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TYPE MATERIAL OF THE TYPE SPECIES OF THE CLASSIC THEROPOD FOOTPRINT GENERA *EUBRONTES, ANCHISAURIPUS,* AND *GRALLATOR* (EARLY JURASSIC, HARTFORD AND DEERFIELD BASINS, CONNECTICUT AND MASSACHUSETTS, U.S.A.)

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ABSTRACT—The classic Early Jurassic age theropod footprints *Eubrontes giganteus, Anchisauripus sillimani,* and *Grallator parallelus* were established by Edward Hitchcock in 1836–1847 and are the type ichnospecies of their respective ichnogenera. We identify, describe, and figure the type specimens in detail for the first time since they were named. We also figure and describe the other elements of the type series as well as specimens mistakenly thought to be the types. All of the tracks come from cyclical lacustrine and marginal lacustrine to fluvial strata from an interval spanning about one million years in the Early Jurassic age Meriden and Agawam groups of the Hartford and Deerfield basins of Connecticut and Massachusetts. Based on osteometric comparisons with skeletal material, these three ichnospecies were most likely made by theropod dinosaurs, as usually assumed. Although treated here as distinct ichnogenera, it is possible that their major proportional differences derive from allometric growth with individuals of several related species in one genus or even within one species of trackmaker. The rigorous establishment of these classic ichnological taxa forms a basis for more wide ranging studies of theropod diversity in the early Mesozoic.

INTRODUCTION

The famous footprint assemblages from Early Jurassic strata of the Connecticut Valley of Connecticut and Massachusetts (Fig. 1) were first described in a series of classic papers by Edward Hitchcock from 1836 to 1865. These included the first descriptions of dinosaurian material from the Western Hemisphere as well as the first dinosaur footprints described anywhere. The footprint taxa described by Hitchcock were subsequently reviewed and revised by Hay (1902) and especially Lull (1904, 1915, 1953) who also added one more ichnogenus (*Anchisauripus*) to an already very long list. Of the more than 47 ichnogenera listed as valid by Lull (1953) only *Eubrontes, Anchisauripus, Grallator, Anomoepus, Otozoum,* and *Batrachopus* have attained wide use, some presently being recognized worldwide in strata of Triassic–Cretaceous age (see Haubold, 1971, 1984). One ichnogenus, *Eubrontes,* has even become the state fossil of Connecticut (Conn. State Statute Sec. 3-110g).

Despite the attention paid to these ichnotaxa, the type specimens of the type ichnospecies of all but two (*Gigandipus* and *Grallator*) of these classic Connecticut Valley ichnogenera have been incorrectly identified for over 100 years. None has ever been figured by photographs or accurate drawings, and all are surrounded by nomenclatural confusion. In this paper we review the type material of the three classic ichnogenera most often assigned to theropod dinosaurs: *Eubrontes, Anchisauripus,* and *Grallator.* The other classic ichnotaxa will be dealt with in subsequent papers.

MATERIAL AND METHODS

The specimens described here are either natural molds or casts of reptile footprints preserved in fine siltstone to coarse sandstone that are housed in the Hitchcock Ichnology Collection at the Pratt Museum of Amherst College (abbreviated AC), Amherst Massachusetts. Specimen photographs were digitally scanned and modified to improve contrast and luminosity and to produce composites of large specimens (using Adobe Photoshop™ software on a Macintosh™ computer). Halftones for publication were produced using the same software and equipment. Except as noted, specimens are illuminated from the upper left. All relevant published illustrations of the type specimens are reproduced here from digitally scanned originals.

New drawings were prepared from photographs of the original specimens outlined in white water-soluble paint using the method described by Olsen and Baird (1986) or prepared by tracing photographs with the original tracks at hand. In all of the new drawings, lines are drawn along the surfaces of maximum curvature (Olsen and Baird, 1986). Composite drawings are shown as impressions of the right pes and were prepared by digitally superimposing drawings of successive tracks (with the opposite tracks reversed), emphasizing the elements of the tracks thought to be least affected by the processes of impression and preservation.

The conventions for obtaining quantitative measurements from the tracks are shown in Figure 3, which are derived from Baird (1957), Leonardi (1987), and Farlow and Lockley (1993). In specific, we follow Baird's (1957) methodology for osteological reconstructions, in which joints between bones are assumed to lie at the center of pads on the track. In addition to the usual measurements, we use a measure of the projection of digit III beyond the length of the rest on the pes we call the projection ratio (Fig. 3). We use a correction to the length of the rear of the phalangeal part of the pes (R) to account for the differences in interdigital angles (θ) among tracks that would otherwise produce spurious variation in the projection ratio. To do this we trigonometrically adjust R as if digits II and IV were parallel to digit III. This trigonometric approximation for this "corrected" R, R′ is:

$$R' = R * [1/\cos(\theta / 2)]$$

The "corrected" projection ratio (P) therefore becomes:

$$P = R' / (T - R')$$

where T is the length of the phalangeal part of the pes skeleton (as inferred from the track as in Fig. 3) and T—R′ is the "corrected" projection of digit III anteriorly past that of II and IV. In fact, the range of possible ways that track morphologies could be measured has not yet been extensively explored, and we use only a few of the range of possibilities here.

We have found that this corrected projection ratio has con-

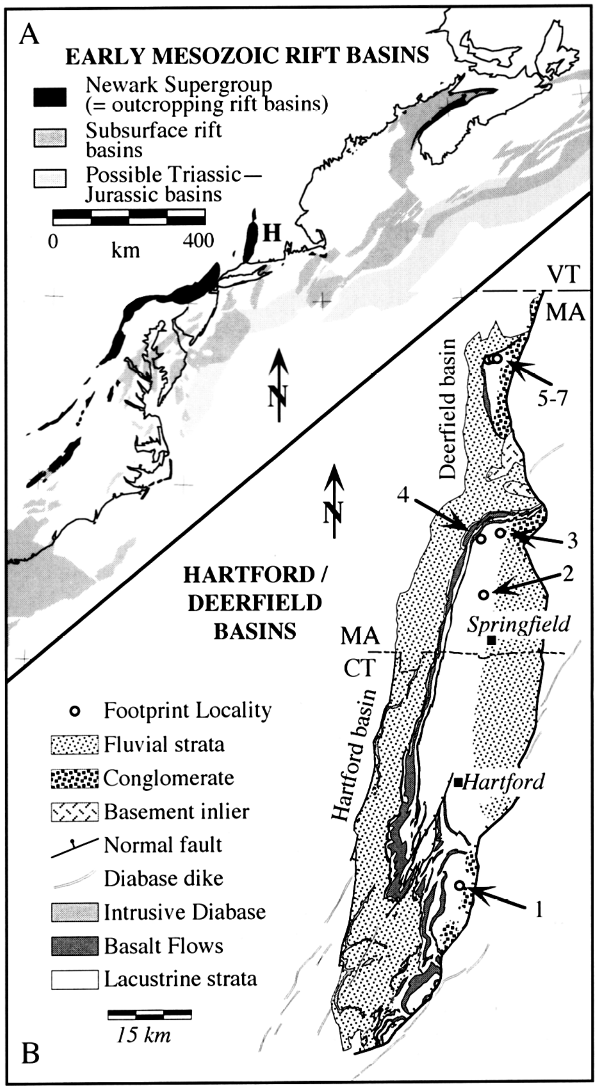

FIGURE 1. Localities for the type specimens and related footprints of *Eubrontes, Anchisauripus,* and *Grallator.* **A**, distribution of Newark Supergroup rift basins in eastern North America: **H**, indicates the Connecticut Valley basin comprised of the Hartford and Deerfield basins shown in **B**. map adapted from Olsen (1997). **B**, map of the Hartford and Deerfield basins showing distribution of major facies and rock types and position of the footprint localities discussed in the text: **1**, Portland quarries, Portland, Connecticut; **2**, Chicopee Falls, Chicopee, Massachusetts; **3**, Moody homestead, South Hadley, Massachusetts; **4**, Dinosaur Footprint Reservation, Holyoke, Massachusetts; **5**, Turners Falls on the Montague shore, Turners Falls, Massachusetts; **6**, old ferry landing in Gill, Gill, Massachusetts; **7**, Field's Orchard in Gill, Gill. Massachusetts. Details for localities are given in Table 2.

siderably less apparent variability in successive footprints in trackways and results in better clustering of ichnotaxa.

The history of the names and status of the ichnotaxa described here is rife with error and confusion. Nearly every citation after Hitchcock (1836) is in some way incorrect or even purposely misleading, and there are objective and subjective synonyms that could be justified as having priority over the generally accepted names in all cases. For taxonomy, we follow the rules and guidelines of the 4th edition of the International Code of Zoological Nomenclature (ICZN, 1997) as applied to ichnotaxa. It is important to note that we only list citations in the synonymies below that refer specifically to the holotypes as we understand them.

The specimen numbers in the Hitchcock collection have a convoluted history, and understanding that history has proved essential for recognizing the type specimens. Edward Hitchcock seems to have begun numbering his specimens prior to 1848, because specimen numbers are used in his "Fossil Footmarks of the United States" of that date. These are simple Arabic numbers preceded by a "No." carved into the rock and are referred to here as "old" numbers. When the Appleton Cabinet at Amherst College was constructed in 1855, all of the specimens received a new numbering system based on their location within the displays. These new numbers consist of a fraction in which the numerator represented a wall, table, or case and the denominator reflected the specimen number in that specific area. These numbers are used by E. Hitchcock in his 1858 "Ichnology of New England" and are referred to as numbers of "1858" where they differ from the numbers used in 1865. Once the numbers of 1858 were introduced, the "old" numbers are never mentioned in print again or correlated to the newer numbers, which is one of the reasons the correct type specimens have been misidentified for so long. In E. Hitchcock (1865) (edited and amended by C. H. Hitchcock) a few of the 1858 numbers are changed to reflect new positions within the Appleton Cabinet, and these changes are generally pointed out in the catalogue of that supplement. The 1865 numbers are used to the present day; however, because the collection was relo-

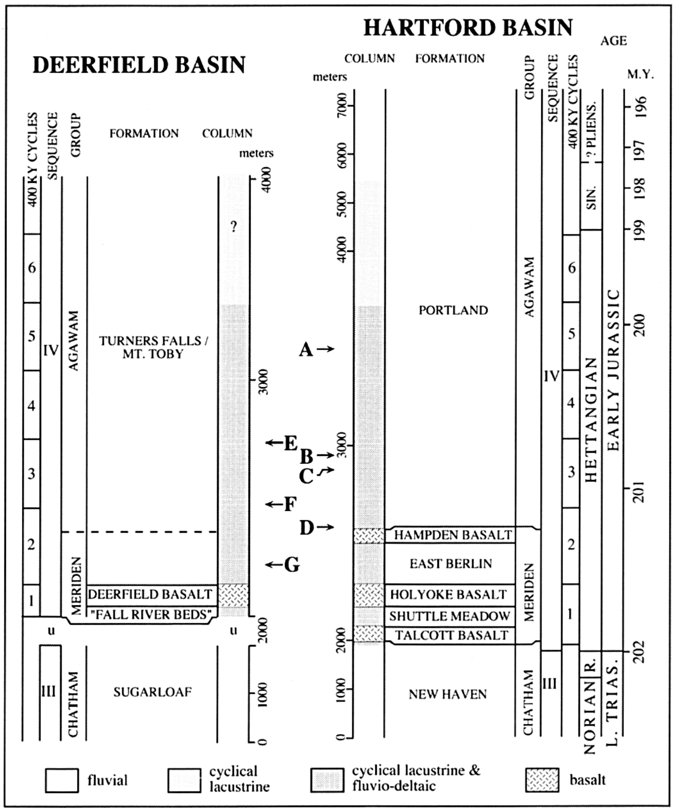

FIGURE 2. Stratigraphic sections of the Hartford and Deerfield basins, expressed on a common age scale for the strata of Jurassic age, showing the position of the localities discussed in the text. **A**, Chicopee Falls, Chicopee, Massachusetts; **B**, Portland quarries, Portland, Connecticut; **C**, Moody homestead, South Hadley, Massachusetts; **D**, Dinosaur Footprint Reservation, Holyoke, Massachusetts; **E**, Field's Orchard in Gill, Gill. Massachusetts; **F**, old ferry landing in Gill, Gill, Massachusetts; **G**, Turners Falls on the Montague shore. Note the difference in thickness scale between the two basin sections and the change in time scale along the Hartford basin section and the changes in thickness scales in both sections. "u" indicates the presence of a possible minor unconformity.

