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Earliest records of *Batrachopus* from the southwestern United States, and a revision of some Early Mesozoic crocodylomorph ichnogenera

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Introduction

During the field season of 1983, a field party from the University of California investigated the faunas of the Kayenta and Moenave formations in northeastern Arizona, on lands of the Navajo and Kaibab–Paiute nations. This fieldwork was a continuation of paleontological, sedimentologic, and biostratigraphic reconnaissance of the region begun in 1981 and supported by grants from the National Geographic Society and the Museum of Paleontology of the University of California (UCMP). Work to date has been summarized by Clark and Fastovsky (Chapter 23) and by Padian et al. (1982). The tracks described here were discovered by J. M. Clark, and collected by Clark, K. Padian, S. M. Gatesy, and E. Cobabe. Upon arrival at Berkeley, the sandstone slabs bearing the footprints were washed and cleaned with a soft brush to remove dirt; latex molds of the best preserved individual tracks and trackways were made by Kyoko Kishi.

The purpose of this chapter is to describe these tracks, the first southwestern records of the crocodylomorph ichnogenus *Batrachopus*. To do so, however, it has proved necessary to revise the ichnogenus *Batrachopus* and other named ichnogenera, mostly from the Newark Supergroup of eastern North America. We also review the stratigraphic distribution of trackways comparable to *Batrachopus*, and we conclude that the basis of first records suggests correlation of the Dinosaur Canyon Member of the Moenave Formation with the Early Jurassic horizons of the Newark Supergroup.

The trackways described here were collected from two different areas in the Dinosaur Canyon Member of the Moenave Formation. The first locality, V85012, is some 500 m east of the type locality of *Protosuchus richardsoni* (UCMP locality V3828)

near “Protosuchus Pillar,” worked by Barnum Brown and field crews from the American Museum of Natural History (AMNH) in 1931 and 1934. As Colbert and Mook (1951) noted, eight *Protosuchus* specimens came from the “Protosuchus Pillar” area in Dinosaur Canyon during those years; seven are AMNH specimens, and the eighth is a UCMP specimen (36717) discovered by Dr. S. P. Welles (locality V4120). From this same region, less than half a kilometer south–southeast of Protosuchus Pillar, six protosuchian skeletons and the first set of footprints mentioned above were discovered within 100 m of each other by James M. Clark in 1983. The tracks came from the base of a cross-bedded orange-red sandstone bed, 1.5–3.0 m thick, with blue–white spheres and burrows; the crocodile skeletons were higher in this bed. Clark (UCMP field notes, 1983) determined that the type specimen of *Protosuchus* is from the next higher sandstone horizon, similar to the lower bed but without cross bedding, and separated from it by one meter of shaly sandstone, brown with green–white spheres and tunnels. Clark concluded, and we agree, that all the *Protosuchus* localities in this area are much higher in the Moenave Formation than Colbert and Mook (1951) realized: Locally, the Moenave is a graded sandstone terrace, above which the talus and cliffs of Dinosaur Canyon rise. The cliffs are primarily formed of Kayenta rocks, with a cap of Navajo Sandstone, and the Moenave–Kayenta contact is probably within fifteen meters of the highest occurrence of *Protosuchus*.

The second footprint locality, V84239, is about two miles (3.5 km) south–southeast of the Landmark, north of Tanahakaad Wash, Coconino County, Arizona, near the base of the Adeii Eechii Cliffs. [A third record of *Batrachopus*, uncollected, occurs in the Dinosaur Canyon Member of the

Moenave Formation in Tanahakaad Wash, in association with other skeletons of *Protosuchus* (J. M. Clark pers. comm.)]

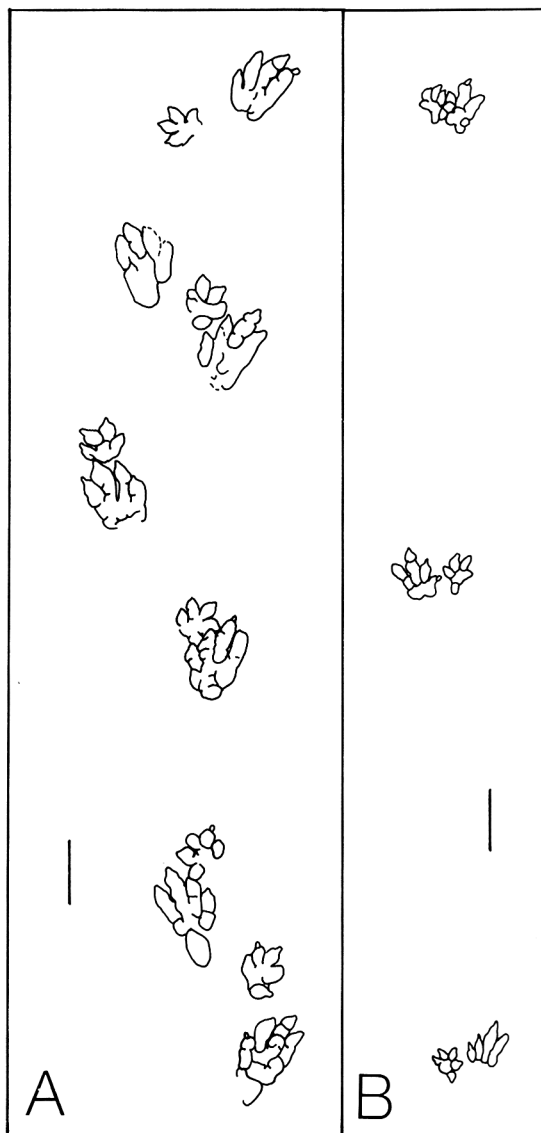
The footprints from both localities are preserved in slabs of coarse orange-red sandstone, badly weathered and friable, up to 2 cm thick, interbedded between layers of finer orange-red mudstone that have been easily washed from the footprint-bearing layers. In the first locality surveyed (V85012), about 0.4 m² of track-bearing sandstone was collected; from the second locality (V84239), about 1.8 m² were collected. We took measurements and made composite drawings of the manus and pes from latex molds of the footprints. When we compared our molds, drawings, and composites to specimens, photographs, and drawings of similar ichnites, we were able to assign the new tracks to the ichnogenus *Batrachopus* E. Hitchcock 1845, which was first recognized in the Early Mesozoic Newark Supergroup of the Connecticut Valley.

As noted above, the purpose of this chapter is to describe the Moenave footprints and to justify their assignment to *Batrachopus*. We also discuss their biostratigraphic significance, especially with respect to the age of the Moenave Formation. In the course of our study, however, it became clear that the ichnogenus *Batrachopus* required substantial revision and comment before any tracks could be referred to it.

The standard reference for Connecticut Valley footprints is Lull (1915, revised 1953). Unfortunately, several pervasive problems with Professor Lull's work must be frankly discussed, specifically those dealing with diagnosis and reconstruction of the trackways that constitute most of the paleovertebrate evidence of the Connecticut Valley. In many cases, including the ichnogenus *Batrachopus*, Lull incorrectly identified the type specimens designated by Edward Hitchcock in the mid 1800s, and often incorrectly recognized nominal priority. Lull's inferences about the possible trackmakers of most tracks, including many badly preserved ones, have generally stood up very well. On the other hand, his drawings of the trackways are often not reliable. They are less drawings of specimens than idealizations of footprint forms. In contemporary ichnological work, composites of manus and pes are normally made by comparing prints in a series, reversing and superimposing tracings of successive tracks to ascertain their consistent features. It is clear that Lull did not do this, and often (e.g., Lull 1953, fig. 54) merely repeated reversed drawings of single impressions to simulate trackways. His reconstructions of trackways suffer because he did not faithfully reproduce three important components: the distances between manus and pes, the distances between successive left and right prints, and the

orientation of manus and pes prints with respect to each other and to the direction of movement. Finally, although he did recognize the importance of ontogenetic growth to the relative proportions of footprints (e.g., Lull 1953, pp. 295–307), it did not seem to affect his acceptance of many of Hitchcock's form genera as valid, regardless of their similarities to slightly larger tracks or of their unique features resulting from substrate differences or poor preservation. To begin with, therefore, we will revise the ichnogenus *Batrachopus*.

Figure 20.1. Trackways of *Batrachopus deweyi*. Scale is 3 cm. A, Neotype trackway of *Batrachopus deweyi* (A.C. 26/5 and 26/6; locality unknown) showing the impression of digit V in the first two pedal impressions. B, Type trackway of *B. "gracilis"* (A.C. 42/3; Turners Falls Sandstone of Massachusetts).



