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INTERPRETATION OF THE TETRAPOD FOOTPRINTS FROM THE EARLY PENNSYLVANIAN OF ALABAMA

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ABSTRACT: Discoveries of tetrapod footprints from the lower part of the upper Pottsville Formation in Alabama (USA) from the 1990s to the present constitute the most representative record, both in quality and quantity, hitherto known from the Early Pennsylvanian (Westphalian A age). These discoveries succeed and considerably broaden the first finds published by Aldrich (1930) from the roofrock of the Jagger coal seam near Carbon Hill, Walker County. The recent investigation of the available material from several sites near Carbon Hill and Jasper concerns, first and foremost, specimens from the Union Chapel Mine, and, in addition, those from the Kansas and Fern Springs Mines, as well as the surviving specimens remaining in the Alabama Museum of Natural History described by Aldrich, which were presumably collected from the Holly Grove Mine near Carbon Hill. After a detailed investigation of several hundred specimens we are able to identify a significant ichnofauna of the following content:

Temnospondyl trackways: *Nanopus reidiae* n. isp., *Matthewichnus caudifer* Kohl & Bryan, 1994;
Anthracosaur trackways: *Attenosaurus subulensis* Aldrich, 1930;
Amniote trackways: *Cincosaurus cobbi* Aldrich, 1930, and *Notalacerta missouriensis* Butts, 1891.

The identification and determination of these ichnotaxa can be established because of the exceptionally large sample size from the Union Chapel Mine in combination with the evidence known from other localities. All are related stratigraphically to the Mary Lee coal zone at the base of the upper Pottsville Formation. The preservation of the footprints is related to the environment of estuarine tidal flat deposits. The so-called *Cincosaurus* beds above the Mary Lee coal are exposed at the Union Chapel Mine. The Fern Springs Mine and Kansas sites presumably belong to the lower horizon of the Jagger coal.

INTRODUCTION

The Knowledge of Carboniferous Tetrapod Footprints

The scientific description of Carboniferous tetrapod footprints, in particular those from the Pennsylvanian, begins with King (1845, 1846), who named *Ornithichnithes* and *Thenaropus* and changed the latter into *Spheropezium*. These forms remained problematic until Lea (1849) next introduced *Sauropus* as a common form of tracks of the Coal Measures, and Dawson (1863, 1868, 1872, 1882) applied this name to footprints from the Paleozoic. Dawson (1882) used the form of the impression for classification and distinguished digitigrade (*Hylopus*) and plantigrade (*Sauropus*) morphs. This procedure related tracks that had been separated by other students. Other criteria of classification are the number of toes, a chirotherian pattern of *S. unguifer*, and an elephantine tread of *S. sydnensis*. Butts (1891) summarized under *Notalacerta* digitigrade, plantigrade, pentadactyl and tetradactyl tracks. Hay (1902) recognized that the name *Sauropus* was first used for tracks from the Triassic (preoccupied by Hitchcock), and substituted *Palaeosauropus* for all Carboniferous tracks called *Sauropus* by former authors.

Previously Matthew (1903b: p. 109f.) argued that the Carboniferous forms encompassed under the name *Sauropus/Palaeosauropus* appear quite diverse from each other. Therefore, they cannot be unified under a single generic name. *Sauropus primaevus* Lea is quite different from *S. sydnenesis* Dawson, and several other ichnospecies included under *Palaeosauropus* by Hay (1902) can be included under generic names of previous authors. As Matthew (1903b) stated, for the type of footprint represented by *S. primaevus*, several generic names have been used — *Thenaropus/Theranopus*, *Notalacerta*, *Anthracopus*, and *Sauropus* — with as many different species. A similar number of generic names and species can be found in other groups of these footprints. By 1903 it was clear how difficult it was to determine a common basis for the classification of footprints. Matthew stated that tail marks and drag marks of the belly are less significant as the basis for a classification; instead, he used the number of toes, and as subordinate characters the "weight" and "strength" of the impression.

Marsh (1894) noted the morphological variation in the footprints he described under certain generic names. This was, from the modern point of view, one of the first realistic, well-founded classification *caveats*. The arguments of Marsh suggest that the main reason for the apparent diversity in Permo-Carboniferous track genera is that authors of this time described only one or a few prints, and gave each separate, new generic names. The paper by Matthew (1903b, p. 110) was intended to reduce this redundancy of names, divide the footmarks into related groups under generic names, and present a tentative arrangement. The numbers of toe marks of manus and pes are the primary criteria used for the classification of batrachian tracks from North America. Of secondary value are slenderness or stoutness of the toes, the weight of the heel, etc. Unfortunately, Matthew used the recorded number of toe marks without regard to the potential incompleteness of the record; e.g. *Dromopus agilis* appears in group 4 with a pentadactyl manus, and *Nanopus caudatus* represents group 9 with a pentadactyl pes and tridactyl manus. Matthew classified 11 groups represented by the following genera:

1. *Notalacerta* Butts, 1891
2. *Hylopus* Dawson, 1882
3. *Pseudobradypus* Matthew, 1903
4. *Dromopus* Marsh, 1894
5. *Batrachichnus* Woodworth, 1900
6. *Thenaropus* King, 1845
7. *Limnopus* Marsh, 1894
8. *Baropus* Marsh, 1894
9. *Nanopus* Marsh, 1894
10. "*Apatichnus*"? with *Hylopus* ? *trifidus* Dawson, 1895
11. "*Ornithichnites*" King, 1845.

Matthew (1903b, p. 111) astutely emphasized that the method of representing tracks by drawings "is wide scope for the exercise of imagination." Thereafter, photography became the principal standard for objective determination. The ultimate goal is to be able to compare the footprints to the animals which made them, and this must await discovery of their skeletons.

The framework formulated by Matthew (1903a,b,c, 1905) has been continued by Baird (1952) and Haubold (1970, 1971). However, over the following 100 years there was no significant progress or solution, as shown in the attempt at a revision by Haubold (1970, 1971) and the overviews by Cotton et al. (1995) and Hunt et al. (1995). At present we are confronted with 56 generic names primarily introduced for tetrapod footprints of the Carboniferous (Table 1), and an additional 10 generic names related first to Permian finds. The number of primary ichnospecies introduced for Carboniferous specimens totals 97, with 43 later binominal combinations. As shown by the origin of generic and species names, the majority of tetrapod footprints were found in North America: 42 ichnogenera and 75 ichnospecies were first described from Carboniferous formations in North America. The remaining 12 ichnogenera and 24 ichnospecies were introduced by studies in western Europe.

Now, one century after Matthew's attempt at a unified classification scheme, it seems possible to correlate at least some tracks, or some ichnotaxa with the foot skeletal structures of tetrapods known from Permo-Carboniferous deposits. This is due to the remarkable accumulation of knowledge concerning skeletons of terrestrial tetrapods from the Carboniferous and to the discoveries of footprints in the Pottsville Formation in Alabama in hitherto unequaled quantities. This large sample size allows critical insights into the modes of origin and preservation that control the recorded morphology of footprints. The detailed investigation and comparison of the specimens from the Union Chapel Mine, and the delamination of several footprints layer by layer, together with an objective documentation by photographs as proposed by Matthew (1903b), creates an optimal chance to establish an understanding of Carboniferous footprints free from imagination, and free from taxonomic oversplitting or oversimplified lumping.

Occurrences in Alabama

The tetrapod footprints investigated for this paper come from the Mary Lee coal zone of the basal upper Pottsville Formation. This is the interval from the Jagger to the New Castle coal beds (see Pashin, 2005). All sites (Union Chapel Mine, Holly Grove Mine, Fern Springs Mine, and Kansas) are located near Carbon Hill, Walker County, Alabama.

Material

UCM - Union Chapel Mine, with suffix identifying the collectors: AA - Ashley Allen, TPA - T. Prescott Atkinson, SM - Steven C. Minkin, RB - Ronald J. Buta, BR - Bruce A. Relihan, JT - Jay Tucker, JL - James A. Lacefield, DA - David Ausmus, GB - Gerald Badger.

FSM - Fern Springs Mine, specimens collected recently by members of the Alabama Paleontological Society are not yet cataloged.

Kansas - Specimens from the outcrops near Kansas collected by J. Lacefield in 1993. The remaining specimens are not yet cataloged.

AMNH - Alabama Museum of Natural History, Tuscaloosa, houses the surviving specimens described by Aldrich (1930) and holds a portion of the UCM specimens.

HH - specimens in the collection of Hartmut Haubold from UCM and FSM.

RM - Redpath Museum, McGill University, Montreal. Casts of some specimens from Joggins, Nova Scotia, originals of Matthew (1905).

TABLE 1. The 56 primary ichnogenera introduced for tetrapod footprints and trackways of Carboniferous formations (asterisks refer to names related to discoveries from North America)
*_Allopus_ Marsh, 1894
“Acripes" Langiaux & Sotty, 1975 (praeocc.)
*_Ancylopus_ Carman, 1927
*_Anomoeichnus_ Carman, 1927
*_Anthracopus_ Leidy, 1880
*_Anticheiropus_ Sarjeant & Mossman, 1979 (praeocc.)
*_Asperipes_ Matthew, 1903
*_Attenosaurus_ Aldrich, 1930
*_Barillopus_ Matthew, 1903
*_Baropezia_ Matthew, 1904
*_Baropus_ Marsh, 1894
*_Batrachichnus_ Woodworth, 1900
*_Bipedes_ Aldrich, 1930
*_Cincosaurus_ Aldrich, 1930
*_Collettosaurus_ Cox, 1874
*_Ctenerpeton_ Aldrich, 1930
*_Crucipes_ Butts, 1891
*_Cursipes_ Matthew, 1903
*_Dromillopus_ Matthew, 1905
*_Dromopus Marsh_, 1894,
*_Hydromedichnus_ Kuhn, 1963 for _Hydromeda_ Aldrich, 1930
*_Hylopus_ Dawson, 1881, 1895
Leptopus Langiaux & Sotty, 1975
*_Limnopus_ Marsh, 1894
*_Limnosauripus_ Kuhn, 1959 for _Limnosaurus_ Aldrich, 1930
*_Matthewichnus_ Haubold, 1970
*_Megabaropus_ Baird, 1952
*_Megapaezia_ Matthew, 1903
*_Nanopus_ Marsh, 1894
*_Notalacerta,_ Butts 1891
*_Notamphibia_ Butts, 1891
Okypes Langiaux & Sotty, 1975
*_Onychopus_ Martin, 1922
*_Ornithoidipus_ Sternberg, 1933
*_Ornithoides_ Matthew, 1903
*_Palaeosauropus_ Hay, 1902 for _Sauropus_ Lea, 1849
*_Parvives_ Willard & Cleaves, 1930
*_Peratodactylopus_ Sarjeant & Mossman, 1979
Pinguipes Langiaux & Sotty, 1975 [= _Stephanopus_ syn. of same year]
Platytherium Barkas, 1873
Prolacertipes Dolle et al., 1970
*_Pseudobradypus_ Matthew, 1903
*_Quadropedia_ Aldrich, 1930
Salichnium Müller, 1962
Schmidtopus Haubold, 1970
Sormiensipes Langiaux & Sotty, 1975 [= _Stephanopus_ syn. of same year]
*_Sphaeropezium_ King, 1845 (replaced Thenaropus King, 1844)
*_Steganoposaurus_ Branson & Mehl, 1932
Stephanopus Gand, 1975
Tenuipes Langiaux & Sotty, 1975
*_Thenaropus_ King, 1844
Tridactylosaurus Barkas, 1883
*_Trisaurus_ Aldrich, 1930

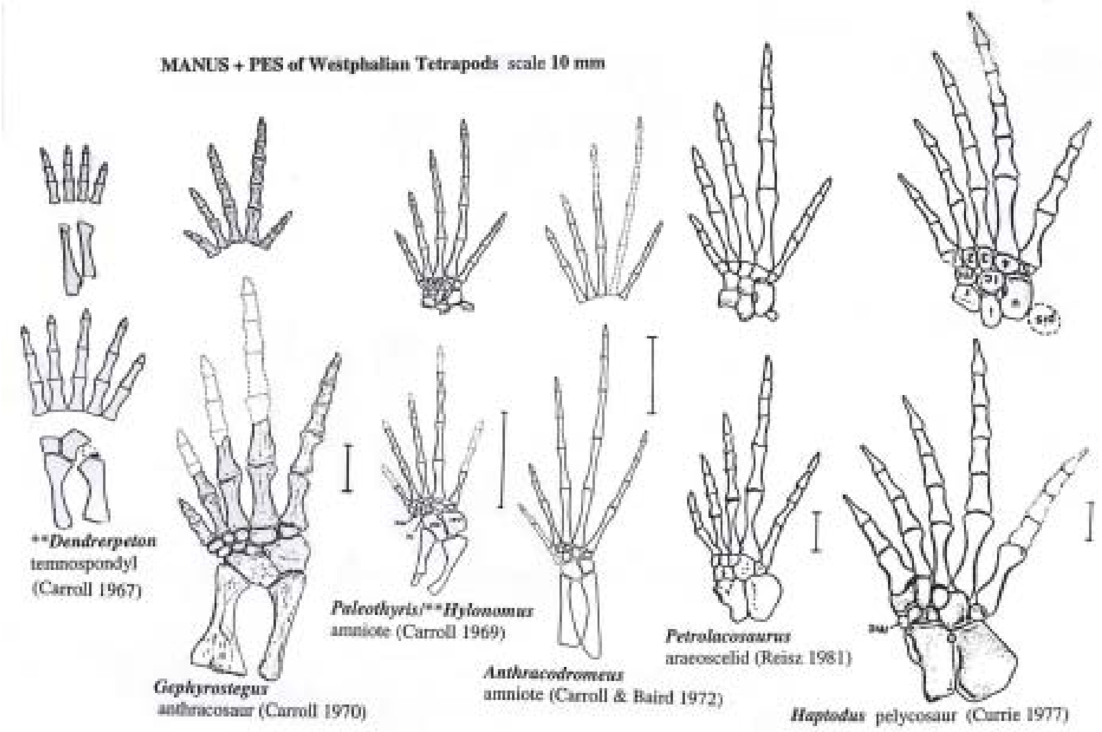

FIGURE 1. Manus and pes skeletons of Westphalian terrestrial tetrapods. Scale 10 mm. *Dendrepeton* after Carroll (1967 a), *Gephyrostegus* after Carroll, (1970), *Paleothyris* (manus) and *Hylonomus* (pes) after Carroll (1969b), *Anthracodromeus* after Carroll and Baird (1972), *Petrolacosaurus* after Reisz (1981), and *Haptodus* after Currie (1977).

