

The Early Jurassic Ornithischian Dinosaurian Ichnogenus *Anomoepus*

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A*nomoepus* is an Early Jurassic footprint genus produced by a relatively small, gracile ornithischian dinosaur. It has a pentadactyl manus and a tetradactyl pes, but only three pedal digits normally impressed while the animal was walking. The ichnogenus is diagnosed by having the metatarsal-phalangeal pad of digit IV of the pes lying nearly in line with the axis of pedal digit III in walking traces, in combination with a pentadactyl manus. It has a proportionally shorter digit III than grallatorid (theropod) tracks, but based on osteometric analysis, *Anomoepus*, like grallatorids, shows a relatively shorter digit III in larger specimens. *Anomoepus* is characteristically bipedal, but there are quadrupedal trackways and less common sitting traces. The ichnogenus is known from eastern and western North America, Europe, and southern Africa. On the basis of a detailed review of classic and new material, we recognize only the type ichnospecies *Anomoepus scambus* within eastern North America. *Anomoepus* is known from many hundreds of specimens, some with remarkable preservation, showing many hitherto unrecognized details of squamation and behavior.



In 1836, Edward Hitchcock described the first of what we now recognize as dinosaur tracks from Early Jurassic Newark Supergroup rift strata of the Connecticut Valley (Hartford and Deerfield basins) (figures 19.1

and 19.2). Because skeletons of dinosaur feet were not known at the time, he naturally attributed the footprints to birds. By 1848, however, he recognized that some of the birdlike tracks were associated with impressions of five-fingered manus, and he gave the name *Anomoepus*, meaning “unlike foot,” to these birdlike

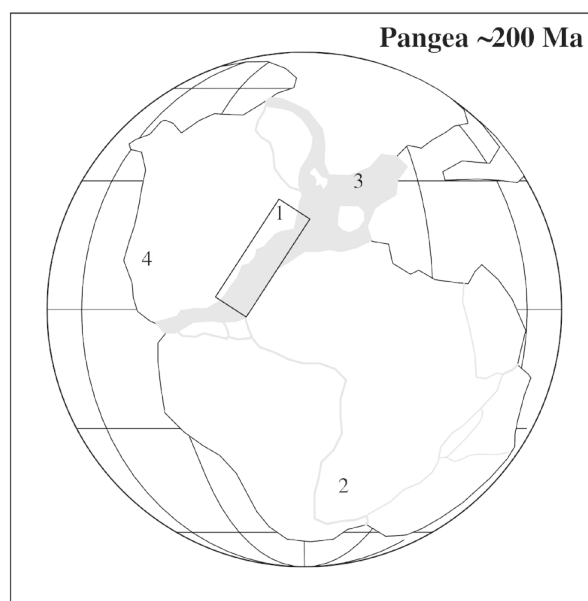


FIGURE 19.1 Pangea at approximately 200 Ma, showing the areas producing *Anomoepus* discussed in this chapter: 1, Newark Supergroup, eastern North America; 2, Karoo basin; 3, Poland; 4, Colorado Plateau. The boxed area is shown in detail in figure 19.2A. (Modified from Kent et al. 1995)

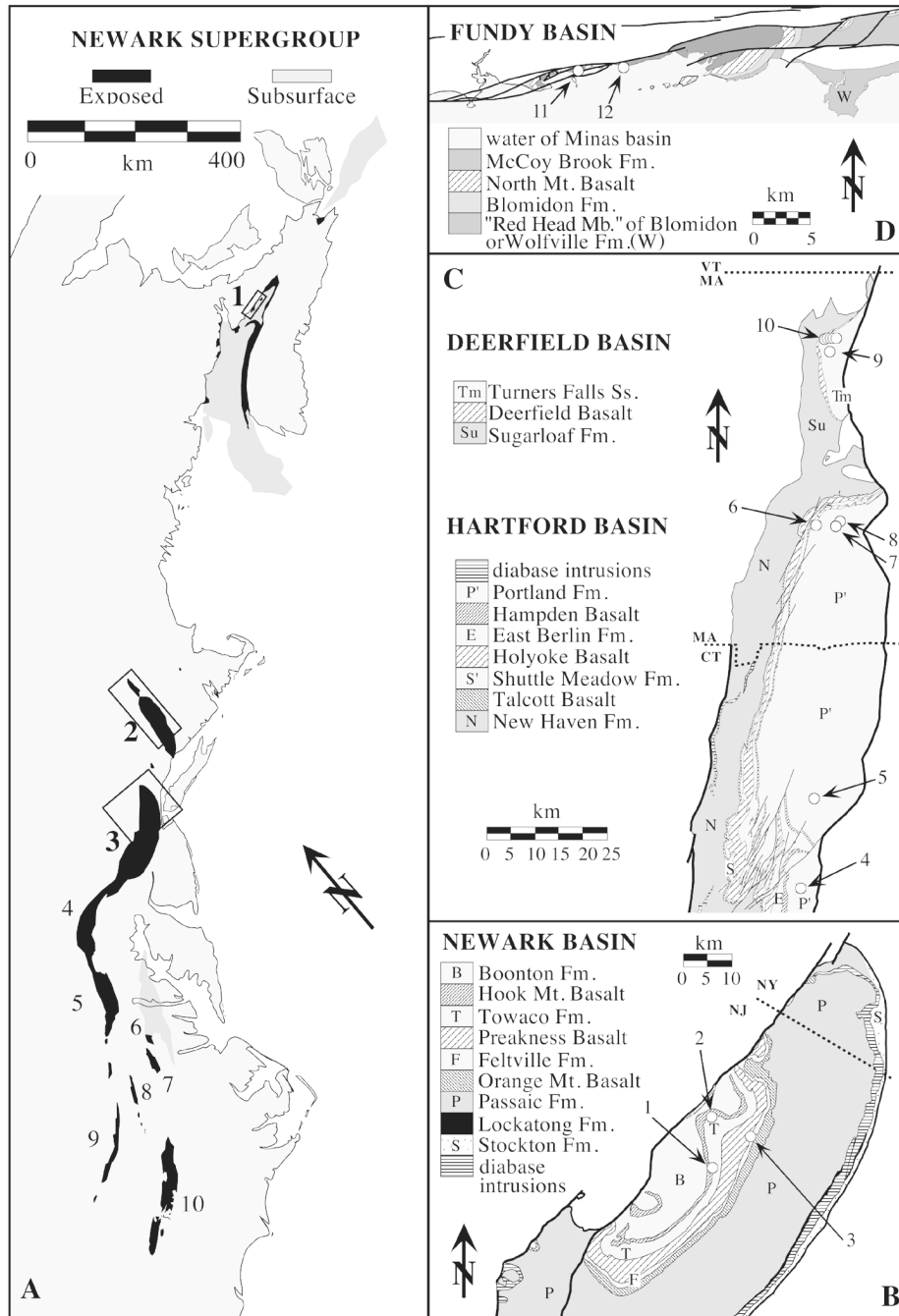


FIGURE 19.2 Newark Supergroup and localities for *Anomoepus*. (A) Newark Supergroup, showing the locations of the maps shown in B, C, and D (rectangles); basins: 1, Fundy; 2, Hartford and Deerfield; 3, Newark; 4, Gettysburg; 5, Culpeper; 6, Taylorsville; 7, Richmond; 8, Farmville and associated basins; 9, Dan River; 10, Deep River. (B) Northern Newark basin: 1, Roseland Quarry; 2, Vreeland Quarry; 3, Shrump Quarry. (C) Deerfield basin and the northern three-quarters of the Hartford basin: 4, Portland brownstone quarries; 5, Wethersfield Cove; 6, Dinosaur Footprint Reservation; 7, Dickinson Quarry; 8, Moody Homestead; 9, Montague City; 10, localities near the Connecticut River near Turners Falls (from west to east: near basalt in Turners Falls; "Turners Falls"; old ferry landing, Gill; Howland's Farm, Gill; Field's Orchard, Gill; Lily Pond Quarry, Gill). (D) North-central part of Minas subbasin, Fundy basin, Five Islands region: 11, McKay Head; 12, Blue Sac. Details of localities for specific specimens are in the caption for figure 19.3 and in table 19.1.

tracks with hands. Despite having been named more than 150 years ago and widely cited, the type material of the species included in the genus has never been attributed or described properly, nor has the wealth of remarkably detailed material been appreciated. Here we describe and figure the type material of all eastern North American species along with key additional materials from other localities, placing them all in stratigraphic and temporal context (figure 19.3). We also compare the eastern North American forms with material from varied locales showing the global distribution of the ichnotaxon. The large amount of well-

preserved material allows the trackmaker to be recognized as an early ornithischian and reveals details of locomotory and other aspects of behavior that have not been demonstrated by the analysis of ornithischian skeletal material alone.

MATERIAL AND METHODS

Virtually all classic Newark Supergroup taxa have a very confused history, resulting in a nomenclatural quagmire that has remained to the present day (Olsen, Smith, and McDonald 1998). Indeed, characteristic of

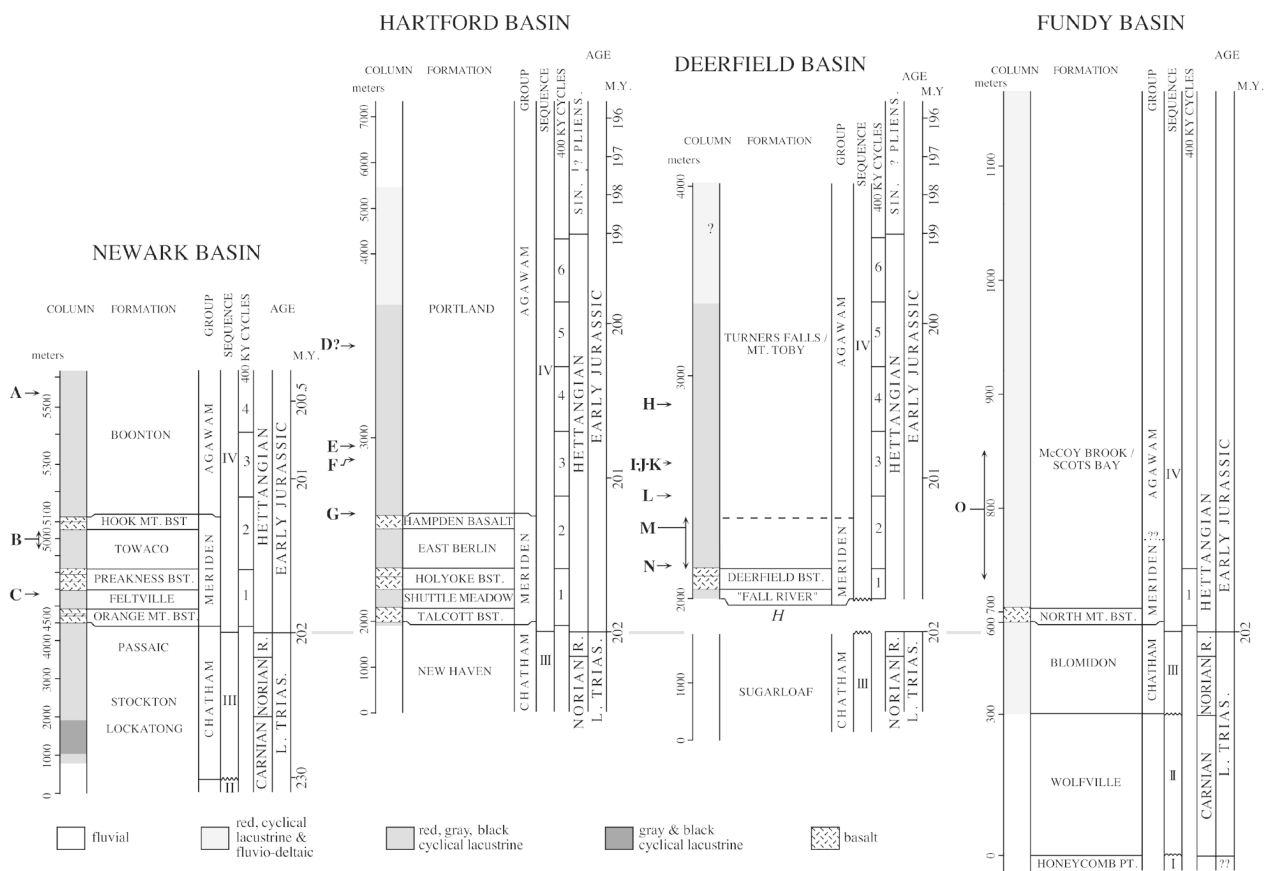


FIGURE 19.3 Stratigraphic sections of the Deerfield, Hartford, Newark, and Fundy basins, expressed on a common age scale for the Jurassic age strata, showing the position of the localities discussed in the text; A, Rockaway River, Boonton, New Jersey; B, Roseland Quarry, Roseland, New Jersey, and Vreeland Quarry, Towaco, New Jersey; C, Shrumpp Quarry, Pleasantdale (Roseland), New Jersey; D, Wethersfield Cove, Wethersfield, Massachusetts; E, Portland brownstone quarries, Portland, Connecticut; F, Moody Homestead and Dickinson Quarry, South Hadley, Massachusetts; G, Dinosaur Footprint Reservation, Holyoke, Massachusetts; H, Lily Pond Quarry, Gill, Massachusetts; I-J-K, Field’s Orchard and Howland’s Farm, Gill, Massachusetts, and Montague City on the old Boston Road; L, old ferry landing, Gill, Massachusetts; M, general “Turners Falls” localities; N, Turners Falls, near basalt, Turners Falls, Massachusetts; O, McKay Head and Blue Sac, Cumberland County, Nova Scotia. Note the difference in thickness scale between the basin sections and the change in timescales within the basin sections. The wavy line indicates unconformity, and the gap at H indicates possible duration of hiatus. (Stratigraphy based on Olsen 1997)

the classic Connecticut Valley taxa is massive confusion of homonyms and of objective and subjective synonyms that previously rendered the taxonomy indecipherable. *Anomoepus* is no exception. There fortunately is enough information in the early published literature and on specimen labels (including those carved into the specimen) to permit a massive streamlining of nomenclature.

The principal basis for this chapter is the Hitchcock Ichnological Collection at the Pratt Museum of Amherst College (AC; Amherst, Massachusetts), consisting of natural molds and casts of footprints, mostly from the Deerfield and Hartford basins of the Newark Supergroup. One Hartford basin track described here is in the collection of the Montshire Museum of Science (MM; Norwich, Vermont), consisting of the remnants of the collection of the Museum of Dartmouth College (Hanover, New Hampshire). Additional tracks are described from other parts of the Newark Supergroup, including the Newark and Fundy basins, and these specimens reside in the collections of the Yale Peabody Museum (YPM; New Haven, Connecticut), the American Museum of Natural History (AMNH; New York City), Dinosaur State Park (DP; Rocky Hill, Connecticut), Rutgers University (RU; New Brunswick, New Jersey), the New Jersey State Museum (NJSM; Trenton, New Jersey), the Fundy Geological Museum (FGM; Parrsboro, Nova Scotia), and the private collection of Eldon George (EG; Parrsboro, Nova Scotia). Specimens in the Museum of Mount Holyoke College (MHM; South Hadley, Massachusetts) were destroyed by fire in the early twentieth century.

Analog and digital photographic and drawing methods are the same as those described in Olsen, Smith, and McDonald (1998). Composite drawings are shown as impressions of the right pes (figures 19.4 and 19.5), prepared by digitally superimposing drawings of successive tracks (with the opposite tracks reversed). The elements of the tracks thought to be least affected by the processes of impression and preservation are emphasized. Conventions for quantitative measurements are shown in figure 19.4, as described by Olsen, Smith, and McDonald (1998). We follow the rules and guidelines of the fourth edition of the *International Code of Zoological Nomenclature* (ICZN; International Commission on Zoological Nomenclature 1999) as applied to ichnotaxa. Only citations in the synonymies referring specifically to the types are listed.

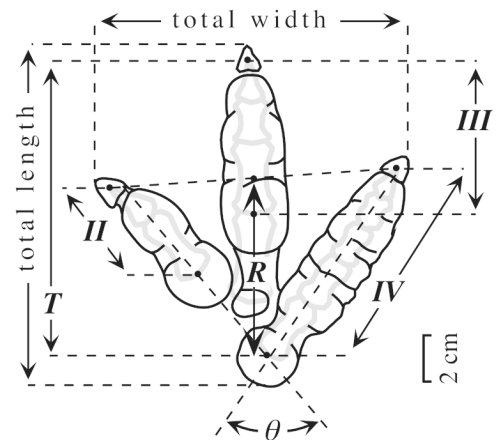


FIGURE 19.4 Definitions of measurements used in the text and in figure 19.19, based on the composite *Anomoepus scambus* in figure 19.5 and the reconstructed skeleton in figure 19.33.

Specimens in the Hitchcock Ichnological Collection presently are numbered according to the catalog of Edward Hitchcock's son Charles H. Hitchcock (1865). However, as described by Olsen, Smith, and McDonald (1998), the specimen numbers were not consistent across E. Hitchcock's publications. Numbers used prior to 1858 are Arabic numerals usually preceded by a "No." carved into the rock (prefixed herein by "old no."). Where the number used by E. Hitchcock (1858) differs from that used by C. H. Hitchcock (1865), the former is distinguished herein by "1858" after the specimen number. In the numbering systems of both 1858 and 1865, the specimen numbers were based on their location within the displays and consist of a fraction with the numerator corresponding to a wall, table, or case and with the denominator indicating the specimen number in that specific area. These different numbering schemes are important because they are the only unambiguous tool allowing individual specimens to be traced through the Hitchcocks' tortuous nomenclatural maze in the absence of explicit drawings or descriptions.

Osteometric Methods

Baird (1957) argued that the characters of tracks most useful for classification are those that reflect the osteology of the trackmaker, and this approach has proved very fruitful. The most important track landmarks localizing osteological features are the pads of the digits, which generally underlie the joints in large reptiles and birds, and thus serve as osteological landmarks

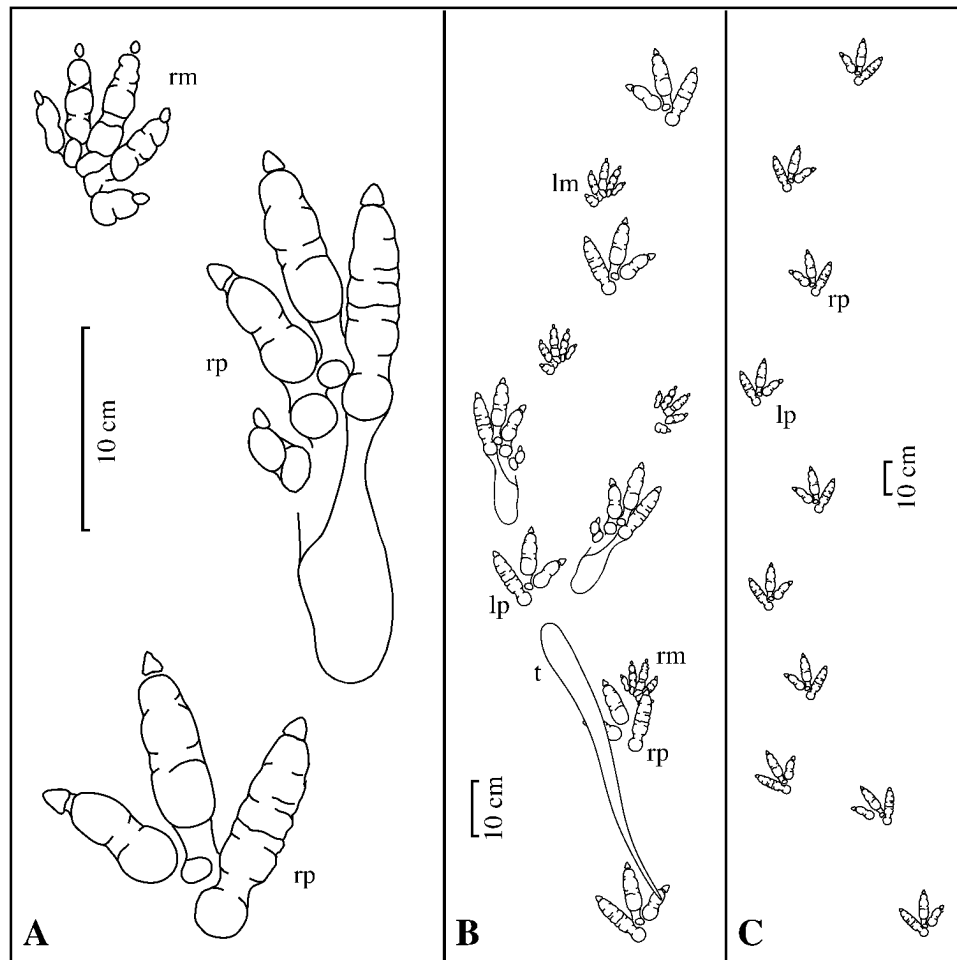


FIGURE 19.5 *Anomoepus scambus*. (A) Composite of walking and sitting manus and pes, based on all available material scaled largely to the Rutgers main slab shown in figure 19.29. (B) Composite trackway with sitting trace, based mostly on main Rutgers slab and on AC 16/5. (C) Composite trackway, normal bipedal locomotion, based mostly on AC 48/1; *lm*, left manus; *lp*, left pes; *rm*, right manus; *rp*, right pes; *t*, tail impression (not a drag trace; see figures 19.11 and 19.25).

(Peabody 1948; Baird 1954, 1957; Padian and Olsen 1984; Olsen and Baird 1986; Olsen and Padian 1986; Farlow and Chapman 1997). It follows that the most useful measurements for comparisons among tracks and between tracks and osteological material are those taken from the center of the pad impressions and from the center of the claws (figure 19.4). Tracks in which the pads are not preserved are therefore of minimal value (Smith and Farlow, chapter 17 in this volume). As far as is known, the lengths of the phalanges of early dinosaur manus and pedes decrease distally, which provides an additional constraint on reconstructions. Measurements on the tracks that are thought to reflect the osteology of the trackmaker can then be used to

assess qualitatively the similarity among tracks and between track and biological taxa using the osteometric methods outlined by Farlow and Lockley (1993), Olsen, Smith, and McDonald (1998), and Smith and Farlow (chapter 17 in this volume).

Our experience suggests that one of the least useful track measurements is digital divarication (*contra* Demathieu 1970, 1990). The apparently greater digital divarication of *Anomoepus* unfortunately has been used routinely to distinguish it from gallatorids (Lull 1904, 1915, 1953). Digital divarication is not only a function of anatomy but also an important function of the foot interacting with the substrate. In individual trackways with deep impressions, variation can span

the full range of all the Connecticut Valley dinosaurian genera. Without other more detailed data, such as specific pad position and manus impressions, identification of *Anomoepus* is unreliable.

A simple adjustment, the cosine correction (Olsen, Smith, and McDonald 1998), removes nearly all the effects of variation in pedal digit divarication angle on measurements of lateral digit length between tracks within the same trackway, within different trackways, and in drawings of osteological material. The cosine correction consists of the following approximation of the average length of digits II and IV as they would project parallel to digit III, termed here R' :

$$R' = R * (1/\cos(\tau/2))$$

where R is the length of the rear of the phalangeal part of the foot as defined in figure 19.4, and τ is the divarication angle between digits II and IV. This approximation is used because with rare but informative exceptions the metatarsal-phalangeal pad of digit II is almost never impressed, precluding the explicit measurement of the length of the first phalanx of digit II.

GEOLOGICAL PROVENANCE

The North American tracks described herein come from the eastern North American Newark Supergroup, consisting of the exposed erosional remnants of rift basin strata formed during the initial stages of the breakup of Pangea (Olsen 1997) (figure 19.1). Much of the supergroup is distinctive in that it consists of cyclical lacustrine sequences, the shallower-water facies of which are often spectacularly rich in reptile footprints. This is particularly true of the Jurassic age strata, belonging to Tectonostratigraphic Sequence IV of Olsen (1997) and comprising the Meriden and Agawam groups of Weems and Olsen (1997) (figure 19.3). In the former group, the largely lacustrine strata are interbedded with extensive basalt flows.

The classic material of *Anomoepus* and synonymous forms of the Hitchcock Ichnological Collection come entirely from the Connecticut Valley, specifically from the Turners Falls Formation of the Deerfield basin and the lower Portland Formation of the Hartford basin (figures 19.2 and 19.3). Additional Hartford basin material is from a level higher in the Portland Formation (Portland brownstone quarries). Other *Anomoepus*-de-

scribed here come from the Newark basin in the Feltville, Towaco, and Boonton Formations and from the McCoy Brook Formation of the Fundy basin (figures 19.2 and 19.3). The geographic and stratigraphic positions of the localities discussed here are shown in figures 19.1, 19.2, and 19.3, and in table 19.1.

As is true with Newark Supergroup tracks in general, most *Anomoepus* tracks are found in tabular beds of oscillatory to unidirectionally rippled siltstone within the transgressive or regressive portions of lacustrine cycles (Olsen 1980, 1988) in shoreline or mudflat facies. However, the Moody Homestead (Hartford basin), Portland brownstone quarries (Hartford basin), and McCoy Brook Formation (Fundy basin) localities are in units with a strong fluvial influence within largely lacustrine sequences.

SYSTEMATIC PALEONTOLOGY

Ichnogenus *ANOMOEPUS* E. Hitchcock 1848

Anomoepus E. Hitchcock 1848:220

?*Harpagopus* E. Hitchcock 1848:247, in part

Apatichnus E. Hitchcock 1858:99, in part

Plesiornis E. Hitchcock 1858:102, in part

?*Antipus* E. Hitchcock 1858:115, in part

Moyenisauropus Ellenberger 1974:25

The details of the synonymy for the Connecticut Valley material are given in appendix I.

Type species: *Anomoepus scambus* E. Hitchcock 1848.

Etymology: *Anomo-*, “unlike, different,” *-pus*, “foot.”

