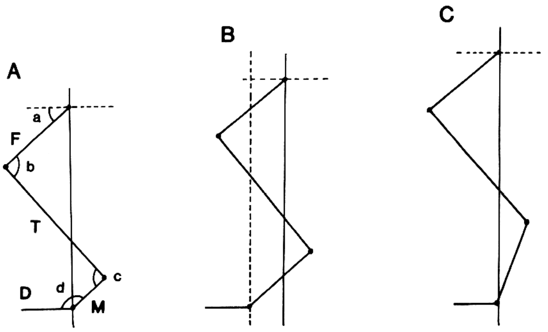


Figure 24.3. Why are the rhea's proximal phalanges not apparent in its footprints? **A** represents a schematic dinosaur hindlimb, with the center of gravity (vertical line) arbitrarily passing through the hip joint and ground contact point. In **B,** the metatarsus has elongated, but no other change has been made. This forces the center of gravity backwards. In **C,** to maintain the original alignment, the orientation of the metatarsus has changed to a more vertical position (but angles *a* and *b* have remained constant). This pulls the metatarsal–phalangeal joints off the ground — a possible answer to the question. Abbreviations: D = digits, F = femur, M = metatarsus, T = tibia.

3. In those portions of the trackbed in which the rhea walked in a straight line and without hesitation, the trackways show two important characteristics: first, one foot is placed almost directly in front of the other; and, second, the third toe (the main weight-bearing axis of the foot) is directed straight ahead or even toed slightly inward. These observations are corroborated by the trackways of birds figured by Hitchcock (1858 Pls. VII, XXXI, LIV), Deane (1861 Pl. III), and later workers.

Comparison of the Tracks of the Rhea with Those of Mesozoic Dinosaurs

In addition to examining the Mesozoic dinosaur trackways in the literature cited below, we photographed and mapped a slab in the Hitchcock Ichnological Collection of the Pratt Museum at Amherst College (A.C. 49/1). It was collected in 1862 from the south side of Turner's Falls, Massachusetts (Early Jurassic, probably Portland Formation), but was never previously figured. Hitchcock (1865 p. 82) referred the numerous tracks on this slab to *Brontozoum validum, B. exsertum,* and *B. sillimanium,* which we regard as synonymous with *Anchisauripus* sp. following Olsen (1980). We have mapped two *Anchisauripus* trackways in Figure 24.4, to compare with those of the rhea. Trackway A, proceeding down the right side of the slab, consists of four prints separated by 82, 82, and 84 cm respectively. Trackway B, proceeding up the left side, comprises three prints separated by 113 and 109 cm respectively. Lengths of digits II–IV are approximately 10, 15, and 10 cm respectively for both trackways. The disparity in pace length suggests that the animal that made trackway B was traveling faster.

Compared to the rhea trackway, A.C. 49/1 shows some similarities and some differences. The angles between the digits are much smaller than in the rhea, averaging 20° (range 19°–21°) and 16° (range 14–17°), respectively, for angles II–III and III–IV. Like the rhea, one foot is placed almost directly in front of the other. This can be seen in other theropod trackways (e.g., Hitchcock 1858 Pls. XXXIII, XXXVIII, XXXIX, XL, XLI, XLII, XLVII Figs. 3 and 6, and LIII Fig. 5; Lull 1953; Thulborn and Wade 1984 Fig. 3; etc.). In the tracks on A.C. 49/1, unlke those Mesozoic tracks just cited, the toes are directed just slightly outward, as they are in some living bird tracks (e.g., Hitchcocck 1858 Pl. XXXII Fig. 2, Pl. LIV Fig. 3). (The reasons for this bear further investigation, but are outside our present study.) We illustrate A.C. 49/1 to show this variation in fossil theropod trackways, but the majority of them are directed inward, as our cited references indicate. Several of these are reproduced diagrammatically in Figure 24.5.

We have stressed the similarity between the trackways of the rhea and those of Mesozoic theropods because of their close phylogenetic relationship. However, we should point out that some of the characteristics of all the trackways mentioned above also apply to the trackways of ornithisichian dinosaurs: for instance, *Anomoepus* trackways typically show one foot planted directly in front of the other (or nearly so) and are toed inward. We have given an example of this (A.C. 52/10, after Hitchcock 1865 Pl. XV) in Figure 24.6. The evidence suggests that these features were present in the common ancestor of saurischians and ornithischians, as we will explain in the next section.

Hindlimb Anatomy and Kinematics

We argue that the footprints of rheas and Mesozoic theropods are similar in these derived respects because their basic patterns of stance and gait have not changed since the Late Triassic. To support this, we must show (*contra* Tarsitano 1983) that the hindlimb anatomy and kinematics of these two groups have the same patterns.