Systematic paleontology**Batrachopus** E. Hitchcock 1845

E. Hitchcock 1845, p. 25

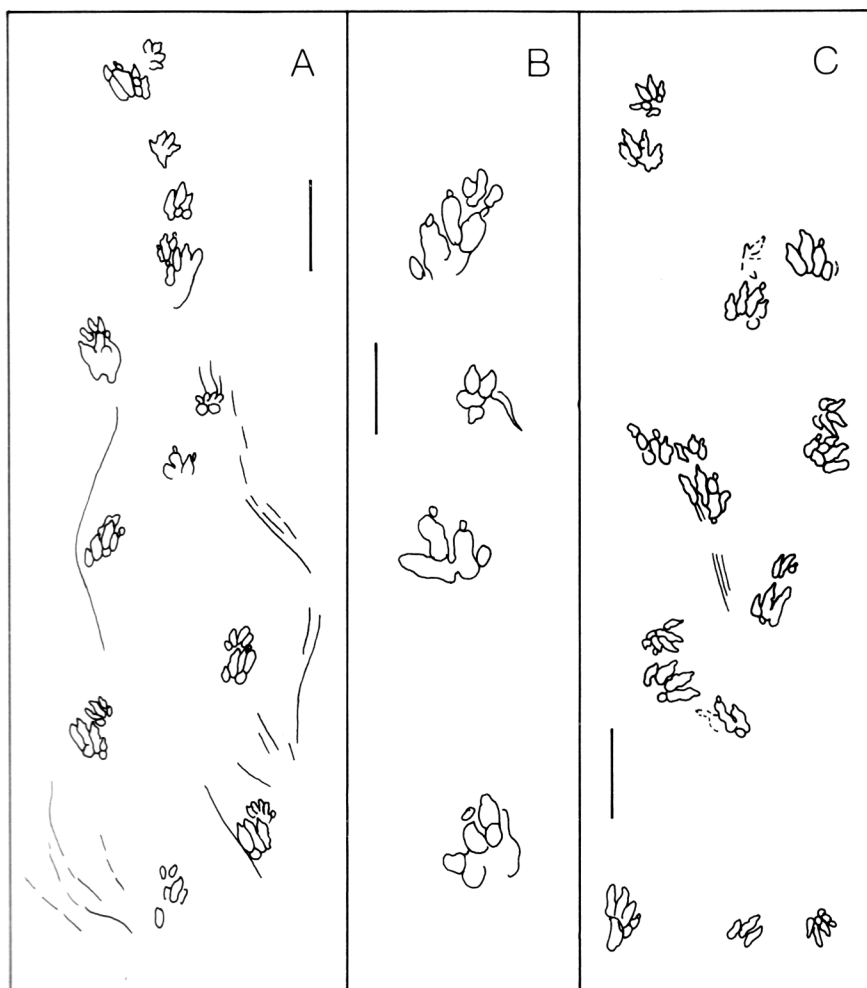
Sillimanius E. Hitchcock 1845, p. 24 (in part)*Palamopus* E. Hitchcock 1845, p. 24*Anisopus* E. Hitchcock 1848, p. 226*Cheirotheroides* E. Hitchcock 1858, p. 130*Arachnichnus* E. Hitchcock 1858, p. 117*Shepardia* E. Hitchcock 1858, p. 131*Macropterna* E. Hitchcock 1858, p. 24*Exocampe* E. Hitchcock 1858, p. 142*Chelonoides* E. Hitchcock 1858, p. 140*Sustenodactylus* E. Hitchcock 1858, p. 116*Orthodactylus* E. Hitchcock 1858, p. 114*Antipus* E. Hitchcock 1858, p. 115*Comptichnus* E. Hitchcock 1865, p. 9*Anisichnus* C. H. Hitchcock 1871, p. xxi*Parabatrachopus* Lull 1942, p. 421*Type species: Batrachopus deweyi**Included species: deweyi, parvulus, dispar**Emended diagnosis:*

Small quadrupedal archosaurian ichnite. The manus has five toes and is usually rotated so that digit II points forward, digit IV points laterally, and digit V points posteriorly. The pes is functionally tetradactyl and digitigrade. Digit V of the pes, when impressed, is reduced to an oval pad posterior to and nearly in a line with digit III. Digit III of the pes is longest and digit I is shortest. (See Figs. 20.1, 20.2.) The pes length, from the base of digit I to the tip of digit IV, ranges between approximately 2 and 8 cm.

Geologic range:

?Latest Triassic (but see below), Early Jurassic, Newark Supergroup of eastern North America: McCoy Brook Formation of Fundy Basin; Turners Falls Sandstone of Deerfield Basin; Shuttle Meadow, East Berlin, and Portland formations of Hartford Basin; Feltsville, Towaco, Boonton, and uppermost meter of Passaic formations, Newark Basin (Olsen 1980a-c, 1981, 1983; Olsen and Baird 1982; Olsen

Figure 20.2. Type trackways of species synonymous with *Batrachopus deweyi*. Scale is 3 cm. **A**, Two parallel trackways that make up the type of *B. "gracilior"* (A.C. 46/3; ?Turners Falls ss.; locality unrecorded). **B**, Type trackway of *B. "bellus"* (A.C. 26/21; Turners Falls ss.). **C**, Two intersecting trackways that make up the type of "*Chirotheroides pilulatus*" (A.C. 34/37; ?Turners Falls ss.; locality unrecorded).



and Galton 1984). Infra-Lias (?Hettangian) of Vendée, France; Upper Stormberg Group (Early Jurassic) of southern Africa; La Cantera Formation (Early Cretaceous) of Argentina (see remarks and references in the section entitled Biogeographic and Stratigraphic Implications below).

Batrachopus deweyi

(E. Hitchcock 1843) E. Hitchcock
1845, emend.

Objective synonyms

- Sauroidichnites deweyi* E. Hitchcock 1843, p. 261, Plate 11, Fig. 9
Batrachopus deweyanus E. Hitchcock 1845, p. 25
Anisopus deweyanus E. Hitchcock 1848, p. 226, Plate 16, Figs. 5, 6; E. Hitchcock 1858, p. 60, Plate 9, Fig. 3; Plate 41, Fig. 2; Plate 43, Fig. 1–2; Plate 53, Fig. 8; Plate 58, Fig. 11
 Lull 1904a, p. 483; Lull 1915, p. 175, Fig. 32; Lull 1953, p. 237, Figs. 104–5

Subjective synonyms

- Anisopus gracilis* E. Hitchcock 1845; 1848, p. 228, Plate 16, Figs. 3–4; E. Hitchcock 1858, p. 61, Plate 9, Fig. 4; Plate 35, Fig. 5; Plate 36, Fig. 1; Plate 43, Figs. 3–5; Plate 58, Fig. 9
Anisichnus gracilis C. H. Hitchcock 1889, p. 119
Batrachopus gracilis Lull 1904a, p. 484; Lull 1904b, p. 381, Figure (“Probable footprint of *Stegomosuchus longipes*”); Lull 1915, p. 177, Fig. 34; Lull 1953, p. 238, Fig. 107
Anisopus gracilior E. Hitchcock 1863, p. 54; E. H. Hitchcock 1865, p. 6, Plate 1, Fig. 3
Anisichnus gracilior C. H. Hitchcock 1889, p. 119
Batrachopus gracilior Lull 1904a, p. 484; Lull 1915, p. 177, Fig. 35; Lull 1953, p. 239, Fig. 108 (wrong specimen citation listed in Fig. 108, but correct in text)
Apatichnus bellus E. Hitchcock 1858, p. 101, Plate 17, Fig. 6; Plate 35, Fig. 8; Plate 45, Fig. 6
Batrachopus bellus Lull 1904a, p. 485; Lull 1915, p. 178; Lull 1953, pp. 239–40
Cheirotheroides pilulatus E. Hitchcock 1858, p. 130, Plate 23, Fig. 4; Plate 36, Fig. 6; Plate 54, Fig. 3
 Lull 1904a, p. 485; Lull 1915, p. 170, Fig. 37; 1953, pp. 240–1, Figs. 110–11
Arachnichnus dehiscens E. Hitchcock 1858, p. 117, Plate 20, Figs. 12–13; Plate 37, Fig. 2; E. Hitchcock 1865, p. 24, Plate 17, Fig. 2
 Lull 1904a, p. 539; Lull 1915, p. 261, Fig. 122; Lull 1953, pp. 265–6, Figs. 140–1

Tentative subjective synonyms

- ?*Comptichnus obesus* E. Hitchcock 1865, p. 9, Plate 5, Fig. 4; Plate 18, Fig. 6; Lull 1904a, p. 538; Lull 1915, p. 260, Fig. 121; Lull 1953, pp. 241–2, Figs. 112–13. Holotype A.C. 55/5

- ?*Shepardia palmipes* E. Hitchcock 1858, p. 131, Plate 24, Fig. 2; Lull 1904a, p. 538; Lull 1915, p. 260, Fig. 120; Lull 1953, p. 243, Fig. 114. Holotype A.C. 33/47
 ?*Palamopus palmatus* E. Hitchcock 1841, p. 483, Plate 34, Figs. 15–16. Holotype A.C. 27/3
 ?*Palamopus gracilipes* E. Hitchcock 1858, p. 129, Plate 23, Fig. 6; Plate 34, Fig. 1. Holotype A.C. 35/23
 ?*Palamopus rogersi* E. Hitchcock 1841, p. 496, Plate 45, Fig. 41 (in part). Holotype A.C. 36/52
 ?*Exocampe arcta* E. Hitchcock 1858, p. 142, Plate 25, Figs. 5, 6, 10; Plate 49, Fig. 5. Holotype A.C. 35/24
 ?*Exocampe ornata* E. Hitchcock 1858, p. 143, Plate 25, Fig. 11; Plate 48, Figs. 1, 6. Holotype A.C. 39/69
 ?*Exocampe minima* E. Hitchcock 1865, p. 11, Plate 18, Fig. 3. Holotype A.C. 55/4
 ?*Chelonoides incedens* E. Hitchcock 1858, p. 140, Plate 31, Fig. 3. Holotype A.C. 6/1
 ?*Sustenodactylus curvatus* E. Hitchcock 1858, p. 116, Plate 20, Fig. 11; Plate 34, Fig. 3. Holotype A.C. 34/43
 ?*Orthodactylus floriferus* E. Hitchcock 1858, p. 114, Plate 20, Fig. 7; Plate 45, Fig. 2. Holotype A.C. 6/1
 ?*Orthodactylus intro-vergens* E. Hitchcock 1858, p. 114, Plate 20, Fig. 8; Plate 51, Fig. 1. Holotype A.C. 34/32
 ?*Orthodactylus linearis* E. Hitchcock 1858, p. 115, Plate 20, Fig. 9; Plate 48, Fig. 4. Holotype A.C. 27/15
 ?*Antipus flexiloquus* E. Hitchcock 1858, p. 115, Plate 20, Fig. 10. Holotype A.C. 41/52

Neotype

A.C. 26/5 and 26/6 (counterparts) as given by Lull (1904a) (see discussion, below, for details). Locality data unrecorded, but matrix looks like East Berlin Formation, Hartford Basin, at Mount Tom, Massachusetts.

