FOSSIL FOOTPRINTS FROM THE GRAND CANYON: SECOND CONTRIBUTION

(WITH 21 PLATES)

BY

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Curator of Vertebrate Paleontology,
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(PUBLICATION 2917)

CITY OF WASHINGTON
PUBLISHED BY THE SMITHSONIAN INSTITUTION
JULY 30, 1927
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INTRODUCTION

In continuation of an investigation of the fossil footprints of the Grand Canyon, so successfully begun in 1924,¹ I was enabled, through an allotment granted by the Marsh Fund committee of the National Academy of Sciences, to visit the Canyon again in the early spring of 1926. This expedition had as its purpose the acquisition of additional fossil tracks from the Coconino and Hermit formations, and the extension of the investigation into the older Supai formation in which the discovery of fossil tracks had been reported by Mr. J. R. Eakin, Superintendent of the Grand Canyon National Park. The expedition was successful far beyond expectations, the collection made for the United States National Museum comprising a series of slabs some 2,700 pounds in weight, on which are animal tracks from three distinct and successive geological formations.

The old locality in the Coconino sandstone on the Hermit Trail was explored laterally and a large series of beautifully preserved tracks and trails secured, including many forms new to this ichnite fauna, and the Hermit shale, some 1,400 feet below the level of the Canyon rim, yielded both fossil tracks and plants. The discovery of a wing impression of a large dragonfly-like insect records for the first time the presence of such forms in the latter formation. Finally in the Supai formation at a level about 1,800 feet below the rim, another footprint horizon was located and a few poorly preserved tracks were collected from this level on both the Hermit and Yaki trails. It is upon these collections that the systematic part of the present paper is based. Even with the diversity of forms now available, it is still quite evident that further collecting will add many more varieties to the known ichnite faunas of these three formations.

I am under especial obligations to Dr. John C. Merriam and his associates on the Marsh Fund committee of the National Academy of

Sciences for the financial assistance which made this investigation possible. The loan of type specimens by Dr. R. S. Lull, Peabody Museum of Natural History, Yale University, Dr. Witmer Stone of the Philadelphia Academy of Natural Sciences, and Dr. John J. Tilton of the University of West Virginia, was of the greatest assistance in the study of the material. I wish also to express my appreciation for the help and many courtesies rendered by the various members of the Park organization. To Superintendent J. R. Eakin I am deeply indebted for the use of equipment, and assistance of personnel; to Mr. E. T. Scoyen, chief ranger, for the detail of ranger assistants, and for his personal interest on many occasions; and to Mr. G. E. Sturdevant, ranger naturalist, whose efficient help and familiarity with fossil localities contributed so much to the successful outcome of the expedition. Mr. Arthur Metszer, who acted as my assistant on this as well as on my previous trip, furnished intelligent and industrious help in making the collections, and throughout the work exhibited a personal interest in the success of the expedition second only to my own.

GEOLOGICAL OCCURRENCE OF FOSSIL TRACKS

In the Grand Canyon National Park, the tracks of extinct animals occur in three distinct geological formations which, named in descending order, are the Coconino, Hermit, and Supai. Credit for the discovery of fossil tracks in the Grand Canyon goes to Professor Charles Schuchert of Yale University, who, in 1915, while making a study of the geology of the Hermit Trail section, noted the presence of tracks in all three formations. After reading his account of their occurrence it is quite apparent that he was unaware at the time of their great abundance and variety. Fossil tracks occur in considerable abundance in all of these formations and at several levels. These later investigations show that in the great variety of footprints found and in the perfection of their preservation, there are few localities that outrank this one. It is further unique in being probably the only place in the world where fossil tracks of three successive faunas may be found in one nearly vertical geological section, separated by such great geological intervals.

Tracks occur throughout a zone 130 feet thick in the lower part of the Coconino (see fig. 1), the bottom 20 feet being barren of impressions. In the Hermit shale, tracks, plants, and insects were found in the hollows or troughs eroded in the top of the underlying

Supai sandstone from 30 to 40 feet above the Hermit-Supai contact. In the Supai, two levels some 25 or 30 feet apart near the middle of that formation are track-bearing. Thus these evidences of past life range through over 800 feet of strata. These horizons lie, roughly stated, as follows: Coconino, 900 to 1,030 feet; Hermit, 1,350 to 1,400 feet; and Supai, 1,760 to 1,800 feet below the top of the Canyon wall.

At the present time tracks are known in these formations on the Yaki and Hermit Trails only, but doubtless their geographical range will be rapidly extended now that their precise levels have been ascertained. A more detailed discussion of the occurrence and character of the beds in which the tracks are found is given below.

*Coconino sandstone.*—The Coconino sandstone and the manner of occurrence of its fossil footprints was discussed at some length in my previous paper, and at this time it seems only necessary to record such observations as resulted from my later visit to the Canyon.

The curious fact that the trend of nearly all of the tracks and trails was in one direction, that is, up the slope of the crossbedded sandstones, has previously been noted, and examination of many additional hundred square feet of track-covered surface of the Coconino verifies this original observation. In all of the hundreds of trails seen, only three exceptions were found. It should also be mentioned that where tracks were seen in situ on the Yaki Trail, this same condition obtained.

The vertical range of tracks in the Coconino seems to be confined to the basal 150 feet of the formation of which the lowermost 20 are barren, and this same condition was found to prevail in the newly

discovered locality on the Yaki Trail. More extended exploration of the Hermit Trail locality shows that tracks are abundant on both sides of the trail wherever physical conditions are such as to allow search being made for them. The track called *Laoporus noblei* Lull is the predominating species and is apparently present wherever tracks are found. Footprints of several of the species described in my former paper were recognized in the field, but only exceptional examples of these were collected as the object in mind was to secure as many different kinds as possible, in order that the complete fauna might be made known. In this we were successful to the extent of procuring specimens sufficiently well preserved on which to base three genera and ten species all new to the fauna, thus nearly doubling the faunal list; but, as stated before, it is quite apparent from a study of the new materials that a considerable number of undescribed forms may yet be found.

The ichnite fauna of the Coconino now consists of the following described genera and species:

**VERTEBRATES**

*Agostoporus matheri* Gilmore  
*Agostoporus medius* n. sp.  
*Agostoporus robustus* n. sp.  
*Allopus ? arizonae* Gilmore  
*Barypodus pachypodus* n. gen. and sp.  
*Barypodus palmaeus* Gilmore  
*Barypodus tridactylus* n. sp.  
*Barypodus metszeri* n. sp.  
*Baropus coconinoensis* n. sp.  
*Baropezia eakini* Gilmore  
*Dolichopodus tetradactylus* Gilmore  
*Laoporus noblei* Lull  
*Laoporus schucherti* Lull  
*Laoporus coloradoensis* (Henderson)  
*Nanopus merriami* Gilmore  
*Nanopus maximus* n. sp.  
*Paleopus regularis* Gilmore

**INVERTEBRATES**

*Mesichnium benjamini* Gilmore  
*Octopodichnus didactylus* n. gen. and sp.  
*Paleohelcura tridactyla* Gilmore  
*Triavestigia niningeri* n. gen. and sp.  
*Unisulcus sinuosus* n. sp.

In the Coconino formation, fossil tracks are now known to occur at three distinct localities. On the Hermit Trail some little distance
below the "White Zig Zags," where the upper part of the track-bearing horizon is marked by large cleared slabs by the side of the trail showing the footprints in situ, an out-of-doors exhibit was prepared on a former visit to the locality. Exploration of the slope to the north and south of this point disclosed track-covered surfaces wherever the local conditions permitted search for them. A second locality at "Dripping Springs" at the head of Hermit Gorge was not visited, although I was informed that tracks were to be found there. Dr. David White, accompanied by G. E. Sturdevant, visited this locality during the summer of 1926, and in a personal letter says: "On the Dripping Springs trail the tracks are very numerous and large ones in particular are abundant." The third locality is on the new Yaki Trail where it crosses the lower 150 feet of the Coconino sandstones some three and one-half miles east of Grand Canyon. Conditions here were not so favorable for examination of the sandstone surfaces, but numerous tracks and trails were seen; these were so poorly preserved, however, that no attempt was made to collect them. In so far as one may rely on field identifications the tracks seemed to pertain to the same species as those found in Hermit Basin, some seven or eight miles distant in an air line. Several tracks of the common Laoporus nobiei were recognized.

That other localities yielding fossil footprints will be found in this formation there seems no question, but the precipitous face of the formation does not allow searching for them except at a few favored localities.

**Hermit shale.**—Schuchert, who was the first to discover fossil tracks in the Hermit shale, makes the following comments on their occurrence:¹

Just below the sign "Red Top" in the lower turn of the Hermit Trail and immediately above the thick upper sandstones [of the Supai] are seen thin-bedded red shaly sandstones alternating with deep-red zones of shale. The surfaces of the glistening and smooth platy sandstones are replete with fillings of the small prisms of interbedded suncracked shales, often rain-pitted, and further marked by the foot impressions of freshwater amphibians described elsewhere in this number of the Journal by Professor Lull,² as Megapezia ? coloradensis and Exocampe ? delicatula. Some of the tracks are distinct impressions of the feet, and others are mere strokes of the toes. In these same beds also occur plant remains in very fragmentary condition which were badly macerated and coated with a slime of red mud during their entombment.

No further collection of tracks was made from the Hermit shale up to the time of the present expedition and consequently the known

ichnite fauna was confined to the two species mentioned above. Under the guidance of G. E. Sturdevant, who had previously made one or more prospecting trips over the Hermit shale at the head of Hermit Gorge (see pl. 1, figs. 1 and 2), we were led without loss of time to the locality from which many of the specimens described in this paper were collected. This locality may be roughly stated as being about one-quarter of a mile west of the sign "Red Top" on the slopes facing north or toward the entrance of Hermit Gorge into the main Canyon of the Colorado, and from 30 to 40 feet above the Hermit-Supai contact. The red shales that carry the tracks and plant remains lie in troughs eroded in the upper part of the Supai sandstone (see fig. 2). In some instances the knolls of sandstone rise 50 feet above the base of the hollow, and all of the tracks found

![Diagram](image)

**Fig. 2.—Diagram to illustrate erosional contact between the Hermit shale and Supai sandstone, and to indicate the position of the track and plant bearing horizon at X. (Modified from Schuchert.)**

...in situ came from two levels, one about 30 feet and a second 40 feet above the base of one of these troughs. Both track and plant remains were found also on the loose slabs covering these slopes even well around toward the head of Hermit Gorge opposite "Dripping Springs," but, as previously mentioned, only two thin layers were found in place. Noble,¹ however, reports finding plant remains "from beds at the base of the Hermit shale resting in depressions in the unconformity near 'Red Top' in Hermit Basin."

The Hermit shale, so named by Noble in 1922, was formerly included in the Supai formation and has a thickness in the Hermit Trail section of 317 feet measured from the base of the deepest depression in the disconformity in the top of the Supai, and 267 feet measured from the top of the highest knoll.

The Hermit shale is described by Noble as follows:²

The beds differ little from one another in composition and consist essentially of sandy mud colored red by ferritic pigment. The beds that I have desig-

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¹ Prof. Paper No. 131, U. S. Geol. Surv., 1922, p. 66.
nated sandstone in the section are massive and relatively compact as contrasted with the beds that I have designated shale, which are thinly laminated, but the distinction between sandstone and shale is unimportant. All the strata are friable. Many beds exhibit sun-cracks and rain-prints, some are ripple-marked. ** * Everywhere the formation makes a slope which is in strong topographic contrast with the sheer cliff of the overlying Coconino sandstone and with the steplike cliffs and ledges of the underlying Supai.

The beds containing the tracks in place are horizontal, and, where exposed to the weather, split into thinly laminated sheets; but as work was continued back into the hillside the layers became more massive.

In removing these layers it was found that one surface might be covered with tracks and plant remains and the very next one beneath devoid of all fossil evidence. Often a trackway could be clearly traced for a short distance only to become more and more indistinct and finally to entirely disappear, probably due to the varying degrees of softness of the surface at the time the animal passed over it. Some few of the trails have the imprints beautifully distinct but in many the details are destroyed by the inflowing mud after the withdrawal of the foot, which would suggest that they may have been made beneath a slight depth of water. No doubt tracks could be found in the Hermit shale at many other localities were search made for them, but such prospecting as was done where the Yaki Trail crosses the formation failed to disclose any, although plant remains were found in some abundance.

The recognition of many forms of the same genera as those described from other Carboniferous areas is of interest, especially those from Joggins and Paraboro, Nova Scotia. The conditions under which these tracks were made in such widely separated localities, seem to have been very similar as evidenced by the many resemblances not only in fauna but in the structural and lithologic features of the track-bearing rocks.

The fauna of the Hermit shale as known at this time consists of the following forms:

**VERTEBRATES**

*Batrachichnus delicatula* (Lull)
*B. obscurus* n. sp.
*Collettosaurus pentadactylus* n. sp.
*Crusipes* sp.
*Dromillopus parvus* n. sp.
*Hyloidichnus bifurcatus* n. gen., n. sp.
*Hylopus hermitus* n. sp.
*Parabaropus coloradensis* (Lull)

**INVERTEBRATES**

Dragonfly-like insect
This ichnite fauna is quite distinct from that of the Coconino which came after, or the Supai which preceded it.

*Supai formation.*—The Supai formation in the Hermit Trail section, as estimated by Noble, has a total thickness of 950 feet. The first evidence of footprints occurring in this formation was noted by Schuchert in 1915. Apparently no one gave the discovery further attention until 1925 when well defined tracks were found by G. E. Sturdevant on loose blocks of sandstone lying below the new Yaki Trail on the north end of O’Neill Butte, at a point slightly more than two miles down from the top. This information was, together with other discoveries made in the same locality, given to me by Superintendent J. R. Eakin. In all of the early discoveries the tracks were on detached blocks found lying on the hillside, and it was not until the late winter of 1926 that Dr. John C. Merriam of the Carnegie Institution of Washington, accompanied by Mr. Sturdevant, found tracks *in situ* (see pl. 2, fig. 2). These were in a sandstone layer estimated to lie in about the middle of the formation.