The anatomy and kinematics of the rhea pelvis and hindlimb are straightforward. The femur is subhorizontally and slightly laterally oriented and its distal end moves up and down during locomotion, while the tibiotarsus moves parasagittally. The long tarsometatarsus also moves parasagittally because the metatarsal ankle, like the knee, allows movement in only the fore-and-aft plane.

The recent discovery of the pelvis and hindlimb of a primitive theropod dinosaur (cf. *Coelophysis*) in the Petrified Forest National Park, Arizona (Chinle Formation, Late Triassic, Late Carnian or Early Norian), allows some unusual insight into anatomical and kinematic patterns of early theropods. This specimen (University of California, Museum of Paleontology V82250/129618) has recently been described by Padian (1986); readers are refered to this paper for further details and illustrations. Here, only a few func-

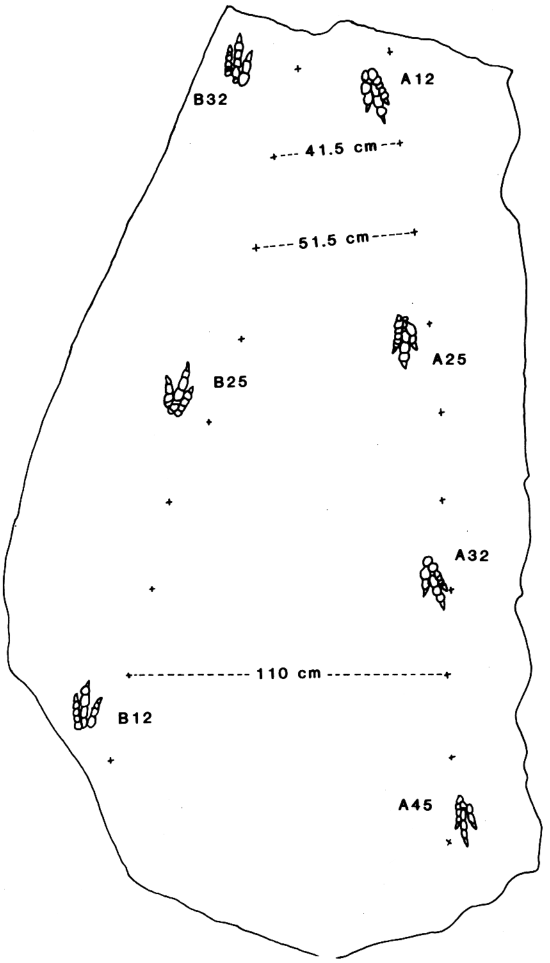


Figure 24.4. Diagram of *Anchisauripus* sp. trackway (A.C. 49/1).

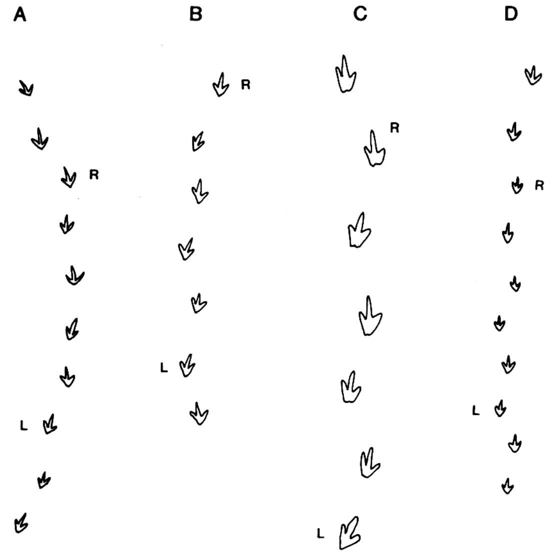


Figure 24.5. Toed-in theropod trackways, with successive footprints very nearly in a straight line. **A,D,** after Hitchcock 1858 Pl. XLI Fig. 2. **B,C,** *ibid.* Pl. XLII Fig. 2. L = left; R = right.

tional considerations will be provided.

The pelvis of UCMP 129618 has a long, low ilium with a pronounced posteroventral arch behind the ischial peduncle, an overhanging supraacetabular crest, a corresponding crest on the inside of the acetabulum, and a pronounced bifaceted antitrochanter on the posterior border of the acetabulum at the junction of the ilium and ischium (Fig. 24.7). The proximal end of the femur is flat, and the head is offset 90° from the shaft. The flat proximal end of the femur abuts against the antitrochanter when the hip is articulated. The broad head can fit into the ovoid acetabulum only when the femur is subhorizontal to horizontal. If it is held more vertically, it snaps off the supraacetabular crest and will not fit in the acetabulum. Furthermore, when the proximal end of the femur is properly fitted against the antitrochanter, the head angles upward at approximately 45° into the acetabulum (Fig. 24.7). In this orientation, as Padian (1986) showed, it is more correct to regard the dinosaurian femur as bowed in two planes (the shaft dorsoventrally, the distal end laterally), not "sigmoid."