Emended diagnosis

Batrachopus in which the complete manus impression is about 75 percent of the length of the pes, including the metatarsophalangeal pads. Pedal digits IV and II are subequal in length, and the distal phalangeal pad of digit I is approximately opposite the crease between the two most proximal phalangeal pads of digit II. The pes length, from the base of digit I to the tip of digit IV, ranges between approximately 2 and 6 cm.

Geologic range

?Latest Triassic (but see below), Early Jurassic, Newark Supergroup: Portland, East Berlin, and Shuttle Meadow formations of the Hartford Basin, Turners Falls Sandstone of the Deerfield Basin, and Feltville, Towaco, Boonton, and uppermost Passaic formations of the Newark Basin (see references listed for the genus, above).

Discussion

The first Connecticut Valley ichnite recognized as quadrupedal was named *Sauroidichnites deweyi* by E. Hitchcock in 1843 (Plate XI, Fig. 9). The slab figured shows a partial trackway and an isolated manus–pes set. No locality was given for this specimen, and no number was given to it. No slab matching its description is listed in E. Hitchcock's (1865) catalog of the Amherst collection; the figured specimen is not mentioned in the 1843 paper. Our attempts to locate the specimen at Amherst have failed. Lull (1904a, 1915, 1953) cited a clearly different specimen (A.C. 26/5 and 26/6) as the type. This specimen also lacks locality data, but Hitchcock did include it in *deweyi* in 1858. It is clear from E. Hitchcock's (1843) lithograph that digit I of the pes is relatively longer than in *B. parvulus* (see below), and in all ways it seems to belong to the same ichnospecies as the slab that Lull designated as the type. Because the type specimen appears to be lost, but the species is apparently still valid, we accept as the neotype the specimen that Lull believed was the holotype.

The neotype (A.C. 26/5 and 26/6) of *deweyi* is an excellent trackway with seven manus–pes sets that show all the characters typical of the genus and species (see Fig. 20.1A); it falls in the upper part of the known size range. The two most posterior manus–pes impressions show a well-defined pad for digit V, which we have occasionally observed in other specimens referable to the genus.

The species *deweyi* was originally included in the higher group name *Sauroidichnites*. Hitchcock used higher names, such as *Ornithichnites* and *Sauroidichnites*, not as generic names of actual specimens, but rather as classificatory ideals (Lull, 1915, pp. 171–2). Therefore, they do not have priority over *Batrachopus* (see also Baird 1957). In 1845, E. Hitchcock applied generic names to the specimens themselves, with a clear table of synonymy. Included in this list was the new genus *Batrachopus*, which included the single species *deweyanus* (a new spelling of *deweyi*). The date of establishment for *Batrachopus* is thus 1845. In the same list, Hitchcock named two other genera, *Sillimanus* and *Palamopus*, which we regard as subjective synonyms of *Batrachopus*. They are poor specimens that cannot be diagnosed to the specific level, and thus are inappropriate as the basis of a genus.

Batrachopus gracilis (Fig. 20.1B) was also named by E. Hitchcock in 1845, but he did not figure or describe it until 1848. The type specimen (A.C. 42/3) consists of a long row of clear manus–pes sets. Digit I of the pes is definitely longer than in *B. parvulus*, and its most distal pad lies opposite the crease between the first and second phalangeal pads of digit II (Fig. 20.3). The manus is about 75 percent of the pes in length. Apart from its smaller size, longer pace, and the lack of impressions of digit V in the pes, this form is identical to *B. deweyi*, and we therefore synonymize the two.

The type slabs of *Batrachopus gracilior*, *B. bellus*, *Arachnichnus dehiscens*, and *Cheirotheroides pilulatus* consist of trackways that show no appreciable differences from *Batrachopus deweyi* other than size, when all of the manus–pes sets are considered and their composites compared (Figs. 20.1, 20.2, 20.4). We thus consider these taxa subjective synonyms of *B. deweyi*. The differences among them as illustrated by Lull (1904a, 1915, 1953) result from

inaccurate renderings of isolated manus–pes sets that do not represent entire trackways.

The ichnotaxa listed above as “tentative subjective synonyms,” as well as their objective synonyms (which Lull listed in 1953), cannot be distinguished from *Batrachopus deweyi*; unfortunately, the specimens are too poorly preserved for us to tell if they share all of the characters of the genus and species *B. deweyi*.

Batrachopus parvulus

(E. Hitchcock 1841) E. Hitchcock
1845, emend.

Ornithichnites parvulus E. Hitchcock 1841, Plate 39,
Fig. 26.

Holotype

20/4 A.C., Amherst College; collected from the sidewalks of Middletown (E. Hitchcock, 1865) or Middlefield (Lull, 1915, 1953), Connecticut, by Dr. Joseph Barratt around 1835. (Middlefield was separated from Middletown in 1886; the latter is more likely to have been paved with large flagstones in 1835). Judging from town records, the slab, which is of the same lithology as typical middle Portland Formation sandstone, probably was excavated from the old Portland quarry across the Connecticut River. This slab also bears the holotype of *Sauropus barrattii*. No referred specimens.

Emended diagnosis

Batrachopus distinguished by a very short pedal digit I, with its most distal pad lying about opposite the most proximal phalangeal pad on digit II. Digits IV and II are about equal in their forward projection. The manus is about 71 percent of the length of the pes.

Geological range

Early Jurassic, Middle Portland Formation, Hartford Basin, Newark Supergroup of eastern North America.

Discussion

What E. Hitchcock called *Ornithichnites parvulus* in 1841 was the first named ichnospecies of what he later called *Batrachopus*. The trackway consists of two successive manus–pes impressions on the same slab as the type of *Sauropus barrattii* (see Chapter 6). In 1843, when E. Hitchcock named *Sauroidichnites deweyi*, he recognized that *parvulus* might be the same sort of track. In 1845, when he named *Batrachopus*, he did not list *parvulus* as one of the species. In 1858, however, he explicitly synonymized *parvulus* with *deweyi*, and never mentioned *parvulus* afterward; in fact, in the 1865 Supplement to the *Ichnology*, E. Hitchcock described the type specimen of *parvulus* as *Anisopus gracilis*.

Examination of the type slab (Fig. 20.3) suggests that *parvulus* is a determinate species, distinguished principally by its shorter digit I. It comes from the middle Portland Formation of the Hartford Basin, whereas all the other type specimens of *Batrachopus* come from either the Turners Falls Sandstone of the Deerfield Basin or the East Berlin Formation of the Hartford Basin.

***Batrachopus dispar* Lull 1904**

Lull 1904a, p. 483, Fig. 2; Lull 1915, p. 176, Fig. 33; Lull 1953, p. 237–8, Fig. 106.

Holotype

21/7 A.C., Amherst College, from the Turners Falls Sandstone of Lily Pond, Gill, Massachusetts, Deerfield Basin, Newark Supergroup. No referred specimens.

Emended diagnosis

Large *Batrachopus*, supposedly distinguished by a relatively small manus impression, but the manus is too incomplete for comparison.