Unaware, at the time, of Schuchert’s previous discovery of tracks in the Supai, I made this locality the first object of search in the spring of 1926, accompanied by Mr. Sturdevant. Our prospecting disclosed many additional tracks and we located a second track-bearing horizon in a light colored sandstone some 30 feet above those found by Merriam and Sturdevant.

Numerous tracks and trackways were found on blocks of stone in the débris which had been thrown below the trail in the course of excavating. No further attention was given the Supai tracks until near the close of operations when an attempt was made to locate these same track-bearing horizons in the Hermit Trail section in order that they might be considered with the other track-bearing formations in a single geological section. In this we were successful, finding the first recognizable footprints in a whitish friable sandstone to the left and below the Hermit Trail at a point about one-half mile below “Santa Maria Spring.” Rather poorly preserved tracks of at least three kinds of animals were seen. The most distinct series collected is shown in plate 21. This is probably the same horizon in the formation in which Schuchert made the original discovery. The following day search was made for the lower horizon and passing backward underneath the cliff after descending the first short zig-zags above “Breezy Point,” tracks were found, thus establishing their position in the section as identical with those previously found in the Yaki

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Trail section. That there is a distinct ichnite fauna in this formation is clearly evident though unfortunately the extreme hardness of the sandstone—and hence its failure to cleave in most instances—makes the collecting of tracks a problem requiring special tools and trained personnel.

Schuchert's description of the Supai as exposed on the Hermit Trail is as follows:

The lower Supai formation [Supai of modern nomenclature] begins with a thick-bedded and cross-bedded cliff-making sandstone of about 150 feet in thickness. Beneath it are red sandy shales with two bands of sandstones that together have an estimated thickness of 200 feet. At the base of this zone is another horizon of thin flaggy beds with some sun-crack fillings and an abundance of rain-prints of the mammillary kind, interpreted as having been made by long continued rain. Midribs of either ferns or cycadofilies were seen and probably also indistinct feet imprints of amphibians. The trail runs along this zone for about two miles and one has a fine opportunity to study the sediments and to note the abundance of rainprints and a few rill markings.

The next lower zone is a cliff-making sandstone about 50 feet in height. Then follows one of shales 100 feet thick, that near the top has beds of septaria-like limy concretions embedded in a dark purple sandy mud. * * * associated are also thin zones of intraformational conglomerates with flat and somewhat rounded small pebbles; the shale pieces have blackened surfaces.

In the field it was estimated that the tracks occurred about 1,800 feet below the rim, but upon checking up with Noble's measurements of this section the conclusion is reached that the lowermost horizon would be about 1,767 feet down and the highest track-bearing layer about 1,717 feet below the top.

As redefined by Noble in 1922 the Supai formation is of Pennsylvanian and ? Permian age and rests with possible unconformity on the underlying Mississippian Redwall limestone. The sandstone has its grains bound together by calcareous cement as contrasted with the siliceous binding materials of the Coconino. Noble points out that the thick layers are conspicuously cross-bedded and that the prevailing dip is south as in the Coconino, and further it was noticed that in the majority of instances the trackways were ascending the slopes of the cross-bedding as in the Coconino.

As this paper was going to press, the National Museum received a slab of footprints, presented by Mr. G. E. Sturdevant, which was found by him in the Supai formation at one side of the Bright Angel Trail. In addition to its being an undescribed genus and species, it also records a new locality for tracks in the Grand Canyon.

It is also worthy of mention that Mrs. G. E. Sturdevant found a small section of the trail of some invertebrate animal in the Bright Angel shale, Cambrian, a specimen that was also donated to the National collections.

1 As this paper was going to press, the National Museum received a slab of footprints, presented by Mr. G. E. Sturdevant, which was found by him in the Supai formation at one side of the Bright Angel Trail. In addition to its being an undescribed genus and species, it also records a new locality for tracks in the Grand Canyon.

The tracks occur in Noble's subdivision B of this formation, and he is inclined to regard the entire Supai as of Pennsylvanian age. The fossil tracks so far collected are all new genera and species and offer no evidence bearing on this question.

The ichnite fauna of the Supai sandstone as known at this time consists of the following described genera and species:

**VERTEBRATES**

Anomalopus sturdevanti n. gen., n. sp.
Stenichnus yakiensis n. gen., n. sp.
Tridentichnus supraictisis n. gen., n. sp.

LIST OF DESCRIBED TRACKS FROM THE CARBONIFEROUS OF NORTH AMERICA

The following list of Carboniferous footprints is a complete roster of all tracks described up to the present time. This list, consisting of 34 genera and 60 species, is badly in need of revision, a task that would doubtless decrease rather than increase the totals given. In order to add to its value as a reference list, the geological horizon and general locality of each is recorded. The geological occurrence of many of the earlier described species was given as Coal Measures, but in the present list, in so far as I have been able, I have made more precise assignment of these, following the more recent age determinations.

<table>
<thead>
<tr>
<th>Name</th>
<th>Horizon</th>
<th>Locality</th>
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</thead>
<tbody>
<tr>
<td>Agostopus matheri</td>
<td>Gilmore Permian</td>
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<td>Anthracopus ellangowensis</td>
<td>Pennsylvanian</td>
<td>Mahanoy Coal Field, Leidy.</td>
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<td>Asperipes avipes</td>
<td>Matthew Coal Measures</td>
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<td>Asperipes caudifer</td>
<td>(Dawson) Coal Measures</td>
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<td>Asperipes flexilis</td>
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<td>Pseudobradypus unguifer (Dawson)</td>
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Name       Horizon               Locality
Punctatumvestigium circuli-formis Butts.  Pennsylvanian ......Kansas City, Mo.
Thenaropus leptodactylus King...Coal Measures......Westmoreland Co., Pa.
Thenaropus macnaughtoni             Coal Measures......Nova Scotia.
                               (Matthew).
Thenaropus ovoidactylus King...Coal Measures......Westmoreland Co., Pa.
Thenaropus pachydactylus King...Coal Measures......Westmoreland Co., Pa.
Thenaropus sphaerodactylus         Coal Measures......Westmoreland Co., Pa.
                               King.

SYSTEMATIC DESCRIPTION OF GENERA AND SPECIES

In the systematic description the genera and species are divided into distinct faunas beginning with that of the Coconino formation, those of the Hermit and Supai following successively. Since none of the genera passes over from one formation into the other, it was thought this manner of treatment would be more convenient for reference than any attempt to group related forms.

Following the policy inaugurated in my first study of Grand Canyon footprints, only the best preserved and most characteristic specimens were selected for description. In most instances the type specimens consist of trackways showing several steps and usually both the right and left sides of the trail. Had it seemed wise to describe all of the various kinds of imprints found, the faunal lists would have been considerably augmented, but after noting the variations found in the imprints in a trackway of a single individual, the more conservative method was adopted. This study has resulted in nearly doubling the known ichnite fauna of the Coconino, has established an adequate fauna for the Hermit, and has made a beginning in the development of a fauna for the Supai. One of the interesting facts established is that these three faunas are distinct, one from the other. A few of the tracks may be assigned with some assurance to the class in which they belong, but many more remain in doubt, and with our present information, there is little hope of clearing up these enigmas.

FAUNA OF THE COCONINO SANDSTONE

Genus DOLICHOPODUS Gilmore


Newly discovered material makes possible some slight emendation of the generic characters of this genus, particularly in verifying some points previously in doubt.
Generic characters.—Quadrupedal. Pes long and narrow with four digits; fourth long, slender and curved outward. Manus smaller than pes, three digits. Toes of both fore- and hindfeet acuminate. Feet turned strongly inward toward line of movement.

Genotype.—Dolichopodus tetradactylus Gilmore.

Dolichopodus tetradactylus Gilmore, Charles W., Smithsonian Misc. Coll., Vol. 77, No. 9, 1926, p. 6, pl. 4, fig. 1.

A second series of tracks (No. 11,503, U. S. N. M.) referable to Dolichopodus tetradactylus was found by the 1926 expedition at the Hermit Trail locality and in the same horizon in the Coconino sandstone in which the type occurred. It is of interest as furnishing confirmatory evidence of the original description and illustration, in addition to throwing further light on the structure of the forefeet, of which the type specimen showed little more than the presence of three sharply pointed digits. The present specimen shows the sole to be narrow and the foot, as a whole, smaller than the hindfoot. In the type the hindfoot was placed in advance of the fore, but in this specimen the forefoot impression is usually slightly in advance or at one side of the hindfoot. This placing of the feet, however, may be due to the irregularity of the stride as no two steps measure the same, varying from 160 to 250 mm. in length. None of the tracks of the forefoot gives evidence of more than three toes, although some are deeply impressed. The forefoot, measured from the back of the heel to the tip of the longest toe, has a length of 16.5 mm. and a width in the opposite diameter of 19 mm. The hindfoot has essentially the same proportions as the type. A third slab (No. 11,495 U. S. N. M.) also has a few impressions attributable to this species, but these are scattered tracks made by the hindfeet and add nothing to our previous understanding of them.

Genus Nanopus Marsh


Marsh's conception of this genus as set forth in his description of the type species can now, with the discovery of two new species, be greatly emended as follows:

Generic characters.—Quadrupedal, semiplantigrade. Four digits in pes, three in manus. Manus usually smaller than pes. Toes acuminate or bluntly rounded. Lateral toes of pes either shorter or subequal
in length with median toes. Forefoot placed in front of hind. Feet turned slightly inward toward line of movement. With or without tail drag.

*Genotype.—* *Nanopus caudatus* Marsh.

**KEY TO SPECIES**

Small size. Toes stout with obtusely rounded ends. Lateral toes of pes shorter than median toes.

*N. caudatus* Marsh

Small size. Toes slender, with acutely pointed ends. Lateral toes of pes shorter than median toes.

*N. merriami* Gilmore

Large size. Toes slender, acutely pointed. Lateral toes of pes subequal in length with median toes.

*N. maximus* n. sp.

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![Tracks of *Nanopus obtusis* Matthew.](image)

**Fig. 3.**—Tracks of *Nanopus obtusis* Matthew. *1a*, hindfoot; *1b*, forefoot. Natural size. (After Matthew.)

![Tracks of *Nanopus quadratus* Matthew.](image)

**Fig. 4.**—Tracks of *Nanopus quadratus* Matthew. *1a*, hindfoot; *1d*, forefoot. Natural size. (After Matthew.)

The two species *N. obtusis* and *N. quadratus* from the Coal Measures of Nova Scotia referred to this genus by Matthew show such a radically different foot plan as to indicate that their affinities lie elsewhere than in the genus *Nanopus*. Reference is made to the divergent fifth or outer toe, the progressive shortening of the digits inward, and the placing of the hindfoot in advance of the forefoot impression.
N. quadratus Matthew¹ quite certainly belongs in the genus Dromil-
lopus with which its small size, digital formula of 4 and 4, and gen-
eral arrangement and relative length of toes are in full accord. For
these reasons it is unhesitatingly transferred to this genus to be
known hereafter as Dromilopus quadratus (Matthew).

Unfortunately the case of N. obtusis cannot be so satisfactorily
settled. The impression of the hindfoot offers no difficulties to its
assignment to Dromilopus but the forefoot shows only three toes
and the foot as a whole (see fig. 4) is quite out of accord with any
described Carboniferous ichnite. This is probably due to distortion,
as pointed out by Matthew,² so that the number of digits and the form
of the foot as shown in figure 4 is probably not to be depended upon
as expressing the true characters of the normal manus imprint. For
that reason and as a temporary expedient this species is provisionally
assigned to the genus Dromilopus to be known as D ? obtusis (Mat-
thew) until such time as the discovery of better preserved specimens
shall disclose its true generic affinities.

NANOPUS MERRIAMI Gilmore

Plate 4, fig. 1

Nanopus merriami Gilmore, Charles W., Smithsonian Misc. Coll., Vol. 77,
No. 9, 1926, pp. 9-12, pl. 4, fig. 2, text fig. 5.

A specimen of Nanopus merriami (No. 11.516, U. S. N. M.) is of
interest as recording a second occurrence of this species in the lowest
track-bearing level of the Coconino formation a considerable distance
north of where the type specimen was collected. It was found in situ
about 30 feet above the Coconino-Hermit contact, immediately above
the spring which supplies water for the trail caretaker’s house in
Hermit Basin. It would now seem that this species is confined to the
lowermost horizon of the Coconino as no tracks attributable to it
have been observed in the upper levels.

NANOPUS MAXIMUS, new species

Plate 3

Type.—Catalogue number 11.506, U. S. N. M. A large slab of
light-colored fine-grained sandstone on which is an irregular track-
way showing impressions of all four feet.

Type locality.—Hermit Trail, Hermit Basin, Grand Canyon Na-
tional Park, Arizona.

Geological occurrence.—Coconino sandstones (about 150 feet above base), Permian.

Description.—Stride (average) about 277 mm., width of trackway (estimated) about 300 mm. Both of these measurements are subject to revision with the discovery of better material for it is quite apparent that the type specimen does not represent a continuous normal trackway. This is indicated by the irregularity of the stride and the great variation in the relative position of the tracks of the fore- and hindfeet, although the manus is always placed in front of the pes. The longest stride measures 320 mm., while the shortest of that same side is only 225 mm. Hindfoot: Greatest length 65 mm., greatest width 85 mm. Four toes acuminete and subequal in length. First and fourth more slender than median pair, both curving inward from their respective sides of the foot. Second and third having their tips directed slightly outward. Sole equal to length of toes, suboval, broadly rounded behind. That there were sharp well developed claws on all four toes is shown by the long deep scratches where the foot had slipped as may be seen on the left side of the trackway in plate 3. Length of digit I, 34 mm., digit II, 34 mm., digit III, 34 mm., digit IV, 36 mm. Forefoot: Length (estimated) about 43 mm., width about 52 mm. Three toes, acuminete, clawed, and probably subequal in length. The sole in most of the imprints is obscure but in the best
preserved one (see A, fig. 5) it is relatively short fore and aft. The outer toe is somewhat set off from the median one. Sole broadly rounded behind. Judging from the depth of the imprints the weight of the animal was largely carried by the hind limbs. The length of digits in the manus varies so much in the different imprints that it seems useless to record their measurements. The outline of the manus as given in figure 5, A, is made from the best preserved imprint on the slab, but the relative length of toes is subject to revision when better specimens are found.