Emended diagnosis: Small (pes < 20 cm long), mostly bipedal and tetradactyl, but functionally tridactyl pedal ichnite characterized by sitting tracks with metatarsal and pentadactyl manus impressions. This pes is unique among early Mesozoic ichnites in having the metatarsal-phalangeal pad of digit IV almost directly or directly in line with the axis of digit III in walking tracks. Pedal digit I (hallux) is relatively long and often at least partially impressed, especially in sitting tracks. Digit III is longest in the manus, with the other digits decreasing in size symmetrically away from that digit, although in poor impressions the manual digits can appear subequal in length. Tail trace is usually present in sitting tracks. Fully bipedal as well as quadrupedal walking trackways occur. Differs from *Atreipus* (figure

TABLE 19.1 Specimens Described and Their Stratigraphic Position and Geographic Positions

Specimen No.	No. of 1858 or Figure No.	No. of 1848	Basin	Formation	Locality	Latitude and Longitude
AC 1 / 1	—	—	Deerfield	Turners Falls Fm.	Field's Orchard, Gill, Mass. ¹	42°36'33"; 72°32'08"
AC 1 / 3	—	—	Deerfield	Turners Falls Fm.	Lily Pond quarry, Gill, Mass. ²	42°36'10"; 72°32'01"
AC 1 / 7	—	—	Deerfield	Turners Falls Fm.	Lily Pond quarry, Gill, Mass. ²	42°36'10"; 72°32'01"
AC 5 / 8	—	—	Deerfield	Turners Falls Fm.	Lily Pond quarry, Gill, Mass. ²	42°36'10"; 72°32'01"
AC 6 / 1	—	—	Deerfield	Turners Falls Fm.	Lily Pond quarry, Gill, Mass. ²	42°36'10"; 72°32'01"
AC 9 / 11	—	—	Deerfield	Turners Falls Fm.	Lily Pond quarry, Gill, Mass. ²	42°36'10"; 72°32'01"
AC 11 / 2	—	—	Deerfield	Turners Falls Fm.	Old ferry landing in Gill, Mass. ³	42°36'29"; 72°32'58"
AC 12 / 3	—	—	Deerfield	Turners Falls Fm.	Near basalt, Turners Falls, Mass. ⁴	42°36'46"; 72°33'08"
AC 14 / 5	—	—	Deerfield	Turners Falls Fm.	"Turners Falls", Mass. ⁵	42°36'43"; 72°33'08"
AC 16 / 1	—	—	Deerfield	Turners Falls Fm.	Lily Pond quarry, Gill, Mass. ²	42°36'10"; 72°32'01"
AC 16 / 2	—	61 ⁶	Hartford	Portland Fm.	Moody homestead, South Hadley, Mass. ⁷	42°16'36"; 72°33'55"
AC 16 / 5	—	—	Deerfield	Turners Falls Fm.	"Turners Falls", Mass. ⁵	42°36'43"; 72°33'08"
AC 16 / 10	—	—	Deerfield	Turners Falls Fm.	"Turners Falls", Mass. ⁵	42°36'43"; 72°33'08"
AC 16 / 11	—	—	Deerfield	Turners Falls Fm.	"Turners Falls", Mass. ⁵	42°36'43"; 72°33'08"
AC 16 / 14	—	—	Deerfield	Turners Falls Fm.	"Turners Falls", Mass. ⁵	42°36'43"; 72°33'08"
AC 19 / 4	—	—	Deerfield	Turners Falls Fm.	Old ferry landing in Gill, Mass. ³	42°36'29"; 72°32'58"
AC 19 / 14	—	—	Deerfield	Turners Falls Fm.	"Turners Falls", Mass. ⁵	42°36'43"; 72°33'08"
AC 19 / 16	—	132	Deerfield	Turners Falls Fm.	Montague City, Montague, Mass. ⁸	42°35'17"; 72°34'31"
AC 19 / 18	—	60 ⁶	Deerfield	Turners Falls Fm.	"Turners Falls", Mass. ⁵	42°36'43"; 72°33'08"
AC 20 / 4	—	1	Hartford	Portland Fm.	Portland brownstone quarries, Portland, Mass. ⁹	41°34'36"; 72°38'37"
AC 20 / 6	—	—	Deerfield	Turners Falls Fm.	Lily Pond quarry, Gill, Mass. ²	42°36'10"; 72°32'01"
AC 23 / 2	—	137 ⁶	Deerfield	Turners Falls Fm.	"Turners Falls", Mass. ⁵	42°36'43"; 72°33'08"
AC 23 / 3	—	152	Deerfield	Turners Falls Fm.	"Turners Falls", Mass. ⁵	42°36'43"; 72°33'08"
AC 23 / 8	—	—	Deerfield	Turners Falls Fm.	Old ferry landing in Gill, Mass. ³	42°36'29"; 72°32'58"
AC 26 / 10	—	136 ⁶	Deerfield	Turners Falls Fm.	Field's Orchard, Gill, Mass. ¹	42°36'33"; 72°32'08"
AC 29 / 1	—	—	Deerfield	Turners Falls Fm.	Lily Pond quarry, Gill, Mass. ²	42°36'10"; 72°32'01"
AC 31 / 84	—	62 ⁶	Deerfield	Turners Falls Fm.	"Turners Falls", Mass. ⁵	42°36'43"; 72°33'08"
AC 31 / 86	—	159 ⁶	Hartford	Portland Fm.	Wethersfield Cove, Wethersfield, Conn. ¹⁰	41°43'22"; 72°39'16"
AC 32 / 1	—	—	Deerfield	Turners Falls Fm.	"Turners Falls", Mass. ⁵	42°36'43"; 72°33'08"
AC 32 / 57	—	—	Deerfield	Turners Falls Fm.	"Turners Falls", Mass. ⁵	42°36'43"; 72°33'08"
AC 33 / 35	—	—	Deerfield	Turners Falls Fm.	"Turners Falls", Mass. ⁵	42°36'43"; 72°33'08"
AC 33/50	—	—	Deerfield	Turners Falls Fm.	"Turners Falls", Mass. ⁵	42°36'43"; 72°33'08"

AC 34 / 19	—	—	Deerfield	Turners Falls Fm.	“Turners Falls”, Mass. ⁵	42°36'43"; 72°33'08"
AC 34 / 40	142	—	Deerfield	Turners Falls Fm.	“Turners Falls”, Mass. ⁵	42°36'43"; 72°33'08"
AC 37 / 9, 37 / 10	40 / 2	—	Deerfield	Turners Falls Fm.	“Turners Falls”, Mass. ⁵	42°36'43"; 72°33'08"
AC 37 / 18	129	—	Deerfield	Turners Falls Fm.	“Turners Falls”, Mass. ⁵	42°36'43"; 72°33'08"
AC 40 / 5	59	—	Hartford	Portland Fm.	Footprint Preserve, Holyoke, Mass. ¹¹	42°14'03"; 72°14'03"
AC 42 / 5	—	—	Deerfield	Turners Falls Fm.	Lily Pond quarry, Gill, Mass. ²	42°36'10"; 72°32'01"
AC 48 / 1	—	—	Deerfield	Turners Falls Fm.	Old ferry landing in Gill, Mass. ³	42°36'29"; 72°32'58"
AC 50 / 1, 3	—	—	Deerfield	Turners Falls Fm.	Howland's farm, Gill, Mass. ¹²	42°36'29"; 72°32'13"
AC 52 / 10	—	—	Deerfield	Turners Falls Fm.	Lily Pond quarry, Gill, Mass. ²	42°36'10"; 72°32'01"
AC 55 / 112	—	—	Deerfield	Turners Falls Fm.	Field's Orchard, Gill, Mass. ¹	42°36'33"; 72°32'08"
—	209 ^{6,13}	—	?	?	?	?
AMNH 7639	—	Fig. 27	Newark	Feltville Fm.	Shrump Quarry, Pleasantdale, N.J. ¹⁴	40°48'44"; 74°15'54"
DP 01.1	—	Fig. 18	Hartford	Portland Fm.	Portland brownstone quarries, Portland, Conn. ⁸	41°34'36"; 72°38'37"
EG	—	Fig. 17C	Fundy	McCoy Brook Fm.	McKay Head, Nova Scotia ¹⁵	45°23'44"; 64°12'39"
EG	—	Fig. 17D	Fundy	McCoy Brook Fm.	McKay Head, Nova Scotia ¹⁵	45°23'44"; 64°12'39"
EG	—	Fig. 17F	Fundy	McCoy Brook Fm.	McKay Head, Nova Scotia ¹⁵	45°23'44"; 64°12'39"
RU main slab	—	Fig. 29A, B	Newark	Towaco Fm.	Vreeland Quarry, Towaco, N.J. ¹⁶	40°55'02"; 74°19'51"
Fig. 15A ¹³	—	—	Newark	Towaco Fm.	Roseland Quarry, Roseland, N.J. ¹⁷	40°48'23"; 74°19'35"
Fig. 15B ¹³	—	—	Newark	Towaco Fm.	Roseland Quarry, Roseland, N.J. ¹⁷	40°48'23"; 74°19'35"
Fig. 15C ¹³	—	—	Newark	Towaco Fm.	Roseland Quarry, Roseland, N.J. ¹⁷	40°48'23"; 74°19'35"
Fig. 15D ¹³	—	—	Newark	Towaco Fm.	Roseland Quarry, Roseland, N.J. ¹⁷	40°48'23"; 74°19'35"
Fig. 15E ¹³	—	—	Newark	Towaco Fm.	Roseland Quarry, Roseland, N.J. ¹⁷	40°48'23"; 74°19'35"
Fig. 15F ¹³	—	—	Newark	Towaco Fm.	Roseland Quarry, Roseland, N.J. ¹⁷	40°48'23"; 74°19'35"
Fig. 15G ¹³	—	—	Newark	Towaco Fm.	Roseland Quarry, Roseland, N.J. ¹⁷	40°48'23"; 74°19'35"
Fig. 15H ¹³	—	—	Newark	Towaco Fm.	Roseland Quarry, Roseland, N.J. ¹⁷	40°48'23"; 74°19'35"
Fig. 30 ¹³	—	—	Newark	Boonton Fm.	Rockaway River, Boonton, N.J. ¹⁸	40°53'40"; 74°23'51"
Fig. 31B ¹³	—	—	Newark	Towaco Fm.	Roseland Quarry, Roseland, N.J. ¹⁷	40°48'23"; 74°19'35"
Fig. 31C ¹³	—	—	Newark	Towaco Fm.	Roseland Quarry, Roseland, N.J. ¹⁷	40°48'23"; 74°19'35"
Fig. 33	—	—	Karoo	upper Elliot Fm.	See Ellenberger, 1974	—
MHM 105-MM 5125	—	—	Hartford	Portland Fm.	Dickinson Quarry, South Hadley, Mass. ¹⁹	42°16'25"; 72°34'00"
NJSM 20321	—	Fig. 14	Newark	Towaco Fm.	Roseland Quarry, Roseland, N.J. ¹⁷	40°48'23"; 74°19'35"
NJSM 19325	—	Fig. 31D	Newark	Towaco Fm.	Roseland Quarry, Roseland, N.J. ¹⁷	40°48'23"; 74°19'35"
RU main slab	—	Fig. 29C	Newark	Towaco Fm.	Vreeland Quarry, Towaco, N.J. ¹⁶	40°55'02"; 74°19'51"
YPM 8665	—	Fig. 17A	Fundy	McCoy Brook Fm.	Blue Sac, Nova Scotia ²⁰	45°23'44"; 64°12'39"
Fig. 17B	—	uncollected	Fundy	McCoy Brook Fm.	McKay Head, Nova Scotia ¹⁵	45°23'44"; 64°12'39"

(continued)

Notes to Table 19.1:

- ¹Field's Orchard, Gill, Mass.. The Orchard of Roswell Field was adjacent to his former home, marked on the map of Beers et al. (1871) and relocated by the authors. Lull (1904, 1915, 1953) places it in the wrong locality.
- ²Lily Pond quarry, Gill, Mass.. We place this locality at the Lily Pond, in the Barton Cove Reservation. It is possible, however, that the locality is instead that indicated by "footprint quarry" on Beers's (1871) map near the Lily Pond; however, the topography is very inaccurate in this part of Beers's map.
- ³Old ferry landing in Gill, Mass. Relocated by the authors as the submerged ledges just to the east of the north pier for the old "Red Bridge," Riverside, Gill, Mass. Position of ferry landing itself shown on map of Beers (1871).
- ⁴Near basalt, Turners Falls, Mass. Probably outcrops of contact on west side of Fall River, just south of its confluence with the Connecticut River, but could be on the west side of Fall River at the confluence of the two rivers.
- ⁵"Turners Falls," Mass. A loose and nonspecific locality name, could apply to anywhere reasonably close to the falls itself, in Gill or Turners Falls proper.
- ⁶Part of type series of *Aethyopus minor* of Hitchcock 1848, listed as coming from Turners Falls and South Hadley, which would be in the Deerfield or Hartford basins, respectively.
- ⁷Moody homestead, South Hadley, Mass. Lull (1904, 1915, 1953) places this locality at Moody Corner as does C. H. Hitchcock (1865). It is very likely that placement is erroneous because the Moody locality is always cited by E. Hitchcock as in South Hadley, but the village of "Moody Corner" proper is in Granby. In addition, information from the Moody family places the location as follows: "Serj. Ebenezer Moody, settled at time of marriage in South Hadley, Mass. He received by Will part of the homestead and estate of his uncle Dea. Daniel Moody, the same being confirmed to him after decease of the latter (Prob. rec. Hamp. Co., Mass.). The house he built and occupied till his decease is on a rise of ground about forty rods south-west of the bridge in 'Moody Corner' [the bridge is in South Hadley, southwest of the village of Moody Corner, Granby, proper]. It is on the west side of the road and directly opposite the curve which the same now forms, the road there formally having passed in a south-west direction to the meeting house in South Hadley" (Moody 1856). The road mentioned is an old and now bypassed, part of Amherst Road. Finally, there are no outcrops in the vicinity of Moody Corner (Balk 1957).
- ⁸Montague City, Montague, Mass. This locality is given as "City," in Montague, a few rods east of the canal, on the old Boston road" by Hitchcock (1858). It would seem to be a ridge of sandstone on the west side of Solar Road, in Montague City, Montague, Mass.
- ⁹Portland brownstone quarries, Portland, Mass. Another loose designation applying to any of the quarries on the east bank of the Connecticut River opposite Portland, Conn.
- ¹⁰Wethersfield Cove, Wethersfield, Conn. Locality identified by P. M. LeTourneau and N. G. McDonald (personal communication, n.d.) on the west bank of the Connecticut River at Wethersfield Cove.
- ¹¹Footprint Preserve, Holyoke, Mass. Dinosaur Footprint Preserve, on the west bank of the Connecticut River in Holyoke, Mass. This part of Holyoke originally was in Northampton, and the locality is referred to by the latter name in Hitchcock's publications.
- ¹²Howland's farm, Gill, Mass. Relocated by the authors as on the ridge extending southwest from residence of H. H. Howland, as indicated on Beers's (1871) map.
- ¹³Presumed lost.
- ¹⁴Shrump Quarry, Pleasantdale, N.J. North side of Eagle Rock Avenue, Pleasantdale, N.J.
- ¹⁵McKay Head, Nova Scotia. Beach ridges approximately 300 m west of mouth of McCoy Brook on the west side of McKay Head, Cumberland County, Nova Scotia.
- ¹⁶Veelands Quarry, Towaco, N.J. Old quarry on west side of Valley Road, Towaco, N.J.
- ¹⁷Roseland Quarry, Roseland, N.J. Northwest corner of Riker Hill, Roseland, N.J.
- ¹⁸Rockaway River, Boonton, N.J. The only known suitable outcrops of the Boonton Formation are along the Rockaway River, Boonton, N.J. Much of the outcrop was covered by the construction of the dam for the Boonton Reservoir.
- ¹⁹Dickinson Quarry, South Hadley, Mass. According to Estell and Leslie Dickinson, the "Dickinson quarry" was most likely the small quarry worked by the Dickinsons that is at the crest of the hill crossed by The Knolls Road, South Hadley, Mass. However, another possibility is the quarry indicated on Balk's (1957) map, near the end of Woodridge Road in South Hadley, because that is closer in position to that shown by Lull (1904) for this locality.
- ²⁰Blue Sac, Nova Scotia. Beach ridges near Moose River at the western sections at Blue Sac, Cumberland County, Nova Scotia.

19.6) in the position of the metatarsal-phalangeal pad on digit IV, usually lacking an impression of the metatarsal-phalangeal pad of digit II (except in sitting position), having a consistently wider divarication between digits II and IV, and having a relatively larger manus in which digits I and V often impress.

Distribution: Early Jurassic: Newark Supergroup, eastern North America; Glen Canyon Group, southwestern United States (Olsen and Galton 1977; Lockley and Hunt 1995); Holy Cross Mountains, Poland

(Gierlinski 1991); upper Elliot Formation, Karoo basin, southern Africa (Ellenberger 1974).

Discussion

Lull diagnosed the genus *Anomoepus* as “bipedal in gait, the manus impressing only when seated. Pes tetradactyl, but functionally tridactyl, digitigrade with an elongated metatarsal segment in evidence when the animal rests. Hallux half rotated, claw occasionally impressing. Limbs moderately long. Tail trace when slowing, but never when moving at a normal gait” (1953:193). As Ellenberger (1974) points out, this diagnosis corresponds to at least four other Connecticut Valley genera as defined by Lull (1904, 1915, 1953). In addition, parts of Lull’s diagnosis correspond to characters of the supposed trackmaker that are difficult to interpret, such as the articulation of the hallux and the length of the legs, and several other characters are simply wrong. The diagnosis given here is a new one, based on the discussion of the species.

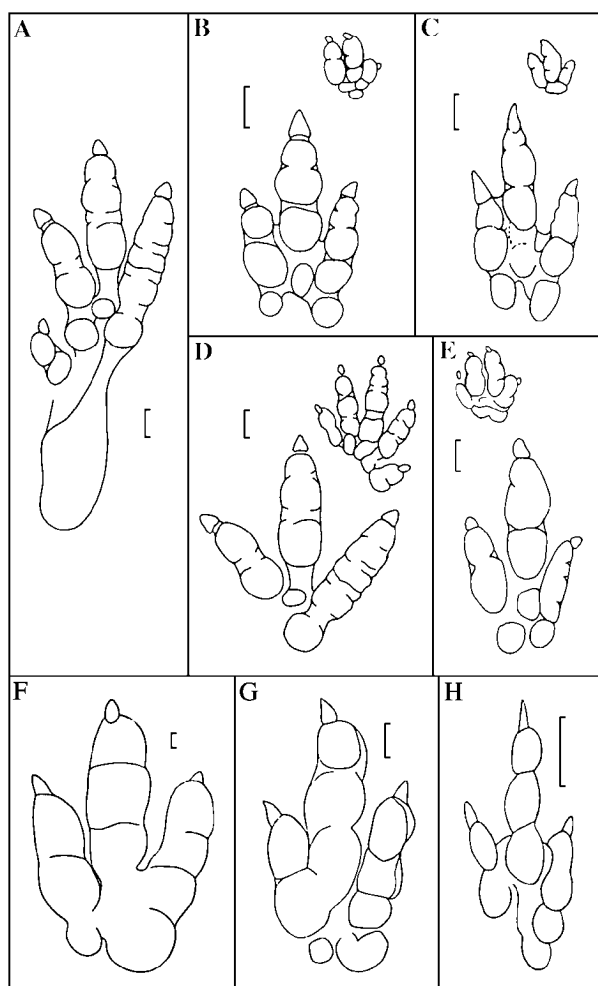


FIGURE 19.6 Comparison of composites of *Anomoepus*, *Atreipus*, and grallatorid ichnogenes. (A) *Anomoepus scambus*, sitting pes (from figure 19.5A). (B) *Atreipus milfordensis*. (C) *Atreipus sulcatus*. (D) *Anomoepus cambus*, walking manus–pes set (based on figure 19.5A and B). (E) *Atreipus acadianus*. (F) *Eubrontes giganteus* (AC 45/1). (G) *Anchisauripus tuberosus* (AC 31/73). (H) *Grallator parallelus* (AC 4/1a). Scale bars are 2 cm. (B, C, and E from Olsen and Baird 1986; F, G, and H from Lull 1953).

- ANOMOEPUS SCAMBUS* E. Hitchcock 1848
Ornithoidichnites cuneatus E. Hitchcock 1841:488, pl. 48 (fig. 55)
Ornithoidichnites fulvicoides E. Hitchcock 1843:258, pl. XI (figs. 3 and 4)
Ornithoidichnites gracillimus E. Hitchcock 1844:305, pl. III (fig. 4)
Fulicopus minor E. Hitchcock 1845:23
Eubrontes gracillimus E. Hitchcock 1845:23
Brontozoum gracillimum E. Hitchcock 1848:175, pl. II (fig. 3)
Aethyopus minor E. Hitchcock 1848:179, pl. 4 (figs. 2 and 3)
Anomoepus scambus E. Hitchcock 1848:222, pl. 13 (figs. 1–6)
 ?*Harpagopus giganteus* E. Hitchcock 1848:247, pl. XVIII (fig. 5)
Brontozoum isodactylum E. Hitchcock 1858:69, pl. XII (fig. 3), pl. XL (fig. 1), pl. XLVI (fig. 3), pl. XVII (fig. 4)
Anomoepus minor E. Hitchcock 1858:57, pl. IX (figs. 1 and 2), pl. XXXIV (fig. 2)
Grallator gracillimus E. Hitchcock 1858:73, pl. XIII (fig. 5), pl. XXIX (fig. 2)

- Apatichnus circumagens* E. Hitchcock 1858:100, pl. XVII (fig. 5), pl. XXXV (fig. 6)
- Plesiornis quadrupes* E. Hitchcock 1858:102, pl. XVII (fig. 7), pl. XXXV (figs. 1 and 2), pl. XLV (fig. 5)
- ?*Antipus bifidus* E. Hitchcock 1858:116, pl. XXVI (fig. 8), pl. XLVIII
- Anomoepus curvatus* E. Hitchcock 1863:48, fig. 1
- Anomoepus intermedius* E. Hitchcock 1865:2, pl. I (fig. 1), pl. XV (fig. 1)
- Anomoepus minimus* E. Hitchcock 1865:5, pl. II (fig. 2)
- Anomoepus gracillimus* C. H. Hitchcock 1865:6 (footnote in E. Hitchcock 1865)
- Anomoepus isodactylus* C. H. Hitchcock 1889:118
- Anomoepus cuneatus* C. H. Hitchcock 1889:118
- Apatichnus crassus* C. H. Hitchcock 1889:118
- Anomoepus crassus* Lull 1904:503, fig. 23
- Moyenisauropus natator* Ellenberger 1974:27, pls. C, D, VIII, X–XIII, XV, XVI
- Moyenisauropus natatilis* Ellenberger 1974:35, pl. E
- Moyenisauropus dodai* Ellenberger 1974:38, pls. G, XVII
- Moyenisauropus vermivorus* Ellenberger 1974:40, pls. F, XVII
- Moyenisauropus minor* Ellenberger 1974:47, pls. G, XVII
- Moyenisauropus longicauda* Ellenberger 1974:50, pls. H, III, XX
- Moyenisauropus levicauda* Ellenberger 1974:76, pl. K

The details of the synonymy for the Connecticut Valley material are given in appendix I.

Lectotype: AC 34/40 (figures 19.7 and 19.8; appendix I)

Etymology: *scambus*, “crooked leg.”

Diagnosis: Same as for genus.

Discussion

From 1836 until his death in 1864, Edward Hitchcock named a very large number of ichnospecies from what we believe to be a very modest number of diagnosable track forms. This disparity appears to be a consequence of four factors: (1) a series of assumptions that

Hitchcock made about the kinds of animals that made the tracks; (2) a typological view of taxa that dominated natural history at that time; (3) the lack of a consistent set of rules of systematic nomenclature; and (4) the increase in apparent variability that was a consequence of more than 25 years of track collection.

At first, Hitchcock named and classified the tracks themselves (E. Hitchcock 1836), but later he determined to name the *animals* that made the tracks (E. Hitchcock 1845), which to us seems an existential process (Olsen, Smith, and McDonald 1998). The early tracks he described were bipedal, and he not surprisingly assumed that they were made by birds—hence the original name of the bipedal tracks, *Ornithichnites* (E. Hitchcock 1836; amended to *Ornithoidichnites* [E. Hitchcock 1841]). Relying on Cuvier’s (1828) principle of the correlation of parts, Hitchcock assumed that creatures with feet like birds could have neither hands nor long tails. Thus when he observed tail drag marks or manus impressions in association with bird-like footprints, he had to place the latter in new genera and new higher taxonomic categories (e.g., *Gigandipus caudatus* E. Hitchcock 1858) (Weems, chapter 18 in this volume). Hitchcock knew that in previous geologic periods there had existed animals with combinations of features seen in different major groups of living animals, but because he never employed evolutionist or transmutationalist hypotheses, once he ruled out a bird, any combination of characters was as likely as any other. Track genera, therefore, proliferated as more and more tracks with combinations of characters, precluding the possibility of avian trackmakers.

James Deane (1845, 1847) was the first to describe and figure tracks with a very birdlike hind foot associated with a pentadactyl fore foot, but he deferred to Hitchcock to name them. The first specimens that Hitchcock could be sure had these characters he named *Anomoepus* (unlike foot) (E. Hitchcock 1848) (figures 19.7 and 19.8). However, identical pes impressions, lacking manus tracks, were part of the type series for several previously named forms (e.g., *Ornithoidichnites fulicoides* E. Hitchcock 1843) (figures 19.9 and 19.10), a fact that Hitchcock for the most part did not acknowledge in print.

Size played a very important role in the taxa that Hitchcock described. Most of his descriptions are dominated by measurements of the lengths of parts of the tracks. Variations in measurements from the type

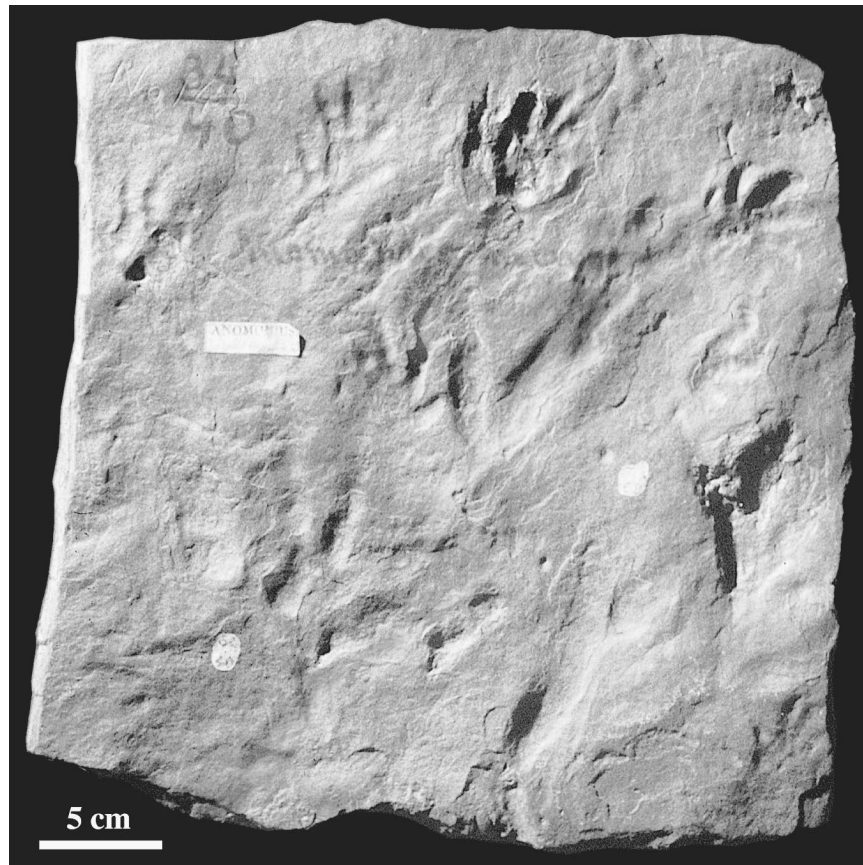


FIGURE 19.7 Lectotype of *Anomoepus scambus* (AC 34/40), natural mold. Note the numerous metatarsal impressions and overlapping manus impressions (figure 19.8).

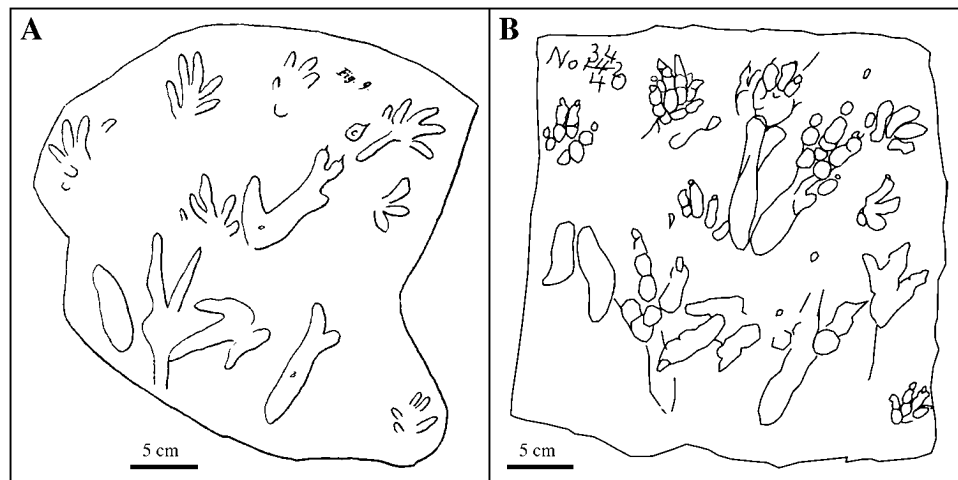


FIGURE 19.8 Lectotype of *Anomoepus scambus* (AC 34/40 [old no. 142]). (A) Drawing by Hitchcock (1848:pl. 20, fig. 4). Note that he evidently did not recognize the faint pes impressions associated with the manus at that time. (B) Our drawing of the same specimen. Note that several manus impressions are double-struck.

series were grounds for him to establish new species because he assumed that the tracks were made by animals with determinate growth, such as birds or marsupials, and that the tracks of young animals were not to be found. In addition, he usually described as new species those tracks that varied in shape, even slightly, from the original type series, even if that variation was limited to the impressions of one foot in a trackway (e.g., *Anomoepus curvatus*). Hitchcock thus employed a strict typological approach, resulting in different size or shape variations being given different names. The concept of allometry was not usually part of the fabric of taxonomy at the time, and thus the change in shape with growth could not be accommodated easily in a species description, although exceptional allometric phenomena were widely discussed (Geoffroy Sainte-Hilaire 1836; Gould 1966, 1977).