Discussion

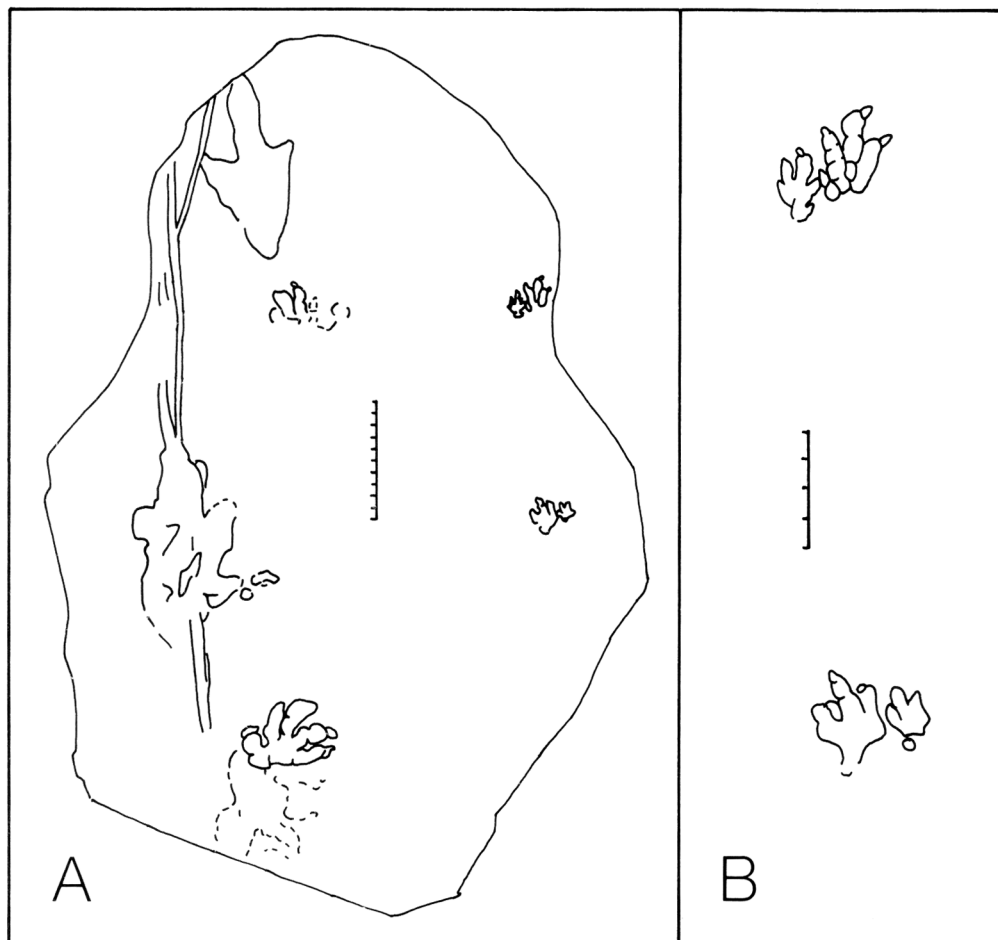
The type specimen of this species unfortunately has only one well-defined manus impression, and it is very lightly impressed: it shows only digits II, III, and IV (not four toes as shown by Lull 1904a, 1915, 1953) (Fig. 20.5). The digits impressed are, however, as long proportionally as in *B. deweyi*. Digits II and IV are subequal. The apparent

difference in manus size could result from the incomplete manus impression in *B. dispar*. The pedes are identical, except for size. The pes of *B. dispar* is roughly 60 percent longer than that of *B. deweyi* and is the largest *Batrachopus* in the Amherst collection. Because of the size difference and the lack of complete information on the manus, we provisionally retain *dispar* as a valid species pending the description of better material.

Description of the Moenave Formation specimens

The trackways collected from the Moenave Formation (UCMP 130583–130596) are preserved in slabs of coarse orange–red sandstone about 1.0–1.5 cm thick. Footprints are abundant on the slabs and are usually impressed to a depth of 3–5 mm. All the footprints appear to be of the same type, though they range in size from about 20 to 60 mm pedal length. Some tracks are poorly preserved and yield

Figure 20.3. Type of *Batrachopus parvulus* (A.C. 20/4; Portland Formation, sidewalk, Middletown, Connecticut), a natural cast. **A**, Entire type slab, including the type of *Sauropus barrattii* (the larger, five-toed track), the type of *Batrachopus parvulus* (on right), and several badly worn ?grallatorid tracks and possible tail drag marks. Scale is 10 cm. **B**, Detail of *Batrachopus parvulus* trackway in **A**. Scale is 4 cm.



little information; these are frequently the deeper tracks, which suggests high water content and poor substrate competence at the time the tracks were made. Manus impressions are variably present and are usually less distinct than pedal impressions.

All of the relatively clear footprints show the same diagnostic characters of *Batrachopus deweyi*. The line drawings of specimens in Figures 20.6 and 20.7, the composite restoration in Figure 20.8, and the photographs in Figure 20.9 obviate long discussion of characteristics. In all the manus–pes sets in which the digits can be discerned, the manus is outwardly rotated and there is no impression of pedal digit V in all but the deepest tracks. These features are typical of *Batrachopus*. The manus is about 75 percent of the length of the pes, and the distal pad of pedal digit I is approximately opposite the crease between the two most proximal phalangeal pads of digit II, as in *Batrachopus deweyi*.

Comparison of *Batrachopus* to other ichnotaxa

As Baird (1954, 1957) noted, *Batrachopus* illustrates the culmination of the large-scale trend, visible through the early Mesozoic, of the reduction in the significance of digit V in the dominant quad-

Figure 20.4. Composites of trackways of *Batrachopus deweyi* and *B. dispar*. Scale is 1 cm. All drawn as right manus–pes sets. **A**, Composite of slabs A.C. 26/5 and 26/6 (see Fig. 20.1A), type of *Batrachopus deweyi*, showing impression of digit V. **B**, Composite of type trackway of *B. “gracilis”*, A.C. 42/3 (see Fig. 20.1B). **C**, Composite of slab A.C. 46/3 (Fig. 20.2A), type of *B. “gracilior”*. **D**, Composite of slab A.C. 26/21 (Fig. 20.2B), type of *B. “bellus”*. **E**, Composite of slab A.C. 34/37 (Fig. 20.2C), type of “*Cheirotheroides pilulatus*”. **F**, Best manus–pes set of slab A.C. 21/7 (Fig. 4), *B. dispar*.

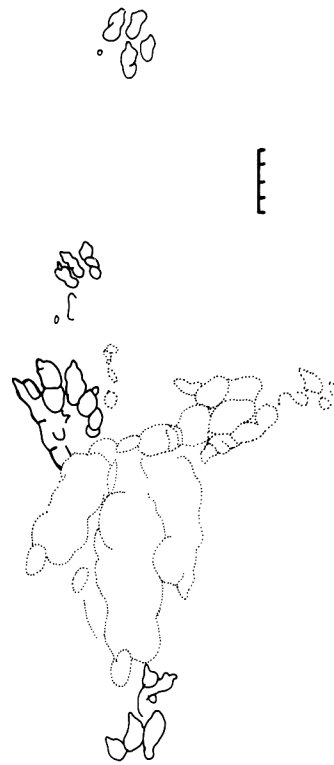
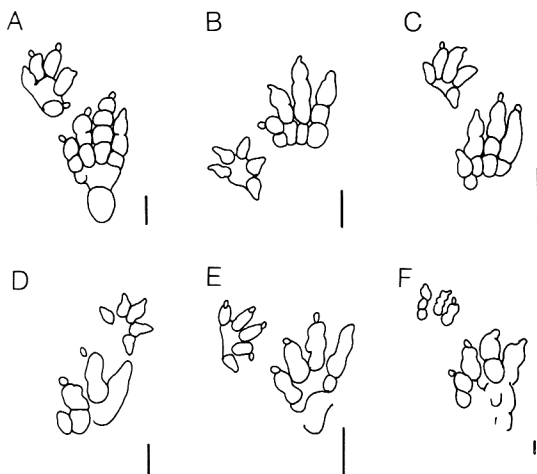
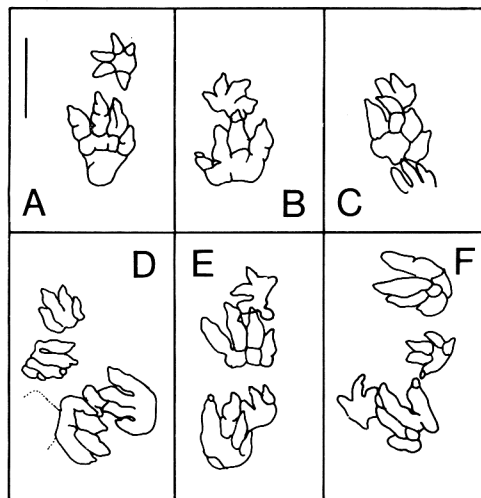


Figure 20.5. Type slab of *Batrachopus dispar* (A.C. 21/7; Turners Falls ss., Massachusetts). Extraneous tracks, mostly *Grallator spp.*, in dotted lines. Scale is 4 cm.

Figure 20.6. *Batrachopus deweyi* from the Dinosaur Canyon Member, Moenave Formation, northeastern Arizona. Scale is 3 cm. UCMP specimen numbers 130587 (A), 130594 (B), 130586 (C), 130588–91 (D), 130592–3 (E), and 130596 (F).