PRINCIPLES OF INTERPRETATION

Skeletal record

The interpretation of tetrapod footprints presented below follows the principle of correlating footprint and skeletal evidence known from the Pennsylvanian in general and from the Westphalian A in particular. Terrestrial tetrapods have been recorded from the Westphalian (*genera known from the Westphalian A of Joggins, Nova Scotia); most of the other forms are known from the late Westphalian, localities including Florence, Nova Scotia, Linton, Ohio, and Nyrany, Czech Republic. The following list includes terrestrial groups known by certain genera (assembled from Carroll, 1964a, b, 1967a, b, 1969a, b, 1970, 1982, 1986; Carroll and Baird, 1968, 1970; Currie, 1977; Holmes et al., 1998; Reisz, 1975).

TEMNOSPONDYLI: *Dendrerpeton**, *Amphibamus*
MICROSAURIA (Tuditanomorpha): *Asaphestra**, *Archerpeton**, *Tuditanus*
REPTILIOMORPHA
  Anthracosauria: *Gephyrostegus*
  Diadectomorpha: *Diadectes, Limnoscelis*
AMNIOTA
  Anapsida, Protorothyrididae: *Hylonomus**, *Palaeothyris, Anthracodromeus, Cephalerpeton*
  Synnapsida: *Protoclepsydrops**
  Ophiacodontidae: *Archaeothyris, Clepsydrops, Ophiacodon*
  Haptodontidae: *Haptodus, Macromerion*

In deciphering the tetrapod footprints from the Alabama localities, we can use a well-established record of terrestrial tetrapods representing temnospondyls, microsaurs, anthracosaurs, and amniotes. Several taxa are represented by rather complete skeletons. In some cases we have sufficient Westphalian skeletal material inclusive of the manus and pes: *Dendrerpeton*, *Gephyrostegus*, *Hylonomus* in combination with *Palaeothyris*, *Anthracodromeus* and *Haptodus* (Fig. 1). Added to this assemblage is the manus and pes skeleton of the first diapsid *Petrolacosaurus* (Reisz, 1981) from the Stephanian (Missourian) of Garnett, Kansas, to show that the fully developed lacertoid foot and track pattern of diapsid amniotes, well known with the ichnotaxon *Dromopus*, is not yet recorded from Westphalian time.

Ichnotaxonomy

The footprint record itself, and also its analysis and interpretation, are intriguing in many respects. Part of the complex of problems includes standardizing the methodology of describing and distinguishing tetrapod footprints, the meaning of an ichnotaxon, relationships between the original imprint and the potential undertracks in general and the observed undertracks in the Westphalian *Cincosaurus* beds in particular. Due to the extraordinarily large sample size originating from UCM, we are confronted with an excellent opportunity to understand the distinction of original tracks from undertracks. This is of prime importance in reducing the potential for misinterpretation in the ichnotaxonomy of Permo-Carboniferous tetrapod footprints.

In the case of the Union Chapel site and the Westphalian A tracks from Alabama, we must deal with opposing positions taken by others in their efforts to recognize extramorphology and avoid the creation of phantom taxa — the approaches of the so-called "lumpers" and "splitters". On one side is the separation of every track morph as described by Aldrich (1930), and at the other side the unification of all track morphs under *Cincosaurus cobbi* as proposed by Pyenson and Martin (2001, 2002; see also Martin and Pyenson, 2005). We propose a middle road, utilizing the experience of so-called extramorphology in tetrapod footprints. Extramorphology may be simply explained using the following observation: through influences other than those relating to foot shape, the trackways and tracks of any tetrapod may appear identical or quite different. When measuring all tracks, one usually gets a range of variation that might suggest high diversity. When the sample size is as large and close to complete as that from the UCM, the measurements of high diversity might be instead interpreted as evidence of low diversity.

This apparent contradiction results from the fact that, in a large amount of specimens, all potential variants of preservation may be documented, and the record is thus a continuum. In contrast, where only a few specimens are known, some may represent extreme morphs in size and preservation. Therefore, each morph might be given separate taxonomic status because transitional morphs are unknown or unavailable, as done by Aldrich (1930). (This can be expressed simply in a statement: The larger the sample size, the lower the diversity, and vice versa, the lower the sample size, the larger the diversity.) A consequence of the very extensive record at UCM is the conclusion that all footprints from Westphalian formations might be identified as *Cincosaurus cobbi*. This means all tracks from 5 mm up to 25 cm of any aspect or preservation. And indeed, the diversity of UCM tracks, identified by Pyenson and Martin (2001, 2002) as a single ichnotaxon, might be attributed to such an effect of large ichnological sample size.

There is a solution that lies between both positions. To better reflect objective reality in identifying the tetrapods that produced the ichofauna, one must follow a different line. This strategy for interpreting diversity utilizes only those imprints that record the anatomy of the manus and pes without, or nearly without, extramorphological deformation. Such deformation may be due to gait, substrate qualities and differences, and the downward diminution of foot pressure that results in undertracks. In undertracks, in particular, a gradational change or loss of anatomical control related to morphology can be observed. In undertrack layers, track digits may appear shorter or longer than the digits that made them, or may disappear completely because strongly impressed digits and body impressions may dominate over lightly impressed digits. Such modifications are facies- and substrate-controlled and might cause morphologically disparate imprints to appear similar. Some impressions may appear significant but in reality represent extramorphological phantoms.

Here is the definition of *extramorphology* formulated by Peabody (1948, p. 296-7), and Haubold et al. (1995, p. 136): "In the study of trackways recorded by any living tetrapod it is possible to distinguish trackway characters which portray the anatomy of the animal from those which tend to obscure the portrayal. The latter kind may be termed 'extramorphologic' and include characters arising from the type of recording material and from the gait and variable speed of the animal. If a trackway exhibits a mixture of morphologic, sedimentary, and dynamic characters that are not clearly differentiated from the others, the trackway has little significance. The only trackways to be described (*determined* and *named*) are those which are clearly impressed and are as free as possible from extramorphological characters. Considerable effort was made to obtain a large number of consecutive footprints so that their composite detail would provide a picture of the pedal morphology, and in the trackway would clearly demonstrate the gait and general body from their arrangement."

In continuing this line of argument, Haubold (1996, p. 35) formulated the term *phantom taxon*: Ichnogenera and ichnospecies introduced by footprints or trackways that exhibit a mixture of morphologic, sedimentary, and dynamic characters are not clearly differentiated from one another, and are, therefore, considered phantom taxa. If the significant traits are so deformed that the anatomy of the manus and pes prints are not recorded, the footprints and trackways cannot be correctly identified and interpreted. The "fingerprint of the architect" is lost. A common basis for introducing phantom taxa are footprints and trackways preserved as undertracks, because their high potential for producing variation may lead to an artificially high number of ichnotaxa. In summary, the experience of observing extramorphology and phantom tracks clearly suggests that individuals of a single species of animals may produce very different deformed tracks (phantoms), and vice versa — similar phantom tracks might be produced by different animals.

The extensive examination by the authors of specimens from the Westphalian A of Alabama cannot be presented here at length. Instead this paper's systematics section relies only upon those specimens that display an optimal anatomically controlled record. In other words, we focus on specimens that clearly preserve manus and pes imprints along trackways recorded at surfaces at or very close to the layer of track origin. In these cases extramorphological influences can be excluded so far as possible, and the observed morphology gives an anatomical basis for characterizing certain ichnotaxa. The evidence of original surfaces includes the composition of several layers as well as telltale characteristics recorded in the slab's surface, such as rounded digit impressions. In contrast, undertracks show digit imprints sharpened by the transfer of weight through the sedimentary layers. Also indicative of an original layer can be the presence of a tail or body impression, which usually disappear at undertrack levels within a few millimeters. One surprising and remarkable observation was made during investigation of UCM specimens: that the imprints recorded at undertrack levels are usually sharper at depth than those at the original surface. This is caus-

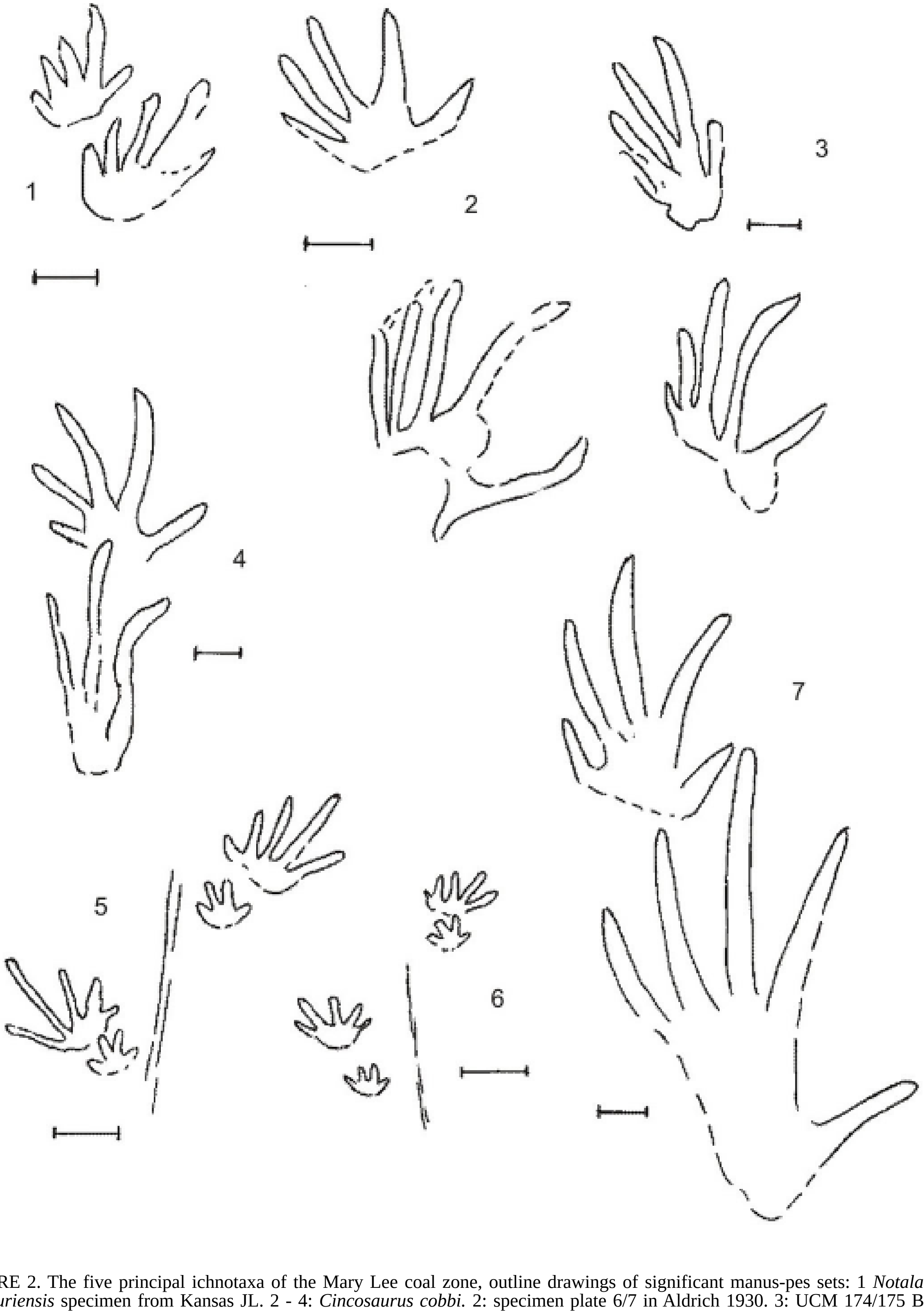

FIGURE 2. The five principal ichnotaxa of the Mary Lee coal zone, outline drawings of significant manus-pes sets: 1 *Notalacerta missouriensis* specimen from Kansas JL. 2 - 4: *Cincosaurus cobbi.* 2: specimen plate 6/7 in Aldrich 1930. 3: UCM 174/175 BR. 4: UCM 263 JT. 5: *Matthewichnus caudifer* UCM 469 BR. 6: *Nanopus reidiae* UCM 1141/1142 TPA (holotype). 7: *Attenosaurus subulensis* assembled from specimens UCM 205, 242, 1214 and 1216 SM. Scale: 1 cm.

ally related to the mechanisms of the origin of tetrapod footprints and the sedimentological conditions controlling their record. These aspects have not been analyzed sufficiently for Permo-Carboniferous track beds. Some examples are discussed below. Due to the greater distinctness of imprints or of their central parts at depth, undertracks might have been preferred to original surfaces when tracks were being collected and selected for exhibition and education. However, as noted by Buta and Minkin (2005), all UCM material was taken seriously by some collectors, and this bias is not as important a problem as it might be in other collections.

SYSTEMATIC PALEONTOLOGY

Trackways Attributed to Temnospondyls

Based upon the published record (Aldrich, 1930) the small track types from specimens collected in the *Cincosaurus* beds of the Union Chapel Mine and the layers of Fern Springs Mine, presumably of temnospondyl origin and here described as *Matthewichnus* and *Nanopus*, are new for the Pottsville Formation in Alabama. In particular, from the UCM surfaces, undertracks of these small tracemakers are very common and look attractive, some surfaces displaying extensive trackways. Only a few specimens are preserved at or close to the original surfaces and, therefore, record an actual, anatomically controlled foot morphology and trackway pattern that might be useful for determination, differentiation, and interpretation. The unquestionably tetradactyl manus imprints suggest temnospondyl origins for both types.

Matthewichnus Haubold, 1970

Dromopus, Matthew, 1905: 86 (*D. velox*).
Matthewichnus Haubold, 1970: 107.
Matthewichnus, Kohl and Bryan, 1994: 661.

The ichnogenus was introduced based on type *Dromopus velox* Matthew, 1905 from the Westphalian of Joggins, Nova Scotia, by Haubold (1970). The elongate digits and plantigrade imprints distinguish this ichnogenus from others. But because knowledge of the trackways is incomplete, this ichnogenus remains problematic. A substantial contribution was the description of a trackway from the Cross Mountain Formation, Westphalian A, of Tennessee, by Kohl and Bryan (1994) as a new ichnospecies of *Matthewichnus* that shows plantigrade imprints with elongated digits. The species name *caudifer* (“tail-bearer”) should not be confused with the previously described *Palaeosauropus (Hylopus) caudifer* (Dawson, 1882). It is also different from *Nanopus caudatus* Marsh, 1894 (see below).