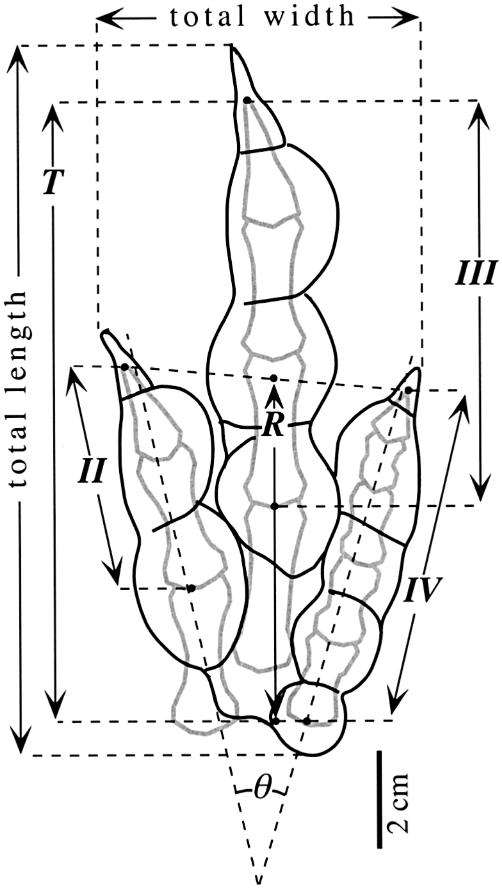

FIGURE 3. Conventions of footprint and skeletal measurements used in this paper shown on Lull's (1953) drawing of his concept of *Anchisauripus sillimani* (AC 9/14) (adapted from Farlow and Lockley (1993) and Leonardi (1987)). Measurements are: **T** = total length of phalangeal part of foot skeleton; **R** = length of rear of phalangeal part of foot; **θ** = divarication angle of digits II–IV; $\mathbf{R}' = R * [1/\cos(q/2)]$ = corrected R; $P = \mathrm{R}' / (T - \mathrm{R}')$ = projection ratio; *II* = length of phalanges II2 + II3; *III* = length of phalanges III2 + III3 + III4; **IV** = total length of phalanges IV1 through IV5.

cated twice from the Appleton Cabinet these numbers no longer correspond to locations.

GEOLOGICAL PROVENANCE

The core of the Hitchcock footprint collection comes from the Jurassic age strata of the Hartford and the Deerfield basins (Figs. 1, 2). The specimens described here come from four localities in the Hartford basin (Dinosaur Footprint Reservation in Holyoke, Moody homestead, Portland quarries, Chicopee Falls), and three localities in the northern Deerfield basin (Turners Falls on the Montague shore, the old ferry landing in Gill, and Field's Orchard). These localities and their stratigraphic positions have been relocated (Fig. 1; Table 1) and at least their approximate stratigraphic positions identified (Fig. 2).

The Jurassic age section of the Hartford and Deerfield basins consists of four parts, all belonging in tectonostratigraphic sequence IV (TS IV) of Olsen (1997). In the Hartford basin, TS IV can be divided into five parts (from the bottom up) (Fig. 2): (1) uppermost New Haven Formation made up of red to gray sandstone and mudstone; (2) the extrusive zone (Meriden Group = Talcott Basalt through Hampden Basalt and Granby Tuff; Weems and Olsen, 1997) consisting of a cyclical lacustrine sequence interbedded with basalt flow and tuff formations; (3) the lower Portland Formation consisting of a cyclical lacustrine sequence; (4) the middle Portland Formation made up of fluvio-lacustrine sequences; and (5) the upper Portland Formation which is predominantly of fluvial origin. The Portland Formation comprises the Agawam Group of the Hartford basin (Weems and Olsen, 1997). All of the lacustrine units coarsen towards the edges of the basin, passing locally into alluvial fan sequences next to the border faults (LeTourneau, 1985; Olsen, 1997). The Hartford basin footprints described herein come from the cyclical lacustrine sequences of the lower Portland Formation of the Agawam Group.

TS IV in the Deerfield basin section consists only of only two divisions: (1) a lower extrusive zone (Fall River beds of Olsen et al., 1992 and Deerfield Basalt; and (2) an upper cyclical lacustrine sequence divided into two time-equivalent formations, the relatively fine-grained Turners Falls Formation and the conglomeratic Mount Toby Formation. The Fall River beds, Deerfield Basalt, and lower Turners Falls and Mt. Toby formations are within the Meriden Group, while the upper Turners Falls and Mt. Toby formations are in the Agawam Group of the Deerfield basin (Weems and Olsen, 1997). All of the Deerfield basin footprints described here are from the Turners Falls Formation.

Like correlative strata in the Newark basin (Olsen et al., 1996; Olsen, 1995a, 1997) the cyclical lacustrine strata of the lower part of TS IV and all of that of the Deerfield basin, is comprised of a regular hierarchy of lake level cycles produced by precipitation fluctuations controlled by Milankovitch-type climatic variations. The thinnest recognized are the transgressive-regressive Van Houten cycles, which were produced by the ~20 ky cycle of climatic precession. Variations in Van Houten cycles trace out several orders of compound cycles, produced by the 100 ky, 400 ky and 2 my "eccentricity cycles." The physical stratigraphy produced by this cyclicity in the Newark, Hartford, and Deerfield basins is extemely similar, and was controlled by the same regional climate system (e.g., Olsen, 1995a). In the Newark basin the sedimentary sequences we attribute to the 400 ky cycles are called McLaughlin cycles (Olsen et al., 1996), and they have proved extremely useful for mapping. While the Newark basin section is known from extensive coring as well as outcrops, the Hartford and Deerfield sections are known almost entirely from discontinuous outcrop. Nonetheless, McLaughlin cycles are apparent in the Hartford and Deerfield basins allowing a tentative correlation of all three basins. At least at the 400 ky level, this allows all of the contained fossils to be placed in a common time scale. In this paper, the McLaughlin cycles are counted upward from the transition of fluvial sequences of the Triassic age part of the section (i.e., New Haven or Sugarloaf formations) into the Jurassic age lacustrine deposits (Fig. 2).

Hartford Basin Localities

The Dinosaur Footprint Reservation in Holyoke is the locality for the type specimen of *Eubrontes giganteus* (AC 15/3) (Table 1). This locality was originally called "the quarry in Northampton, on the east side of Mount Tom" (Hitchcock, 1836:4, 13), and is in the basal Portland Formation (Figs. 1, 2). It is in the upper part of the McLaughlin cycle that begins in the underlying East Berlin Formation (McLaughlin cycle 2). About 30 m of variegated red and gray flaggy sandstone and mudstone are discontinuously exposed, beginning about directly above the Granby Tuff. All of the exposed units bear footprints. The lithology of AC 15/3 most closely resembles the lowest 5 m of strata exposed in color, grain size, and bedding, and trackways from this same interval were described by Ostrom (1972). The environment appears to have been a very shallow lake and

TABLE 1. Data on locality and status of specimens discussed in text.

Specimen number	Taxon[b]	Status	Reference	Locality	Latitude and longitude
15/3	*Eubrontes giganteus*	holotype	E. Hitchcock, 1836	Dinosaur Footprint Reservation	42°14'03" 72°37'25"
4/6	*Anchisauripus sillimani*	holotype	E. Hitchcock, 1843	Chicopee Falls	42°09'06" 72°35'00"
35/41	"*Ornithichnites sillimani*"	figured	E. Hitchcock, 1841	Chicopee Falls	72°35'00"
4/1a[a]	*Grallator parallelus*	holotype	E. Hitchcock, 1847	Moody homestead	42°16'36" 72°33'55"
39/1	*Anchisauripus tuberosus*	holotype	E. Hitchcock, 1841	Turners Falls on the Montague shore	42°36'58" 72°33'16"
23/2	"*Grallator parallelus*"	figured	E. Hitchcock, 1841	old ferry landing in Gill	42°36'29"
23/2	"*Antipus bifidens*	holotype	E. Hitchcock, 1858		72°32'58"
9/14	"*Anchisauripus sillimani*"	figured	Lull, 1904	Portland Quarries	41°34'36" 72°38'37"
54/8	"*Anchisauripus parallelus*"	figured	E. Hitchcock, 1865	Field's Orchard[c]	42°36'33" 72°32'08"
45/8	"*Eubrontes giganteus*"	—	E. Hitchcock, 1865	unrecorded	—
45/1	"*Eubrontes giganteus*"	figured	E. Hitchcock, 1865	unrecorded	—

[a] We designate as AC 4/1a the specimen originally numbered as old N. 234. AC 4/1b is the other half of mounted material that was collected later and is not part of the original trackway (Hitchcock, 1865).

[b] Names in quotes are those given to the specimen by the cited reference and may or may not be a correct assignment.

[c] Only the position of the currently outcropping locality is given.

playa. No reliable locality data are recorded for AC 45/8, the specimen substituted for the real type by Hitchcock (1865).

The Moody homestead locality for AC 4/1a is about 300 m above the base of the lower Portland Formation in a portion of the basin in which the cyclical lacustrine sequences have significant amounts of sandstone and conglomerate (Table 1). Hitchcock originally referred to this locality as "the north part of South Hadley" (1841:485). The locality is about 70 m above the dark gray and black units exposed along Bachelor Brook described by Meriney (1988) in the Portland Formation, a total of about 280 m above the Granby Tuff and Hampden Basalt. This places the site in the upper middle of McLaughlin cycle 3 of the Hartford basin. Although there is presently very little outcrop at this locality, based on the slabs in the Hitchcock collection and what little outcrop remains, the main footprint-bearing units are thin red mudstones interbedded with brown to gray sandstones. The depositional environment was marginal, shallow-water lacustrine and small-scale fluvial.

Red and brown sandstones exposed in the Portland quarries (the name consistently used by Hitchcock, 1858), in Portland, Connecticut, were probably the source of AC 9/14 (Table 1), which was found while it was serving as a flagstone in Middletown, Connecticut. The quarries are about 530 m above the base of the Portland Formation and appear to belong to the upper part of the third McLaughlin cycle. There are still very good exposures at the flooded quarries and the depositional environments were predominately fluvial and possibly eolian (LeTourneau, pers. comm., 1996).

The Chicopee Falls locality, in Chicopee, Massachusetts, is in the upper part of the lower Portland Formation, and is in the lower part of McLaughlin cycle 5, about 900 m above the base of the formation (Table 1). Hitchcock (1841:487) refers to this locality as "Chicopee Factories in Springfield", a name that appears to apply to quarries in the bed of the Chicopee River (p. 466).The sequence crops out along the Chicopee River and consists of four well-developed Van Houten cycles. The small river bed quarries that produced the footprints are in the second or third Van Houten cycle, the third also containing the "Chicopee fish bed" in its deepest-water part. The dark gray, oscillatory rippled sandy mudstone with the footprints AC 4/6 and 35/31 was probably deposited in an ephemeral lake or playa existing during the regressive part of the lake cycles. These are the youngest of the footprints described in this report.