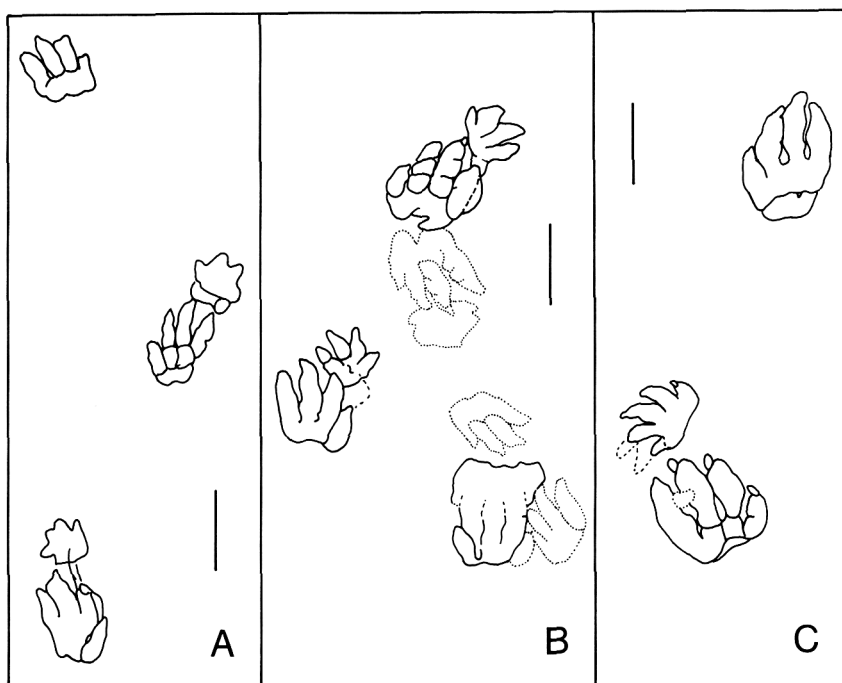
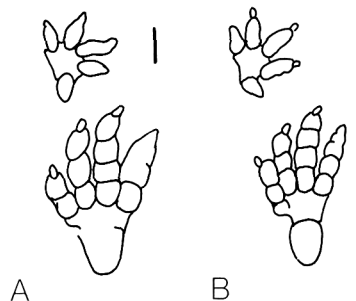


Figure 20.7. Trackways of *Batrachopus deweyi* from the Dinosaur Canyon Member, Moenave Formation, northeastern Arizona. Scale is 3 cm. UCMP specimen numbers 130595 (A), 130585 (B), and 130584 (C) (also shown in Fig. 20.11).

rupedal, nondinosaurian archosaur ichnofaunas (Fig. 20.10). In *Batrachopus*, digit V is only very rarely impressed, and when it is, only an oval pad posterior to digit III is present. *Otozoum* (Fig. 20.10) is considered a scaled-up, graviportal version of its contemporary *Batrachopus* (Baird 1954, 1957). *Brachychirotherium*, characteristic of the Late Triassic horizons of the Newark and of the Early to Late horizons of the German Keuper, has a slightly larger pad for digit V that projects slightly laterally and is present in almost all trackways. *Chirotherium*, dominant in the Early and Middle Triassic, has the least reduced digit V, and in most tracks it projects strongly laterally and is usually recurved (Fig. 20.10).

Along with the loss of a functional digit V in the pes, the manus of *Batrachopus* shows a greater outward rotation than in any other nondinosaurian archosaurs. The manus in *Chirotherium* and *Brachychirotherium* are partially rotated outward, with digit V pointing laterally in most trackways. In *Batrachopus*, however, digit V of the manus usually points backward. A similar orientation is seen in the manus of the related crocodylomorph track *Pteraichnus* (Padian and Olsen 1984) and in the unrelated dinosaur track *Anomoepus*.

Figure 20.8. Composites of *Batrachopus deweyi* material. Scale is 1 cm. All drawn as right manus-sets. **A**, Composite of Moenave material, based on material drawn in Figs. 20.6 and 20.7. **B**, Composite of Newark Supergroup material, based on material drawn in Figure 20.1–20.4. Note that the impression of pedal digit V, as shown here, occurs only rarely.



To avoid confusion, we note that we are using the terms “crocodylian” and “crocodylomorph” in their osteotaxonomic sense. Crocodylians (= Crocodylia) include the traditional grades Protosuchia, Mesosuchia, and Eusuchia (Romer 1966); Crocodylomorpha includes Crocodylia plus their closest relatives, the sphenosuchids and pedeticosaurs *sensu lato* (genera include, for example, *Sphenosuchus*, *Pedeticosaurus*, *Saltoposuchus*, *Hesperosuchus*, *Pseudhesperosuchus*, *Terrestrisuchus*). The sphenosuchids and pedeticosaurs are small, lightly built, terrestrial, possibly bipedal forms. We will suggest below that *Batrachopus* could have been made by a crocodylian *sensu stricto*, but we are not sure about

the other crocodylomorphs mentioned above, because their pedal structures are poorly known. Therefore, the presence of noncrocodylian crocodylomorph bones in Late Triassic rocks does not necessarily imply that *Batrachopus* would have been present there as well.

Possible trackmakers of *Batrachopus*

A pedal digit V reduced as much as it is in *Batrachopus* is seen in several Mesozoic archosaurs, including *Lagosuchus* (Romer 1972; Bonaparte 1975), *Lagerpeton* (Romer 1972), crocodiles, and

Figure 20.9. Photograph of UCMP 130584, *Batrachopus deweyi*, from the Moenave Formation, Dinosaur Canyon Member, Arizona. Diameter of lens cap is 54 mm.

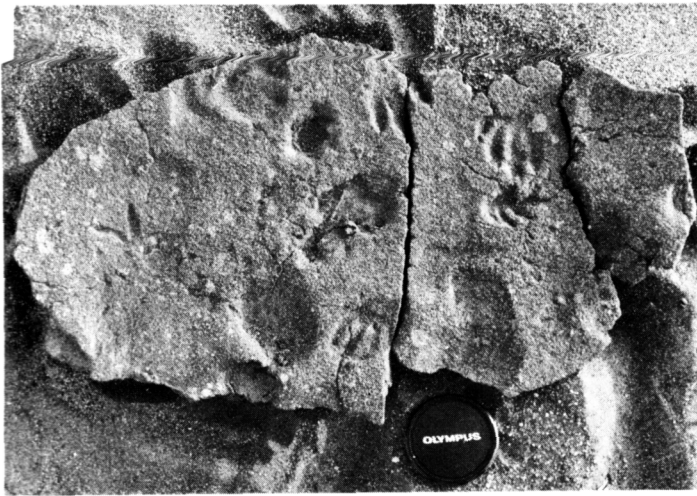
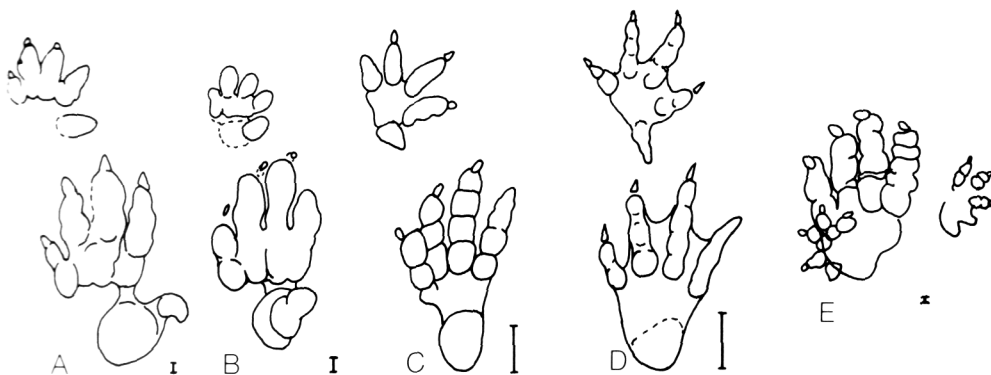


Figure 20.10. Comparison of ichnites similar to *Batrachopus*, all drawn as right manus–pes sets. Scale is 1 cm. A. *Chirotherium barthi*, from the Moenkopi Formation of Arizona (after Baird, 1957), Early Triassic. B. *Brachychirotherium parvum*, from the Passaic Formation of New Jersey (after Baird, 1957), Late Triassic. C. *Batrachopus deweyi*, from the Newark Supergroup. D. *Alligator ?mississippiensis*, drawn from lithograph in Dean (1861; Plate 21), with manus and pes positioned according to trackways of *Caiman* sp. in Padian and Olsen (1984). E. *Otozoum moodii*, from the Portland Formation of Massachusetts, drawn reversed from A.C. 15/14.



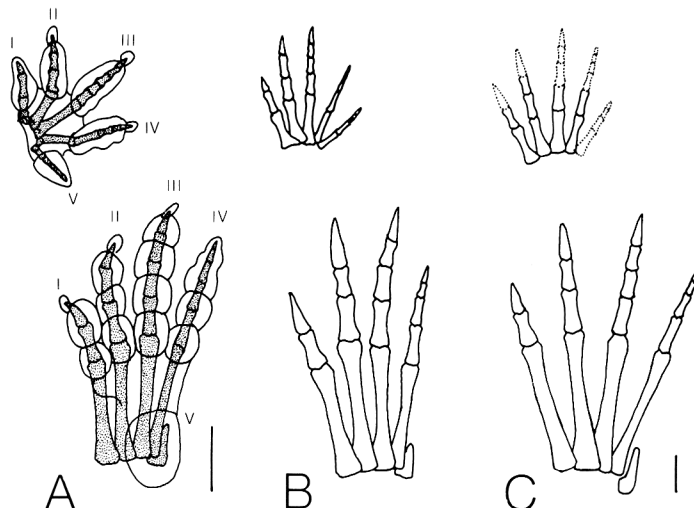
dinosaurs. The basic form of the rest of the pes of *Lagosuchus* and *Lagerpeton* is very different from the form of the reconstructed pes of *Batrachopus*, but the possibility cannot be eliminated that a very primitive, as yet unknown dinosaur could have made *Batrachopus* tracks. This is because *Batrachopus* retains a number of features plesiomorphic to all archosaurs, which most dinosaurs modified, and which today are found only in crocodiles: for example, quadrupedality, five digits in both the manus and pes, and four long toes with the third toe longest.