Matthewichnus caudifer Kohl and Bryan, 1994

Figures 2 (5), 3A-C

Matthewichnus caudifer Kohl and Bryan, 1994: 661, figs. 3 - 6.

The identity of the UCM material with *Matthewichnus caudifer* Kohl and Bryan, 1994 from the Westphalian of Tennessee is confirmed by specimen UCM 469 BR with footprints in original surface preservation at several layers. Additional evidence of *M. caudifer* is known from uncataloged specimens from the Fern Springs Mine; one trackway in the collection of BR shows along a length of 60 cm about 120 manus-pes sets.

Known distribution. Cross Mountain Formation, Westphalian B, Campbell County, Tennessee, and basal upper Pottsville Formation, Westphalian A, Union Chapel Mine and Fern Springs Mine, Walker County, Alabama.

Diagnosis. Manus tetradactyl, roughly as wide as long. Digits II and III of roughly equal length, slightly more than half the length of the entire print. Digits I and IV also subequal, approximately one-third the length of the entire print. Pes pentadactyl, larger than manus, with digits of increasing length from I to IV, digits III and V subequal. (condensed from Kohl and Bryan, 1994).

Material from Walker Co. Alabama. UCM 469 BR (several surfaces), UCM 969 BR, UCM (H002) BR, UCM 652 TPA, UCM 285 AA; Fern Springs Mine — one unnumbered specimen BR, four specimens in the collection of HH.

Description and discussion. With extensive evidence, knowledge of the characters of these ichnospecies becomes more precise. Most significant is the comparison with other small pes prints having an elongate digit IV, usually directed outward. The axis of pes digit III is directed slightly outward; the smaller manus imprints are placed closer to the midline and directed inward. The presence of a tail impression, and the dimensions of imprints and trackway parameters mentioned in the original diagnosis of Kohl and Bryan (1994), must be modified to include the UCM specimens or, like the tail impression, are not diagnostically significant. The value of the tail impression, as with other ichnotaxa from the Pottsville Formation, lies in the demonstration of a track record at the original surface. This is the optimal, anatomically controlled record of the manus and pes morphology, sometimes with plantigrade imprints (Figs. 3 A-C). All the determinable specimens therefore show the tail impression. A long trackway with at least 120 manus-pes sets along 60 cm from Fern Springs Mine shows the smallest manus size, about 5 mm long; the pes is about 8 mm long. In other trackways collected by HH from the FSM, the pes length is greater than 20 mm. In trackways from the UCM, the known pes length does not exceed 15 mm. Due to different lithofacies of the UCM and FSM surfaces, the tracks’ preservation shows some variation in morphology that might be quantified by further studies.

Nanopus Marsh, 1894

Nanopus Marsh, 1894: 82.
Nanopus, Matthew, 1905: 98.
Nanopus, Haubold, 1970: 96.
Anthichnium, Haubold, 1970: 89 (*partim*).

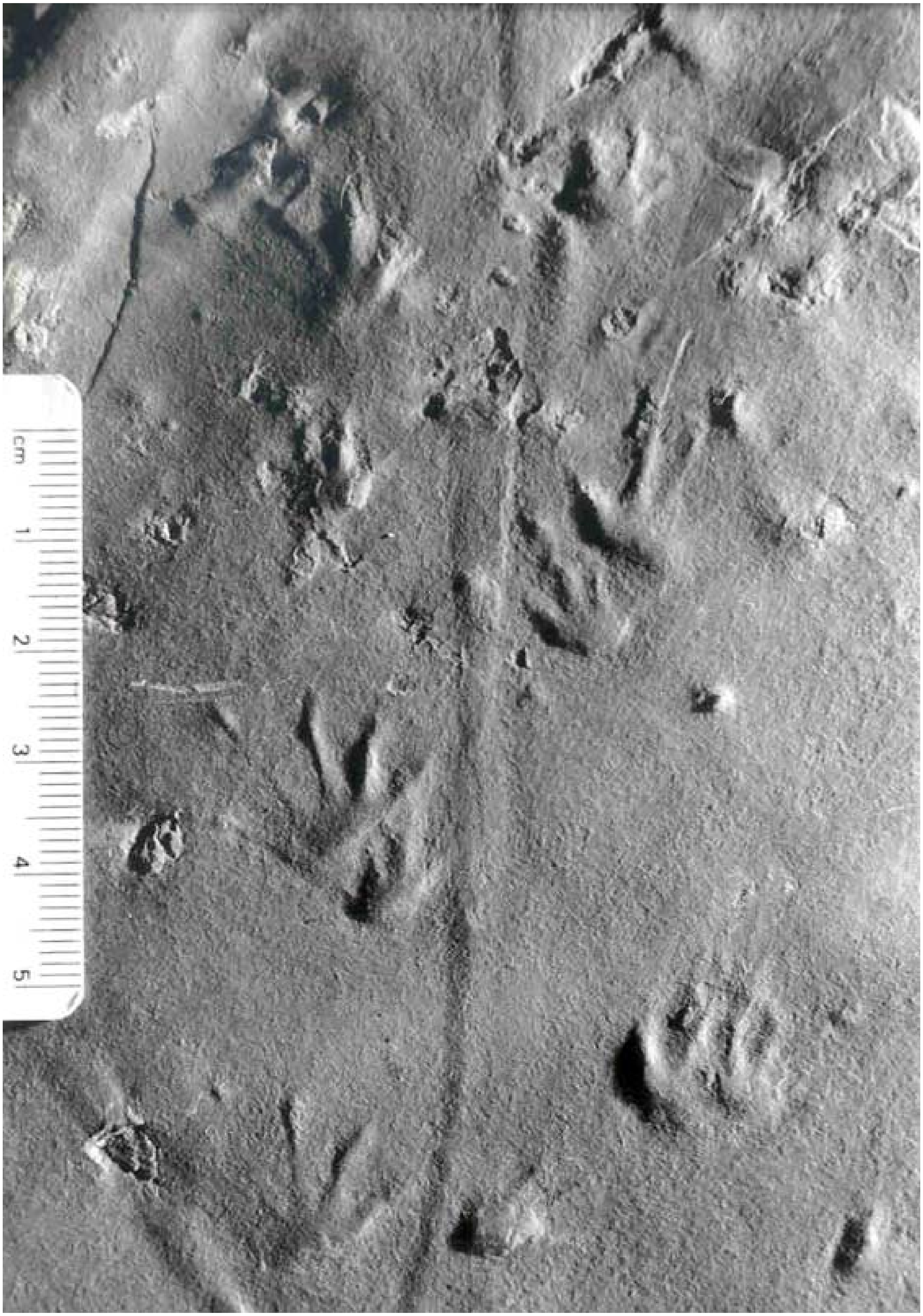

FIGURE 3A. UCM 469 BR.

FIGURE 3. *Matthewichnus caudifer* Kohl and Bryan, 1994 (photographs, scale mm and cm). A: UCM 469 BR. B: UCM 652 TPA. C: specimen from Fern Springs Mine, segment of a long trackway, coll. BR.

FIGURE 3B. UCM 652 TPA.

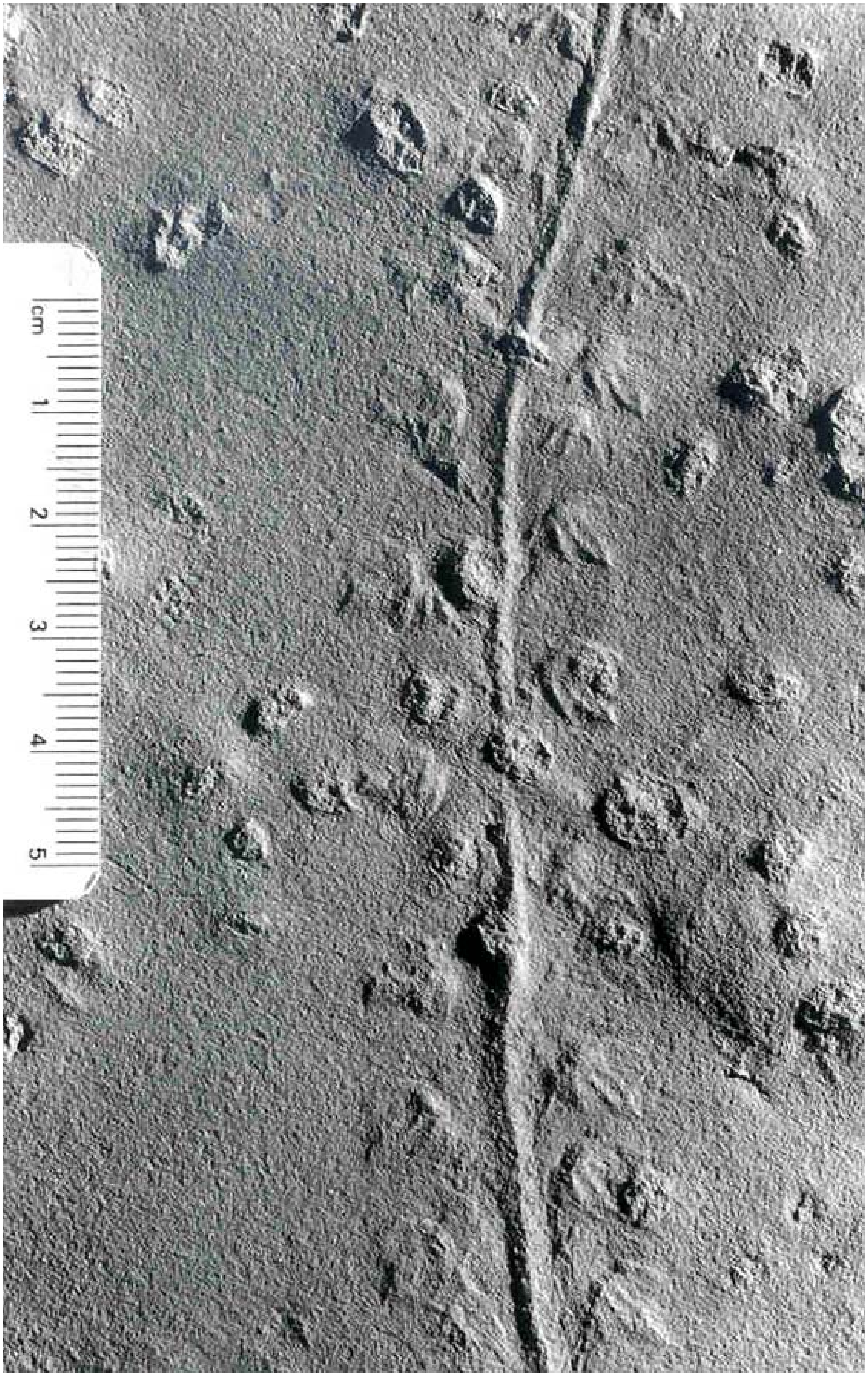

FIGURE 3C. UCM (H002) BR.

The ichnogenus was introduced by Marsh (1894) with *Nanopus caudatus* as type, for a relatively long trackway found in the Upper Pennsylvanian Wabaunsee Group of Kansas. Under *Nanopus quadratus* and *N. obtusus*, Matthew (1905: 98) named similar salamander-like tracks and trackways from the Westphalian A of Joggins. Haubold (1970, 1971) synonymized the *Nanopus* specimens from Joggins erroneously with *Anthichnium*. At this time several data points were not available, such as the knowledge of *Batrachichnus*, type species *B. plainvillensis*. After the investigation of specimens from Lower Permian Red Beds the validity of *Batrachichnus* was recommended (Haubold, 1996), and after inspection by HH of the cast of the holotype from the Missourian of Massachusetts in the collection of Don Baird, the validity of *Batrachichnus* is confirmed. In common with *Batrachichnus*, *Nanopus* from Joggins has a pentadactyl manus, but the proportions of the digits and imprints are different from those of *Batrachichnus plainvillensis* and *B. delicatulus/salamandroides*. The number of digits in the species of the genus described by Marsh (1894) is obviously incomplete in most impressions. However, some imprints of the type specimen (Yale Peabody Museum 539) show a tetradactyl manus. Together with the information from the specimens of *N. quadratus* and *N. obtusus* from Joggins (RM 2.1134. 2.1134a, 2.1135, and 12.59 studied in casts) and the evidence from UCM, the ichnogenus *Nanopus* can be reestablished with a separate, new ichnospecies.

***Nanopus reidiae* n. isp.**

Figs. 2(6), 4A-F

Holotype. UCM 1141/1142 TPA.

Paratypes (referred material). UCM 311 AA, UCM 159 BR, UCM 196 BR, UCM 629-TPA, UCM 364 AA, UCM 60 GB, UCM 649 TPA. All specimens listed as paratypes allow in regard to their preservation at the original surface a sufficient identification of the manus and pes proportions, in particular of the digit length and arrangement, which is the main character in which it differs from *Matthewichnus caudifer*.

Etymology. The species is named in honor of Mrs. Dolores Reid, the owner of UCM when the initial specimens were recovered. Her generosity is arguably the single most important factor in the salvage of this large collection of tracks from the elements and from eventual destruction during reclamation.

Locality and Horizon. Union Chapel Mine, Walker County, Alabama, *Cincosaurus* beds above the Mary Lee coal bed, lower part of the upper Pottsville Formation.

Diagnosis. Footprints of tetrapods with tetradactyl manus and pentadactyl pes imprints. The length of pes digits I to V are nearly equal, pes digit III parallels the midline (direction of trackway), and digits I to V are outspread at an angle of 90°. The manus imprints are smaller, only 60% of the size of the pes imprints. Along a trackway manus and pes imprints appear close together in sets with a changing pattern. The manus is usually positioned behind the pes, but sometimes it is partially overstepped by the pes or may occasionally appear in front of the pes. Where the trackway curves, the manus imprints may face outward from the middle line (axis) of the trackway. This points to a somewhat elongated trunk of the trackmaker; the coupling value (ratio of the length of trunk to the length of front + hind limb) might be more than 1:1.5. Observed pes lengths are about 10 mm or greater. In trackways associated with tail impressions the manus and pes imprints become increasingly plantigrade. The closely related *N. caudatus* and *N. quadratus* show an imprint pattern of shorter and broader digits.