Deerfield Basin Localities

The somewhat vague designation of "Turners Falls on the Montague shore" for AC 39/1 (Hitchcock, 1841:487) probably refers to the outcrops on the southeast side of the Connecticut River at or below the dam at Turners Falls (Table 1). If so, this locality is in the lower Turners Falls Formation, about 130 m above the base of the formation, and probably in the lower to middle part of McLaughlin cycle 2 of the Deerfield basin. On the whole, the outcrops correlate with the lower three-quarters of the East Berlin Formation of the Hartford basin. The sequence in this part of the Turners Falls Formation is dramatically cyclical, although the red platy bedded sandstone in which AC 39/1 is preserved could have been from anywhere within the red parts of the section.

The locality for AC 23/2 that Hitchcock called "Turners Falls in Gill" (1847:51), "Turners Falls at the Ferry" (1858:116), and "Turner's Falls" (1865:56) is obviously difficult to pin down precisely. The old ferry at Turners Falls landed on two shores of the Connecticut River above the dam, one on the south in the Village of Turners Falls (town of Montague), and the other on the north shore in the town of Gill (see Beers et al., 1871). Combining the information from the three citations, the locality may be the old ferry landing in Gill (Table 1). Although no exposures are evident at this spot at the present, the horizon should be about 370 m above the Deerfield basalt and should be in the lower part of McLaughlin cycle 3, close to the as yet undefined boundary between the Meriden and Agawam groups (Weems and Olsen, 1997).

Field's Orchard in Gill (for AC 54/8, Hitchcock, 1865:7) refers to small quarries originally located in the orchard of Mr. Roswell Field of Gill, Massachusetts (Table 1). A "Footprint Quarry" is shown on the maps of Beers et al. (1871) at a spot now submerged about 100 m west of Barton Island. However, tracks from small presently exposed quarries in rocks of the same lithology as typical for Field's orchard in Gill are found just to the west of what was the Roswell Field home in Gill about 1 km to the west-northwest of the spot shown for the "footprint quarry" in the maps of Beers et al. (1871). The two locations are along strike, and the discrepancy makes no stratigraphic difference. These beds are located about 700 m above the base of the Turners Falls Formation and are probably in the

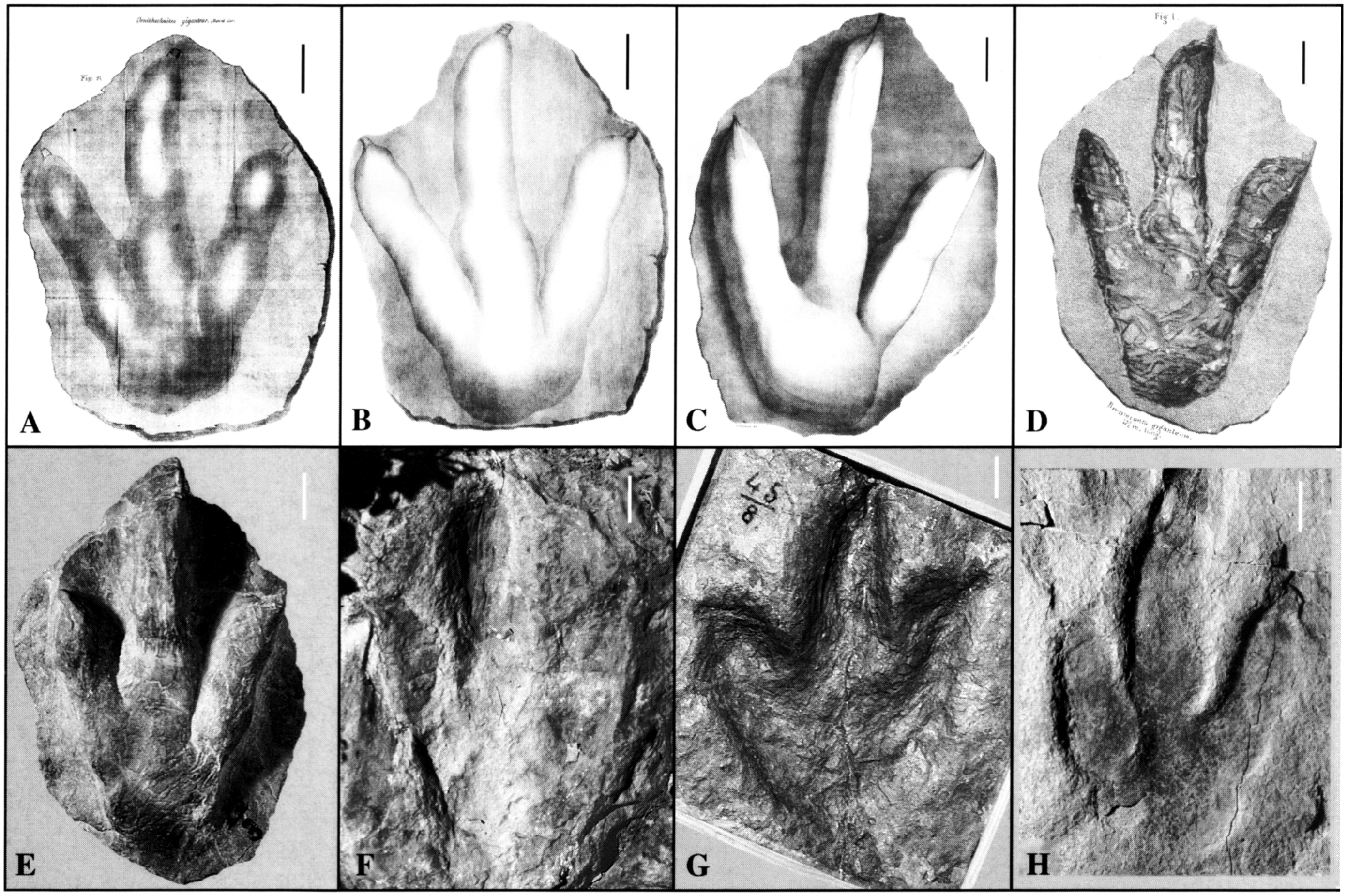

FIGURE 4. Lithographs and photographs of *Eubrontes giganteus* and referred specimens. **A**, Hitchcock (1836, fig. 21); **B**, Buckland (1836, pl. 26b, fig. 1); **C**, Hitchcock (1848, pl. 1, fig. 1); **D**, Hitchcock (1858, Pl. 57, fig 1); **E**, type of *Eubrontes giganteus* AC 15/3; **F**, specimen referable to *Eubrontes giganteus*, in situ, at the locality for AC 15/3, the Dinosaur Footprint Reservation, Holyoke, Massachusetts; **G**, AC 45/8, the specimen substituted for the type of *Eubrontes giganteus* by Hitchcock (1865); **H**, AC 45/1, specimen figured by Lull (1904, 1915, 1953) as a referred specimen of *Eubrontes giganteus*. Scale is 5 cm. Scale bar in the lithographs, added by us.

upper part of McLaughlin cycle 2 or the basal part of McLaughlin cycle 3.

SYSTEMATIC PALEONTOLOGY

Ichnogenus *EUBRONTES* E. Hitchcock, 1845

E. Hitchcock 1845, p. 23
Brontozoum E. Hitchcock 1847, p. 50.

Type Ichnospecies—*Eubrontes giganteus* (Figs. 4A, 5).

Diagnosis—Large (>25 cm long) bipedal, functionally tridactyl ichnite with a relatively short digit III, a broad pes, and a hallux which is rarely, if ever, impressed. Divarication of outer digits averaging 25°–40°.

Eubrontes giganteus E. Hitchcock, 1845

E. Hitchcock, 1845, p. 23.
Ornithichnites giganteus Hitchcock, 1836:317, fig. 21.
Ornithoidichnites giganteus Hitchcock, 1841:484, pl. 36, fig. 18.
Brontozoum giganteum Hitchcock, 1847:57; 1848:169, pl. 1., fig. 1; 1858:64, pl. 57, fig. 1.

Holotype—AC 15/3 (old No. 38), a natural cast in gray fine sandstone from the Dinosaur Footprint Reservation in Holyoke, Massachusetts (loc. 1, Figs. 1, 2), Portland Formation, collected 1835 (Figs. 4A, 5).

Diagnosis—Large (>30 cm long), functionally tridactyl ichnite in which the digit III projection ratio is about 2.2, and the length to width ratio is about 1.4 to 1.5. Projection of digits II and IV along the axis of digit III about equal. Divarication of outer digits 30°–40° (Table 2).

Discussion—*Ornithichnites giganteus* was the name given by E. Hitchcock in 1836 to a large three-toed footprint from what now is called the Dinosaur Footprint Reservation in Holyoke, Massachusetts. Figure 21 of Hitchcock (1836) is a full tone drawing, clearly of specimen AC 15/3 (Fig. 4A). The other figures of *Ornithichnites giganteus* in that paper are rather crude drawings of trackways that cannot be recognized as any particular specimen in existing collections. According to Hitchcock (1865), AC 15/3 was the first specimen of the ichnospecies ever found and is the "original type of the ichnospecies." Thus AC 15/3 must be the holotype of *Ornithichnites giganteus* by original designation. Figures of AC 15/3 appeared in William Buckland's Bridgewater Treatise VI (1836, v. 2:pl. 26b, fig. 1) as well as in E. Hitchcock's papers of 1841, 1848, and 1858. This was the first dinosaur footprint to be formally described.

In 1836 Hitchcock established the name *Ornithichnites* as a name for bird footprints in general (literally "stony bird tracks"), not as a genus name of an animal per se. In 1841,

TABLE 2. Data (in mm) for the footprints discussed in text and graphed in Figure 198. See Figure 3 for definitions.

