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Tetrapod tracks from the Mauch Chunk Formation (middle to upper Mississippian) of Pennsylvania, U.S.A.

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ABSTRACT.— Evidence of tetrapods is scarce in the early Mississippian. Following Romer's Gap, a time of some 15 million years at the beginning of the Mississippian when remains of tetrapods and other continental organisms are rare, only sporadic skeletal and footprint fossils are found. We report here on new specimens of the tetrapod ichnogenera *Hylopus* and *Palaeosauropus* from the middle of the Mauch Chunk Formation (middle to upper Mississippian) of Eastern Pennsylvania. These document walking and swimming behaviors by at least two basal tetrapod taxa, perhaps an anthracosaur and a temnospondyl, and show evidence for the beginning of the second period of tetrapod diversification.

Key words: Carboniferous, Mississippian, tetrapod, trace fossil, ichnofossil, Mauch Chunk Formation.

INTRODUCTION

Tetrapod trackways occur only sporadically in the Mississippian and yet such materials document the early stages in the invasion of the land by vertebrates and can indicate aspects of the palaeobiology of early tetrapods. Fossil tracks from the early Mississippian are especially important because of the rarity of skeletal fossils through that time. Tetrapods originated in the Late Devonian, and apparently diversified to some extent, but their fossil record is especially weak for the first 15 million years of the Mississippian (Tournaisian and early Viséan; about 360-345 million years ago). This time span is known as as Romer's Gap, named for Alfred Sherwood Romer who first noted the hiatus (Ward *et al*. 2006). This interval was assumed to represent a time of poor preservation, but Ward *et al*. (2006) argue that the gap was a time of genuine low diversity of tetrapods because of unusually low atmospheric oxygen levels. Only after the recovery of oxygen levels 345 Ma did tetrapods begin their terrestrialization phase in earnest.

Among tetrapods, this second phase of radiation is marked by the appearance of several tetrapod lineages, the basal Crassigyrinidae, Baphetidae, Colosteidae, and Adelogyrinidae, as well as the Aïstopoda, Microsauria, Temnospondyli, and Anthracosauria, together representing a major radiation of tetrapods that continued through the Mississippian (Ruta *et al*. 2003). The Mauch Chunk Formation of Pennsylvania is generally accepted as middle to upper Mississippian (c. 320-340 million years ago), but lower parts may be Viséan in age based on fossil plants (Jennings 1985). So, this unit probably immediately postdates Romer's Gap (Ward *et al*. 2006).

Tetrapod tracks have long been known from the Mississippian of Pennsylvania (Lyell 1843; Lea 1849; Dawson 1863; Leidy 1879). Lea (1849) named the ichnogenus *Palaeosauropus* (*Sauropus*) from the Mauch Chunk Formation in Pennsylvania, but little else has been published from the state (Cotton *et al*. 1995). New trackway material from the Mauch Chunk Formation in Pennsylvania has recently been added to the collections at the Academy of Natural Sciences in Philadelphia (ANSP). The purpose of this paper is to describe the new material and to put it in context of the early radiation of tetrapods on land.

GEOLOGY

The Mauch Chunk Formation occurs in several drainage basins in Pennsylvania, Maryland and West Virginia, and for the most part is a monotonous sequence of 100m to 1000 m thickness of red and grey siltstones, fine sandstones, and shales that is largely unfossiliferous. Orogenic uplift in the southeastern corner of the state during the late middle Mississippian created the Mauch Chunk delta, and by the late Mississippian this delta had prograded to the northeastern corner of the state (Edmunds *et al*. 1979). The Mauch Chunk Formation has been subdivided informally into three members by Wood *et al*. (1969): the lower and upper members consist of alternating grey and red beds,

and the middle member consists of greyish red beds. The upper member intertongues with the overlying Pottsville Formation, and the lower member intertongues with the underlying Pocono Formation. The top of the formation is placed somewhat arbitrarily at the top of the last of the red beds, so there is some debate about whether the contact with the Pottsville Sandstone is conformable or unconformable (Edmunds *et al*. 1979). Calcareous sandstone is found in some sections, and occasional limestone beds are found in the western part of the state where the formation is more differentiated and has been subdivided stratigraphically (Edmunds *et al*. 1979).