The presence of three and four digits in the manus and pes, parallel arrangement of the two middle toes of the hindfoot, short, broadly rounded sole, and forefoot placed in front of hindfoot, are characters found in the genus Nanopus.

The large size of Nanopus maximus at once distinguishes it from the other species of the genus, all of which are small. From N. merriami from this same formation, but apparently restricted to the lower part of the track-bearing horizon, it may be distinguished not only by its much greater size, but also by having the two lateral toes of the pes subequal in length with the two median toes, whereas in both N. caudatus Marsh and N. merriami Gilmore the two lateral digits are shorter than the median. From N. caudatus it is further distinguished by the more slender and acuminate form of the digits as contrasted with the heavy rounded toes of that species. The specific name is suggested by its great size as contrasted with the smaller footprints of the other species of the genus.

Genus LAOPORUS Lull


Generic characters (emended).—Quadrupedal, semiplantigrade, with four digits in manus and five in the pes; fifth toe often not impressing. Lateral digits always shorter than median pairs. Sole broad, digits usually short. Feet usually grouped in pairs with front foot always placed in front of hind.

1After the manuscript of the present paper had been accepted for publication an article on British Permian Footprints by George Hickling (Manchester Lit. and Philos. Soc., Memoirs, Vol. 53, 1909, Art. 22, pp. 1-24, pls. I to IV) came to my attention for the first time. Although too late to be discussed in the present article, I wish in this note to call attention to the fact that many of the British tracks show striking resemblances to those of the Coconino and that the genus Laoporus is quite certainly represented in the Pernith Red sandstone; see figs. 10 and 11, pl. II, of the article cited. This brief note will bring to the attention of those interested the above mentioned fauna, and a more complete discussion of it will be included in my next publication dealing with footprints of the Grand Canyon.
Genotype.—Laoporus schucherti Lull.

Two species, *L. schucherti* and *L. noblei*, were described by Lull from the Coconino formation, but only a single specimen of the former species has been recognized in my collections although the other occurs in great abundance.

Fig. 6.—*Laoporus noblei*. No. 11,494, U. S. N. M. Diagram of a portion of the trackway to show the relatively long median toes of the manus. No indication of the fifth toe of the pes in this trackway. About 3/4 natural size.

**LAOPORUS NOBLEI** Lull

Plate 4, fig. 2


Footprints of *Laoporus noblei* Lull are by far the most abundant of all the animal tracks found in the Coconino sandstone. Usually the trackway of this species can be recognized at once by the uniform-


ity of the stride and by the pairing of the impressions made by the fore- and hindfeet, the former always being placed in front of the latter. One trackway (No. 11,494 U. S. N. M.) among a considerable number collected in 1926 deserves special mention because of the unusual length of the median toes of the forefeet. These toes considerably exceed in length the longest toes of the hindfoot (see fig. 6) whereas the opposite condition usually prevails. Furthermore, in this specimen the fore and hind tracks are subequal in size whereas the forefoot impression is usually smaller. None of the pes tracks gives indication of the presence of a fifth digit. The rather meager evidence of its presence in the hindfoot may, however, now be considered as absolutely established by two specimens (Nos. 11,491 and 11,512 U. S. N. M.) both of which show several pes tracks with five toes clearly registered.

**Genus BARYPODUS Gilmore**


The genus _Barypodus_ was originally characterized on rather scanty materials so that with the discovery of other species referable to this genus, it now becomes necessary to emend the original definition as follows:

*Generic characters.*—Quadrupedal, plantigrade with three parallel digits in both manus and pes. Digits long, either slender or stout, well separated, and with or without webbing between the toes. Sole of pes subtriangular in outline with heel hooking outward. Sole as long as or longer than digits. Forefoot placed in front of hind.

*Genotype.*—_Barypodus palmatus_ Gilmore.

**KEY TO SPECIES**

**Large size.** Toes long, slender, joined by web. Outer toe of manus one-half length of inner. Palm of manus longer than digits with outward hook of heel.

\[B. \text{palmatus}\]

**Medium size.** Toes long, slender, without webbing. Outer toe of manus longer than inner. Palm of manus longer than digits with decided outward hook of heel.

\[B. \text{tridactylus}\]

**Medium size.** Toes, moderate length, stout without webbing. Outer toe subequal in length with inner. Palm of manus apparently shorter than digits, without outward hook.

\[B. \text{metszeri}\]
BARYPODUS TRIDACTYLUS, new species

Plate 5

Type.—Catalogue number 11,502, U. S. N. M. Consists of the positive and negative slabs on which is a beautifully preserved trackway.

Type locality.—Hermit Trail, Hermit Basin, Grand Canyon National Park, Arizona.

![Trackway Diagram](image)

Fig. 7.—Barypodus tridactylus. Type. No. 11,502, U. S. N. M. Diagram of trackway. Toes indicate position of the hindfeet. About \( \frac{1}{2} \) natural size.

Geological occurrence.—Coconino sandstone (about 150 feet above base), Permian.

Description.—Stride about 140 mm., width of trackway about 175 mm. Hindfoot: None of the impressions made by the pes is sufficiently clear to provide measurements. The presence of three digits is distinctly indicated by several tracks (see pl. 5). Measured across the toes the foot has a width of 44 mm. Digits shorter than those of manus. Length of first digit about 15.5 mm., second about 23 mm., third 26 mm. It will be seen from these measurements that the toes grow progressively longer toward the outside of the foot. The
smaller size of the digits and the indistinctness of the impressions raises the question of these imprints having been made by the pes, but when critically examined, the fact that some of the impressions were made upon the slightly raised flow of sand forced out by the sole of the preceding foot, seems to leave no alternative conclusion than that they were made by the pes. If this interpretation be correct, then we have the very unusual condition of having the hindfoot apparently bearing less of the weight of the animal, as evidenced by the shallowness of the imprints. The sole is not distinctly impressed (see fig. 7) in any of the tracks and on that account no idea of its shape, extent, or peculiarities is to be gained from this specimen. Forefoot: Length 81 mm., width 46 mm. Three digits, long, parallel and sharply acuminate. Toes directed straight forward in relation to axis of trackway. Digit I is 37 mm. long, digit II, 43 mm., digit III, 42 mm. Sole sub-rectangular with a blunt, hook-like protuberance on the outer posterior angle as in B. palmatus. There is no deviation of the lateral toes as in so many three toed tracks, notably those of the Connecticut-Triassic, but in both fore- and hindfeet the toes are placed nearly parallel. All of the toes are equally well impressed. The resemblance in form of the palm of the manus to B. palmatus seems to indicate that the original interpretation of the position of the hook-like protuberance as being on the inside of the foot was in error. In the specimen now before me it is clearly shown to be on the outer side. This indicates that the type of B. palmatus belongs to the right side, a fact that was indeterminable at the time of description, due to the paucity of the type materials.

Although there are many resemblances to be found in a comparison of the two species here discussed, they may be at once distinguished by the smaller size of B. tridactylus, the absence of webbing between the toes, and the smaller relative size of the hindfoot as contrasted with the fore. Differences found in the relative length of digit III of the forefoot also furnish another distinguishing character.

**Barypodus Metszeri, new species**

Plate 6

*Type.*—Catalogue number 11,505, U. S. N. M. Consists of a trackway about 560 mm. in length showing impressions of all four feet.

*Type locality.*—Hermit Trail, Hermit Basin, Grand Canyon National Park, Arizona.

*Geological occurrence.*—Coconino sandstone (about 150 feet above base), Permian.
Description.—Stride about 235 mm., width of trackway (estimated) about 210 mm. Hindfoot: Length about 88 mm., width about 65 mm. Three stout sharply pointed toes of moderate length, well separated. Two outer toes having their outer borders curved inward, which gives these digits the appearance of turning inward toward the median one, when in reality they are nearly parallel. Length of digits, I = 22 mm.; II = 28 mm.; III = 30 mm. Sole deeply impressed; elongate, narrowed, obtusely pointed heel that hooks slightly outward. Sole nearly twice as long as the digits. Toes turned strongly inward. Forefoot: Length (estimated) 54 mm., width
about 58 mm. Three toes more slender and more acutely pointed than toes of hindfeet. Inner toe more widely set off from middle toe than is the outer one. Toes all strongly bent inward, the second and third especially so. The palm is so lightly impressed in all of the imprints that its outline is not clearly indicated, so that much doubt exists as to the correctness of the illustration of this portion of the foot in figure 8. It has therefore been shown in a broken line. The forefoot is placed in advance of the hindfoot and slightly outside. That the claws were acuminate is not only clearly indicated by the shape of the digits, but also by the long, deep scratches in the rock as shown on the left side of the trackway (see fig. 8). In both fore- and hindfeet, distinct cross ridges indicate the presence of deep creases on the bottom of the foot, at the base of the toes. The footprints are deeply and clearly registered and there is little probability of additional toes ever having been present since they did not register here.

This species is referred to the genus Barypodus largely on the ground of there being three digits on both fore- and hindfeet, and the presence of an elongate sole. From B. palmatus it is at once distinguished by the shorter, stouter, curved toes and the absence of webbing between the digits. Likewise it may be distinguished from B. tridactylus by the short toes with curved claws and a shorter palmar impression lacking pronounced outer hook.

The specific name is in honor of Mr. Arthur Metszer who collected the type specimen and whose efficient services contributed so largely in bringing together this fine collection of footprints.

Genus BAROPUS Marsh


The genus *Baropus* was founded by Marsh on a series of tracks from the Coal Measures of Kansas. With the additional material collected in the Grand Canyon, it may be characterized as follows:

*Generic characters.*—Large size. Quadrupedal, plantigrade. Four toes on both manus and pes. Toes short, thick with rounded extremities, clawless. Forefoot subequal in size or smaller than hindfoot. Soles of feet large.

*Genotype.*—*Baropus lentus* Marsh.

**KEY TO SPECIES**

Imprints of fore and hindfeet subequal in size, with hindfoot placed in rear of forefoot. Sole of pes elongate, subtriangular in outline, with heavy protuberance on inner side.

* B. lentus
Imprint of forefoot smaller than that of hindfoot, with hindfoot placed in front of forefoot. Sole of pes truncate, subquadrangular in outline, without protuberance on inner side.

B. coconinoensis

BAROPUS COCONINOENSIS, new species

Plate 7

Type.—Catalogue number 11,514, U. S. N. M. Consists of a slab on which are four tracks made by the fore- and hindfeet of the left side.

Fig. 9.—Baropus coconinoensis. Type. No. 11,514, U. S. N. M.
Diagram of left side of trackway. About 1/6 natural size.

Type locality.—Hermit Trail, Hermit Basin, Grand Canyon National Park, Arizona.

Geological occurrence.—Coconino sandstone (about 125 feet above base), Permian.

Description.—Stride about 300 mm., width of trackway unknown. Hindfoot: Length about 108 mm., width about 138 mm. Four toes
of moderate subequal length, thick, with broadly rounded extremities, apparently without claws. First and second toes slightly diverted from the outer two which are more or less parallel. Foot turned strongly inward. Sole broad, subrectangular in outline. Approximate length of toes: I, 30 mm., II, 30 mm., III, 35 mm., IV, 35 mm. Forefoot: Length 75 mm., width (estimated) about 100 mm. There are probably four toes although only three can be observed. Both of the imprints have had at least one toe obliterated by the hindfoot stepping upon them so that their entire number is in doubt. The toes are stout, of moderate length, and, as in the pes, have rounded ends without claws. First digit slightly set off from the others. Sole wider than long and broadly rounded behind. Foot turned strongly inward and placed inside the line of the hindfoot impressions. Palm about twice the length of the longest toe, subquadrate in outline and broadly

Fig. 10.—Baropus lentus Marsh. Diagram of trackway. About \( \frac{1}{2} \) natural size. (After Marsh.)
rounded behind. The missing toe has been tentatively restored as shown in figure 9.

The specimen selected as the type is the trackway of a large quadrupedal animal and consists of four imprints from the left side. The tracks are deeply impressed and the softness of the sand at the time they were made is indicated by the flows behind the impressions displaced by the impact of the feet.

The hindfoot with four toes, in size, shape and arrangement of digits has its closest resemblance to Baropus lentus Marsh from the Coal Measures of Kansas. It differs in having the forefoot smaller than the hind, sole of pes relatively broader, less elongate, and without inner protuberance (compare figs. 9 and 10). In this specimen the hindfoot is placed in front and outside of the forefoot impression, whereas in B. lentus the hindfoot is behind the forefoot. It seems quite probable, however, that the trackway now before me does not represent the normal walking stride of the animal. That the creature was climbing a slope is evidenced by the position of the slab in situ and also by the mounds of sand behind the imprints, displaced by the pressure of the feet. The weight seems to have been equally distributed between fore and hind limbs, as indicated by the subequal depth of the tracks.

This form may be distinguished at once from Allopus ? arizonae occurring in these same beds by its much larger size, and the lesser number of digits in the pes.

Genus AGOSTUS Gilmore


The genus Agostopus was established on well preserved specimens from the Coconino sandstone as exposed on the Hermit Trail section. A slightly emended characterization of the genus follows:

Generic characters.—Quadrupedal, semiplantigrade, with five digits in manus and four in the pes; broad soled with either two or three clawed digits in the pes. Feet directed inward, hindfoot placed in front of forefoot impressions. Short limbed, wide bodied.

Genotype.—Agostopus matheri Gilmore.

KEY TO SPECIES

Hindfoot with three long acutely pointed digits, all directed forward.

A. matheri

Hindfoot with two long acutely pointed digits, both bent strongly outward.

A. medius
AGOSTOPUS MEDIUS, new species

Plate 8

Type.—Catalogue number 11,509, U. S. N. M. Consists of a trail 870 mm. in length, showing consecutive impressions of all four feet.

Type locality.—Hermit Trail, Hermit Basin, Grand Canyon National Park, Arizona.

Geological occurrence.—Coconino sandstone (about 150 feet above the base), Permian.