These features demonstrate the restrictions on the femoral position in even the earliest theropods. Martin (1983) correctly noted this orientation of the femur in the acetabulum of *Archaeopteryx,* which we conclude is a synapomorphy of theropods and probably of dinosaurs in general. Martin also argued that the partial internal closure on the inside of the acetabulum in *Archaeopteryx* was primitive for archosaurs, but not found in saurischian dinosaurs. However, it is present in UCMP 129618, in *Syntarsus* (Raath 1969), and in *Dilophosaurus* (Welles 1984), to name only a few primitive theropods, and Gauthier (1984) has shown that this feature is synapomorphic at the level of Dinosauria. These features are probably not an adaptation for jumping in *Archaeopteryx* as Martin (1983) suggested, but for upright posture. In order for the acetabulum to accommodate the head of the femur, the distal end must be abducted slightly from the parasagittal plane, thus enabling the hindlimb to clear the abdominal region (birds have retained this structural complex).

As Figure 24.7 also shows, the condyles of the distal end of the femur are subterminal. The lateral condyle fits between the tibia and fibula, as in birds. The available range of movement therefore occurs around the natural position of a 90° bend in the knee. Both the knee and ankle move parasagittally, as in birds (Fig. 24.8), and this follows from the features of hingelike, nonrotary joints, parallel surfaces, bilateral symmetry, and straight shafts (Schaeffer 1941,

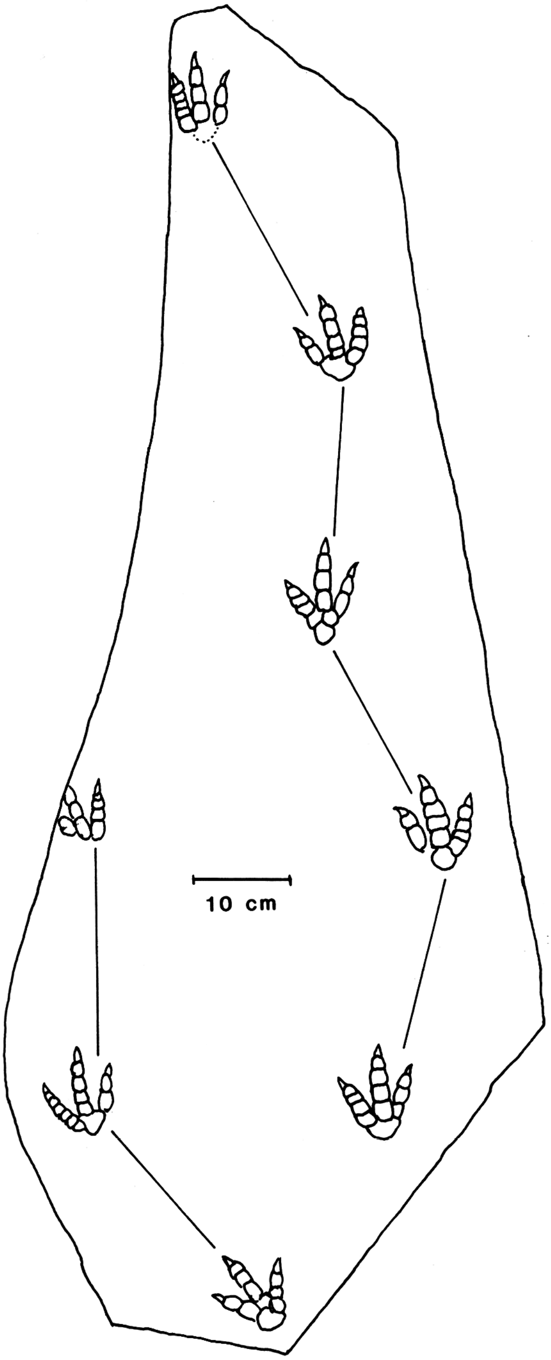


Figure 24.6. Diagram of the ornithischian trackway *Anomoepus* (A.C. 52/10), after Hitchcock 1865 Pl. XV.

