Reports

Swimming Ability of Carnivorous Dinosaurs

Abstract. *Dinosaur tracks from Lower Jurassic rocks at Rocky Hill, Connecticut, were apparently made by a floating or half-submerged animal that was pushing along the bottom with the tips of its toes. These tracks were probably made by large carnivorous dinosaurs (Theropoda) and are apparently the first evidence of swimming by such animals.*

Direct evidence for the swimming ability of dinosaurs is necessarily rare, one of the few documented cases being a set of sauropod forefoot prints made by a partially submerged animal (*1*). Hadrosaurs have often been called amphibious, yet, except for alleged webbing between the fingers (*2*), little direct evidence exists for such an interpretation (*3*). Scant attention has been given to the swimming ability of carnivorous dinosaurs (Theropoda), although large lakes and streams have been visualized as an escape route and refuge for harried vegetarians, especially sauropods and hadrosaurs, inferring lesser swimming ability for pursuing predators. Bakker (*4*) hypothesized, by analogy with ostriches, that theropods were passable swimmers, propelled by strong kicks of the back legs. Unusual tracks at Connecticut State Dinosaur Park, Rocky Hill, brought to my attention by Richard L. Krueger, state geologist, entirely support Bakker's theory.

Since Ostrom (*5*) reported dinosaur tracks at Rocky Hill, a storm overturned the temporary building covering the site and the footprints were buried for protection. A new, permanent building has been constructed adjacent to the original exposure, and an entirely new set of prints has been uncovered on the same (?) bedding plane of the East Berlin Formation (Lower Jurassic) (*6*). Some of these prints, unlike any on the earlier exposure, were apparently made by a partially submerged theropod that was kicking along a muddy bottom with the tips of its toes.

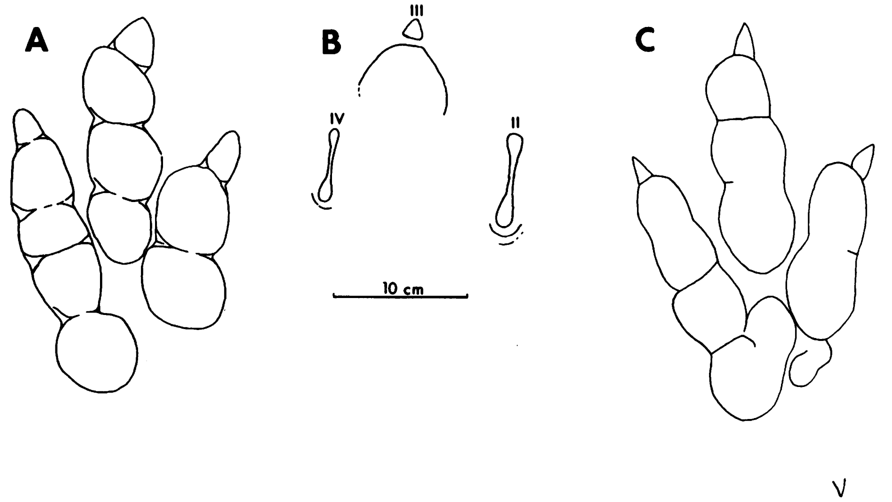

Fig. 1. (A) *Eubrontes platypus*, type, left footprint. (B) Left footprint made by a swimming dinosaur, tentatively identified as *Eubrontes* sp.; a composite restoration based on three footprints. (C) *Anchisauripus minusculus*, type, left footprint. A hallux imprint (ungual of digit I) pointing to the rear is present in the type of *A. minusculus*, but not in the type of *E. platypus*.