The formal nomenclatural rules of de Candolle's *Lois* of 1867 had not been adopted prior to Hitchcock's death, so he felt free to change the names of taxa at will and often. Thus he changed the name of *Anomoepus scambus* E. Hitchcock 1848 to *A. minor* E. Hitchcock 1858 simply because he did not think the specific epithet *scambus*, meaning "crooked leg," really applied to the species. C. H. Hitchcock apparently did not follow de Candolle's (1867) rules in the 1880s, even though by then they were fairly widely accepted. All these factors were mutually reinforcing as more and more tracks came to light.

Matters were not improved by the revisions of Hay (1902) or Lull (1904, 1915, 1953), neither of whom attempted to trace out the history of individual specimens. Instead, they mostly followed C. H. Hitchcock's (1865) catalog, in which he attempted to execute what he thought were his father's nomenclatural wishes. An example is AC 16/5, identified as the type of *Anomoepus minor* by C. H. Hitchcock (1865) and as a co-type of *A. scambus* by Lull (1904, 1915, 1953) (appendix I), even though the specimen was not collected until five years after the type species was named (figures 19.11 and 19.12)!

The result is a nomenclatural morass. We thus have found it necessary to trace the history of all the individual specimens that fall within *Anomoepus* (appendix I). Were the rules of priority, synonymy, and homonymy followed strictly, the genus name *Anomoepus* could not stand because several prior generic and specific names have been used up to the present (appendix



FIGURE 19.9 Lithograph of *Ornithoidichnites fulvicoides* (E. Hitchcock 1843:pl. XI, fig. 3). The specimen that this lithograph represents should be the holotype of *O. fulvicoides*; it may be AC 19/18 (figure 19.10).

I). However, we believe the type species name *A. scambus* should be conserved because it is so well known and because the earlier names have not been in use for the concept of *Anomoepus* for more than 90 years (see appendix I, where we apply reversal of precedence [ICZN, art. 23.9 (International Commission on Zoological Nomenclature 1999)] to the prior synonyms).

As summarized in appendix I, Hitchcock's (1848) type series of *Anomoepus scambus* can include only the specimens owned by T. Leonard, Esq. (E. Hitchcock 1848:pl. 21, figs. 1 and 2) and three specimens in Hitchcock's possession at that time: AC 19/14 (E. Hitchcock 1848:pl. 21, fig. 3), AC 34/40 (old no. 142; E. Hitchcock 1848:pl. 20, fig. 9), and AC 37/9 and 37/10 (part and counterpart, old no. 170 and 40/2 of 1858; E. Hitchcock 1848:pl. 13, fig. 3). With Leonard's specimen and AC 19/14 apparently lost, and with no holotype designated in 1848, only AC 34/40 (figures 19.7 and 19.8) and AC 37/9–10 (figure 19.13) remain as candidates for a lectotype. Of these, AC 34/40 has clear manus impressions and at least two recognizable pedes and was the specimen on which Hitchcock based the species name; hence we designate it the lectotype of *A. scambus* (figures 19.7 and 19.8).

Anomoepus scambus is now represented by hundreds of specimens from four Newark Supergroup basins (figures 19.2 and 19.3). The pes is tetradactyl; the manus, pentadactyl. The size range is fairly large, in-



FIGURE 19.10 Lectotype of *Ornithoidichnites fulvicoides* (= *Plesiornis quadrupes*) (AC 19.18), natural mold.

cluding what are almost certainly babies (figures 19.14–19.16), with the largest forms occurring in the youngest strata (figures 19.17 and 19.18). All the ichnotaxa named by Edward and Charles H. Hitchcock that we believe should be classified as *A. scambus* fall into a narrow range of shapes that vary with size as shown by our osteometric analysis (figure 19.19). Because there are no clear discontinuities of form, we recognize only one ichnospecies, *A. scambus*, among these specimens (figures 19.5–19.8), although we acknowledge that further work on existing material may allow recognition of additional species.

Small specimens of *Anomoepus* are characterized by a pedal digit III that is proportionally longer than in larger forms. This same allometric change is seen in grallatorids (i.e., the *Grallator-Anchisauripus-Eubrontes* complex) (Olsen 1980; Olsen, Smith, and McDon-

ald 1998; Smith and Farlow, chapter 17 in this volume). *Anomoepus* is distinct from grallatorids in this relationship, as expressed in the projection of digit III beyond the rest of the foot, clearly seen in osteometric analysis (figure 19.19A). In both groups, the ratio between the length of the back of the foot (R of appendix II) and the projection of digit III beyond the back of the foot ($R'/T - R'$ of figure 19.19A and appendix II) increases with increasing size, indicating that larger tracks have a proportionally shorter digit III. However, in *Anomoepus*, digit III is proportionally shorter than in grallatorids for all sizes. Thus, in regard to the overall proportions of the foot, a medium-size *Anomoepus* has the shape of a *Eubrontes* (*sensu stricto*) (figure 19.6F). *Otozoum*, on the contrary, lies clearly along the same trend as *Anomoepus* in its relative projection of digit III (figure 19.19A), as do all but one of the plotted prosauropod feet. However, the change to a shorter digit III in larger specimens is gradual and not as pronounced as in grallatorids (figure 19.6F–H).

The separation between the common Connecticut Valley dinosaurian taxa is much less clear when comparing the relative lengths of digits II and IV (figure 19.19B). The fields of *Anomoepus* and the grallatorids overlap, and the field of *Otozoum* is completely enclosed by that of *Anomoepus*. Nonetheless, it is clear that, again, digit III of grallatorids tends to be relatively longer than in either *Anomoepus* or *Otozoum*, except in the largest forms of *Eubrontes* and *Anchisauripus*.

Of note is the very large range of measurements from trackways of single individuals (figure 19.19B). As is true for their morphology in general, this large range highlights the extreme danger in attaching much significance to measurements of single tracks, especially for ratios of measurements of relatively small tracks in which measurement error and substrate-induced differences between tracks is amplified.

The smallest forms of *Anomoepus scambus* are known from the Towaco Formation of the Newark basin (figures 19.14 and 19.15) and from the Deerfield basin (figure 19.16). In the latter basin, C. H. Hitchcock (1865) referred to some well-preserved small examples as *Corvipes lacertoideus* (figure 19.16; see also appendix I). In the Towaco Formation, there are examples of very small sitting traces, showing the same posture as larger examples (figure 19.14). Slightly larger forms were given the names *A. minimus*, *A. gracillimus*, and *Apatichnus circumagens* (figures 19.20–



FIGURE 19.11 AC 16/5, the specimen that C. H. Hitchcock (1865) and Lull (1904, 1915, 1953) incorrectly identified as the type of *Anomoepus scambus*. (A) Natural mold, illuminated from lower right. (B) Our drawing of the same specimen. Note the probable tail impression overprinting the first pes track (compare with figure 19.24). A and B are to the same scale.

19.22). E. Hitchcock classified medium-size forms as *Anomoepus scambus* itself (figures 19.11 and 19.12), *A. curvatus* (figure 19.23), *A. intermedius* (figures 19.24 and 19.25), and *Brontozoum isodactylum* (figure 19.26). These forms are common in the Connecticut Valley (e.g., the Hitchcock collection) and also occur in the Feltville Formation of the Newark basin (figure 19.27). The largest forms from the Deerfield and Hart-

ford basins were called *Plesiornis quadrupes* E. Hitchcock (1858) (figures 19.9 and 19.10) and *A. cuneatus* C. H. Hitchcock (1889) (figure 19.28), and similar forms from the Towaco Formation of the Newark basin were named *Apatichnus crassus* by C. H. Hitchcock (1889) (figure 19.29). A track identical in form was found by I. C. Russell in the Boonton Formation (figure 19.30). Previously undescribed examples of the

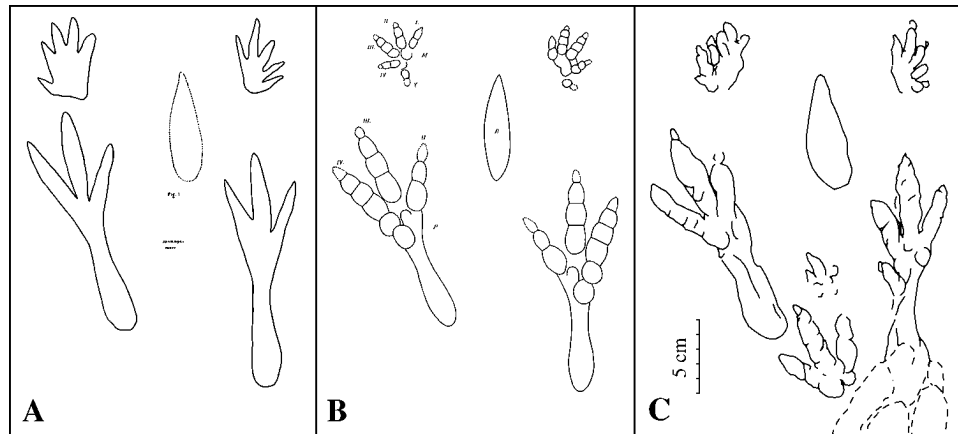


FIGURE 19.12 AC 16/5. (A) Drawing by Hitchcock (1858:pl. IX, fig. 1). (B) Drawing of the same specimen by Lull (1904:fig. 19). (C) Our drawing, from figure 19.11. Note that the left manus of the sitting track is double-struck.

largest known Newark forms occur in the Portland Formation of the Hartford basin and in the McCoy Brook Formation of the Fundy basin (figures 19.17 and 19.18). However, complete sitting traces are not known in the largest *Anomoepus*. The large sitting traces described as cotypes of *Anomoepus major* are not *Anomoepus*, as shown by Gierlinski (1994), but very rare examples of sitting gallatorids (see also Farlow and Galton, chapter 15 in this volume; figure 19.10; appendix II).

In sitting traces, it is common for both metatarsi to

be impressed (figures 19.5, 19.7, 19.8, 19.11, and 19.12). In many such cases, including the lectotype of *A. scambus*, the impression of the pes itself is very shallow and indistinct (figure 19.7). Often only the portion of the metatarsal impression in line with the axis of digit IV is continuous with the foot. Digit I is occasionally impressed for its entire length in tracks with metatarsal impressions (figures 19.11 and 19.29). As has been noted previously (Lull 1904), digit divarication tends to be greater in *Anomoepus* than in gallatorids, except in sitting traces, and greatest in the larg-

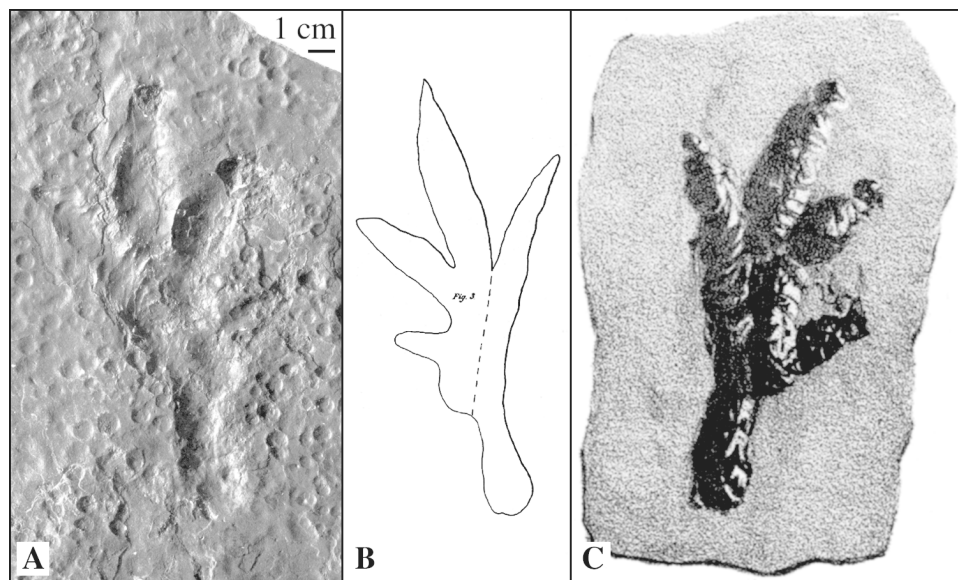


FIGURE 19.13 (A) AC 37/9, natural mold. (B) Drawing of 37/10 (counterpart to AC 37/9) (E. Hitchcock 1848:pl. 13, fig. 3). (C) Lithograph of AC 37/9 (E. Hitchcock 1858:pl. LIX, fig. 4).



FIGURE 19.14 Natural cast of juvenile *Anomoepus scambus* from the Towaco Formation of the Newark basin (Roseland Quarry) (NJSM 20321). Note the sitting tracks with manus.

est specimens (appendix II). Digit I is also impressed to some extent in most sitting tracks, and the tip of the unguis of that digit frequently leaves a small mark on many walking traces.

An impression of the “breast region” has been reported in *Anomoepus* (Lull 1904, 1915, 1953), occurring on AC 16/5 (figures 19.11 and 19.12). However, we believe that the impression interpreted as the “breast region” is actually an example of an isolated metatarsal impression (figures 19.11 and 19.12) because it is identical in outline to the other metatarsal impressions and is comparable to impressions of the metatarsus where the phalangeal impressions are preserved extremely lightly or not at all (figures 19.7 and 19.8).

Although *Anomoepus* is very unusual in having the metatarsal-phalangeal pad of digit IV lying nearly along the axis of digit III, this feature is seen only in walking traces. In sitting traces, with the metatarsus impressed, the metatarsal-phalangeal pads of digits II, III, and IV make a triangle in the same position as in grallatorids, with the metatarsal-phalangeal pad of digit IV lying lateral to the axis of digit III (figures 19.5 and 19.29). As seen in AC 16/5 and other examples

(figures 19.11, 19.24, 19.25, 19.27, and 19.29), pedal digit divarication is high in walking traces and much lower in sitting traces within a single trackway. In fact, in such sitting traces (figure 19.6A) the pes impression tends to look much like a larger grallatorid such as *Eubrontes* (figures 19.5 and 19.29) or the Late Triassic ichnite *Atreipus* (figure 19.6B, C, and E), which it closely resembles (Olsen and Baird 1986). When the animal was sitting, the pes impressions were directed more forward, but with much variation.

Pads on the best-preserved *Anomoepus* pedal impressions are of a distinctly different style than those seen in contemporary grallatorids. The pedal pads and the manus pads are often separated by two creases, instead of by the single crease seen in grallatorids (figures 19.5, 19.23, 19.29, and 19.31B). However, on specimens lacking skin impressions, this distinction is not at all obvious. In many tracks, no crease or constriction at all is seen between the most distal pads of digit III of the pes (figures 19.15 and 19.31C and D), which parallels the condition seen in the Triassic ichnotaxon *Atreipus* (Olsen and Baird 1986) (figure 19.6B, C, and E).

The digits of the manus generally radiate forward and outward in both sitting and walking tracks in *Anomoepus* (figures 19.5, 19.11, and 19.12). Although by no means completely clear in any single specimen but based on the best manus impressions (figure 19.31), in addition to the impression of the unguis tips, digit I has two main phalangeal pads; digit II has three main phalangeal pads; digit III has three or four main phalangeal pads; digit IV has three main phalangeal pads; and digit V has one phalangeal pad. Digit V usually is offset slightly from the other digits and often has a pad impressed for the proximal part of the metacarpus, but sometimes leaves no impression at all. Pads underlying parts of the distal metacarpus are also often impressed (figure 19.31B).

Scale impressions on both the manus and the pes are similar, with the skin being covered with small, rounded, and randomly aligned scales (figures 19.24 and 19.31). Similar but larger scales are present on the metatarsal impressions. On the tail (figure 19.25), as seen in one spectacular specimen (AC 48/1), there are rows of rectangular scales proximally and a ventral keel of scales (?) more distally. No feather impressions are apparent. Trackways sometimes have a small discontinuous tail drag consisting of a narrow groove.

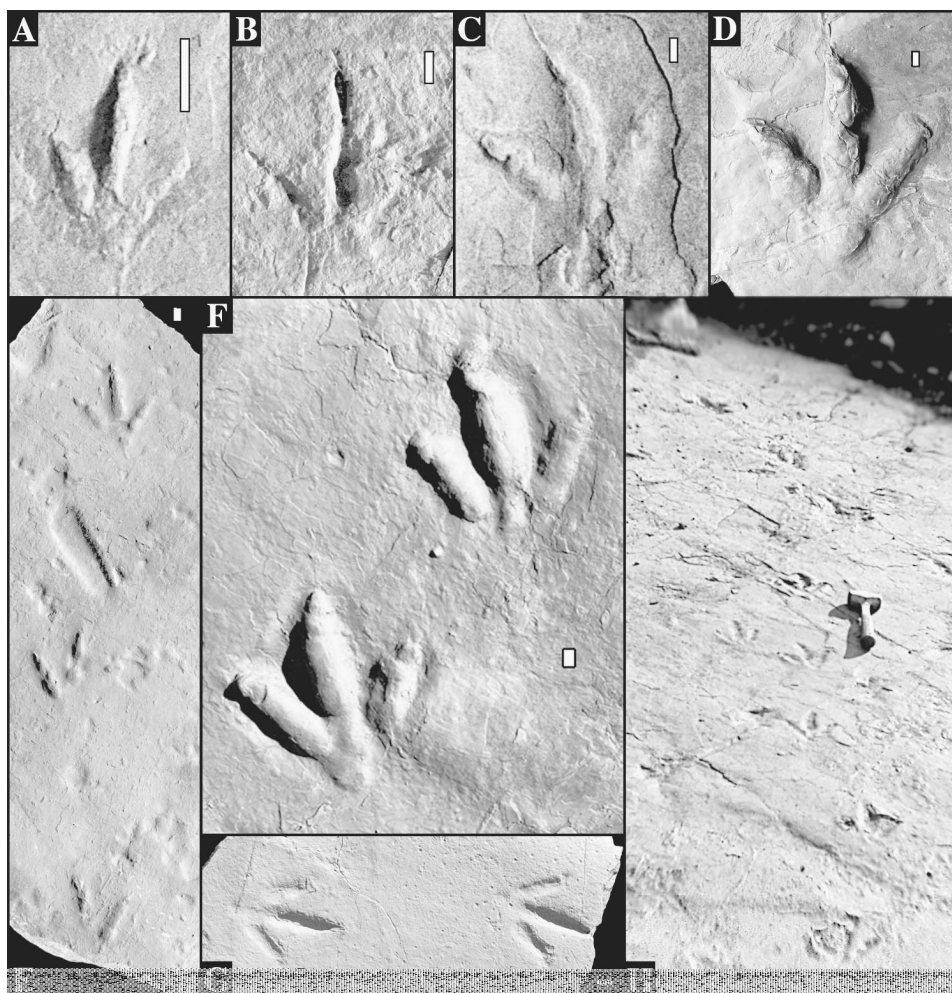


FIGURE 19.15 *Anomoepus scambus* from the Towaco Formation of the Newark basin (Roseland Quarry). (A–D) Series of pedal tracks, showing changes in proportions with size: (A) natural cast (NJSM 20321); (B) natural mold, illuminated from right, specimen presumed lost; (C) natural cast, specimen presumed lost; (D) natural cast (counterpart to track in trackway shown in H), specimen presumed lost. (E) Natural mold of trackway of small *Anomoepus scambus*, specimen presumed lost. (F) Natural cast of successive pes impressions of *Anomoepus scambus* (counterpart to trackway in H). (G) Natural molds of *Anomoepus scambus*. (H) Trackway of *Anomoepus scambus* in situ, not collected (counterpart to F, next to hammer). Scale in A–G is 1 cm.

Anomoepus trackways are usually bipedal. In such walking tracks, the pes impressions are directed slightly medially so that the trackway is distinctly “pigeon-toed” (figures 19.5, 19.10, 19.22, 19.23, and 19.26). However, in addition to the sitting traces with manual impressions, there are not uncommonly quadrupedal walking traces. Most notable is slab AC 16/5 (figure 19.11): the tracks impressed before the sitting trace indicate typical quadrupedal walking. On the underside of the same slab (figure 19.16B–D), there are numerous trackways of small *Anomoepus*

that C. H. Hitchcock (1865) placed within *Corvipes lacertoideus*.

There are a large number of classically described ichnospecies that were probably made by the same kind of trackmaker as *Anomoepus* but that we regard as indeterminate ichnotaxa, because they do not show pads, are under- or overprints, are caved-in tracks, or show significant variation between successive tracks. These ichnites include the quadrupedal *Tarsodactylus expansus* (C. H. Hitchcock 1867), *Xiphopeza triplex* (E. Hitchcock 1848), *Plectropterna gracilis* (E. Hitchcock

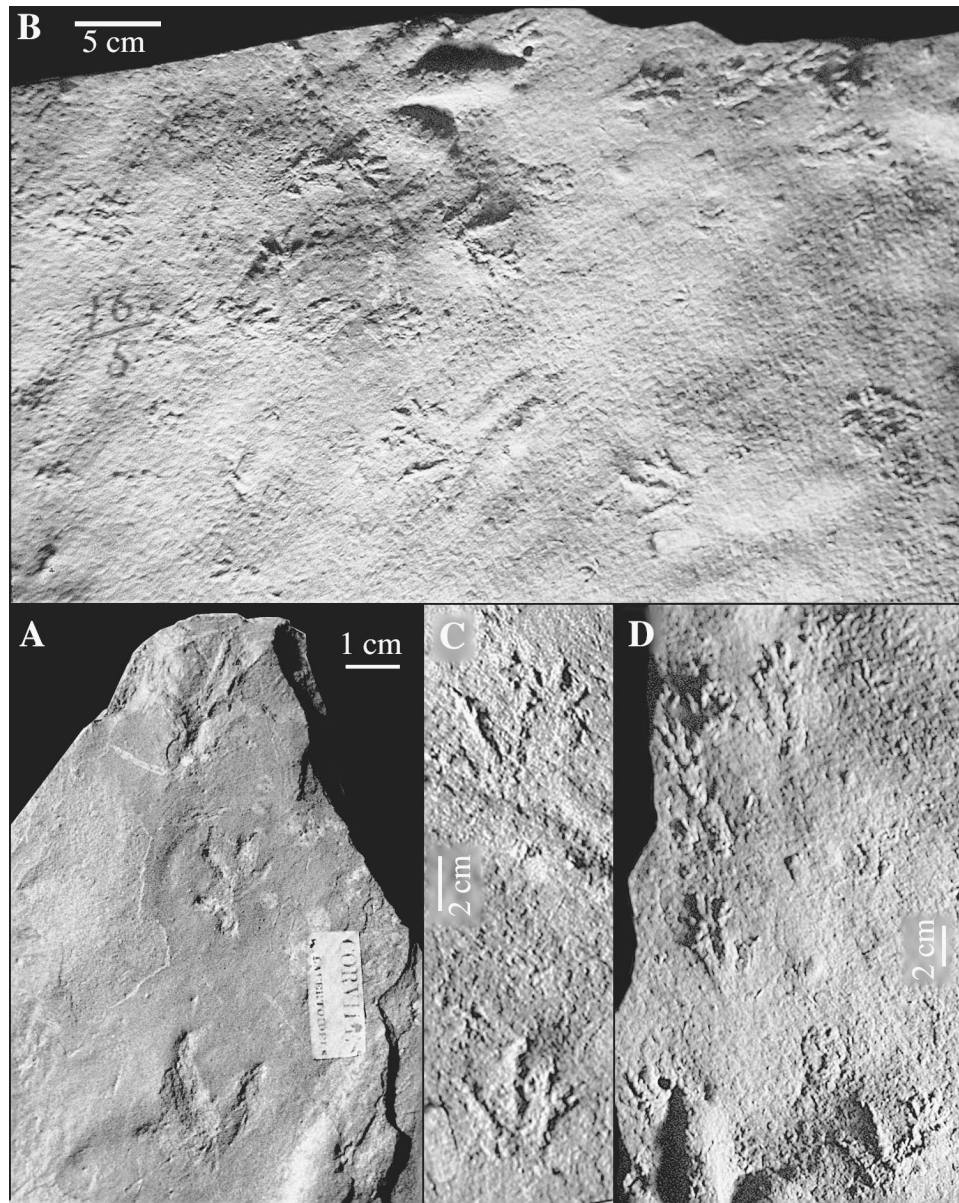


FIGURE 19.16 Juvenile *Anomoepus*. (A) Holotype of *Corvipes lacertoideus* (AC 32/1). (B–D) Portions of the underside of AC 16/5, natural casts. The top side of AC 16/5 is shown in figure 19.11.

1858), *P. lineans* (E. Hitchcock 1858), *P. minitans* (E. Hitchcock 1858), *Harpedactylus tenuissimus* (E. Hitchcock 1845), *H. gracilior* (E. Hitchcock 1865), *H. crassus* (E. Hitchcock 1865), and *Ammopus marshi* (Lull 1915); the bipedal *Typopus abnormis* (E. Hitchcock 1845); and probably several others. These tracks are not diagnosable as taxa. Drawings of them in the works of Hitchcock and Lull fail to convey the enormous amount of variation between successive tracks in trackways, and in some cases the drawings are so

subjective as to be virtually unrecognizable as the same specimens (e.g., *Tarsodactylus caudatus* as figured in Lull 1904, 1915, 1953). In any case, they should not be thought of as any sort of proxy for biological taxa, although they may provide details of locomotion in substrates of varying consistencies.