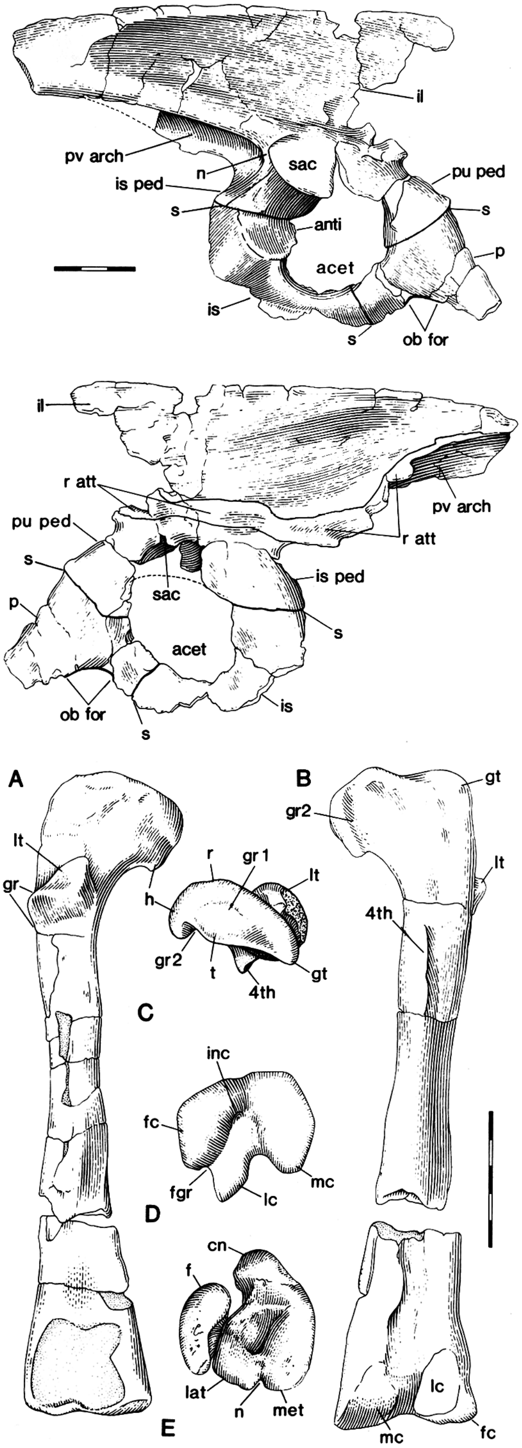


Figure 24.7. Pelvis and hindlimb bones of a small theropod, cf. *Coelophysis bauri*, UCMP 129618 (Late Triassic: Chinle Formation). Above: right pelvis in lateral (upper) and medial (lower) views. Below: **A–D,** right femur in dorsal (A), ventral (B), proximal (C), and distal (D) views. **E,** left tibia and fibula in proximal view. Scale divisions = 1 cm. After Padian (1986).

Coombs 1978, Brinkman 1980, Padian 1983). These features also appear to apply to early sauropodomorphs (e.g., *Plateosaurus)*, ornithischians (e.g., *Heterodontosaurus)*, and dinosaurs outside the saurischian–ornithischian dichotomy (e.g., *Herrerasaurus)*, and hence characterize the ancestors of dinosaurs. Padian (1983) has shown that these also apply to pterosaurs, and therefore most probably to the common ancestor of pterosaurs and dinosaurs. We therefore suggest that theropod hindlimb articulation and kinematics have not changed in any substantial details since the Late Triassic. This conclusion appears to be supported by the evidence of Early Mesozoic theropod footprints detailed above. It would be falsified if it were demonstrated that we have incorrectly assembled and manipulated the pelvis and hindlimb, or that the footprint patterns have been misinterpreted.

Crocodilian vs. Avian Paradigms for Mesozoic Theropods

The need to learn more about dinosaurian posture and gait has long led paleontologists to dissect the structures of living reptiles and compare them to those of extinct dinosaurs; Romer's doctoral dissertation work (1923a,b, 1927) is a classic case in point. This tradition has continued to the present day, but one problem common to all studies of paleobiological structure and function has yet to be solved: how can the effectiveness of a paradigm be assessed, and how can the limits of an analogy be recognized? The answer seems to be that homology is generally better than analogy, and evidence better than models. We will demonstrate some consequences of these differing approaches.

Tarsitano (1983) recently assessed the stance and gait of theropod dinosaurs of the Mesozoic. Because he disagreed with the evidence that shows that birds evolved from small coelurosaurs of the Mesozoic (e.g., Ostrom 1976, Gauthier and Padian 1985, Gauthier 1986), he had to regard most features shared by theropods and birds as convergent. In his 1983 paper, Tarsitano claimed that in birds

> the tibiotarsus bone–muscle complex is the primary system of locomotion. In thecodonts, crocodilians and dinosaurs it is the tail–femoral bone–muscle complex which is most important in locomotion. Thus, in order to interpret the osteology and muscle scars of theropods, it is better to compare theropods to crocodilians which have the same morphology as the pseudosuchian predecessors of theropods.