Description.—Average length of stride about 170 mm., width of trackway about 230 mm. Hindfoot: Length about 75 mm., hindfoot placed in front of forefoot, the sole usually obliterating toes of the manus. Sole wider than long, palmate, broadly rounded behind. Sole longer than digits. Four, possibly five, toes, the two middle ones sharply pointed and strongly curved outward. First and fourth short and heavy, with bluntly rounded terminations apparently without claw; first often not impressing. Length of digits, I = 4 mm.; II = 23 mm.; III = 30 mm.; IV = 16 mm. While the trackway as a whole gives the impression of being clearly defined, when it comes to considering the details of the foot plan the specimen leaves much to be desired. On the type slab there are ten imprints made by the two hind-feet, but only two of these in the lower left hand side (see pl. 8) show the undoubted presence of a short, obtuse first digit. It is either missing entirely from the other tracks or else there is only the slightest trace of its existence. Where the imprint is missing, the inward extension of the sole is always sufficient to have carried it. In a few of these tracks on both sides a projecting protuberance on the outer posterior angle of the sole (see fig. 11) may represent the presence of a fifth digit, but additional specimens are necessary before this point can be definitely decided. Forefoot: Length (estimated) about 40 mm., width about 72 mm. Sole suboval in outline. Smaller than pes. Number of digits uncertain, probably five, apparently reducing inward. All short, stout, with broadly rounded terminations and apparently without claws. Fifth set off from the others. The uncertainty regarding the digits of the manus is largely brought about by their partial obliteration by the flow of sand crowded back upon them by the impact of the heel of the hindfoot.

A portion (negative) of this same trackway was collected in 1924 and presented to the Grand Canyon National Park Museum, while the positive portion (No. 11,136, U. S. N. M.) was brought to Washington under the impression that the tracks were duplicated in other specimens in the collection. Critical study demonstrated its distinct-
ness from all others, but in the expectation of again visiting the locality, its description was deferred until another section of the trail could be secured. In addition there is a second specimen (No. 11,500, U. S. N. M.) in the 1926 collection that may also be referred to this

Fig. 11.—*Agostopus medius*. Type, No. 11,509, U. S. N. M. Diagram of trackway. About ½ natural size.

genus and species, but the preservation is such that it throws no additional light on the detailed foot structure, and needs no further mention here.

The characteristic foot structure of this short-legged, wide-bodied animal shows it to be clearly referable to the genus *Agostopus*. From
the single known species, *A. matheri*, it is to be distinguished by its larger size, the relatively wider soles, and the short, stout form of digit IV.

**Genus AMBLYOPUS, new genus**

*Generic characters.*—Quadrupedal, plantigrade. Toes of both manus and pes not differentiated but inclosed in the foot mass. Impressions of feet reniform in outline, being longer than wide. Pes tracks placed partly upon those of manus, and forming rows inside them.

*Genotype.*—*Amblyopus pachypodus*, new species.

**AMBLYOPUS PACHYPODUS, new species**

*Plate 9*

*Type.*—Catalogue number 11,511, U. S. N. M. Consists of a slab 830 mm. long, having a trackway running the entire length.

*Type locality.*—Hermit Trail, Hermit Basin, Grand Canyon National Park, Arizona.

*Geological occurrence.*—Coconino sandstone (about 130 feet above base), Permian.

*Description.*—Stride about 210 mm.; width of trackway about 330 mm. Hindfoot placed partly upon the imprint made by the forefoot. *Hindfoot:* Length about 100 mm. None of the footprints, and most of them are well impressed, gives any indication of the presence of separate toes, but in the deepest part of the pes tracks two longitudinal parallel tapering depressions (see fig. 12) evidently indicate the presence of at least two digits, but these were wholly inclosed within the mass of the foot. It is this peculiarity that has suggested the specific name *pachypodus*. The anterior portion of the imprints gives the impression of their having been made by a single broad toe, which had a broadly rounded ungual. This end measures 53 mm. in transverse diameter. On the inner side and a little posterior to its midlength a pronounced indentation may represent the division between toes and sole. The outline of the hindfoot impression as a whole may be said to be reniform. The sole is subquadrate in outline and well impressed in nearly all of the tracks, especially the series of the right side. *Forefoot:* The placing of the hindfoot wholly or in part upon the impression made by the forefoot has obliterated most of the details of its structure. It is quite evident that the feet were of about equal size, and from what little can be seen of them, that there was a similarity of structure. These resemblances are clearly shown
in plate 9, the outer right-hand row being those made by the forefoot, the second inner row being those of the hindfeet of that side.

The depth of the tracks, wide trackway, short stride, and large size of the imprints indicates they were made by a heavy, squat animal, with a relatively short body, for otherwise it would be quite impossible for the hindfoot to have been set upon the imprints of

![Diagram of part of the trackway. Outer row of tracks made by the forefoot; inner row, made by the hindfoot, and placed partly upon the tracks of manus. About \( \frac{1}{6} \) natural size.](image)

... the forefeet. No evidence of a tail drag was found. This specimen occurred at a slightly lower level in the horizon than the one from which the major part of the Coconino tracks were collected.

**Genus OCTOPODICHNUS, new genus**

*Generic characters.*—Apparently eight footed with tracks arranged in groups of four, alternating, two anterior impressions didactyle, two posterior unidactyle.

*Genotype.*—*Octopodichnus didactylus,* n. sp.
OCTOPODICHNUS DIDACTYLUS, new species

Plate 10, fig. 2

Type.—Catalogue number 11,501, U. S. N. M. Consists of a slab 440 mm. long, having a trail traversing the entire length. A small portion of the obverse slab is also present.

Type locality.—Hermit Trail (500 feet to left of trail going down), Hermit Basin, Grand Canyon National Park, Arizona.

Geological occurrence.—Coconino sandstone (about 150 feet above the base), Permian.

Description.—The trail here described consists of two lines of imprints arranged in groups of four, the groups of the two sides alternating. These groups are arranged in a row of three regularly spaced tracks with the fourth offset inward and slightly behind the most posterior imprint of the line of three. A line passed through the three tracks has its axis everted 45° to the line of direction of movement (see fig. 13), this inclination of course being reversed in the groups of tracks on the opposite side. The direction of movement is clearly indicated by the displaced sand caused by the impact of the heel (see pl. 10). The tracks are subequal in size, the two anterior imprints being bifurcated, with the outer toe or claw slightly longer and more robust than the inner; the two posterior imprints seem to be unidactyle. The outer toe of the third imprint of each group, enumerated from the front, especially of the right side, has a heavy inward projecting heel. The toes have the same direction as the line of tracks. The stride, if the movement may be so designated, is 106 mm. The greatest width of trackway is about 94 mm., space between single imprints usually 21 mm., there being a slight variation; the fourth or offset impression is about 15 mm. inside the third. The three tracks in line occupy a linear space of 58 to 63 mm. Single tracks have a length of 13 mm., a width of 7 mm.

Much uncertainty exists as to the nature of the animal that made this trail. Some of the living crustaceans have didactyle extremities and that is the chief reason for the suggestion about to be made that the trail may be the tracks of a member of that group. While there seems to be no living crustacean that would make such a trail, in Permian times there may have been such an animal. The trackway is distinct from all others found at this locality and in all of the hundreds of square feet of sandstone surface examined only one other such trail was discovered. A second poorly preserved specimen (No. 7,846, U. S. N. M.) was collected in this same general locality in 1924, but the preservation was such that its principal characteristics were not recognized at that time.
The stride as compared with the width of trackway would seem to indicate an animal with considerable length of leg, and it is inconceivable that the imprints are other than those made by feet on separate legs, a conclusion substantiated by the direction of the claws or toes. While the tracks give the impression that all four were moved forward simultaneously, it may be that one leg was moved forward at a time after the manner of progression of many existing invertebrates.

**GENUS TRIAVESTIGIA, new genus**

*Generic characters.*—A continuous trail of three parallel sets of markings, between two of which there is a faintly impressed tail
drag. Longer axes of feet impressions placed slightly diagonal to
direction of movement, alternating. Feet apparently unidactyl.

Genotype.—Triavestigia niningeri n. sp.

TRIAVESTIGIA NININGERI, new species

Plate 10, fig. 1

Type.—Catalogue number 11,510, U. S. N. M. Consists of a slab
about 260 mm. long, having a trail traversing about two-thirds of
its length.

Type locality.—Hermit Trail, Hermit Basin, Grand Canyon Na-
tional Park, Arizona.

Geological occurrence.—Coconino sandstone (a loose slab from
hillside about 100 feet above the base), Permian.

Description.—The trail here described consists of three parallel
rows of impressions, between two of which the intermittent drag of
a tail is faintly but clearly recorded. Width of the trackway 14 mm.,
width of the paired rows 8.5 mm. Length of step is about 7.5 mm.
The feet seem to have been unidactylus, and made single mark-like
depressions that stand diagonal to the axis of the line of movement.
Curiously enough all of the markings forming the three rows have
the same diagonal angle as shown in figure 14. The impressions forming the two rows on either side of the tail drag are regularly alternating. The outer or third row is composed of the largest and most distinct markings, but their spacing is the same as those of the other two rows. The impressions found on either side of the tail drag are quite certainly made by the feet, but as to the origin of the third row, one cannot be certain whether it was made by a foot or by some other appendage. However, the regularity of spacing and close conformity to the other rows leaves no other conclusion than that all were made by the same animal. Whether the normal trail would consist of four rows of tracks, as in Bifurcula pes, which in some specimens shows only three, there is no way of determining at this time. Only by the discovery of additional specimens can we hope to clear up this point. While I have been unable to definitely classify these tracks they give every indication of having been made by some invertebrate animal and for the present at least they will be so regarded.

The specific name is in honor of Prof. H. H. Nininger of McPherson, Kansas, who found the type specimen and generously donated it to the national collections.

**PALEOHELCURA TRIDACTYLA** Gilmore

*Paleohelcura tridactyla* Gilmore, Charles W., Smithsonian Misc. Coll., Vol. 77, No. 9, 1926, pp. 31-34, pl. 12, fig. 1, text fig. 20.

The discovery of a second specimen (No. 11,499, U. S. N. M.) of *Paleohelcura tridactyla* is of interest because the tracks were found *in situ* in the Coconino sandstone, at about 150 feet above the base of the formation and not far distant from where the type was discovered. The type was a loose slab found lying on the hillside below the Hermit Trail about 125 feet above the base.

The second specimen adds nothing new to our knowledge of the species, as it exhibits the same tridactyle impressions with a tail drag in the center of the trackway.

Genus **UNISULCUS** Hitchcock


The genus *Unisulcus* was established by Hitchcock for a group of simple trails which he regarded as having been made by naked

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1 Hitchcock, Edward, Ichnology of New England, 1858, pp. 153, 154, pl. 30
worms or annelids. The genus was characterized as "trackway a single continuous groove."

Genotype.—Unisulcus marshi Hitchcock.

A specimen found in the Coconino sandstone bears a trail which appears to have been made by some crawling, legless animal whose affinities seem to fall in this genus.

UNISULCUS SINUOSUS, new species

Plate II

Type.—Catalogue number 11,498, U. S. N. M. Consists of a small slab of sandstone carrying three trackways.

Type locality.—Hermit Trail, Hermit Basin, Grand Canyon National Park, Arizona.

Geological occurrence.—Coconino sandstone (about 150 feet above base), Permian.

Description.—Trackway a continuous groove having an average width of 3 mm. and usually slightly sinuous. Sand on one side of trail slightly raised forming a slight ridge; the opposite side lower and somewhat rounded. On the ridged side the wall of the groove is nearly perpendicular, while the opposite side is beveled. At bottom the trail gives the impression of being grooved rather than rounded. The abrupt ending of one trail in the center of the slab as shown in plate II suggests that it was made by an animal that was able to move backward as well as forward. However, there is no accumulation of sand at this end such as has been observed by Hitchcock in trails of a somewhat similar nature. Slightly beyond the intersection of two of these trails, both are flattened and widened out and the bottom is sculptured by three distinct shallow, longitudinal grooves.

Of the Mesozoic ichnites assigned to this genus, the present species most closely resembles Unisulcus marshi in size and especially in width of groove, but is at once distinguished from that form by the more sinuous nature of the trackway, and by the grooved character of the furrow. The reference of this specimen to the genus Unisulcus by no means implies that it is regarded as having been made by a crawling worm, though such may have been the case. It seems more probable that it is the track of a mollusk, for the dragging shell would better account for the grooved appearance of the trail as well as the ridge of sand on one side, although in living mollusks the trail is usually ridged on both sides of the groove.

The type is the only specimen of this species observed in all of the hundreds of square feet of sandstone surface examined.
Genus BATRACHICHNUS Woodworth

Batrachichnus Woodworth, J. B., Bull. Geol. Soc. Amer., Vol. 11, 1900, p. 542, pl. 40, text fig. 2.

This genus may be characterized as follows:

Generic characters.—Small forms, quadrupedal, with four and five toes on manus and pes respectively. With or without median groove. Toes slender, radially arranged.

Genotype.—Batrachichnus plainvillensis Woodworth.

This genus contains two species from widely separated localities, B. plainvillensis Woodworth from the Carboniferous of Massachusetts, and B. celer (Matthew) from the Carboniferous of Nova Scotia. The species Exocampe ? delicatula Lull, a form of small size with similar digital formula is provisionally referred to this genus to be known hereafter as B. delicatula (Lull). The digital formula of Notalacerta jacksonensis Butts 1 suggests its affinities also to be with this genus to which it is now referred. Its 4 and 5 short, bluntly rounded toes as contrasted with the five long and acuminate toes on both manus and pes in the type species of Notalacerta (N. missouriensis) certainly justify its removal from that genus. It is, however, quite possible that a comparison of the type specimens might show that B. jacksonensis and B. plainvillensis are cospecific, in which event the latter would become a synonym of the former on the ground of priority. This matter could only be settled satisfactorily by a restudy and comparison of the type specimens, which is outside the scope of the present study.