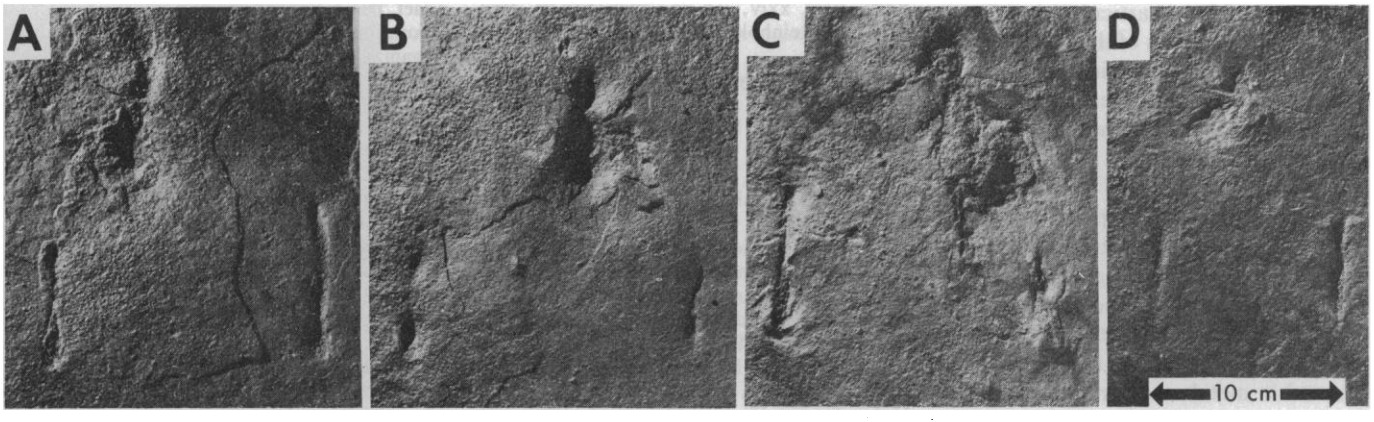

Fig. 2. Representative prints made by a swimming dinosaur. (A) Left *Eubrontes* print with exceptional clarity in the lateral claw scratches. (B) Right *Eubrontes* print with very deep digit III ungual and pad imprints. (C) Right *Eubrontes* print with slight mounding at the back of the lateral claw scratches. (D) Left *Anchisauripus* print from a sequence of eight footfalls made by one individual (see Fig. 3). Digit III is longer (extends farther forward) relative to the lateral claw scratches in *Anchisauripus* compared to *Eubrontes* footprints.

The basic footprint has the following features (Figs. 1 and 2): pes digit III is represented by a small, semicircular claw imprint followed by a broad shallow depression made by the first interphalangeal pad; the pad print of digit III lies in front of a line connecting the tips of the lateral claw imprints; digit III is offset laterally (that is, it is closer to digit IV than to digit II); imprints of digits II and IV each start with a depression or pit made by initial impact of the claw tip, followed by a shallow groove scratched by the claw as the foot was flexed, and each terminates with a second depression or pit made by the claw at the final push of the foot. Some prints have small mounds of mud piled up around the back of each lateral claw trace (Fig. 2). As the animal flexed the pes to propel itself for-

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ward, digit III acted as a fixed pivot with digits II and IV sliding slightly to the rear.

There are at least 43 prints conforming to the pattern just described (four are shown in Fig. 2), which fall into a more common larger and less common smaller size category. Some prints are superbly clear, others rather faint, and some sequences have been "stepped on " by typical, full-foot trackways. Some swimmer tracks are deeply imprinted, others are very shallow. The longest sequence unequivocally made by a single individual has eight footfalls, with an average step length of 104.7 cm (Fig. 3). In this sequence the step length with the right foot forward (average, 114.7 cm) is always longer than that with the left foot forward (average, 97.3 cm), perhaps indicating a "gallop" rhythm to the swimming strokes. Another sequence of five footfalls has an average step length of 130 cm, but does not have the alternating long-short step pattern. The sequences of footprints begin and end abruptly, and many are single, isolated footprints as would be expected from the hypothesized mode of formation.

Imperfect, partial footprints are sometimes formed when the substrate includes several layers of mud and the dinosaur's weight presses the track through all layers. A good print is formed on the uppermost surface, but the deeper layers, exposed by splitting the hardened sediment, have only vague outlines of the original footprint. Such prints, called "ghost prints" or "under prints" (*7*), typically retain a crude outline of the entire foot and never have the delicate claw scratches described above. Clearly, the prints described here are not ghost prints. Tracks made on firm or almost dry mud or on a very thin layer of mud also typically record the entire length of each toe, and bear little resemblance to the tracks described above. Only a partially submerged animal could make such tracks.