In other words, according to Tarsitano, theropods evolved from "pseudosuchians," which are allegedly very much like crocodilians, so it is legitimate to base restorations of theropod musculature and functional morphology on the model of a crocodile. This overlooks the obvious difference in anatomy and kinematics between crocodiles and theropods. However, the real problem with the terms of this comparison is the lack of definition of the groups with which theropods are to be compared. Tarsitano (1983 p. 255) asserted "It is apparent that all saurischian dinosaurs have evolved from a pseudosuchian ancestry since the remnants of the crocodilian tarsus is [sic] to be seen in theropods, sauropods and prosauropods. The ischia and pubes of pseudosuchians are decidedly saurischian and not crocodilian."

In these and other passages, Tarsitano did not supply the membership of the "pseudosuchians" or tell us how they differ from crocodilians or other "thecodonts". The difficulty with this, as Gauthier and Padian (1985) pointed out, is that the groups commonly called "thecodonts" and "pseudosuchians" are not defined or united by any shared derived evolutionary features and therefore cannot be diagnosed. As a result, it is difficult to generalize about most aspects of their evolution, including stance and gait.

Gauthier (1984, 1986) suggested that the name "thecodont" be discarded and the name "pseudosuchian" be restricted to crocodilians and all archosaurs closer to crocodiles than they are to birds. He proposed the name "ornithosuchian" for all archosaurs closer to birds than to crocodiles. If, in the above passages, this concept of "ornithosuchian" is substituted for the word "pseudosuchian," the statements are now true in a phylogenetic sense but not in an anatomical sense, because crocodilians and ornithosuchians have different ankle joints ("crocodile-normal" versus "crocodile-reversed"). Morever, in advanced ornithosuchians (*Lagosuchus*, *Lagerpeton*, Pterosauria, and Dinosauria) a metatarsal ankle evolved, with many concomitant changes in the pelvis, femur, and tibia–fibula (Gauthier 1984, 1986; Padian 1984). Theropods should not be compared to crocodiles, a different evolutionary lineage, but to other ornithosuchians. Birds are living theropods and living ornithosuchians, and retain more "remnants" of the plesiomorphic dinosaurian structure.

The consequence of these different views for locomotion and trackway studies can be seen by contrasting Figure 24.8 with Figure 24.9, which is an adaptation of Tarsitano's (1983) view of how the theropod hindlimb was articulated, using the example of *Tyrannosaurus rex.* Note that in his figure the femur moves in a 90° arc about the vertical plane, with the knee joint nearly straight. According to our conclusions described above, in Tarsitano's left figure the hip joint is severely dislocated and the knee is nearly hyperextended. It is probable that *Tyrannosaurus*, like other very large dinosaurs, secondarily adapted to some graviportal characteristics, including a more columnar stance. But even large theropods made tracks (e.g., *Eubrontes)* like smaller ones (see Thulborn and Wade 1984).

If, as Tarsitano seems to be suggesting, crocodiles are a better model for theropodan stance and gait than are birds, theropod trackways should be considerably broader, with lower step angles, than is actually the case. We do not expect that Tarsitano's crocodilian theropod could have made the tracks in the fossil record ascribed to theropods, because the distal end of the femur would have to have been positioned considerably lateral to the proximal end (as in birds) in order to clear the body cavity. In this position the tibia articulates in columnar fashion against the distal end of the femur, not its asymmetrical subterminal condyles. As positioned, it is unlikely that the tibia could have sloped back underneath the body to produce trackways so close to the body midline, and even toed slightly inward. Birds can do this because the subterminal distal femoral condyles are asymmetrical, and when the knee articulates at a 90° angle, the disparity in the position of the condyles angles the tibia–fibula medially underneath the body. This seems to have been the plesiomorphic condition for dinosaurs.

We agree with Tarsitano on a different point: that the vertebral column in Mesozoic non–avian theropods was probably held at an angle of about 20°, rather than the 0° or 50° models advocated by other authors. But we conclude on the basis of comparative anatomy and kinematics of theropods, living and extinct, that there were no substantial differences in hindlimb function, despite sweeping changes in the pelvis, tail, and mode of life that occurred during the evolution of birds. Our independent evidence for this conclusion is the ichnological record, which demonstrates no change in trackmaking pattern since the Early Mesozoic. If we are correctly interpreting Tarsitano's ideas about the stance and gait of theropods, then we have no choice but to conclude that, if he were right, then the Mesozoic footprints ascribed to theropods must be misidentified. It seems more likely that a crocodile is not a good model for theropod stance and gait.