As reconstructed from the trackways, the bones of the manus and pes of *Batrachopus* cannot be distinguished from those of crocodilians. Moreover, the strongly out-turned, five-fingered manus is definitely present in the tracks of modern crocodiles (Dean 1861; Schaeffer 1941; Padian and Olsen 1984). [The five-fingered manus is also out-turned in *Anomoepus* (Lull 1953, p. 194, Fig. 61), usually considered an ornithischian track; however, the pes is functionally tridactyl in the latter, which proves that the two trackmakers were very different.] The osteology of the manus and pes of *Batrachopus*, using the rules worked out by Peabody (1948) and Baird (1954, 1957) strongly resembles those of both modern and Early Mesozoic crocodiles (Fig. 20.11). Finally, in both the Newark Supergroup and the Glen Canyon Group, crocodile skeletons in the same size range as *Batrachopus* occur in the same strata (*Protosuchus* in the Moenave Formation of the Glen Canyon Group and *Stegomosuchus* in the Newark). In fact, J. M. Clark discovered six protosuchian skeletons less than 100 m from the *Batrachopus* trackways collected from locality V85012.

The inferred association of *Batrachopus* with crocodilian skeletons has an interesting history. Lull (1904a) suggested that *B. "gracilis"* (our *B. deweyi*) is probably the trackway of *Stegomosuchus longipes*, a small armored reptile known from a partial, incompletely preserved skeleton discovered in the Portland Formation near Longmeadow, Connecticut. At first, the skeleton was referred to the small aetosaur *Stegomus*, of which one species, *S. arcuatus*, was known from a much lower horizon in the New Haven Arkose of New Haven, Connecticut. Differences of the carapaces and limbs of the two specimens convinced Lull to erect a separate genus, and he did so noting the long foot of the new form, which lacked a fifth free digit. He therefore suggested (Lull 1904b, p. 381) the possible association of *Stegomosuchus* with *Batrachopus*, regarding the former (and hence the trackmaker of the latter) as a quadrupedal "pseudosuchian" allied to the aetosaurs but distinctly different. As it turns out, Lull's view of the association appears to be a good inference, but *Stegomosuchus*, instead of aetosaurid, is properly regarded as a crocodile (Walker 1968). This supports our assessment on independent grounds that *Batrachopus* is the footprint of a crocodylomorph.

It is important to note, however, that as strong as the osteological resemblance is between the reconstructed *Batrachopus* feet and those of protosuchid and modern crocodiles, the same resemblance could be shared with many noncrocodilian crocodylomorphs, for which complete pedes have not been preserved. Unfortunately, the foot is not well-known in "paracrocodyles" (Walker 1970) in gen-

Figure 20.11. Comparison of reconstructed pes of (A) *Batrachopus deweyi* with (B) manus and pes of *Alligator* sp. [from Romer (1956)], and with (C) manus and pes of *Protosuchus richardsoni* [from Colbert and Mook (1951)]. Scale is 1 cm. All drawn as right manus-pes sets.



eral. *Terrestrisuchus*, from the Late Triassic Carboniferous limestone fissure fills of Cowbridge, Glamorgan, Wales (Crush 1984), is an exception because it appears to have a digit V with two small phalanges. *Batrachopus* shows no evidence of phalanges on pedal digit V, although *Chirotherium* and *Brachychirotherium* do, so we can presume to eliminate *Terrestrisuchus* and similar forms from consideration as the trackmaker of *Batrachopus*. We conclude that the trackmaker was most probably a true crocodylian or a crocodylomorph with a pedal digit V reduced to the state seen in crocodylians.

Stratigraphic implications

Batrachopus was originally discovered in a sandstone slab probably from the East Berlin Formation of the Hartford Basin, Newark Supergroup, and has since been found in nine additional formations in the Hartford and four other basins. In every case, *Batrachopus* is restricted to horizons directly below the oldest basalt and sediments interbedded and above it. These horizons, long thought to be Triassic in age, have been reassigned to the Lower Jurassic on the basis of radiometric dating of the basalt flows and by biostratigraphic correlation of palynomorphic and vertebrate fossils (Cornet, Traverser, and McDonald 1973; Olsen and Galton 1977; Cornet 1977; Olsen 1980a–c; Cornet and Olsen 1985).

Footprints from three other regions have been referred to *Batrachopus*. The stratigraphically oldest form so ascribed is *B. varians*, from the Middle Triassic of France (Demathieu 1970). The pes is proportionally very similar to *Batrachopus*, specifically *B. deweyi*, but the manus points straight ahead and is not of the *Batrachopus* type, which Demathieu, working only with Lull's figures, could not have realized. The existing material of *B. varians* suggests to us a brachychirotheriid rather than a true *Batrachopus*.

Another supposedly Middle Triassic form is *Batrachopus (Parabatrachopus) argentina* (Lull 1942), from what Lull listed as the Paganzo Beds III of the Sierra de la Quijadas, Argentina. Lull also described a species of *Grallator*, as *Anchisauripus australis*, from the same beds. However, the basin exposed in the Sierra de la Quijadas is the San Luis Basin (see Anderson and Anderson 1970), in which the Paganzo Beds proper do not occur. Instead, Stipanovic (1956) listed the track-bearing strata as Division III of the San-Luisense interval, and noted similarities between this sequence and the Botucatu Group of Brazil, which contains a lower sequence of possible Early Jurassic age (Cordani, Kawashita, and Filho 1978) and an upper sequence of lavas and interbedded sediments of Early Cretaceous age. However, the stratigraphy of the *Batrachopus*-

bearing beds has since been revised (Criado Roque, Mombru, and Moreno 1981; Bonaparte 1981), and these beds are now recognized as from the La Cantera Formation (Flores 1969) of the Gigante Group. The La Cantera Formation has produced a Neocomian pollen assemblage and has, therefore, been reassigned to the Early Cretaceous (Yrigoyen 1975). The La Cantera footprint faunule is completely separate from the Triassic, *Chirotherium*-bearing Los Rastros beds of the Ischigualasto–Ville Union Basin, with which it is often listed (e.g., Haubold 1971).

Other occurrences of *Batrachopus* were reported from the Infralias (probably Hettangian) of Veillon, Vendée, France. Lapparent and Montanet (1967) named these *Batrachopus gilberti*. These appear to be true *Batrachopus* and are indistinguishable from *B. deweyi*. Similar tracks occur in the Upper Stormberg Group of southern Africa and were named *Plateotetrapodiscus rugosus*, *Suchopus bakoenaorum*, *Molapentapodiscus pilosus*, and *Synaptichnium motutongense* (Ellenberger 1970, 1974). Although the available material fits within the range of variation known in *Batrachopus* trackways, it has no diagnostic features; definite assignment to that genus must await the discovery of better material (Olsen and Galton 1984). The Upper Stormberg is thought to be of Early Jurassic age on the basis of associated reptile and mammal remains, tetrapod ichnofossils (Olsen and Galton 1977, 1984), and some limited palynological information and radiometric dates (Aldiss, Benson, and Rundel 1984).

The diagnostic features of the *Batrachopus* trackways and their absence in earlier strata form an interesting pattern. Virtually all *Batrachopus* reported from eastern North America, Europe, and South Africa occur in strata of Early Jurassic age, where dates can be assigned or correlated on other grounds. The one exception is a faunule with *Batrachopus* from the uppermost meter of the Passaic Formation, Newark Basin, Newark Supergroup. Olsen and Galton (1977) and Olsen (1980a,b, 1983) considered the age of this assemblage Late Norian (Rhaetian of earlier authors). However, strata in the same position in other parts of the Newark Basin have produced good Early Jurassic palynoflorules, in which the transition to Late Triassic palynoflorules occurs some 10–20 m lower (Cornet 1977; Cornet and Olsen 1985). The Passaic *Batrachopus* assemblage may, therefore, also be Early Jurassic (Hettangian) in age. This faunule overlies and is completely distinct from the older *Brachychirotherium*–*Apatopus* footprint assemblage characteristic of the rest of the Passaic Formation (Chapter 6), and in all other biostratigraphic particulars is of typical “Jurassic” aspect.

We conclude from the above that, apart from the possibility that *Batrachopus* may yet be found in

horizons of latest Triassic age, its known distribution is Hettangian to Neocomian (Early Jurassic to Early Cretaceous). We qualify this generalization for several reasons. Bones of crocodylomorphs are known from sediments of Norian and younger age, although at present records of crocodylomorphs with clearly reduced fifth pedal digits are restricted to Hettangian and younger sediments. Protosuchian crocodiles are known from the Los Colorados Formation of Argentina (Bonaparte 1971), which we regard as of Norian age. Known protosuchians lack phalanges on the fifth digit, so it can be presumed that *Batrachopus*-type footprints could be found in horizons slightly earlier than their known range. The Los Colorados fauna is a good admixture of typical Norian and Liassic faunal types, and could well be transitional. At present, it provides the only datum suggesting potential extension of the known range of inferred track-makers of *Batrachopus*, that is, crocodylomorphs with reduced pedal digit V.