BATRACHICHNUS DELICATULA (Lull)

Plate 12


Lull’s original description, based on rather scanty materials from these same deposits, follows:

The smallest of the forms collected by Professor Schuchert consists of a very delicately impressed fore- and hindfoot in relief on mud-cracked red shale. The hindfoot is the larger and shows four slightly radiating digits, but no trace of sole. The manus is also apparently four-toed with distinct impressions of terminal claws. The digits radiate more widely, but here again there is no palmar impression. The form may therefore be described as digitigrade. Faint indications which may represent phalangeal limitations may be

1 The Kansas City Scientist, Vol. 5, 1891, p. 18, text fig.
seen on the second digit of the manus. This form resembles most closely the genus *Eocampe* of the Connecticut Trias, but is a generalized track which almost any small amphibian, such as a modern salamander for instance, might make and while it may for convenience be placed within the mentioned genus, genetic relationship with the creatures that made the tracks so designated is not of necessity implied.

*Specific characters.*—Manus somewhat smaller than the pes, with three well-defined, radiating digits, the middle one of which is directed forward. An

![Diagram](image)

Fig. 15.—*Batrachichnus delicatula* (Lull). No. 11,519, U. S. N. M.

A, diagram of trackway showing normal track. B, showing trackway made by the hindfeet only. Note that the stride has lengthened and the trackway is narrower than in A. Dotted lines connect impressions made by the hindfeet. Both figures 1/2 natural size.

obscure impression of an additional digit lying on the inner side of and more nearly parallel to the second is indicated. There is also at the base of the second digit what may represent a palmar pad. It may, however, be accidental, as there are other such on the slab.

*Pes.*—The four phalangeal impressions are more or less ovoid without indications of claws or phalanges and, except for the first, curve slightly outward. There is a faint mark which may indicate a fifth digit. The pes impression lies immediately behind that of the manus and a little apart from it as the figure indicates. There lies in advance and to the left of the impres-
sions we have discussed a series of five minute rounded marks, whose relative position is precisely the same as the termini of the pedal toes in the track described. These marks seem therefore to indicate the impression of the right pes. If so they give a trackway width of 33 mm. and an estimated stride of the same foot of 42 mm., thus indicating a rather wide-bodied, short-legged form. This form is provisionally included in the genus *Exocampe* Hitchcock, the species being designated as *delicatula* in allusion to its delicate proportions.

A series of footprints, one of several trackways impressed on the undulating surface of a large slab of Hermit shale (No. 11,519, U. S. N. M.), seems to be referable to this species. The specimen was found one-quarter of a mile west of the sign "Red Top" on the Hermit Trail, at the head of Hermit Gorge by Mr. G. E. Sturdevant, of the Park Service, who discovered it lying loose on a slope about 30 feet above the Hermit-Supai contact where it had been exposed to weathering, which to some extent accounts for the distinctness of the minute tracks impressed upon the upper surface.

![Figure 16](image)

Fig. 16.— *Batrachichnus delicatula* (Lull). Type. No. 2,146, Yale Museum; right manus (a) and pes (b) natural size. (After Lull.)

The trackway, 300 mm. in extent, crosses the lower right hand portion of the slab shown in plate 12. The hindfoot has a length of 10.5 mm. and width of 13 mm. There are five digits, and a tracing of the foot plan, when placed upon Lull's figure of the pes, though slightly larger, agrees precisely in the placement and arrangement of the toes. The digits are slender, radiating, progressively lengthening toward the outside. The fifth, much reduced in length and widely set off from the others, has its origin far back on the sole and is directed strongly outward. As in the type, the sole is indistinct, though a few imprints seem to indicate that it was broadly rounded behind. The hindfoot, as shown by Lull, is placed directly behind the forefoot.

The forefoot has a length of 7 mm., a greatest width from tip to tip of first and fourth digits of 10 mm. There are four widely radiating digits apparently without claws, although Lull thought he detected "distinct impressions of terminal claws." Manus turned strongly inward toward the axis of the direction of movement. First
and fourth toes usually in line across the palm of the foot, the former pointing inward and backward, the latter outward and forward as shown in figure 16. As in the pes the palmar impressions are hardly more than a suggestion. Forefeet usually inside the line formed by the hindfeet.

Such differences as may be noted between the forefeet of this and Lull's type may be more apparent than real for it must be remembered that Lull had but a single impression of the manus (see fig. 16) in the type, and as we well know the same trackway often exhibits differences in the toe plan in successive imprints made by the same foot (see fig. 15). It is, therefore, important to have trackways of some length in order to be sure of the precise arrangement of the digits.

Comparative Measurements

<table>
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<th>No. 11,519 U. S. N. M.</th>
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<tr>
<td>Width of trackway</td>
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<tr>
<td>Width of manus</td>
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</tr>
<tr>
<td>Length of pes</td>
<td>7.0</td>
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</tr>
<tr>
<td>Width of pes</td>
<td>7.0</td>
<td>13.0</td>
</tr>
</tbody>
</table>

A second series of small five-toed tracks on this same slab (see B, fig. 15) but crossing the trackway just described at right angles, is of interest as showing the apparent capability of this animal to walk entirely on the hind legs. This series, which may be clearly traced for a length of 290 mm., gives nowhere any evidence of the front feet. Furthermore the lengthened stride, 82 mm., and narrowed trackway, 34 mm., give corroborative evidence in support of this conclusion. In proportions of foot and relative arrangement of the digits the impressions of the hindfeet in the two trails are essentially identical and while both may not have been made by the same individual, they were quite certainly made by the same kind of an animal. That small, crawling quadrupedal animals often assume the bipedal mode of progression for short distances has often been observed among the small lizards of the southwestern United States, as has been convincingly portrayed by Sayville Kent in excellent photographs. However, it is rather surprising to find an amphibian doing likewise since our living amphibians are usually slow and sluggish of movement.
A salamandroid feature of the feet is seen in the inward toeing of the forefeet and the more outward direction of the toes in the hind-feet. The widely radiating toes of the forefoot and the digital formulas of 4 and 5 are particularly characteristic of the salamander group and it would seem quite probable that the affinities of these tracks fall into that group.

The assignment of this species to the genus *Batrachichnus* Woodworth, founded on a specimen from the Carboniferous shales of Massachusetts, is chiefly on the basis of a similar digital formula supplemented by its small size, with slender toes radially arranged. Its original reference to the Mesozoic genus *Exocampe*, as mentioned by Lull, was a temporary expedient and not intended to imply genetic relationship. The different digital formula as now definitely known shows at once that its affinities lie outside the genus *Exocampe* which has four digits in the pes and five in the manus.

The type species *Batrachichnus plainvillensis* shows a decided median groove (see fig. 18) of which there is no indication in *B. delicatula*, but in common with Matthew in referring *Dromopus celer* to this genus, this feature is not here regarded as of great classificatory importance.

*B. delicatula* is distinguished from *B. plainvillensis* and *B. celer* by its much larger size, more widely radiating toes, especially of the forefoot, and lack of sole impressions. Its distinction from the Jog-gins species is rendered difficult because of inadequate illustration and description.

**BATRACHICHNUS OBSCURUS, new species**

**Plate 13**

*Type.*—Catalogue number 11,529, U. S. N. M. Consists of a trail about 500 mm. in length; on this same slab are plant impressions and a few tracks of *Hylopus* sp.

*Type locality.*—About one-fourth mile west of the sign “Red Top” on Hermit Trail, at head of Hermit Gorge, Grand Canyon National Park, Arizona.

*Geological occurrence.*—Hermit Shale (about 30 feet above Hermit-Supai contact), Permian.

*Description.*—Stride 23 mm., width of trackway 23 mm., width of median groove 8 mm. *Hindfoot:* Length 9 mm., width 6 mm. There appear to be five short digits; third and fourth subequal in length and directed straight forward; fifth much shortened but not especially set off from other toes; second and first progressively shortened inward (see fig. 17). Although the trail is of considerable length...
only a few of the impressions show toe marks, and of the hindfoot none shows the full complement, all but one imprint lacking the fifth toe. The sole is relatively narrow, elongate and obtusely rounded.

![Diagram of part of trackway. About \( \frac{1}{4} \) natural size.](image17)

**Fig. 17.**—*Batrachichnus obscurus*. Type. No. 11,529, U. S. N. M.  
Diagram of part of trackway. About \( \frac{1}{4} \) natural size.

behind. *Forefoot*: Length about 5 mm., width 4.5 mm. Four digits. First slightly set off from the others and directed forward and inward, others extending almost straight forward. The forefeet im-

![Diagram of trackway. Natural size. (After Woodworth.)](image18)

**Fig. 18.**—*Batrachichnus plainvillensis* Woodworth. Genotype. Diagram of trackway. Natural size. (After Woodworth.)

pressions are even more obscure than the hind, evidently due to the fact that the tracks were made in very soft mud which, in most instances, ran into the track as soon as the foot was withdrawn, leaving only a slight depression. The contour of the palm is not fully indicated in any of the tracks.
In the length of stride, which is equal to width of trackway, in size of tracks, number of digits, and presence of a median groove, these tracks bear a strikingly close resemblance to those of *Batrachichnus plainvillensis* from the Carboniferous shales of Massachusetts. The great width and depth of the median groove seem to indicate that it was made by the dragging belly. The course is irregularly sinuous and at one end the animal turned sharply to the left and with a more moderate bend to the right, and where these bends were made the median groove is much widened and smoothed out. (See pl. 18.)

It is quite evident that the tracks were made by a salamandroid, shortlegged crawling animal, which in moving about dragged the belly. The foot structure also suggests its amphibian origin. No other trails or tracks exactly comparable to it have been found at this locality.

From *B. plainvillensis* this species may be distinguished by the shorter toes, their more forward direction, and the wider and deeper median groove. It is distinguished at once from *Dromillopus*, also a small form in these same deposits, by the greater number of toes on the hindfoot. The specific name is suggested by the obscure condition of most of the tracks.

**Genus DROMILLOPUS Matthew**


Matthew characterizes the genus as follows:

*Generic characters.*—Small digitigrade batrachians. Toes slender, directed forward in a radial manner; imprint showing only four toes to each foot.

*Genotype.*—*Dromillopus quadrifidus* Matthew.

This genus was established by Matthew on a series of small tracks from the Carboniferous Coal Measures of Joggins, Nova Scotia.

**DROMILLOPUS PARVUS,** new species

Plate 14

*Type.*—Catalogue number 11,537, U. S. N. M. Consists of a small slab of shale showing the trackway and tail drag of a small animal.

*Type locality.*—About one-fourth mile west of the sign “Red Top” on Hermit Trail near the head of Hermit Gorge, Grand Canyon National Park, Arizona.

*Geological occurrence.*—Hermit shale (about 40 feet above Hermit-Supai contact), Permian.
Description.—Stride about 36 mm.; width of trackway about 33 mm. This small slab of reddish colored shale has impressed on its surface some few beautifully preserved tracks (see pl. 14), although the trackway as a whole is obscure in several important details.

This obscurity is due to two conditions, first, the intermingling on the left-hand side of the tracks of two small animals; and second, the failure of one pair of feet to impress clearly. The feet most clearly registered correspond almost precisely in size and in number and arrangement of the digits with the so-called hindfoot described by
Matthew\(^1\) as \textit{Dromillopus quadrifidus} from the Coal Measures of Joggins, Nova Scotia. The presence of a distinct tail drag, and its absence in the Joggins trackway (compare figs. 19 and 20), differences found in the structure of the forefeet, longer stride, and greater width of trackway all point to its specific distinctness from the Nova Scotian species; hence the specific name \textit{parvus} is proposed for its reception. **Hindfoot**: Length 9 mm., width 8 mm. Four digits of which the outer is set off from the other three. These are long and slender, regularly increasing in length toward the outside of the foot, the third being the longest, the fourth considerably shorter.

![Image](https://example.com/image.png)

\textbf{Fig. 20.—} \textit{Dromillopus quadrifidus} Matthew. Type. Diagram of trackway. About natural size. (After Matthew.)

The sole is well impressed and the full rounded outline of the heel is shown in figure 19, whereas in the Joggins species the sole is scarcely distinguishable. The foot is shown to have been semiplantigrade, not digitigrade as originally characterized by Matthew. **Forefoot**: Length about 8 mm., width 8 mm. While none of the so-called hindfoot impressions show the detailed structure plainly, it is clearly evident there were only four toes on the manus. The sole seems to be more broadly rounded than in the pes. A description of the other details of the foot must await the discovery of better preserved specimens.

The imprints connected by dotted line in figure 20 were regarded by Matthew as having been made by the hindfeet. No reasons were

given for this conclusion, though their slightly larger size may have influenced his decision. The relative position of these tracks suggests that their identity may be the reverse of Matthew's conception. The same condition prevails in the trackway now before me, but no positive evidence in solution of this suggestion is offered and for the present Matthew's identification will be followed. Between the rows of tracks is a distinct, well defined groove probably made by a dragging tail, which registers the movement of the animal as indicated by the undulating character of the impression.

A second series of tracks of this species is found on the upper side of the slab carrying the basi-relief tracks of *Hyloidichnus bifurcatus* (No. 11,598, U. S. N. M.). It is a short trackway that is in

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<td>Length of manus track</td>
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<td>Width of manus track</td>
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accord in all particulars with the type specimen. The tail drag is not continuous as in the type but left its trace only on the crests of the ripple marked surface across which the trail runs.

**Genus HYLOPUS Dawson**


The genus *Hylopus* was briefly characterized by Dawson as follows: "Smaller footprints [than *Sauropus* Lea], digitigrade, and made by animals having a long stride and hind and forefeet nearly equal. Five toes. Probably footprints of Microsauria and possibly of Dendrerpeton." In all Dawson described five species. These named in chronological order are: *Hylopus logani*, *H. hardingi*, *H. caudifer*, *H. minor* and *H. tri跌us*. All are from the Coal Measures of Nova Scotia.

Subsequently Matthew¹ reviewed the genus and reached the conclusion "that there is so much variation in the form of these foot-

prints that they cannot all be contained in the genus *Hylopus*." He then shows that *H. hardingi*, *H. minor*, and *H. logani* should be retained in the genus and at the same time selects *H. hardingi* as the genotype. He also concludes (p. 85) "that five toe-marks of the hindfoot and four in the fore is the typical number for *Hylopus*." It is this conclusion that leads him to question the propriety of retaining *H. minor* which has a digital formula of 5-5. *H. caudifer* is removed to the genus *Asperipes*, and *H. tridus* to the genus *Ornithoides*.