Coarsening-upwards fluvial cycles are seen throughout the Mauch Chunk Formation and have been interpreted by Griesmer (1980) as an indication of deltaic progradation. The absence of large-scale cross bedding, the presence semi-directional ripple marks and the presence of both walking and swimming traces indicate a shallow, semi-aquatic environment. Barrell (1907) interpreted the whole of the Mauch Chunk Formation as having been deposited in a subaerial/fluvial setting in a semi-arid climate. Desiccation cracks and raindrop imprints throughout the formation indicate a semi-arid climate, though it was never dry enough to produce evaporites. The footprint slabs described here, and field observations by MBV, confirm aspects of the sedimentology of the Mauch Chunk Formation. ANSP 22651 is a slab of medium/fine grained reddish-brown sandstone with a muddy, rough texture, and convex hyporelief raindrop imprints on the underside of the slab. ANSP 22652 and 22653 were found *in situ* at Tamaqua, Pennsylvania, where the entire formation is only 115 m thick, in a bed some 20 m below the obscure contact between the Mauch Chunk and Pottsville formations. Bed thickness varies throughout the section, but individual beds are some 60-100 mm thick. The tracks are found near the top of a fining-upward fluvial cycle composed of fine-grained, grey sandstone overlaid by red mudstone. There is an erosive contact at the base of the cycle, and the upper surfaces of some beds including those with tracks, show shallow ripple marks, with those near the top of the section being more linguoid in shape. Shales at the top of the cycle show desiccation cracks, raidnrop imprints, and rare plant impressions.

Fossils are generally rare in the Mauch Chunk Formation. Lea (1849) was first to report tetrapod footprints from Mount Carbon, Schuylkill County, Pennsylvania, and since then further finds have been reported, all from the middle member of the formation (Fillmore *et al*. 2006; Lucas *et al*. 2006). Other fossils include fish fragments and worm burrows (Hoque 1968), as well as isolated invertebrates (Edwards *et al*. 1979) and plants reported from the middle member, about 300 m below the top of the formation (Jennings 1985).

The age of the Mauch Chunk Formation is debated. It is usually dated as Mississippian, and most often middle to upper Mississippian, because the underlying Pocono Sandstone Formation is dated as middle Mississippian and the overlying Pottsville Formation as Pennsylvanian. Edmunds (1996) notes the age of the Mauch Chunk Formation spans about half of the Osagean Age, the entire Meramecian and Chesterian Ages, and a small part of the Morrowan Age based on intertonguing marine beds and determinations of age from marine fossils. This is confirmed by freshwater bivalves in the Mauch Chunk Formation itself (Busanus and Hoare 1991). The maximum age range, on this estimate, corresponds to the time from Viséan to earliest Bashkirian on the international scale (Gradstein *et al*. 2004), suggesting duration from 352 to 318 million years ago at most. Magnetostratigraphic evidence (Opdyke and DiVenere 2004) confirms this and suggests that the entire Mauch Chunk Formation spans more than 18 magnetozones representing some 16 million years. Jennings (1985) reported fossil plants that confirmed a Viséan age for the middle member of the Mauch Chunk Formation, so it is still unclear whether the unit spans a long time interval or contains many gaps. The trackways all come from the middle member, equivalent to the late Meramecian/ early Chesterian time interval (Edmunds 1996), and so perhaps some 340 Ma.

SYSTEMATIC PALAEONTOLOGY

Ichnogenus *Hylopus* Dawson, 1882
Ichnospecies *Hylopus hardingi* Dawson, 1882

Material.—ANSP 22651, a slab with 12 prints.

Locality.—Banks of the Nescopeck Creek under an overpass of US I-80, near Hazleton, Luzerne County, Pennsylvania. ANSP 22651 was found as float in an area underlain by the Mauch Chunk Formation and the lithology is consistent with Mauch Chunk lithofacies.

Occurrence.—*Hylopus* is known from the Horton Group (Tournaisian to lower Viséan), Nova Scotia; Bluefield Formation (middle Mississippian), West Virginia and Mauch Chunk Formation (middle to upper Mississippian), Pennsylvania.

Description.—ANSP 22651 (Figure 1) shows a series of 12 concave epirelief footprints including five manus and pes pairs. The pes and most of the manus of one pair found in the middle of the slab are partly obscured by sediment. The footprints on the upper half of the slab are slightly deeper than those on the lower half, most likely due to the slight inclination of the bedding surface. The trackway is 74 mm wide.

