FOSSIL FOOTPRINTS FROM THE GRAND CANYON

(With Twelve Plates)

BY

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Curator of Vertebrate Paleontology, United States National Museum

(Publication 2832)

CITY OF WASHINGTON
PUBLISHED BY THE SMITHSONIAN INSTITUTION
JANUARY 30, 1926
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INTRODUCTION

Tracks of extinct quadrupeds were first discovered in the Grand Canyon in 1915 by Prof. Charles Schuchert, and specimens collected by him at that time were made the basis of a short paper by Dr. R. S. Lull in which were described two species, *Laophorus schucherti* and *L. nobeli*, from the Coconino sandstone.

In the summer of 1924, the locality was visited by Dr. John C. Merriam, president of the Carnegie Institution of Washington, who made a small collection of tracks which were later presented to the United States National Museum. While at the locality, Doctor Merriam conceived the idea of having a permanent exhibit of these footprints *in situ* on the Hermit Trail, to teach a lesson as to the great antiquity of the animal life that once roamed over these ancient sands—a lesson that could not fail to be understood by the veriest tyro in geological phenomena. This plan was presented to Hon. Stephen F. Mather, director of the National Park Service, who immediately became interested in the project, and, with the aid of friends of the Park Service, arrangements were perfected whereby, in the late fall of 1924, the writer was detailed to visit the locality and prepare such an exhibit, and at the same time to make a collection of the footprints for the United States National Museum. Both of these undertakings were successfully carried out.

The collection made for the Museum, consisting of a series of slabs some 1,700 pounds in weight and carrying a great variety of excellently preserved imprints, is of more than usual interest, especially in coming from a locality and formation in which but the two species of Ichnites mentioned above have been recognized previously. Even with the diversity of forms now secured, it is quite

apparent that all varieties to be found at this locality are not repre-
sented. It is upon this collection and the one made by Doctor M.
riam earlier in the year that the present study is based.

FIELD EXHIBIT OF FOSSIL FOOTPRINTS

A preliminary survey of the locality on the Hermit Trail showed
that the natural conditions were most favorable for the preparation
of an exhibit of the tracks in situ. The rather steep slope of the
cross-bedded sandstone on whose surface the tracks are imprinted
stands at an inclination of nearly 30 degrees facing toward the Trail
over which, in the course of a year, hundreds of tourists travel on
mule back in making their pilgrimage to the bottom of the canyon.
Furthermore, it was found that the upper superimposed layers of
laminae scaled off in large sheets, thus uncovering the tracks and
trails beneath. The preparation of this exhibit required first the re-
moval of the overburden of loose dirt and broken rock down to the
more compact layers, and then the quarrying off of the loose
upper laminae until a solid and continuous face covered with foot-
prints was reached. In this way a smooth surface 8 feet wide and
25 feet long was uncovered, as shown in plate 1, figure 1. The upper
surface of this large slab has a great many tracks and trails leading
up the slope, a few passing over and under the more or less hori-
total strata shown at the top. At the side of the slab and leading up
from the trail a flight of stone steps was laid in order to facilitate
examination by those interested in a closer inspection of the foot-
prints. At the base of this main exhibit, other large slabs lying close
to the trail were similarly cleared off (see pl. 1, fig. 2), so that
there are now several hundred square feet of rock surface forming
a permanent exhibit of the various tracks and trails that are to be
found here.

The great antiquity of these footprints, which occur from 900 to
1,080 feet below the level of the present rim of the canyon, is clearly
demonstrated at this locality. It is obvious that since the day when
those animals impressed their feet in what at that time was moist
sand, more than 1,000 feet of rock-making materials were piled up
in successive strata above them, and this does not take into account
many hundreds of feet more that have been eroded off from the
present top of the canyon wall. The great length of time required
for the cutting away or erosion of the rock to form the deep canyon,
and the even longer time necessary for the original deposition
of this great vertical mass of stone is, when translated into terms of
years, if that were possible, so stupendous as to be almost beyond human comprehension.

It is hoped that the object lesson so graphically taught by this unique exhibit may serve as an example to stimulate the preparation and preservation of other natural phenomena to be found in our government-controlled parks, monuments, and reservations.

GEOLOGICAL OCCURRENCE

The Coconino sandstone of the Hermit Trail in which these tracks occur is considered Permian in age. In this section it has a total thickness of 350 feet, but, so far as known, footprints are found only in the lower half. The greater part of the material here described was collected from one level about 150 feet above the base of the formation (see fig. 1). A few tracks were found at a level of 20 feet above the base, the lowest point at which imprints appeared. Between these two extremes, tracks were observed at several levels, and there is reason for believing that they may prevail continuously throughout the lower part of the sandstone. At the 150 foot level, tracks were traced laterally for a distance of 700 to 800 feet.

The Coconino sandstone is described by Noble as follows:

The Coconino sandstone is a pale-buff fine-grained cross-bedded sandstone whose distinctive features are its massive appearance, the huge scale of the cross-bedding, and the uniform fineness of the component grains of sand. The massiveness of the sandstone, which is due to the coarseness of the cross-bedding, causes it to weather into the highest and most precipitous cliff in the upper wall of the canyon.

The formation is made up of lenticular beds, each of which is truncated by the bed above it in such a way that, as outlined in cross section or cliff faces, the beds commonly form irregular wedges whose sides are sweeping curves. Each wedge consists of innumerable thin inclined laminae. Horizontal bedding is absent except near the base of the formation, where it is inconspicuous. . . . The laminae form parallel curves that flatten downward. Commonly at the top of a wedge they are inclined at angles of 15° to 25°, or exceptionally 30°, but near the base of a wedge they bend and become horizontal or nearly horizontal.

The fossil tracks occur on the upper surface of these inclined laminae. In removing the laminae it was found that the underlying surfaces were often devoid of tracks, while the very next layer might be thickly covered. Sometimes as many as four distinct kinds of tracks were found on one surface. Some slabs were literally covered with imprints and curiously enough all pointed in the same direc-

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tion—up the steep slope of the sandstone layer, suggesting an old trail leading to the water, or possibly recording a great migration of animal life such as is occasionally known to take place among the animals of the present time. Of all the trails collected and the still greater number observed in the field, but one exception to the uphill movement was noted, this being the tracks of a large quadruped, which clearly pointed down the hill (see p. 30). In this connection it is interesting to quote from Sir William Jardine’s *Ichnology of Annandale* (p. 5):

It is a curious fact that nearly all the footprints are impressed as if the animal had walked from west to east or from where we presume water to have been toward the land.

No doubt tracks occur in the Coconino sandstone at many other localities, having been reported on the rocks near “Dripping Spring,” also in the Hermit Basin, but the usual precipitous face of the formation, except in a few favorable places, does not permit searching for them.

Because of the many resemblances in structural and lithologic features to the De Chelly, Navajo, and Wingate sandstones, all of which Gregory regards as most certainly comprised of dune deposits, Noble is of the opinion that the Coconino sandstone is essentially of aeolian origin.

That the evidence afforded by footprints of extinct animals may, in the absence of other fossil criteria, be of value in the correlation of widely separated formations, seems to be indicated by the recognition of generically like, if not specifically similar, tracks found in the Coconino sandstone of the Grand Canyon.

and in the Lyons sandstone of Colorado. The latter is regarded by
Henderson\(^1\) as late Pennsylvanian, but Willis T. Lee, in an unpub-
lished manuscript, reaches the conclusion that the sandstones carry-
ing the footprints in Colorado are Permian, which would seem to
be more nearly in accord with the evidence furnished by the fossil
tracks. Doctor Lee, in a letter under date of June 18, 1925, has
kindly furnished the following statement in advance of the publica-
tion of his paper:

In this manuscript it is shown that the rocks formerly called Lyons include
representatives of two distinct formations, one of Pennsylvanian age and one of
Permian age and that the name Lyons sandstone is now restricted by the
U. S. Geological Survey to the cross-bedded sandstone near Lyons, Colorado,
which has been quarried extensively—that is, to the upper 100 feet of the rocks
formerly called Lyons. The upper sandstone was found to overlap older for-
mations and to be closely associated with rocks containing invertebrates believed
to be of Permian age. These invertebrates are found in many places in lime-
stone stratigraphically above the Lyons sandstone—that is, in the lower part
of the Lykins formation. The Lyons sandstone as restricted is structurally
more closely associated with the Lykins formation of probable Permian age
than with the underlying Ingleside formation, of Pennsylvanian age, and is
therefore regarded as Permian.

SYSTEMATIC DESCRIPTION OF GENERA AND SPECIES

The best preserved and most characteristic of the fossil footprints
collected from the Hermit Trail are described in the following pages.
The list of described forms might have been lengthened had it seemed
wise to include all of the various kinds of imprints found, but in
several instances the evidence was so meager as to deter one from the
adoption of such a course. The possibility of acquiring still further
material from this locality in the immediate future made it injudicious
to describe tracks of which only a few imprints are known.

This study has resulted in the founding of a considerable number
of new genera and species representing the only adequate Permian
ichnite fauna known from North America. Its chief value, however,
is in recording a fauna which, as previously stated, may, in the ab-
sence of other fossil criteria, be of value in geological correlation.
It has not been possible to place, with assurance, more than one
or two of these newly described forms in a definite class. In a few
instances suggestions are made as to the animal to which certain
of the tracks may be attributed, but there now seems no possibility
of definitely connecting them. Should there eventually be found a
way of uniting the two lines of evidence, it is hoped that these tracks

may aid in bringing about a better understanding and interpretation of the habits and characteristics of the animals that made them.

Genus **DOLICHOPodus**, new genus

*Generic characters.*—Quadrupedal. Pes long and narrow. Fourth digit long, slender, and curved outward. Three (?) toes in manus, which is placed behind and outside tracks of the pes. Toes acuminate, clawed, fifth digit of pes wanting. Feet turned strongly inward toward line of movement.

**DOLICHOPodus TETRADACTYLUS**, new species

*Plate 4, fig. 1*

*Type.*—Catalogue number 11,123, U. S. N. M. A slab carrying a consecutive series of eight footprints.

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

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

*Description.*—Stride about 230 mm.; width of trackway, 51 mm. *Hindfoot:* Four digits, fifth wanting, fourth long, slender, curved outward. Three inner digits progressively shortened. All toes acuminate except possibly the first. Heel rounded. Length of track 32 mm., width 15 mm. Length of digit I, 4 mm.; digit II, 5 mm.; digit III, 7 mm.; digit IV, 16 mm. *Forefoot:* Three (?) parallel digits, toes acuminate. Placed behind and outside hind foot.

The selected type of this species is a consecutive series of eight footprints divided equally between the fore- and hindfeet of the right and left sides of an animal walking in a straight course. The imprints made by the forefoot are so indistinct as to be visible only by special lighting, and this, combined with the narrow trackway and length of stride at first gave the impression that the track was made by a bipedal animal. These front impressions fall behind and outside of the deeper imprints of the hindfeet, and in an oblique light three short parallel digits are clearly discernible, the outer two being of equal length and sharply pointed. The inner toe is much shortened. The toes of both feet are directed strongly inward toward the median line of the trackway.

The striking feature of the more deeply impressed tracks of the hindfeet, which, by the way, are quite unlike any others yet found at this locality, is the presence of a long, slender fourth digit terminated by a sharp claw that curves outward. On the inner side
of this long toe distinct impressions of three digits which become progressively shortened toward the inner posterior side of the foot are to be noted in two of the tracks. The second and third toes are sharply pointed with a tendency to turn outward as does the fourth. The termination of the short first toe is imperfect but it seems to have a rounded end. It is strongly divergent and is directed straight inward at a right angle to the long axis of the foot. There is no evidence of a fifth digit, but if present it would certainly have been registered because of the depth of the foot impressions as a whole. All of the toes with the exception of the first of the hindfoot are directed forward in line of the course of movement.

The unusual feature of the tracks of the hindfeet being strongly in advance of those of the forefeet, the reverse of the usual condition, raises the question of their proper identification. The reasons for considering the deeply impressed tracks as having been made by the hindfeet are their larger size, narrower trackway, and deeper impression, for otherwise the weight of the body must have rested chiefly on the forefeet—an unreasonable supposition.