Dawson in his characterization and also in his first published figures before the species was named, shows five digits on the forefoot. In the light of the many other resemblances to these tracks found in specimens from the Grand Canyon, in which there are five distinct toe impressions on the forefoot, it would seem that Dawson was probably correct, and that Matthew was in error in thinking there were only four toes on the manus. Because of the close resemblances found in these footprints from the Hermit shale to those of *H. hardingi* Dawson, especially in relative length of digits, stride and width of trackway, I refer the following new species to *Hylopus*, which may now be characterized as follows:

*Generic characters* (emended).—Quadrupedal, semidigitigrade. Manus subequal or smaller than pes. Five toes in both manus and pes; toes in both thick with bluntly pointed extremities; fourth longest, progressively decreasing in length inward; fifth in both fore- and hindfeet much shortened and strongly set off from others. Stride long, hindfoot placed behind forefoot.

*Genotype.*—*Hylopus hardingi* Dawson.

Matthew also points out that all of the species except *H. logani* have the print of the sole preserved, and on that account infers that Dawson was in error in regarding the feet as being digitigrade. This conclusion is fully sustained by the semi-plantigrade character of the impressions of the specimen about to be described.

**HYLOPUS HERMITANUS**, new species

Plate 15

*Type.*—Catalogue number 11,517, U. S. N. M. Consists of a slab on which is a trail showing many of the tracks of both fore- and hindfeet beautifully impressed.

*Type locality.*—One-fourth mile west of sign post "Red Top" on Hermit Trail, head of Hermit Gorge, Grand Canyon National Park, Arizona.

1 Air-Breathers of the Coal Period, Montreal, 1863, pl. 1, figs. 2, 2a.
Geological occurrence.—Hermite shale (30 feet above base), Permian.

Description.—Stride about 144 mm.; width of trackway about 114 mm. Hindfoot: Length about 38 mm.; width 40.5 mm. Five toes. The fourth toe is longest, the others progressively shorter inward. The fifth is shortened, divergent, and with a tendency to turn backward. There seem to have been sharp claws on the second, third, and fourth digits as in H. minor Dawson, but the fifth had a
bluntly rounded end and was apparently without claw. If a claw was present on the first digit it must have been obtusely pointed. In all of the tracks, the sole is rather faintly impressed in so far as its exact posterior outline is concerned. As determined it is relatively short, but broad, and apparently without prominent palmar pads. *Forefoot:* Smaller than hindfoot. Length 32 mm.; width from tip to tip of first and fifth toes is 36 mm. Five toes, arranged much as in the hindfoot. Fourth is longest, progressively shortening inward.

![Fig. 22.—Hylopus hardingi Dawson. Trackway. (After Matthew.)](image)

Fifth more widely divergent from fourth than in the pes, with an inclination to turn backward, and apparently without claw. The palm is short, and rounded behind.

A second series of tracks (No. 11,524, U. S. N. M.) from this same locality, occurring on the weathered surface of a small slab of shale found on the hillside below the ledge where the type was found in place, is identified as belonging to this same genus and species. It is smaller than the type (see table of measurements) but otherwise is in close agreement as to the proportions and arrangement of the digits. Other scattering imprints of *Hylopus* are present on several slabs of shale from this same locality.
Examination of the type (see pl. 15) shows that the animal was in the habit of placing the hindfoot directly in line with but a variable distance behind the forefoot, never overlapping. That the digits were flexible is indicated by the strongly bent ends of digits three and four in the lower impression of the pes as shown in figure 21, whereas the very next impression forward shows them perfectly straight. Since the straight form of digits predominates they are regarded as representing the normal shape of these toes.

### Comparative Measurements

|                | No. 11,524 U. S. N. M. | No. 11,517 U. S. N. M. Type | *Hylopus hardingi* *
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<td>Stride</td>
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<td>Width of hindfoot</td>
<td></td>
<td>40.5</td>
<td>33.0</td>
</tr>
<tr>
<td>Length of digit I</td>
<td>5.0</td>
<td>5.0</td>
<td>4.5</td>
</tr>
<tr>
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</tr>
<tr>
<td>Length of digit III</td>
<td>11.5</td>
<td>14.0</td>
<td>15.0</td>
</tr>
<tr>
<td>Length of digit IV</td>
<td>14</td>
<td>18.5</td>
<td>20.5</td>
</tr>
<tr>
<td>Length of digit V</td>
<td></td>
<td>7.0</td>
<td>6.0</td>
</tr>
<tr>
<td>Length of forefoot</td>
<td>21</td>
<td>32.0</td>
<td>...</td>
</tr>
<tr>
<td>Width of forefoot</td>
<td>26</td>
<td>36.0</td>
<td>...</td>
</tr>
<tr>
<td>Length of digit I</td>
<td>6</td>
<td>7.5</td>
<td>...</td>
</tr>
<tr>
<td>Length of digit II</td>
<td>7</td>
<td>8.0</td>
<td>9.0</td>
</tr>
<tr>
<td>Length of digit III</td>
<td>10</td>
<td>10.5</td>
<td>13.5</td>
</tr>
<tr>
<td>Length of digit IV</td>
<td>12</td>
<td>15.0</td>
<td>16.5</td>
</tr>
<tr>
<td>Length of digit V</td>
<td>4.5</td>
<td>6.0</td>
<td>5.7</td>
</tr>
<tr>
<td>Forefoot in front of hindfoot</td>
<td>...</td>
<td>12 to 30</td>
<td>...</td>
</tr>
</tbody>
</table>

*Measurements of Hylopus hardingi taken from Matthew's illustration.

Matthew\(^1\) depicts a fore- and hindfoot of *Hylopus hardingi* which in the explanation of figures he attributes to the right side. By comparison with the tracks of *Hylopus hermitanus* now before me, and especially with Matthew’s figure 2, plate 6, it becomes at once apparent that they pertain to the left side. It will be noted that in Matthew’s illustration of the hand, the side from which the first digit would spring is left unfinished (see fig. 23), implying that the evidence for its absence was inconclusive. In view of the close resemblance to the specimen here described and in their close agreement

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of relative proportions as shown in the table of comparative measurements, and especially by Dawson's original determination, it would seem there can be but little doubt that the creature making the tracks called *Hylopus hardingi* had five digits on the forefoot. The liability of toes not to impress is clearly shown in the specimen now before me for although in most of the tracks forming this short trail all toes are indicated, one hindfoot impression shows only the dimmest record of digit four and no trace at all of the outer toe.

*Hylopus hermitanus* most closely approaches *H. hardingi* in size and arrangement of the digits of the feet, but may be distinguished from that species by the more widely separated and more divergent toes, and especially by the more forward position of the fifth toe. In both *H. hardingi* and *H. minor*, the fifth toe is given off far back on the side of the sole. In the forefeet of both of these species the lateral toes are much less divergent than in the specimen here described (compare figs. 21 and 22).

In offering conjectures about the known animals which might have been responsible for the Nova Scotian tracks, Sir William Dawson suggests they may have been made by some microsaurian-like *Hylopeton* or *Hylonomus*. In any event, all of the tracks here discussed seem to conform more nearly to those made by amphibians than to those of any known reptile.
In figure 24 is shown a diagram of the foot plan of *Anthracopus ellangowensis* Leidy from the Coal Measures of Pennsylvania, which displays such striking resemblances to the forefoot of *Hylopus hermitanus* as to allow the suggestion that with the recovery of better preserved specimens of the Pennsylvanian species they will be found to be congeneric. Through the courtesy of Dr. Witmer Stone, director of the Philadelphia Academy of Sciences, I have had the opportunity of examining the type of *Anthracopus ellangowensis* and find on one imprint a faint suggestion of the presence of a fifth digit, although none of the other five tracks preserved gives any hint of its existence. The evidence is, therefore, inconclusive. The absence of the fifth digit in *A. ellangowensis* is the only important difference found in a comparison of these two species, and its absence may be due to its not impressing, a condition observed in at least one track of the type of *H. hermitanus*. In general form, relative length and
divergence of the digits, and shape of palmar impression there is
great similarity between the two. Attention should also be called to
certain resemblances found between *H. hermitanus* and *Ichnium sphaerodactylum* described by Pabst from the Permian (Tauback) of Thuringen. In the general plan of the feet there is a striking similarity, though the absence of the first digit in the manus and the heavier toes with bluntly rounded extremities in *I. sphaerodactylum* effectually distinguishes it from the Arizona form.

**Genus HYLOIDICHNUS, new genus**

*Generic characters.*—Quadrupedal, semidigitigrade. Both manus and pes have five digits. Manus smaller than pes and placed in front of hindfoot. Toes terminated either with pellets or having bifurcated ends.

*Genotype.*—Hyloidichnus bifurcatus.

1 Pabst, W., Deutsche geol. Gesell., Vol. 48, 1896, pp. 638 and 808, text fig. 2.
HYLOIDICHNUS BIFURCATUS. new species

Plate 16

Type.—Catalogue number 11,518, U. S. N. M. Consists of the obverse slab on which is a trackway about 500 mm. in extent.

Type locality.—Hermit Trail, one-fourth mile west of sign "Red Top" head of Hermit Gorge, Grand Canyon National Park, Arizona.

Geological occurrence.—Hermit shale, 30 feet above Hermit-Supai contact, Permian.

Description.—Stride about 180 mm.; width of trackway about 125 mm. Forefoot somewhat smaller than hind and is placed in front of it. Hindfoot: Length 42 mm., width 40.5 mm. There are five toes, progressively longer toward the outside, the fourth being the longest. The fifth digit is much shortened, and somewhat set off from the others. Fourth digit is more than twice the length of the sole and extending directly forward as in Hylopus. First and fifth toes terminated by pellets, second, third and fourth usually

![Diagram of trackway](image-url)
having bifurcated ends with inner branch longer than outer (see fig. 25). These have suggested resemblance to the bifurcated digits of the living *Rhacophorus maximus*, a tree frog of Sumatra, which has the unguals split to give better support to the terminal disks. This reference should not convey the idea of relationship but simply calls attention to an interesting similarity of structure. Sole narrow antero-posteriorly but wide transversely. Digits have the following lengths. I = 7.3 mm., II = 17 mm., III = 23 mm., IV = 30 mm., V = 13 mm. Forefoot: Length about 32 mm., width 31.2 mm. Five digits as in the pes, which grow progressively longer toward the outside, the fourth being the longest. The fifth shorter than the first and especially set off from the other toes as in the hindfoot. All of the toes seem to be terminated by pellets. None of the imprints show bifurcated toes. First toe more widely separated from the others than in the hindfoot. The digits have the following lengths: I = 10 mm., II = 14.5 mm., III = 17.5 mm., IV = 20 mm., V = 9 mm. These tracks may be classed as digitigrade, as shown by the extreme shortness of the sole impression. They were evidently made by a quadrupedal batrachian, evidently of the walking type as indicated by the alternating position of the steps of opposite sides.

In such features as the digital formula, and their radiating arrangement, these tracks bear a close resemblance to *Hylopus* found in these same beds, but the longer and more slender toes terminated either by pellets or bifurcated ends at once distinguish them from that genus as well as all others coming under my observation. It is therefore regarded as new, the specific name *bifurcatus* being in reference to the divided ends of a few of the toes on the hindfeet.

Only one specimen referable to this species was found in the collection of 1926.

**Genus PARABAROPUS, new genus**

The discovery of additional specimens that appear to be referable to Lull's species *Megapezia? coloradensis*\(^1\) indicates the necessity of establishing a new genus for its reception. Its original assignment to the Nova Scotian genus *Megapezia* was regarded by Lull as provisional, largely on account of the paucity of the materials at his command. Certain resemblances to the genus *Baropus* suggest the name *Parabaropus*, which may be characterized as follows:

**Generic characters.**— Quadrupedal, plantigrade, with five digits in both manus and pes. Forefoot smaller than hind; toes in both rela-

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tively short with rounded extremities, without claws; sole of pes elongated, narrowed behind. Forefoot turning strongly inward and placed in front of hindfoot.

Genotype.—Parabaropus coloradensis (Lull)

**PARABAROPUS COLORADENSIS** (Lull)

Plate 15, fig. 7


In establishing this species, Lull had as type materials "three small slabs of red impure sandstone, one apparently of the manus obscured by crushing and mud-cracking, another of the pes, and a third with two impressions each of hand and foot, which determine the width of trackway but not the length of stride." From a study of these composite materials he depicted the plan of the feet as shown in figure 26.

A series of tracks (No. 11,598, U. S. N. M.) of the left side from the Hermit shale and from the same general locality as the type specimens, shows such striking resemblances to the tracks figured by Lull, except for their slightly larger size, as to at once raise the question of the proper association of the imprints as illustrated by Lull. This series, which is in relief, has been cast and thus affords all of the evidence of the original imprints. The manus is shown to be smaller than the pes, and the digits of the former resemble those of the latter in being relatively short with rounded ends without claws. This fact is entirely in accord with the large number of trackways in the collection from this same region in that the toes of the manus are always similar to those of the pes in the character of their termination. In other words, if one has the toes acuminate, they will be pointed in the other; if rounded in the hindfoot, they will be rounded in the forefoot, etc., etc. In the large collection of trackways now available from this same region, not a single exception to this rule can be found. This reason alone appears to be sufficient to show that these imprints have been incorrectly associated.

That Lull recognized this incongruity of foot structure is shown by the following remarks:

The difference in character of manus and pes is so great, except for an agreement in size, that one would not, perhaps, be justified in associating them together were it not for the third slab.

Examination of the type materials made possible through the kindness of Dr. R. S. Lull, who forwarded them to the National Museum, all goes to confirm my above conclusions. The third slab, on which
reliance was placed for the original association of the detached im-
prints, was found to have on its surface the tracks of no less than
four kinds of animals, all rather indistinctly recorded in so far as
their exact details are concerned. None of these can be positively
identified with either of the detached tracks. The footprint which has
suggested resemblances to the pes track figured by Lull is much
smaller, but disregarding this difference in size, the preservation is
such as to render its positive identification with that track out of the
question.