Conclusions

The first conclusion that we wish to emphasize is the importance of phylogeny in understanding function. From the above considerations, it is unlikely that Mesozoic theropods differed from living birds in their mode of walking, except in individual details (for example, in large forms such as *Tyrannosaurus*, which are clearly secondarily derived). It is a precept of comparative anatomy that functional inferences are most likely to be correct when the structural similarities on which they are based are phylogenetically homologous. As the phylogenetic level becomes more specific, the functional inference becomes more powerful. Modern birds are descended from Mesozoic theropods, and crocodilians represent an outgroup that retains many primitive archosaurian patterns, as well as its own derived ones. With this phylogenetic paradigm as an independent body of evidence, some reasons emerge for the functional similarities of living birds and Mesozoic theropods.

The second conclusion is that footprints can serve as an independent test of functional or ecological hypotheses. On the basis of comparative anatomy alone, we could have hypothesized that the locomotory patterns of the rhea and other birds were essentially unchanged from those of *Coelophysis*. A comparison of their footprints was perhaps the only possible independent test of this hypothesis. In our view, the hypothesis has proven robust. We expect that this conclusion will not surprise most workers; we will be content if it helps to lay to rest some

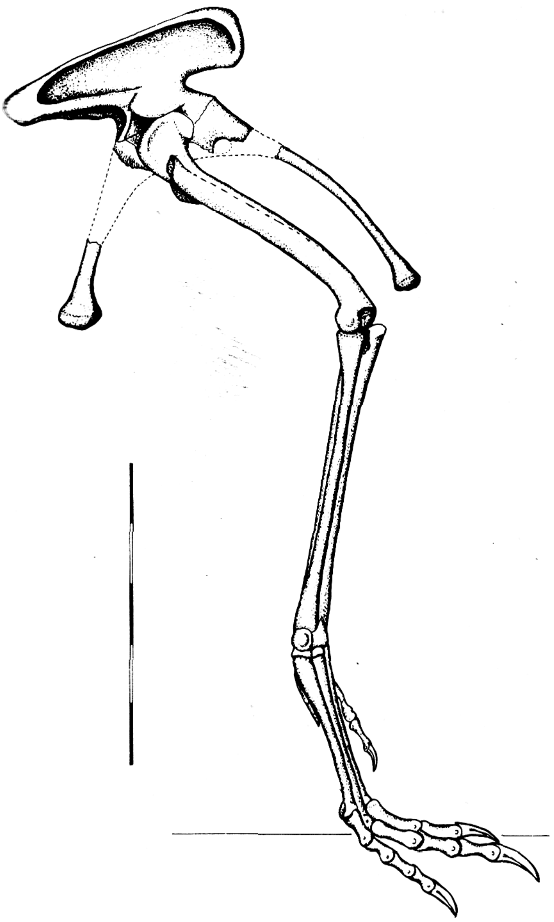
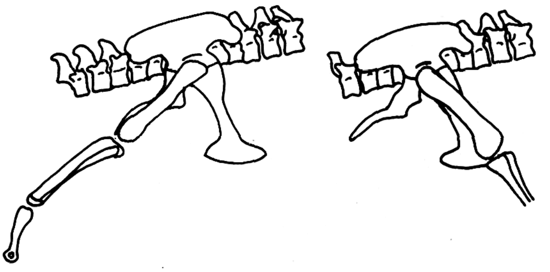


Figure 24.8. Reconstruction of pelvis and hindlimb of *Coelophysis bauri*, partly based on UCMP 129618. The femur is drawn slightly forward of its actual articulation in the acetabulum in order to show the position of the head with respect to the trochanter. Also, the position of the femur as shown is near maximum retraction, toward the end of the propulsive phase of the hindlimb. Scale division = 5 cm.

Figure 24.9. Tarsitano's (1983) reconstruction of hindlimb kinematics in *Tyrannosaurus*, with restored muscles removed for clarity.



arguments about the paleobiology of Mesozoic dinosaurs that are not supported by several independent lines of evidence.

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References

Archey, G. 1941. The moa: a study of the Dinornithiformes. *Auckland Institute Museum Bull.* 1:1–119, XV Plates, Tables A–O.

Avnimelech, M. A. 1966. Dinosaur tracks in the Judean hills. *Proc. Israel Acad. Sci. Humanities, Section Sci.* 1:1–19.

Baird, D. 1954. *Chirotherium lulli*, a pseudosuchian reptile from New Jersey. *Bull. Museum Comparative Zool., Harvard Univ.* 111:165–192.