The impressions of the forefeet offer but little opportunity for comparison with described forms, but those of the hindfeet bear certain resemblances to the tracks

Fig. 2.—Dolichopus tetradactylus. Type, No. 11,123. U. S. N. M. Diagram of series of footprints. About 1/2 natural size.
of *Dromopus agilis* Marsh, such as the long, curved fourth digit, with curved claw, as shown in figure 3. The absence of a fifth on the outside of the foot, the reversed curvature of the digits, and the hindfoot impression behind the fore show, however, that the two sets of tracks were made by quite different animals.

The footprints of *Dolichopodus tetradactylus* appear to have been made by an active animal with long hind limbs and a comparatively light body. That this creature carried the greater part of its weight almost entirely upon the hind limbs seems to be shown by the greater depth of the imprints made by the hindfeet.

![Diagram of footprints](image)

**Fig. 3.** *Dromopus agilis* Marsh. Diagram of left fore and hind footprints. 1/2 natural size. (After Marsh.)

A survey of the known vertebrate fauna of the Permian discloses only one form, *Araeoscelis*, which, in its structure, is suggestive of a type of animal that might make a trackway similar to the footprints under consideration. Perusal of Williston's osteological description shows that a complete pes of this animal is unknown, but the restoration (see fig. 4) shows a fifth digit. In commenting on the number of digits Williston says:

> Only four metatarsals are preserved together in any one specimen, though the presence of the first tarsal would seem definitely to indicate the presence of the full five.

It would seem, therefore, that *Araeoscelis* must be ruled out of consideration as the maker of these tracks. On the other hand, the lack of evidence of a fifth toe in the tracks may be due to its failure to

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impress, but the depth of the hindfoot impressions as a whole leads to the conclusion that this digit was probably absent. An important distinction is thus furnished also between Dolichopodus and Dromopus which in many other features closely approach each other. If correctly restored the feet of Araeoscelis fulfil nearly all requirements for their correlation with the footprints called Dromopus agilis by Marsh.

Resemblances in the general plan of the footprints here described to the feet of Araeoscelis leave but little doubt of their reptilian origin.

**NANOPUS MERRIAMI, new species**

*Plate 4, fig. 2*

*Type.*—Catalogue number 11,146, U. S. N. M. One slab (obverse) on which there is a consecutive series of tracks about 450 millimeters in length.
Type locality.—Hermit Basin, Hermit Trail, Grand Canyon National Park, Arizona.

Geological occurrence.—Coconino sandstone (about 20 feet above the base), Permian.

Description.—Stride 62 mm., width of trackway, 50 mm. Hindfoot: Length 15 mm., width 12.7 mm.; four toes, the inner slender, sharp, and closely parallel to the second, the two median toes parallel and directed straight forward, tips acuminate, clawed. Outer toe shortened and well set off from the third. Sole suboval, weakly impressed, nearly as long as the toes. Length of digit I, 5 mm.; digit II, 7.5 mm.; digit III, 7.2 mm.; digit IV, 4.5 mm. Forefoot: Length about 11 mm., width 9.5 mm.; three toes, outer slightly divergent, inner and outer digits shorter than median and subequal in length. Sole small, suboval, weakly impressed. Toes appear to bear slender, pointed claws. Length of digit I, 4.5 mm.; digit II, 6 mm.; digit III, 4.6 mm. The weight of the animal, judging from the depth of the

Fig. 5.—Nanopus merriami. Type, No. 11, 146, U. S. N. M. Diagram of series of footprints. About \( \frac{1}{3} \) natural size.
The imprints of the feet, must have been about equally distributed between the fore and hind limbs.

The series of tracks selected as the type of the new species *Nanopus merriami* are of especial interest from the fact that they mark the lowest horizon in the Coconino sandstone where fossil footprints were found *in situ*. This level is about 20 feet above the base of the Coconino sandstone, or about 1,080 feet below the rim of the canyon. Only the obverse of the foot impressions was secured (see pl. 4, fig. 2), but a plaster cast shows the imprints as clearly as they were on the original rock surface.

The presence of three and four digits respectively on the manus and pes; parallel grouping of the two middle toes of the hindfoot, which are subequal in length; forefoot placed in front of the

![Footprints Image](image)

**Fig. 6.—Nanopus caudatus Marsh.** Outline of left fore and hind footprints. Natural size. (After Marsh.)

...
After careful consideration of the characters briefly reviewed above, the weight of evidence seems to favor the reference of the present specimen to the genus *Nanopus*. Three species have previously been described, *N. caudatus* Marsh, *N. obtusus* Matthew, and *N. gamratus* Matthew.

The specific distinctness of *Nanopus merriami* from *N. caudatus* is shown by the more slender form of the digits terminated by slender claws, relatively shorter soles, smaller size, and lack of tail traces. The last mentioned feature is probably unimportant, for the dragging of the tail must often have depended on the occupation of the animal. The lack of claws, strongly divergent outer toe, unequal length of the two middle digits of the pes, heavier digits, quadratoform

![Image](image.png)

Fig. 7.—*Barilopus arctus* Matthew. *a*, Left hindfoot; *b*, left forefoot. About twice natural size. (After Matthew.)

the sole, and forefoot placed behind the hind, effectually distinguish the Canadian species from *Nanopus merriami*.

No tracks referable to this species were found in the higher track-bearing levels of the Coconino sandstone, but larger collections are necessary before one can be assured that they are confined to the lowermost part.

Marsh was of the opinion that *Nanopus caudatus* in all probability favored a reference to the Amphibia, but the nature of the animal indicated by the impressions of *N. merriami*, although a matter of conjecture, might with equal probability be considered reptilian.

The species is named for Dr. John C. Merriam, president of the Carnegie Institution of Washington, who was instrumental in bringing about the arrangements whereby this excellent series of footprints was acquired for the national collections.
The genus *Laoporus* is characterized by Lull as follows:

**Generic characters.**—Quadrupedal, without tail trace, with four digits in the manus and five in the pes, semiplantigrade, broad-soled, with short digits which in the impressions lack phalangeal pads. Traces of claws appear to be present but they have no grasping predatory function. Feet turned inward toward the line of march.

Footprints of the genus *Laoporus* are found more commonly than any other at the Hermit Trail locality. The large slab shown in plate 1, figure 1, has nearly one-half of its surface literally covered with these tracks, and a second slab (see pl. 1, fig. 2) is similarly decorated.

The closest affinities of *Laoporus* seem to be with *Limnopus* (see fig. 8), and while the latter has a similar digital formula, the heavy, thickened toes with rounded extremities apparently lacking claws, the strongly divergent fifth digit, and the overlapping of the hindfoot impressions on those of the forefoot, seem sufficient to distinguish this genus from *Laoporus*.

Lull's comments on the character of the animals making the tracks ascribed to *Laoporus* as follows:

The creatures which made the footprints were quadrupeds of moderate size, with broad, stumpy feet, apparently clawed, and having at least four toes in front and five behind. The hindfoot, which is somewhat larger, bore a proportionately greater share of the creature's weight, especially in the smaller species (*L. schucherti*). The limbs were apparently short, with a wide trackway, implying a bulky body. No trace of a dragging tail is discernible on any of the specimens, and the body was carried clear of the ground.

These observations apply equally well to the new materials discussed in the following pages. At this time I see no way of definitely determining whether the impressions are amphibian or reptilian in origin.

**Laoporus Nobeli** Lull

Plate 5, fig. 2; plate 6


A beautifully preserved trackway (No. 11,148, U. S. N. M.) from a level 150 feet above the base of the Coconino sandstone (see pl. 5, fig. 2) is identified as pertaining to *Laoporus nobeli* Lull,

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and while none of the imprints have more than three toes registered, the close agreement in foot proportions, width of trackway, and length of stride all point to its affinities with the above mentioned genus and species.

As originally determined by Lull, *Laoporus* has four toes on the manus and five on the pes, this being fully substantiated by the paratype (No. 8422, U. S. N. M.) upon which the genus is partially based, and which has been of the greatest assistance in arriving at a proper identification of the recently acquired material. The shallowness of the prints on slab No. 11,148, U. S. National Museum, largely explains the absence of the missing toe impressions, and that there were other toes is evidenced by the lateral projection of the foot mass, entirely sufficient to have carried the proper number of additional digits.

![Figure 8: Limnopus vagus Marsh. Outline of fore and hind footprints of left side. Natural size. (After Marsh.)](image)

A second slab (No. 11,122, U. S. N. M.) from the same level has on its surface a considerable number of footprints (see pl. 6) which also seem to belong to this genus and species. While these do not form a well-defined trackway, the clearness of many of the imprints contributes to a much better understanding of the detailed structure of the feet than has hitherto been obtained. All of the better impressed tracks are slightly larger than those of the type and other specimens, as may be seen by reference to the table of comparative measurements (p. 16), but those of the forefoot are almost identical in all other features with the paratype.

A study of the paratype in combination with these new specimens gives such a different conception of the plan of the feet from those depicted by Lull as to require a new drawing which is shown in figure 9. The manus, as clearly shown in the paratype, has only four digits, but they are distinctly separated at their bases, with a short, slender first digit and a slightly longer but divergent fourth. Digits
two and three are parallel, subequal in length, and distinctly separated. The palm is narrow antero-posteriorly, with the heel strongly rounded off toward the external side. In all of these respects the new material is in perfect accord with the excellent impression of the forefoot of the paratype, as shown in figure 9A. This figure was made from a cast, the specimen showing the obverse side of the imprint only.

The digits of the pes, instead of being short and blunt as originally depicted, are relatively long and distinctly separated. Only one of the footprints on the slab numbered 11,122 shows any evidence of a fifth toe (see fig. 9C) and its presence in the other tracks of this genus and species would be unsuspected if it were not for the claw drag showing five in the paratype. The evidence is conclusive in this respect, as first recognized by Lull, for where the creature dragged the hindfoot of the left side there are five distinct narrow scratches. The first toe, although relatively short, is distinct; the second, third, and fourth are of subequal length; the fifth is seldom plainly impressed. All are acuminate.

A critical examination of Lull's illustration of the type1 specimen shows that the imprints are rather shallowly impressed and for that reason fail to give a true conception of the foot plan, especially as to the character of the digits. This will explain the great disparity existing between the original figures and the present conception (see fig. 9) based upon more abundant and better preserved specimens.

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1 *Loc. cit., pl. 2, fig. 1.*
In addition to the specimens mentioned above, the collection contains numerous short series of tracks, none of which is worthy of special mention. In plate 9 is shown a trackway of *Laoporus nobeli* diagonally crossing that of *Baropezia eakini*.

**Comparative Measurements**

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**Laoporus Coloradoensis** (Henderson)

Plate 7, figs. 1, 2

*Limnopus (?) coloradoensis* Henderson, Junius, Journ. Geol., Vol. 32, No. 3, 1924, p. 228, figs. 1, 2, 3.

Through the courtesy of Prof. Junius Henderson of the University of Colorado, the type and figured specimens of *Limnopus coloradoensis* (Nos. 13238, 14140 and 14141, Univ. of Colo.) from the Lyons sandstone (Permian), Lyons, Colorado, were loaned me for study and comparison with the footprints from the Grand Canyon.

In the original description this species was questionably referred to the genus *Limnopus* founded by Marsh upon tracks from the Coal Measures of Kansas. (See fig. 8.) The presence of five distinct digits in the pes and four in the manus, with traces of claws,

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lack of phalangeal pads, broad soles and feet turned inward toward the line of movement, with forefoot placed in front of the hind, are all features indicating its affinities with the genus *Laoporus*. The dimensions of the imprints, width of trackway, and length of stride indicate its closest affinities to be with the smaller of the two described species, *L. schucherti* Lull, but the distinct separation of the fifth digit from the fourth of the pes, and the shorter length of digits one and four of the manus appear to show its distinctness from that species.

A rather indistinct trackway (No. 11,176, U. S. N. M.) collected by Dr. J. C. Merriam at the Hermit Trail locality shows a few hind-foot impressions that, except for their larger size, are indistinguishable from those of *Laoporus coloradoensis*, to which species they are referred. (See pl. 7, fig. 1, and compare A and B, fig. 10.)

More abundant specimens may show that *L. coloradoensis* and *L. schucherti* are synonymous, in which event, on the ground of priority, the specific name *coloradoensis* must be abandoned. For the present it seems best to retain both names, even though they cannot be adequately distinguished.