In front of this track are two smaller tracks, one slightly encroach-
ing upon the other, which in the light of newly discovered specimens
can quite certainly be identified as the manus and pes tracks of

*Fig. 26.—*Megapezia? coloradensis* Lull. Type, No. 2,145, Yale
Museum. *a,* right manus. *b,* right pes. ½ natural size. (Reduced
from Lull.)

*Hyloidichnus bifurcatus.* The other tracks present on this slab are
inferior in their preservation and deserve no further mention at this
time.

After study of the type materials it is my conclusion that no evi-
dence exists for the association of these detached footprints and on
that account the track illustrated by Lull as the pes (see fig. 26) is
selected as the type of the species *P. coloradensis.*

Comparison of the manus track of the newly discovered trackway
(see fig. 27) with the type of *P. coloradensis* (Lull) (see fig. 28)
shows such close resemblances between them as to leave no doubt
that the type track pertains to the manus rather than the pes as
originally determined. These tracks are practically of the same size,
as may be seen in the table of comparative measurements and further
resemblances are found in the short radiating digits, with rounded
extremities, without claws, and short, broad sole rounded behind. The type shows the presence of only four digits but the faint impression of the sole which gradually fades out on the right hand side of the track indicates that it was sufficiently wide to carry a fifth toe. A tracing made from the type track without restoration is shown in figure 28.
Although the evidence is not entirely conclusive, in view of the many similarities pointed out specimen No. 11,598, U. S. N. M., is provisionally referred to the present species, and our knowledge of the species may now be elaborated by its description.

This specimen was found in situ in the Hermit shale about one-quarter mile west of the sign post "Red Top," on the Hermit Trail.

Comparative Measurements of Forefeet

<table>
<thead>
<tr>
<th>Specimen</th>
<th>No. 11,598 U. S. N. M.</th>
<th>Type No. 2,145 Yale Museum</th>
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</thead>
<tbody>
<tr>
<td>Length</td>
<td>48 mm.</td>
<td>48.5 mm.</td>
</tr>
<tr>
<td>Breadth</td>
<td>70 mm.</td>
<td>50.0 mm.</td>
</tr>
<tr>
<td>Length of digit I</td>
<td>12 mm.</td>
<td>12.6 mm.</td>
</tr>
<tr>
<td>Length of digit II</td>
<td>14 mm.</td>
<td>15.0 mm.</td>
</tr>
<tr>
<td>Length of digit III</td>
<td>14 mm.</td>
<td>17.0 mm.</td>
</tr>
<tr>
<td>Length of digit IV</td>
<td>13 mm.</td>
<td>15.5 mm.</td>
</tr>
<tr>
<td>Length of digit V</td>
<td>11 mm.</td>
<td>...</td>
</tr>
</tbody>
</table>

in Grand Canyon National Park, Arizona, about 30 feet above the Hermit-Supai contact. The length of stride is about 240 mm., width of trackway unknown. Forefoot smaller than hind and placed in front of the hindfoot impression. Hindfoot: Plantigrade, length about 80 mm., greatest width 80 mm. Five relatively short digits having rounded terminations, without claws. Fifth toe set off from the others and directed strongly outward. Sole elongate, more than three times as long as the longest toe. Digits have the following lengths: I = 14 mm., II = 21 mm., III = 23 mm., IV = 18 mm., V = 16 mm. Forefoot: Length about 48 mm., width about 70 mm. Five toes radially arranged. Toes as in the pes, short with rounded terminations without claws. Palm nearly twice as wide as long, and broadly rounded behind. The foot as a whole is turned inward.

Fig. 28.—Parabaropus coloradensis (Lull) Type. No. 2,145, Yale Museum. Outline of manus, un-restored. About 

\frac{1}{2} natural size.
whereas the hindfoot is directed straight forward (see fig. 26). The relative lengths of the digits are given in the table of comparative measurements (see p. 57). The form of the elongated hindfoot impression has a considerable resemblance to the pes track of Baropus lentus Marsh (see fig. 10), but is distinguished from that genus by the presence of five toes and in having the forefoot considerably smaller than the hind, and its much smaller size as a whole.

Genus COLLETTOSAURUS Cox


In reviewing the literature relating to Carboniferous footprints it became at once apparent that many of the authors gave but scant attention to the work done by their predecessors, a procedure that has resulted in the creation of a number of synonyms. While it is far beyond the scope of the present paper to attempt a revision of the entire subject, in order to secure a working basis for the proper classification of the specimens here considered it becomes necessary to make the nomenclatural changes herewith suggested.

In 1874 Cox proposed the genus Collettosaurus based on an adequate specimen from the Carboniferous of Warren County, Indiana. No attempt was made to characterize the genus, but from his rather meager description and illustration it may now be defined as follows:

Generic characters.—Quadrupedal. Five digits on both manus and pes. Toes relatively slender, acuminate, radiating, with fifth somewhat set off from the others; feet about equal in size; hindfoot placed behind forefoot.

Genotype.—Collettosaurus indianaensis Cox.

In February 1891, Butts\(^1\) described the new genus and species Notalacerta missouriensis (see fig. 30) from the Upper Coal Measures of Kansas City, Missouri, and in March of the same year he established a second genus Notamphibia magna (see fig. 29), each having five slender sharply pointed toes on both fore- and hindfeet.

A critical comparison of these three genera fails to disclose differences of genetic importance, and on the grounds of priority Notalacerta and Notamphibia are considered synonyms of Collettosaurus, the species to be known hereafter as Collettosaurus missouriensis (Butts) and C. magna (Butts).

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\(^1\) Butts, Edward, The Kansas City Scientist, Vol. 5. 1891, p. 18.
Fig. 29.—Collettosaurus magna (Butts). Type. Imprint of right side. About natural size. (After Butts.)

Fig. 30.—Collettosaurus missouriensis (Butts). Type. Imprints of fore- and hindfoot of left side. Natural size. (After Butts.)
Dromopus velox Matthew from the Lower Carboniferous of Nova Scotia (see fig. 31), likewise appears to have its affinities within this genus, and were it not for the uncertainty of the digital formula of the forefoot, I should unhesitatingly refer it to the present genus. The hindfoot with five slender digits, digits three and four subequal in length, and the first slightly divergent, are all features in common with the pes impressions of the species to be described below.

Matthew was in doubt as to whether there were three or four toes in the manus of Dromopus velox, but in view of the close similarities noted above in the hindfeet, it would seem not unlikely that five may be found in this foot when better preserved specimens are known.

![Fig. 31.—Dromopus velox Matthew. Type. a, right hindfoot impression; 2b, right forefoot impression. From Joggins, Nova Scotia. Both natural size. (After Matthew.)](image)

Footprints from the Hermit shale, having a similar digital formula, with slender sharp pointed toes are tentatively referred to Collettosaurus.

**Collettosaurus Pentadactylus**, new species

Plate 19, fig. 1

*Type.*—Catalogue number 11,527, U. S. N. M. Consists of a slab of shale 390 mm. in length carrying a consecutive series of tracks evidently made in very soft mud.

*Type locality.*—One-fourth mile west of sign post "Red Top" on Hermit Trail, head of Hermit Gorge, Grand Canyon National Park, Arizona.

*Geological occurrence.*—Hermit shale (about 30 feet above base), Permian.

Description.—Stride about 330 mm.; width of trackway 120 mm. Hindfoot: Five digits, third and fourth long, slender, subequal in length, and usually directed straight forward in the direction of movement. The fifth digit originates well back on the side of the sole and is diverted strongly outward. The first is weak and about half the length of the median digits. Sole apparently long, but none of the hindfoot impressions is sufficiently clear to show the precise shape of the sole. Roughly estimated the pes may have a total length of

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**Fig. 32.—Collettosaurus pentadactylus.** Type No. 11,527, U.S.N.M. Diagram of trackway. About 1/4 natural size.
about 50 mm. The length of the digits may tentatively be recorded as follows: digit I, 14 mm.; digit II, 24 mm.; digit III, 28 mm.; digit IV, 28 mm.; digit V, 22 mm. These figures are subject to revision since the impressions may have been lengthened by slipping in the mud. *Forefoot*: Length about 54 mm.; width measured from tip of digit I to the tip of digit V, 41 mm. Five digits, inner and outer, shorter than median toes, both somewhat divergent, and both originate well back on the opposite sides of the palm behind the bases of the median digits. The first is weak, and, as in the hindfoot impressions, about one-half as long as the middle toes. Sole long, narrow, and obtusely pointed behind. Length of digit, I, 13 mm.; digit II, 26 mm.; digit III, 27 mm.; digit IV, 25 mm.; digit V, 20 mm. In walking the forefoot is placed forward and directly in front of the hindfoot. The weight of the animal, judging from the depth of the impressions of the feet, was about equally distributed between the fore and hind limbs. Forefoot but little smaller than hind.

From *Collotetosaurus magna* (Butts) the present species may at once be distinguished by the much shorter digit I in both manus and pes and by the greater relative narrowness of the imprint as a whole.
Unfortunately Butts neglected to state whether the imprint figured by him was of the hand or the foot, nor did he designate whether right or left, but from comparison with the specimens under consideration it becomes quite apparent that the track was made by a foot of the right side of the animal, clearly indicated by the posterior position of the fifth digit.

The tracks here described seem to have been made by a long-legged quadruped walking rapidly through soft mud, for when the foot was withdrawn the ooze closed in from either side in many instances leaving only a narrow streak to indicate the imprint of the toe. There are no indications of a tail drag.

The foot plan, especially of the manus, shows some striking resemblances to that of the living Iguana (compare figs. 32 and 33). The long slender acuminate toes; two median digits of subequal length; divergent fifth toe and narrow pointed palmar impression, are all features in common between the fossil tracks and those of the Iguana, and at least permit the suggestion that in all probability these fossil tracks were reptilian if not Sauri in origin.

**Genus CURSIPES Matthew**


The genus *Cur sipes* was established by Matthew on specimens from the Carboniferous of Joggins, Nova Scotia. The chief characters distinguishing *Cur sipes*, as extracted from Matthew’s description would seem to be as follows:

*Generic characters.*—Quadrupedal. Five digits in pes, three in manus. Toes long and slender in both feet. Sole small in both manus and pes.

The presence of this genus in the Hermit formation seems to be indicated by the rather inferior specimen briefly described below.

**CURSIPES, sp.**

Plate 17, fig. 2

A series of footmarks (No. 11,521, U. S. N. M.) more or less obscured by the tracks of other animals stepping upon them, seems to be referable to the genus *Cur sipes*, and if correctly identified marks the first recognized occurrence of this genus in the Hermit ichnite fauna. This specimen was found in the same locality as the other Hermit specimens described herein.

As shown best on the upper right hand side of the slab, the print of the three toed forefoot was distinct from the hind and placed some
distance in front of it. The stride is about 115 mm., width of trackway about 125 mm. Hindfoot: Length about 30 mm., width about 33 mm. There are five digits. Toes widely spread as in Hylopus. Fifth toe strongly set off from the other. Second and third toes subequal in length, others progressively shorter toward the outside of the foot. Sole rather lightly impressed. Considerable variation in the length of toes is noted in the several impressions available; the length of toes as given below are measurements taken from the two most clearly impressed tracks. Length of toes: I = 9 mm.; II = 11 mm.; III = 10.5 mm.; IV = 10 mm.; V = 9 mm. Forefoot: Length about 28 mm., width about 20 mm. There are three long slender toes, the outer slightly spreading from the inner two. Toes subequal in length, none less than 18 mm. long. Sole indistinctly impressed.

The digital formula of five in the pes and three in the manus at once distinguishes this trackway from all others found in the Hermit fauna, but in the Joggins, Nova Scotia, fauna two genera, Asperipes and Cursipes, are found with a similar number of digits. The elongated nature of the toes, especially in the manus, and the relatively small soles seems to show that its affinities lie in the genus Cursipes to which it is provisionally referred.

The much larger size of the tracks, and differences noted in the plan of the feet, especially in the relatively shorter and stouter toes of the pes, are characters that might serve to distinguish it from the described species, C. dawsoni and C. levis Matthew, but on account of the unsatisfactory nature of the evidence to be obtained from this single specimen its designation as a distinct species is deferred for the present. It is sufficient at this time to call attention to the presence of Cursipes in this fauna in the expectation that better specimens may be found, which will permit its adequate characterization.

**INZERTE SEDIS**

Plate 17, fig. 2; plate 18

Under this heading, attention is called to certain ichnites occurring in the Hermit formation that are apparently new to the fauna, but due to the paucity of information to be obtained from specimens in hand it seems undesirable to name them.

Specimen No. 11,528, U. S. N. M. (see pl. 18), is notable as being the largest footprint yet discovered in the Hermit formation, and as such it appears worthy of this brief description.

This specimen was found by Mr. G. E. Sturdevant and was presented by him to the national collections. It was picked up on the
hillside about one-fourth mile west of the sign "Red Top" on the Hermit Trail, in Hermit Basin, and from 30 to 40 feet above the Hermit-Supai contact. The single track is deeply impressed on the sun-baked surface of a slab of reddish sandy shale. There are five toes and a tapering heel of moderate length. If correct in regarding it as being the imprint of a right foot (probably the hind), the fifth toe is somewhat set off from the others and subequal in length with the fourth. The fourth is the longest digit, the others progressively reducing in length toward the inside of the foot. The toes give the impression of all being acuminate. The track has a greatest length of 128 mm.; a greatest spread of toes of 130 mm. Length of digits as follows: I = 20? mm.; II = 30 mm.; III = 40 mm.; IV = 52 mm.; V = 50 mm. On the lower left hand corner of this slab, about 165 mm. posterior to the above described tracks are three toe marks, but whether made by the same foot cannot be determined. In size, narrowing of the heel, presence of five digits, toes reducing in length inward with a divergent fifth digit, this track suggests affinities with *Chirottherium heterodactylum* (King) from the Carboniferous of Pennsylvania. The much shorter digits with other minor differences would separate it from that species if more perfect specimens should show its affinities to lie within that genus.

A second specimen (No. 11,530, U. S. N. M.) from this same locality and geological horizon, and likewise consisting of a single track made by a much smaller animal, also seems to represent an undescribed member of this Ichnite fauna. Its principal characteristics are well shown in plate 17, figure 3. It has four long, tapering, acuminate toes, two of which are curved. A short spur extending outward from the base of the larger toe on the left hand side of the specimen may represent a very short fifth digit. The heel is largely missing. Greatest spread of toes 46 mm. Length of digits taken from left to right is as follows: I = 5 mm.; II = 15 mm.; III = 26 mm.; IV = 34 mm.; V = 31.5 mm.