1957. Triassic reptile footprint faunules from Milford, New Jersey. *Bull. Museum Comparative Zool., Harvard Univ.* 117:449–520.

Beebe. 1906. *The Bird: Its Form and Function.* (Henry Holt & Co.) 496 pp.

Benham, W. B. 1913. Notes on footprints of the moa. [Note in paper by K. Wilson.] *Trans. New Zealand Institute* 45:211.

Brinkman, D. 1980. The hindlimb step cycle of *Caiman sclerops* and the mechanics of the crocodile's tarsus and metatarsus. *Canadian Jour. Zool.* 58 (12):2187–2200.

Charig, A. J. 1972. The archosaur pelvis and hindlimb: an explanation in functional terms. *In* Joysey, K. A., and Kemp, T. S. (ed.). *Studies in Vertebrate Evolution* (Winchester Press) pp. 121–156.

Colbert, E. H. 1968. *Men and Dinosaurs: The search in field and laboratory.* (E. H. Dutton Company) 283 pp.

Coombs, W. P. 1978. Theoretical aspects of cursorial adaptations in dinosaurs. *Quart. Rev. Biology* 53:393–418.

Deane, J. 1861. *Ichnographs from the Sandstone of the Connecticut River.* (Little, Brown & Co.) 91 pp.

Desmond, A. J. 1975. *The Hot-Blooded Dinosaurs: A revolution in paleontology.* (Blond and Briggs) 238 pp.

Gauthier, J. A. 1984. A cladistic analysis of the higher systematic categories of the Diapsida. Ph.D. thesis, Department of Paleontology, University of California, Berkeley. Dissertation #85–12825, University Microfilms, Ann Arbor, Michigan.

1986. Saurischian monophyly and the origin of birds. *In* Padian, K. (ed.). *The Origin of Birds and the Evolution of Flight. Mem. California Acad. Sci.* 8:1–55.

Gauthier, J. A., and Padian, K. 1985. Phylogenetic, functional, and aerodynamnic analyses of the origin of birds. *In* Hecht, M. K., Ostrom, J. H., Viohl, G., and Wellnhofer, P. (ed.). *The Beginnings of Birds.* (JuraMuseum) pp. 185–197.

Gillies, T. B. 1872. On the occurrence of footprints of the moa at Poverty Bay. *New Zealand Institute Proc. Trans.* 4:127–128.

Haubold, H. 1971. *Ichnia Amphibiorum et Reptiliorum fossilium. Handbuch der Palaeontologie, Teil 18.* (Gustav Fischer) 124 pp.

Heilmann, G. 1926. *The Origin of Birds.* (Appleton) 210 pp.

Hitchcock, E. 1836. Ornithichnology. Description of the footmarks of birds *(Ornithichnites)* on New Red Sandstone in Massachusetts. *Amer. Jour. Sci.* 29:307–340.

1858. *Ichnology of New England. A report on the sandstone of the Connecticut Valley, especially its fossil footmarks.* (William White) 199 pp. + LX pls.

1865. *Supplement to the Ichnology of New England.* (Wright and Potter) 96 pp. + XX pls.

Hutton, F. W. 1899. On the footprint of a kiwi-like bird from Manaroa. *Trans. and Proc. New Zealand Institute* 31:486, Pl. XLV.

Huxley, T. H. 1868. On the animals which are most nearly intermediate between the birds and reptiles. *Annals and Magazine Nat. Hist.* 2 (4):66–75.

1870. Further evidence of the affinity between the dinosaurian reptiles and birds. *Quart. Jour. Geol. Soc. London* 26:12–31.

Jaeger, E. 1948. *Tracks and Trailcraft.* (Macmillan) 381 pp.

Lambrecht, K. 1933. *Handbuch der Palaeornithologie.* (Gebrüder Borntraeger Verlag) 1024 pp.

Lull, R. S. 1915. Triassic life of the Connecticut Valley. *Connecticut State Geol. Nat. Hist. Surv. Bull.* 24:1–285.

1953. Triassic life of the Connecticut Valley (revised). *Connecticut State Geol. Nat. Hist. Surv. Bull.* 81:1–331.

Martin, L. D. 1983. The origin of birds and of avian flight. *In:* Johnston, R. (ed.). *Current Ornithology* 1:105–129.

Mountford, C. P. 1946. *Spinifex* town. *Nat. Hist.* 55 (1):62–68.

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, New York State Geological Association. Geology Dept., Rutgers Univ.* pp. 352–398.

Olsen, P. E., and Padian, K. 1986. Earliest records of *Batrachopus* from the southwestern United States, and a revision of some Early Mesozoic crocodylomorph ichnogenera. *In* Padian, K. (ed.). *The Beginning of the Age of Dinosaurs.* (Cambridge University Press) pp. 259–276.