Description and discussion. Within the spectrum of related ichnotaxa of small presumed temnospondyls, the most significant characters for *Nanopus* are those mentioned in the diagnosis: digit proportions and the orientation of the pes within the trackway. This is important for the differentiation to other small ichnogenera including the type *Matthewichnus* from the Westphalian A, and from *Batrachichnus* from younger beds of the Permocarboniferous. A more objective characteristic in differentiation of *Nanopus* and *Matthewichnus* is possible by comparing the photographs (Figs. 3 and 4) with some helpful assistance from the added line drawings (Fig. 2).

The vast majority of the small tracks found at UCM may belong as well to *Nanopus*, but because of the preservation as undertracks the determination cannot be established definitely for all specimens. Examples of such undertracks are: UCM 2 SM, 4 SM, 11 SM, 140 BR, 167 BR, 177 BR, 191 BR, 195 BR, 281 AA, 302 AA, 312 AA, 313 AA, 318 AA, 357 AA, 447/8 TPA, 833/1031 AA, 973 BR. Long trackways, each with about 100 manus/pes sets, are 76/84 TPA, 249 JT, and 571 DA, providing evidence of the potential for change and variation during undertrack preservation. The list of specimens might be expanded considerably. Those mentioned are only a few representative specimens that have been studied and documented recently in detail.

In contrast to the specimens referred to as *holotype* and *paratypes*, undertrack specimens look more attractive and are rather easy to recognize during field work in the *Cincosaurus* beds at UCM. However, they are not significant for ichnotaxonomy, for shedding light on the behavior of the trackmaker, or for understanding the environment in which they were laid down. They are highly variable extramorphologically disguised impressions, a result of the action of sedimentological mechanics during the preservation of these tracks in the *Cincosaurus* beds at UCM and in many other Permo-Carboniferous formations. This phenomenon of preservation is the reason for the apparent uniformity of small and large tracks in the Pottsville Formation. Indeed, the undertracks of the small *Nanopus*, the medium-sized *Cincosaurus* and the large *Attenosaurus* look alike. However, with the knowledge of sedimentology, track preservation and extramorphology, such similarity is nothing more than an illusion (see earlier under ichnotaxonomy). Moreover, such undertracks are named very differently and interpreted in every possible way from most Permo-Carboniferous footprint formations in North America and Europe.

This context is the background in using names of

FIGURE 4A. UCM 1141 TPA.

FIGURE 4. *Nanopus reidiae* n.isp. (photographs, scale cm and mm). A: UCM 1141 TPA, holotype specimen. B: UCM 311 AA. C: UCM 060 GB. D: UCM (H003) BR, trackway preserved at original surface and in the following part at a 1 mm deeper undertrack surface. E: UCM 973 BR the undertracks of manus and pes are reduced to a record of three digits. F: UCM 357 AA, one example of the attractive *Nanopus* trackways, the "little gems" of the Union Chapel Mine *Cincosaurus* beds. These undertracks display manus and pes partially complete.

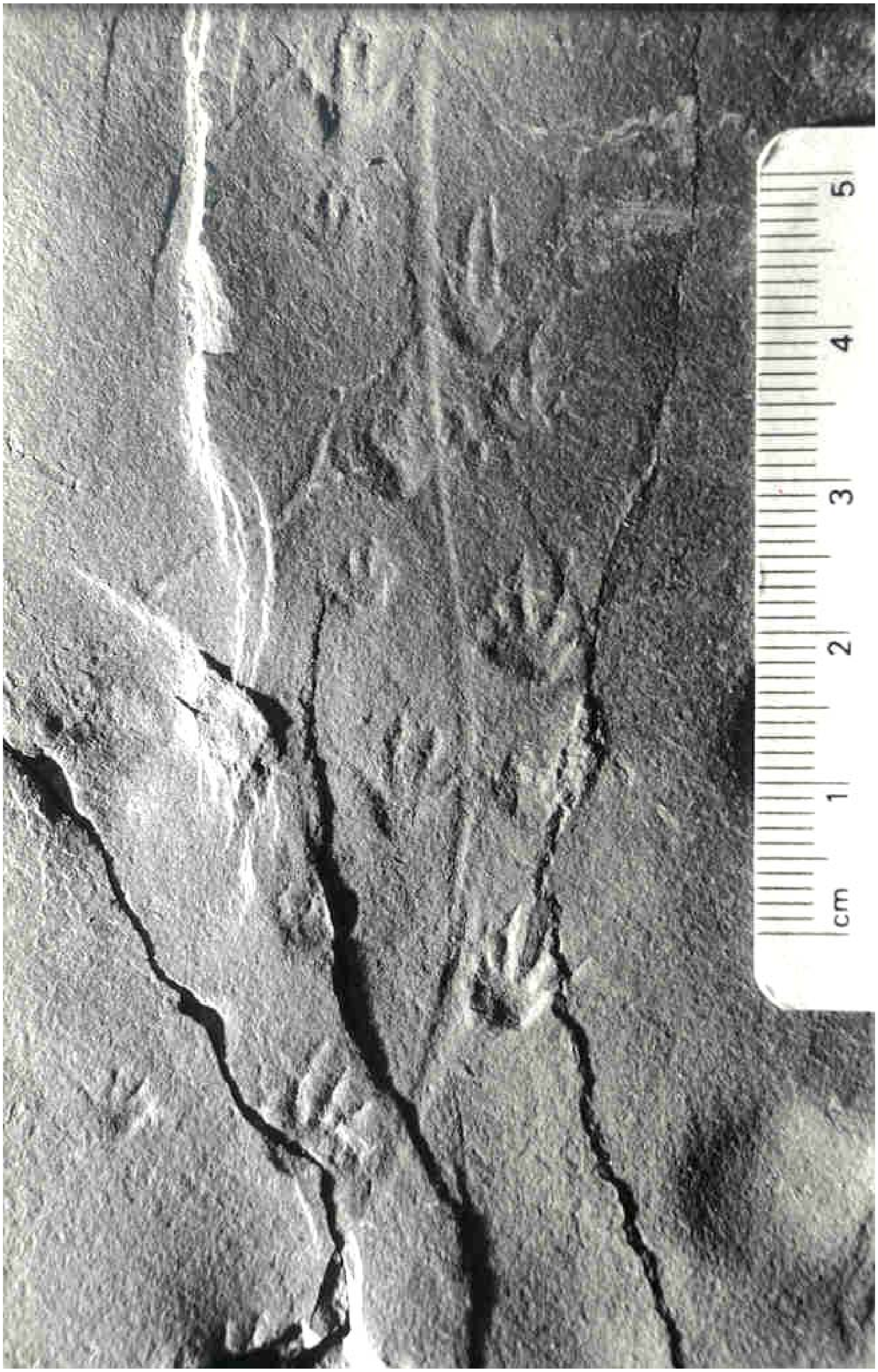

FIGURE 4B. UCM 311 AA.

FIGURE 4C. UCM 60 GB.

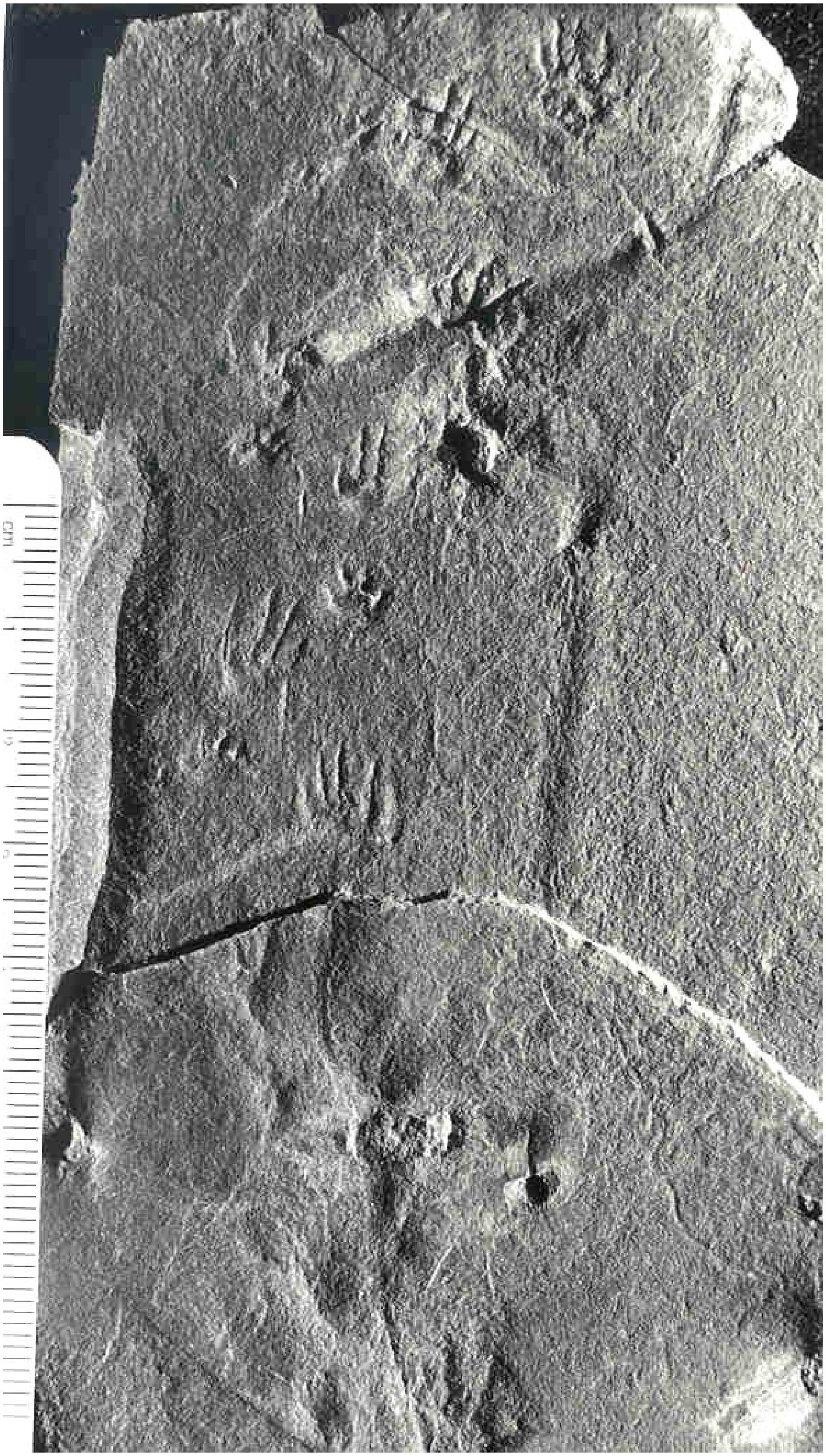

FIGURE 4D. UCM (H003) BR.

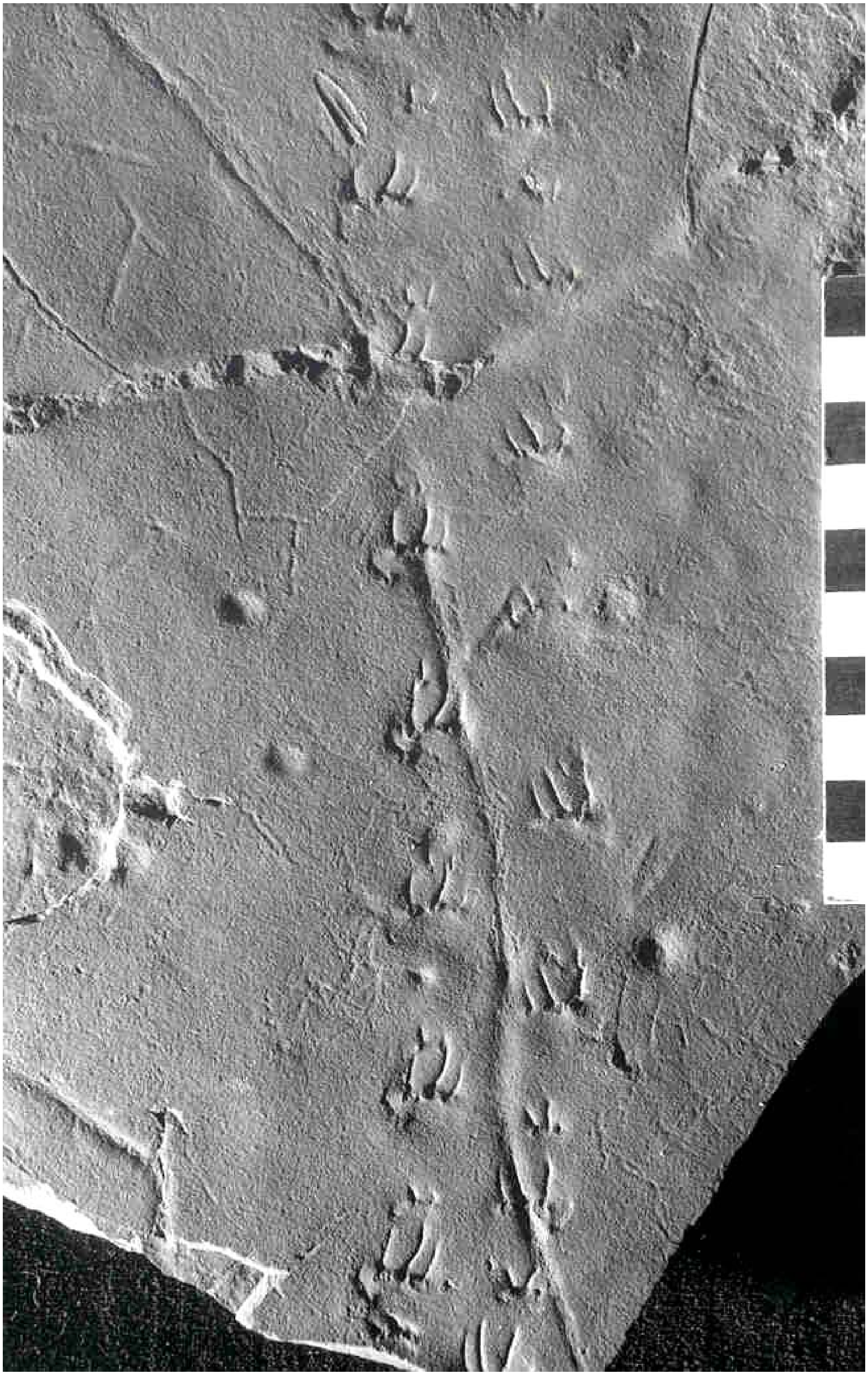

FIGURE 4E. UCM 973 BR.