**FAUNA OF THE SUPAI FORMATION**

**Genus STENICHTHUS**, new genus

*Generic characters.*—Quadrupedal, plantigrade. Four toes on both fore- and hindfeet. Toes long, slender, and acuminate. Hindfoot placed upon the impression made by the forefoot.

*Genotype.*—*Stenichthys yakiensis*, new species.

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STENICHNUS YAKIENSIS, new species

Plate 19, fig. 2

_Type._—Catalogue number 11,533, U. S. N. M. Consists of a slab on which is a trackway about 330 mm. in length.

_Type locality._—Yaki Trail (about 2 miles down from top), east side of O'Neill Butte, Grand Canyon National Park, Arizona.

Fig. 34.—_Stenichnus yakienensis._ Type. No. 11,533, U. S. N. M.
Diagram of trackway. About \( \frac{1}{2} \) natural size.

_Geological occurrence._—Supai formation (about middle), Pennsylvanian.

_Description._—Stride about 81 mm., width of trackway (estimated) 94 mm., hindfoot placed forward and partially upon forefoot. Forefoot nearly equal to hindfoot in size. _Hindfoot:_ Length about 45 mm., width across the toes 23.5 mm., across sole 18 mm. There are four long, slender toes. Toes nearly equal to length of sole, and inner three directed straight forward, outer toe slightly divergent. Two
median toes subequal in length, lateral toes slightly shorter. The sole longer than wide, practically the same length as the toes, obtusely rounded behind. Forefoot: Length about 40 mm., width across palm

![Diagram of trackway from Coal Measures, Joggins, Nova Scotia. Natural size.](image-url)

about 18 mm. In most of the imprints three toes are registered, but the hindfoot, in the greater number of instances, was partially placed upon the fore and wiped out the imprint of the shortened inner toe. Although plainly present on the right side, in these tracks the outer
toe failed to impress. Sole shorter than in pes, being wider than long. As in the hindfoot the two median toes are longest, the inner much shortened and the outer somewhat shorter than the second and third. All seem to be directed forward.

In slenderness of the toes and narrow sole, these tracks bear a striking resemblance to *Ornithoides* ? *adamsi* Matthew, from Nova Scotia, but the greater number of toes and larger size of the present specimen serves to distinguish the two genera. A comparison of the two, however, leads me to wonder whether the Nova Scotian species is not also four-toed, the outer toe failing to register as on the right side of the specimen now before me. In his original description of the species Matthew remarks: "It may be associated with *O. trifidus*, though the examples do not exhibit the characters of this genus fully." Matthew's inability to distinguish fore- and hindfoot impressions adds a further resemblance to the specimen in hand. Its reference to the present genus would seem most appropriate.

**Genus ANOMALOPO*US, new genus**

*Generic characters.*—Quadrupedal. Four digits in pes, three in manus. Forefoot smaller than hind, with hind placed in front of fore. Outer toe of both manus and pes stout with rounded clawless extremity directed outward and forward; other toes acuminate. Inner toe of pes short as in *Agostopus*.

*Genotype.*—*Anomalopus sturdevanti*, new species.

**ANOMALOPO*US STURDEVANTI, new species**

*Plate 20*

*Type.*—Catalogue number 11,577, U. S. N. M. Consists of a slab of sandstone 475 mm. long having a trail of 13 imprints traversing its entire length.

*Type locality.*—Yaki Trail, Grand Canyon National Park, Arizona.

*Geological occurrence.*—Supai formation. Pennsylvanian.

*Description.*—Stride about 155 mm., width of trackway about 200 mm. *Hindfoot:* Length about 90 mm., width about 80 mm. Four digits. First toe very short, heavy, with rounded extremity; fourth toe stout with rounded end much diverted outward from the others. The fourth digit on the left hindfoot has a more pointed end and projects more directly outward than the fourth of the right side. It has the appearance of having suffered injury, which would fully account for the differences noted. The second and third toes are long, comparatively slender, with sharply pointed extremities. These me-

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Fig. 36.—Anomalopus sturdevanti. Type, No. 11,577, U. S. N. M. Diagram of a portion of trackway. About ½ natural size.
dian toes, although directed straight ahead in the direction of movement, have a tendency to turn outward. The sole of the foot is relatively narrow and supplied with palmar pads. The toes have the following lengths: \( I = 5 \text{ mm.} \); \( II = 35 \text{ mm.} \); \( III = 35 \text{ mm.} \); \( IV = 26 \text{ mm.} \). Hindfoot placed in front of forefoot and the impression of the sole usually obliterating the toes of the forefoot. Forefoot: Length about 68 mm.; width measured from tip of digit I to tip of digit III, 53 mm. Three digits. Outer toe stout, with broadly rounded extremity and spreading outward from the others. Digit I and II as in the pes, long, comparatively slender, parallel acuminate and directed straight forward. Sole relatively narrow with broadly rounded heel. Length of toes as follows: \( I = 29 \text{ mm.} \); \( II = 27 \text{ mm.} \); \( III = 18 \text{ mm.} \).

This series of footprints is impressed on a fine grained pinkish colored sandstone that is covered with worm trails. The footprints are deeply impressed and clearly defined except that portions of the forefoot track are destroyed by the hindfoot partially stepping upon it.

The species is named for Mr. Glen E. Sturdevant, ranger naturalist of the Grand Canyon National Park, who discovered and collected the specimen, and through whose efforts it was presented by the Park Service to the United States National Museum.

**Genus TRIDENTICHNUS, new genus**

*Generic characters.*—Quadrupedal, semiplantigrade. Five toes in pes, three ? in manus. Manus smaller than pes, with hindfoot placed behind forefoot.

*Genotype.*—*Tridcntichnus supaiensis*, new species.

**TRIDENTICHNUS SUPAIENSIS, new species**

*Plate 21*

*Type.*—Catalogue number 11,534, U. S. N. M. Consists of a slab on which is a trackway of eight imprints divided equally between the feet of the two sides.

*Type locality.*—Hermit Gorge (to the left of Hermit Trail, descending, about one-half mile below Santa Maria Spring), Grand Canyon National Park, Arizona.

*Geological occurrence.*—Supai formation (upper track bearing horizon; about 350 feet below top), Pennsylvanian.

*Description.*—Stride about 185 mm., width of trackway about 187 mm. Forefoot placed about 18 mm. in front of hindfoot; in
one pair of tracks slightly outside of it. Forefoot smaller than hindfoot. *Hindfoot:* Length about 68 mm., width about 70 mm., five toes, the three median ones subequal in length and directed forward; first much shortened and extending forward and inward, while the fifth is widely set off from the others and is directed almost straight outward. Three median toes bluntly acuminate, second and fourth having a tendency to turn in toward the third (see fig. 37). Sole broader than long and broadly rounded behind. Digits have the following lengths: $I = 10 \text{ mm.}; \ II = 23 \text{ mm.}; \ III = 26 \text{ mm.}; \ IV = 26 \text{ mm.}; \ V = 13 \text{ mm.}$ *Forefoot:* Length (estimated) about 40 mm., width of three toes 48 mm. Three toes impressed, but there may have been more in the complete complement. The three median toes bear a strikingly

Fig. 37.—*Tridentichnus supaiensis.* Type. No. 11,534, U. S. N. M. Diagram of a portion of trackway. About $\frac{1}{3}$ natural size.
close resemblance to those of the hindfoot, in size, shape, and relative positions to one another. The presence of lateral toes is suggested by a toe scratch on the inner side of one impression, and on the outer side of this same print the sand shows disturbance as if a fifth toe was present, but one cannot be sure and the other forefoot tracks are not sufficiently well impressed to give any additional evidence on this point. The sole is imperfectly impressed and this fact may account for the faintness of the evidence relating to the lateral digits. Width of three digits 48 mm., same as those of the hindfoot. Lengths: \( II = 22.5 \text{ mm.}; \ III = 26 \text{ mm.}; \ IV = 26 \text{ mm.} \)

The variation in the different tracks is clearly indicated in figure 37.

A second occurrence of this genus and species seems to be indicated by a comparison of figure 2, plate 2, with the trackway above described. In the illustration the three-toed front foot may be seen in its proper position in front of the hind foot, which, except for the lack of a fifth digit, agrees in all essentials with the type of the present genus and species. If this long range identification is correct it shows the presence of this form at the Yaki locality some seven or eight miles distant in an air line from the type locality.

**SUMMARY**

The study of these fossil footprints has resulted in the establishment of adequate ichnite faunas for the Coconino and Hermit formations and the beginning of a fauna for the older Supai. The various forms described are, with few exceptions, based upon trackways showing impressions of all four feet, a procedure that should give the minimum trouble in the identification of specimens that may be subsequently discovered. The faunal lists could have been considerably augmented had it seemed expedient to describe inferior material, but a more conservative course was adhered to.

Comparison of these three faunas shows them to be absolutely distinct from one another as not a single genus has yet been found common to any two of the formations. In so far as the Hermit is concerned, this fact occasions no particular surprise, even though the difference in geological level be disregarded, for the environmental conditions were such as to lead one to expect an entirely different assemblage of animal life than would be found in either the Coconino or Supai. The muddy character of the sediments with sun-cracked surfaces, with associated ferns and other water-loving plants are all indicative of the low lying nature of the region at the time these animals inhabited it. The many amphibian-like footprints, and tracks
left by crawling, short-legged creatures who dragged their tails and bellies in the mud appear typical of such an environment.

The Coconino fauna is nearly doubled in the number of known species but the facies of the fauna remains as stated in a previous paper—"Carboniferous in aspect, as shown by the relatively small size of the animals, all of which are quadrupedal, as contrasted with the considerable number of very large forms and many three-toed bipedal animals of the Triassic." Taken as a whole, this fauna now consists of 15 genera and 22 species and seems to have closer relationships to the ichnite fauna from the Middle Coal Measures of Kansas, described by Marsh than to the more extensive fauna from the Coal Measures of Nova Scotia made known by Dawson and Matthew.

On the other hand the Hermit fauna has its closest affinities with that from Nova Scotia, for of the eight genera now known, four are common to both and the facies of the two faunas taken as a whole shows striking resemblances. That similar environmental conditions prevailed in these two widely separated localities is indicated by the similarity in the character of the sediments in which the imprints occur.

The Supai fauna, known at present by three genera and as many species, shows no close relationships with tracks from other localities, although it may be said to be Carboniferous in aspect. It apparently represents an ichnite fauna new to North America and consequently has little correlative value at this time.

Aside from the trails of invertebrate animals found all others were made by quadrupedal creatures, but only a comparatively few give any certain clue as to whether they pertain to the Reptilia or Amphibia.

Animals having a digital formula of 5 and 5 predominate in the Hermit, while those having a lesser number are more abundant in the Coconino. Whether this fact has any significance remains to be determined. Search of the literature shows that all Permian animals in which the foot structure is known have five digits in both manus and pes and of the Coal Measures Amphibia none shows fewer than four digits in the manus and five in the pes. It would seem therefore either that none of the Permian animals known from their skeletons may be considered as the makers of the three and four toed tracks, or else certain digits consistently fail to leave their impressions.

In an attempt to identify some of the known Permian vertebrates as being responsible for certain of these tracks, tracings were made of all of the available fore- and hindfeet of animals of that period, in order that these tracings might be placed directly upon the tracks,
in order to more accurately compare them. No information of importance resulted, as so many unknown factors enter into such a comparison as to render any likenesses found to be of little consequence. At present there appears but little likelihood of definitely correlating the footprints with fossil skeletons. The chief importance of these footprints, it now seems, is the establishment of adequate faunas for each of these three formations, which in the absence of other fossil criteria may be of future use in correlating these deposits with other track-bearing formations of distant localities.

LITERATURE


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EXPLANATION OF PLATES

Plate 1

Fig. 1. General view of fossil footprint locality at head of Hermit Gorge. Most of the specimens of fossil tracks and plants from the Hermit shale were collected from the slope above the massive sandstones in the middle foreground. The disconformable Hermit-Supai contact is plainly indicated on the left side of the photograph. The cross indicates the level where footprints, plants, and insect wing were found in situ............................. 6

2. Close up view of the fossiliferous ledge indicated by the cross in fig. 1. The projecting ledge extending to the right from the base of the cedar tree, which is estimated to be 30 feet above the Hermit-Supai contact, contained footprints, plants, and insect impressions.

Plate 2

Fig. 1. Looking up Yaki trail from a point two miles down from the top of the rim, where the trail cuts through a massive sandstone in the middle Supai formation on the east side of O'Neill Butte. Numerous tracks and trails occur in the upper light-colored sandstone seen in the right of the picture................................. 8

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*Barypodus metscheri*, new species. Type. No. 11,505, U. S. N. M. Irregular trackway. × 3

Plate 7

*Baropus coconinoensis*, new species. Type. No. 11,514, U. S. N. M. Left side of trackway. × 3.2

Plate 8

*Agostopus medius*, new species. Type. No. 11,509, U. S. N. M. Trackway. × 3.46

Plate 9

*Amblyopus pachypodus*, new genus and species. Type. No. 11,511, U. S. N. M. Trackway; outer rows of impressions made by forefeet, inner, those of the hindfeet. × 4.57

Plate 10

Fig. 1. *Triavestigia minuscula*, new genus and species. Type. No. 11,510, U. S. N. M. Tail drag clearly shown between the parallel rows of tracks on the left side. × 1.3

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Plate 11

*Unisulcus sinuosus*, new species. Type. No. 11,497, U. S. N. M. Three trails crossing slab. × 2

Plate 12

*Batrachichnus delicatula* (Lull) No. 11,519, U. S. N. M. Large slab whose surface is thickly covered with minute tracks. × 4.5

Plate 13

*Batrachichnus obscurus*, new species. Type. No. 11,529, U. S. N. M. Trail showing where belly dragged in the mud. Plant impressions. Large tracks those of *Hylopus hermitensis*. × 2.7

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