Upon examination of the two slabs of footprints (Nos. 14,140 and 14,141, Univ. of Colo.) illustrated by Henderson I am quite assured that they have been properly referred to *L. coloradoensis*. Specimen No. 14,140 has quite a different arrangement of the tracks in that they form a continuous series not set off in pairs as in the type and other figured specimen. The width of trackway, however, agrees with the other two. The change of gait may have been brought about as Henderson suggests, by the animal creeping up a steep bank where travel was difficult. All details of the imprints on these two referred slabs are obscure. The foot structure is well shown in the accompanying figures, and their proportions are given in the table of measurements.

1 *Loc. cit., figs. 1 and 3.*
Comparative Measurements

<table>
<thead>
<tr>
<th></th>
<th>Type of L. schucherti</th>
<th>Type of L. coloradosensis</th>
<th>Specimen No. 11,137 U. S. N. M.</th>
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<tr>
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<td>mm.</td>
<td>mm.</td>
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<td>Width of impressions</td>
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<tr>
<td>Length of digit III</td>
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<tr>
<td>Width</td>
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<td>Length to tip of digit III without claw</td>
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<td>Length of digit II</td>
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<tr>
<td>Length of digit V</td>
<td>6.0</td>
<td>4.0</td>
<td>3.5</td>
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<tr>
<td>From tip to tip of outer digits</td>
<td>16.00</td>
<td>17.0</td>
<td>24.0</td>
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</table>

* = average.

Genus BAROPEZIA Matthew

This genus was founded by Matthew on specimens from the Coal Measures of Nova Scotia and included two species, Baropezia sydnetensis (Dawson) and B. abcissa Matthew. Footprints from the Grand Canyon have a considerable resemblance to those of B. sydnetensis in size, triangular form of the imprints of the pes, and smaller manus with short, heavy toes radially arranged, and I therefore tentatively refer the following new species to this genus.

BAROPEZIA EAKINI, new species

Plates 8 and 9

Type.—Catalogue number 11,137, U. S. N. M. Consists of a short consecutive series of deeply impressed tracks of which the obverse side is also preserved.

Paratype.—Catalogue number 11,138, U. S. N. M. Consists of a large slab of consecutive tracks that are less deeply impressed than the type.

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

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

Description.—Stride about 123 mm.; width of trackway about 144 mm. Hindfoot: Length 44 mm.; width 51 mm. Sole subtriangular, deeply impressed in type. There were five distinct subequal toes; digits short, with broadly rounded terminations without trace of claws, though there may have been a bluntly rounded nail. Fifth digit slightly divergent. Forefoot: Length about 28 mm.; width about 47 mm. Sole suboval, inside and front most deeply impressed. Five distinct radially arranged toes, and, as in the pes, short with bluntly rounded extremities, first much reduced, others apparently subequal in size; fourth and fifth divergent.

This species has the print of five toes on the hindfoot and apparently five on the fore. The tracks made by the hindfoot of the right side differ so from those of the left (compare fig. 11 and pl. 8) as to clearly indicate that the right has suffered injury causing two toes, the fourth and fifth, to protrude prominently outward from the side of the foot. This same peculiarity, though less distinctly indicated, is noted in the paratype (pl. 9) which leads to the conclusion that both series of tracks were made by the same individual. The paratype, a beautifully preserved trackway, is a striking example of the unreliability of the information to be obtained from fossil foot-
prints, even when the tracks seem to be fairly well impressed. Of more than 30 distinct tracks, none registers more than three toes, and were it not for the deformity of the toes of the right hindfoot, showing that the tracks of both type and paratype were made by the same animal, there might be some doubt as to their reference to the same species.

The digital formulae of *B. sydnensis* and *B. iberissa* (figs. 12 and 13) as determined by Matthew, are 4-3 and 4-4 respectively. That both may have additional toes which did not register seems quite probable, especially in the light of the two series of tracks discussed above. That Matthew was cognizant of such a possibility is indicated by his comment on the pes of *B. sydnensis* that “the first digit may be potentially present.” Considered from the evidence furnished by this new material, it would seem quite certain that *B. sydnensis* has a formula of 5 and 4 digits instead of 4 and 3. There is also reason for thinking that Matthew may have been mistaken in his identification of the relative positions of the two tracks. In the narrowness, fore and aft, of the sole impression, the divergence of digit one, and in the relative size and arrangement of the other
digits, the imprint called hindfoot by Matthew certainly bears a closer resemblance to the track of the manus in *B. eakini* than to that of the pes. Furthermore, the subtriangular sole of the so-called forefoot has its nearest counterpart in the pes of *B. eakini*. For these reasons it would appear that *B. sydnensis* also agrees with *B. eakini* in planting the forefoot in front of the hind instead of behind it as originally determined by Matthew.

The average distance between fore and hind tracks of the same side of *B. eakini* is about 16 millimeters. The feet turn in strongly toward the median line of the trackway. The front of the feet is always deepest impressed, probably because the animal was climbing a slope, an inference substantiated by the flow structure behind the tracks made by the material displaced by the feet. The toes of
both fore- and hindfeet are short and rounded without trace of claws, though they may have been terminated by blunt, rounded nails. In all, there are on the two slabs 45 tracks about equally divided among the four feet of the animal.

The creature making these tracks was apparently a short, squat quadruped with a wide body, and evidently slow of movement as indicated by the short stride. There is no evidence of a tail drag on either of the slabs. The forefoot impression is always placed in front and slightly outside the hind.

In reviewing the known Permian animals in search of the possible makers of these tracks, two forms were found, *Cacops aspidephorus* and *Trematops milleri,* either of which appears to have the proper proportions to leave a trackway similar to the one under discussion, both being relatively short, wide bodied creatures with short, stubby tails and large five-toed feet without claws (see figs. 12, 13).

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Either of these animals would seem to fulfil all requirements in so far as the character of an animal can be visualized from a study of its tracks. The absence of a tail drag would also be accounted for by the presence of this short, stubby tail. According to Williston, Cacops has a length over all of about 20 inches, whereas Trematos is 36 inches long. If the above suggested correlation has any merit whatsoever, these tracks are at once placed as belonging to the stegocephalian branch of the Amphibia.

The specific name of Baropesia eakini is in honor of Mr. J. R. Eakin, superintendent of the Grand Canyon National Park, whose generous assistance contributed so much to the success in making this collection of fossil tracks.

**Genus AGOSTOPUS, new genus**

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

**AGOSTOPUS MATHERI, new species**

*Plate 10*

*Type.*—Catalogue number 11,135, U. S. N. M. Consists of a trackway some 700 millimeters in length, showing consecutive imprints of all the four feet.

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

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

*Description.*—Length of stride, 134 mm.; width of trackway, 199 mm. *Hindfoot*: Length about 67 mm., width 65 mm. Sole broad, palmate, quadrately rounded, longer than digits. Four digits, median two curved outward, outer three acuminate, probably terminated by sharp claws. First digit short, heavy, obtusely rounded, without claw. Length of digits, I = 4 mm., II = 18 mm., III = 22 mm., IV = 18 mm. *Forefoot*: Length (estimated) 35 mm., width about 63 mm. Sole suboval, smaller than hindfoot; apparently five short digits, fifth reduced and projecting outward at a right angle to the long axis of the foot.

In addition to the slab of footprints selected as the type, the collection contains two slabs (Nos. 11,133 and 11,150) pertaining to this species. The imprints, especially of the hindfoot, are clearly pre-
served, but the toes of the forefeet are usually cut off by the flow of sand crowded out by the heel of the hindfoot, thus destroying the evidence for a positive determination of the length of the toes of the manus.

In the presence of four toes on the hindfoot and five on the fore, these tracks closely resemble *Megapezia pineoi*¹ from the Lower Carboniferous of Nova Scotia, but here their similarity practically ends, since they differ so much in size, length and arrangement of

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The digits, and in the proportions and shape of the sole as to fully indicate their generic distinctness. It therefore becomes necessary to erect a new genus for their reception and the name *Agostopus* Matiliani is proposed. The specific name is for Hon. Stephen F. Matiliani, director of the National Park Service, whose personal interest was so largely responsible for the opportunity of making this important collection of fossil footprints.

The stride is comparatively short for so large an animal and the steps, as well as the width between the right and left rows, are remarkably uniform. The forefoot is placed behind and a little outside the line of tracks made by the hindfoot. The heel seems to be broadly rounded, as indicated by the broken line shown in figure 16. The heavier outer line of the pes tracks represents the outline of the disturbed sand which was pressed out by the impact of the foot. All of the tracks show distinct imprints of the soles, as may be seen in Plate 10.

Omnisuchus as the hindfoot is set partly on the toe marks of the precedent impression of the forefoot, it resembles *Barillopus* Matiliani, but its much larger size, sole longer than digits, different digital formula, and lack of tail mark at once distinguish it from that genus.

On the forefoot there are apparently five toes, all of which appear short. In arriving at the number of digits it was assumed that the divergent projection on the outside of the imprint represents a fifth toe. Such a protuberance is present in several of the tracks though there is a variation in shape and size, as indicated in figure 16. Both fore- and hindfeet turn inward toward the center of the line of march. The creature making these tracks was evidently a short-bodied, wide-bodied animal, apparently of sluggish habits.

**Genus Palaeopus, new genus**

*Generic characters.*—Quadrupedal, hindfoot somewhat the larger, always most deeply impressed. Five digits in pes, three or more in manus. Manus in direct line of pes tracks. Sole longer than toes. Short toes without a trace of claws. Feet directed straight forward. Long limbed with regular stride.

**Palaeopus Regularis, new species**

*Plate 5, fig. 1*

*Locality.*—Catalogue number 11,143, U. S. N. M. Slab containing a straight series of tracks of a single individual 1,200 millimeters in length.
Paratype.—Catalogue number 11,144, U. S. N. M. Reverse slab on which is a consecutive series of footprints in millimeters in length. The paratype shows agreement except of stride, which is shorter than in the type. Hindfoot, 25 mm. in both type and paratype, 26 mm. in paratype. Stumpy and directed straight forward. Overlapping track of manus.

Forefoot: Length of type, 10 mm., paratype, 9 mm.; width, 20 mm. in both type and paratype. Digits IV and V opposed by web. Smaller and more shallow than pes, and with (?) toes, short and directed forward. Placed directly in parallel with hindfoot.

The trail made by the latter is distinctive on account of the straight trackway and regularity of the imprints, especially those made by the pes. The paratype was from the Hermit Basin, Grand Canyon National Park.

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

Geological occurrence.—Conino sandstone (about 1,000 feet above base). Paratype is a slab 9 feet west of the type locality.

Description.—Comparison of type and paratype shows a high degree of agreement except in the length of stride, which is shorter in the paratype than in the type. Hindfoot, 25 mm. in both type and paratype, 26 mm. in paratype. Stumpy and directed straight forward. Overlapping track of manus.

Forefoot: Length of type, 10 mm.; width, 20 mm. in both type and paratype. Digits IV and V opposed by web. Smaller and more shallow than pes, and with (?) toes, short and directed forward. Placed directly in parallel with hindfoot.

The trail made by the latter is distinctive on account of the straight trackway and regularity of the imprints, especially those made by the pes. The paratype was from the Hermit Basin, Grand Canyon National Park.

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

Geological occurrence.—Conino sandstone (about 1,000 feet above base). Paratype is a slab 9 feet west of the type locality.
...slab 9 feet in length, the trackway extending the full length without the slightest deviation to the right or left.

The forefoot impressions are usually dimly impressed or absent. In many places on the type slab this is due to the hindfoot having been placed directly on top of the fore, thus obliterating the imprints. Often, however, only the posterior half is thus wiped out. In the paratype the hindfoot is shown falling in advance of the fore, evidently caused by a slower gait and slightly shorter stride. Judging from the relative depth of the impressions of the fore- and hind feet, the greater part of the weight of the animal was borne by the latter. The ratio of foot length to length of stride is about 1 to 8.

The feet were broad and stumpy with digits largely buried in the mess of the foot. A few of the impressions made by the pes show long, short, rounded toes (fig. 17). None of the forefoot impressions of the type gives any idea of the number of digits, but in the paratype a few are suggestive of the presence of at least three.