Name	No.*	AC	*T*	*II*	*III*	*IV*	*θ*	*III/II*	*III/IV*	*R*	*T* − *R′*	*P*
type *E. giganteus*		15/3	335	148	195	240	32	1.32	0.81	227	99	2.39
type *A. sillimani*		4/6	150	62	90	96	32	1.45	0.94	85	62	1.44
type *G. parallelus*	1	4/1	67	22	41	33	29	1.91	1.24	38	28	1.41
	2	4/1	68	23	40	34	22	1.74	1.18	39	28	1.41
	3	4/1	70	24	39	36	25	1.64	1.07	35	34	1.05
	4	4/1	70	23	42	39	28	1.83	1.08	40	29	1.43
	average	4/1	69	23	40	36	28	1.78 ± 0.12	1.14 ± 0.08	38	30 ± 2	1.32 ± 0.18
type *A. tuberosus*		39/1	160	70	105	105	24	1.5	1.00	98	60	1.68
type *O. moodi*	1	4/1a	240	115	130	190		1.13	0.68	195	45	4.33
	2	4/1a	240	110	137	200	22	1.25	0.69	190	46	4.17
	3	4/1a	230	110	140	170	21	1.27	0.82	195	32	6.26
	4	4/1a	240	115	142	180	18	1.23	0.79	190	48	4.04
	average	4/1a	238	113	137	185	20	1.22 ± 0.06	0.74 ± 0.07	193	42 ± 5	4.66 ± 1.05
O. moodi	1	4/1b	235	110	120	180	23	1.09	0.67	185	46	4.09
	2	4/1b	250	120	145	205	22	1.21	0.71	195	51	3.87
	3	4/1b	245	115	140	190	27	1.22	0.74	185	55	3.48
	4	4/1b	250	120	150	210	24	1.25	0.71	195	51	3.94
	5	4/1b	260	115	155	200	25	1.35	0.78	187	68	2.80
	average	4/1b	248	116	142	197	24	1.22 ± 0.09	0.72 ± 0.04	190	54 ± 9	3.61 ± 0.52
type *A. parallelus***	a	54/8	145	48	90	101	30	1.88	0.89	90	51	1.56
A. hitchcocki††	b	54/8	91	41	58	60	26	1.41	0.97	54	36	1.56
A. sillimani††	c	54/8	130	57	82	83	30	1.44	0.99	80	47	1.76
A. hitchcocki††	d	54/8	93	36	53	56	20	1.49	0.95	50	42	1.20
A. tuberosus††	e	54/8	210	88	123	142	19	1.4	0.87	122	86	1.43
G. parallelus†	a1	23/2	89	35	60	50	9	1.71	1.20	49	40	1.23
	a2	23/2	89	34	60	57	10	1.76	1.06	53	36	1.49
	a3	23/2	90	36	60	55		1.67	1.09	52		
	average	23/2	89	35	60	54	10	1.72 ± 0.05	1.12 ± 0.07	51	38 ± 1	1.36 ± 0.80
Anomoepus sp.	b1	32/2	85	32	52	65	55	1.63	0.80	62	15	4.63
Eubrontes sp.††	a1	45/1	315	145	180	222	38	1.24	0.81	210	93	2.39
	a2	45/1	310	130	175	225	33	1.35	0.78	200	101	2.06
	a3	45/1	305	130	175	222	32	1.35	0.79	210	87	2.52
	average	45/1	310	135	177	223	34	1.31 ± 0.06	0.79 ± 0.02	207	94 ± 5	2.31 ± 0.24
Eubrontes sp.††	b1	45/1	310	130	180	220	36	1.38	0.82	215	84	2.69
	b2	45/1	305	130	170	230	40	1.31	0.74	200	82	2.31
	average	45/1	308	130	175	225	38	1.35 ± 0.05	0.78 ± 0.06	208	88 ± 4	2.49 ± 0.27
A. tuberosus††	c	45/1	180	72	111	115	18	1.54	0.97	110	69	1.62
	d	45/1	105	45	65	70	22	1.44	0.93	65	39	1.71
	e	45/1	165	70	95	120	27	1.36	0.79	100	62	1.65
	f	45/1	180	75	115	117	32	1.53	0.98	115	60	1.98
type *Anomoepus scambus*		37/10	70	25	38	53	66	1.52	0.72	46	15	3.62
Grallator sp.††	a1	9/14	103	39	58	59	30	1.49	0.98	56	45	1.29
	a2	9/14	104	37	63	59	27	1.7	1.07	60	42	1.46
	a3	9/14	104	38	58	58	24	1.53	1.00	56	46	1.24
	average	9/14	104	38	60	59	27	1.57 ± 0.11	1.02 ± 0.04	57	45 ± 1	1.32 ± 0.12
Gallator sp.††	c1	9/14	112	37	64	60	21	1.73	1.07	56	55	1.03
	c2	9/14	110	35	60	58	20	1.71	1.03	60	49	1.24
	c3	9/14	110	38	65	60	18	1.71	1.08	55	54	1.03
	average	9/14	111	37	63	59	20	1.72 ± 0.01	1.06 ± 0.02	57	53 ± 1	1.10 ± 0.12
A. sillimani††	d1	9/14	120	40	67	67	25	1.68	1.00	64	54	1.20
	d2	9/14	127	41	74	71	30	1.8	1.04	67	58	1.20
	average	9/14	124	41	71	69	28	1.74 ± 0.09	1.02 ± 0.03	66	56 ± 5	1.20 ± 0.00
A. sillimani††	f1	9/14	120	43	74	72	22	1.72	1.03	72	47	1.57
	f2	9/14	119	43	73	74	24	1.7	0.99	70	47	1.51
	average	9/14	120	43	74	73	23	1.71 ± 0.02	1.01 ± 0.03	71	47 ± 1	1.54 ± 0.04
A. sillimani††	g1	9/14	119	43	72	71	25	1.67	1.01	71	46	1.57
	g2	9/14	120	41	71	71	20	1.73	1.00	70	49	1.45
	g3	9/14	120	41	72	72	18	1.76	1.00	71	48	1.49
	average	9/14	120	42	72	71	21	1.72 ± 0.04	1.00 ± 0.01	71	48 ± 0	1.51 ± 1.15

[a] A letter designates the individual. A number designates one track of a trackway, in the order they were made.

***Grallator parallelus* of Hitchcock (1865); homonym and synonym of *G. parallelus* of Hitchcock (1947).

†Second of the type series, not the holotype.

††Name as it would be applied by Lull (1953). May not be correct.

Hitchcock changed the name to *Ornithoidichnites* to reflect the concept that they were bird-like tracks. Hitchcock in 1845 decided he could name genera of animals that made the tracks rather than the tracks themselves and provided the name *Eubrontes* for the track maker of *O. giganteus* as well as generic names for all of the other ichnospecies then named. Thus, *Ornithichnites giganteus* became *Eubrontes giganteus.* However, for unknown reasons, E. Hitchcock never again referred in print to *Eubrontes,* substituting the name *Brontozoum* instead in 1847 and sticking to that name until his death. Hay (1902) recognized that *Eubrontes* had priority over *Brontozoum* and regarded *Ornithichnites* as an invalid name because it was never intended to be the name of an animal. This interpretation was followed by all subsequent workers (Lull, 1953). It is worth noting however, that the practice of naming an animal on the basis of a track is essentially an existential operation. Short of finding a

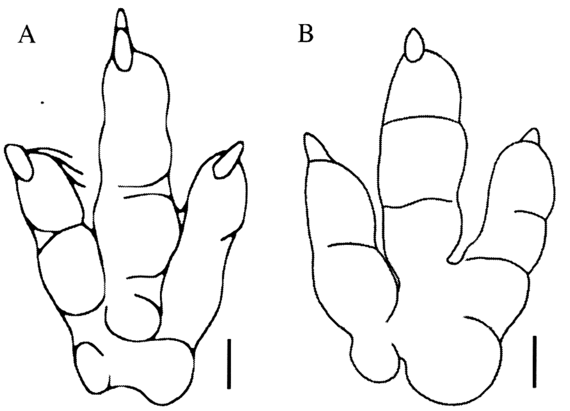

FIGURE 5. Outline drawing of AC 15/3, the type specimens of *Eubrontes giganteus* (**A**) compared to (**B**) AC 45/1, specimen figured by Lull (1904, 1915, 1953) as a referred specimen of *Eubrontes giganteus*. Scale bar is 5 cm.

skeleton of a diagnosible animal in a trackway, we can never be certain of the trackmaker. Even if we had such an occurrence how could we establish that other species might not have made identical tracks? This is one of the main reasons for the separation of ichnotaxonomic nomenclature from biological taxonomy (Sarjeant and Kennedy, 1973). Current procedure dictates that the track be named, not the unknowable animal that made it (see ICZN, Art. 23g [iii]). Although, we believe that *Ornithichnites* should serve as the valid senior synonym of *Eubrontes,* we do not argue for adoption of this. Rather we follow ICZN, Art. 23j(i), and validate *Eubrontes* because the name *Ornithichnites* has not been in use for 151 years, and it would be extremely disruptive to substitute the latter name for the well known and popular *Eubrontes.* By "page priority" in the 1836 paper, *Eubrontes giganteus* remains the type ichnospecies of the ichnogenus, a status it was also assigned by Baird (1957).

Although 15/3 was unambiguously established as the type specimen of *Eubrontes giganteus* in 1836 by E. Hitchcock, his son, C. H. Hitchcock replaced AC 15/3 with AC 45/8 as the type of the ichnospecies in E. Hitchcock's (1865) posthumously published "Supplement to the Ichnology of New England". The stated rationale was that 45/8 conformed more closely to his late father's concept of the ichnospecies because the newer specimen has thicker toes (Fig. 4G). This was done despite the fact that the specimen was not collected until nearly 29 years after the ichnospecies was named (Hitchcock, 1865:23). The designation of AC 45/8 as the type specimen has been repeated in all subsequent works (e.g., Lull, 1953:179), although it is clearly in error. AC 45/8 is a very large but unclear track, most likely an underprint, not showing distinct pads and is in any case indeterminate (Fig. 4G).

Specimen AC 15/3 is a high-relief, natural cast of a right pes with somewhat indistinct pads (Figs. 4, 5). The absence of skin impressions and the overall softness of the outline of the print suggests it is a cast of an over-print close to the impression surface. The natural cast of digit III is severely undercut and had clearly broken off at some time, the fracture being mended with gray cement. This damage slightly obscures the division between phalangeal pads 1 and 2 of that digit. The great depth of the track makes some measurements, especially of the length of digit III, somewhat subjective (Table 2).

Digits II and IV project about equally far along the axis of digit III and the ratio of the length of the rear of the pes to the projection of digit III (the projection ratio) is about 2.2 (Fig. 3; Table 2). The two distal pads of digit IV and the distal pad of digit II lie opposite each other and the posterior ½ of phalangeal pad 2 of digit III. The claw marks are large, but the claws may have dragged out of the track, and they are somewhat damaged. The center of metatarsal-phalangeal pad of digit III lies opposite the crease between the metatarsal-phalangeal and proximal phalangeal pads of digit II, and just behind the middle of the proximal phalangeal pad of digit IV. The crease between the proximal phalangeal pads of digit III is in front of the creases between the phalangeal pads of digit II. The metatarsal-phalangeal pads of digits II, III, and IV make a triangle with sides of the ratio 1.00/1.03/1.25.

A large number of tracks still in situ at the Dinosaur Footprint Reservation (Ostrom, 1972) are very similar to AC 15/3 and one or more trackways could represent the same individual (Fig. 4F). The tracks exposed are all impressions and along with specimens previously collected from the site in the Hitchcock Ichnological Collection at the Pratt Museum of Amherst College, these could comprise an excellent sample for analysis of variation within an ichnospecies.

Track AC 15/3 is similar to the track figured by Lull (1904, 1915, 1953) as *Eubrontes giganteus* (AC 45/1; Figs. 4H, 5B), differing primarily in being larger and in seeming to have narrower toes. The latter is probably due to partial collapse of the sides of the deeper track of AC 15/3 when the foot was withdrawn.

Ichnogenus *Anchisauripus* Lull

Ornithichnites (in part) E. Hitchcock 1841:486.
Eubrontes (in part) E. Hitchcock 1845:23.
Brontozoum (in part) E. Hitchcock 1847:50.
Lull 1904:486; 1915:181; 1953:166.

Type ichnospecies—*Anchisauripus sillimani* (Figs., 6A, B, 7)

Diagnosis—Medium sized (15–25 cm long) bipedal, functionally tridactyl ichnite. Digit III projects relatively further anteriorly than in *Eubrontes* and not as far as Grallator (digit III projection ratio >1.3 and <1.8). Foot narrower than in *Eubrontes,* but not as narrow as in *Grallator* (length/width ratio near 2). Hallux rarely if ever impressed. Divarication of outer digits 20°–35°.

Anchisauripus sillimani (E. Hitchcock)
Ornithichnites tuberosus (in part) E. Hitchcock 1841:486, pl. 37, fig. 21.
Ornithichnites tuberosus (in part) E. Hitchcock 1843:256.
Ornithichnites sillimani E. Hitchcock 1843:255.
Eubrontes dananus E. Hitchcock 1845:23.
Brontozoum sillimani E. Hitchcock 1847:49.
Brontozoum sillimanium E. Hitchcock 1848:49.
Anchisauripus dananus Lull 1904:288.
Anchisauripus sillimani Lull 1915:181.
Anchisauripus dananus Lull 1953:168.
Grallator (*Anchisauripus*) *sillimani* Olsen et al. 1992:507, fig. 12B.

Holotype—AC 4/6 (23/13 of E. Hitchcock, 1865; old No. 48) natural mold in gray siltstone from Chicopee Falls, Massachusetts (Figs. 1, 2), Portland Formation, collected prior to 1841 (Figs. 6A, B, 7).

Diagnosis—Medium sized (~20 cm long) functionally tridactyl ichnite in which the digit III projection ratio averages about 1.4, and the length to width ratio is about 2.0 (Table 3). Digit II tends to project more than IV along the axis of digit III. Divarication of outer digits averages 27° (Table 2).