A composite restoration of manus and a pes (Figure 2), made using multiple footprint overlays to correct for

distortion and incomplete preservation (Table 1), shows five digits on each, although digit I is not always preserved on the pes print. The average manus and pes lengths are 23 mm and 24 mm, and average widths are 26 mm and 28 mm, respectively (Table 2). The digits on both manus and pes are generally straight, with only slight curvature in digit IVof the manus. Free lengths of each digit vary (Table 1). In the manus, digit IV is the longest, while digits II, III and V are all roughly the same length; digit I (if present), is much shorter than the others. Interdigital angles vary (Table 3). The right manus prints show an irregularity: digits I, II and III are curved slightly counter-clockwise. This may represent an injury or some pathological effect.

A tail drag is preserved in the upper half of the slab as a shallow groove approximately 30 mm long running between the uppermost manus/pes pair. The drag may be preserved here because the mud surface was convex upwards, and it may be absent elsewhere because there was a slightly greater distance between the animal and the substrate.

Remarks.— Although previous records of footprints in Pennsylvania have most often been linked to *Palaeosauropus*, ANSP 22651 cannot be referred to that ichnotaxon because it is much smaller and lacks the characteristic thick and broadly rounded digits. The specimen is, however, very similar to *Hylopus*, a common track from the Mississippian of eastern North America. *Hylopus* was established by Dawson (1882), and later descriptions were made by Matthew (1904), Sarjeant and Mossman (1978), Sundberg *et al*. (1990) and Cotton *et al*. (1995). Lucas *et al*. (2006) recognize *Hylopus* in a collection of Mauch Chunk tracks at the Reading Public Museum, Reading, Pennsylvania. Although six ichnospecies of *Hylopus* have been described, Sundberg *et al*. (1990) consider that only two of these are valid: *H. hardingi* and *H. hamesi*. The former is a walking trace, while the latter is a combination of toe marks and foot scrapes made most likely while swimming.

H. hardingi, as described by Sundberg *et al*. (1990), has a pentadactyl manus and pes, though digit I is reduced and barely visible. Digits on the manus display unequal free lengths, with digit IV being the longest. They also display slight counter-clockwise curvature, with the exception of digit II, which is straight. Divarication angles between the digits are large, primarily between digits III and IV. Sole length is short. The digits on the pes are straight except for digit IV, which shows slight counter-clockwise curvature. All pes digits have similar free lengths as well as similar divarication angles (except for digits IV-V), and are all forward facing except for digit V which angles outwards.

ANSP 22651 is very similar in size, morphology and digital layout to *H. hardingi*. Most notably, ANSP 22651 displays the elongate and curved digit IV of *H. hardingi* as well as the reduced digit I. It differs only in the length/width ratio of the pes, and the more limited pes overlap. ANSP 22651 is the first record of tail drag in *Hylopus*.

Ichnogenus *Palaeosauropus* Lea, 1849

Material.— ANSP 22652, 22653.

Locality.— A large outcrop adjacent to a railway bed/public bike trail along the east side of Rt. 309, one mile south of Tamaqua, Schuylkill County, Pennsylvania. The two footprint-bearing slabs were found *in situ* in successive, vertically dipping beds.

Occurrence.— *Palaeosauropus* is known from the Horton Group (Tournaisian to lower Viséan), Nova Scotia; Mauch Chunk Formation (middle to upper Mississippian), Pennsylvania and Tar Springs Formation (middle Mississippian), Indiana.

Description.— ANSP 22652 contains two trackways (Figure 3), both in concave epirelief. The first trackway runs the length of the slab (0.5 m), and consists of five manus/pes pairs, showing slight overlap of the pes digits on to the base of the manus sole. The footprints are poorly defined, with the large, deep sole imprint being the defining feature. These are not believed to be undertracks however as the underside of the beds seen *in situ* directly above ANSP 22652 and 22653 contained no convex hyporelief prints.

For the first trackway, the external width is 150 mm, stride length is 140 mm, length of pace 80 mm, oblique pace 120 mm (based on manus/pes pairs), pace angulation (PA), 82°. A tail/body drag is present as a 10 mm wide groove across the upper quarter of the slab following the midline of the first trackway, and parallel to it is a dark, sediment-filled groove. Though its origin is unclear, this may be a mud crack, rather than a trace fossil.