Dark gray mudstones at Rocky Hill were deposited along the margins of a large permanent lake that fluctuated in size with irregular climatic changes (*8*). During prolonged dry periods full aerial exposure of these soft yet cohesive muds created an environment ideally suited to preservation of typical, full-foot dinosaur tracks. Judged from step length and the hypothesized posture of the swimming dinosaur (Fig. 3), the water depth at the time the swimmer tracks were made was probably 1.5 to 2.5 m (*9*). Ripple marks, groove and flute casts, and other current indicators ubiquitous in rocks of the East Berlin Formation are almost totally absent from the bedding plane containing these footprints. Relatively still water of modest depth standing over a bed of soft mud combined to preserve these unusual footprints, although the muds were probably sufficiently cohesive to retain tracks even had ripple marks been subsequently imposed (*10*). The fact that these are lacustrine, not floodplain, muds suggests that the dinosaurs entered the water intentionally and were not trapped by a sudden flood.

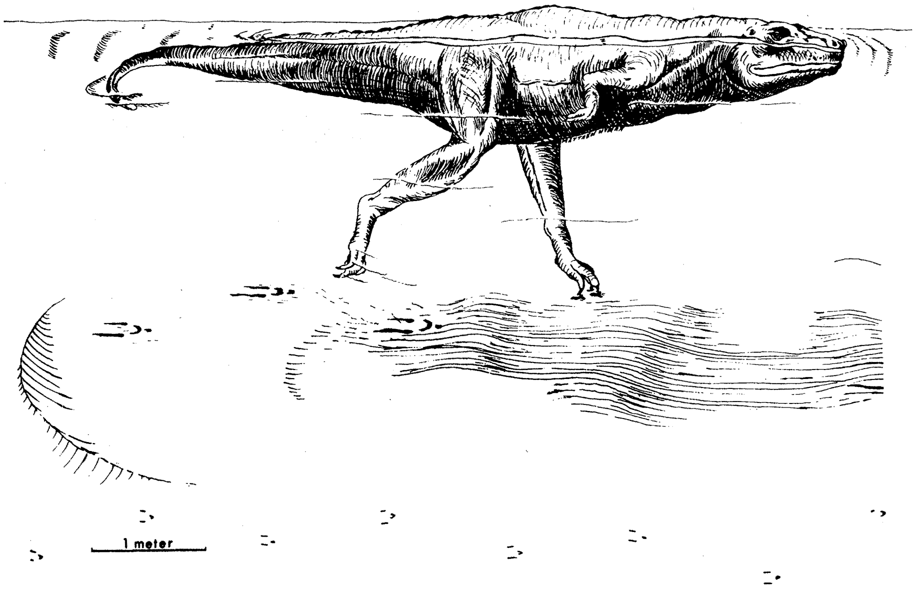

Fig. 3. Restoration of the *Eubrontes* track-maker patterned after *Megalosaurus* and shown in the hypothesized swimming posture. Below is a map of eight footprints made by a smaller animal, possibly *Anchisauripus*. [Restoration by Matthew Hyman]

The swimming track-maker was a tridactyl biped of large size (*11*). Spacing of the toes on the more common, larger tracks is similar to that of *Eubrontes* footprints, especially *E. platypus*, although the toe spacing is also similar to prints of *Anchisauripus minusculus* (Fig. 1) (*12*). Insofar as *Eubrontes* is the most common taxon represented by full-foot imprints at Rocky Hill (*5*), the larger swimming tracks are referred to *Eubrontes* sp. A sequence of eight prints (Fig. 3) was made by a smaller dinosaur with a very long step (average width of prints, 94 mm, about half the width of typical *Eubrontes* prints; average step length, 104.7 cm). Ichnite taxa with comparably narrow feet have far shorter step lengths (for example, for *Grallator formosus* the width is 110 mm, the step 65.5 cm; for *Anchisauripus tuberosus* the width is 86 mm, the step 44 cm) (*12*). Two factors account for the narrow foot/long step combination: (i) angulation of the distal metatarsal ginglymi draws the toes together when the foot is strongly flexed, and (ii) the smaller dinosaur glided or floated slightly between footfalls, thus exaggerating the step length. The less common, smaller swimming tracks are tentatively identified as *Anchisauripus* sp.