Gierlinski (1991) has named a new species, *Anomoepus pienkovski*, from the Early Jurassic of the Holy Cross Mountains of Poland. According to Gierlinski, this species differs from *A. scambus* in being quadru-

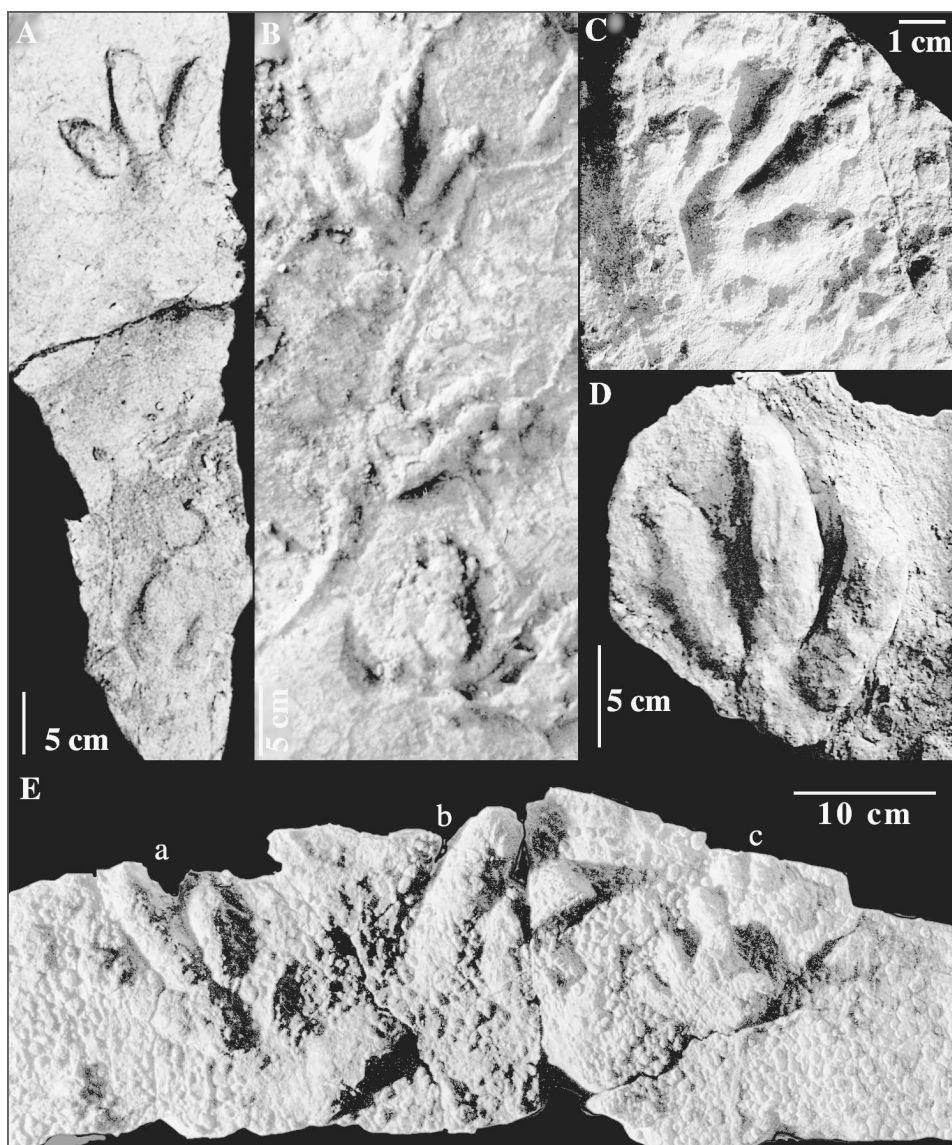


FIGURE 19.17 Natural casts of *Anomoepus scambus* from the McCoy Brook Formation of the Fundy basin (Blue Sac and McKay Head, Cumberland County, Nova Scotia). (A) YPM 8665. (B) Not collected. (C) Manus in Eldon George collection. (D) Large pes, somewhat distorted, in Eldon George collection. (E) Large *Anomoepus* in two trails (FGM-994-GF 2): a, trail 1, single pes; b, pes of trail 2 with metatarsal impression; c, double-struck manus impressions of trail 2.

pedal, in having a larger manus relative to the pes, and in having the manus impressions farther from the midline. All these features are seen in AC 16/5, regarded by Lull (1904, 1915, 1953) as the type specimen of *A. scambus*. However, *A. pienkovski* does appear more massive than any Newark Supergroup example of *Anomoepus* or of African *Moyenisauropus* and therefore may be a valid species. Additional, better-preserved material should help clarify this ambiguity.

SYNONYMY OF *ANOMOEPUS* AND *MOYENISAUROPUS* AND THEIR DISTRIBUTION

Ellenberger (1974) gave the name *Moyenisauropus* to tracks with sitting and manus impressions from the upper Elliot Formation of the Stormberg Group of the Karoo basin of southern Africa (figure 19.32). The ichnogenus includes the type species *Moyenisauropus*

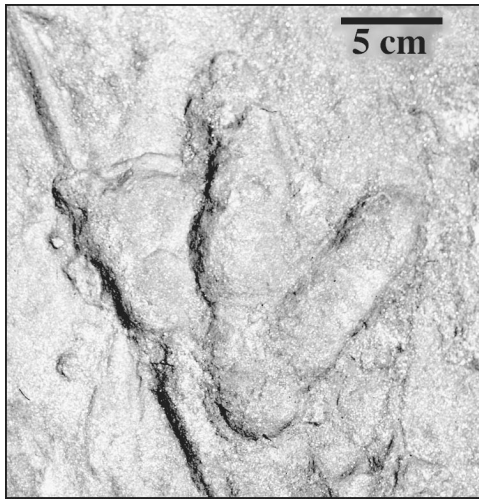


FIGURE 19.18 Natural cast of very large *Anomoepus scambus* from the Portland Formation (DP 01.1).

natator as well as *M. natatilis*, *M. dodai*, *M. vermivorus*, *M. minor*, *M. longicauda*, and *M. levicauda*. Even the largest of these named ichnospecies falls within the size range of Newark Supergroup forms, and there do not seem to be any qualitative differences from *Anomoepus scambus*. One of us (Rainforth) recently examined the type material of the various *Moyenisauropus* species (casts in the collections of the Université de Montpellier II, Laboratoire de Paléontologie) and can confirm the synonymy with the species *A. scambus*. In addition, we will describe the forms called *Moyenisauropus* by Ellenberger in more detail in a future paper.

According to Ellenberger (1974), *Moyenisauropus* is similar to *Anomoepus* as defined by Lull (1953) but departs in the characters that are dealt with individually in the following points.

1. In *Moyenisauropus*, pedal digits II, III, and IV are widely divergent when walking but come together when stopped. This pattern is seen in all the trackways of *Anomoepus* in which walking trackways lead into sitting traces, including AC 16/5, which Lull (1904, 1915, 1953) supposed was the type specimen of the type species of the genus (figure 19.11), as well as in the main Rutgers slab of *Anomoepus crassus* (figure 19.29).
2. In *Moyenisauropus*, digit I of the pes is often impressed in sitting traces, even for its entire length. In fact, the hallux is often impressed for its entire length in sitting *Anomoepus*. Examples

include AC 34/40 (the lectotype) (figures 19.7 and 19.8), AC 37/9 and 37/10, part of the original type series (figure 19.13), and the main Rutgers slab (figure 19.29).

3. The nature of the creases between the pads is different in *Moyenisauropus*. This character is difficult to assess because Ellenberger never says exactly how the creases differ from those in *Anomoepus*. However, the photographs Ellenberger (1974) provided show creases overlapping the range of variation seen in *Anomoepus*.
4. In *Moyenisauropus*, the metatarsal bundle makes an asymmetrical rather than a symmetrical pad in sitting traces, with only metatarsal IV making an impression its entire length. This is exactly the condition seen in many sitting traces of *Anomoepus* (figures 19.5, 19.11, 19.29, and 19.33). Lull's drawings show the impression of the metatarsal bundle as symmetrical, but this is an error. As shown by Ellenberger's (1974) drawing, this feature is also highly variable in *Moyenisauropus*, as it is in *Anomoepus*.
5. The manus is extremely mobile in *Moyenisauropus*, sometimes impressed several times while stopped, in a very large circle, sometimes anterior and medial to the pes, other times lateral to the pes. Ellenberger's knowledge of *Anomoepus* is based completely on Lull (1953). Lull's drawings of sitting *Anomoepus* unfortunately are excessively stylized composites (figure 19.12). Lull makes this fact explicit only in his 1904 work. Indeed, most sitting traces of *Anomoepus* have multiple manus impressions, although none are known to make a circle, which, in any case, based on Ellenberger's figures, is never really achieved in *Moyenisauropus* either.
6. *Moyenisauropus* shows a tendency for what Ellenberger calls metacarpograde, which presumably means a tendency for there to be an impression of the metacarpus. AC 34/40 seems to show this character (figure 19.7), and AC 16/14 definitely has an impression of the distal metacarpus (figure 19.31A). However, it is difficult to tell exactly what Ellenberger means because no figures are shown of this condition in *Moyenisauropus*.

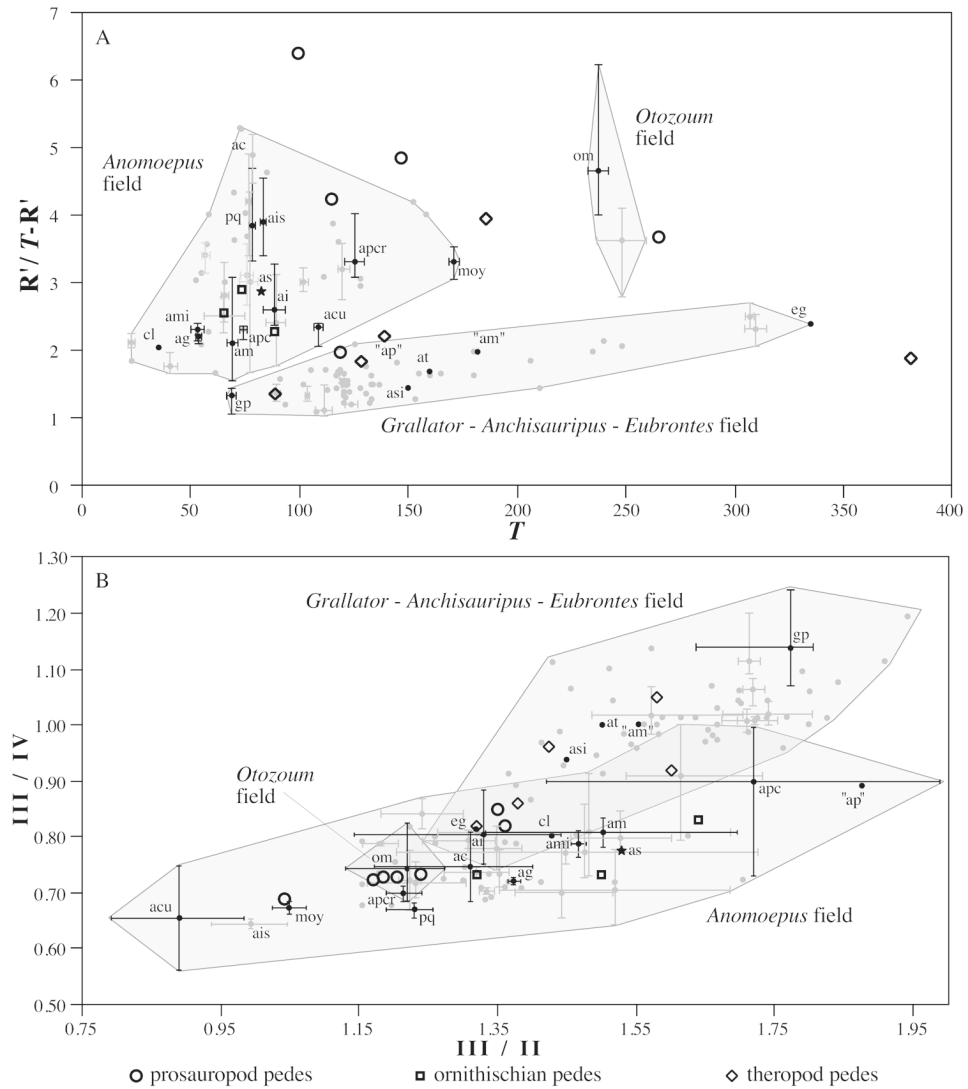


FIGURE 19.19 Relationships between osteometric measurements for tracks and skeletal material. Black dots are type specimens; gray dots are additional specimens for comparison; the bars show the ranges for single tracks within trackways made by single individuals; skeletal remains are indicated by circles (prosauropods), squares (ornithischians), and diamonds (theropods). Lengths of elements are defined in figure 19.4. (A) Relationship between the length of the foot (T) and the projection of digit III beyond the other digits ($RN/T - R'$) (figure 19.4). (B) Relationship between the lengths of digits II and IV scaled to the length of digit III. Darker polygons are areas of overlap between fields; *ac*, *Anomoepus curvatus*; *acu*, *Anomoepus cuneatus*; *ag*, *Anomoepus gracillimus*; *ai*, *Anomoepus intermedius*; *ais*, *Anomoepus isodactylus*; *am*, *Anomoepus minor* (AC 16/5); “*am*,” “*Anomoepus*” *major*; *ami*, *Anomoepus minimus*; “*ap*,” “*Anchisauripus parallelus*”; *apc*, *Apatichnus circumagens*; *apcr*, *Apatichnus crassus*; *as*, *Anomoepus scambus*; *asi*, *Anchisauripus sillmani*; *at*, *Anchisauripus tuberosus*; *cl*, *Corvipes lacertoides*; *eg*, *Eubrontes giganteus*; *gp*, *Grallator parallelus*; *moy*, *Moyenisauropus*; *om*, *Otozoum moodii*; *pq*, *Plesiornis quadrupes*. For original data and specimen numbers, see appendix II.

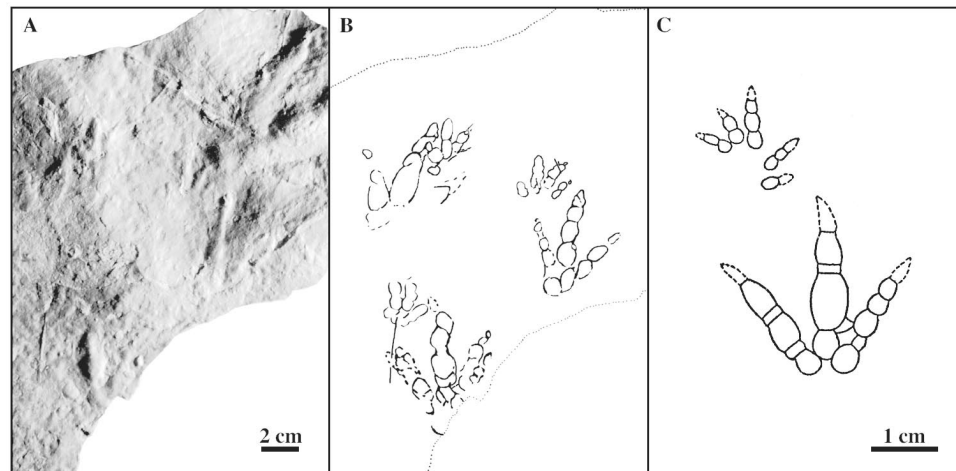


FIGURE 19.20 Holotype of *Anomoepus minimus* (AC 55/112), natural molds. (A) Photograph. (B) Our drawing. (C) Drawing by Lull (1904:fig. 66).

7. The ischial mark of *Moyenisauropus* is in the form of three small crescents fitted together, differing from the circular mark of *Anomoepus*. None of the so-called ischial marks of *Anomoepus* are impressed clearly enough to compare with what Ellenberger figures in *Moyenisauropus*, and it is by no means clear that what he describes actually reflects the anatomy of the trackmaker.
8. A “breast mark” is never present in traces of seated *Moyenisauropus*. What Lull (1904, 1915, 1953) calls a breast mark is seen only in AC 16/5 (figures 19.11 and 19.12). As noted earlier, the so-called breast mark is most likely an isolated metatarsus impression, and thus *Anomoepus* lacks this character as well.
9. The tail mark is often complete in sitting *Moyenisauropus*. Tail traces obviously are present in sitting *Anomoepus*, most blatantly seen in AC 48/1, the type slab of *A. intermedius* (figure 19.25). AC 16/5 also seems to have one, although scale impressions are absent (figure 19.11).
10. A snout mark is sometimes present in stopped *Moyenisauropus*. This character is difficult to assess because it is so unclear and inconsistent in *Moyenisauropus* itself, as shown by Ellenberger. In addition, there are marks lateral to the trackways in *Anomoepus* that might be interpreted as snout marks. In any case, because all dinosaurs presumably had snouts, it is difficult to know how the presence of a rare snout mark alone can define an ichnotaxon, unless there is a specific character of the snout that is critical.
11. Webs between digits II, III, and IV are impressed in walking traces. Webs have been reported in numerous ichnotaxa. However, these webs, we think, have been interpreted correctly as a “pressure wave” of mud in front of the track (Lull 1953; Seilacher 1997), as we feel is also the case in *Moyenisauropus*. A feature can be demonstrated to be a web only if scale impressions are present in it, which is not the case in *Moyenisauropus*.
12. *Moyenisauropus* has claws rather than nails. Although Ellenberger attributes to Lull the interpretation that ornithischian nails rather than claws are present, Lull only says that “the affinities of this genus [*Anomoepus*] lie with the Orthopodous, Camptosaur-like dinosaurs” (1953:193) and says nothing about claws while discussing affinities. Further, *Anomoepus* clearly has claws (figures 19.5, 19.15, 19.25, 19.29, and 19.33), regardless of its supposed affinities.
13. The feet of *Moyenisauropus* are turned inward when walking (i.e., a “waddling” gait), while they turn out while sitting. Exactly this pattern is seen in *Anomoepus* (figures 19.5, 19.11, and 19.15), although not in Lull’s drawings.

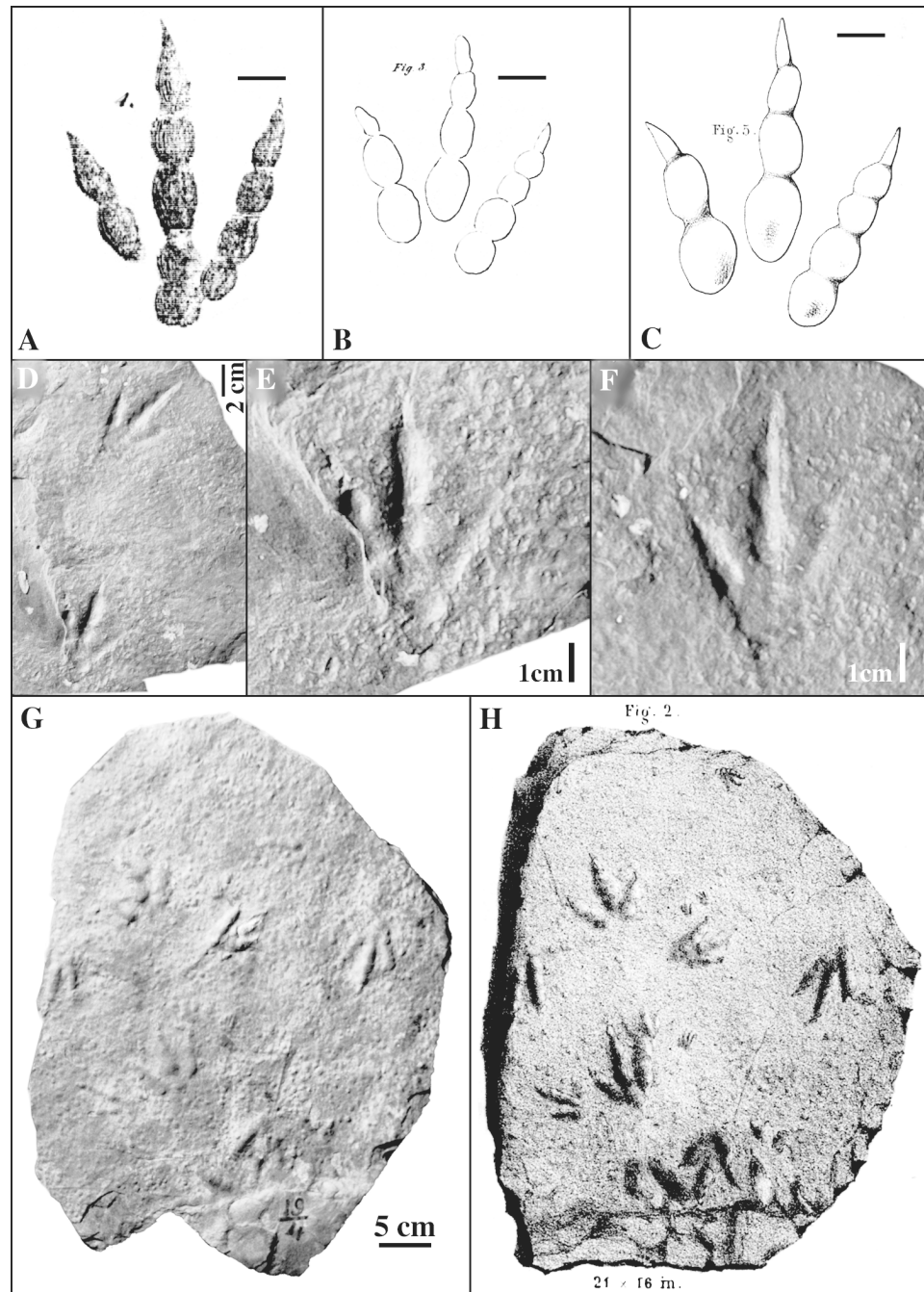


FIGURE 19.21 *Anomoepus gracillimus*. (A) Drawing by Hitchcock (1844:pl. III, fig. 4), probably of AC 37/18 (old no. 129). (B) Drawing by Hitchcock (1848:pl. 2, fig. 3). (C) Drawing by Hitchcock (1858:pl. XIII, fig. 5). (D–F) Photographs of AC 37/18, probably the specimens in A–C (especially A): (D) both tracks; (E) first track; (F) second track. (G) Photograph of slab AC 19/4, with *A. gracillimus*, natural molds. (H) Lithograph of AC 19/4 (E. Hitchcock (1858:pl. XXXIX, fig. 2) assigned, with footprints to *Anomoepus gracillimus*, *A. minor*, *Grallator tenuis*, and *Anisopus gracilis*. Scale in A–C is 1 cm.



(A)

(B)

FIGURE 19.22 Referred trackway of *Apatichnus circumagens*. (A) AC 20/6, natural cast (counterpart to AC 1/3). (B) AC 1/3, natural molds, illuminated from right.



FIGURE 19.23 Holotype of *Anomoepus curvatus* (AC 52/10). (A) Natural mold of slab. (B) Track 1 of A (left pes). (C) Track 2 of A (right pes). (D) Track 3 of A (left pes).

14. There are swimming traces in *Moyenisauropus*. Ellenberger attributes a number of trackways to swimming *Moyenisauropus*. One of us (Olsen) has seen similar trackways in *Anomoepus* in the Towaco Formation (in situ in the Roseland Quarry, but not collected).

15. The various species of *Anomoepus* show a great variety of form, whereas those of *Moyenisauropus* are more similar to its type species. As shown in the discussion of *A. scambus*, most of the variation between supposed species of *Anomoepus* is a result of differences in preserva-

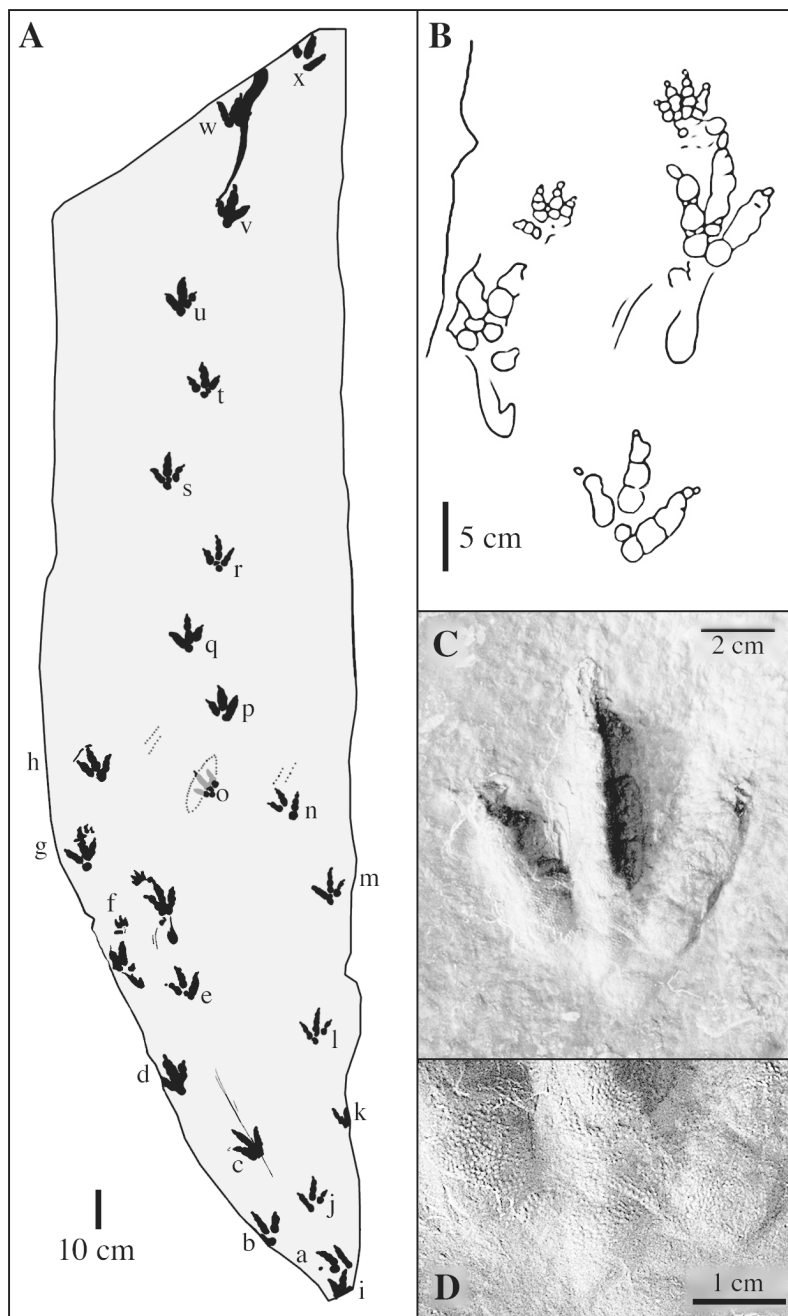


FIGURE 19.24 Holotype of *Anomoepus intermedius* (AC 48/1), natural mold. (A) Drawing of the entire slab, with only the largest tracks (*A. intermedius*) drawn in. (B) Sitting trace (*e* and *f* in A). (C) Particularly detailed pes impression (*r* in A). (D) Detail of C, showing skin impression. Each track on the specimen has a label, *a*–*x*. For details of the individual tracks, see figure 19.25.

tional mode or illustration technique (see also appendix I).