Discussion—*Anchisauripus sillimani* began its complicated history with the second ichnospecies named and described by E. Hitchcock (1836), *Ornithichnites tuberosus* (his Figs. 2, 5, unnumbered figure). The figures in that paper unfortunately do

TABLE 3. Data (in mm) for the skeletal remains graphed in Figure 16. See Figure 3 for definitions.

Name	*T*	θ	*III/II*	*III/IV*	*R*	*T* − *R*′	*P*	Source*
Ornithischia								
Lesothosaurus	79	31	1.64	0.83	56	25	2.25	1, 2
Scutellosaurus	65	26	1.50	0.73	48	19	2.56	1, 2
Heterodontosaurus	73	21	1.32	0.73	55	19	2.91	1, 2
Theropoda								
Coelophysis	128	12			83	46	1.83	1
			1.46	0.91				2
			1.39	1.01				2
Syntarsus	139	17	1.60	0.92	96	44	2.22	1, 2
Liliensternus	184	35	1.32	0.82	152	39	3.95	1, 2
Dilophosaurus	381	34	1.38	0.86	257	135	1.90	1, 2
Procompsognathus	88	24	1.58	1.05	52	38	1.37	1, 2
Prosauropoda								
Massospondylus			1.14	0.72				2
			1.15	0.72				2
			1.27	0.79				2
			1.17	0.68				2
Plateosaurus	265	28			213	58	3.67	1
			0.99	0.68				2
			1.21	0.68				2
			1.19	0.71				2
			1.21	0.73				2
			1.29	0.75				2
			1.38	0.78				2
			1.23	0.72				2
			1.14	0.77				2
Lufengosaurus			1.16	0.76				2
			1.32	0.70				2
Ammosaurus	146	19	1.17	0.72	123	25	4.85	3
Sellosaurus	118	46	1.35	0.85	82	42	1.96	1, 2
Anchisaurus	114	14	1.36	0.82	93	22	4.23	3
Yunnanosaurus	99	21	1.04	0.99	86	14	6.40	4

*Sources: 1, Farlow and Lockley, 1993, Figure 2; 2, Farlow and Lockley, 1993, Figure 1; 3, Galton, 1976; 4, Galton, 1990.

not allow for identification of actual specimens. In 1841, however, Hitchcock provides full tone lithographs of three specimens included under *O. tuberosus* (Fig. 6). These are easily recognized as actual specimens presently in the collection (Fig. 6) and we identify them as follows: his pl. 37, fig. 20 is AC 39/1 (old No. 54) from Turners Falls on the Montague shore (Turners Falls Formation); pl. 37, fig. 21 is AC 4/6 (23/13 of E. Hitchcock, 1865; old No. 48) from Chicopee Falls (Portland Formation); pl. 38, fig. 22 is AC 35/31 (old No. 52) also from Chicopee Falls (Portland Formation). None of these were explicitly designated as the type specimen although they must constitute the type series. However, Hitchcock in 1843 (p. 224) noted in reference to his paper of 1836 that, "A moment's inspection of these figures shows a striking difference between Fig. 20 of Plate 37 and the other two figures [21 of Pl. 37 and 22 of Pl. 38]. But as the former was destitute of claws, I thought it was safest not to separate it from the others. Having since, however, found the claws on numerous specimens, I shall describe this variety as the *O. tuberosus*; excluding the other figures above referred to." After describing *O. tuberosus,* based on pl. 37, fig. 20 of his paper of 1841 and new specimens, Hitchcock writes, "The variety of *O. tuberosus* . . . differs so much from the other varieties given in Plate 37, figure 21, and Plate 38, figure 22. that I hesitate not to describe the latter as a distinct species. . .. This new species which I found upon the figures of my Report, I propose to denominate *O. sillimani,* as a testimony of my respect for the character and the valuable and long continued labors of Professor Silliman in the cause of science." (p. 255). Thus, AC 4/6 and 35/31 become the type series of *O. sillimani.* (pointed out to P.E.O. by Donald Baird, pers. comm., 1975; Olsen, 1980). No specific designation of a holotype was given, but because AC 4/6 is a deeper and clearer impression we designate it as the lectoholotype of *O. sillimani* (Fig. 7). *Ornithichnites sillimani* again appears in Hitchcock's classification of footprints of 1844 (p. 317).

When Hitchcock (1845) established the names of the animals that made the tracks he placed the specimens in his *O. sillimani* in *Eubrontes* but then without explanation changed the specific epithet to *dananus* (p. 23). Again without explanation the ichnospecies reappears in 1847 as *Brontozoum sillimani* (p. 44). Specimens AC 4/6 and 35/31 (using the old numbers, 48 and 52) are explicitly listed as *B. sillimanium* in 1848, with no explanation of the change in the spelling of the specific epithet and the later name is then used throughout the rest of E. Hitchcock's works.

In the "Ichnology of New England" Hitchcock (1858) makes note of a beautiful slab of tracks from Middletown, Connecticut (AC 9/14), that he includes in *Brontozoum sillimanium*, calling it the "gem of the Cabinet" (see Fig. 8). Oddly enough, however, specimens AC 4/6 and 35/31 are no longer listed as specimens in *B. sillimanium.* Instead, AC 35/31 is listed in his new ichnospecies *Grallator formosus* (p. 75). It is possible, however, that specimen AC 23/13 is actually mislabeled as 22/13 in the list (1858) of specimens of *B. sillimanium.* Specimen AC 9/14 is again referred to as the "gem of the Cabinet" in the "Supplement" in 1865. In the Anonymous post-1865 "Synopsis" of the ichnogenera and ichnospecies in the Hitchcock collection, this slab is listed as the type specimen of *Brontozoum sillimanium.* Presumably this citation is what led Lull (1904) to list AC 9/14 as the type specimen of the type ichnospecies of his new ichnogenus *Anchisauripus,* although he gives it as *Anchisauripus dananus* rather than *A. sillimani,* which has priority. Lull (1915, 1953) later corrects this error in the specific epithet and refers to the correct prior synonym. Clearly the holotype of *A. sillimani* must be AC 4/6 not the more famous AC 9/14, be-

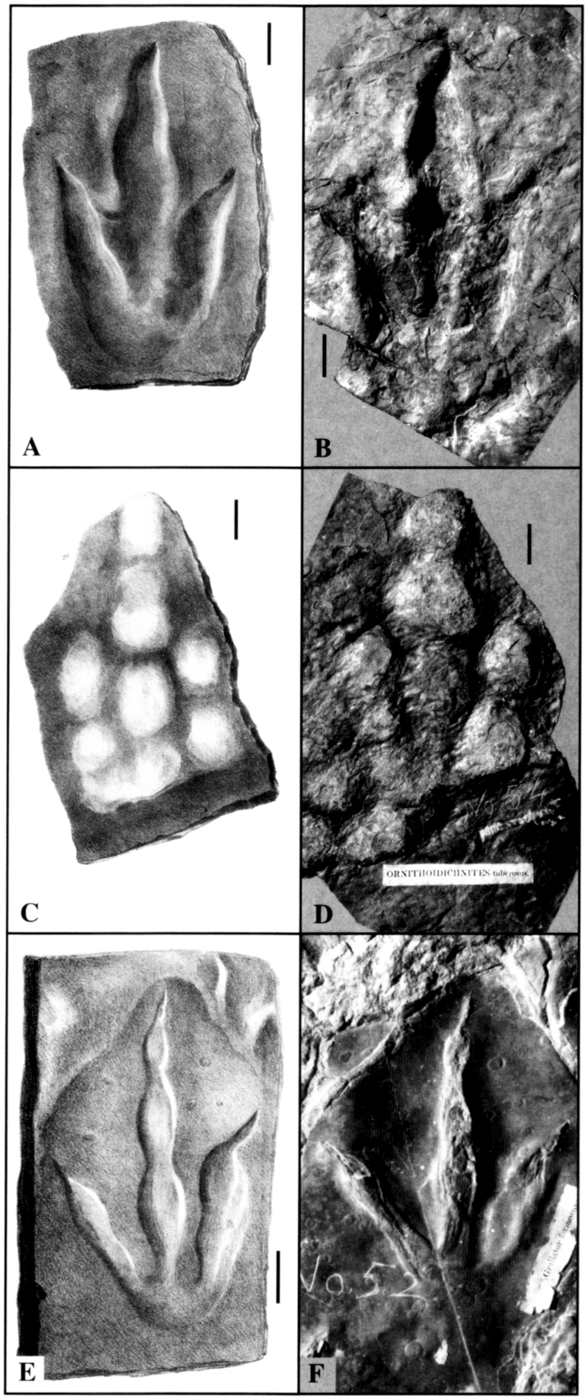

FIGURE 6. Lithographs of the original type series of *Ornithichnites tuberosus* and *O. sillimani* and photographs of the specimens they represent. **A**, *Ornithichnites sillimani* of Hitchcock (1841, pl. 37, fig. 21); **B**, AC 4/6, the type specimen of *Anchisauripus sillimani*. **C**, *Ornithichnites tuberosus* of Hitchcock (1841, pl. 37, fig. 20); **D**, AC 39/1, the type specimen of *Anchisauripus tuberosus*. **E**, second *O. sillimani* of Hitchcock (1841, pl. 38, fig. 22). **F**, AC 35/31, indeterminate dinosaurian footprint, second of the type series of *O. sillimani*. Scale bar is 2 cm. Scale in the lithographs, added by us.

cause the latter was not discovered until many years after the former.

Incidentally, Lull (1904, 1915, 1953) cites AC 31/73 as the type specimen of *O. tuberosus*. However, what he figures as that specimen is actually AC 31/72, clearly collected after 1841.

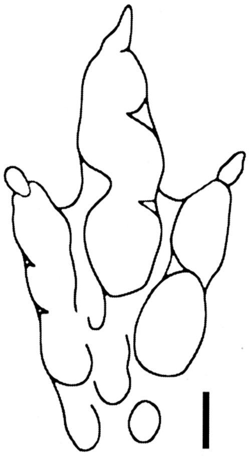

FIGURE 7. Outline drawing of AC 4/6, type specimen of *Anchisauripus sillimani*. Scale bar is 2 cm.

However, as described above, AC 39/1 must be the holotype of *O. tuberosus* (E. Hitchcock, 1841:486–487; 1843:224) (Fig.6).

The true holotype of *A. sillimani* (AC 4/6) is a natural mold with somewhat indistinct pad impressions. It is an underprint from close to the actual layer trod upon. There are a few breaks in the rock that impinge on the morphology of the track, especially posteriorly (Fig. 7).

Digit II projects slightly further anteriorly than IV along the axis of digit III, and the projection ratio of digit III is about 1.4 (Table 2). Hence digit III is relatively longer than in *E. giganteus.* Digit II is relatively long relative to IV (based on the *III/IV* and *III/II* ratios; Table 2) compared to *Eubrontes giganteus.* The two distal pads of digit IV and the distal pad of digit II lie opposite each other, while the middle of the proximal phalangeal pad of digit III lies opposite the crease between the distal pads of digits II and opposite the two distal pads of IV. Relative to each other, the claws on digits II and III appear fairly large, and that of digit IV appears relatively small. The metatarsal-phalangeal pad of digit III is indistinct, but appears to lie about opposite the creases between the proximal phalangeal pads and the metatarsal-phalangeal pads of digits II and IV. The metatarsal-phalangeal pads of digits II, III, and IV make a triangle with sides of the ratio 1.00:1.00:0.96.