Digits I-IV of the manus are all straight, forward-facing, and of similar length (ca. 15 mm). Only one manus and one pes imprint are clearly pentadactyl. Average manus length and width (where measurable) are 42 and 50 mm; average pes length and width are 40 and 53 mm (Table 4). All visible digits seem to have roughly equal free lengths, though digit V appears slightly shorter than the rest. The inter-digital angles for pes and manus are small for digits I-IV (< 15°), and greater between digits IV-V (< 50°). Total digit divarication for the pes is ca. 120÷ , and less for the manus.

The second trackway on ANSP 22652 runs at approximately 45° to the first. It consists of only one manus/pes pair, represented by shallow toe marks. These have approximately the same width as prints in the first trackway, though an accurate measurement is impossible. The toe prints of the manus are longer than those of the pes, and the pes imprints overlap slightly onto the manus imprints.

ANSP 22653 also contains two trackways in convex

TABLE 1. *Hylopus* sp. (ANSP 22651), key measurements of the composite manus and pes, in mm. Abbreviations: **L**, length; **SW**, sole width; **W**, width. Measurement definitions according to Leonardi (1987).

	Footprint Dimensions		Digit Free Length					Divarification of Digits				
	L/SW	W/SW	I	II	III	IV	V	I-II	II-III	III-IV	IV-V	Total
Manus	2.8	2.9	12	11	11	14	-	30	31	32	-	93
Pes	3	2.9	12	12	12	16	11	10	13	19	37	79

TABLE 2. *Hylopus* sp. (ANSP 22651), footprint dimensions, in mm. Only footprints 1-6 from the upper half of the trackway were measured. Abbreviations: **m**, manus; **p**, pes.

Footprint	Length	Sole Length	Width	Sole Width
1(m)	24	11	22	17
2(p)	25	11	29	18
3(m)	20	11	24	11
4(p)	24	7	32	12
5(m)	25	11	31	16
6(p)	24	10	22	14

TABLE 3. *Hylopus* sp. (ANSP 22651), interdigital angles, in degrees. Abbreviations: **m**, manus; **p**, pes.

Footprint	I-II	II-III	III-IV	IV-V	Total
1(m)	25	44	30	—	98
2(p)	8	16	27	41	91
3(m)	< 17 >		—	—	97
4(p)	30	25	39	63	157
5(m)	18	42	47	—	108
6(p)	30	12	< 37 >		80
7(m)	—	—	—	—	—
8(p)	—	—	—	—	—
9(m)	28	46	25	—	100
10(p)	—	—	—	—	—
11(m)	23	35	37	—	95
12(p)	—	—	—	—	—