Thus most of the differences between *Anomoepus* and *Moyenisauropus* are a result of the Hitchcocks' and

Lull's incomplete or incorrect documentation of specimens in the Hitchcock collection. Gierlinski and Potemka (1987) and Gierlinski (1991) have provided an emended diagnosis of *Moyenisauropus* in which they stress the tendency for the distal and penultimate pad

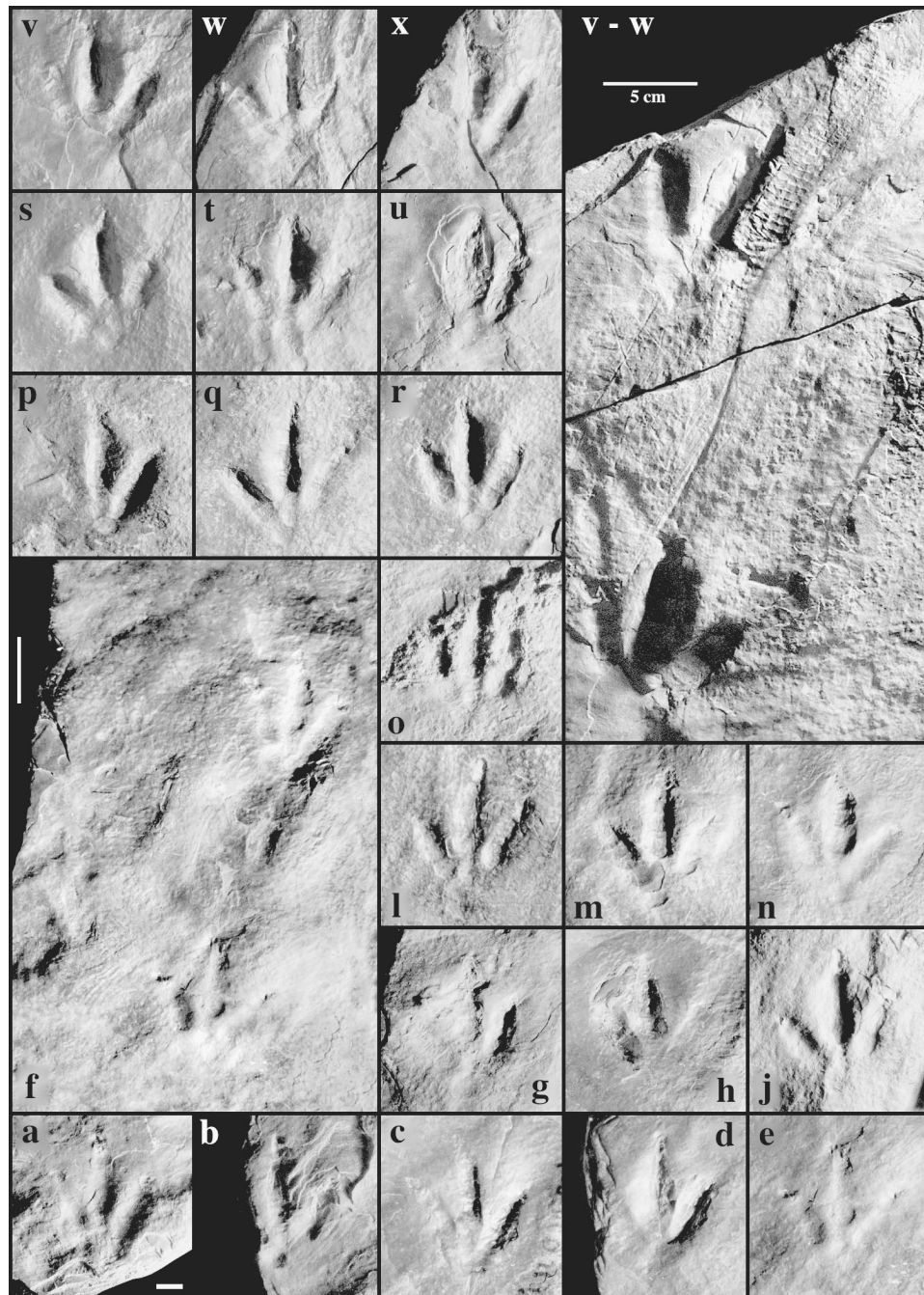


FIGURE 19.25 *Anomoepus intermedius* (AC 48/1), details of individual tracks. Letters correspond to track labels given in figure 19.24A. Note the detailed impression of the tail in *v* and *w*. Scale in *a* is 2 cm, and individual tracks *b*–*x* are the same scale. Scale bar in *f* is 5 cm.

on digit III to be conjoined in this genus as opposed to in *Anomoepus*. This feature may be a function of size or simply of preservational mode, as it is clearly seen in some Connecticut Valley examples (figures 19.11, 19.12, 19.15, and 19.29) as well as in many

Anomoepus from the Towaco Formation. Gierlinski (1991) also stresses the massive and short shape of the manual and pedal digits as well as the inward direction of the walking pes in *Moyenisauropus*. Again, we can see no differences in these features between *Moyeni-*



FIGURE 19.26 Specimen with tracks assigned to *Brontozoum isodactylum* by Hitchcock (1858). This is the specimen plowed up by Pliny Moody in around 1802 (the date varies with various Hitchcock references) and referred to by Dr. E. Dwight of South Hadley, Massachusetts, as “probably the tracks of Noah’s Raven” (E. Hitchcock 1844:297).

sauropus and *Anomoepus* that cannot be accounted for by size and preservational mode. Based on comparisons between the two genera, we therefore conclude that there are no grounds for ichnogenic distinction between *Anomoepus* and *Moyenisauropus*. Indeed, we can see no justification for separation of the southern African material from the American species *Anomoepus scambus*.

Gierlinski (1991) has described several new species of *Moyenisauropus* from Early Jurassic strata of the Holy Cross Mountains of Poland. These species indeed appear more massive than any other *Anomoepus* or *Moyenisauropus*, and although the preservation is not ideal, they may be either valid ichnospecies within *Anomoepus* or a new ichnogenus.

As thus described, *Anomoepus* may be monotypic and is nearly cosmopolitan, being definitively present in eastern North America, southern Africa, and probably Europe (Poland). In addition, tracks probably ref-

erable to *Anomoepus* are present in the Early Jurassic age Glen Canyon Group (Olsen and Galton 1977; Lockley and Hunt 1995; E. C. Rainforth, personal observation). Its temporal distribution is limited to the Early Jurassic. However, as described later in the chapter and by Bakker (1996), *Anomoepus* tracks could have been made by a wide variety of relatively primitive ornithischians, including groups that survived to the end of the Cretaceous. Thus we should expect to find *Anomoepus* in significantly younger strata such as the possible ?Early Cretaceous example cited by Currie (1989).

ASPECTS OF THE BEHAVIOR OF THE MAKER OF ANOMOEPUS

One of the diagnostic characters of *Anomoepus* is to have the metatarsal-phalangeal pad of digit IV in line or nearly in line with the axis of digit III in walking trackways (figures 19.5, 19.10, 19.11, 19.15, 19.23, 19.25, and 19.26). In sitting traces, however, a much more typical dinosaurian configuration of pads is seen; digit III lines up with the metatarsal axis, and the digital divarication decreases (figures 19.5, 19.11, 19.24, and 19.29). This is most clearly seen in the Rutgers main slab (figure 19.29). As one of us (Olsen 1995) pointed out, this configuration of pads demands that the phalanges must be rotated medially relative to the metatarsus while the animal is walking (figure 19.33A). Perhaps this seemingly peculiar way of walking is related to a particularly large abdomen or to the backward position of the gut in ornithischians. Grallatorid walking or sitting tracks, presumably made by theropods (Olsen, Smith, and McDonald 1998), show no such pattern (Gierlinski 1994), and neither does the possible ornithischian track *Atreipus* (Olsen and Baird 1986).

As previously mentioned, it is also common in *Anomoepus* sitting traces for the phalangeal portion of the pes to be very lightly impressed or not impressed at all, with most of the animal’s weight clearly being born on the metatarsal bundle during implantation and removal (figures 19.7, 19.11, and 19.29).

Sitting tracks of *Anomoepus* often have multiple impressions of the same manus, often striking over one another (figures 19.7, 19.11, and 19.29). This pattern shows that the trackmaker repeatedly patted or stomped the ground, perhaps in a display such as the one Ellenberger (1974) suggested for the southern African *Anomoepus* (his *Moyenisauropus*). In addition,

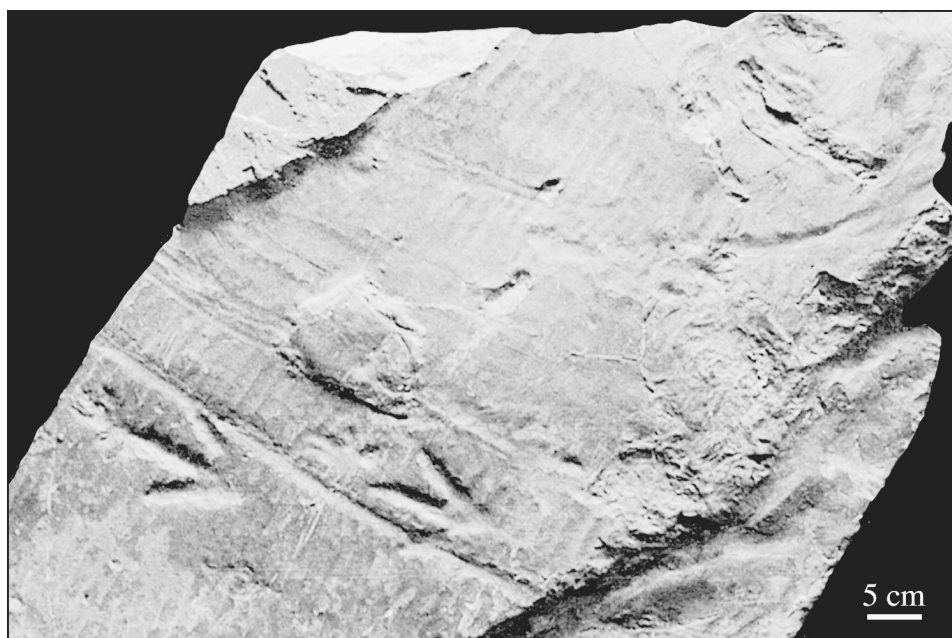


FIGURE 19.27 Natural mold of *Anomoepus scambus* from the Feltville Formation of the Newark basin (AMNH 7639), illuminated from above. Note the distinctly impressed walking quadrupedal tracks and faint sitting tracks of a different individual (both *A. scambus*) and the faint, isolated pes imprint of a grallatorid.

both specimens of the trace called *Harpagopus giganteus* (E. Hitchcock 1848) are associated with trackways of *Anomoepus* and may represent repeated symmetrical and stereotyped motion of the manus away from or toward the midline (figure 19.34).

Finally, *Anomoepus* frequently occurs on slabs with individuals of many sizes (figures 19.15, 19.16, and 19.27). Often the size distribution is not continuous, with many very small *Anomoepus* and a fewer number of larger individuals (Olsen 1995). Not only does the very strong dominance of *Anomoepus* on these slabs suggest gregarious behavior, but it also suggests that baby trackmakers of *Anomoepus* stayed with larger individuals (Olsen 1995). Multiple species associations and track sequences of different-size individuals passing at different times are also plausible explanations, but ones that we think are less parsimonious, given the consistent preservational quality on the slabs.

ORNITHISCHIAN ORIGIN OF *ANOMOEPUS*

The ornithischian origin of *Anomoepus* has been asserted for more than 90 years (Lull 1904, 1915, 1953) and affirmed by most later workers (Haubold 1971,



FIGURE 19.28 Lectotype of *Anomoepus cuneatus* (MM 5125; counterpart to MHM 105, now destroyed).

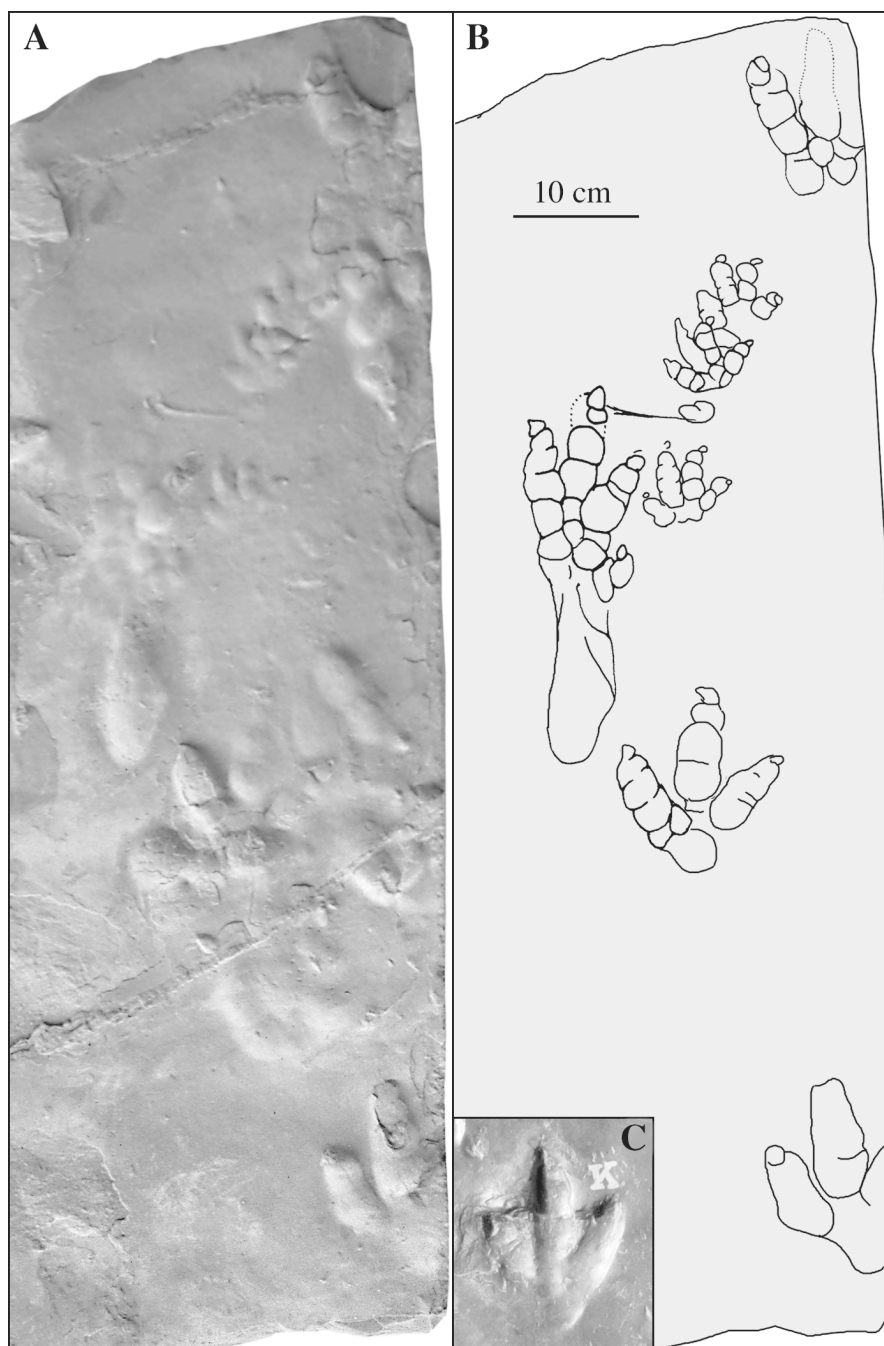


FIGURE 19.29 Rutgers specimens of *Apatichnus crassus* from the Towaco Formation of the Newark basin. (A) Counterpart of display slab. (B) Drawing of A, showing only the tracks of sitting individual. (C) Single track (K) of long trackway of main Rutgers display slab, which may be the holotype of *A. crassus*. Scale in A and C is the same as in B.

1984; Olsen and Galton 1984; Olsen and Baird 1986; Gierlinski 1991). The most striking aspect of *Anomoeopus* that ties it to the Ornithischia is the manus. It is primitive at the archosaur level in having five subequal digits. However, it has the dinosaurian shared derived

character of having a reduced number of phalanges in manual digits IV and V (figures 19.6D, 19.31, and 19.33) and having the distinctively dinosaurian pes. The only known dinosaurs that lack enlarged digits I, II, and III and yet show the dinosaurian reduction in



FIGURE 19.30 *Anomoepus scambus* from the Boonton Formation. (Reproduced from a photograph [Donald Baird private collection] by I. C. Russell of a specimen collected before 1900)

manual phalangeal formula are ornithischians. There is significant dispute, however, on the character polarity of the enlargement of digits I, II, and III, typical of theropods and of the earliest dinosaurs with preserved manus (*Eoraptor* and *Herrerasaurus* [Serenó 1993; Sereno et al. 1993]), as well as of the Jurassic ornithischian *Heterodontosaurus* (Santa Luca 1980). The overall structure of the pes in *Anomoepus* is, unfortunately, primitive at a level below that of the Dinosauria. Apart from the presumed mesotarsal ankle that *Anomoepus* must have had as a dinosaur (but see Dyke 1998), the basic pedal phalangeal formula is primitive at a level below that of the Dinosauria. However, the seemingly peculiar kinematics of walking in *Anomoepus* suggest the expression of morphological characters not obvious from present skeletal descriptions. There may well be phylogenetic information in these as yet undescribed characters.

An ornithischian that appears to match skeletal reconstructions of *Anomoepus* is the “fabrosaur” *Lesothosaurus* from southern Africa (Olsen and Baird 1986) (figure 19.33), although the manus is known incompletely and the forelimbs seem relatively too small (Thulborn 1972; Sereno 1991). Early thyreophorans, such as *Scutellosaurus* (Colbert 1981), are other candidates for *Anomoepus* (figure 19.33). Because the phylogenetic level of generality of the walking method of *Anomoepus* is unknown, we can limit possible trackmakers of *Anomoepus* to only primitive members of

several ornithischian clades, including not only the “fabrosaur” and the Thyreophora, but also probably primitive members of the Marginocephalia and Ornithopoda. A potentially distinctive character of *Anomoepus* seems to be a relatively long metatarsus. It seems proportionally longer than any of the dinosaur material shown in figure 19.33. It is difficult to assess the meaning of this character, however, because there appears to be confusion about the length of the metatarsals relative to the phalanges in *Lesothosaurus*, and the metatarsus of *Scutellosaurus* is incomplete (reconstructed on the basis of *Hypsilophodon* [Colbert 1981]) (figure 19.33). Thus we conclude that the trackmaker of *Anomoepus scambus* was a relatively small, gracile, facultatively bipedal ornithischian.

AGE OF ANOMOEPUS

All examples of *Anomoepus* found to date in the Newark Supergroup rifts of eastern North America occur in strata above the lowest basalts. The Triassic–Jurassic boundary, as identified with palynomorphs, occurs below the oldest basalt, and therefore all *Anomoepus* are Early Jurassic in age (figure 19.3). However, *Anomoepus* has not been found in the strata between the boundary and the oldest basalts, although admittedly there is only one region (in the northeastern Newark basin) where abundant dinosaur tracks have been found at this level.

The restriction of *Anomoepus* to strata in eastern North America dated palynologically as Early Jurassic was one of the main lines of evidence suggesting an Early Jurassic age for many sequences traditionally thought to be Late Triassic, such as the Glen Canyon Group of the western United States and the upper Stormberg Group of southern Africa (Olsen and Galton 1977, 1984). These strata generally are accepted now as Early Jurassic in age (e.g., Shubin and Sues 1991).

It is now becoming clear that the continental tetrapod assemblages of the Early Jurassic were very different from those of the latest Triassic. In the latest Triassic, nondinosaurian archosaurian herbivores were dominant in the equatorial regions, whereas prosauropods and nondinosaurian archosaurian herbivores were dominant in the midlatitudes. Although the ichnite *Atreipus* was abundant in the first three-quarters of the Late Triassic, indicating a common dinosaurian

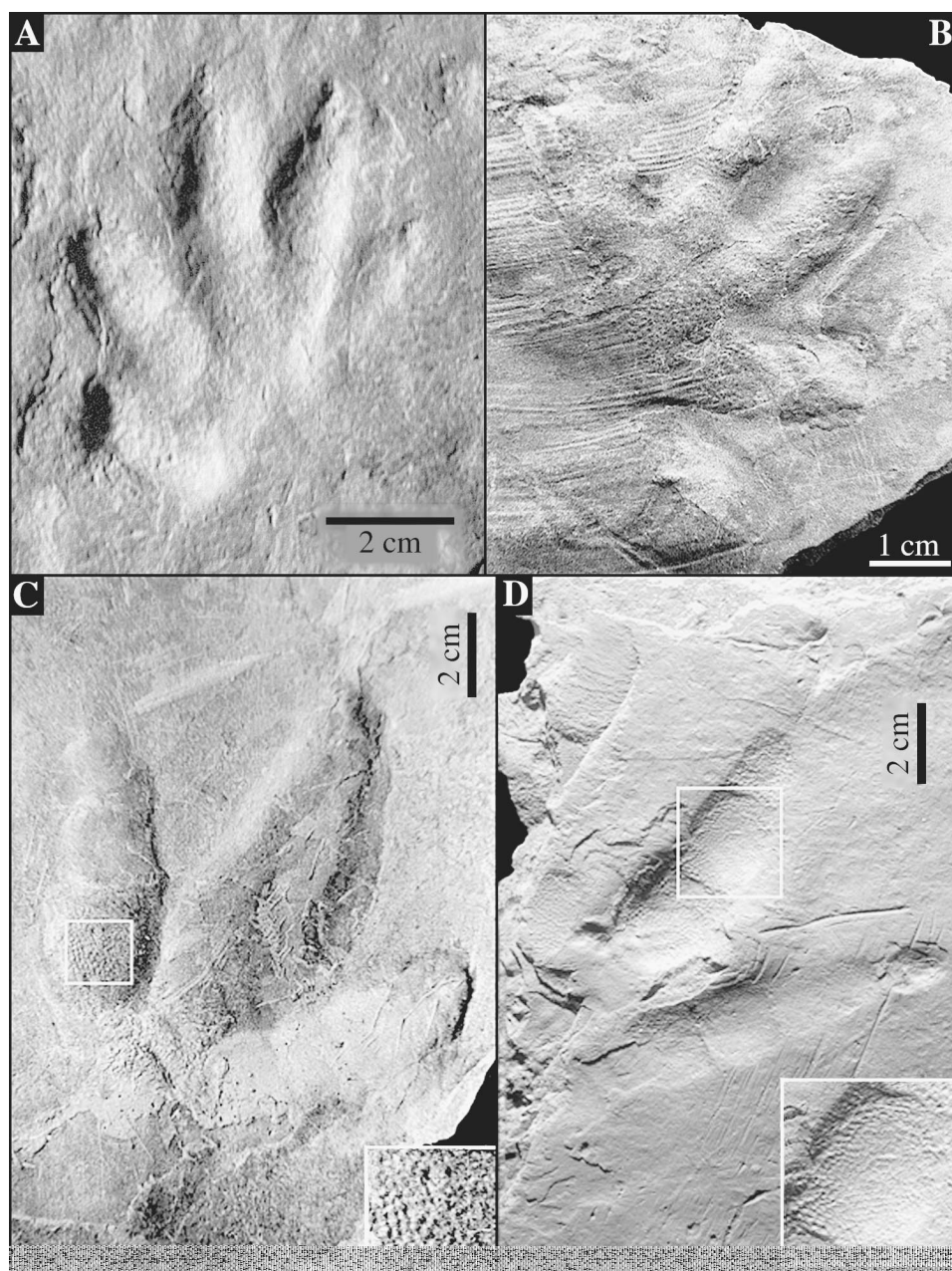


FIGURE 19.31 Unusual preservation in manus and pes impressions of *Anomoepus*. (A) Manus in AC 16/14. (B) Isolated natural cast of manus of *Anomoepus*, with skin impressions, from the Towaco Formation (Roseland Quarry), presumed lost. Note the drag mark of a claw on digit V. (C) Natural cast (presumed lost) and (D) mold of pes impressions from the Towaco Formation (Roseland Quarry) (NJSM 19325).

herbivore in the equatorial zone to the midlatitudes, it is absent from all latest Triassic (late Rhaetian) track assemblages. Track data from eastern North America (Olsen et al. in press) indicate an abrupt end to the Late Triassic–type assemblages at or very close to the

palynologically dated Triassic–Jurassic boundary, with a replacement by a grallatorid-*Batrachopus-Rhynchosauroides* assemblage (i.e., theropods, crocodylomorphs, lepidosaurs). Shortly thereafter (within 50,000 years, based on cyclostratigraphy), *Anomoepus*

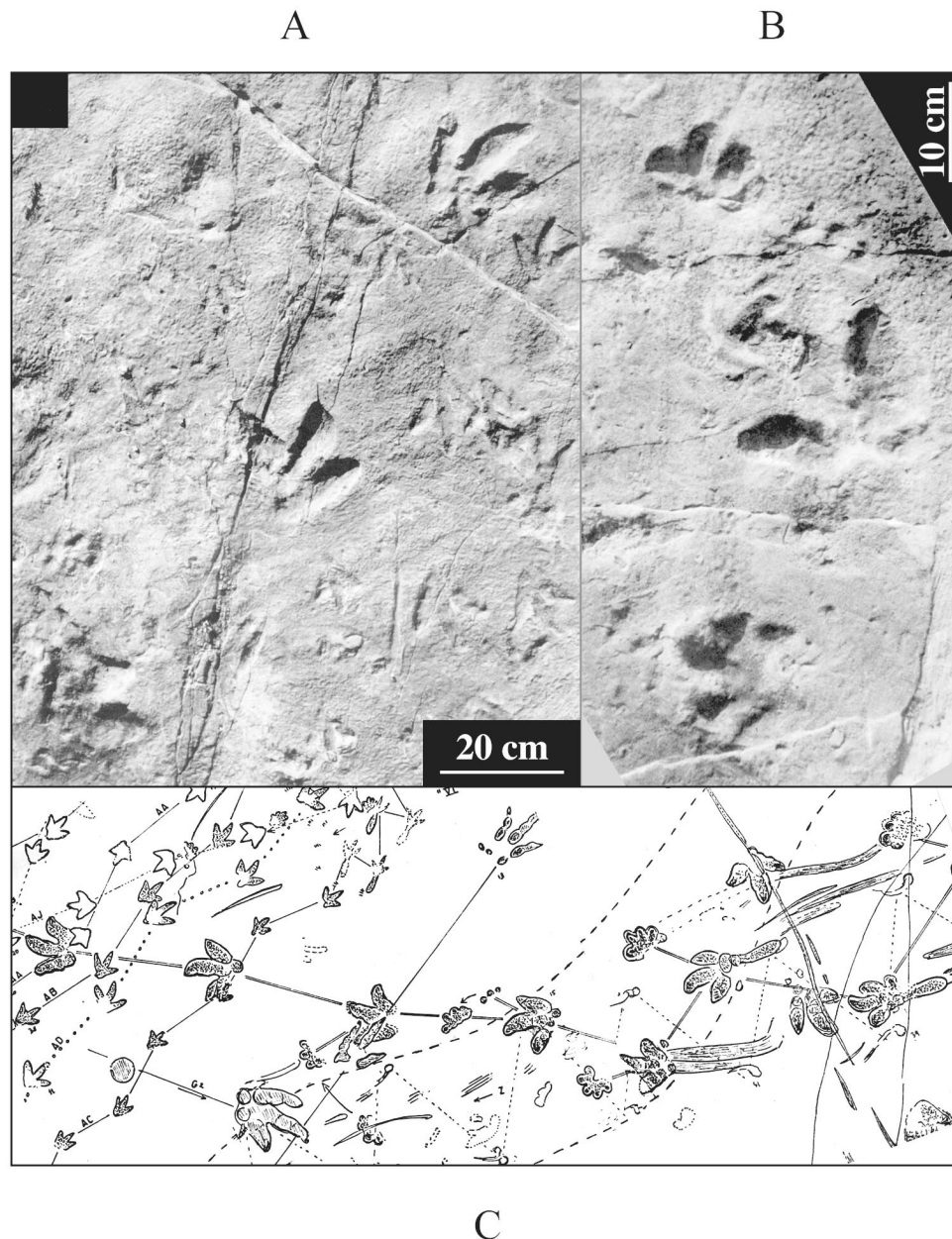


FIGURE 19.32 *Moyenisauropus natator*, natural molds. (A) Holotype (trackway of a large individual going from lower left to upper right). (B) Manus and pes of holotype. (C) Drawing by Ellenberger of holotype trackway (X). (From Ellenberger 1974)

became abundant, *Rhynchosauroides* very rare, and the track assemblage subsequently remains consistent through the remainder of the Early Jurassic part of the Newark Supergroup. *Otozoum* also appears in the Early Jurassic, although it remains a rare form (Rainforth 2000) except in the most northern basins. Indeed, the appearance of track assemblages with *Anomoepus* represents the stabilization of dinosaurian

dominance that would last for the next 135 million years.