On the type slab (see pl. 5, fig. 1, reproduced from a photograph) a few shallow, half obliterated footprints of the manus may be seen immediately in advance of those of the pes; in the paratype the imprints of the manus fall behind those of the pes.

The creature making these tracks was evidently narrow-bodied, with long legs, and walked with an upright, mammalian-like stride. Such an arrangement of quadrupedal tracks could be accounted for only in this way. The straightness of the trackway and regularity of the stride at once distinguishes the trail of *Palaeopus regularis* from others found at the locality.

**Genus BARYPODUS, new genus**

*Generic characters.*—Quadrupedal, with three digits in both manus and pes. Digits long, nearly parallel, well separated; appear to be joined by web. Sole subquadrate, longer than digits. Forefoot placed well forward of hind, both turned strongly inward.

**BARYPODUS PALMATUS, new species**

*Type.*—Catalogue number 11,134, U. S. N. M. Consists of a slab on which are single impressions of a fore- and hindfoot.

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

*Geological occurrence.*—Coconino sandstone (150 feet above base), Unnamed.
Description.—Length of stride unknown. **Hindfoot:** Length, 127 mm., width, 87 mm.; sole palmate, longer than toes and longer than wide. Three toes, long, directed forward, and apparently without claws. Length of first digit, 37 mm.; second, 54 mm.; third, 38 mm. First digit slightly divergent, third protrudes slightly beyond border of the web. **Forefoot:** Length, 108 mm., width, 88 mm. Outline of foot semi-rectangular with a distinct blunt, hook-like tubercle on inner posterior angle of heel. There seem to be three toes, the inner one being short, the outer two long, slender, and directed straight forward, all within the mass of the foot. The middle toe, as in the pes, is most deeply impressed. Extremities of the toes show no trace of claws. Length of inner digit, 15 mm.; second, 52.5 mm.; third, 47 mm. At the base of the toes distinct cross lines indicate the presence of creases. Forefoot 135 mm. in advance of the hindfoot impression.

Although the specimen selected as the type of this genus and species furnishes rather meager information concerning the track...
GRAND CANYON FOSSIL FOOTPRINTS—GILMORE

They are so distinct from the other footprints forming the collection from this locality that they seem worthy of description.

This form is remarkable for the large, heavy, semiquadrate soles and the apparent presence of web-like flanges that seem to extend between and beyond the tips of the toes. The presence of such a flange is indicated in both manus and pes, but more especially the latter, by the depression of the sand between the toes and the numerous cross ridings marking the surfaces. Its distinct outline is shown in Plate I, fig. 11.

The large size of the animal making these tracks is indicated by the size of the footprints and depth of the impressions. Further material will be needed to elucidate the outlines of the feet, and it would not be at all surprising to find that there were additional toes. The web-like character of the feet is also found in the Triassic Allopus? but this fact does not necessarily imply any relationship since the great size and different digital formula of the Mesozoic tracks at once distinguishes them. Although subequal in size with tracks here designated Allopus? arizonae, those of Barypodus palmae are at once distinguished by the long, slender, webbed toes, and the lengthened quadrate form of the sole impressions.

A correlation of these tracks with any of the known Permian animals cannot be attempted without additional material, whereby details of foot structure, length of stride, and width of body could be determined. The largest animals now known from the Permian are Dimetrodon and Edaphosaurus, either one of which may have been sufficiently large and heavy to make these tracks, for both have five well-developed digits, and it is hardly probable that either had webbed feet.

ALLOPUS? ARIZONAE, new species

Plate II, fig. 2

Type.—Catalogue number 11.123, U. S. N. M. Consists of a negative series of footprints 8½ feet in length.

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

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

Description.—Stride about 530 mm. width of trackway about 30 mm. Hindfoot: Length about 60 mm., width about 85 mm. Apparently five toes which are very short with bluntly rounded ex-....

1 Hitchcock, Edward, Ichnology of New England, 1858, p. 123, pl. 33, fig. 4.
and toes with blunt, rounded extremities without claws, these show a marked resemblance to *Allopus littoralis* Marsh from the Cretaceous Measures of Kansas. I shall, therefore, tentatively refer these tracks to the genus *Allopus*, although there are differences which suggest that they probably pertain to a distinct genus.

The tracks are deeply impressed, but the sand was apparently so soft that the detailed foot plan was not recorded. Furthermore, the trail is crossed diagonally by the trackway of a second large animal, apparently of the same species, which in several instances stepped upon the footprints of the first, thus contributing still further to the difficulty of their proper interpretation. The last three pairs on the left side are the most distinct and the description is based almost entirely upon these six impressions of the fore- and hindfeet.

The consecutive series of tracks is unique from the fact that it was the only trackway found at this locality leading down the declined slope; all others were ascending. For that reason there

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GRAND CANYON FOSSIL FOOTPRINTS—GILMORE

Some doubt as to the length of stride and the relative position of the imprints as representing the normal gait. For example, the imprints regarded as having been made by the manus falls behind and slightly inside the line of the larger impression made by the pes. In Allopus littoralis, as interpreted by Marsh, the positions are reversed.

The less number of digits on the manus and greater on the pes serves at once to distinguish this species from Allopus littoralis with its two and four respectively. However, until the detailed structure of the feet of this new form is more completely and positively known, it appears best to refer it to this established genus.

Marsh regarded the tracks of Allopus as having been made by a large labyrinthodont animal but the reduced number of digits in the manus does not suggest their assignment to any of those forms known from their skeletons.

As noted above, at the time this series of tracks was made the sand must have been thoroughly saturated with water as evidenced by the fact that it flowed back into the tracks from both sides, leaving a narrow longitudinal depression at the center where the flows failed to merge. Furthermore, on the down-hill side of the imprints, especially those made by the pes, the displaced sand has flowed downward for a distance of 200 to 225 millimeters. Three successive flows, one above the other, are registered, as indistinctly shown in figure 2, plate 11.

These features raise the question as to how an aeolian deposit on a slope of 30 degrees could become so fully saturated with water. It could hardly be accounted for by submergence for under that condition the smaller tracks would hardly be registered so distinctly as many of them are. It permits of the suggestion that a further study of their origin, in the light of this new evidence, may bring about a modified conception of the aeolian theory accounting for the original deposition of these sandstones.

Genus PALEOHELCURA, new genus

Generic characters.—Foot apparently tridactylous; long axis of each cluster of three placed strongly diagonal to direction of movement. Tail trace.

PALEOHELCURA TRIDACTYLA, new species

Plate 12, fig. 1

Type.—Catalogue number 11,145, U. S. N. M. Consists of a slab about 560 mm. long, having a trail traversing the entire length.
Type locality.—Hermit Trail, Hermit Basin, Grand Canyon National Park, Arizona.

Geological occurrence.—Coconino sandstone (a loose slab from hillside at a point about 125 feet above the base), Permian.

The trail here described consists of two parallel lines of tracts between which the drag of a caudal appendage is clearly registered. The lateral lines are formed by clusters of three imprints, evidently made by tridactyl, pointed extremities, the longer axis of which stands at about 45 degrees to the line of direction. The clusters alternate on the two sides. This alternating movement of the limbs of opposite sides is indicated in the undulating movement of the trail, which is quite clearly shown in plate 12, figure 1. The direction of movement is indicated by the drag of the toes as being in the direction shown by the arrow (fig. 20). The inner toe seems to be the smallest; the outer two are subequal in size. The greatest width of the trackway is 22 millimeters, length of stride about 11 millimeters, distance between single imprints of each cluster about 3 millimeters, and width of each cluster of three about 8.5 millimeters.

![Diagram of trackway](image-url)
In looking at this specimen, one is struck by the general distinctness of the outlines and the perfection of preservation, but an attempt to refer it to a particular class of animals results in great perplexity. The wonder is that an animal, apparently so small and light, should have left any impression that could be converted into rock. It is quite unlike any of the described trails attributed to crustaceans, myriapods, or insects, and yet it gives every indication of having been made by some invertebrate animal. The specimen has been examined by the several specialists in the United States National Museum dealing with these groups, and all disclaim its relationship to any with which they are familiar.

Regardless of my inability to definitely classify these tracks, their distinctive character makes it desirable to name them, and the new genus and species *Paleohelcura tridactyla* is proposed for their reception. It is my impression that they represent the trail of some invertebrate; they certainly do not display features indicative of the foot of any known vertebrate animal.

On a recent visit to the United States National Museum, the distinguished paleontologist, Prof. Othenio Abel, called my attention to a series of tracks preserved in the museum at Weimar which bear a certain resemblance to the tracks under consideration. These are shown in figure 21, reproduced from a sketch by Professor Abel who generously permitted its use. This series of tracks is from the Buntsandstein (Triassic) between Schönalkarden and Trowback near Nesselberg, and are therefore somewhat younger than the Grand Canyon specimen. They show the same grouping in threes set at an oblique angle to the median line of movement, and with a similar relative width of trackway. They differ, however, in their larger size, lack of tail trace, and in having the clusters of the two sides opposite, whereas the clusters alternate in the Arizona form. While these distinctions are important, the Austrian specimen is of interest in being
the only one known which bears any great resemblance to those here described.

A second slab (No. 11,141, U. S. N. M.) which was originally a part of that bearing the type, has on its surface a continuation of the *Paleohelcura* trail evidently made by the same individual. It differs from the type in having only a single toe mark on each side of the tail drag for one-half of its linear extent, the remaining half showing two imprints. In only three or four instances are all three toes registered. This serves to emphasize the necessity of securing abundant material for the study of fossil tracks if the chances of error are to be reduced to the minimum.

**Genus MESICHNIUM, new genus**

*Generic characters.*—Digital formula unknown. Row of regularly spaced oval depressions between the parallel lines of tracks.

**MESICHNIUM BENJAMINI, new species**

Plate 12, fig. 2

*Type.*—Catalogue number 11,155, U. S. N. M. Consists of a small slab on which is a trail about 300 millimeters in length.
Type locality.—Hermit Trail, Hermit Basin, Grand Canyon National Park, Arizona.

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

In plate 12, figure 2, is shown a photographic reproduction of two parallel lines of footprints which clearly represent the trail of some animal, but which, in most of its details, is quite obscure. The one distinctive feature is the presence of a median row of suboval depressions regularly spaced and for half the length of the trail deeply impressed; on the other half they are either shown faintly or missing entirely. The width of the trackway is 22.4 millimeters; distance between depressions of median row averages about 15 millimeters, which also represents the length of stride. Whether these median pits were formed by a caudal appendage or by a descending ventral protuberance on the body is of course impossible to determine. It would seem most logical to regard them as having been made by a short, stubby tail.

The direction of movement is shown on the forward border of the track by the drag made by the appendage causing the oval depressions, as contrasted with the more perpendicular posterior side of the imprint.

The trail is quite different from any other in the collection, and I find nothing like it described. That it was made by some invertebrate there is little doubt, but no clue has been found as to the particular animal.

The specific name is in honor of Dr. Marcus Benjamin, who for many years has so ably edited the scientific publications of the United States National Museum.

SUMMARY

That both vertebrate and invertebrate animals are present in this collection of footprints is certain, but with the exception of the classes Reptilia and Amphibia among the former, quite certainly represented by the tracks designated *Dolichopodus tetractylus* and *Haplopus eukini* respectively, it was found impossible to assign the other forms to their proper class with any degree of assurance.

No skeletal remains are known from the Coconino sandstone and consequently no direct clue is offered as to the makers of any of these tracks. A study was made of the Permian vertebrate fauna found in the adjacent regions in the hope that forms might be found whose structure would indicate responsibility for some of the imprints. This search was not entirely in vain, for in the Permian *Araeoscelis*...
with its light body, long, slender limbs, and lizard-like foot structure, we have a reptile which fulfils all essentials for the type of animal that made the tracks designated *Dolichopodus tetradactylus*; and in *Trachypus* and *Cacops*, with wide, short bodies and short, heavy limbs, are amphibians of the right proportions to have made trails similar to those called *Baropezia eakini* and *Agostopus matheri*. I do not wish to imply that the tracks were made by these animals, but the type of creature to which they may be attributed is quite certainly represented. The evidence for such correlation must not be taken too seriously, since at present there seems no way of definitely linking up the two lines of evidence.