Ostrom, J. H. 1970. Terrestrial vertebrates as indicators of Mesozoic climates. *Proc. North Amer. Paleont. Conv.* Part D:347–376.

1976. *Archaeopteryx* and the origin of birds. *Biological Jour. Linn. Soc. London* 8:91–182.

1985. The meaning of *Archaeopteryx*. *In* Hecht, M. K., Ostrom, J. H., Viohl, G., and Wellnhofer, P. (ed.). *The Beginnings of Birds* (JuraMuseum) pp. 161–176.

Owen, R. 1842. Report on British fossil reptiles, part II. *Report British Assoc. Adv. Sci. 11th Meeting Plymouth* 1841:60–294.

1879. *Extinct Wingless Birds of New Zealand; with an Appendix on Those of England, Australia, Newfoundland, Mauritius, and Rodriguez.* (John Van Voorst) pp. 451–453, pl. CXVI.

Padian, K. 1983. A functional analysis of flying and walking in pterosaurs. *Paleobiology* 9 (3):218–239.

1984. The origin on pterosaurs. *In:* Reif, W.-E., and Westphal, F. (eds.). *Third Symposium on Mesozoic Terrestrial Ecosystems* (Attempto Verlag) pp. 163–168.

1986. On the type material of *Coelophysis* Cope (Saurischia: Theropoda), and a new specimen from the Petrified Forest of Arizona (Late Triassic: Chinle Formation). *In* Padian, K. (ed.). *The Beginning of the Age of Dinosaurs: Faunal change across the Triassic–Jurassic boundary.* (Cambridge University Press) pp. 45–60.

Padian, K., and Olsen, P. E. 1984a. The track of *Pteraichnus:* not pterosaurian, but crocodilian. *Jour. Paleont.* 58:178–184.

1983b. Footprints of the Komodo dragon and the trackways of fossil reptiles. *Copeia* 1984 (3):662–671.

Peabody, F. E. 1959. Trackways of living and fossil salamanders. *Univ. California Publ. Zool.* 63 (1):1–72.

Raath, M. A. 1969. A new coelurosaurian dinosaur from the Forest Sandstone of Rhodesia. *Arnoldia (Rhodesia)* 4:1–25.

Rich, P. V., and Green, R. H. 1974. Footprints of birds at South Mt. Cameron, Tasmania. *The Emu* 74 (4):245–248.

Romer, A. S. 1923a. Crocodilian pelvic muscles and their avian and reptilian homologues. *Bull. Amer. Museum Nat. Hist.* 48:533–552.

1923b. The pelvic musculature of saurischian dinosaurs. *Bull. Amer. Museum Nat. Hist.* 48:605–617.

1927. The pelvic musculature of ornithischian dinosaurs. *Acta Zoologica* 8:225–275.

Schaeffer, B. 1941. The morphological and functional evolution of the tarsus in amphibians and reptiles. *Bull. Amer. Museum Nat. Hist.* 78:395–472.

Sollas, W. J. 1879. On some three-toed footprints from the Triassic Conglomerate of South Wales. *Quart. Jour. Geol. Soc. London* 35:511–517.

Sternberg, C. M. 1926. Dinosaur tracks from the Edmonton Formation of Alberta. *Canada Dept. Mines Geol. Surv. Bull.* 44 (Geological Series 46):85–87, 134–135.

Tarsitano, S. 1983. Stance and gait in theropod dinosaurs. *Acta Palaeont. Polonica* 28 (1–2):251–264.

Thomas, T. H. 1879. Tridactyl uniserial ichnolites in the Trias at Newton Nottage, near Porthcawl, Glamorganshire. *Cardiff Naturalists Soc. Reports Trans.* 10:72–91, pl. II.

Thulborn, R. A., and Wade, M. 1984. Dinosaur trackways in the Winton Formation (Mid-Cretaceous) of Queensland. *Mem. Queensland Museum* 21 (2):413–517.

Voy, C. D. 1880. On the occurrences of footprints of *Dinornis* at Poverty Bay, New Zealand. *Amer. Naturalist* 14:682–684.

Welles, S. P. 1984. *Dilophosaurus wetherilli* (Dinosauria, Theropoda): osteology and comparisons. *Palaeontographica* 185A:85–180.

Williams, W. L. 1872. On the occurrence of footprints of a large bird, found at Turanganui, Poverty Bay. *New Zealand Inst. Proc. Trans.* 4:124–2127.

Wilson, K. 1913. Footprints of the moa. *Trans. New Zealand Inst.* 45:211.