Eubrontes footprints are generally regarded as having been made by a large theropod such as *Megalosaurus* or *Teratosaurus* (*12*) because: (i) Late Triassic, Early Jurassic bipedal ornithopods known from skeletons are too small to have made *Eubrontes* footprints (*13*), and (ii) *Eubrontes* prints have sharply pointed unguals rather than the broad hooves or semiclaws of large bipedal herbivores (*14*). *Anchisauripus* prints are also thought to belong to a carnivouous dinosaur, possibly a coelurosaur (*15*). However, it is ecologically implausible that up to 90 percent of the large terrestrial vertebrates in the Connecticut Valley could have been top predators, and *Eubrontes* prints may have been made by an otherwise unknown herbivore. In deference to prevailing opinion, the swimming *Eubrontes* has been restored as a large carnivore patterned after *Megalosaurus* (Fig. 3). The fact that both a large, heavy-bodied theropod and a small, gracile form are represented by swimming tracks suggests that ability to swim was common rather than exceptional among Theropoda. If this interpretation is correct, traditional hypotheses of escape behavior by herbivorous dinosaurs as well as of pursuit tactics of predatory theropods will have to be revised.

W. P. COOMBS, JR.

Western New England College,
Springfield, Massachusetts 01119,
and *Pratt Museum, Amherst College,*
Amherst, Massachusetts 01002

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9. Hubert *et al.* (*8*) estimate the minimum size of the perennial lake as 2160 km^2 and the maximum size as possibly greater than 5000 km^2. The minimum central depth is estimated to have exceeded 20 m and might have exceeded 80 m. Throughout this report the track-maker is described as swimming, although in the hypothesized restoration the dinosaur's feet necessarily touch bottom and the animal is arguably "wading," and not in the strictest definition "swimming." It is certain that all or nearly all the animal's mass was buoyed up by water, so the animal was at least floating. Also, sequences of footprints begin and end abruptly, and there are several single prints that are isolated within a large surface obviously suitable for the preservation of tracks. Unless these were made by a deus ex machina, the track-maker must have been truly swimming at times. The estimate of water depth at the time the tracks were made is based on the assumption that the proportions and posture given in the restoration (Fig. 3) are approximately correct, with a suggested hip height of about 2 m. However, there is always the possibility that the animal was completely submerged, and pushing along the bottom hippo-style, in which case the water depth would have been considerably greater.
10. J. F. Hubert, personal communication.
11. An exact determination of the dinosaur's size is not possible. Under the hypothesized mode of track formation the width of each footprint is less than normal and the stride length is probably abnormally long. Moreover, stride length is notoriously unreliable for calculating the size of a track-maker because the parameter varies over a wide range of values depending on the animal's speed. If the proportions of the restored animal are approximately correct (Fig. 3), a total length of 6 to 7 m is estimated.
12. R. S. Lull, *Conn. State Geol. Nat. Hist. Surv. Bull. 81* (1953), p. 1.
13. Some prosauropods, especially *Plateosaurus*, are large enough to have made *Eubrontes* prints, but these animals have a peculiar entaxonic tetradactyl foot that has long been associated with *Otozoum*-form footprints.
14. Bipedal dinosaurs may have one of three major ungual patterns: (i) sharply pointed, laterally compressed, or nearly circular, strongly hooked true claws; (ii) pointed, dorsoventrally compressed, flat-bottomed, narrow semiclaws; and (iii) broadly rounded, dorsoventrally flattened hooves. Among Jurassic dinosaurs, only stegosaurs combine true hooves with a tridactyl pes. Most pre-Cretaceous ornithopods have semiclaws. True claws, found only in the Theropoda, can be recognized in footprints by their tendency to form an isolated, nearly circular pit just anterior to the distalmost interphalangeal pad. Semiclaws lie flatter against the substrate, leaving an elongate, sharply pointed triangle at the end of each toe. *Eubrontes* prints have a diversity in the shape of the ungual imprints, and on this feature alone such prints could not be identified with certainty as theropod rather than ornithopod.
15. P. M. Galton, *J. Paleontol.* **45**, 781 (1971).
16. Amherst College contributed toward the preparation of this report.