FIGURE 4F. UCM 357 AA.

FIGURE 5. UCM 26 SM, cf *Matthewichnus caudifer*, the trackway started from a possible resting or aestivation trace, or some kind of hatching event.

Aldrich (1930) by Schult (1995) for the determination of several footprints from the Robledo Mountain Formation in New Mexico. The partial, apparently bipedal trackways called *Salichnium* — the name points to the hitherto enigmatic phenomenon of apparent leaping traces — first named by Müller (1962; cf. Haubold, 1970, p. 86; 1971, p. 11) from the Westphalian D of Zwickau, Germany, are simply undertracks identical to many specimens from the *Cincosaurus* beds. The number of examples is endless, like the synonymy of *Batrachichnus* (Haubold, 1996). The taxonomic establishment and comparison of the ichnospecies unified under *Nanopus* — *N. caudatus*, *N. obtusus*, *N. quadrifidus*, and *N. reidiae* — must be elaborated in detail later. Aside from UCM, there are some finds (TPA collection) from the Birmingham region that resemble the imprint pattern with short broad digits known from *N. caudatus* and *N. quadratus*. The description and differentiation of these ichnotaxa have to be investigated later; here we concentrate on the evidence characterizing *N. reidiae*.

Specimens UCM 949 BR and UCM (H003) BR are significant in proving the change in the preservation between tracks at the original surface and undertracks at surfaces a few millimeters below. In UCM 949 BR the original surface displays an extended trace of the tail and body beside rather few manus and pes imprints. Following our observations, this appearance is, in most cases, characteristic for the record of *N. reidiae* at or close to the primary surface. In contrast, some 3 mm to 5 mm below the surface of UCM 949 BR, undertracks display medially sharpened and elongated digit impressions of manus and pes that are related to the record from the original surface. Much more instructive is specimen UCM (H003) BR (Fig. 4D). A segment of the trackway is preserved along the original surface with tail impression and other imprints, a few of which allow determination as *N. reidiae*; the trackway continues into a segment of undertracks exposed on a layer only 1 mm deeper, visible because the layer above has delaminated. These undertracks show sharp, elongate and pointed digits; the tail impression is lacking.

The manus imprints in both *Matthewichnus* and *Nanopus* are tetradactyl and significantly smaller than those of the pes. *Nanopus* shows pes digits of rather similar length; this proportion might be comparable with the pattern known from the temnospondyl *Dendrerpeton* (Fig. 1) of Joggins. In *Matthewichnus* the length of the pes digits increases strongly from I to IV, IV is the longest, and digit V is as long as digit III. No comparable foot morphology is yet known from temnospondyls of Westphalian age. The trackway pattern of both ichnospecies points, along with a coupling value between 1 and 1.5, to an elongated trunk region. This may allow as well a correlation with microsaurs. However, the foot morphology and the tetradactyl manus have the standard morphology of several other kinds of Permo-Carboniferous tracks that are interpreted as having been made by temnospondyls.

An extraordinary and enigmatic record is displayed in specimen UCM 26 SM (Figure 5). The first interpretation in the UCM database argued for an act of predation, because the trackway apparently ends here. Instead, this is where the trackway of a small tetrapod begins and moves away. There are two potential interpretations. It is 1) a resting or aestivating situation, or 2) indicative of some kind of hatching event. Concerning the first argument there are no traces in the surrounding sediment. The second argument corresponds with the trace situation; however, it is highly speculative, especially because it points to the absence of an "amphibian larval stage" in the temnospondyl trackmaker, and the idea should be attributed to the senior author alone. Still, in this case a temnospondyl origin should not necessarily be excluded. The reproductive strategies of terrestrial temnospondyls must not necessarily be the same as those of amphibians in a strict sense. Moreover, in view of some current discussions concerning a modified amphibian status of microsaurs (Carroll, 2001), the hatching trace associated with a trackway of cf. *Matthewichnus* could argue for an origin of this group of early tetrapods as well. At present there are only preliminary ideas regarding specimen UCM-026 SM. Any further discussion and interpretation must consider the surface in relation to the environment of the track-bearing layers at UCM.

TRACKWAYS ATTRIBUTED TO ANTHRACOSAURS

Attenosaurus Aldrich, 1930
Attenosaurus subulensis Aldrich, 1930

Figures 2 (7), 6A-B

Attenosaurus subulensis Aldrich, 1930, p. 13, pl. 2.

The largest form, already introduced as an ichnotaxon by Aldrich (1930), is *Attenosaurus subulensis*. It is known from Holly Grove Mine and Union Chapel Mine. Although the original specimen described by Aldrich is lost, the ichnotaxon can be well established by reference to the UCM samples. By dimension (up to 25 cm pes length), trackway pattern, and digit proportions (the pentadactyl manus and pes imprints IV is shorter than III), the manus and pes morphology of *Attenosaurus* is therefore different from that of *Cincosaurus*. However, it might be possible in view of the restricted undertrack record, and from a more generalized formal point of view, to understand *Attenosaurus* and *Cincosaurus* as size-controlled extremes of a single ichnotaxon. In particular, under the spectrum of *Cincosaurus*, e.g., with taxa named as separate by Aldrich that are synonymized below under *Cincosaurus*, we apparently have evidence of transitional forms from *C. jonesii* to *A. subulensis*. This is, again, one example of the intriguing information of undertracks. If the ichnotaxonomy concerns the optimal recorded specimens, figured by Aldrich (1930, pl. 2 and 6, 7), together with specimens from UCM, these are separate ichnotaxa, not only in dimension but also, particularly, in foot morphology. An extended record of the large forms might allow a further ichnotaxonomic differentiation of specimens assigned to *Attenosaurus*. As long as we are dependent on undertracks, further detailed discrimination of certain forms remains premature.

In this context and in the forefront of taxonomical problems of tetrapod footprints of the Pennsylvanian in principle, the generic splitting of *Attenosaurus* tracks into three ichnogenera as proposed by Hunt et al. (2004) needs to be briefly discussed. The interpretation as pelycosaurs concerns only two or three specimens assigned to *Dimetropus*, and tentatively identified as *Dimetropus* isp. This rather formal argumentation surpasses the reality in interpreting tetrapod footprints of Pennsylvanian age in particular. And although the limitations of undertracks and extramorphological elongations and shortenings of digits are noted by Hunt et al. (2004) repeatedly, such characters are used for the ichnogeneric discrimination. Above all, the extended record of several hundred footprints of large animals within the the UCM specimens contradicts the generic separation presented by Hunt et al. The mentioned specimens UCM 24 ("*Alabamasauripus*"), UCM 21 ("*Dimetropus*"), and UCM 199/200, UCM 270 ("*Attenosaurus*") are a fragmentary selection from an extended number of specimens that record all possible morphological-extramorphological transitions. Before any future ichnotaxonomical conclusions, the undertrack phenomena of the footprint-bearing formation in Alabama and other occurrences in North America should be analyzed. The understanding of larger tetrapod tracks of the Carboniferous is too incomplete yet, and there are enough ichnogeneric names available that need to be revised before new names should be introduced.

The most plausible interpretation of *Attenosaurus* points to anthracosaurs as represented by *Gephyrostegus* (Fig. 1) from the later Westphalian deposits. However, the huge size of *Attenosaurus* appears in principle rather enigmatic within the hitherto known skeletal record of terrestrial tetrapods of the early Westphalian. An origin by pelycosaurs, respectively early synapsids, is excluded by the large size of *Attenosaurus*, although it may appear only as a relative argument. At first sight, a transition in size and, therefore, in origin appears possible. However, the wide trackway pattern of *Attenosaurus* is different from the very narrow pattern of the pelycosaurian *Cincosaurus*. In all known specimens *Attenosaurus* is recorded as undertracks, and digits II, III, IV and sometimes V, belonging mainly to the pes, appear very elongate in the undertracks. Some prints pushed through several centimeters of sediment and the number of visible digits is reduced, a phenomenon already reported by Aldrich (1930, pl. 1) as *A. indistinctus*. In some cases only the imprints of the larger foot, presumed to represent the pes, are recorded. Due to its large size, the knowledge of the trackway pattern is limited. The blocks of roof shale slabs or surfaces of larger extent, such as the uncataloged slab in the Aldrich collection at the ALMNH from the Aldrich collection (Fig. 6 B) and UCM 645/1074 TPA, are the exception. The stride was measured from UCM 270 AA with 420 mm related to a pes length of 130 mm. Some additional significant selected specimens representing *Attenosaurus* from Union Chapel Mine are 9, 16, 24/25, 205, 219, 242, 1206 and 1216 (all SM) as well as 270, 282 AA, and 1470-72 (all RB). Several additional specimens are documented in Haubold et al. (2005).

Although in most aspects the restricted preservation of *Attenosaurus* does not allow a clear description, and it may have a status of a phantom taxon, this significant and comparable gigantic element of the Pottsville ichnofauna should be accepted at present as valid. The missing type material of *A. subulensis* is a formal problem in the nomenclature. But this not a substantial argument against a distinct tetrapod ichnotaxon.

FIGURE 6A. UCM 645 TPA.

FIGURE 6. *Attenosaurus subulensis* Aldrich, 1930 (photographs scale in cm). A: UCM 645 TPA trackway segment with two manus and pes imprints. B: ALMNH uncataloged from Holly Grove Mine; the trackway displays pes-undertracks only.

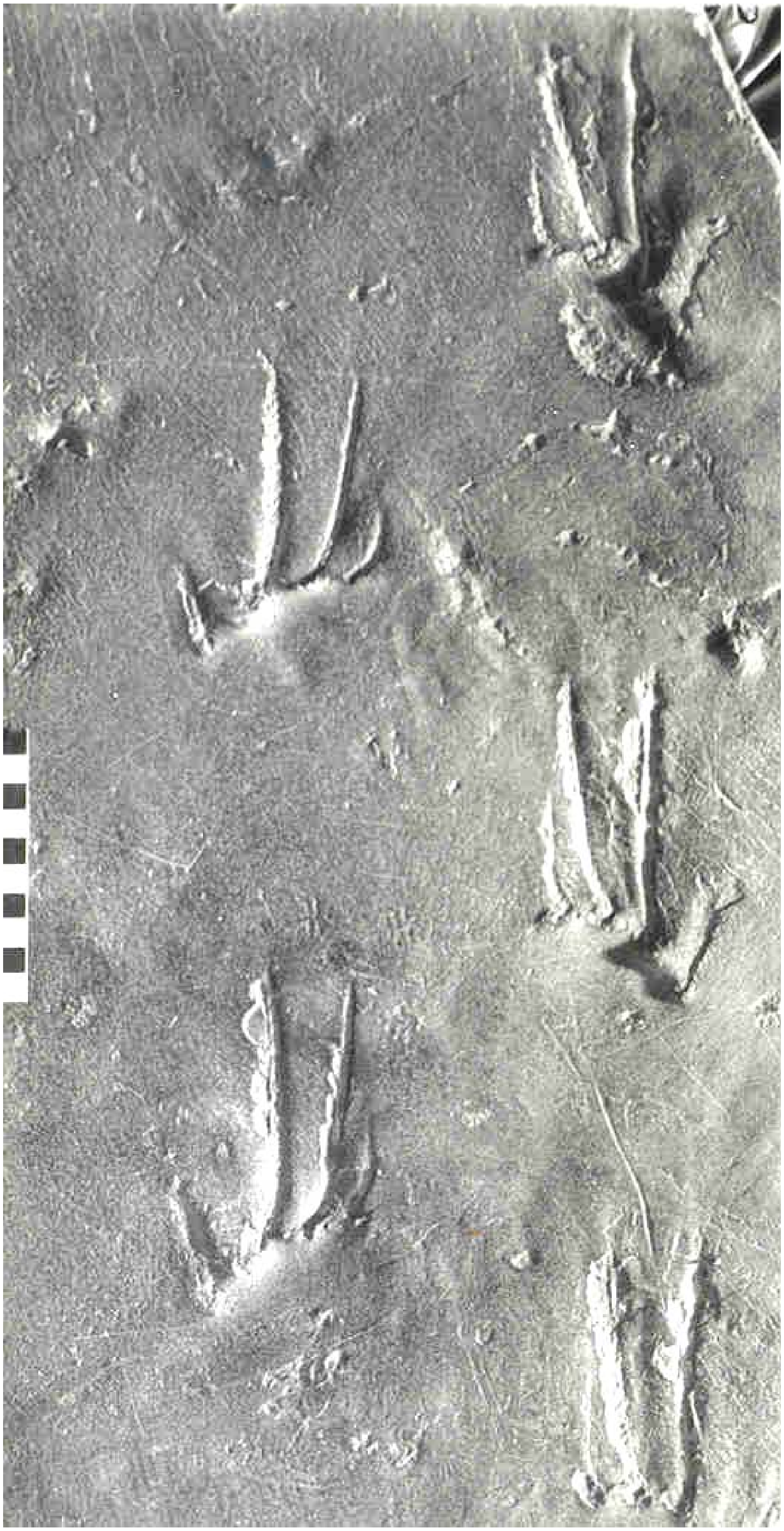

FIGURE 6B. ALMNH specimen.

TRACKWAYS ATTRIBUTED TO AMNIOTES

The amniote interpretation of ichnotaxa *Cincosaurus* and *Notalacerta* is supported by the pentadactyl manus and by the trackway pattern, which shows a more advanced, less sprawling gait that reflects the progress in terrestrial abilities of early amniotes. *Notalacerta* can be optimally correlated in accordance with Chesnut et al. (1994) to protorothyridid anapsids such as *Hylonomus* (Fig. 1) known from the Westphalian A of Joggins. In contrast, *Cincosaurus* might be represented, in view of its digit proportions and remarkable high pace angulation pattern, by early synapsids resembling *Haptodus* (Fig. 1), although such skeletal evidence is known only from the late Westphalian onward.

Notalacerta Butts, 1891

Notalacerta missouriensis Butts, 1891

Figs. 2 (1), 7A-D

Notalacerta missouriensis Butts, 1891: 18, Fig.
Notalacerta missouriensis, Chesnut et al., 1994: 155, Fig. 3-6
footprints from Kansas, Alabama, Lacefield 2000: Figs. on p. 68 and 69.