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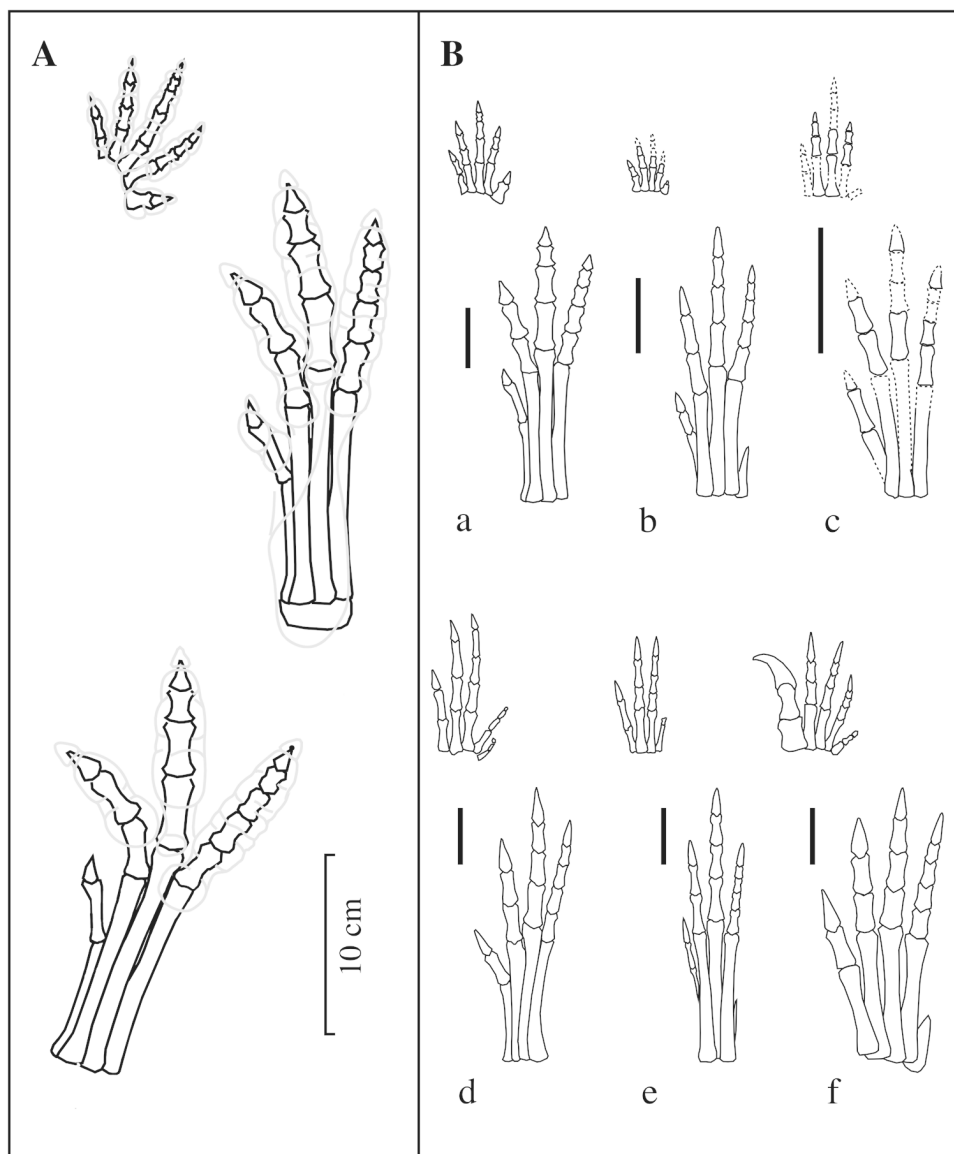


FIGURE 19.33 Skeletal reconstruction of the manus and pes of *Anomoepus* compared with those of other early Mesozoic dinosaurs. (A) Manus and pes of *Anomoepus*, reconstructed. Note that rotation of the metatarsus is necessary in order to reconcile the walking and sitting pes impressions. Metatarsal length is drawn to allow for distal tarsals, astragalus, and pedal extensor tendons. (B) Skeletal reconstructions of various dinosaurian manus and pedes; a, *Anomoepus scambus*; b, *Lesothosaurus diagnosticus* (pes after Thulborn 1972; manus after Sereno 1991); c, *Scutellosaurus lawleri* (after Colbert 1981); d, *Heterodontosaurus tuckii* (after Santa Luca 1980); e, *Coelophysis bauri* (after Colbert 1989); f, *Anchisaurus coelurus* (after Galton 1976). Scales in B are 5 cm.

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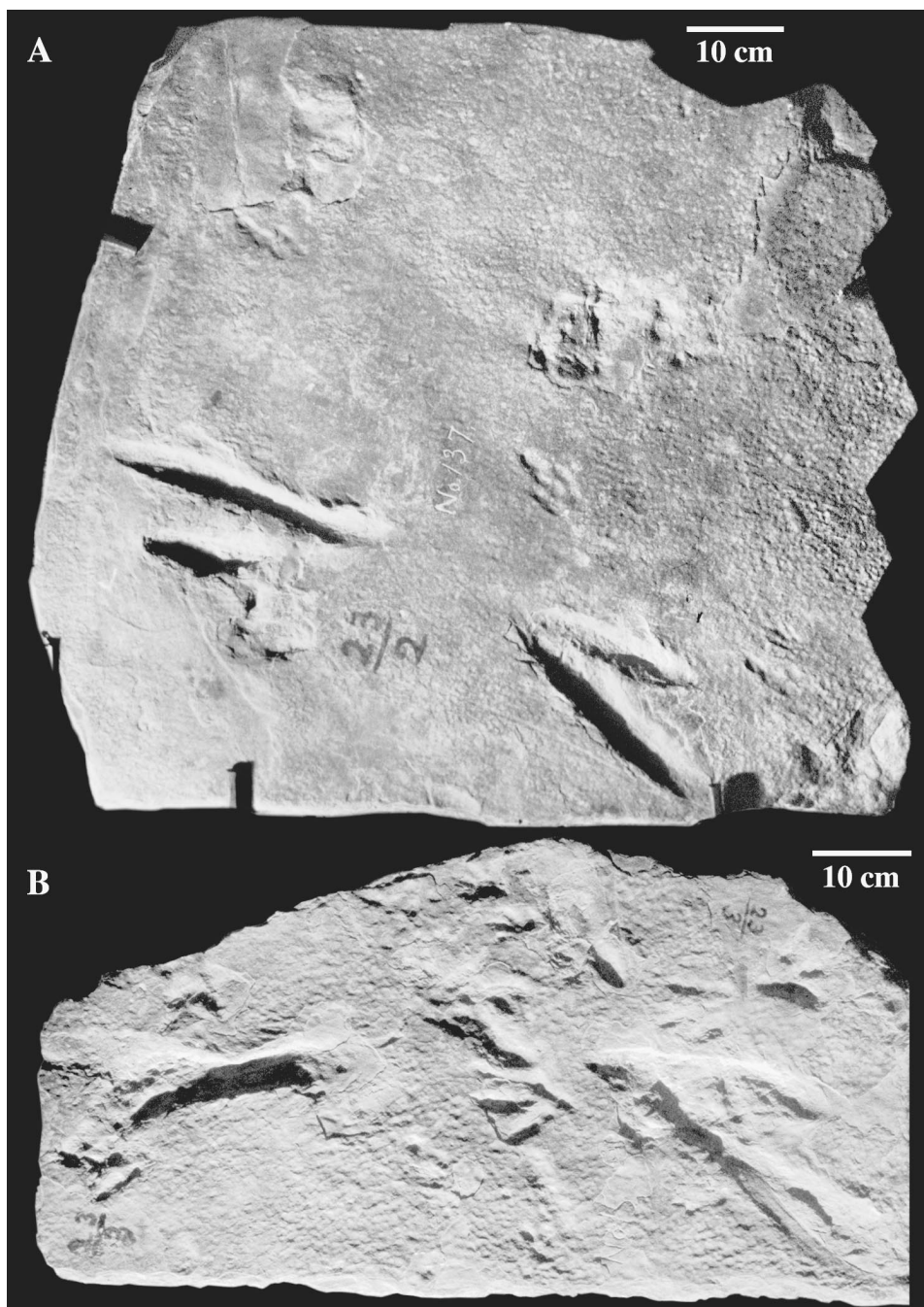


FIGURE 19.34 Natural molds, illuminated from below, of *Harpagopus giganteus*. (A) Holotype (AC 23/2). Note the faint *Anomoepus* trackway going from lower left to upper right. (B) AC 23/3 referred specimen. Note that whereas AC 23/2 has two pairs of grooves, AC 23/3 apparently has three.

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APPENDIX I

Material and Systematics

The purposes of this appendix are to trace the complex details of the synonymy presented in this chapter and to identify the key specimens.

Tridactyl footprints with associated manus impressions were first described and figured by James Deane (1845, 1847), although he deferred to Edward Hitchcock to assign a name to these tracks. Hitchcock found it necessary to erect a new genus, *Anomoepus* (E. Hitchcock 1848), for these quadrupedal ichnites, describing *A. scambus* (the type species) and referring *Sauroidichnites barratti* (E. Hitchcock 1837) to the new genus. The latter ultimately became the basis for *Sauropus barratti*, the type of which (AC 20/4) is an indeterminate ichnotaxon (for a full discussion of *S. barratti*, see Olsen and Baird 1986).

SENIOR SYNONYMS OF *Anomoepus scambus*: Reversal of Precedence

When Edward Hitchcock began naming ichnotaxa, he was applying the names to the footprint morphologies. However, in 1845, he took the new approach of naming the animals that made the footprints rather than the tracks themselves. Hence he replaced the genus *Ornithoidichnites* with several new genera, including *Eubrontes* and *Fulicopus*. In 1848, Hitchcock replaced the generic names given in 1845, explaining that because “the names were not accompanied by drawings or descriptions, they would not be allowed as authoritative by the rules adopted among naturalists; and therefore, in this paper, I have made several alterations, as well as additions” (1848:134). Indeed, he never again refers to the names given in 1845! However, many (if not all) of the 1845 taxa are actually valid because published descriptions already existed (albeit within the genera *Ornithichnites* and *Ornithoidichnites*) (ICZN, art. 12 [Names Published Before 1931; International Commission on Zoological Nomenclature 1999]).

Prior to 1848, Hitchcock was not sure that there were any quadrupeds with a birdlike pes among Connecticut Valley tracks. Hence on the basis of pes impressions alone, he had named several taxa that subsequently were placed within *Anomoepus*. We propose

that *Anomoepus scambus* be considered a *nomen protectum*, the senior synonyms not having been used since the 1840s. In the next section, we provide documentation in accordance with ICZN, article 23.9 (Reversal of Precedence) (International Commission on Zoological Nomenclature 1999).

Ornithoidichnites cuneatus E. Hitchcock 1841

In either 1836 or 1837, Dr. Joseph Barratt of Middletown, Connecticut, verbally named and described *Ornithichnites cuneatus* for footprints on a slab found in Middletown. The species is listed in the 1837 classification scheme of Hitchcock. In 1841, Hitchcock replaced the name *Ornithichnites* (E. Hitchcock 1836; type species *O. giganteus*), meaning “stony bird tracks,” with *Ornithoidichnites*, meaning “resembling the track of a bird.” This publication also provided the first written description of *Ornithoidichnites cuneatus* (E. Hitchcock 1841:488). Barratt’s original specimen was figured in that work as plate 48, figure 45 (also figure 106); Hitchcock also discussed a specimen from South Hadley that subsequently became known as “Noah’s raven” (AC 16/2; E. Hitchcock 1841:pl. 48, fig. 55; in this chapter, figure 19.26). A third specimen was also figured (E. Hitchcock 1841:pl. 39, fig. 25). These three illustrated specimens thus constituted the type series. We have been able to identify and locate only AC 16/2 and thus designate it the lectotype.

Ornithoidichnites fulcoides E. Hitchcock 1843

Ornithoidichnites fulcoides was named for material from Turners Falls resembling footprints of *Fulica americana* (coot). On the basis of the trackway configuration, Hitchcock speculated that the trackmaker was quadrupedal, although manus impressions were lacking. It is not known how many specimens Hitchcock examined; two figures were provided (E. Hitchcock 1843:pl. XI, figs. 3 and 4), and therefore these represent the type material. However, it is unclear from this work and from subsequent works by Hitchcock whether the single footprint in his figure 3 (our figure 19.9) is from the slab illustrated in his figure 4. The slab was originally in the possession of Dr. James Deane of Greenfield, Massachusetts, who divided it in two and gave half to Hitchcock (AC 19/18). The portion remaining in Deane’s collection unfortunately was destroyed (E. Hitchcock 1843). We therefore designate AC 19/18 (figure 19.10) the lectotype of *O. fulcoides*.

Hitchcock (1843) tentatively referred AC 16/2 to *O. fulcoides*; he subsequently referred all material previously classified as *O. cuneatus* to *O. fulcoides* (E. Hitchcock 1844) on the grounds that the former was too poorly preserved.

Ornithoidichnites gracillimus

E. Hitchcock 1844

Ornithoidichnites gracillimus was named for footprints resembling *O. fulcoides*, but smaller. These footprints originally were mentioned and figured by Deane (1844:pl. 11, cited in E. Hitchcock 1844:305), although he deferred to Hitchcock to name them. Deane referred to three slabs bearing the new species, one of which was disposed of to the British Museum before Hitchcock had a chance to study it. However, Hitchcock mentioned that he had a single specimen, from Turners Falls, in his own possession (E. Hitchcock 1844:pl. III, fig. 4), although it is not clear whether this is one of the slabs Deane described. This specimen is therefore the holotype of *O. gracillimus*. Although the match is not exact, the figured specimen (figure 19.21) most closely resembles AC 37/18 (old no. 129) from Turners Falls.

Eubrontes gracillimus E. Hitchcock 1845

The type species of *Eubrontes* is *E. giganteus*, formerly *Ornithichnites giganteus* (E. Hitchcock 1836:317) and *Ornithoidichnites giganteus* (E. Hitchcock 1841:484). The material previously referred to *O. gracillimus* was renamed *E. gracillimus*. The holotype is therefore that of *O. gracillimus* (E. Hitchcock 1844:pl. III, fig. 4; possibly AC 37/18).

Fulicopus minor E. Hitchcock 1845

The type species of *Fulicopus* is *F. lyellianus*, the replacement name for *O. lyellii* (E. Hitchcock 1843:257). *F. minor* was the name given to the trackmaker of *O. fulcoides*, and the name applied to all the material formerly called *O. fulcoides*. The lectotype material is therefore the same as that for *O. fulcoides* (i.e., AC 19/18).

Aethyopus minor E. Hitchcock 1848

The replacement name for *Fulicopus* was *Aethyopus* (the type species being *A. lyellianus*), although *O. fulcoides* (rather than *F. minor*) is the only synonym listed. However, it is not stated whether this name is a

simple replacement of the name *Fulicopus* (in which case *A. minor* is a junior synonym of *O. fulcoides*, and AC 19/18 is the lectotype specimen) or whether the genus was named for new material, with the *O. fulcoides* specimens then referred to *Aethyopus*. If the latter, then the type series of *Aethyopus minor* is composed of all the specimens listed in 1848 (i.e., AC 16/2 [old no. 61], 16/3 [old no. 130], 19/18 [old no. 60], 23/2 [old no. 137], 26/10 [old no. 136], 31/86 [old no. 159], 31/84 [old no. 62], and old no. 209 [specimen not located and presumed lost]). Figures 2 and 3 of plate 4 (E. Hitchcock 1848) are line drawings of individual footprints of *A. minor*; however, it is not possible to identify what specimens these tracks may belong to. However, the latter figure might represent the same footprint as illustrated for *O. fulcoides* (E. Hitchcock 1843:pl. XI, fig. 3). In addition, figures are provided of three slabs containing *A. minor* that were (in 1848) in the possession of Dexter Marsh (E. Hitchcock 1848:pl. 20, fig. 10; pl. 23, fig. 3; pl. 24, fig. 3). Of these three slabs of Marsh's, we have been able to locate only one—that illustrated by Hitchcock (1848) in his plate 20, figure 10—in the Hitchcock Ichnological Collection at the present time. This specimen subsequently was cataloged as AC 26/10 and figured again by Hitchcock (1858: pl. XL, fig. 1). We have not been able to determine whether Hitchcock ever acquired the other two figured slabs owned by Marsh; at any rate, they do not appear to be in the Pratt Museum now. Given Hitchcock's rationale for constructing this new species, from the list of specimens in the original type series, we designate AC 19/18—our lectotype of *O. fulcoides*—to be the lectotype of *Aethyopus minor* (for the same reasons that AC 19/18 is designated the lectotype of *O. fulcoides*).

Brontozoum gracillimum E. Hitchcock 1848

Brontozoum (E. Hitchcock 1848; type species *B. giganteum*, formerly *Ornithichnites giganteus* or *Ornithoidichnites giganteus*) was another of the genera Hitchcock named in 1848, when he dismissed his earlier (1845) trackmaker names. *B. gracillimum* was erected to replace *Ornithoidichnites gracillimus*. It is therefore a junior synonym of *Eubrontes gracillimus* because the latter taxon *had* been described and figured as *O. gracillimus* (by application of ICZN, art. 12 [International Commission on Zoological Nomenclature 1999]; *contra* E. Hitchcock 1848:134). Therefore,

the type specimen of *B. gracillimum* is the specimen figured in Hitchcock (1844) as plate III, figure 4 (possibly AC 37/18). Hitchcock referred several specimens to *B. gracillimum* (old nos. 89 [AC 31/6], 129 [AC 37/18], 130 [AC 16/3], 158 [AC 32/45], 134, 135, and 167 [we have not been able to locate the latter three in the Hitchcock Ichnological Collection]), including that which we have identified tentatively as the holotype of *O. gracillimus*, and he figured the species in his plate II, figure 3.



To summarize, we believe that *Aethyopus minor* is an objective junior synonym of *Fulicopus minor*, both of which are objective junior synonyms of *Ornithoidichnites fulicoides*. *Brontozoum gracillimum* is an objective junior synonym of *Eubrontes gracillimus*, which is in turn an objective junior synonym of *Ornithoidichnites gracillimus*. *Ornithichnites cuneatus* is a *nomen nudum*. *Ornithoidichnites fulicoides* is a junior subjective synonym of *Ornithoidichnites cuneatus*. Hence, of the names that might have priority over *Anomoepus scambus*, only *Ornithoidichnites cuneatus* and *O. gracillimus* are valid.

However, we propose that because the name *Ornithoidichnites* has not been used or been considered valid since 1844, it be considered a *nomen oblitum* in favor of its junior synonyms *Fulicopus* and *Eubrontes*; these synonyms in turn should be considered *nomina protecta*, leaving *F. minor* and *E. gracillimus* as senior synonyms of *Anomoepus scambus*. Neither of these two species is the type species of their respective genera; they differ significantly from their type species. We believe that these differences justify moving *F. minor* and *E. gracillimus* into a different genus. Hitchcock erected *Anomoepus* for specimens of quadrupedal trackways, although noting that the pes impressions were extremely similar to those of some of his previously named bipedal trackways—for example, *F. minor* and *E. gracillimus*. Therefore, we consider *F. minor* and *E. gracillimus* to be subjective synonyms of *Anomoepus scambus*. We propose that *F. minor* and *E. gracillimus* be considered *nomina oblita* in favor of *A. scambus* (which thus becomes a *nomen protectum*) because they have not been considered valid taxa since 1845, whereas *Anomoepus* has been used widely since 1848 (Lull 1953; Kuhn 1963; Haubold 1971, 1984, 1986;

Ellenberger 1974; Olsen and Galton 1984; Thulborn and Wade 1984; Clark and Fastovsky 1986; Olsen and Baird 1986; Olsen and Padian 1986; Olsen and Sues 1986; Gierlinski and Potemka 1987; Pienkowski and Gierlinski 1987; Weems 1987; Zhen et al. 1989; Gierlinski 1991, 1996; Farlow and Lockley 1993; Morales and Bulkley 1996; Rainforth and Lockley 1996; Farlow and Chapman 1997; Lockley 1997; Wright 1997; Lockley et al. 1998; Le Loeuff et al. 1999; Lockley and Matsukawa 1999; see also the references in Chure and McIntosh 1989, McDonald 1996, and this chapter). The type specimens of *A. scambus* are discussed in the next section.

THE LECTOTYPE OF *ANOMOEPIUS SCAMBUS*

Anomoepus scambus was based on four slabs from Turners Falls, Massachusetts, although none was designated the holotype.

The first slab described by Edward Hitchcock was owned by T. Leonard, Esq., of Greenfield, Massachusetts (E. Hitchcock 1848:pl. 21, figs. 1 and 2; pl. 13, figs. 1 and 2), and at the time Hitchcock stated that it was the best example. Unfortunately, there is no evidence that this or any other specimen owned by Leonard ever made it into the Hitchcock Ichnological Collection, so this slab is presumed lost.

The second slab on which Hitchcock based the species was in the collection of Dexter Marsh at the time (AC 19/14; E. Hitchcock 1848:pl. 21, fig. 3). The slab was acquired for the Hitchcock collection at Marsh's auction in Greenfield, Massachusetts, in 1853 (C. H. Hitchcock 1865) and was refigured in 1858 (plate XLIV, figure 1). We unfortunately have been unable to locate this specimen within the Hitchcock Ichnological Collection.

The third slab, AC 34/40 (old no. 142; E. Hitchcock 1848:pl. 20, fig. 6), is the slab for which the specific epithet ("crooked leg") is derived (figure 19.7), although Hitchcock adds that the name "may prove inappropriate for the species." James Deane, who was apparently the first to notice this distinctive genus (Deane 1845, 1847), presented this specimen to Hitchcock before or during 1848. However, Deane did not at first recognize the presence of birdlike feet associated with metatarsal and manus impressions. This specimen, although acquired originally by Deane, does not

seem to have been one of the several that Deane described, which were instead in Leonard's collection. We designate the specimen AC 34/40 as the lectotype of *Anomoepus scambus*.

The fourth specimen (counterparts AC 37/9 and 37/10; both parts together, old no. 170 of 1848 and 40/2 of 1858) consists of an isolated pes and metatarsus impression (E. Hitchcock 1848:pl. 13, fig. 3). This specimen was refigured as *Chimaera barratti* in 1858 (plate 21, figure 1; plate 59, figure 4). These slabs are currently in the Hitchcock Ichnological Collection (figure 19.13).

In 1858, Hitchcock subsumed *A. scambus* into *A. minor*, listing among the specimens of the new species both AC 19/14 and AC 34/40, again with no specimen being designated as the type. However, C. H. Hitchcock (1865) declared AC 16/5 to be the type of the species of *A. minor* (figure 19.11). Specimen AC 16/5 is from Turners Falls and was purchased at Marsh's auction of 1853 (C. H. Hitchcock 1865). Although it is not listed as *A. minor* in 1858, it is figured in plate IX, figure 1, of that work and stated to be in Hitchcock's collection. Lull (1904, 1915, 1953) curiously regarded *A. minor* as a junior synonym of *A. scambus*, but he listed AC 16/5 as a cotype of the older species, along with AC 34/40. This listing was incorrect because Hitchcock did not have AC 16/5 or figure it in 1848, when he named the senior species!

JUNIOR SYNONYMS OF *ANOMOEPUS SCAMBUS*

Based on examination of specimens (where possible), we consider the following to be synonyms of *Anomoepus scambus*.

Anomoepus minor E. Hitchcock 1858

In 1858, Edward Hitchcock replaced the specific epithet *scambus* with *minor*. *Anomoepus minor* therefore included all the material previously attributed to *A. scambus*. *A. minor* is obviously an objective synonym of *A. scambus*.

Plesiornis quadrupes E. Hitchcock 1858

Hitchcock erected this taxon for some of the material previously included in *Ornithichnites fulvicoides* and *Aethyopus minor*. The type series comprised AC 16/14,

19/18, 20/7, 21/30, 37/28, and 39/28 (the last number is an error and probably should be 37/29). Lull (1904, 1915) lists *Plesiornis quadrupes* as a subjective synonym of *Anomoepus intermedius*. However, in Lull (1953), *Plesiornis quadrupes* is again recognized as valid, and AC 19/18, 37/28, and 37/29 are listed as the type series. We consider AC 19/18 (figure 19.10) to be the lectotype, the taxon being an objective synonym of *Aethyopus minor* and thus of *Anomoepus scambus*.

Grallator gracillimus E. Hitchcock 1858

Grallator gracillimus is a replacement name for *Ornithoidichnites gracillimus* (and hence of *Eubrontes gracillimus* and *Brontozoum gracillimum*). It is therefore an objective junior synonym of *Eubrontes gracillimus* (*nomen oblitum*; senior synonym of *Anomoepus scambus*, *nomen protectum*). Thirteen specimens are referred; however, only those specimens from Turners Falls that were in the Hitchcock Ichnological Collection in 1844 can be part of the original (i.e., *O. gracillimus*) type series. Of the specimens Hitchcock listed, AC 16/3, 16/10, 16/14, 32/18, 32/45, and 37/18 are all from Turners Falls, although it is not known when they came into his possession. As noted previously, we believe that AC 37/18 may be the specimen figured in 1844, which would make it the holotype. However, we consider *A. scambus* to be the valid synonym of *E. gracillimus*.

Brontozoum isodactylum E. Hitchcock 1858

In 1858, Hitchcock named *Brontozoum isodactylum*, listing *Ornithoidichnites fulvicoides* (E. Hitchcock 1843) and *Aethyopus minor* (E. Hitchcock 1848) as prior synonyms. The species was figured in plates XII, figure 3; XL, figure 1; XLVI, figure 3; and LVII, figure 4. The type series consisted of AC 6/3, 16/2, 16/3, 16/5, 17/2, 21/4, 22/5, 22/12, 26/10, 28/2, 31/86, 33/10, 35/4, 35/31, 35/37, 35/40, 37/22, 37/27, 39/2, 40/6, 41/21, and 41/34. On December 10, 1862 (E. Hitchcock 1866:86), at a meeting of the American Academy of Arts and Sciences (AAAS, proceedings not published until 1866), he stated that the name *B. isodactylum* was not reliable and should be dropped. He reiterated this suggestion in 1865, stating that *B. isodactylum* "ought not be retained. It is hardly necessary to offer here the particular reasons which led to [its] rejection" (E. Hitchcock 1865:2). Most of the specimens of *B. isodactylum* were moved into the new species *A. in-*

termedius (E. Hitchcock 1865:2), and the remainder were placed in the new species *B. divaricatum* (E. Hitchcock 1865:7). (It should be noted that in 1862 Hitchcock considered all the specimens of *B. isodactylum* to be *A. intermedius* and used the name *B. isodactylum* for a new species of larger tridactyl tracks [E. Hitchcock 1866:86]. This new formulation of *B. isodactylum* presumably is the same as *B. divaricatum* of 1865.) We consider *B. isodactylum* (E. Hitchcock 1858) to be a subjective synonym of *A. scambus*.

***Anomoepus curvatus* E. Hitchcock 1863**

Anomoepus curvatus was named by Hitchcock in 1863 and illustrated (his figure 1) with an outline drawing of what is clearly AC 52/10 (our figure 19.23) in a paper that expanded on the oral report given to the AAAS in December 1862 (E. Hitchcock 1866). He made no mention of *Anomoepus curvatus* in this latter work; however, *Apatichnus curvatus* was named, and the type specimen was listed as AC 44/2, although Hitchcock was “not sure it is an *Apatichnus*, for as yet we find no fore-foot” (1866:86). It seems likely that after the oral presentation of 1862 Hitchcock decided that the specimen (AC 44/2) tentatively named *Apatichnus curvatus* belonged instead within *Anomoepus*. He gave a description of *Anomoepus curvatus* in 1865 in which he noted that the forefoot is “not yet found on any specimen” (E. Hitchcock 1865:5). Among the referred specimens, he listed AC 44/2, and C. H. Hitchcock (1865) noted that *Anomoepus curvatus* is one of several taxa represented on that slab. However, because AC 52/10 was the first specimen to be described and figured, we believe it to be the holotype. It has no sitting or manus impressions. The right pes impression on the slab looks somewhat more slender and more curved than *A. scambus*, but the left pes impression of the two trackways on the slab are indistinguishable from *A. scambus* only by being slightly larger (figure 19.23). The differences among the successive tracks of the single individual and with *A. scambus* reflect individual variation, and *A. curvatus* is a junior subjective synonym of *A. scambus*.