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Oxygen Ion–Conducting Ceramics: A New Application in High-Temperature–High-Pressure *p*H Sensors

Abstract. *Membrane electrodes fabricated from yttria-stabilized zirconia, a representative oxygen ion–conducting ceramic, show a linear voltage response to* pH *over the range 3 to 8 at 285°C and a pressure of 1200 pounds per square inch (82 atmospheres). Test units have been operated continuously at 285°C without failure for periods as long as 9 days. Unlike sensors which are based on electron transfer couples, such membrane electrodes are insensitive to changes in the oxidation-reduction environment and, in turn, exert no influence upon the environment. Such ceramic membranes can therefore be used for the direct measurement of the* pH *of geothermal brines, of water in nuclear reactors, and in high-temperature thermodynamic studies on aqueous systems.*

There has long been a recognized need for a stable sensor for measuring the *p*H of high-temperature solutions such as geothermal brines, water in nuclear reactors, and in high-temperature thermodynamic studies on aqueous systems (*1*). In response to this need, attempts have been made to develop suitable sensors based upon the palladium hydride electrode (*2*), the glass electrode (*3*), and metal-metal oxide couples (*4*). Quite surprisingly, no effort appears to have been directed toward the application of oxygen ion-conducting ceramic membranes for this purpose in spite of certain parallels to well-known inorganic ion-specific sensors such as the lanthanum fluoride electrode for fluoride ion (*5*) and the extensive electrochemical studies of stabilized zirconia ceramics in connection with high-temperature fuel cells (*6*) and oxygen sensors (*7*).

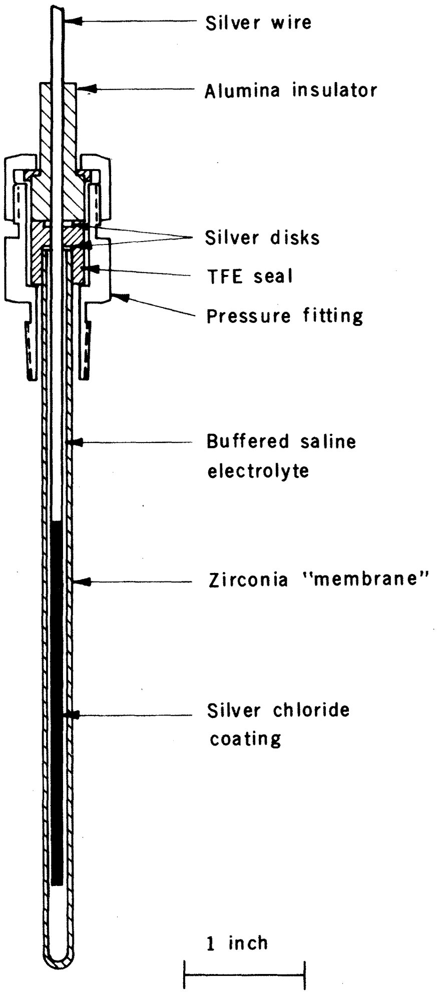

Fig. 1. Schematic diagram of the sensor; *TFE*, Teflon.

I have recently discovered that such oxygen ion conductors, as exemplified by yttria-doped zirconia, show excellent response to *p*H when incorporated into structures reminiscent of the conventional glass electrode. In this form they apparently function as typical membranes with the oxygen ion serving as both the current carrier and the potential-determining species in equilibrium with the hydrogen ion in the aqueous phase. In the work reported here, yttria-stabilized zirconia tubes of the type used in fuel cells and oxygen sensors were prepared by conventional slip casting and plasma spraying techniques (*8*). The tubes [6 inches long and 0.25 inch in inside diameter with a wall thickness of 1/32 inch (1 inch = 2.54 cm)] were stabilized with 8.0 and 16.9 percent yttria (by weight).

The first indication that the ceramic membranes could function as *p*H sensors was obtained from experiments performed at ambient temperature in which zirconia tubes containing 0.1*m* NaCl buffered to *p*H 7.0 as an internal electrolyte were used. An insulated, chlorided silver wire served as the internal electrode, and measurements were made against the reference arm of an Ingold combination electrode as the system was equilibrated with solutions of different *p*H including 0.1*m* HCl, 0.1*m* NaOH, and phosphate buffers. From comparisons of the response to that of the Ingold glass electrode, I found that the behavior of the zirconia membrane as a *p*H sensor was excellent. Because of its high impedance (> 10^{11} ohms at 25°C), however, the sig-