Known distribution. Top of Cement City Limestone, Chanute Formation, Missourian of Kansas City, Missouri (original locality); Rock Lake Member of Stanton Formation near Garnett, Kansas (Chesnut et al. 1994); Rockcastle Sandstone Member (Westphalian A) of the Le Formation, McCreary County, Kentucky (Chesnut et al., 1994); Mary Lee Coal Zone, Kansas, Holly Grove Mine and Union Chapel Mine, Walker County, Alabama.

This hitherto problematic ichnotaxon was reestablished by the description of a new find in the Westphalian A of Kentucky by Chesnut et al. (1994). Their paper contains several important comments that originated from the experience of Don Baird (1982). Besides the description of a new specimen, Chesnut et al. (1994) presented a composite sketched from topotypes and photographs of the lost types.

Exceptionally preserved additions to *N. missouriensis* are specimens collected by JL in 1993 near Kansas, west of Carbon Hill, Alabama. Along several trackways with tail mark are recorded imprints of the pentadactyl manus about 18 mm long, and pes about 22 mm long. The manus is directed inward, and the pes outward along trackways with a stride of 50 mm to 65 mm, and manus pace angulation of 90°. This relatively wide trackway pattern is significant and allows the tentative identification of specimens displaying trackways with undertracks of manus imprints not only from Kansas, Alabama, but also trackways with fragmentary imprints in the pattern of *N. missouriensis* from the Union Chapel Mine (UCM 223, 229 and 1209 SM) and two trackways on slabs of Aldrich's collection from the Holly Grove Mine (ALMNH P.985.1.15 and 17). The relatively wide trackway pattern, together with the digit proportions of the manus, are important for the differentiation of *N. missouriensis* from *Cincosaurus cobbi*.

Cincosaurus Aldrich, 1930

Cincosaurus Aldrich, 1930: 27

Cincosaurus cobbi Aldrich, 1930

Figs. 2 (2-4), 8A-H

Cincosaurus cobbi Aldrich, 1930: 27, pl. 6, 7
cf. *C. fisheri* Aldrich, 1930: 27, pl. 8
cf. *C. jaggerensis* Aldrich, 1930: 28, pl. 9 (ALMNH P 985.1.8)
cf. *C. jonesii* Aldrich, 1930: 28, pl. 10 (ALMNH P 985.1.9), pl. 11
cf. *Quadropedia prima* Aldrich, 1930: pl. 15 (ALMNH P 985.1.7)
cf. *Limnosaurus alabamensis* Aldrich, 1930: 49, pl. 14 (ALMNH P 985.1.5)
cf. *Hydromeda fimbriata* Aldrich, 1930: 45, pl. 13 (ALMNH P 985.1.1)
cf. *Trisaurus secundus* Aldrich, 1930: pl. 17 (ALMNH P 985.1.14)

Known distribution. Mary Lee coal zone, lower part of the upper Pottsville Formation, Holly Grove Mine, Union Chapel Mine, and Kansas, all in Walker County, Alabama. There is no correct determined record known from outside Alabama.

Diagnosis. Tetrapod trackways with pentadactyl imprints of manus and pes, both in reptilian-like arrangement, the length of digits increases from I to IV, and V is shorter and positioned backward and outward. The known size range measured for the manus is 15 mm to 35 or even 40 mm in length. The pes is slightly larger than the manus. The majority of average trackways show the manus directed inward, and the pes parallels the midline, each related to the orientation of digit III. The trackway pattern is narrow with a pace angulation of succeeding manus imprints usually higher than 100° and up to 120°.

Discussion. The proof of the tentative synonymy above is given by the record from UCM specimens 17 SM, 18 SM, 87 TPA, 174/175 BR, 208 SM, 237 SM, 250 to 263 JT, 1075 TPA, and 1476 RB. Together, they may show transitions comparable to the types separated by Aldrich. After more detailed inspection of these tracks, the concept of transitional preservation may come under question, but the observed differences might, in part, have derived from the somewhat different substrate consistency of the Holly Grove samples in comparison to the thin laminated mudstones of the UCM layers. The best agreement with *C. cobbi* is given for the type specimen of *Quadropedia prima*: along the trackway segment, inward-directed manus imprints are visible, and from the pes are recorded short and shallow marks of only two digits. This corresponds with undertrack modifications; in most trackways of *C. cobbi* only the inward-directed pentadactyl manus imprints are completely recorded. This is identical to a specimen from Kansas, Alabama, collected by JL that displays a pace angula-

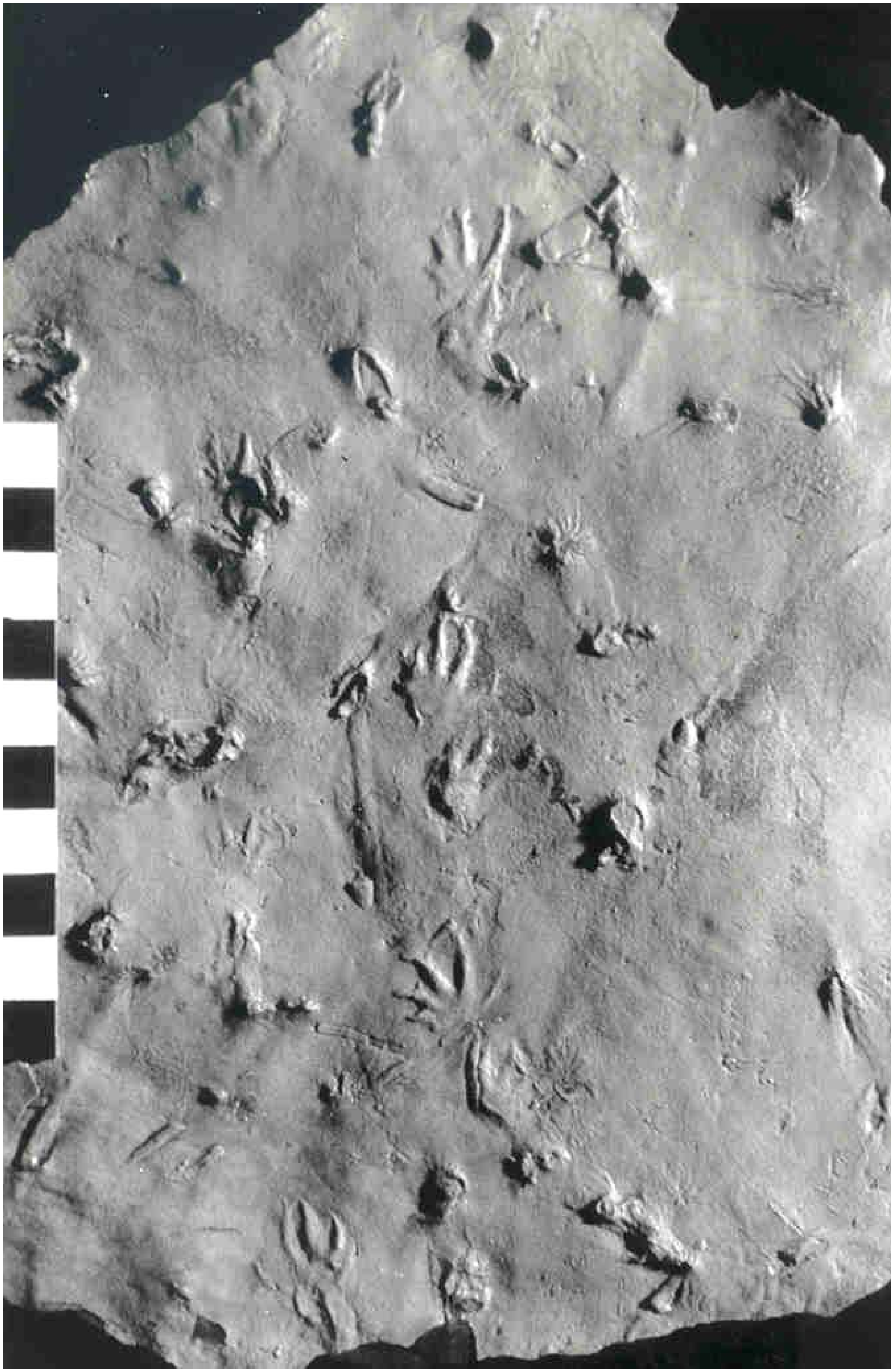

FIGURE 7A. Unnumbered specimen from Kansas, Alabama.

FIGURE 7. *Notalacerta missouriensis* Butts, 1891 (photographs, scale in cm). A: Trackway with 6 manus-pes sets, unnumbered specimen from Kansas, coll. JL. B: two subparallel trackways, unnumbered specimen from Kansas, coll. JL. C: ALMNH P.985.1.15 from Holly Grove Mine. D: UCM 229 SM, specimen with undertracks displaying the trackway pattern of *N. missouriensis*.

FIGURE 7B. Unnumbered specimen from Kansas, Alabama.

FIGURE 7C. ALMNH P.985.1.15.

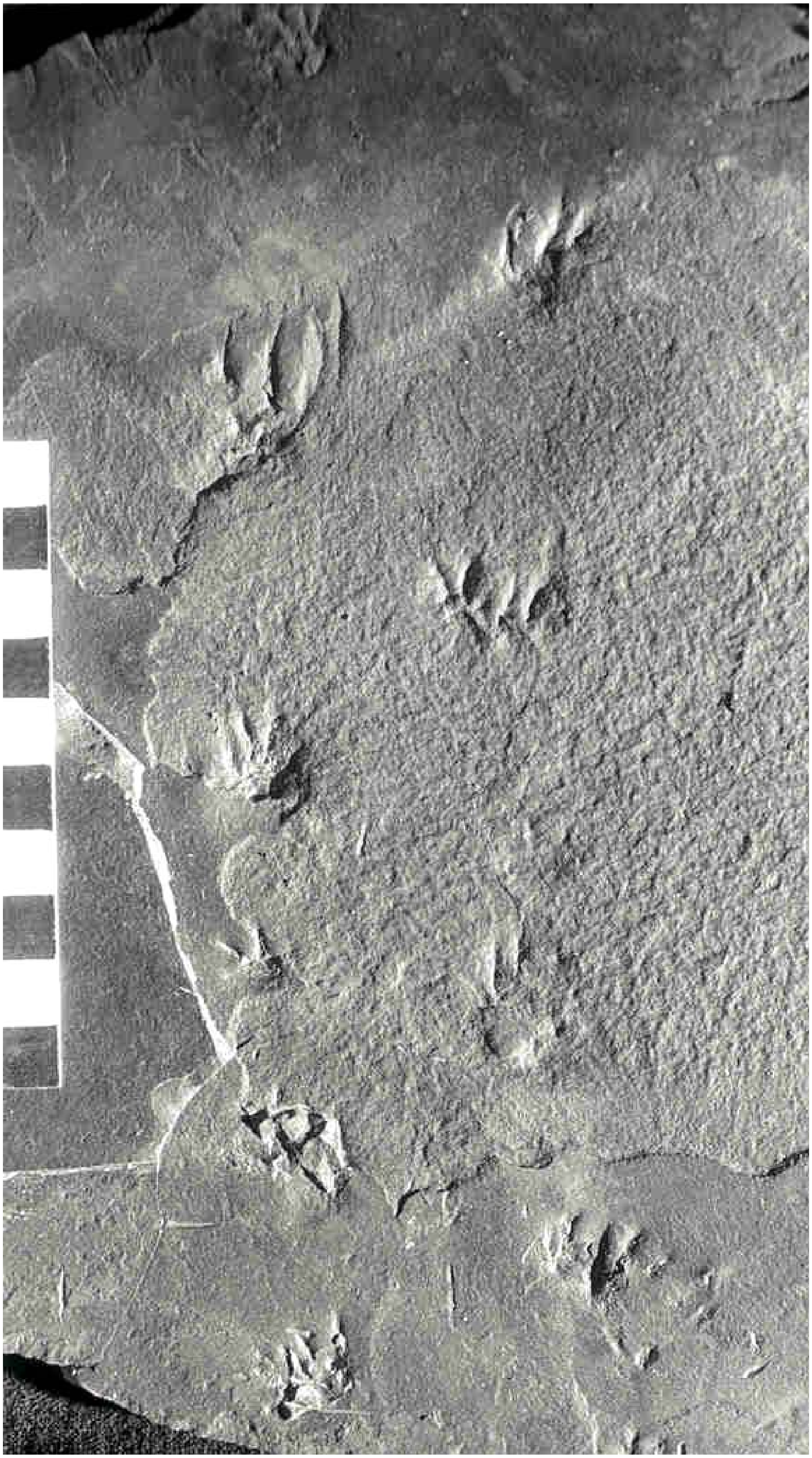

FIGURE 7D. UCM 229 SM.