No strictly bipedal animals have yet been found in this fauna, all being quadrupedal, and these vary greatly in size from one or two inches in length to the largest which may have attained a length of several feet.

Attention should be called to the fact that probably none of these trails shows the normal walking gait, due to the fact that all were impressed by animals climbing a steep slope in soft sand, and this effort has probably, in all instances, shortened the stride. That all of the trails observed, with one exception, lead in a common direction—that is, up the face of the slope—is difficult of explanation. This applies not only to the level where most of the collection was made but also to all other levels in the Coconino where tracks were seen, both perpendicularly and horizontally. It is also of interest to note that the three series of footprints of *Laoporus coloradoensis* from the Lyons sandstone of Colorado show the same characteristic.

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

**VERTEBRATES**

*Dolichopodus tetradactylus*, n. gen., n. sp.
*Nanopus merriami*, n. sp
*Laoporus schucherti* Lull
*Laoporus nobeli* Lull
*Laoporus coloradoensis* (Henderson)
*Baropezia eakini*, n. sp.
*Agostopus matheri*, n. gen., n. sp.
*Paleopus regularis*, n. gen., n. sp.
*Barypodus palmatus*, n. gen., n. sp.
*Allopust arizonae*, n. sp.

**INVERTEBRATES**

*Paleoheleura tridactyla*, n. gen., n. sp.
*Medichnium benjaminii*, n. gen., n. sp.
The above fauna, taken as a whole, shows that its affinities lie nearest to those described from the Carboniferous Coal Measures rather than to the later Mesozoic Ichnites. This is indicated by the presence in the Coconino of two and possibly three genera common to the Carboniferous, whereas not a single genus of the Triassic was recognized. Furthermore, the facies of the fauna is Carboniferous in aspect as shown by the relatively small size of the animals, all of which are quadruped, as contrasted with the considerable number of very large forms and the many three-toed bipedal animals of the Triassic. The Coconino footprint fauna also seems to have closer relationships to the Ichnite fauna from the Middle Coal Measures of Kansas, described by Marsh, 1 than to the more extensive faunas from the Coal Measures of Nova Scotia described by Dawson 2 and Matthew. 3

The present fauna is founded upon specimens having well-marked characters, and being from a single locality and well-established horizon, have a value of their own in throwing light upon the land vertebrate life during the deposition of the Coconino sandstone. If they have but little value in themselves, they may eventually shed much light on the habits and characteristics of the Permian animal life.

PSEUDO-TRACK-LIKE MARKINGS

Plate 2, fig. 2

Under this heading attention is called to some peculiar track-like markings found on a massive sandstone of the Supai formation in that part of the Grand Canyon known as "Fossil Bay." While these are not regarded as having been made by animals, they are of interest on account of their superficial resemblance to tracks made by horses' hoofs, and since their origin is as yet unexplained, these notes are published in the hope that it may lead to a fuller investigation.

These markings were called to my attention by Mr. Samuel Hubbard, leader of the Doheny Scientific Expedition of 1924, who had long known of their existence through information obtained from the Supai Indians who regarded them as tracks made by a band of horses. They thickly cover an area of several hundred square feet in extent and have the appearance of semi-oval rings, frequently with the two posterior extremities prolonged backward, but seldom con-

verging sufficiently to meet behind. All the rounded or oval ends, as may be seen in the illustration (pl. 2, fig. 2) are pointing in a common direction. They vary in size but their general contours are fairly alike.

None of these markings occurred in regular sequence and none were found giving evidence of having been impressed into the surface of the sand. After a careful examination it was my conclusion that they do not present a series of fossil tracks, but were nothing more than a staining of the sandstone, the deeper coloration making them stand out clearly against the lighter colored background of sandstone. A few through weathering showed surface depression but a section obtained in one place clearly indicated that this deep coloration extended downward into the sandstone for at least four inches.

In a search of the literature in an attempt to get light on the origin of these curious markings, it was of interest to find that Hitchcock had described supposed tracks (see fig. 23) from the Triassic of Connecticut which bear a striking resemblance to those under consideration. Their resemblance to a horse's hoof was apparently recognized.

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1 Hitchcock, Edward, Ichnology of New England, 1859, p. 134, pl. 21, figs. 377.
by Hitchcock who applied to one the name *Hoplicnus equus*. Although unable to reach any conclusion as to the class of animals to which they might be attributed, Hitchcock was of the opinion that they were true tracks and not discolorations. He attempts to show that they occurred in regular sequence and were depressed below the general surface level. Hay remarks: "It is doubtful whether or not this genus of foot marks was produced by a vertebrate animal."

Sir William Jardine described some hoof-like tracks from the New Red Sandstone of Scotland under the name *Chelichnus gigas*. While these have the same hoof-like shape without the appearance of toes or claws, they do show a distinct pace and uniform alternate progression.

May it not be that the Supai markings are stains resulting from the decay of some gelatinous medusa-like animals that were stranded on a sandy beach?

2 Ichnotology of Annandale, 1853, p. 9, pl. 1.
EXPLANATION OF PLATES

PLATE 1.

Fig. 1. Slab of footprints in situ on the Hermit Trail, Grand Canyon National Park. This slab is 8 by 25 feet and located 950 feet below the rim or 150 feet above the base of the Coconino sandstone. The mule trail may be seen in the lower left-hand corner.

2. The same, but taken from a point farther down the trail. The surface of the slab in the foreground is also covered with numerous tracks. The slab shown in plate 9 was collected from the exposed layer. Continuation of the trackway may be seen in the center foreground.

PLATE 2.

Fig. 1. Pack mules loaded with slabs of footprints starting up the trail for the top of the canyon. All the specimens were transported to the top of the canyon in this manner.

2. Unidentified track-like markings found on the sandstones of the Supai formation in “Fossil Bay,” Grand Canyon National Park. These occur on a massive band of sandstone 1,673 feet below the level of the canyon rim.

PLATE 3.

General view of the foot track locality on Hermit Trail looking east. Photograph taken before clearing off the débris from the hillside. Photograph by Robert Carson of the Doheny Scientific Expedition.

PLATE 4.

Fig. 1. Dolichopodus tetradactylus, new genus and species. Type, No. 11,123, U. S. N. M. Imprints of digits of the manus are dimly shown behind and slightly outside those of the pes. Less than ¼ natural size.

2. Nanopus merriami, new species. Type, No. 11,146. U. S. N. M. About ¼ natural size.

PLATE 5.

Fig. 1. Palaeopus regularis, new genus and species. Type, No. 11,143. U. S. N. M. Imprints of forefeet occasionally seen directly in front of those made by the hindfeet. About ¼ natural size.

NO. 9 GRAND CANYON FOSSIL FOOTPRINTS—GILMORE

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Above, Transporting slabs of fossil footprints.
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(For explanation, see page 40)
General view of fossil footprint locality, Grand Canyon National Park.
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(For explanation, see page 40)
Fossil footprints from the Grand Canyon.
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Fossil footprints from the Grand Canyon.
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FOSSIL FOOTPRINTS FROM THE GRAND CANYON: SECOND CONTRIBUTION

(WITH 21 PLATES)

BY
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Curator of Vertebrate Paleontology,
United States National Museum

(CITY OF WASHINGTON
PUBLISHED BY THE SMITHSONIAN INSTITUTION
JULY 30, 1927)
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(WITH 21 PLATES)

INTRODUCTION

In continuation of an investigation of the fossil footprints of the Grand Canyon, so successfully begun in 1924, 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. Nadin, 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 their encouragement and for the facilities provided.

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 range 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 feet barren, and this same condition was found to prevail in the newly

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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**

_Agostopus matheri_ Gilmore  
_Agostopus medius_ n. sp.  
_Agostopus robustus_ n. sp.  
_Alopus ? arizonae_ Gilmore  
_Amblyopus pachyodus_ n. gen. and sp.  
_Barypodus palmatus_ Gilmore  
_Barypodus tridactylus_ n. sp.  
_Barypodus metszeri_ n. sp.  
_Baropus coconinoensis_ n. sp.  
_Baropezia eakini_ Gilmore  
_Dolichopodus tetractylus_ 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 noblei 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 thinbedded 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 sun-cracked 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 Megapedia † delicosanis and Exocompe † delicatula. Some of the tracks are distinct impressions of the feet, and others are mere strokes of the toes. In these beds also occur plant remains in very fragmentary condition which were badly macerated and coated with a slime of red mud during their accumulation.

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

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² Lull, R. S., Ibid., pp. 337-346.
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 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 a little way toward the head of Hermit Gorge opposite "Dripping Springs," but, as previously mentioned, only two thin layers were found in place. Noble, 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 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:

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 described sand treated with but the di strata are ripple-marked strongly topped sandstone a;

The beds exposed to the work was massive.

In remote covered with debris void of tracked for and finally of softness few of the the details of the form beneath a the Hermit but such p formation in some ab

The recorded for those from which these seem to have not only in track-bearing

The faun the followin
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 Parrboro, 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.
Crustipes sp.
Dromillopus parvus n. sp.
Hyloidichnus bifurcatus n. gen., n. sp.
Hylops 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,\(^1\) has a total thickness of 950 feet. The first evidence of footprints occurring in this formation was noted by Schuchert in 1915.\(^2\) 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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\(^1\) *Op. cit.*, pl. 19.
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 cycadslices 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 ? Permain 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.

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 supaiensis* 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>
</tr>
</thead>
<tbody>
<tr>
<td>Agostopus matheri</td>
<td>Permian</td>
<td>Grand Canyon, Ariz.</td>
</tr>
<tr>
<td>Allopus ? littoralis</td>
<td>Pennsylvanian</td>
<td>Osage Co., Kans.</td>
</tr>
<tr>
<td>Anthracopus ellangowensis</td>
<td>Pennsylvanian</td>
<td>Mahanoy Coal Field, Pa.</td>
</tr>
<tr>
<td>Asperipes avipes</td>
<td>Coal Measures</td>
<td>Joggins, Nova Scotia</td>
</tr>
<tr>
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<td>Osage Co., Kans.</td>
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<tr>
<td>Barypodus palmatus</td>
<td>Permian</td>
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NO. 3  GRAND CANYON FOSSIL FOOTPRINTS—GILMORE

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The offer of time has been sting that
and the structures have scent...
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 tetradoactylus Gilmore.

DOLICHOPODUS TETRADACTYLIUS Gilmore

Dolichopodus tetradoactylus 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 tetradoactylus 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.

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

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 Matthew quite certainly belongs in the genus Dromilopbus with which its small size, digital formula of 4 and 4, and general 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 Dromillopus 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 Dromillopus 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, 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 Dromillopus to be known as D? obtusis (Matthew) 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. 9-13, 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 trackway showing impressions of all four feet.

Type locality.—Hermit Trail, Hermit Basin, Grand Canyon National 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 acuminate 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, acuminate, 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.

![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 1/2 natural size.](image)

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 hind foot (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. 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. 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. 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.

![Diagram of trackway](image)

**Figure 7.—Barypodus tridactylus.** Type. No. 11,502, U. S. N. M.
Diagram of trackway. Toes indicate position of the hindfeet.
About ¼ 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 11,595, 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 Barpyodus 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 Baryopus 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.

![Diagram of left side of trackway. About 1/2 natural size.](image)

*Fig. 9.—Baropus coconinoensis. Type. No. 11,514, U.S. N. M. Diagram of left side of trackway. About 1/2 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 130 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
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 AGOSTOPUS** 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 hindfeet, 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 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

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**Fig. 11.—*Agostopus medius*. Type. No. 11,509, U. S. N. M. Diagram of trackway. About \( \frac{1}{4} \) natural size.**
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 II,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 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**

*Genetic 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.

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**Fig. 13.—Octopodichnus didactylus.** Type. No. 11,501, U. S. N. M. Diagram of trackway. About \( \frac{1}{2} \) natural size.
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.

Fig. 14.—Triavestigia niningeri. Type. No. 11,510, U. S. N. M.
Diagram of trackway. About ¼ natural size.

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 Bifurculapes, 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.

**PALEOHLECURA 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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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 11

*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 11 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.