Age of the Moenave Formation

The Moenave Formation has long eluded a well-founded assessment of age; various proponents have argued for either a Late Triassic or an Early Jurassic age based on isolated factors (reviews in Harshbarger, Repenning, and Irwin 1957; Pippingos and O'Sullivan 1978; Peterson and Pippingos 1979). The Glen Canyon Group, which includes the Wingate, Moenave, Kayenta, and Navajo formations, has yielded relatively few fossils of any kind until recently, and there are as yet no radiometric age determinations for any part of the Glen Canyon Group. However, recent palynological investigations of the Whitmore Point Member of the Moenave Formation have provided indications that the Glen Canyon Group, with the exception of the basal Rock Point Member of the Wingate Formation (see below), is probably entirely Jurassic in age. Based on a series of comparisons of Whitmore Point pollen to pollen from the Newark Supergroup (detailed in Peterson and Pippingos 1979, pp. 31–3), Bruce Cornet and his colleagues have correlated the Moenave locality with the upper–lower to lower–middle part of the Portland Formation of the Newark Supergroup, which is late Sinemurian to early Pliensbachian in age (Peterson, Cornet, and Turner-Peterson 1977). Cornet based these determinations both on the predominance of striate *Corollina*, the principal palynomorphic indicator of Liassic horizons in Europe, and on the presence of forms referable to *Corollina itunensis*, *Chasmatosporites apertus*, and *Callialasporites*, known only from Liassic and younger strata (the first species only from middle Liassic and younger rocks). Peterson and Pippingos agreed with Cornet's conclusion that the entire Glen Canyon Group above the Rock Point

Member of the Wingate Formation was Liassic in age (middle Sinemurian to late Toarcian). However, it should be mentioned that the Whitmore Point Member, from which pollen samples were taken, is stratigraphically just above the Dinosaur Canyon Member, from which the *Protosuchus* and *Batrachopus* were collected (Harshbarger et al. 1957).

Unfortunately, repeated attempts to find additional palynofloras have failed. In 1981, Carol Hotton of the UCMP field party collected twenty-eight pollen samples and tested nine others from the Kayenta Formation of northeastern Arizona, all of which proved barren (Chapter 23; Padian et al. 1982). Two samples from the Whitmore Point Member of the Moenave Formation were tested, but only the one from the locality sampled by Cornet proved fossiliferous. The predominance of striate *Corollina* suggested a Lower Jurassic age. In the sample she studied, Hotton did not find *Corollina itunensis* or *Callialasporites*, but also found no taxa characteristic of Late Triassic European horizons. Although further testing is always desirable, we accept the Liassic determination of Peterson, Cornet, and Turner-Peterson, in view of the high correspondence of the Moenave and Portland palynofloras.

Vertebrate fossils from the Moenave have also been sparse; Clark and Fastovsky (Chapter 23) review the fauna. The crocodile *Protosuchus*, one candidate for the *Batrachopus* trackmaker, has been the most common vertebrate fossil collected. Eight specimens were recovered from the Dinosaur Canyon Member of the Moenave Formation by field parties from the American Museum of Natural History and the Museum of Paleontology of the University of California between 1931 and 1941. In 1983 the UCMP field party, as mentioned above, found six other skeletons less than half a mile from the original *Protosuchus* locality. These, like the other specimens, were found near the top of the Moenave Formation, close to its contact with the Kayenta Formation. Considerably lower in the Whitmore Point Member, at the same pollen locality discussed above, J. M. Clark and members of the UCMP field party collected bone scraps of fishes and reptiles in 1981 and 1983. These included the first records of turtles (a partial shell) and theropod dinosaurs (a vertebra) from the Moenave Formation. The subholostean fish *Semionotus* and the conchostracan *Cyzicus* have also been collected from the Whitmore Point Member (discussed in Olsen, McCune, and Thomson 1982), and several species referable to *Semionotus* (including *Lepidotes*) have come from the Springdale Sandstone or upper Dinosaur Canyon Member farther north (review in Harshbarger et al. 1957). S. P. Welles and other UCMP investigators have collected similar fish remains from the Moenave Formation near Kanab, Utah.

None of the paleovertebrate taxa recovered from the Moenave Formation is diagnostic of Triassic or Jurassic horizons. Therefore, the age of the Moenave should not be based only on vertebrate correlations. However, given the abundance of Moenave crocodiles, and the absence of Late Triassic crocodiles or crocodyloid tracks anywhere in the world except for the questionably dated Los Colorados Formation of South America (Cornet and Olsen 1985), we suggest that the *Batrachopus*-bearing horizons may be correlative and of Early Jurassic age (Peterson et al., 1977). This inference seems to be supported by a strong correspondence between Moenave and Portland palynofloras. In addition, there is a marked universal nonconformity near the base of the Glen Canyon Group, separating the Rock Point Member of the Wingate Formation (which intergrades with the uppermost Chinle Formation) from the Lukachukai Member of the Wingate [which intergrades with overlying Kayenta and Navajo Formations in an apparently continuous sequence of deposition (Pipiringos and O'Sullivan 1978)]. The Rock Point Member has yielded typical Late Triassic Chinle vertebrates, a fauna much different from those of overlying Glen Canyon sediments. Although there is no evidence either way for the age of the earliest Moenave and Wingate deposits, the possibility exists that this unconformity discussed by Pipiringos and O'Sullivan separates the available Triassic and Jurassic records in the southwestern United States. At this point, all available evidence points to an Early Jurassic age for the Glen Canyon Group proper, excluding the Rock Point Member, and including the vertebrate-, footprint-, and pollen-bearing horizons discussed here.

Note added in proof

Fr. Giuseppe Leonardi, the eminent Brazilian paleoichnologist, has recently informed us that *Batrachopus* has been discovered in the Prado region of southwestern Colombia, in sediments dated by ammonites as late Norian (below the traditionally recognized "Rhaetian") in age. This information corresponds to our prediction in this paper that footprints of crocodylomorphs, such as *Batrachopus*, would be discovered in sediments from the Late Triassic (Norian), from which age skeletal material of crocodylomorphs has been known for some years. At the same time, if this new record is correctly identified, it extends the stratigraphic range of *Batrachopus*, which by itself can no longer be regarded as evidence for a maximal Jurassic age. The footprints described to us by Fr. Leonardi have not yet been published; it will be interesting to see the degree to which they conform to known records of *Batrachopus* from sediments of Jurassic and later age.

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References

- Aldiss, D. T., J. M. Benson, and C. C. Rundel. 1984. Early Jurassic pillow lavas and palynomorphs of eastern Botswana. *Nature (London)* 310:302-4.
- Anderson, H. M., and J. M. Anderson. 1970. A preliminary review of the biostratigraphy of the uppermost Permian, Triassic, and lowermost Jurassic of Gondwanaland. *Palaeontol. Afr.* 13 (Suppl.): 1-22.
- Baird, D. 1954. *Chirotherium lulli*, a pseudosuchian reptile from New Jersey. *Mus. Comp. Zool. (Harvard Univ.)*, *Bull.* 1:163-92.
1957. Triassic reptile footprint faunules from Milford, New Jersey. *Mus. Comp. Zool. (Harvard Univ.)*, *Bull.* 117: 449-520.
- Bonaparte, J. F. 1971. Los tetrapodos del sector Superior de la Formación Los Colorados, La Rioja, Argentina (Triásico Superior): I Parte. *Opera Lilloana* 22: 1-183.
1975. Nuevos materiales de *Lagosuchus talampyensis* Romer (Thecodontia-Pseudosuchia) y su significado en el origen de los Saurischia. Chañarenses Inferior, Triásico Medio de Argentina. *Acta Geol. Lilloana*. 13: 5-90.
1981. Los fósiles mesozoicos. In M. Yrigoyen (ed.), *Geología y Recursos Naturales de la Provincia de San Luis. Relatorio del VII Congreso Geológico Argentino*. (Buenos Aires: Asociación Geológica Argentina), pp. 97-9.
- Colbert, E. H., and C. C. Mook. 1951. The ancestral crocodile *Protosuchus*. *Am. Mus. Hist.*, *Bull.* 97: 143-82.
- Cordani, U. G., K. Kawashita, and A. T. Filho. 1978. Application of the rubidium-strontium method to shales and related rocks. *Am. Assoc. Petrol. Geol., Stud. Geol.* 6: 93-117.
- Cornet, B. 1977. The palynostratigraphy and age of the Newark Supergroup. Ph.D. thesis, Department of Geosciences, University of Pennsylvania.
- Cornet, B., A. Traverse, and N. G. McDonald. 1973. Fossil spores, pollen, fishes from Connecticut indicate Early Jurassic age for part of the Newark