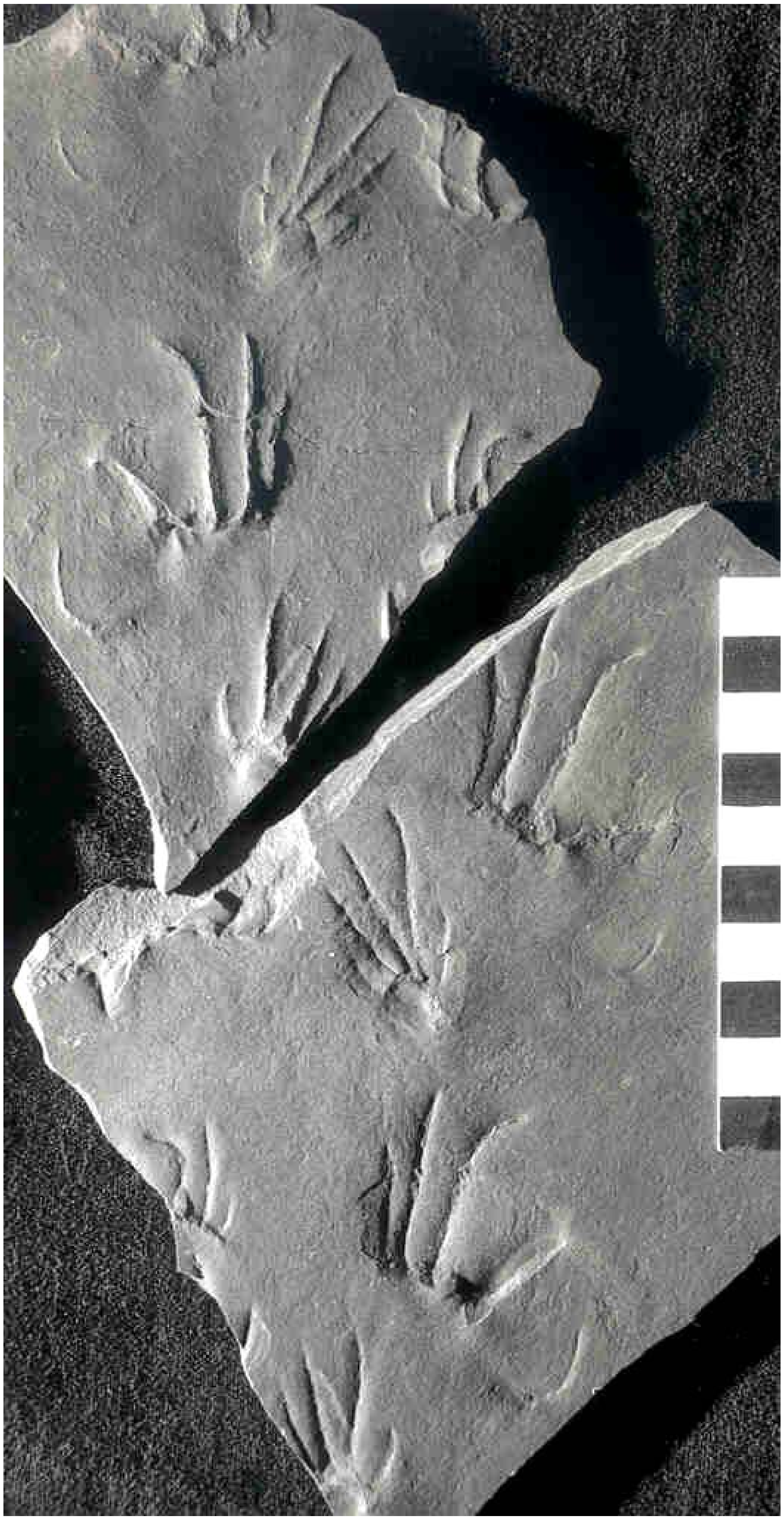

FIGURE 8A. UCM 174/175 BR.

FIGURE 8. *Cincosaurus cobbi* Aldrich, 1930 (photographs, scale cm). A: UCM 174/175 BR, manus and pes are recorded with five digits each, and narrow digit ankles. B: UCM 263 JT, the common undertrack preservation with incomplete pes and pentadactyl inward directed manus imprints. C: UCM 1075 TPA, subparallel trackways, with elongated digit imprints. D: ALMNH P.985.1.16 Holly Grove Mine. E + F: UCM 1476/1477 RB undertrack surface with sharp manus imprints and original surface of the same trackway with confused marks and significant lateral impressions of the fifth digits. G: UCM 17 SM, undertracks of manus imprints close together due to slow gait. H: ALMNH P.985.1.7 holotype of "*Quadropedia prima*"; the trackway segment shows complete manus imprints besides few marks of two pes digits.

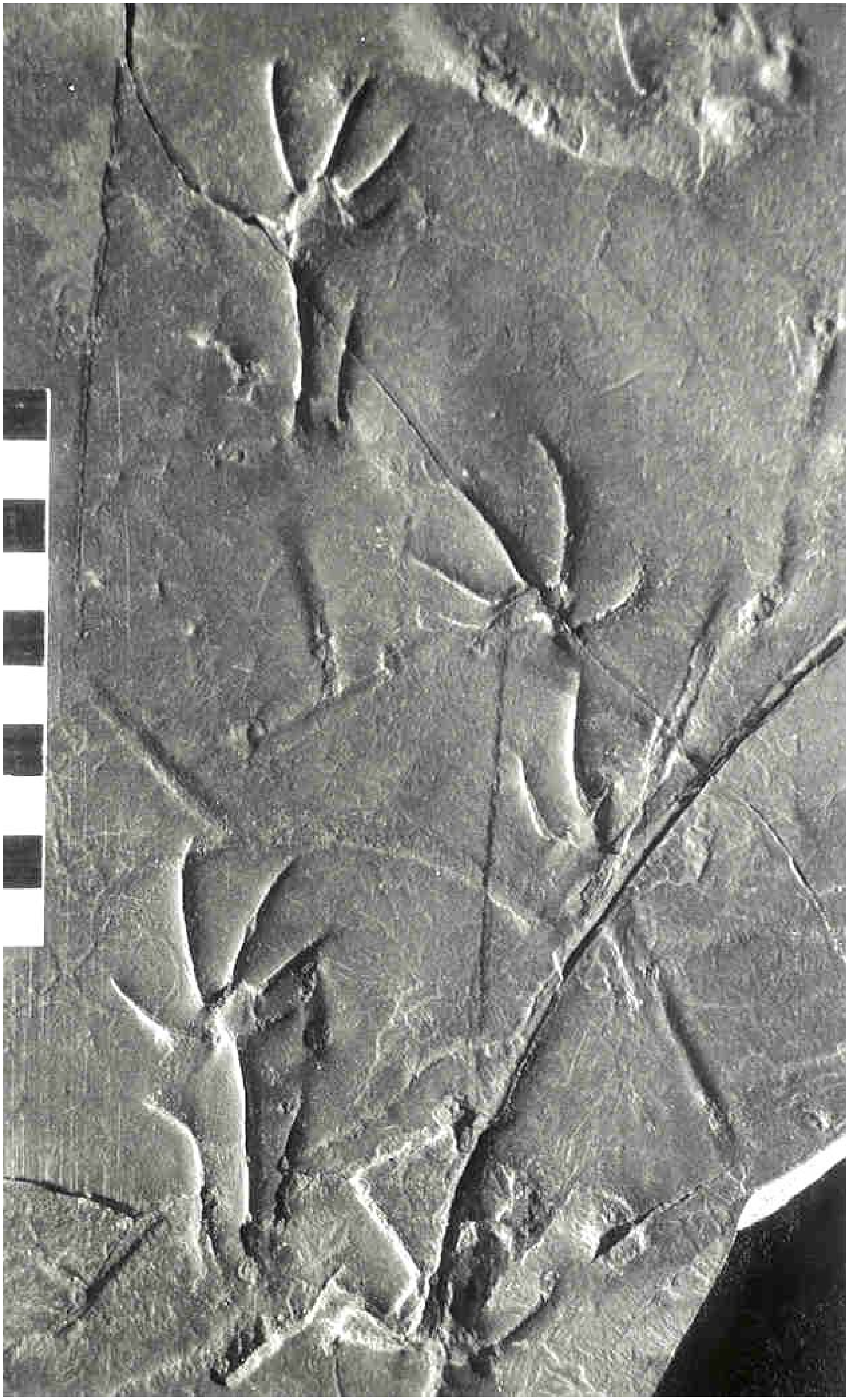

FIGURE 8B. UCM 263 JT.

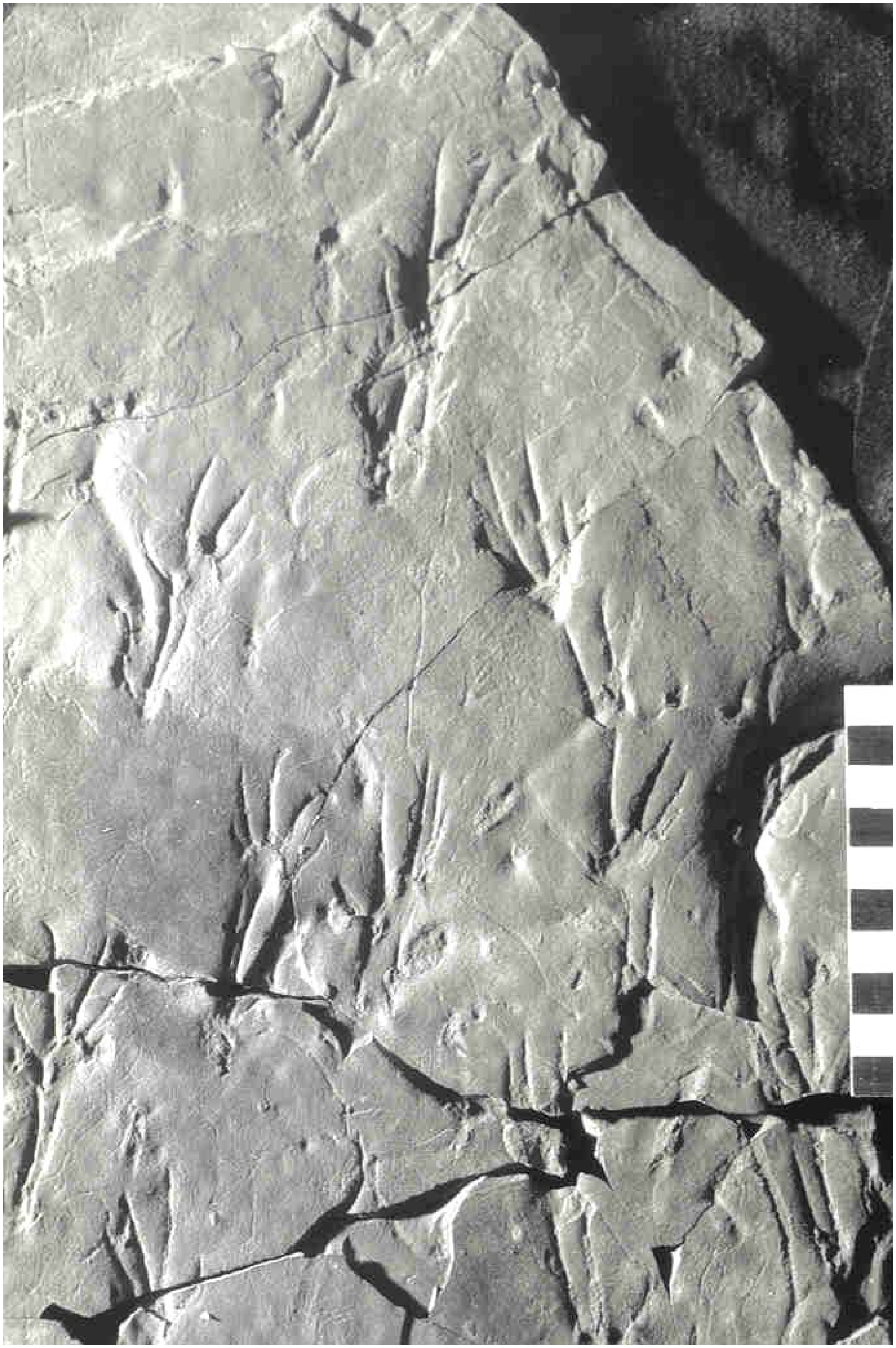

FIGURE 8C. UCM 1075 TPA.

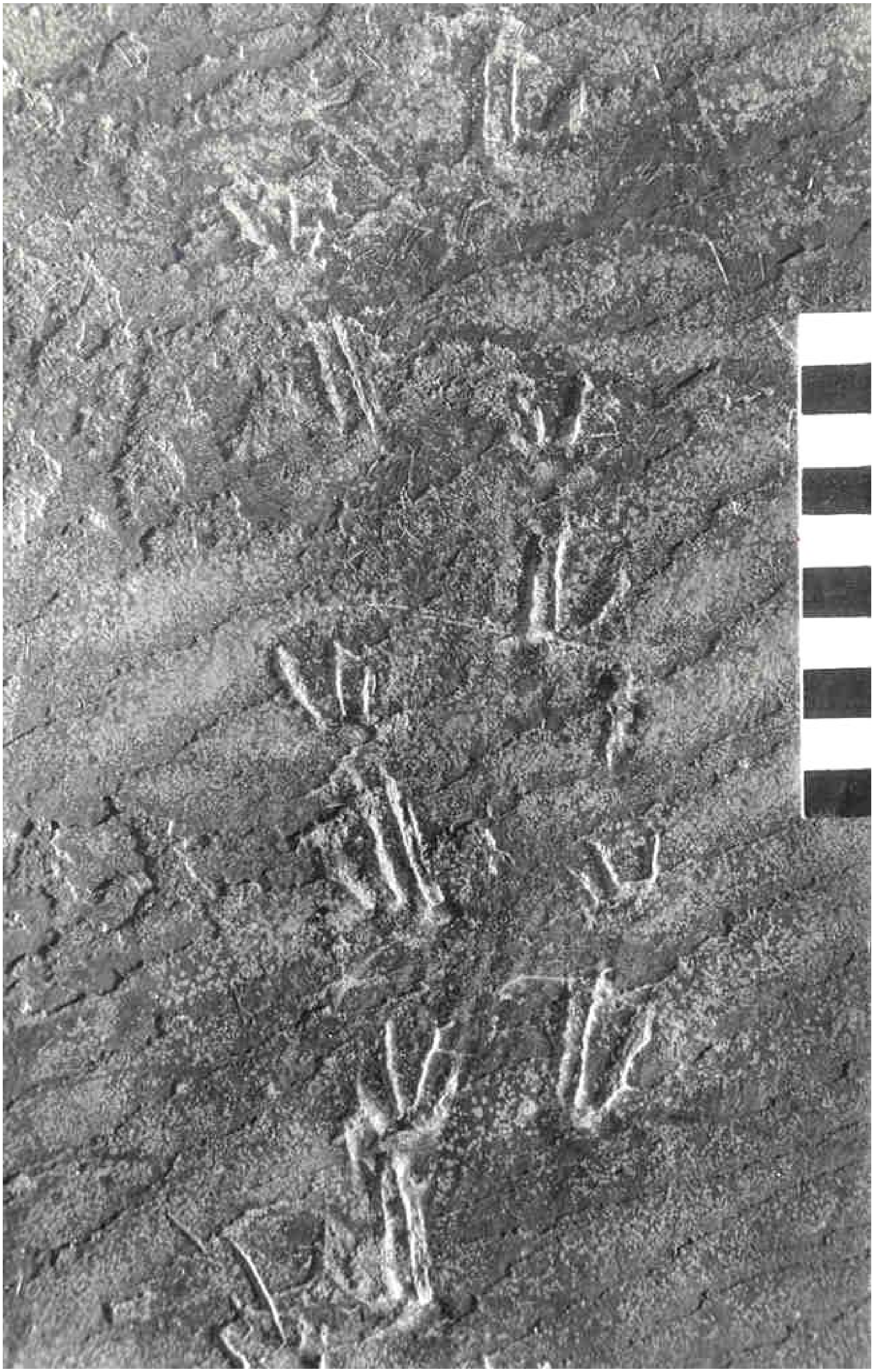

FIGURE 8D. ALMNH P.985.1.16.