_Genericotype._—_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 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 conspecific, 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 *Exocampe* 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 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: *Bairachichnus delicatula* (Lull). Type. No. 2,146, Yale Museum; right manus (a) and pes (b) natural size. (After Lull.)](image)

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**

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<td>Width of manus</td>
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</tr>
<tr>
<td>Length of pes</td>
<td>mm.</td>
<td>7.0</td>
<td>10.5</td>
</tr>
<tr>
<td>Width of pes</td>
<td>mm.</td>
<td>7.0</td>
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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 hindfeet. 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* Woodward, 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 Joggin species is rendered difficult because of inadequate illustration and description.

**BATRACHICHNUS OBSCURUS**, new species

*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

Fig. 17.—Batrachichnus obscurus. Type. No. 11,529, U. S. N. M. Diagram of part of trackway. About ¼ 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-

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 as *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 *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.

![Diagram of trackway](image)

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

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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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<tr>
<td>Length of manus track</td>
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</tr>
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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. triâdus. 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. trifidus* 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.—Hermit 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.

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**

<table>
<thead>
<tr>
<th></th>
<th>No. 11,544</th>
<th>No. 11,547</th>
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<tr>
<td></td>
<td>U. S. N. M.</td>
<td>U. S. N. M.</td>
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<tr>
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<tr>
<td>Length of digit V</td>
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<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 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...
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 *Hylorpeton* or *Hylonomus*. In any event, all of the tracks here discussed seem to conform more nearly to those made by amphibia 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 4 from the Permian (Tauback) of Thüringen. 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.

4Pabst, W., Deutsche geol. Gesell., Vol. 48, 1896, pp. 638 and 808, text fig. 2.
HYLOIDICHNUS BIFURCATUS. new species

Plate 16

Type.—Catalogue number 11,598, 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.

Fig. 25.—Hyloidichnus bifurcatus. Type. No. 11,598, U. S. N. M. Diagram of trackway. About 1/2 natural size.

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
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 *Megapesia ? coloradensis*¹ indicates the necessity of establishing a new genus for its reception. Its original assignment to the Nova Scotian genus *Megapesia* 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-

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. 2.


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. 14,593, 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

![Diagram of track](image)

**Fig. 26.—Megaplesia? 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.

FIG. 27.—Parabaropus coloradensis (Lull) No. 11,598. U. S. N. M. Diagram of left hand side of trackway. About ½ natural size.
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, 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.

<table>
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<tr>
<td><strong>Breadth</strong></td>
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<td></td>
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<tr>
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<td></td>
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<tr>
<td><strong>Length of digit V</strong></td>
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<td>mm.</td>
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</tbody>
</table>

Fig. 28.—*Parabaropus coloradensis* (Lull) Type, No. 2,145, Yale Museum. Outline of manus, unrestored. About 1/4 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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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 ¹ 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.)

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.—Colletosaurus pentadactylus. Type. No. 11,527, U.S. N.M.*

Diagram of trackway. About 1/2 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 Collettosaurus 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 _Cursipes_ was established by Matthew on specimens from the Carboniferous of Joggins, Nova Scotia. The chief characters distinguishing _Cursipes_, 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 _Cursipes_, and if correctly identified marks the first recognized occurrence of this genus in the Hermit ichnological 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.

**INCERTE 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 *Chirotherium 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 STENICHNUS*, 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.*—*Stenichnus yakiensis*, new species.

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.

![Diagram of trackway](image)

FIG. 34.—Stenichnus yakiensis. Type. No. 11,533, U. S. N. M. Diagram of trackway. About \( \frac{1}{4} \) 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 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 ANOMALOPUS, 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.

**ANOMALOPUS 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-

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 mm.; II = 35 mm.; III = 35 mm.; IV = 26 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 mm.; II = 27 mm.; III = 18 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.*—*Tridentichnus 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 mm.; II = 23 mm.; III = 26 mm.; IV = 26 mm.; V = 13 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
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 mm.; III = 26 mm.; IV = 26 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 frontfoot may be seen in its proper position in front of the hindfoot, 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.

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.

2. Casts of footprint impressions (probably Tridentichnus sp.) in Supai sandstone. These were the first tracks to be found in situ on the Yaki Trail. Found and photographed by Dr. J. C. Merriam. These occur at the base of the heavy, darker colored sandstone shown at the right but further down the trail than in fig. 1.

3. Undescribed trackway on a large block of sandstone from the debris blasted out of the upper light colored sandstone (shown in fig. 1) in building the Yaki Trail.

PLATE 3

Nanopus maximus, new species. Type. No. 11,506, U. S. N. M. Showing an irregular trackway. Note the scratches made by a slipping hindfoot on the lower left hand side. X 4.3

PLATE 4

Fig. 1. Nanopus merriami Gilmore. No. 11,516, U. S. N. M. Trackway from lower part of track-bearing horizon in the Coconino sandstone. X 1.77

2. Laoporus nobeli Lull. No. 11,494, U. S. N. M. Showing the especially long second and third digits of the manus. X 3.
Plate 5
Figs. 1 and 2. Barypodus tridactylus, new species. Type No. 11,502, U.S.N.M. Showing trackway. Fig. 1, upper or positive slab; fig. 2, lower or negative slab. X 2.64

Plate 6
Barypodus metszeri, new species. Type No. 11,505, U.S.N.M. Irregular trackway. X 3

Plate 7
Baropus coconinoensis, new species. Type No. 11,514, U.S.N.M. Left side of trackway. X 3.2

Plate 8
Agostopus medius, new species. Type No. 11,509, U.S.N.M. Trackway. X 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. X 4.57

Plate 10
Fig. 1. Triavestigia niningeri, 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. X 1.3
2. Octopodichnus didactylus, new genus and species. Type No. 11,501, U.S.N.M. X 1.7

Plate 11
Unisulcus sinuosus, new species. Type No. 11,407, U.S.N.M. Three trails crossing slab. X 2

Plate 12
Batrachichnus delicatula (Lull) No. 11,519, U.S.N.M. Large slab whose surface is thickly covered with minute tracks. X 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. X 2.7

Plate 14
Dromillopus parvus, new species. Type No. 11,537, U.S.N.M. Trackway with tail drag between. Tracks on left side belong to some five-toed creature. X 1, over natural size
PLATE 15
*Hylopus hermitensis*, new species. Type. No. 11,517, U. S. N. M. Trackway showing variation in successive impressions. × 2

PLATE 16
*Hyloidichnus bifurcatus*, new genus and species. Type. No. 11,518, U. S. N. M. Trackway on the positive slab. × 2

PLATE 17
Fig. 1. *Parabaropus coloradensis* (Lull) No. 11,520, U. S. N. M. Left side of trackway. Photographed from the cast of the original specimen. × 3
2. *Cursipes* sp. Trackway from the Hermit shale. No. 11,521, U. S. N. M. × 1.9
3. Unidentified track. No. 11,530, U. S. N. M. From the Hermit shale. About natural size

PLATE 18
Unidentified track. No. 11,528, U. S. N. M. The largest track yet found in the Hermit formation. × 1.85

PLATE 19
Fig. 1. *Collettosaurus pentadactylus*, new species. Type. No. 11,527, U. S. N. M. Trackway showing how the mud flowed into the tracks as the foot was withdrawn. × 2
2. *Stenichnus yakinsis*, new genus and species. Type. No. 11,533, U. S. N. M. Trackway. × 2

PLATE 20
*Anomalopus sturdevanti*, new genus and species. Type. No. 11,517, U. S. N. M. Trackway on slab. × 2.5

PLATE 21
*Tridentichnus supaiensis*, new genus and species. Type. No. 11,534, U. S. N. M. Trackway on slab. × 2.2
Locality of fossil footprints, Grand Canyon.
(For explanation, see page 76)
1. Looking up Yaki Trail.
2 and 3. Fossil footprints from the Grand Canyon.

(For explanation, see page 76)
Fossil footprints from the Grand Canyon.
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Fossil footprints from the Grand Canyon.

(For explanation, see page 78)
FOSSIL FOOTPRINTS FROM THE GRAND CANYON: THIRD CONTRIBUTION

(WITH FIVE PLATES)

BY

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(PUBLICATION 2956)

CITY OF WASHINGTON
PUBLISHED BY THE SMITHSONIAN INSTITUTION
JANUARY 28, 1928
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INTRODUCTION

A third visit to the Grand Canyon in the late spring of 1927 enabled me to collect additional fossil footprints, some of which are undescribed species. Since there is no immediate prospect of acquiring further specimens, it seems important that these, together with a specimen presented to the Museum by Mr. G. E. Sturdevant, naturalist of Grand Canyon National Park, should be described, in order to perfect as far as possible the record of the ichnites of this region. While the above mentioned specimens from the Hermit and Supai formations form the basis of the present paper, attention is also given to a fourth ichnite fauna recently found in the Tapeats sandstone of the Bright Angel section. These materials are fragmentary and do not warrant systematic description. All are trails of invertebrate animals, probably trilobites, a conclusion reached by the late Dr. Charles D. Walcott from his study of similar trails from this same formation in other parts of the Grand Canyon.

I wish here to express to Dr. John C. Merriam and his associates of the Grand Canyon Exhibit Committee of the National Academy of Sciences my appreciation for the financial assistance which made this third trip possible. I also wish to acknowledge again the help given by various members of the Park organization. Superintendent M. R. Tritton furnished equipment and assistance of personnel; Mr. James Brooks, chief ranger, detailed ranger assistants; and Mr. G. E. Sturdevant, Park naturalist, as on previous visits, contributed freely of his time and energy to the successful outcome of the work in hand.

NEW OBSERVATIONS ON THE GEOGRAPHICAL DISTRIBUTION
OF TRACKS IN THE GRAND CANYON

The geographical range of fossil tracks in the Grand Canyon was considerably extended through the opportunity offered of exploring new localities. It would seem that on the south rim of the Grand

SMITHSONIAN MISCELLANEOUS, COLLECTIONS, VOL. 80, NO. 8
Canyon, tracks can be found in the Coconino, Hermit, and Supai formations wherever local conditions permit of search being made for them.

In the Coconino, footprints were found in débris at the base of the Coconino cliff on the west side of the Bright Angel Trail, and were also noticed by Dr. E. F. Miller of the Marlin Oil Company, on the Grand View Trail where he was engaged in measuring the geological section. Their presence here is further substantiated by a specimen (No. 2367, U. S. N. M.) collected in this same locality in 1903 by the late Dr. Charles D. Walcott. This is some 20 miles east of the nearest known fossil footprint locality, and thus considerably extends their previously recorded range.

Accompanied by Dr. David White and Mr. G. E. Sturdevant, I visited the Dripping Springs locality at the head of Hermit Gorge and, although only a short time was spent there, we observed tracks in great abundance on the sloping ledges immediately to the north and east of the spring, thus fully verifying earlier reports of their occurrence.

Considerable time was spent in searching the track-bearing horizon in the Coconino formation where it is crossed by the Yaki Trail, and although numerous tracks and trails were found, with one exception their preservation was so poor that none was thought to be of sufficient value to collect.

In the Hermit formation, Dr. David White discovered tracks of extinct animals in association with fossil plants in two distinct and widely separated localities—on the Bright Angel Trail and on the Yaki Trail. In both of these localities the preservation of the plants was far superior to that of plants found in Hermit Basin, but the animal tracks were inferior in that only a few imprints were found, never a trackway of any extent. Neither of these places, therefore, seems to be a promising locality for further work, their chief interest being in extending the known geographical distribution of the Hermit ichnites.

In the Supai formation Mr. Sturdevant, as previously mentioned, found a slab of well preserved tracks on the Bright Angel Trail, and numerous footprints were observed by us on blocks that had fallen down from the more or less perpendicular face of the track-bearing bed of sandstone on the point which projects into the Canyon immediately below Yavapai Point.

Several days prospecting in the Supai formation along the western side of O'Neill Butte on the Yaki Trail disclosed a considerable abun-
and variety of tracks. Those found were on blocks lying on
the hillside, though a few were preserved in situ. That this forma-
tion has a large undescribed ichnite fauna is plainly evident, but it is
difficult to obtain specimens for study because of the inaccessible-
ness of the perpendicular track-bearing cliffs, and because the tracks usually
occur in massive blocks of sandstone that do not readily cleave into
layers. If adequate study specimens are to be secured, specially trained
workers with proper equipment must be employed.