- Group. *Science* 182: 1243–7.
- Cornet, B., and P. E. Olsen. 1985. A summary of the biostratigraphy of the Newark Supergroup of eastern North America, with comments on early Mesozoic provinciality. *III Congr. Latin-Am. Paleontología. México. Memoria*, pp. 67–81.
- Criado Roque, P., C. A. Momburu, and J. Moreno. 1981. Sedimentitas mesozoicas. In M. Yrigoyen (ed.), *Geología y Recursos Naturales de la Provincia de San Luis. Relatorio del VII Congreso Geológico Argentino*. (Buenos Aires: Asociación Geológica Argentina), pp. 79–96.
- Crush, P. J. 1984. A Late Upper Triassic sphenosuchid crocodylian from Wales. *Palaeontology* 27: 131–57.
- Dean, J. 1861. *Ichnographs from the Sandstone of the Connecticut River* (Boston: Little, Brown).
- Demathieu, G. 1970. *Les Empreintes de Pas de Vertébrés du Trias de la Bordure Nord-Est du Massif Central. Cahiers de Paléontologie* (Paris: Editions CNRS).
- Ellenberger, P. 1970. Les niveaux paléontologiques de première apparition des Mammifères primordiaux en Afrique du Sud, et leur ichnologie. Etablissement de zones stratigraphiques détaillées dans le Stormberg du Lesotho (Afrique du Sud) (Trias supérieur à Jurassique). *Proc. Pap., 2nd Gondwana Symp. CSIR Pretoria, S. Afr.* 1970: 343–70.
1974. Contribution à la classification des pistes de vertés du Trias. Les types du Stormberg d'Afrique du Sud, (IIème partie: le Stormberg Supérieur — I. Le biome de la zone B/1 ou niveau de Moyeni: ses biocénoses). *Palaeovert., Mém. Extraord., Montpellier*, pp. 1–155.
- Flores, M. A. 1969. El Bolsón de Las Salinas en la Provincia de San Luis. *Actas IV J. Geol. Argent.* 1:311–27.
- Harshbarger, J. W., C. A. Repenning, and J. H. Irwin. 1957. Stratigraphy of the uppermost Triassic and the Jurassic rocks of the Navajo country [Colorado Plateau]. *U.S. Geol. Surv. Prof. Pap.* 291: 1–74.
- Haubold, H. 1971. *Ichnia Amphibiorum et Reptiliorum fossilium. Handbuch der Paläoherpetologie, Teil 18* (Gustav Fischer, Stuttgart).
- Hitchcock, C. H. 1871. Account and complete list of the Ichnozoa of the Connecticut Valley. *Wallings and Gray's Official Topographical Atlas of Massachusetts* (Boston: Wallings and Gray), pp. XX–XXI.
1889. Recent progress in ichnology. *Proc. Boston Soc. Nat. Hist.* 24: 117–27.
- Hitchcock, E. 1841. *Final Report on the Geology of Massachusetts. Amherst and Northampton, Pt. III*, pp. 301–714.
1843. Description of five new species of fossil footmarks, from the red sandstone of the valley of the Connecticut River. *Am. Assoc. Geol. Natural., Trans.* 1843:254–64.
1845. An attempt to name, classify, and describe the animals that made the fossil footmarks of New England. *Proc. 6th Mtg, Am. Assoc. Geol. and Naturalists, New Haven, Conn.*, pp. 23–5.
1848. An attempt to discriminate and describe the animals that made the fossil footmarks of the United States, and especially New England. *Mem. Am. Acad. Arts Sci.* (2)3: 129–256.
1858. *Ichnology of New England. A Report on the Sandstone of the Connecticut Valley, Especially Its Fossil Footmarks* (Boston: William White).
1863. New facts and conclusions respecting the fossil footmarks of the Connecticut Valley. *Am. J. Sci.* (2) 36: 46–57.
1865. *Supplement to the Ichnology of New England* (Boston: Wright and Potter).
- Lapparent, A.-F., and C. Montenat. 1967. Les empreintes des pas de reptiles de l'Infralias du Veillon. *Mem. Soc. Geol. France.* 107: 1–44.
- Lull, R. S. 1904a. Fossil footprints of the Jura-Trias of North America. *Boston Soc. Nat. Hist. Mem.* 5:461–557.
- 1904b. Notes on the probable footprints of *Stegomus longipes*. *Am. J. Sci.* (4)17: 381–2.
1915. Triassic life of the Connecticut Valley. *Conn. State Geol. Nat. Hist. Surv., Bull.* 24: 1–285.
1942. Triassic footprints from Argentina. *Am. J. Sci.* (5)(240): 421–5.
1953. Triassic life of the Connecticut Valley. *Conn. State Geol. Nat. Hist. Surv., Bull.* 81: 1–331.
- Olsen, P. E. 1980a. A comparison of the vertebrate assemblages from the Newark and Hartford Basins (early Mesozoic, Newark Supergroup) of Eastern North America. In Jacobs, L. L. (ed.), *Aspects of Vertebrate History: Essays in Honor of Edwin Harris Colbert* (Flagstaff, Arizona: Museum of North Arizona Press), pp. 35–53.
- 1980b. Triassic and Jurassic Formations of the Newark Basin. In: Manspeizer, W. (ed.), *Field Studies in New Jersey Geology and Guide to Field Trips, 52nd Ann. Mtg. New York State Geol. Assoc., Newark College of Arts and Sciences, Newark, Rutgers University*, pp. 2–39.
- 1980c. Fossil great lakes of the Newark Supergroup in New Jersey. In Manspeizer, W. (ed.), *Field Studies in New Jersey Geology and Guide to Field Trips, 52nd Ann. Mtg. New York State Geol. Assoc., Newark College of Arts and Sciences, Newark, Rutgers University*, pp. 352–98.
1981. Comment on "Eolian dune field of Late Triassic age, Fundy Basin, Nova Scotia." *Geology.* 9: 557–61.
1983. Relationship between biostratigraphic subdivisions and igneous activity in the Newark Supergroup. Southeastern Sect., *Geol. Soc. Am., Abstr. Prog.* 15(2): 71.
- Olsen, P. E., and D. Baird. 1982. Early Jurassic vertebrate assemblages from the McCoy Brook Formation of the Fundy Group (Newark Supergroup, Nova Scotia, Canada). *Geol. Soc. Am., Abstr. Prog.* 14(1–2): 70.
- Olsen, P. E., and P. M. Galton. 1977. Triassic-Jurassic terapod extinctions: are they real? *Science* 197: 983–6.
1984. A review of the reptile and amphibian assemblages from the Stormberg of southern Africa, with special emphasis on the footprints and the age of the Stormberg. S. H. Houghton Memorial Volume. *Palaeontol. Afr.* 25: 87–110.

- Olsen, P. E., A. R. McCune, and K. S. Thomson. 1982. Correlation of the early Mesozoic Newark Super-group by vertebrates, principally fishes. *Am. J. Sci.* (5)282: 1–44.
- Padian, K., J. M. Clark, D. E. Foster, and C. Hotton. 1982. Preliminary biostratigraphic–sedimentologic exploration of the Kayenta Formation of Arizona. *National Geographic Society Research Final Reports* 1982, in press.
- Padian, K., and P. E. Olsen. 1984. The fossil trackway *Pteraichnus*: not pterosaurian, but crocodylian. *J. Paleontol.* 58: 178–84.
- Peabody, F. E. 1948. Reptile and amphibian trackways from the lower Triassic Moenkopi Formation of Arizona and Utah. *Bull. Dept. Geol. Sci., Univ. Calif., Berkeley* 27: 295–468.
- Peterson, F., B. Cornet, and E. C. Turner-Peterson. 1977. New data bearing on the stratigraphy and age of the Glen Canyon Group (Triassic and Jurassic) in southern Utah and northern Arizona. *Geol. Soc. Am. Abst. Prog.* 9(6):755.
- Peterson, F. and G. N. Phipps. 1979. Stratigraphic relations of the Navajo Sandstone to Middle Jurassic formations, southern Utah and northern Arizona. *U.S. Geol. Surv. Prof. Pap.* 1035-B: 1–43.
- Phipps, G. N., and R. B. O'Sullivan. 1978. Principal unconformities in Triassic and Jurassic rocks, Western Interior, United States – a preliminary survey. *U.S. Geol. Surv. Prof. Pap.* 1035-A: 1–29.
- Romer, A. S. 1956. *Osteology of the Reptiles*. (University of Chicago Press, Chicago), pp. 1–722.
1966. *Vertebrate Paleontology*, 3rd ed. (Chicago: University of Chicago Press), pp. 1–468.
1972. The Chañares (Argentina) reptile fauna. XV. Further remains of the thecodonts *Lagerpeton* and *Lagosuchus*. *Mus. Comp. Zool. (Harvard Univ.) Breviora*. 394: 1–7.
- Schaeffer, B. 1941. The morphological and functional evolution of the tarsus in amphibians and reptiles. *Am. Mus. Nat. Hist. Bull.* 78: 395–472.
- Stipanovich, P. N. 1956. El sistema Triásico en la Argentina. *Cong. Geol. Internat., Sec. II, El Mesozoico del Aemisferio Occidental y sus Correlaciones Mundiales* (Durango, Mexico: Editorial Stylo), pp. 73–111.
- Walker, A. D. 1968. *Protosuchus*, *Proterochampsia*, and the origin of phytosaurs and crocodiles. *Geol. Mag.* 105: 1–14.
1970. A revision of the Jurassic reptile *Hallopus victor* (Marsh), with remarks on the classification of crocodiles. *Phil. Trans. Roy. Soc. London B* 257: 323–72.
- Yrigoyen, M. R. 1975. La edad Cretácica del Grupo Gigante (San Luis) y su relación con cuencas circunvecinas. *Actas I Congr. Argent. Paleont. Bioestr.* 2: 29–56.