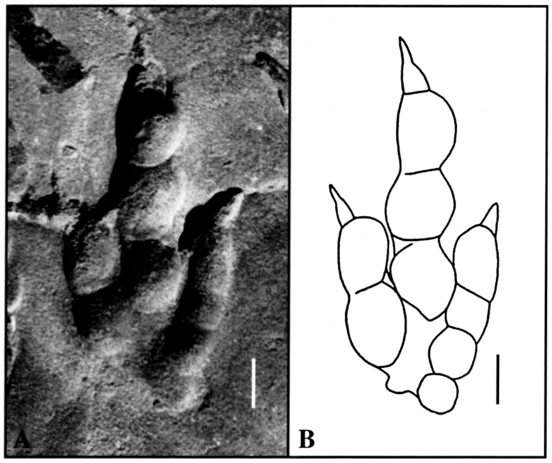

FIGURE 8. One of many natural casts of pes impressions on slab AC 9/14 (**A**) (f1) of table 2), compared to the drawing (**B**) representing that specimen by Lull (1904, 1915, 1953). Lull figured the specimen incorrectly as the type of *Anchisauripus sillimani.* Scale bar is 2 cm.

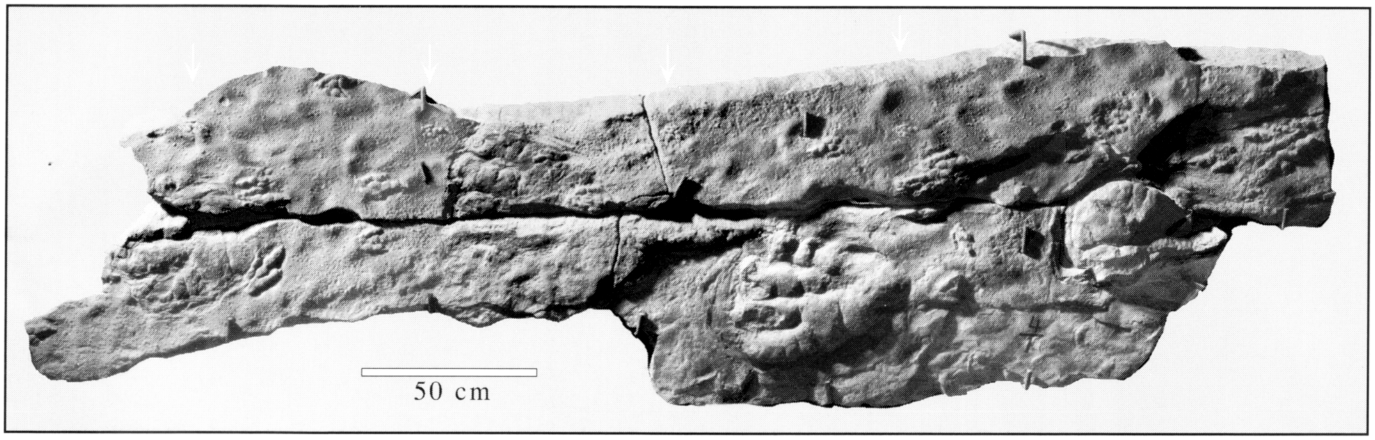

FIGURE 9. Photograph of type of *Otozoum moodii* and *Grallator parallelus*, AC 4/1a. White arrows point to footprints in trackway comprising the type of *Grallator parallelus*.

Although Lull's identification of the type specimen of *A sillimani* was incorrect, the basic morphology of specimen AC 4/6 does correspond fairly closely to that of many of the tracks of similar size on slab 9/14, although there are some differences in the relative proportions of the lengths of the phalanges (Table 3).

Ichnogenus *Grallator* E. Hitchcock

E. Hitchcock, 1858, p. 72.

Type Ichnospecies—*Grallator parallelus* (Figs. 9–11)

Diagnosis—Small (<15 cm long) bipedal, functionally tridactyl ichnite. Digit III projects relatively further anteriorly and the foot is more narrow than in *Eubrontes* and *Anchisauripus* (length/width ratio near or greater than 2). Hallux rarely impressed. Divarication of outer digits 10°-30° (Table 2).

Grallator parallelus E. Hitchcock
Brontozoum parallelum (in part) E. Hitchcock 1847, p. 44, figs. 1, 2a.
Brontozoum parallelum (in part) E. Hitchcock 1848, p. 44, pl. 3, fig. 4.
Grallator cursorius (in part) E. Hitchcock 1858, p. 72, pl. 13, fig. 3; pl. 33, fig. 5, 1865,
Grallator parallelus (in part) E. Hitchcock 1865, p.
Grallator cursorius Lull 1904, p. 494, fig. 12; 1915, p. 200, fig. 53; 1953; fig. 26, 27.

Holotype—Natural cast in brown sandstone of a trackway of four successive pes impressions on slab AC 4/1a (old No. 234) from the Moody homestead, South Hadley, Massachusetts, Portland Formation, collected in 1847 by Pliny Moody (Hitchcock, 1847:figs. 1, 2a). This slab also bears the holotype of *Otozoum moodii* Hitchcock, 1847 (Figs. 9–11).

Diagnosis—Small (<8 cm long) functionally tridactyl ichnite in which the digit III projection ratio is about 1.3, and the length to width ratio is about 2.2 (Table 3). Digit II projects further along the axis of digit III and is more robust than digit IV, which is narrow. Divarication of outer digits averages 28°.

Discussion—In 1847, Pliny Moody (the same person who supposedly in 1802 or 1803 found the footprints jokingly called the tracks of Noah's Raven) collected and presented to E. Hitchcock the large slab (AC 4/1) bearing the natural casts of a trackway of what was to become the basis for the description of *Otozoum moodii* (Hitchcock, 1847), as well as numerous smaller tridactyl footprints (Figs. 9, 10). Hitchcock named the trackway of the smallest tridactyl individual on AC 4/1 *Brontozoum parallelum* (his fig. 1 and 2b) (Figs. 9–11), along with a trackway on a slab from the old ferry landing in Gill (his "Turners Falls in Gill"; his fig. 2a = AC 23/2 = old No. 137) (Figs. 12, 13, 15). The latter slab also bears the type of the peculiar *Antipus bifidus* of Hitchcock (1858) (Fig. 12). Hitchcock was silent on whether AC 4/1 or 23/2 should be the type specimen of *B. parallelum*, although he was uneasy about them being the same ichnospecies. Hitchcock refigured both AC 4/1 and 23/2 in 1848 (pl. 3, fig. 4, and fig. 3, respectively) still identifying them as the only listed specimens of *B. parallelum* (Fig. 15).

However, *Brontozoum parallelum* is not listed in the 1858 "Ichnology"; rather the small trackway on AC 4/1 and the tridactyl tracks on 23/2 are figured as an examples of the first ichnospecies of a new ichnogenus, *Grallator*, and a new ichnospecies *G. cursorius*. (E. Hitchcock, 1858:pl. 13, fig. 3; pl. 33, fig. 5; pl. 58, fig. 4; pl., 36, fig. 8). The fact that these specimens of his new *Grallator cursorius* were the same specimens as his older *B. parallelum* was apparently ignored by Hitchcock (Figs. 9–12). *Grallator cursorius* is thus an objective synonym of *Brontozoum parallelum*. Hitchcock never designated a type of *B. parallelum* or *G. cursorius*. Parenthetically, in the anonymous "Synopsis," AC 23/2 is not listed as an example of *G. cursorius*, and instead specimen AC 21/1 is listed as the type, which is clearly incorrect.

The confusion was compounded when E. Hitchcock (1865) seemingly designated a new ichnospecies, *Grallator parallelus* (Figs. 14, 15). This is the same specific epithet used for *Brontozoum parallelum*, differing only in gender agreement (orthography). The two ichnospecies are thus homonyms. However, Hitchcock (1865) does not list AC 4/1 or 23/2 in the hypodigm of *G. parallelus*, and no mention is made whatsoever of *Brontozoum parallelum* of Hitchcock 1847. Given the fact that E. Hitchcock's publication of 1865 was completed posthumously by C. H. Hitchcock from incomplete notes, we believe that the designation of *Grallator parallelus* as a new ichnospecies was an error by C. H. Hitchcock and that *G. parallelus* was meant to be conceptually the same ichnospecies as *Brontozoum parallelum*. In that case, therefore, *Brontozoum parallelum and Grallator parallelus* are synonyms as well as homonyms, and the correct type ichnospecies of *Grallator* should be *Grallator parallelus*, not *Grallator cursorius*.

Of the specimens listed as syntypical material of *Grallator parallelus* by E. Hitchcock (1865), Lull (1904, 1915, 1953) lists AC 54/8 as the holotype, placing the ichnospecies in his ichnogenus *Anchisauripus*. The ichnospecies *Anchisauripus parallelus* was subsequently commented on by Baird (1957), Hau-

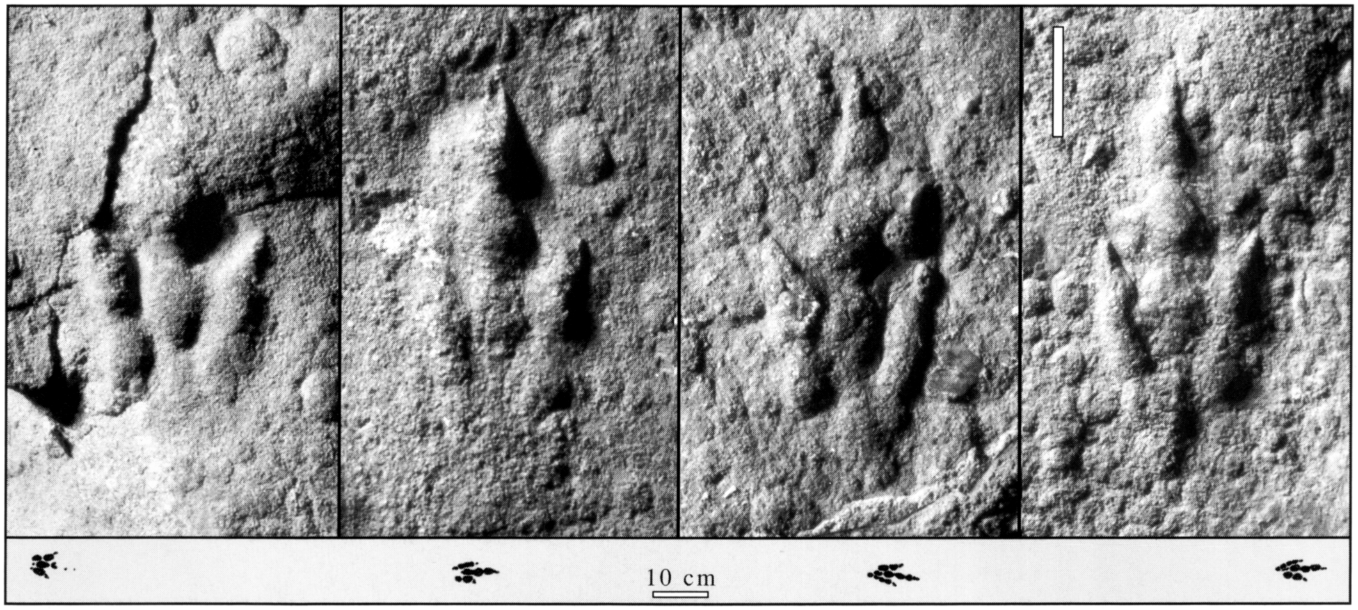

Figure 10. Photographs of natural casts of successive pes impressions of *Grallator parallelus* (above), and silhouettes of the full trackway on slab 4/1a (below) (see Fig. 9). Scale bar is 2 cm in the upper panels.

bold (1971), and Smith (1982), among others. As *Anchisauripus parallelus* has been widely used and is a senior synonym of *Grallator parallelus* it is appropriate to formally recognize the senior synonym. Lull (1904:494–495) selected AC 4/1 as the type specimen *G. cursorius* and listed the latter as the type ichnospecies of the ichnogenus, which also automatically designates AC 4/1 as the type specimen of the objective senior synonym *Grallator parallelus.* Specimens AC 32/2 and 54/8 (Figs. 9, 10) have, therefore, no significance as types.