***Anomoepus intermedius* E. Hitchcock 1865**

Hitchcock named and figured *Anomoepus intermedius* in 1865 (p. 2), although the name is mentioned in the proceedings of the AAAS meeting of December 10, 1862 (E. Hitchcock 1866). In 1863, he compared *A.*

curvatus with *A. intermedius* but did not provide a coherent description, figures, or specimen numbers of the latter. The type series is composed of 18 specimens (AC 16/3, 19/14, 21/3, 26/10, 32/57, 48/1, 50/1, 50/2, 51/1, 51/2, 51/5, 51/9, 51/14, 52/4, 53/5, 53/10, 54/13, and 55/112), including several that earlier had been included in the type series of *Brontozoum isodactylum* (thus *A. intermedius* is a subjective, possibly objective, synonym of *B. isodactylum*, depending on which of the type series one would wish to designate the lectotypes of both species). Specimen AC 32/57 has a paper label saying “*Anomoepus intermedius*. new species? [illegible] no. 16/14.” This specimen was figured originally by Deane (1861:pl. 33). However, C. H. Hitchcock stated that a different, much more spectacular slab (AC 48/1) is “probably the typical specimen of *A. intermedius*, showing the impressions of all four feet and the tail” (1865:82). Lull (1904, 1915, 1953) followed C. H. Hitchcock in considering AC 48/1 the holotype. The lectotype individual is presumably the trackway with the sitting impression. In addition, Lull (1904, 1915, 1953) considered several other species to be junior synonyms of *A. intermedius*: *Sauropus barratti*, *Aethyopus minor* (in part), *Plesiornis quadrupes* (removed from *A. intermedius* in Lull 1953, however), *Plectropterna minitans* (removed from *A. intermedius* in Lull 1915, 1953), and *Apatichnus holyokensis*. Specimen AC 48/1 is a remarkable slab, for in addition to the trackway alluded to previously, the slab has a long trackway of 15 pes impressions, most with clear skin impressions, ending with a unique tail sitting trace (figures 19.24 and 19.25). However, we can see no differences between AC 48/1 or AC 32/57 and *A. scambus* other than a minor difference in size, and thus consider *A. intermedius* to be a subjective synonym of *A. scambus*.

***Anomoepus gracillimus* C. H. Hitchcock**

C. H. Hitchcock (E. Hitchcock 1865:6, footnote) transferred all the specimens of *Grallator gracillimus* to *Anomoepus gracillimus*. This synonymy was followed by Hay (1902) and by Lull (1904, 1915, 1953). Lull, however, lists AC 50/1 as the type, which it cannot be because it was collected in 1862 (E. Hitchcock 1865), long after the species was named. Indeed, the specimen figured by Hitchcock (1844:pl. III, fig. 4; possibly AC 37/18) must be the holotype. As with *Grallator gracillimus*, *A. gracillimus* is an objective junior synonym of

Eubrontes gracillimus (*nomen oblitum*); hence we refer it to *Anomoepus scambus*.

***Anomoepus minimus* E. Hitchcock 1865**

Hitchcock (1865:5, pl. 2, fig. 2) gave the name *Anomoepus minimus* to the smallest tracks he recognized as having *Anomoepus*-type hands. The type specimen as figured by E. Hitchcock (1865) and identified by C. H. Hitchcock (1865) is AC 55/112 (Lull 1904, 1915, 1953). The specimen shows a tridactyl pes and a probable pentadactyl manus (figure 19.20). The specimen differs in size and minor proportional differences from *A. scambus* in ways accountable for by growth (figure 19.19). One specimen listed in the type series of 1865, AC 34/19, was listed in the type series of *Corvipes lacertoideus* (E. Hitchcock 1858) and is now apparently lost. The other specimens listed by E. Hitchcock appear to be small *Anomoepus* indistinguishable from *A. scambus* except by minor size-related differences (figure 19.18), and we consider the species to be a junior subjective synonym of *A. scambus*.

***Anomoepus cuneatus* C. H. Hitchcock 1889**

C. H. Hitchcock apparently first mentioned this species in 1865 in his description of AC 16/11. He described the slab, from Turners Falls, as having “two tracks of *Brontozoum validum*, two of *Apatichnus* (?) *bellus*, one of *Grallator* (?) *tenuis*, one of *A. cuneatus* (?) and others” (C. H. Hitchcock 1865:52). The specific epithet *cuneatus* is otherwise used in the work of 1865 only for *Grallator cuneatus*, which C. H. Hitchcock thought it resembled (possibly “*A.* *cuneatus* is a typographical error replacing “*G.* *cuneatus*”). When C. H. Hitchcock formally proposed the species in 1889, he curiously made no mention of this slab and instead listed two other slabs (AC 29/1 and AC 50/2), with the type specimens designated as a specimen in the Mount Holyoke Museum (listed as no. 105 by Lull 1904, 1915; now destroyed, Lull 1953) and its counterpart at the Museum of Dartmouth College (now in the Montshire Museum of Science: MM 5125, old no. 130) (figure 19.28). The last specimen is indistinguishable from *Anomoepus scambus*, particularly those specimens originally referred to *A. crassus*. The tracks on AC 16/11 are barely discernible and are certainly indeterminate. Because C. H. Hitchcock provided no figures or detailed description in his 1889 paper, it is impossible to tell which of the many *Anomoepus* tracks on AC 29/1 and

AC 50/2 he intended to belong in *A. cuneatus*. As far as we can tell, the species *Anomoepus cuneatus* is thus a *nomen nudum* and hence invalid. In any case, none of the *A. cuneatus* we have examined can be distinguished from *A. scambus*, except by size.

***Apatichnus crassus* C. H. Hitchcock 1889**

C. H. Hitchcock (1889) named *Apatichnus crassus* on the basis of robust specimens from the Towaco Formation at the Vreeland Quarry in Lincoln Park, New Jersey. The type specimen (Rutgers main slab), as designated by C. H. Hitchcock without figures (1889:fig. 29), consists of two consecutive pes impressions, the second of which is a right sitting trace with an unusually clear metatarsal impression and an impression of digit I. Several partially overlapping right manus impressions are also present. The type of *Apatichnus crassus* differs from *A. scambus* only in size and in the incomplete impression of the manus, and we consider it to be a junior subjective synonym. Other material from the Towaco Formation bridges these differences entirely (Olsen 1995) (figures 19.15 and 19.29). In fact, the slab that Lull (1904, 1915, 1953) thought to be the type slab of *A. scambus* (i.e., AC 16/5) has a virtually identical pose and identical proportions (figures 19.11 and 19.29).

***Anomoepus isodactylus* C. H. Hitchcock 1889**

C. H. Hitchcock resurrected the species *Anomoepus isodactylus* in 1889, listing MHM 142 and 128 (counterparts, both destroyed by fire) from the Dickinson Quarry, in South Hadley, Massachusetts, as the holotype, and MHM 112 and 126 as referred specimens. No figures were provided. He stated that the species “may be the same as with certain impressions at first called *Brontozoum isodactylum* by my father, but does not correspond to the reference by him of the most of that species to *Brontozoum divaricatum* in the supplement” (C. H. Hitchcock 1889:125). Of course, the material that E. Hitchcock originally assigned to *B. isodactylum* was referred subsequently to both *B. divaricatum* and *Anomoepus intermedius*.

***Anomoepus crassus* Lull 1904**

Lull (1904) considered the material described as *Apatichnus crassus* (C. H. Hitchcock 1889) to belong instead to *Anomoepus*, which we follow here. However,

we consider *A. crassus* to be a subjective junior synonym of *A. scambus*.

***Anomoepus giganteus* C. H. Hitchcock ed. Grier 1927**

C. H. Hitchcock named *Anomoepus giganteus* for a specimen at Dartmouth College (DC 8), collected from either Granby Crossing or Aldrich's Mills, Massachusetts. However, there is no record of a description or of a figure of this species; hence it is a *nomen nudum*.

***Apatichnus circumagens* E. Hitchcock 1858**

An understanding of the history of this ichnotaxon is hampered by apparent errors in references to figures in Hitchcock (1858), by errors in specimen numbers, and by the loss of several key specimens from the Hitchcock collection. Of the type series of 15 specimens Hitchcock listed, three are missing (AC 11/2, 21/2, and 23/8); one is mislabeled (AC 33/49 belongs in the type series of *Apatichnus* [*Batrachopus*] *bellus*, p. 101); and another is a slab listed as *Grallator gracilimus* on page 73 (figure 19.21). The loss of AC 21/2 is especially unfortunate because it was designated the type specimen by C. H. Hitchcock (1865) but was, according to him, shattered when another specimen collapsed on it (and the fragments subsequently lost). Likewise, AC 23/8 (now lost) was the specimen figured by Lull (1904, 1915, 1953). All but two of the existing specimens (AC 1/3, 5/8, 9/11, 14/5, 29/1, 16/1, and 16/10) are identical to the usual concept of *Anomoepus*, and none has manus impressions. One specimen has the elongate digit III characteristic of grallatorids (AC 33/50), and the possible manus impression associated with it appears not to belong to the pes. Finally, AC 12/3 lacks pads and is indeterminate. Unquestionable manus impressions in the type series evidently were limited to the specimens now lost. From Hitchcock's and Lull's drawings, presumably of these specimens, we see an *Anomoepus*-like form with a slightly asymmetrical pes and a poorly known pentadactyl manus.

The best existing tracks of the type series are on slabs AC 1/3, 29/1, and 20/6, which represent the same individual because these slabs were continuous in the field. An example from the trackway labeled *Apatichnus circumagens* by E. Hitchcock is shown in figure 19.22. The track is indistinguishable from *Anomoepus*

and differs from *A. scambus* in size-related features alone. Given the lack of the designated types and the identity of most of the existing specimens with *Anomoepus*, we consider this ichnospecies a subjective synonym of *A. scambus*.

POSSIBLE JUNIOR SYNONYMS OF *ANOMOEPUS SCAMBUS*

***Corvipes lacertoideus* E. Hitchcock 1858**

Edward Hitchcock (1858) listed 14 specimens as belonging to *Corvipes lacertoideus*, but neither he nor C. H. Hitchcock (1865) designated a type specimen. However, AC 32/1 is labeled as the type specimen in the Hitchcock Ichnological Collection and is so listed in the anonymous list of types compiled probably by C. H. Hitchcock; hence we designate it the lectotype. As defined by this specimen, *Corvipes lacertoideus* has a pentadactyl manus and a tridactyl pes. No pads are visible (figure 19.16). The specimen is indistinguishable from a small *Anomoepus*, but because of its poor preservation it is best regarded as indeterminate. All the other specimens listed by Hitchcock as belonging to this form are also indistinguishable from small *Anomoepus*.

The best example of what Hitchcock considered to be *Corvipes lacertoideus* is seen on AC 16/5, the opposite side of the slab bearing the supposed type of *Anomoepus scambus* as listed by C. H. Hitchcock (1865) and by Lull (1904, 1915, 1953). Several trackways clearly belonging to small *Anomoepus* are present (figure 19.16).

***Tarsodactylus caudatus* E. Hitchcock 1858**

Hitchcock (1858:98) designated several poorly preserved quadrupedal trackways with tail drag marks from Turners Falls as *Tarsodactylus caudatus*. Two specimens (AC 6/1 and AC 33/35) comprised the type series. The latter specimen appears to be lost, and the former is a slab bearing trackways of an *Anomoepus*-like larger ichnite, two trackways of smaller animals, and, on a lower layer, two tracks of grallatorids along with an indistinct trail (one of the type series of *Orthodactylus floriferus* [E. Hitchcock 1858]). One of the two smaller trackways must comprise the lectotype of *Tarsodactylus caudatus*. Both are very poor quadrupe-

dal trackways, which because of a lack of pads and inconsistency between successive tracks must be regarded as indeterminate. However, they are most probably poor examples of *Anomoepus*.

Lull (1904, 1915, 1953) cited AC 42/5 as the type specimen of *Tarsodactylus caudatus*, presumably because C. H. Hitchcock called it “the finest slab of this species in the Cabinet” (1865:78). However, this specimen was not known when the species was named. The slab bears two parallel quadrupedal trackways with tail drags. The trackways are poor; the manus and pes lack pads; and there is no justification for Lull’s (1953:fig. 137) idealized drawings. The trackways are indistinguishable from very poor, small *Anomoepus* trackways.

***Harpagopus giganteus* E. Hitchcock 1858**

Harpagopus giganteus E. Hitchcock (1848:247) is the type species for large groovelike impressions on footprint slabs, in the case of *H. giganteus* associated with *Brontozoum parallelum* and *Aethyopus minor* (E. Hitchcock 1848). The type series consists of AC 23/2 (old no. 137) and AC 23/3 (old no. 152); AC 23/2 is figured in Hitchcock’s (1848) plate 23, figure 5, and thus we designate this specimen the lectotype.

***Antipus bifidus* E. Hitchcock 1858**

Antipus bifidus (E. Hitchcock 1858:116) was named for the groovelike impressions on AC 23/2, 23/3, and 17/2; these specimens are figured in Hitchcock’s (1858) plate XLVIII, figure 10; plate XXXVI, figure 8; and plate XXXVI, figure 7, respectively. *A. flexiloquus* is the type species. Hitchcock made no reference to his earlier taxon *Harpagopus giganteus*, although *A. bifidus* is clearly a junior objective synonym. We interpret these impressions (figure 19.34) as being associated with the *Anomoepus* pes prints and as having been made by a sweeping motion of the manus toward and then away from the midline.

***Apatichnus holyokensis* C. H. Hitchcock 1889**

The type specimen of *Apatichnus holyokensis* was a specimen in the collection of the Mount Holyoke Museum and was destroyed by fire. C. H. Hitchcock listed an additional specimen, AC 52/4, and Lull (1904) synonymized *Apatichnus holyokensis* with *Anomoepus intermedius*. We have been unable to examine AC 52/4.

***Ornithichnites culbertsoni* King 1844**

This species was described for material from the “Coal Measures” of Pennsylvania (King 1844). King (1844:176, fig. 2) initially figured and described the material as *Ornithichnites culbertsoni*. Abel (1935) considered the material to belong to ?*Anomoepus culbertsoni*. Lyell (1846) observed that these traces are native American petroglyphs, and thus we confidently can assign them to *Homo sapiens* rather than to *Anomoepus*.

***Ornithichnites gallinuloides* King 1844**

Like *Ornithichnites culbertsoni*, this footprint is from the “Coal Measures” of Pennsylvania (King 1844:176, fig. 1), and again Abel (1935) considered it to be *Anomoepus? gallinuloides*. Lyell’s (1846) conclusion applies here as well.

***Brontozoum expansum* E. Hitchcock 1841**

The type specimen of *Brontozoum expansum* (old no. 59 [AC 40/5]; E. Hitchcock 1841:pl. 38, fig. 22) has the wide divarication typical for *Anomoepus*, and thus we thought it should be mentioned here. However, it is unusually large and has been damaged badly by preparation; it may instead be a poor grallatorid.

REMOVED FROM ANOMOEPUS

The type specimen of *Anomoepus major*, designated by C. H. Hitchcock (1865:56) and listed in the type series in 1858, is AC 1/1. This specimen has an especially confused history, being confounded with the histories of the ichnogenera *Amblonyx*, *Sauropus*, and *Anchisauripus*. This history is detailed partially in Olsen and Baird (1986). The pes is clearly that of a grallatorid (*Anchisauripus tuberosus*), but there are possible metatarsal, ischial, and manus impressions on the slab, which is what caused Hitchcock to make it a species of *Anomoepus*. C. H. Hitchcock (1865) also listed AC 1/7, a sitting specimen, as a cotype, but that specimen was not described until 1865, although it was mentioned in 1858. We agree with Gierlinski (1994) that both AC 1/1 and AC 1/7 are grallatorids. This conclusion is supported by osteometric comparisons (figure 19.19). Thus the species does not belong to *Anomoepus*; and if these tracks belong to a grallatorid, as argued by Olsen and Baird (1986) and by Gierlinski (1994), then they represent very rare examples of sitting traces of theropods.

APPENDIX II

Data for Figure 13.23

Name	ID.	Catalog Number	T	II	III	IV	T-IV	θ	III/II	III/IV	R	R'	T—R/	R'/T—R'	R/T—R
Type <i>Eubrontes giganteus</i>		AC 15/3	335.0	148.0	195.0	240.0	95.0	32.0	1.318	0.813	227.0	236.1	98.9	2.39	2.30
Type <i>Anchisauripus sillimani</i>		AC 4/6	150.0	62.0	90.0	96.0	54.0	32.0	1.452	0.938	85.0	88.4	61.6	1.44	1.38
Type <i>Grallator parallelus</i>	1	AC 4/1	67.0	21.5	41.0	33.0	34.0	29.0	1.907	1.242	38.0	39.3	27.7	1.41	1.37
	2	AC 4/1	68.0	23.0	40.0	34.0	34.0	22.0	1.739	1.176	39.0	39.7	28.3	1.41	1.38
	3	AC 4/1	70.0	23.5	38.5	36.0	34.0	25.0	1.638	1.069	35.0	35.8	34.2	1.05	1.02
	4	AC 4/1	70.0	23.0	42.2	39.0	31.0	28.0	1.835	1.082	40.0	41.2	28.8	1.43	1.39
ave		AC 4/1	68.8	22.8	40.4	35.5	33.3	28.0	1.780	1.143	38.0	39.2	29.6	1.32	1.28
stdev			1.5	0.9	1.6	2.6	1.5	3.2	0.117	0.082	2.2	2.3	3.0	0.2	0.2
Type <i>Anchisauripus tuberosus</i>		AC 39/1	160.0	70.0	105.0	105.0	55.0	24.0	1.500	1.000	98.0	100.2	59.8	1.68	1.64
Type <i>Otozoum moodii</i>	1	AC 4/1a	240.0	115.0	130.0	190.0	50.0	—	1.130	0.684	195.0	195.0	45.0	4.33	4.33
	2	AC 4/1a	240.0	110.0	137.0	200.0	40.0	22.0	1.245	0.685	190.0	193.6	46.4	4.17	4.09
	3	AC 4/1a	230.0	110.0	140.0	170.0	60.0	21.0	1.273	0.824	195.0	198.3	31.7	6.26	6.16
	4	AC 4/1a	240.0	115.0	142.0	180.0	60.0	18.0	1.235	0.789	190.0	192.4	47.6	4.04	3.99
ave		AC 4/1a	237.5	112.5	137.3	185.0	52.5	20.3	1.220	0.742	192.5	195.6	41.9	4.66	4.59
stdev			5.0	2.9	5.3	12.9	9.6	2.1	0.062	0.072	2.9	2.6	7.4	1.0	1.0
Type <i>Otozoum moodii</i>	1	AC 4/1b	235.0	110.0	120.0	180.0	55.0	23.0	1.091	0.667	185.0	188.8	46.2	4.09	4.00
	2	AC 4/1b	250.0	120.0	145.0	205.0	45.0	22.0	1.208	0.707	195.0	198.6	51.4	3.87	3.80
	3	AC 4/1b	245.0	115.0	140.0	190.0	55.0	27.0	1.217	0.737	185.0	190.3	54.7	3.48	3.38
	4	AC 4/1b	250.0	120.0	150.0	210.0	40.0	24.0	1.250	0.714	195.0	199.4	50.6	3.94	3.85
	5	AC 4/1b	260.0	115.0	155.0	200.0	60.0	25.0	1.348	0.775	187.0	191.5	68.5	2.80	2.73
ave		AC 4/1b	248.0	116.0	142.0	197.0	51.0	24.2	1.223	0.720	189.4	193.7	54.3	3.6	3.6
stdev			9.1	4.2	13.5	12.0	8.2	1.9	0.092	0.040	5.2	4.9	8.5	0.5	0.5
Type “ <i>Anchisauripus parallelus</i> ”	1	AC 54/8	144.5	48.0	90.0	101.0	43.5	30.0	1.875	0.891	90.0	93.2	51.3	1.82	1.75
	2	AC 54/8	91.0	41.0	58.0	60.0	31.0	26.0	1.415	0.967	54.0	55.4	35.6	1.56	1.52
	3	AC 54/8	130.0	57.0	82.0	83.0	47.0	30.0	1.439	0.988	80.0	82.8	47.2	1.76	1.70
	4	AC 54/8	93.0	35.5	53.0	56.0	37.0	20.0	1.493	0.946	50.0	50.8	42.2	1.20	1.18
	5	AC 54/8	210.0	88.0	123.0	142.0	68.0	19.0	1.398	0.866	122.0	123.7	86.3	1.43	1.41
Small grallatorid	1	AC 23/2	89.0	35.0	60.0	50.0	39.0	9.0	1.714	1.200	49.0	49.2	39.8	1.23	1.23
	2	AC 23/2	89.0	34.0	60.0	56.5	32.5	10.0	1.765	1.062	53.0	53.2	35.8	1.49	1.48
	3	AC 23/2	90.0	36.0	60.0	55.0	35.0	—	1.667	1.091	52.0	—	90.0	—	—
ave		AC 23/2	89.3	35.0	60.0	53.8	35.5	9.5	1.715	1.118	51.3	51.5	37.8	1.36	1.36
stdev			0.6	1.0	0.0	3.4	3.3	0.7	0.049	0.073	2.1	2.9	30.2	0.2	0.2
Type <i>Anomoepus scambus</i> with <i>Antipus</i>	4	AC 23/2	85.0	32.0	52.0	65.0	20.0	55.0	1.625	0.800	62.0	69.9	15.1	4.63	4.11
Large grallatorid		AC 45/1	315.0	145.0	180.0	222.0	93.0	38.0	1.241	0.811	210.0	222.1	92.9	2.39	2.26
		AC 45/1	310.0	130.0	175.0	225.0	85.0	33.0	1.346	0.778	200.0	208.6	101.4	2.06	1.97
		AC 45/1	305.0	130.0	175.0	222.0	83.0	32.0	1.346	0.788	210.0	218.5	86.5	2.52	2.43
ave		AC 45/1	310.0	135.0	176.7	223.0	87.0	34.3	1.309	0.792	206.7	216.3	93.7	2.31	2.21
stdev			4.1	7.1	2.4	1.4	4.3	2.6	0.049	0.014	4.7	5.7	6.1	0.2	0.2

Large grallatorid	AC 45/1	310.0	130.0	180.0	220.0	90.0	36.0	1.385	0.818	215.0	226.1	83.9	2.69	2.56
	AC 45/1	305.0	130.0	170.0	230.0	75.0	40.0	1.308	0.739	200.0	212.8	92.2	2.31	2.17
ave	AC 45/1	307.5	130.0	175.0	225.0	82.5	38.0	1.346	0.778	207.5	219.5	88.0	2.49	2.36
stdev		3.5	0.0	7.1	7.1	10.6	2.8	0.054	0.056	10.6	9.4	5.8	0.3	0.3
Large grallatorid	AC 45/1	180.0	72.0	111.0	115.0	65.0	18.0	1.542	0.965	110.0	111.4	68.6	1.62	1.60
Small grallatorid	AC 45/1	105.0	45.0	65.0	70.0	35.0	22.0	1.444	0.929	65.0	66.2	38.8	1.71	1.68
Medium grallatorid	AC 45/1	165.0	70.0	95.0	120.0	45.0	27.0	1.357	0.792	100.0	102.8	62.2	1.65	1.61
Medium grallatorid	AC 45/1	180.0	75.0	115.0	117.0	63.0	32.0	1.533	0.983	115.0	119.6	60.4	1.98	1.91
<i>Anomoepus scambus</i>	AC 37/10	70.0	25.0	38.0	53.0	17.0	66.0	1.520	0.717	46.0	54.8	15.2	3.62	3.04
Type " <i>Anomoepus</i> " major	AC 1/7	182.0	76.0	118.0	118.0	64.0	35.0	1.553	1.000	115.0	120.6	61.4	1.96	1.87
Type <i>Anomoepus curvatus</i>	AC 52/10	78.0	35.0	41.0	60.0	18.0	53.0	1.171	0.683	58.0	64.8	13.2	4.91	4.40
	AC 52/10	78.0	30.0	42.0	59.0	19.0	55.0	1.400	0.712	58.0	65.4	12.6	5.18	4.60
	AC 52/10	79.0	32.0	44.0	58.0	21.0	52.0	1.375	0.759	58.0	64.5	14.5	4.46	4.01
	AC 52/10	78.0	33.0	46.0	60.0	18.0	49.0	1.394	0.767	59.0	64.8	13.2	4.93	4.48
	AC 52/10	78.0	38.0	46.0	57.0	21.0	45.0	1.211	0.807	60.0	64.9	13.1	4.97	4.60
ave	AC 52/10	78.2	33.6	43.8	58.8	19.4	50.8	1.310	0.746	58.6	64.9	13.3	4.87	4.40
stdev		0.4	3.0	2.3	1.3	1.5	3.9	0.110	0.048	0.9	0.3	0.7	0.3	0.2
Type <i>Plesiornis quadripes</i>	AC 19/18	78.0	34.0	40.5	62.0	16.0	71.0	1.191	0.653	50.0	61.4	16.6	3.70	3.02
	AC 19/18	79.0	33.0	41.0	61.0	18.0	69.0	1.242	0.672	50.0	60.7	18.3	3.31	2.73
	AC 19/18	78.0	33.0	41.5	61.0	17.0	72.0	1.258	0.680	52.0	64.3	13.7	4.68	3.79
ave	AC 19/18	78.3	33.3	41.0	61.3	17.0	70.7	1.230	0.669	50.7	62.1	16.2	3.83	3.12
stdev		0.5	0.2	0.3	0.2	0.6	1.5	0.014	0.006	1.0	1.8	2.3	0.7	0.5
Medium grallatorid	AC 9/14	103.0	39.0	58.0	59.0	44.0	30.0	1.487	0.983	56.0	58.0	45.0	1.29	1.24
	AC 9/14	104.0	37.0	63.0	59.0	45.0	27.0	1.703	1.068	60.0	61.7	42.3	1.46	1.42
a1	AC 9/14	103.5	38.0	58.0	58.0	45.5	24.0	1.526	1.000	56.0	57.3	46.2	1.24	1.21
a2	AC 9/14	103.5	38.0	59.7	58.7	44.8	27.0	1.572	1.017	57.3	59.0	44.5	1.32	1.29
a3	AC 9/14	103.5	38.0	59.7	58.7	44.8	27.0	1.572	1.017	57.3	59.0	44.5	1.32	1.29
ave a	AC 9/14	103.5	38.0	59.7	58.7	44.8	27.0	1.572	1.017	57.3	59.0	44.5	1.32	1.29
stdev		0.5	1.0	2.9	0.6	0.8	3.0	0.115	0.045	2.3	2.4	2.0	0.1	0.1
Medium grallatorid	AC 9/14	102.0	33.0	63.0	56.5	45.5	29.0	1.909	1.115	59.0	60.9	41.1	1.48	1.44
Medium grallatorid	AC 9/14	112.0	37.0	64.0	60.0	52.0	21.0	1.730	1.067	56.0	57.0	55.0	1.03	1.02
c1	AC 9/14	110.0	35.0	60.0	58.0	52.0	20.0	1.714	1.034	60.0	60.9	49.1	1.24	1.22
c2	AC 9/14	110.0	35.0	60.0	58.0	52.0	20.0	1.714	1.034	60.0	60.9	49.1	1.24	1.22
c3	AC 9/14	110.0	38.0	65.0	60.0	50.0	18.0	1.711	1.083	55.0	55.7	54.3	1.03	1.01
ave c	AC 9/14	110.7	36.7	63.0	59.3	51.3	19.7	1.718	1.061	57.0	57.9	52.8	1.10	1.08
stdev		1.2	1.5	2.6	1.2	1.2	1.5	0.010	0.025	2.6	2.7	3.3	0.1	0.1
Medium grallatorid	AC 9/14	120.0	40.0	67.0	67.0	53.0	25.0	1.675	1.000	64.0	65.6	54.4	1.20	1.18
d1	AC 9/14	127.0	41.0	74.0	71.0	56.0	30.0	1.805	1.042	67.0	69.4	57.6	1.20	1.16
d2	AC 9/14	123.5	40.5	70.5	69.0	54.5	27.5	1.740	1.021	65.5	67.5	56.0	1.20	1.17
ave d	AC 9/14	123.5	40.5	70.5	69.0	54.5	27.5	1.740	1.021	65.5	67.5	56.0	1.20	1.17
stdev		4.9	0.7	4.9	2.8	2.1	3.5	0.092	0.030	2.1	2.7	2.3	0.0	0.0

(continued)

Data for Figure 13.23 (Continued).