In the Coconino on the south rim of the Grand Canyon, tracks are
now known at Dripping Springs on the west, and on the Grand View
Trail to the east, an extent of about 20 miles. In the Hermit and
Supai, tracks have been found from Hermit Basin on the west to the
Yaki Trail on the east, a distance of about 11 miles. That further
exploration will greatly extend these ranges is now plainly evident.
Tracks have not yet been found in the rocks of the north rim of the
Canyon, but it is confidently expected that their discovery there will
be one of the early announcements.

SYSTEMATIC DESCRIPTION OF GENERA AND SPECIES

Under this heading are included notes and new observations on
described genera and species as well as descriptions of a few that are
new to the ichnite faunas of the Grand Canyon. They are discussed
in the same order as in the preceding papers on this subject, com-
paring those from the Coconino formation and following suc-
cessively with the Hermit, Supai, and Tapeats footprints.

**ICHNITES FROM THE COCONINO FORMATION**

**Genus LAOPORUS Lull**

Mention was made in my previous paper of the similarity exist-
ing between the tracks of *Laoporus* and those figured by Hickling on
the British Permian. Further study and comparison deepens the
conviction that these tracks are congeneric. Their close similarity
in size, number, relative lengths and arrangement of the digits is
clearly indicated in the illustrations (compare figs. 1 and 2). The

[Footnote references are not fully visible in the image.]

[End of text]
British tracks are referred by Hickling to *Chelichnus ambiguus* Jardine, but examination of Jardine's original figures of this species leaves much doubt as to the correctness of this assignment. If correct, it is of interest to note Hickling's observation that in Jat

![Figure 1](image1)

*FIG. 1.*—Footprints from the British Permian which can be properly referred to the genus *Laoparus*. *A*, fore and hind tracks; *B*, manus. All after Hickling. About \( \frac{1}{2} \) natural size.

![Figure 2](image2)

*FIG. 2.*—*Laoporus nobelii* Lull. A, outline of manus track. Paratype No. 8422, U. S. N. M. *B*, manus and pes track of No. 11,122, U. S. N. M. All about \( \frac{1}{2} \) natural size.

specimen, "the fifth digit is nowhere shown," and it is a condition often observed in the trackways of the American *Laoporus*.

**OCTOPODICHNUS DIDACTYLUS** Gilmore


Recently in bringing together all of the miscellaneous fossil footprint materials in the U. S. National Museum, the accumulation of many years, a small slab (No. 2367) was found on whose surface there was a trackway that is clearly referable to the genus *Octopodichnus* and provisionally to the species *O. didactylus* Gilmore. The specimen is of interest as being the third recognizable specimen found of this species and also from the fact of its coming from a new locality for tracks, thus greatly extending their known geographical range.

The specimen was collected by the late Dr. Charles D. Walcott from the Coconino sandstone on the Grand View Trail, Grand Canyon National Park, Arizona, in 1903. This discovery antedates by 12 years the finding of quadruped tracks in the Grand Canyon by Schuchert and by nearly a quarter of a century the discovery of the type specimen (No. 11,501 U. S. N. M.) on which the above genus and species was established.

The considerably smaller size of the trackway and slight differences noted in some of the individual imprints suggest the possibility of

\[1\] *Ichnites of Annandale*, 1853, pls. 6 and 11.
the specimen representing a distinct species, but more perfectly preserved material is needed to determine that point. The trackway shows two parallel lines of imprints arranged as in the type in groups of four, the groups of the two sides alternating. These groups have the usual arrangement of a row of three regularly spaced tracks with the fourth offset inward.

After a study of the type specimen, it was my conclusion that the trackway was probably made by some Permian crustacean. In confirmation of the probable correctness of that conclusion, Mr. Remington Kellogg, of the U. S. Biological Survey, calls my attention to a considerable similarity between these tracks and trails made by the living sand crab *Ocypoda albicans*, recently observed by him in the sands on Hatteras Island, North Carolina.

**ICHNITES FROM THE HERMIT FORMATION**

*Genus HYLOIDICHNUS* Gilmore


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

**HYLOIDICHNUS WHITEI, new species**

Plate 3, fig. 1

*Type.*—Catalogue number 11,692, U. S. N. M. Consists of a small slab on which are four imprints. Collected by Dr. David White, June, 1927.

*Type locality.*—Yaki Trail (“Cedar Ridge”) 500 feet west of trail, Grand Canyon National Park, Arizona.

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

*Description.*—Stride estimated to be about 106 mm., width of trackway about 45 mm. Forefoot slightly smaller than hind and placed almost directly in front of it. *Hindfoot*: Length about 24 mm., width about 22 mm. Five toes. The toes are long and especially slender, fourth longest, others growing progressively shorter toward the inside of the foot. First only faintly impressed, but apparently about the same length as the fifth. Digits II to V having terminations slightly enlarged, the first apparently having bifurcated ends. The toes have the following lengths: $I = 7.5$ mm., $II = 11.1$ mm.,
III = 13 mm., IV = 16 mm., V = 8 mm. Sole not sufficiently impressed to show its outline; it seems to be short and broadly rounded behind. Forefoot: Length about 18.5 mm., width from tip of first to tip of fifth digit 17 mm. Five digits which increase in length from first to fourth. Fifth about one-half as long as the fourth, but longer than first. First and fifth directed strongly forward and outward respectively from the median digits. Digits I and II terminated by pellets; I and IV by asymmetrically bifurcated ends resembling those of the pes in *H. bifurcatus*. All toes especially slender. The digits have the following measurements: I = 6 mm., II = 12 mm., III = 13 mm., IV = 13.5 mm., V = 5 mm. The palm failed to leave a distinct impression and thus its size and contour are unknown.

The general resemblance of the foot plan, the same relative length of toes, and the presence of both bifurcated and pellet toe terminations as in the feet of *Hyloidichnus bifurcatus* Gilmore from this same
formation, indicates that its affinities fall within that genus. Its specific distinctness, however, is shown by its much smaller size, in having the bifurcated toes on the manus, and the more slender form of the toes as a whole.

The species is named in honor of Dr. David White who collected the type specimen.

**PARABAROPUS COLORADENSIS (Lull)**

Plate 1


On the track covered surface of a large slab (No. 11,707, U. S. N. M.) of impure Hermit sandstone of the collection of 1927, obtained from the fossil track locality one-fourth mile west of the sign "Red Top" on the Hermit Trail, is a trackway identified as *Parabaropus coloradensis* (Lull). This trail, the most perfect yet discovered, shows the trackway to have a width of about 190 mm.

On this same slab are numerous trails of *Holopus hermitanus* and a single trackway of *Collettosaurus*, probably *C. pentadactylus*. The large size of this slab, with its undulating surface covered with footprints, presents an interesting section of the old mud flat over which these animals walked and which has preserved a plain record of their ramblings. A view of this specimen is given in plate 1.

The stride of the *Parabaropus* tracks varies from 260 to 340 mm., whereas in specimen No. 11,598, described in my previous paper, the stride is about 240 mm., and it is quite apparent from the measurements of the foot impressions that the two animals were of about the same size.

In the specimen now before me, the pes impressions lack the elongated sole which is such a distinctive feature of the hindfoot in the tracks previously referred to. The difference noted is due, as is clearly apparent from a comparison of specimens, to the difference in depth to which the feet impressed themselves into the mud. In the specimen under discussion, the posterior part of the heel did not register, whereas in the trackway previously described, the whole foot sank deeply into the muddy surface. The proportions of the feet, number of toes, their form and close similarity of arrangement, leave no

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2 Op. cit., p. 56, fig. 27.
doubt as to their being conspecific. The differences noted in a compari-
son of these two specimens illustrates the need of an abundance of,
material in the study of fossil tracks if an investigator is not to be
led astray by differences that are more apparent than real.

In the normal relationships of the tracks, the forefoot is placed in
front of the hind, but in the trackway now before me the forefoot is
occasionally found in the rear of the hindfoot.

**COLLETTOSAURUS PENTADACTYLUS** Gilmore

Plate 1

_Collettosaurus pentadactylus_ Gilmore, C. W., Smithsonian Misc. Coll., Vol. 80,
No. 3, 1927, p. 60, text fig. 32, pl. 19, fig. 1.

A trackway 1300 mm. in length, on slab No. 11,707, U. S. National
Museum (see pl. 1) seems to be clearly referable to the above genus
and species. While this specimen adds nothing to our knowledge of
the feet impressions, the presence of a deep, continuous, but slightly
undulating, tail drag is of interest, since the type specimen (No. 11,527,
U. S. N. M.) showed none. A second specimen (No. 11,710, U. S.
N. M.) identified as pertaining to the same species, although 530 mm.
in length, gives no evidence of a dragging tail. Study of these three
specimens confirms my previous conviction that the presence or
absence of a tail drag has but little significance as a diagnostic charac-
ter for distinguishing fossil tracks.

**ICHNITES FROM THE SUPAI FORMATION**

Genus _AMMOBATRACHUS_, new genus

*Generic characters.*—Quadrupedal. Five digits in pes, four in
manus. Forefoot smaller than hind, with the latter placed in front
of the former. Digits of both manus and pes widely separated, outer
toes of both much reduced in size, fifth of pes widely divergent.

*Genotype.* _Ammobatrachus turbatans_, new species.

**AMMOBATRACHUS TURBATANS**, new species

Plate 2

*Type.*—Catalogue number 11,691, U. S. N. M. Consists of a slab
of sandstone 380 mm. long having a trail traversing its entire length.
Collected by G. E. Sturdevant, 1927.

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

*Geological occurrence.*—Supai formation, Pennsylvanian.
Description.—Stride about 80 mm., width of trackway about 115 mm. Hindfoot: Length about 40 mm., width about 40 mm. Five digits. The first toe is short. Third slightly the longest while second and fourth are subequal. All three acuminate. The second and third curved slightly outward. Fifth toe, short, stout, with bluntly rounded extremity. This digit is directed strongly outward, its longer axis standing nearly at right angles to those of the other toes. In the imprints of the pes on the left side the fifth toe is longer, more slender, and directed more forward than on the right side. The imprint of the second toe is lacking in most of the tracks of the left side. The sole of the foot is relatively long, exceeding the length of the toes, is rounded behind, and had palmar pads. The toes have the following

Fig. 4.—Ammobatrachus turbatans, new genus and species. Type, No. 11,691, U. S. N. M. Diagram of trackway. About ¾ natural size.
IO SMITHSONIAN MISCELLANEOUS COLLECTIONS

lengths: II = 15 mm., III = 17.5 mm., IV = 15 mm., V = 7.5 mm. Hind-foot regularly placed in front of fore, but usually clear of the toes of the manus. Forefoot: Length about 30 mm., width about 30 mm. Four toes. Toes lengthening toward the outside of foot, the outer and inner being short and subequal in length. The outer toe originates well backward on the side of the palm, and is directed forward and outward. Median toes widely separated and divergent anteriorly. All of the digits of the manus have subacute terminations (see fig. 4). The foot as a whole is much smaller than the pes. Sole relatively short, being broader than long and broadly but regularly rounded posteriorly. Length of toes as follows: II = 7.5 mm., III = 12.5 mm., IV = 14.5 mm., V = 7.5 mm. The digital formula of five and four at once distinguishes this genus from all described forms of the Supai ichnite fauna. Batrachichnus of the Hermit, Laoporus and Agostopus of the Coconino, have a similar number of toes, but here their resemblance to Ammobatrachus largely ends. The intermediate size of the footprints under discussion, the wide spreading of the toes, and differences in length and other proportions effectually distinguish these from all other Grand Canyon tracks.

Hickling figures a pes track from the Permian of Corncockle Muir, Scotland, which bears certain resemblances to the pes, but his details of foot plan are uncertain and thus a closer comparison is of little importance.

INVERTEBRATE TRAILS FROM THE SUPAI FORMATION

During the field work of 1927, a considerable number of trails evidently made by invertebrate animals, were observed in the track-bearing horizons of the Supai formation. Owing to the lack of proper facilities, only a few of these were collected. Although many of them clearly show that the impressions were made by animate creatures, their details are not sufficiently clear to depict their principal characteristics, and on that account they seem unworthy of generic and specific designation, but in order to advance our knowledge of the Supai ichnite fauna as far as is consistent with the character of available materials, a few of these specimens are briefly described and illustrated.