Based on the type material, *Grallator parallelus* is one of the more distinctive grallatorids. As an ichnospecies it is distinguished by the relative prominence of digit II and the delicate form of digit IV compared to *Eubrontes* and *Anchisauripus.* The *III/IV* and *III/II* ratios are 1.1 and 1.8, respectively. The middle part of the distal pad of digit II lies opposite the crease between phalangeal pads 1 and 2 digit III, while the front of the distal pad of digit IV projects forward only to that same crease on digit III. The projection ratio of digit III is about 1.3 (Table 2), and hence digit III is relatively quite long. The claws are relatively large, especially that of digit II. The middle of the metatarsal-phalangeal pad of digit III is just posterior to the creases between the proximal phalangeal pad of digit IV. The impression of metatarsal-phalangeal pad of digit II is indistinct at best, but it appears that the metatarsal-phalangeal pads of digits II, III, and IV make a triangle with sides of about equal length.

GENERIC SEPARATION OF *EUBRONTES, ANCHISAURIPUS,* AND *GRALLATOR*

The type specimens described in this paper exhibit most of the shape variability seen in Early Jurassic age tracks generally assigned to theropod dinosaurs (Baird, 1957). The type specimens of *Eubrontes, Anchisauripus,* and *Grallator* are exemplary in this regard. If viewed typologically, outside the context of a contemporaneous population of intermediate sizes, they appear to be quite distinct from one another in proportions and by inference different in the osteology of their track makers. However, tracks made by populations of single species of dinosaurs could be expected to exhibit differences due to morphological variation owing to allometric growth, intrinsic variation in osteology in any single size category, and variation caused by flexibility in the foot during interaction with the substrate. In addition, there could be variation with stratigraphic level, due to evolution within a lineage, or between temporally successive closely related species. In addition, there can be variation due to taphonomic factors (including tectonics) acting on the track subsequent to its creation. However, because the tracks described here come from different localities, widely separated stratigraphic levels, and are mostly represented by single tracks (*Eubrontes* and *Anchisauripus*), we are forced to use a typological approach to their diagnoses as taxa. The meaning of these diagnoses are, therefore, open to serious question, because ichnotaxa should be viewed in their full ontonogenetic and population context, which has not yet been fully explored.

Recent attempts to treat putative theropod tracks as populations have shown that at least some aspects of footprint shape do appear to change continuously with size (Olsen, 1980, 1995a; Smith and Farlow, 1996). This is seen in the length-width relationship, the divarication of the lateral digits, and most clearly in the projection ratio (Figs. 3, 16A). Smaller tracks generally have a high length to width ratio, larger ones tend to have a low length to width ratio. Smaller tracks tend to have narrow angles of divarication, larger tracks are more widely splayed—with much variation. Smaller tracks have a digit III that projects relatively far in front of digits (projection ratio near 1), and in larger tracks digit III projects relatively little (projection ratio near 2) (Fig. 16A). Unfortunately these are the same differences that most clearly separate the type specimens of *Eubrontes, Anchisauripus,* and *Grallator* (Fig 16A). These are also the main characters that have been used to group other ichnospecies in these ichnogenera.

The seemingly continuous variation in these proportional differences led Olsen (1980) to conclude that *Eubrontes, Anchisauripus,* and *Grallator* are not, in fact, generically separable. Olsen (1980) therefore regarded all of the Newark Supergroup ichnospecies within those three ichnogenera as belonging to *Grallator* because that was the oldest named ichnogenus that at the time had an unambiguous type specimen (AC 15/3, the

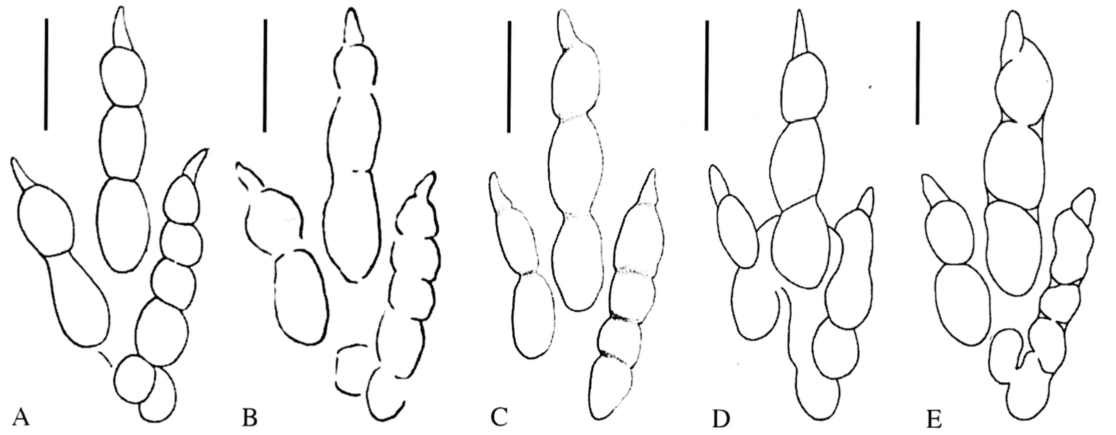

FIGURE 11. Drawings of the type of *Grallator parallelus,* all AC 4/1a: **A**, *Brontozoum parallelum* of Hitchcock (1947, fig. 2a); **B**, *Brontozoum parallelum* of Hitchcock (1948, pl. 3, fig. 4). **C**, *Grallator cursorius* of Hitchcock (1958, pl. 13, fig. 3); **D**, *Grallator cursorius* of Lull (1904, 1915, 1953). **E**, composite outline drawing of type trackway of *Grallator parallelus.* **C** and **D** are shown as mirror images of the originals. Scale bar is 2 cm.

type specimen of *E. giganteus,* was missing in 1980). With the correct type specimen of *Eubrontes* recognized, its ichnogenus name is the one with clear priority. This brings us quite close to Hitchcock's original concept of *Eubrontes* (*Brontozoum*). Up until 1858 his concept of *Eubrontes* included not only large forms, but also small forms, corresponding in fact to Lull's concept of *Eubrontes, Anchisauripus* and *Grallator.* Only in 1858 did he place (tentatively) the smallest forms as a different ichnogenus (*Grallator*), with Lull (1904) creating the third ichnogenus.

There are some other differences among the tracks discussed here that are not so clearly related to size, however. One of the most obvious of these is the relative projection of digits II vs. IV (exclusive of the claw) along the axis of digit III. In the type specimens of *Eubrontes giganteus* and *Anchisauripus sillimani,* digit II and IV appear to project approximately equally, while in the type of *Grallator parallelus* and in AC 36/19 digit II distinctly projects further anterior than IV. In contrast, in AC 45/1 and AC 54/8 digit IV projects distinctly more than II. Assessing these differences is difficult, however, because the relative projection of digits II and IV depend on the alignment of the metatarsal axis with the axis of digit III, and that alignment varies even with individual trackways, as it clearly does in some Early Jurassic age ornithischians (e.g., *Anomoepus* in Olsen, 1995a). Some variation is indeed seen in this character in the type trackway of *Grallator parallelus* (AC 4/1a; Fig. 12; Table 2), but the other two type specimens are isolated tracks.

FIGURE 12. Slab AC 23/2 containing the second individual of the type series of *Grallator parallelus* (arrows), several tracks of *Anomoepus* sp., the type of the enigmatic *Antipus bifidens* (V shaped grooves), and several indistinct tracks. Scale bar is 5 cm.

Recently, Farlow and Lockley (1993) have proposed a new method of recognizing the makers of dinosaurian tracks which is also useful for discriminating different ichnotaxa. Using Baird's (1957) method of reconstructing the osteology of tracks, in which joints are assumed to lie in the center of pads (Fig. 3), Farlow and Lockley (1993) graph the ratio of the length of digit III to digit II, against the ratio of the length of digit III to digit IV (i.e., *III/II* against *III/IV,* Fig. 3). This method has the advantage of being insensitive to the alignment of the digits with the metatarsal axis (assuming no sliding and a clear impression). When the data for the tracks described here are plotted in this manner (Fig. 16), the type specimens are clearly separated from one another. Farlow and Lockley's (1993) method does not take into account allometric growth, however. Larger tracks tend to group towards the lower left and the smaller tracks to the upper right (as is true for the osteological measurements, see below) and this may reflect an allometric relationship. Without information about variations in individuals or populations the meaning of the apparent separation of the specimens on the graph is not clear. The range of variation seen within each of two osteological species shown by Farlow and Lockley (i.e., *Coelophysis bauri* and *Plateosaurus engelharti*) is rather large and suggests that the range of variation seen in all of the putative theropod tracks described here conceivably could have been made by one osteological species exhibiting allometric growth.

It is our opinion that although the ichnogenera *Eubrontes, Anchisauripus,* and *Grallator* might indeed be diagnosable ichnogenera, this cannot be determined by examination of their

FIGURE 13. The trackway of the second individual of the type series of *Grallator parallelus* (**A**). Scale bar is 5 cm. Detail of the three successive tracks (**B–D**). Scale bar is 2 cm.

type specimens alone. It still seems plausible to us that the proportional changes that separate these three ichnogenera may very well be seen in the ontogeny of one osteological species—as well as between species of different adult sizes. The same is true of the ichnospecies placed within those ichnogenera, all of which have been treated typologically. Hopefully, an examination of within-site, or within-stratigraphic level variation, may well clarify the meaning of the differences among these classic forms.

WERE *EUBRONTES, ANCHISAURIPUS,* AND *GRALLATOR* MADE BY THEROPOD DINOSAURS?

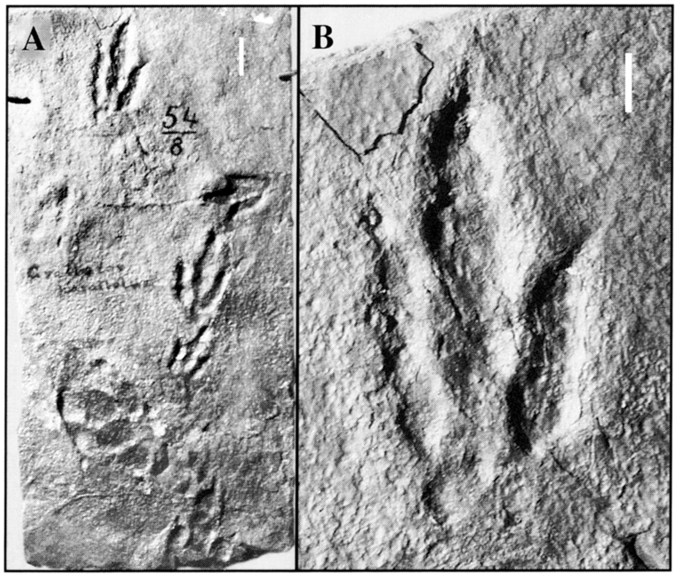

FIGURE 14. **A**, slab AC 54/6 containing the type of *Grallator parallelus* of Hitchcock (1865) (upper left), along with examples of other tracks assignable to (from top to bottom) *Anchisauripus hitchcocki, A. sillimani, A. hitchcocki,* and *A. tuberosus.* Scale bar is 5 cm. **B**, type of *Grallator parallelus* of Hitchcock (1865) (AC 54/6). Scale bar is 2 cm.

Despite many assignments of tracks to potential track makers by a variety of workers, the process is not at all simple. This can be shown by a quick survey of papers giving very different, reasoned conclusions for the same ichnotaxa (e.g., Lull, 1953; Baird, 1957; Olsen and Baird, 1986; Olsen and Padian, 1986; Weems, 1992, 1996; and Farlow and Lockley, 1993). Two fundamentally different approaches have been used. The first is general similarity and the second (much less often used) is cladistics. In the general similarity method, an osteological reconstruction of a track is made and then compared to the pedal structure of known skeletal forms. If a close match is found, the trackmaker is assumed to be identified (at some taxonomic level). The cladistic approach holds that only characteristics of the manus or pes that are shared derived characters for a specific osteological taxon are useful for assigning a track to a potential track maker (Olsen, 1995b; Farlow and Chapman, 1997). Because tetrapod manus and pes specializations are often shared derived characters of biological monophyletic groups, we should potentially be able to recognize at least some of these characters in footprints.