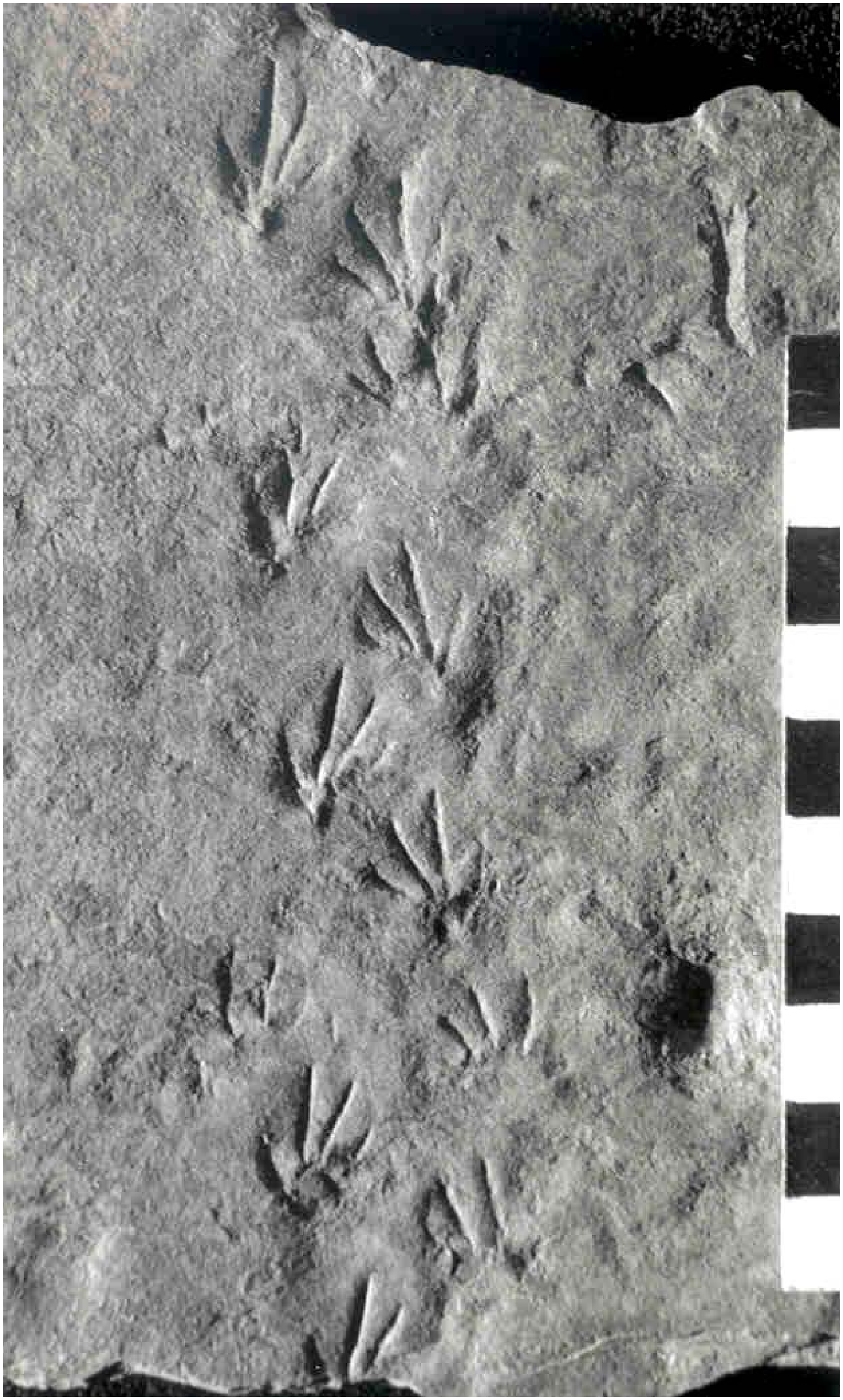

FIGURE 8E. UCM 1476 RB.

FIGURE 8F. UCM 1476 RB.

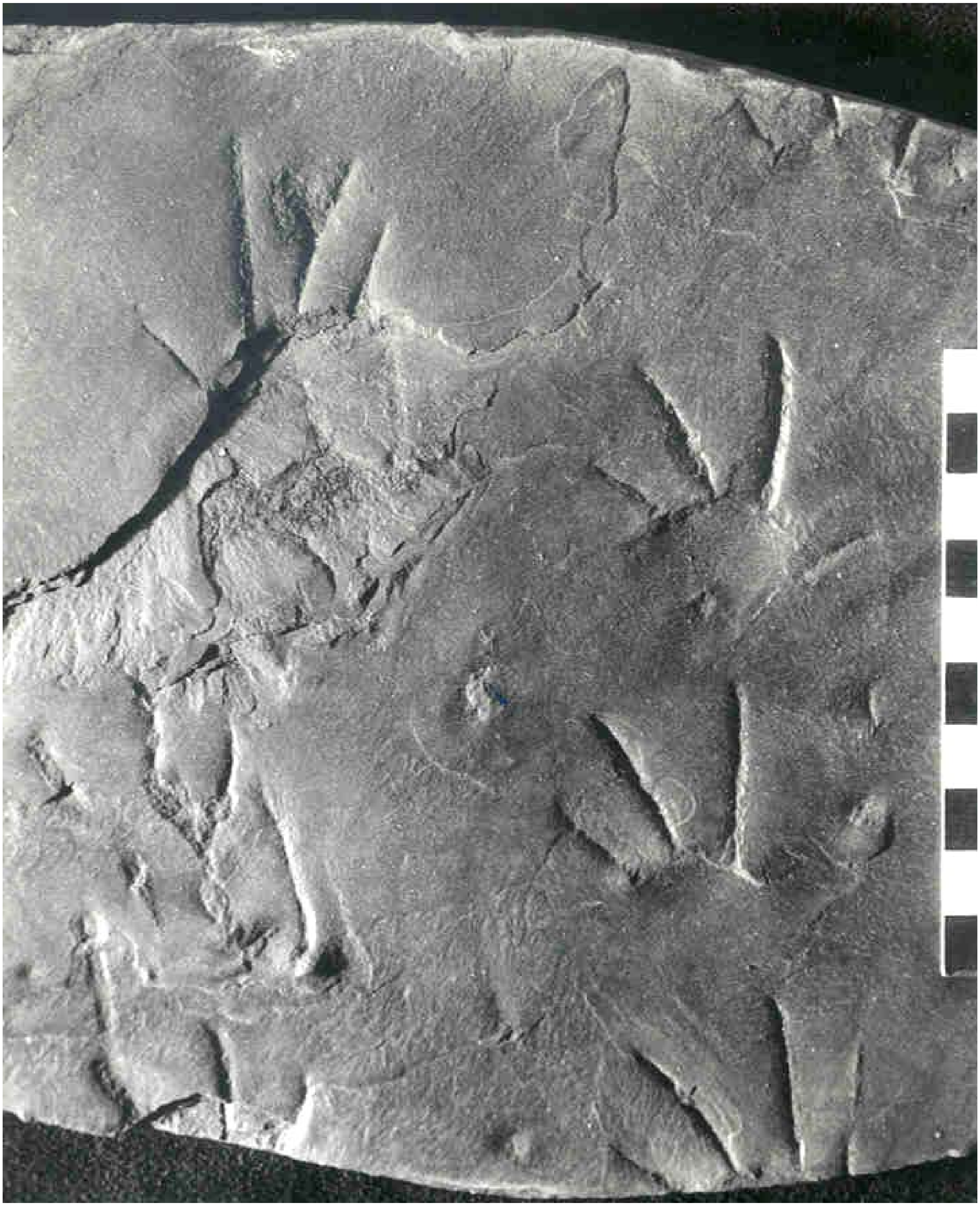

FIGURE 8G. UCM 17 SM.

FIGURE 8H. ALMNH P.985.1.7.

tion of about 110° of manus undertracks — the narrow trackway pattern of *C. cobbi*. In other examples there is a very slow gait with pace angulation of less than 50°, as present on specimen UCM 17 SM, but the visible manus imprints belong unquestionably to *C. cobbi*. Pes imprints can be incomplete or missing along the trackways. A representative record is given with the excellent original specimen, the nondesignated type specimen, of Aldrich. Although this specimen is lost, the figures (Aldrich 1930, pl. 6 and 7) show many significant features of this ichnotaxon. Specimen UCM 174/175 BR shows a comparable degree of completeness to Aldrich's original, but it has a comparably narrow degree of digit divarication. This might be due to a gait controlled pattern of the digits' ankles which is not of ichnotaxonomic value.

The majority of *C. cobbi* specimens from UCM show the manus complete and pentadactyl, whereas impressions of the pes are in general incomplete due to undertrack preservation, recording only two or three digit imprints. Because of both gait as well as undertrack preservation, track digits range from short (UCM 253/256 JT and UCM 1068 TPA) to very elongate (UCM 1075 TPA). Digits IV in manus and pes appear variable in length. Therefore digit IV might appear shorter or longer in several imprints along the trackways than digit III. A remarkable example of *C. cobbi* at the original layer is preserved in UCM 1477 RB. A rather confused trackway can be shown at the surface of the next layer, 4.5 mm deeper, which possesses the characteristic undertrack morphology. This evidence represents the key for the identification of some other enigmatic trackways, e.g., specimens UCM 331 AA, UCM 67 RB, that can now be recognized as *C. cobbi*. These hitherto rare cases of *C. cobbi* tracks from the original layer appear confused in a characteristic way, whereas a much larger proportion of the tracks are visible in undertracks only. However, one significant character that is indicative of both original and undertrack level might be the outward impression of pes digit tip V. In consequence the knowledge of *C. cobbi* remains incomplete, and imprints close to the anatomical manus and pes structure have yet to be confirmed, preferably by additional finds.

Cincosaurus cobbi is presented here as a definite and significant ichnotaxon. We underscore the possibility of misunderstanding when *Cincosaurus* is used in a wide sense, containing all hitherto known footprints from the Mary Lee coal zone. In this case all fossil footprints discovered in Carboniferous formations could be called "*Cincosaurus*". This is without question an untenable position in light of our observations presented here. It should be pointed out that there are no known clearly preserved imprints of *C. cobbi*. Because of this deficiency, this significant type, the most famous one from the Pottsville Formation, is of questionable taxonomic status. The validity of *Cincosaurus cobbi* must be tested by comparative studies of similar tetrapod footprints from related Pennsylvanian formations. However, the only previous description of *C. cobbi* outside the Black Warrior Basin, by Schneck and Fritz (1985) in the Early Pennsylvanian of Georgia, does not show a sufficient morphological relation to the specimens of *C. cobbi* known from Alabama. The same questionable status caused by the restriction of undertrack record might be noted for *Attenosaurus*.

CONCLUSIONS

The five described tetrapod ichnotaxa might be seen as standard elements of the Mary Lee coal zone and in particular of the so-called *Cincosaurus* beds. However, the documented distribution is not uniform for the known sites. From the Union Chapel Mine, within the *Cincosaurus* beds above the Mary Lee coal we recognize the presence of *Nanopus reidiae*, *Matthewichnus caudifer*, *Attenosaurus subulensis*, *Cincosaurus cobbi*, and cf. *Notalacerta missouriensis*.

All the other sites in Walker County may belong stratigraphically to footprint horizons close to the lower Jagger coal. We can list: Kansas: *Notalacerta missouriensis* and *Cincosaurus cobbi*; Fern Springs Mine: *Matthewichnus caudifer;* the Aldrich collection (presumably from the Holly Grove Mine near Carbon Hill): *Cincosaurus cobbi, Attenosaurus subulensis* and cf. *Notalacerta missouriensis*.

Indicative of possible additional ichnotaxa or hitherto not understandable types of preservations are, for example, specimens UCM 78 TPA, UCM 125 JL, UCM 267 AA, UCM 340 AA, UCM 945 BR. Resolution of the status of these types will presumably not be possible alone by additional samples collected at UCM but by specimens to be collected in the future elsewhere in the Pottsville Formation.

It is apparent that the UCM specimens will play a definitive role in clarifying the ichnotaxonomy of Permo-Carboniferous tracks. One aspect of the extraordinary value of the discoveries from the Union Chapel Mine is the evidence of hundreds of specimens that help to illuminate the mechanics of the preservational variations of tetrapod footprints and trackways. Globally, there is no other occurrence in the Permo-Carboniferous where the intriguing variation of undertrack preservation can be better understood than from the Union Chapel Mine. The UCM specimens are one of the basic keys for the revision of Permo-Carboniferous tetrapod footprints. If this key is used correctly in future investigations, it will open the door for a more realistic understanding of the rather enigmatic fossil footprints of Carboniferous age and their interpretation in correlation with the tetrapod skeletal record. The Carboniferous is the crucial period in the early evolution of terrestrial tetrapods. Therefore, the footprints and trackways found in Carboniferous formations are an authentic proof of the standard in locomotion realized by tetrapods, and the early differentiation in pattern of tetrapod locomotion. *The pattern of fossil trackways gives principal insight into locomotion, which is not available from the skeletal record.*

Last but not least, it should be noted: The present attempt to interpret the tetrapod footprints from some strata of the Pottsville in Alabama is not a revision of the ichnofauna from the Westphalian of North America as a whole. This might be underscored by a few personal words: "When I (HH) began my first studies on footprints from Carboniferous formations in the 1960s, I got some helpful and warning arguments from Don Baird. In a letter dated March 19, 1969, Don wrote, 'I knew I would regret the day you were born! And you, too, will regret the day you first set foot in the field of Carboniferous ichnology.' I always kept this sentence in mind since I became aware of the discoveries at the Union Chapel Mine in 2002. The extraordinarily large sample size of footprints dicovered by the engaged and open-minded paleontological community in Alabama motivated me to leave the former conservative principles regarding the rather restricted scientific value of Carboniferous tetrapod ichnofossils. Beyond question, following this contribution there will be much more to do in the future, and whether we come to a sufficient understanding of Carboniferous ichnology remains open."

For additional photographs of vertebrate traces (both tetrapod trackways and fish swimming traces) from the Union Chapel Mine, see Haubold et al. (2005).

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