In figure 1, plate 4, is illustrated a trail (No. 11,740, U.S. N. M.) found lying on the slope west of O'Neill Butte. A second specimen found later on a massive block of sandstone at the base of the track.

bearing sandstone in the middle Supai appears to be identical, but the extreme hardness of the sandstone resisted all attempts to collect it. These were the only trails of this particular kind observed in many days of prospecting in this formation. The trail illustrated (see fig. 5) is impressed on the surface of a pinkish sandstone and has a length of approximately 370 mm. The specimen, which is the positive slab, has been cast, and the replica affords all the evidence of the original. The trackway as a whole is asymmetrical, brought about, it would seem, by the failure of the appendages of the right side to leave their imprints. Two faint impressions on the right side near the midlength lend support to this view. (See pl. 4, fig. 1.) These are elongated depressions set diagonally to the line of movement, and in nearly every way conform to those forming the outer row on the left side of the trackway. If this supposition is correct, the normal trail would have a width of about 46 mm. The longitudinal row of tracks of the left

![Fig. 5—Invertebrate trail from Supai formation. No. 11,740, U. S. N. M. About 1/4 natural size.](image)
side consists of a uniform series of elongated depressions that stand diagonally to the line of direction. These are quite regularly spaced, averaging about 15 mm. apart. The outer ends of the diagonal tracks are somewhat enlarged backward, whereas the inner end gives off a sharp spur that is directed forward and inward. Over all, these diagonal impressions have an average length of about 27 mm. A second, and supposedly median row of elongated impressions, but less clearly registered, parallels those just described. They also have a diagonal trend, parallel in direction but usually alternating with those of the outer row.

This trail seems to be undescribed and when more perfect examples are found, there will be little difficulty in fully characterizing it. The character of the trackway points clearly to its invertebrate origin, though at this time I have no suggestion to offer as to the particular group of animal life to which it may be attributed.

A second trail, No. 11,693, U. S. N. M. (see pl. 4, fig. 2), collected by Mr. G. E. Sturdevant in 1927, from the uppermost track-bearing horizon of the Supai formation, on the west side of O'Neill Butte, represents another undescribed trackway of peculiar kind, the details of which, as in the preceding, are not altogether clear. This trackway has a total length of 330 mm.; width about 65 mm.; length of stride about 25 mm. It consists of two parallel rows of curved, pointed, finger-like markings, between which are irregularly shaped, subround impressions of spasmodic occurrence. The tracks of opposite sides seem to alternate, although in some few instances they are opposite. The finger-like impressions stand diagonally to the line of movement and seem to be directed forward, though from this specimen alone one cannot be sure of the direction of movement. The irregularity of the impressions (see fig. 6), especially of the two rows, does not permit of a satisfactory diagnosis, and for that reason I refrain from naming it, though it undoubtedly represents a form new to this ichnite fauna.

In plate 3, figure 2, is illustrated a kind of track that has been observed on numerous occasions in the Supai formation, but which has not yet been found in the form of a definite trackway. While this type of track may be easily recognized, none of the examples found gives any idea of a continuous trail, the individual tracks being placed here and there and apparently without rhyme or reason. Occasionally two and three will be found, one placed behind the other,
Some of the imprints are tridactyle, others didactyle. The toes are usually sharply pointed and widely divergent. These tracks vary from 14 to 16 mm. in length and from 9 to 12 mm. in width. They give every evidence of having been made by an invertebrate animal to whose identity we have no clue at this time. It is anticipated that sooner or later well-defined trails of this animal will be discovered.
ICHNITES FROM TAPEATS SANDSTONE

Plate 5, figs. 1, 2, 3, and 4

In a previous paper\(^1\) mention was made in a footnote of the discovery by Mrs. G. E. Sturdevant on the Bright Angel Trail of a small section of a trackway which at that time was thought to come from the Bright Angel shale. More extended search of this locality by Messrs. G. E. Sturdevant and Edwin D. McKee has brought to light several additional specimens, and Mr. Sturdevant writes me that all of these specimens, including the one previously found by Mrs. Sturdevant, are from the Tapeats sandstone.

The correctness of his observation is fully confirmed by comparison of the specimens with trails figured by the late Dr. Charles D. Walcott\(^2\) from the Tapeats sandstone of other parts of the Grand Canyon, several of which are identical in character. That there was an extended ichnite fauna in this formation is abundantly shown by the many different kinds of trails figured by Walcott, and by the specimens more recently collected.

Walcott attributes all of the various kinds of trails illustrated by him as being made by trilobites. He points out that the known genera and species of trilobites from the Middle Cambrian give a wide varia-

\(^2\) Smithsonian Misc. Coll., Vol. 67, No. 4, 1918, pls. 37 to 42.
tion in size, and in ventral appendages, quite sufficient perhaps to account for most of the trails found.1

While I have no intention of giving a detailed description of these recently discovered trails, a few of the more characteristic specimens are illustrated here, especially those that differ from the trails published by Walcott, and these figures tell the story of the kinds found.

The discovery of these trails in the Tapeats of the Bright Angel section is especially interesting as recording a fourth track-bearing horizon in this one geological section.

A CORRECTION

In the faunal list of the Coconino, Smithsonian Misc. Coll., Vol. 80, No. 3, 1927, p. 4, a third species of Agostopus, A. robustus is listed. This name was inadvertently included, but it has no standing and should therefore be dropped from further consideration, as a nomen nudum.

Attention is also called to the misspelling of the species Hylopus hermitanus in the same publication. In the list of Hermit ichnites, page 7, H. hermitus, and on page 78, H. hermitensis both should be Hylopus hermitanus Gilmore.

1Idem, p. 175.
EXPLANATION OF PLATES

PLATE 1
Large track-covered slab (No. 11,707, U. S. N. M.) from the Hermit Shale, showing trackways of *Parabaropus coloradensis* (Lull) (large track forming the diagonal trail across left side of slab); *Collettosaurus pentadactylus* Gilmore (trail with distinct tail drag to right of center); and *Hylopus hermitanus* Gilmore (all other tracks on the slab). This slab has a greatest transverse diameter of 6 feet and 5 inches; a greatest vertical diameter of 3 feet and 10 inches.

PLATE 2

PLATE 3
Fig. 1. *Hyloidichnus whitei*, new species. Type. No. 11,692, U. S. N. M. About natural size.
Fig. 2. Unidentified tracks (invertebrate) from the Supai formation, O'Neill Butte, Grand Canyon National Park, Arizona. About natural size.

PLATE 4
Fig. 1. Unidentified trail (invertebrate). No. 11,740, U. S. N. M. From the Supai formation on west side of O'Neill Butte, Grand Canyon National Park, Arizona. About one-half natural size.
Fig. 2. Unidentified trail (invertebrate). No. 11,693, U. S. N. M. From the Supai formation (upper track-bearing horizon), on west side of O'Neill Butte, Grand Canyon National Park, Arizona. More than one-half natural size.

PLATE 5
Trilobite tracks and trails. All from the Tapeats Sandstone, Middle Cambrian, as exposed in the Bright Angel section, Grand Canyon National Park, Arizona. Figs. 1, 2, and 4, about three-fourths natural size. Fig. 3, natural size.
Fossil footprints from Supai formation.
(For explanation, see page 16)
Fossil tracks from the Grand Canyon.

(For explanation, see page 16)
Fossil invertebrate trails from Supai formation.
(For explanation, see page 16)
Trilobite tracks and trails, Tapeats formation.
(For explanation, see page 16)
The fossil tracks of extinct four-footed animals were first discovered in the Grand Canyon of the Colorado in 1915, but the abundance of their occurrence and their great diversity of kind remained unknown until 1924. In that year and again in 1926 collections of them were made for the U. S. National Museum, and my studies of these materials have disclosed the presence of no less than 26 genera and 32 species of fossil footprints. In number of species, and in excellence of preservation of the tracks, this area easily outranks all other known American localities for Permian and Pennsylvanian footprints.

The great antiquity of these fossilized tracks of extinct creatures of a by-gone age is clearly shown by the fact that they occur from 900 to 3,800 feet below the top of the canyon wall. This means that since the first of these animals left their footprints in what was then moist sand, nearly 4,000 feet of rock-making materials were deposited in successive layers above them, not to mention the hundreds of feet more that no doubt were eroded from the present rim of the canyon. Add to this period of up-building, the length of time required for the cutting of the canyon through 4,000 feet of solid rock, and we have an idea of the tremendous age of these fossil footprints.

A third visit to the Grand Canyon under the auspices of the Grand Canyon Exhibit Committee of the National Academy of Sciences, was made in the late spring of 1927 for the dual purpose of locating and preparing exhibits of tracks in situ, and making further collections of fossil footprints for the U. S. National Museum. Both of these projects were successfully carried out.

Two small field exhibits, one in the Coconino, the other in the Supai formation were prepared, the purpose being to show the tracks precisely as they occur in nature in order that they may be viewed by visitors, through fixed telescopes which the committee plans to place in front of the new observation station now being erected on Yavapai Point. In order to find suitable locations for these exhibits
Fig. 8.—Slab of fossil footprints from the Hermit shale, as exposed at the head of Hermit Gorge, Grand Canyon National Park, Arizona. The following forms have been recognized: *Hylopus hermitanus* Gilmore, *Parahoplus coloradensis* (Lull) and *Collettosaurus pentadactylus* Gilmore. This slab is 6½ feet wide and 5 feet long.
Fig. 9.—Footprint exhibit in situ in the Supai formation on the west side of O'Neill Butte, Grand Canyon National Park, Arizona. (Photograph by Matthes.)

Fig. 10.—Fossil trackway on large slab of Supai sandstone, quarried out in building the new Yaki trail along the east side of O'Neill Butte. (Photograph by Matthes.)
which obviously must be visible from the observing station, a considerable amount of exploratory work was necessary. As a result of this, the known geographical range of fossil tracks in the Grand Canyon was greatly extended and a considerable amount of new material was secured for the National collections. Subsequent study has shown some of the tracks to be undescribed, but the most noteworthy specimen collected, from an exhibition viewpoint, is the large slab from the Hermit formation shown in the accompanying illustration. This gives a vivid picture of the diversity of animal life that once roamed over this ancient mud flat.

An interesting development of these investigations was the discovery by Mr. G. E. Sturdevant, Park Naturalist, of a track-bearing horizon in the Bright Angel section of the Middle Cambrian. Thus four distinct ichnite horizons are established in this one geological section, distributed as follows: Coconino sandstone, 900 to 1,030 feet; Hermit, 1,350 to 1,400 feet; Supai, 1,760, to 1,800 feet; and Tapeats, 3,600 to 3,800 feet below the top of the Canyon wall.

On the south rim of the Grand Canyon, tracks have been found on Grand View Trail on the east and Dripping Springs on the west, these two localities being separated by a distance of 27 miles, and this last exploration leads to the belief that tracks can be found in the above mentioned horizons wherever the physical conditions will permit search being made for them. In view of this last statement, it is of interest to add that Mr. Sturdevant has recently discovered fossil tracks in the Coconino and Supai formations on the north rim of the canyon, some 14 miles distant in an air line from those found on the south rim.
DISCOVERY OF FOSSIL TRACKS ON THE NORTH RIM OF THE GRAND CANYON

Fossil tracks of quadrupedal animals were first discovered in the rocks of the Grand Canyon of the Colorado in 1915, but the abundance of their occurrence and their great variety of kind has only recently been made known. During the past three years investigations carried on by the senior author show the presence of no less than 28 genera and 36 species of fossil ichnites. These represent three distinct faunas that named in descending order occur in the Coconino (Permian), Hermit (Permian) and Supai (Pennsylvanian?) formations. All of the specimens on which the above-mentioned determinations are based were obtained entirely from the south side of the canyon, and it is, therefore, of interest to find that fossil footprints also occur on the north side. Mr. Sturdevant, with the assistance of Mr. Charles Nesb, made a special search for tracks on the north rim and on December 3, 1927, and was rewarded by finding well-preserved footprints in both the Coconino and Supai formations.

When collections have been made, it will be a matter of added interest to learn whether the tracks occur in the same horizons and also whether the same genera and species are to be found on both sides of the canyon, which are separated by a distance in an air line of fourteen or more miles.

CHARLES W. GILMORE,
U. S. National Museum

GLENN E. STURDEVANT,
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