Overall, there is a general similarity between the reconstructed osteology of *Eubrontes, Anchisauripus,* and *Grallator* and known theropod footprints. However, there is also an overall similarity with some prosauropod feet and all of the known early Mesozoic bipedal ornithischian feet. A more specific similarity method is that of Farlow and Lockley (1993). Based on the ratios of digital length described above (Figs. 3, 16B) they concluded that there were osteological differences among the feet of theropods, bipedal ornithischians, and prosauropods that could potentially allow their tracks to be distinguished from one another. We have added three more prosauropod taxa to Farlow and Lockley's data (Table 3, Fig. 16) and have plotted all of the tracks discussed in this paper along with the type specimens of *Anomoepus scambus* (AC 37/9) (the type ichnospecies of *Anomoepus*) and *Otozoum moodii* (AC 4/1a). There is some overlap between the fields for all of these major dinosaurian groups. However, these overlap areas are easily separated by the absolute size of the footprints. Only the part of the theropod field with the largest individuals overlaps the prosauropod field, and the overlapping part of the prosauropod field contains data from feet much smaller than those of the similarly proportioned theropods. Similarly, the bipedal ornithischian *Heterodontosau-*

rus has phalangeal length ratios similar to that of the much larger prosauropods. As is true for the theropod field, the smaller prosauropods tend to be in the upper right, while the largest tend to be in the lower left. The bipedal ornithischian osteological taxa do not seem to show such a size trend, however.

All of the tracks described in this paper fall in or close to the theropod field. The holotype of *Eubrontes giganteus* (AC 15/3) falls very close to the theropod *Liliensternus,* but also falls within the prosauropod field in the region of the smaller skeletons. AC 15/3 is, however, larger than the prosauropods included in the area it overlaps. The smallest of the tracks described here, the type of *Grallator,* falls along the projection of the theropod field. The type of *Anomoepus* falls very close to the bipedal ornithischian field, and the type of *Otozoum* falls in the middle of the prosauropod field, which agrees with newer assessments (Farlow, 1992; Lockley and Hunt, 1995; Bakker, 1996). However, we do not know what other reptiles might share these proportions as well, especially within the more primitive Archosauromorpha.

The projection ratios (Fig. 3) of the skeletal remains and the footprints provide additional discrimination ability (Tables 2, 3; Fig. 16A). This ratio is determined in a manner analogous to footprints using the interdigital angle correction from published drawings of skeletons (Fig. 3). Virtually all theropod skeletal remains lie in an elongate field overlapping that of the holotypes of *Eubrontes giganteus, Anchisauripus sillimani,* and *Grallator parallelus,* as well as a large number of related tracks

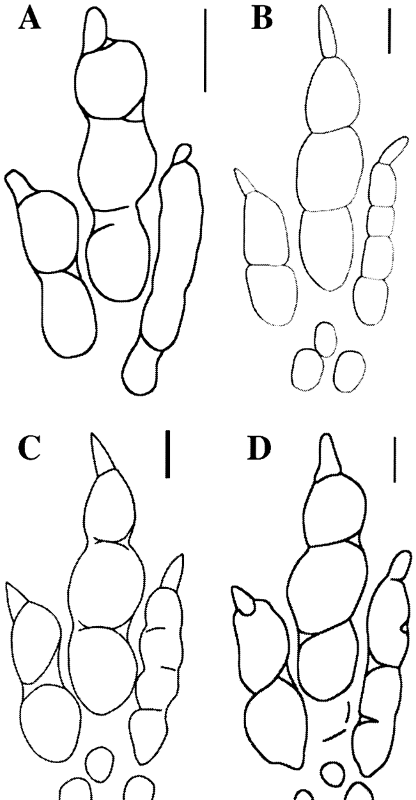

FIGURE 15. **A**, composite drawing of second individual in the type series of *Grallator parallelus* of Hitchcock (1847) (AC 23/2); **B**, *Grallator parallelus* (AC 54/6) of Hitchcock (1858; pl. V, fig. 1: reversed); **C**, *Anchisauripus parallelus* of Lull (1904, 1915, 1953) (fig. 42 of Lull, 1953: reversed); **D**, line drawing (reversed) of (AC 54/6). Scale bar is 2 cm.

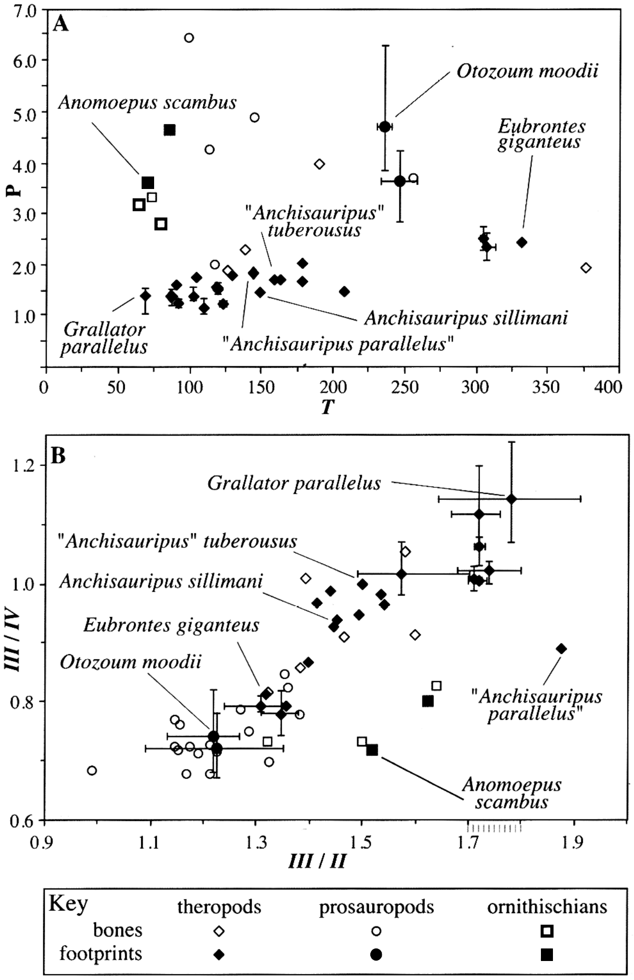

FIGURE 16. Graph comparing the proportions of footprints discussed in text with skeletal material. See Tables 2 and 3 for data. Only the holotypes are labeled. Together, these two graphs successfully separate. *Otozoum* and *Anomoepus* from tracks (*Eubrontes, Anchisauripus, Grallator*) that seem to show continuous variation and change in shape with size. Bars show the range of the dimensions or ratios of successive tracks from trackways. **A**, corrected projection ratio graphed against total length (as defined in Fig. 3). Note that the types of *Grallator parallelus, Anchisauripus sillimani,* and *Eubrontes giganteus* lie in an elongate, linear field with the majority of the theropod feet as well as a large number of other tracks usually placed in those ichnogenera. The type of *Anomoepus scambus* lies close to a referred specimen of *Anomoepus* (on AC 23/2) and close to the Early Jurassic ornithischians. Likewise the type of *Otozoum moodi* (AC 4/1a) lies close to a referred specimen from the same locality (AC 4/1b) and both are within the field of prosauropod feet. **B**, graph of the relative lengths of the digits as defined by Farlow and Lockley (1993) (see Fig. 3). Note that the theropod and prosauropod feet lie overlapping elongate, fields as do nearly all of the *Eubrontes, Anchisauripus,* and *Grallator* footprints. Small tracks and skeletons tend to be on the right, while large tracks and skeletons tend to be on the left of this field. The exception is AC 54/6 the type of "*Anchisauripus parallelus*" of Hitchcock (1865) that we believe to be a distorted track. The holotype of *Anomoepus scambus* and a referred specimen of *Anomoepus* (on AC 23/2) lie off the prosauropod and theropod fields, quite close to two ornithischian skeletons (*Lesthotosaurus* and *Scutellosaurus*).

(see Table 2). The exception is *Liliensternus,* which falls in the prosauropod field. Prosauropod and ornithischian skeletal remains are also well separated from each other and the theropods, with the exception of *Sellosaurus,* which falls within the theropod field. The holotype of *Anomoepus scambus* clearly falls in the ornithischian field close to another referred *Anomoepus* specimen. Similarly, *Otozoum* is within the prosauropod field.

Using the cladistic method, we ask, "are there characters of the type material of *Eubrontes, Anchisauripus,* and *Grallator* that are shared derived characters of the Theropoda"? Gauthier (1986; character 32) lists a reduction in the length of pedal digit IV to approximately the same length as II making the foot symmetrical about digit II as a shared derived character of the Theropoda, within the Saurischia. This character is certainly shared with *Eubrontes, Anchisauripus,* and *Grallator.* However, bipedal ornithischians also have this character, although to a lesser extent, which within Gauthier's scheme, must have been acquired convergently. Thus, for this character to have meaning for *Eubrontes, Anchisauripus,* and *Grallator* these ichnotaxa must have one or more shared derived characters of the Saurischia. Unfortunately, there are no known pedal shared derived characters for saurischians. The manus of theropods is uniquely specialized in a number of respects (Gauthier, 1986; Sereno, 1993), and its overall structure suggests that it was used for grasping rather than locomotion on the ground. The virtual absence of convincing manus impressions associated with the thousands of tracks assigned to *Eubrontes, Anchisauripus,* and *Grallator* argues that the manus was not adapted for ground locomotion or even for resting on the ground (but see Weems, 1992 and Gierlinski, 1994). This is only weak evidence for the manual shared derived characters of the Theropoda in *Eubrontes, Anchisauripus,* and *Grallator.* A useful hypothesis worthy of testing against skeletal remains is that the proportional characters isolating the theropods, as proposed by Farlow and Lockley (1993), may in fact be shared derived characters of the Theropoda (excluding herrerasaurs), if allometry is taken into account (e.g., Fig. 16A). At the present time, we conclude that *Eubrontes, Anchisauripus,* and *Grallator* appear to be theropod footprints but further, more rigorous testing of this hypothesis is required.

CONCLUSIONS

The identification of the true type material of the type ichnospecies of *Eubrontes, Anchisauripus,* and *Grallator* provides a necessary basis for further work. The type specimens of the three ichnotaxa are proportionally distinct from one another using a variety of measurements. However, the types of *Eubrontes* and *Anchisauripus* are isolated tracks, precluding an analysis of variation within trackways, and a lack of population studies hinders assessment of what these proportional differences mean for the separation of the three ichnogenera. A case can be made that they could all be placed within one ichnogenus that allometrically varies in proportion, conforming to Hitchcock's original concept of *Eubrontes.* In addition, there are some morphological grounds for regarding *Eubrontes, Anchisauripus,* and *Grallator* as theropod as usually assumed, although further work on both footprints and osteological material is clearly warranted.

About one million years is covered by the interval that produced the type material of *Eubrontes, Anchisauripus,* and *Grallator* (Fig. 2). Forms nominally assigned to these ichnogenera have been found in strata about a million years younger in the Hartford basin, and the latter two genera occur in strata 23 million years older in the Newark basin (Fig. 2). Through the last eight million years of this record, these tracks are by far the most common dinosaur tracks found, and over this interval they record the rise to ascendancy of theropods as the top terrestrial predators of the Mesozoic. Establishment of the identity of the type specimens of the type ichnospecies of the classic ichnogenera *Eubrontes, Anchisauripus,* and *Grallator* establishes a firm basis for documenting the changes in dinosaurian diversity during this transition.

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