Name	ID	Catalog Number	T	II	III	IV	T-IV	θ	III/II	III/IV	R	R'	T-R/	R'/T-R'	R/T-R
Medium grallatorid	e1	AC 9/14	124.0	48.0	72.0	79.0	45.0	17.0	1.500	0.911	71.0	71.8	52.2	1.37	1.36
	f1	AC 9/14	120.0	43.0	74.0	72.0	48.0	22.0	1.721	1.028	72.0	73.3	46.7	1.57	1.54
	f2	AC 9/14	119.0	43.0	73.0	74.0	45.0	24.0	1.698	0.986	70.0	71.6	47.4	1.51	1.48
	ave f	AC 9/14	119.5	43.0	73.5	73.0	46.5	23.0	1.709	1.007	71.0	72.5	47.0	1.54	1.51
	Stdev		0.7	0.0	0.7	1.4	2.1	1.4	0.016	0.029	1.4	1.3	0.6	0.0	0.0
Medium grallatorid	g1	AC 9/14	119.0	43.0	72.0	71.0	48.1	25.0	1.674	1.014	71.0	72.7	46.3	1.57	1.53
	g2	AC 9/14	120.0	41.0	71.0	71.0	49.0	20.0	1.732	1.000	70.0	71.1	48.9	1.45	1.43
	g3	AC 9/14	120.0	41.0	72.0	72.0	48.0	18.0	1.756	1.000	71.0	71.9	48.1	1.49	1.48
	ave g	AC 9/14	119.7	41.7	71.7	71.3	48.3	21.0	1.721	1.005	70.7	71.9	47.8	1.51	1.48
	Stdev		0.6	1.2	0.6	0.6	0.6	3.6	0.042	0.008	0.6	0.8	1.4	0.1	0.1
Medium grallatorid	h	AC 9/14	122.0	43.0	71.0	73.0	49.0	25.0	1.651	0.973	72.0	73.7	48.3	1.53	1.49
Medium grallatorid	i	AC 9/14	132.0	47.0	80.0	77.0	55.0	22.0	1.702	1.039	71.0	72.3	59.7	1.21	1.19
Medium grallatorid	j	AC 9/14	113.0	40.0	72.0	68.0	45.0	19.0	1.800	1.059	65.0	65.9	47.1	1.40	1.38
Medium grallatorid	k	AC 9/14	153.0	52.0	93.0	85.0	68.0	28.0	1.788	1.094	83.0	85.5	67.5	1.27	1.23
Medium grallatorid	l	AC 9/14	112.0	40.0	69.0	68.0	44.0	24.0	1.725	1.015	69.0	70.5	41.5	1.70	1.66
Medium grallatorid	m	AC 9/14	120.0	42.0	73.0	70.0	50.0	30.0	1.738	1.043	72.0	74.5	45.5	1.64	1.58
Medium grallatorid	n	AC 9/14	117.0	41.0	68.0	69.0	48.0	30.0	1.659	0.986	70.0	72.5	44.5	1.63	1.57
Medium grallatorid	o	AC 9/14	125.0	45.0	77.0	78.0	47.0	70.0	1.711	0.987	69.0	84.2	40.8	2.07	1.69
Medium grallatorid	p	AC 9/14	108.0	35.0	68.0	57.0	51.0	20.0	1.943	1.193	55.0	55.8	52.2	1.07	1.05
Medium grallatorid	q	AC 9/14	133.0	43.0	76.0	75.0	58.0	21.0	1.767	1.013	73.0	74.2	58.8	1.26	1.24
Medium grallatorid	r	AC 9/14	121.0	38.0	67.0	70.0	51.0	23.0	1.763	0.957	67.0	68.4	52.6	1.30	1.27
Medium grallatorid	s	AC 9/14	122.0	40.0	72.0	72.0	50.0	25.0	1.800	1.000	71.0	72.7	49.3	1.48	1.44
Medium grallatorid	t	AC 9/14	128.0	47.0	78.0	73.0	55.0	27.0	1.660	1.068	73.0	75.1	52.9	1.42	1.38
Medium grallatorid	u	AC 9/14	119.0	44.0	71.0	70.0	49.0	25.0	1.614	1.014	73.0	74.8	44.2	1.69	1.65
Medium grallatorid	v	AC 9/14	133.0	48.0	80.0	82.0	51.0	21.0	1.667	0.976	78.0	79.3	53.7	1.48	1.45
Medium grallatorid	w	AC 9/14	118.0	43.0	73.0	70.0	48.0	33.0	1.698	1.043	71.0	74.0	44.0	1.68	1.62
Medium grallatorid	x	AC 9/14	136.0	48.0	80.0	80.0	56.0	29.0	1.667	1.000	79.0	81.6	54.4	1.50	1.45
Medium grallatorid	y	AC 9/14	120.0	42.0	70.0	68.0	52.0	14.0	1.667	1.029	68.0	68.5	51.5	1.33	1.32
Medium grallatorid	z	AC 9/14	117.0	44.0	72.0	71.0	46.0	18.0	1.636	1.014	68.0	68.8	48.2	1.43	1.41
Medium grallatorid	1	AC 9/14	133.0	50.0	79.0	79.0	54.0	18.0	1.580	1.000	81.0	82.0	51.0	1.61	1.59
Medium grallatorid	2	AC 9/14	123.0	43.0	68.0	69.0	54.0	20.0	1.581	0.986	70.0	71.1	51.9	1.37	1.35
Medium grallatorid	3	AC 9/14	120.0	40.0	73.0	72.0	48.0	10.0	1.825	1.014	69.0	69.3	50.7	1.37	1.36
Medium grallatorid	4	AC 9/14	120.0	38.0	70.0	65.0	55.0	18.0	1.842	1.077	65.0	65.8	54.2	1.21	1.20
Medium grallatorid	5	AC 9/14	118.0	42.0	73.0	72.0	46.0	15.0	1.738	1.014	73.0	73.6	44.4	1.66	1.65
Medium grallatorid	6	AC 9/14	130.0	50.0	78.0	78.0	52.0	16.0	1.560	1.000	74.0	74.7	55.3	1.35	1.34
Medium grallatorid	7	AC 9/14	120.0	46.0	73.0	72.0	48.0	18.0	1.587	1.014	71.0	71.9	48.1	1.49	1.48
Medium grallatorid	1	AC 13/4	235.0	111.0	140.0	178.0	57.0	23.0	1.261	0.787	153.0	156.1	78.9	1.98	1.94
Medium grallatorid	2	AC 13/4	240.0	111.0	140.0	175.0	65.0	23.0	1.261	0.800	160.0	163.3	76.7	2.13	2.09
Medium grallatorid	3	AC 13/4	155.0	60.0	93.0	97.0	58.0	20.0	1.550	0.959	95.0	96.5	58.5	1.65	1.62
Medium grallatorid	4	AC 13/4	206.0	78.0	129.0	130.0	76.0	35.0	1.654	0.992	127.0	133.2	72.8	1.83	1.74
Medium grallatorid	5	AC 13/4	160.0	66.0	100.0	96.0	64.0	33.0	1.515	1.042	95.0	99.1	60.9	1.63	1.56
Medium grallatorid	6	AC 13/4	134.0	50.0	85.0	80.0	54.0	27.0	1.700	1.063	78.0	80.2	53.8	1.49	1.45

<i>Anomoepus scambus</i>	2	AC 16/2	78.0	32.0	49.0	58.0	20.0	76.0	1.531	0.845	50.0	63.5	14.5	4.36	3.44
("Noah's Raven")	3	AC 16/2	79.0	33.0	48.0	62.0	17.0	59.0	1.455	0.774	54.0	62.0	17.0	3.66	3.18
	4	AC 16/2	78.0	30.0	48.0	62.0	16.0	59.0	1.600	0.774	55.0	63.2	14.8	4.27	3.71
Average	ave	AC 16/2	78.3	31.7	48.3	60.7	17.7	64.7	1.526	0.797	53.0	62.7	15.6	4.02	3.40
	stdev		0.6	1.5	0.6	2.3	2.1	9.8	0.073	0.041	2.6	0.7	1.3	0.4	0.3
Lectotype <i>Anomoepus scambus</i>	1	AC 34/40	82.0	34.0	52.0	66.0	16.0	51.0	1.529	0.788	55.0	60.9	21.1	2.89	2.61
<i>Anomoepus minor</i>	1	AC 16/5	70.0	25.0	40.0	51.0	19.0	71.0	1.600	0.784	43.0	52.8	17.2	3.07	2.50
	2	AC 16/5	65.0	23.0	39.0	50.0	15.0	65.0	1.696	0.780	38.0	45.1	19.9	2.26	1.91
	3	AC 16/5	70.0	30.0	40.0	48.0	22.0	70.0	1.333	0.833	35.0	42.7	27.3	1.57	1.28
	4	AC 16/5	70.0	28.0	40.0	48.0	22.0	39.0	1.429	0.833	40.0	42.4	27.6	1.54	1.45
Average	ave	AC 16/5	68.8	26.5	39.8	49.3	19.5	61.3	1.514	0.808	39.0	45.8	23.0	2.1	1.8
	stdev		2.5	3.1	0.5	1.5	3.3	15.1	0.164	0.030	3.4	4.9	5.2	0.7	0.5
Type(?) <i>Anomoepus gracillimus</i>	1	AC 37/18	53.0	22.0	30.0	42.0	11.0	51.0	1.364	0.714	33.0	36.6	16.4	2.22	2.01
	2	AC 37/18	55.0	21.0	29.0	40.0	15.0	55.0	1.381	0.725	33.0	37.2	17.8	2.09	1.85
	ave		54.0	21.5	29.5	41.0	13.0	53.0	1.372	0.720	33.0	36.9	17.1	2.2	1.9
	stdev		1.4	11.5	18.6	22.7	8.5	19.9	0.639	0.381	17.3	18.8	9.7	0.7	0.6
<i>Anomoepus scambus</i>	1a	AC 37/18	58.0	28.0	33.0	45.0	13.0	38.0	1.179	0.733	38.0	40.2	17.8	2.26	2.13
	1	AC 19/04	56.0	24.0	30.0	42.0	14.0	51.0	1.250	0.714	36.0	39.9	16.1	2.48	2.23
	2	AC 19/04	64.0	24.0	38.0	49.0	15.0	57.0	1.583	0.776	39.0	44.4	19.6	2.26	1.99
	3	AC 19/04	75.0	32.0	39.0	55.0	20.0	50.0	1.219	0.709	50.0	55.2	19.8	2.78	2.52
Average	ave	AC 19/04	65.0	26.7	35.7	48.7	16.3	52.7	1.351	0.733	41.7	46.5	18.5	2.5	2.2
	stdev		9.5	4.6	4.9	6.5	3.2	3.8	0.202	0.037	7.4	7.9	2.1	0.3	0.3
<i>Anomoepus minimus</i>	1	AC 32/46	77.0	29.0	41.0	57.0	20.0	56.0	1.414	0.719	51.0	57.8	19.2	3.00	2.65
	1	AC 19/05	75.0	31.0	40.0	55.0	20.0	70.0	1.290	0.727	50.0	61.0	14.0	4.37	3.58
	1	AC 55/112	56.0	23.0	34.0	42.0	14.0	55.0	1.478	0.810	35.0	39.5	16.5	2.39	2.12
	2	AC 55/112	50.0	22.0	32.0	42.0	8.0	63.0	1.455	0.762	29.0	34.0	16.0	2.13	1.81
Average	ave	AC 55/112	53.0	22.5	33.0	42.0	11.0	59.0	1.466	0.786	32.0	36.7	16.3	2.3	2.0
	stdev		2.1	0.4	0.7	0.0	2.1	2.8	0.008	0.017	2.1	1.9	0.2	0.1	0.1
<i>Anomoepus scambus</i>	1	AC 37/25	52.0	26.0	30.0	42.0	10.0	75.0	1.154	0.714	31.0	39.1	12.9	3.02	2.40
<i>Anomoepus scambus</i>	1	AC 19/3	61.0	30.0	41.0	55.0	6.0	46.0	1.367	0.745	35.0	38.0	23.0	1.65	1.52
<i>Anomoepus scambus</i>	1a	AC 19/4	70.0	33.0	42.0	58.0	12.0	72.0	1.273	0.724	46.0	56.9	13.1	4.33	3.50
Average	ave	AC 19/4	65.5	31.5	41.5	56.5	9.0	59.0	1.320	0.735	40.5	47.4	18.1	3.0	2.5
	stdev		6.4	2.1	0.7	2.1	4.2	18.4	0.066	0.015	7.8	13.3	7.0	1.9	1.4
<i>Anomoepus scambus</i>	1	AC 16/10	55.0	26.0	30.0	38.0	17.0	55.0	1.154	0.789	37.0	41.7	13.3	3.14	2.78
	1b	AC 16/11	57.0	24.0	29.0	37.0	20.0	63.0	1.208	0.784	38.0	44.6	12.4	3.58	3.06
Average	ave	AC 16/11	56.0	25.0	29.5	37.5	18.5	59.0	1.181	0.787	37.5	43.1	12.9	3.4	2.9
	stdev		1.4	1.4	0.7	0.7	2.1	5.7	0.039	0.004	0.7	2.0	0.6	0.3	0.2

(continued)

Data for Figure 13.23 (Continued).

Name	ID.	Catalog Number	T	II	III	IV	T-IV	θ	III/II	III/IV	R	R'	T-R/ T	R'/T-R'	R/T-R	
Type <i>Anomeopus intermedius</i>	1a	AC 48/1	86.0	38.0	48.0	58.0	28.0	54.0	1.263	0.828	54.0	60.6	25.4	2.39	2.13	
	1b	AC 48/1	90.0	42.0	48.0	61.0	29.0	74.0	1.143	0.787	55.0	68.9	21.1	3.26	2.60	
	1c	AC 48/1	87.0	35.0	48.0	64.0	23.0	68.0	1.371	0.750	52.0	62.7	24.3	2.58	2.14	
	1d	AC 48/1	92.0	37.0	53.0	60.0	32.0	60.0	1.432	0.883	56.0	64.7	27.3	2.37	2.05	
	1e	AC 48/1	87.0	35.0	47.0	62.0	25.0	62.0	1.343	0.758	54.0	63.0	24.0	2.62	2.25	
	1g	AC 48/1	93.0	34.0	49.0	64.0	29.0	60.0	1.441	0.766	57.0	65.8	27.2	2.42	2.10	
	1h	AC 48/1	84.0	38.0	50.0	59.0	25.0	64.0	1.316	0.847	51.0	60.1	23.9	2.52	2.14	
	ave	AC 48/1	88.4	37.0	49.0	61.1	27.3	63.1	1.330	0.803	54.1	63.7	24.7	2.6	2.2	
	stdev		3.3	2.7	2.0	2.3	3.1	3.1	6.4	0.104	0.051	2.1	3.1	2.1	0.3	0.2
	2d	AC 48/1	94.0	38.0	51.0	62.0	32.0	32.0	70.0	1.342	0.823	56.0	68.4	25.6	2.67	2.18
	2f	AC 48/1	90.0	32.0	54.0	62.0	28.0	28.0	60.0	1.688	0.871	54.0	62.4	27.6	2.26	1.95
	2g	AC 48/1	88.0	36.0	50.0	63.0	25.0	25.0	66.0	1.389	0.794	53.0	63.2	24.8	2.55	2.14
	2i	AC 48/1	83.0	25.0	43.0	55.0	28.0	28.0	65.0	1.720	0.782	48.0	56.9	26.1	2.18	1.84
2j	AC 48/1	88.0	38.0	48.0	61.0	27.0	27.0	66.0	1.263	0.787	54.0	64.4	23.6	2.73	2.29	
2k	AC 48/1	90.0	32.0	48.0	63.0	27.0	27.0	63.0	1.500	0.762	55.0	64.5	25.5	2.53	2.16	
2l	AC 48/1	87.0	31.0	52.0	57.0	30.0	30.0	60.0	1.677	0.912	48.0	55.4	31.6	1.76	1.52	
2m	AC 48/1	89.0	38.0	48.0	61.0	28.0	28.0	61.0	1.263	0.787	58.0	67.3	21.7	3.10	2.67	
2o	AC 48/1	91.0	35.0	51.0	70.0	21.0	21.0	61.0	1.457	0.729	54.0	62.7	28.3	2.21	1.91	
2p	AC 48/1	91.0	34.0	51.0	62.0	29.0	29.0	68.0	1.500	0.823	54.0	65.1	25.9	2.52	2.09	
ave	AC 48/1	89.1	33.9	49.6	61.6	27.5	27.5	64.0	1.480	0.807	53.4	63.0	26.1	2.4	2.1	
stdev		2.9	4.1	3.0	3.9	3.0	3.0	3.5	0.171	0.053	3.2	4.1	2.7	0.4	0.3	
Anomoepus <i>scambus</i>	3a	AC 48/1	78.0	31.0	41.0	58.0	20.0	47.0	1.323	0.707	52.0	56.7	21.3	2.66	2.44	
	3b	AC 48/1	74.0	29.0	39.0	56.0	18.0	60.0	1.345	0.696	50.0	57.7	16.3	3.55	3.07	
	ave	AC 48/1	76.0	30.0	40.0	57.0	19.0	53.5	1.334	0.702	51.0	57.2	18.8	3.1	2.8	
	stdev		2.8	1.4	1.4	1.4	1.4	9.2	0.016	0.007	1.4	0.7	3.6	0.6	0.4	
Anomoepus <i>scambus</i>	4a	AC 48/1	76.0	30.0	40.0	58.0	18.0	73.0	1.333	0.690	48.0	59.7	16.3	3.67	2.95	
	5a	AC 48/1	77.0	33.0	43.0	57.0	20.0	58.0	1.303	0.754	52.0	59.5	17.5	3.39	2.96	
	5b	AC 48/1	76.0	37.0	43.0	61.0	15.0	69.0	1.162	0.705	52.0	63.1	12.9	4.89	4.03	
	5c	AC 48/1	77.0	34.0	42.0	61.0	16.0	70.0	1.235	0.689	51.0	62.3	14.7	4.22	3.46	
	ave	AC 48/1	76.7	34.7	42.7	59.7	17.0	65.7	1.233	0.716	51.7	61.6	15.1	4.2	3.5	
stdev		31.9	12.7	17.1	23.7	7.9	24.7	0.522	0.293	20.7	24.4	7.3	1.4	1.2		
Anomoepus <i>scambus</i>	6a	AC 48/1	73.0	34.0	40.0	57.0	16.0	77.0	1.176	0.702	48.0	61.3	11.7	5.26	4.11	
	7qa	AC 48/1	74.0	30.0	41.0	57.0	17.0	73.0	1.367	0.719	50.0	62.2	11.8	5.27	4.24	
	1a	AC 6/3	83.0	37.0	44.0	71.0	12.0	63.0	1.614	0.620	58.0	68.0	15.0	4.54	3.87	
	1b	AC 6/3	84.0	46.0	43.0	66.0	18.0	57.0	0.935	0.652	57.0	64.9	19.1	3.39	2.98	
	2	AC 6/3	83.5	41.5	43.5	68.5	15.0	60.0	1.048	0.635	57.5	66.4	17.1	3.88	3.36	
	ave	AC 6/3	83.8	43.8	43.3	67.3	16.5	58.5	1.0	0.6	57.3	65.6	18.1	3.6	3.2	
	stdev		0.4	3.8	0.4	2.1	2.6	2.6	0.315	0.014	0.4	1.4	1.8	0.5	0.4	

<i>Anomoepus scambus</i>	1	AC 1/3	73.0	27.0	48.0	51.8	21.2	65.0	1.777	0.926	42.0	49.8	23.2	2.15	1.81
	2	AC 1/3	74.0	26.3	53.0	53.3	20.7	72.0	2.017	0.995	42.0	51.9	22.1	2.35	1.90
	3	AC 1/3	75.0	29.2	51.0	54.0	21.0	73.0	1.747	0.944	42.0	52.2	22.8	2.30	1.85
	4	AC 1/3	74.0	29.9	41.0	56.2	17.8	65.0	1.370	0.729	43.0	51.0	23.0	2.22	1.87
	ave		74.0	28.1	48.3	53.8	20.2	68.8	1.728	0.899	42.3	51.2	22.8	2.3	1.9
	stdev		0.8	1.7	5.3	1.8	1.6	4.3	0.267	0.116	0.5	1.1	0.5	0.1	0.0
<i>Anomoepus scambus</i>	1a	AC 16/5	38.0	15.0	23.0	29.0	9.0	58.0	1.533	0.793	22.0	25.2	12.8	1.96	1.71
	1b	AC 16/5	40.0	15.0	26.0	26.0	14.0	52.0	1.733	1.000	23.0	25.6	14.4	1.78	1.60
<i>Anomoepus scambus</i>	2a	AC 16/5	40.0	16.0	26.0	26.0	14.0	45.0	1.625	1.000	23.0	24.9	15.1	1.65	1.52
	2b	AC 16/5	42.0	16.0	25.0	29.0	13.0	48.0	1.563	0.862	24.0	26.3	15.7	1.67	1.53
	ave		40.0	15.5	25.0	27.5	12.5	50.8	1.613	0.909	23.0	25.5	14.5	1.75	1.58
	stdev		1.6	0.6	1.4	1.7	2.4	5.6	0.089	0.103	0.8	0.6	1.2	0.1	0.1
Type <i>Corvipes lacertoides</i>		AC 32/1	35.0	14.0	20.0	18.0	17.0	80.0	1.429	1.111	18.0	23.5	11.5	2.04	1.56
<i>Anomoepus scambus</i>	1	MM 5125	105.0	57.0	56.0	75.0	30.0	54.0	0.982	0.747	65.0	73.0	32.0	2.28	2.03
	2	MM 5125	112.0	53.0	42.0	75.0	37.0	55.0	0.792	0.560	70.0	78.9	33.1	2.39	2.12
	AVE		108.5	55.0	49.0	75.0	33.5	54.5	0.891	0.653	67.5	75.9	32.6	2.33	2.07
	stdev		4.9	2.8	9.9	0.0	4.9	0.7	0.134	0.132	3.5	4.2	0.7	0.1	0.1
<i>Anomoepus scambus</i>	2	DP 01.1	158.0	65.0	90.0	127.0	31.0	74.0	1.385	0.709	101.0	126.5	31.5	4.01	3.20
Type(?) <i>Apatichnus crassus</i>	3	RU main	126.0	58.0	69.0	97.0	29.0	77.0	1.190	0.711	77.0	98.4	27.6	3.56	2.79
	ave		124.0	54.0	67.0	98.0	26.0	43.0	1.241	0.684	87.0	93.5	30.5	3.07	2.85
	stdev		125.0	56.0	68.0	97.5	27.5	60.0	1.215	0.698	82.0	95.9	29.1	3.3	2.8
<i>Anomoepus scambus</i> (Fig. 13.31D)		NJSM 19325	1.4	2.8	1.4	21.2	1.4	2.1	0.138	0.002	7.1	3.5	2.0	0.4	0.0
<i>Anomoepus scambus</i>	1	AMNH 7639	128.0	50.0	67.0	97.0	31.0	64.0	1.340	0.691	81.0	95.5	32.5	2.94	2.49
	ave		102.0	35.0	59.0	77.0	25.0	67.0	1.686	0.766	63.0	75.5	26.5	2.86	2.38
	stdev		100.0	37.0	50.0	78.0	22.0	57.0	1.351	0.641	67.0	76.2	23.8	3.21	2.82
<i>Anomoepus scambus</i> (Fig. 13.15A)		NJSM 20321	1.4	1.4	6.4	14.1	4.2	2.1	0.244	0.053	2.8	0.5	1.9	0.2	0.3
<i>Anomoepus scambus</i> (Fig. 13.15B)	1	Lost	23.0	8.0	11.0	14.0	9.0	59.0	1.375	0.786	13.0	14.9	8.1	1.85	1.61
<i>Anomoepus scambus</i> (Fig. 13.15D)	2	Lost	58.0	25.0	39.0	38.0	20.0	87.0	1.560	1.026	28.0	38.6	19.4	1.99	1.44
<i>Anomoepus scambus</i> (Fig. 13.15E)	3	Lost	118.0	44.0	64.0	96.0	22.0	73.0	1.455	0.667	73.0	90.8	27.2	3.34	2.69
	ave		122.0	47.0	66.0	101.0	21.0	68.0	1.404	0.653	79.0	95.3	26.7	3.57	2.96
	stdev		118.0	45.0	66.0	85.0	33.0	74.0	1.467	0.776	69.0	86.4	31.6	2.73	2.18
<i>Anomoepus scambus</i> (Fig. 13.31C)	1	Lost	119.3	45.3	65.3	94.0	25.3	71.7	1.442	0.699	73.7	90.8	28.5	3.2	2.6
<i>Anomoepus scambus</i> (Fig. 13.15E)	2	Lost	2.3	1.5	1.2	8.2	6.7	3.2	0.033	0.068	5.0	4.4	2.7	0.4	0.4
	ave		111.0	46.0	61.0	86.0	25.0	64.0	1.326	0.709	71.0	83.7	27.3	3.07	2.60
	stdev		58.0	25.0	34.0	48.0	10.0	82.0	1.360	0.708	35.0	46.4	11.6	3.99	3.01

(continued)

Data for Figure 13.23 (Continued).

Name	ID.	Catalog Number	T	II	III	IV	T-IV	θ	III/II	III/IV	R	R'	T—R/	R'/T—R'	R / T—R
<i>Anomoepus scambus</i> (Fig. 13.15G)	1	Lost	65.0	27.0	33.0	44.0	21.0	77.0	1.222	0.750	39.0	49.8	15.2	3.29	2.57
	2		67.0	22.0	38.0	48.0	19.0	69.0	1.727	0.792	39.0	47.3	19.7	2.40	1.98
	ave		66.0	24.5	35.5	46.0	20.0	73.0	1.475	0.771	39.0	48.6	17.4	2.8	2.3
	stdev		1.4	3.5	3.5	2.8	1.4	5.7	0.357	0.029	0.0	1.8	3.2	0.6	0.4
<i>Anomoepus scambus</i> (Fig. 13.14)	1	NJSM 20321	24.0	10.0	13.0	16.0	8.0	72.0	1.300	0.813	13.0	16.1	7.9	2.03	1.64
	2		22.0	11.0	13.0	15.0	7.0	46.0	1.182	0.867	14.0	15.2	6.8	2.24	2.06
	ave		23.0	10.5	13.0	15.5	7.5	59.0	1.241	0.840	13.5	15.6	7.4	2.1	1.9
	stdev		1.4	0.7	0.0	0.7	0.7	18.4	0.084	0.038	0.7	0.6	0.8	0.2	0.3
<i>Anomoepus scambus</i> (Fig. 13.30)	1	Lost	128.0	52.0	60.0	89.0	39.0	76.0	1.154	0.674	76.0	96.4	31.6	3.06	2.41
	2	YPM 8665	115.0	44.0	75.0	104.0	11.0	74.0	1.705	0.721	73.0	91.4	23.6	3.87	3.09
	ave		118.0	58.0	71.0	87.0	31.0	67.0	1.224	0.816	77.0	92.3	25.7	3.60	3.00
	stdev		152.0	71.0	85.0	126.0	26.0	46.0	1.197	0.675	113.0	122.8	29.2	4.20	3.86
<i>Moyenisauropus natator</i> (Fig. 13.32A)	1	EG	166.0	86.0	87.0	131.0	35.0	65.0	1.012	0.664	109.0	129.2	36.8	3.52	2.97
	2		175.0	83.0	90.0	132.0	43.0	65.0	1.084	0.682	111.0	131.6	43.4	3.03	2.56
	ave		170.5	84.5	88.5	131.5	39.0	65.0	1.048	0.673	110.0	130.4	40.1	3.3	2.8
	stdev		6.4	2.1	2.1	0.7	5.7	0.0	0.051	0.013	1.4	1.7	4.7	0.3	0.3