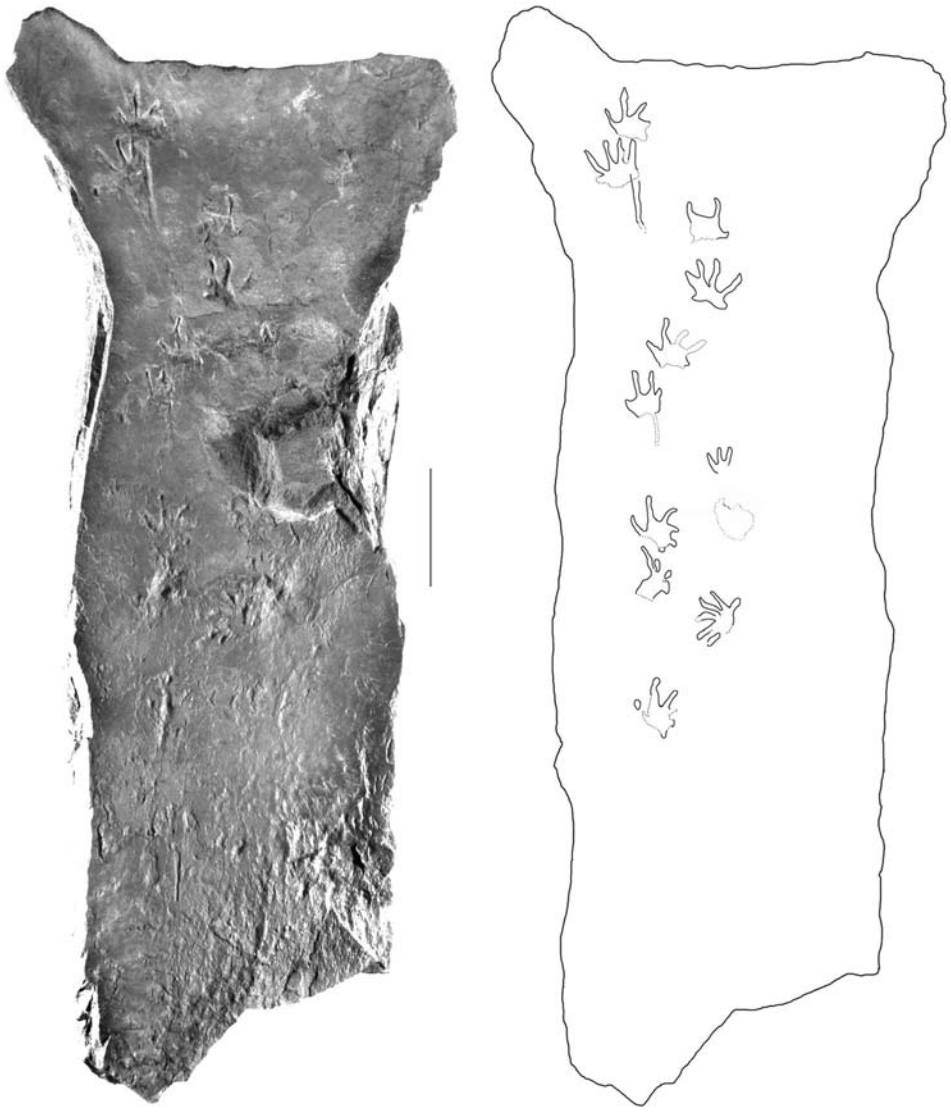

Fig.1. *Hylopus* sp. (ANSP 22651), Mauch Chunk Formation, along Nescopeck Creek near Hazleton, Luzerne County, Pennsylvania. A, slab showing a trackway of 12 footprints. B, tracing of the better preserved prints in the upper half of the slab. Scale bar is 50 mm.

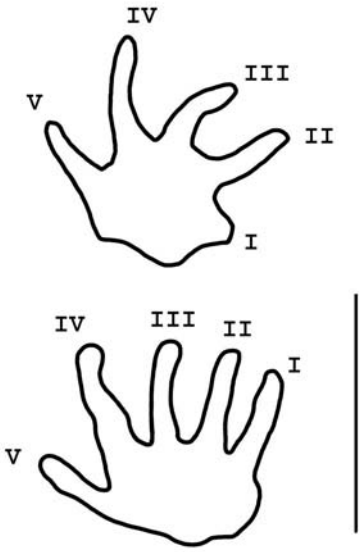

Fig. 2. *Hylopus* sp., reconstructed manus (top) and pes (bottom) prints based on tracings of all prints on ANSP 22651. Scale bar is 25 mm.

epirelief (Figure 4). The first trackway runs along the length of the slab (360 mm), and consists of eight footprints, of which only three manus/pes pairs are discernible. All imprints are poorly defined. Only one footprint is preserved well enough for all five digits to be distinguished. In other prints individual digits appear as convex impressions, but determining the digit number was not possible. On average manus/pes width is 40 mm wide, and PA is ca. 80°.

A convex tail drag impression (< 20 mm wide) is present, and forms a distinct curve across the slab, generally following the midline of the trackway. Running parallel to this drag is a small groove (< 5 mm wide) filled with darker sediment, very like that seen on ANSP 22652. Though is it possible that this groove is non-biological in origin, such an occurrence on both slabs in conjunction with a tail drag is interesting.

The second trackway on ANSP 22653 is located on the lowermost portion of the slab and consists of two consecutive manus/pes pairs along with one additional footprint, rather like the second track prints on ANSP 22652. These prints are represented by shallow toe/digit marks, with slight overlap of the pes onto the manus.

Remarks.—The primary trackways of ANSP 22652 and 22653 are most similar to the Mississippian ichnotaxon *Palaeosauropus*. This ichnogenus has been recorded from three areas in the eastern U.S.A. (Cotton *et al*. 1995), and it

TABLE 4. *Palaeosauropus* sp. (ANSP 22652), footprint dimensions, in mm. Abbreviations: **m**, manus; **p**, pes.

Footprint	Length	Sole Length	Width	Sole Width
1(m)	44	—	45	—
2(p)	47	20	52	32
3(m)	—	—	—	—
4(p)	37	24	52	—
5(m)	—	—	—	—
6(p)	—	—	—	—
7(m)	42	21	51	32
8(p)	31	20	52	36
9(m)	—	—	—	—
10(p)	—	—	—	—
11(m)	42	22	54	29
12(p)	40	19	54	37

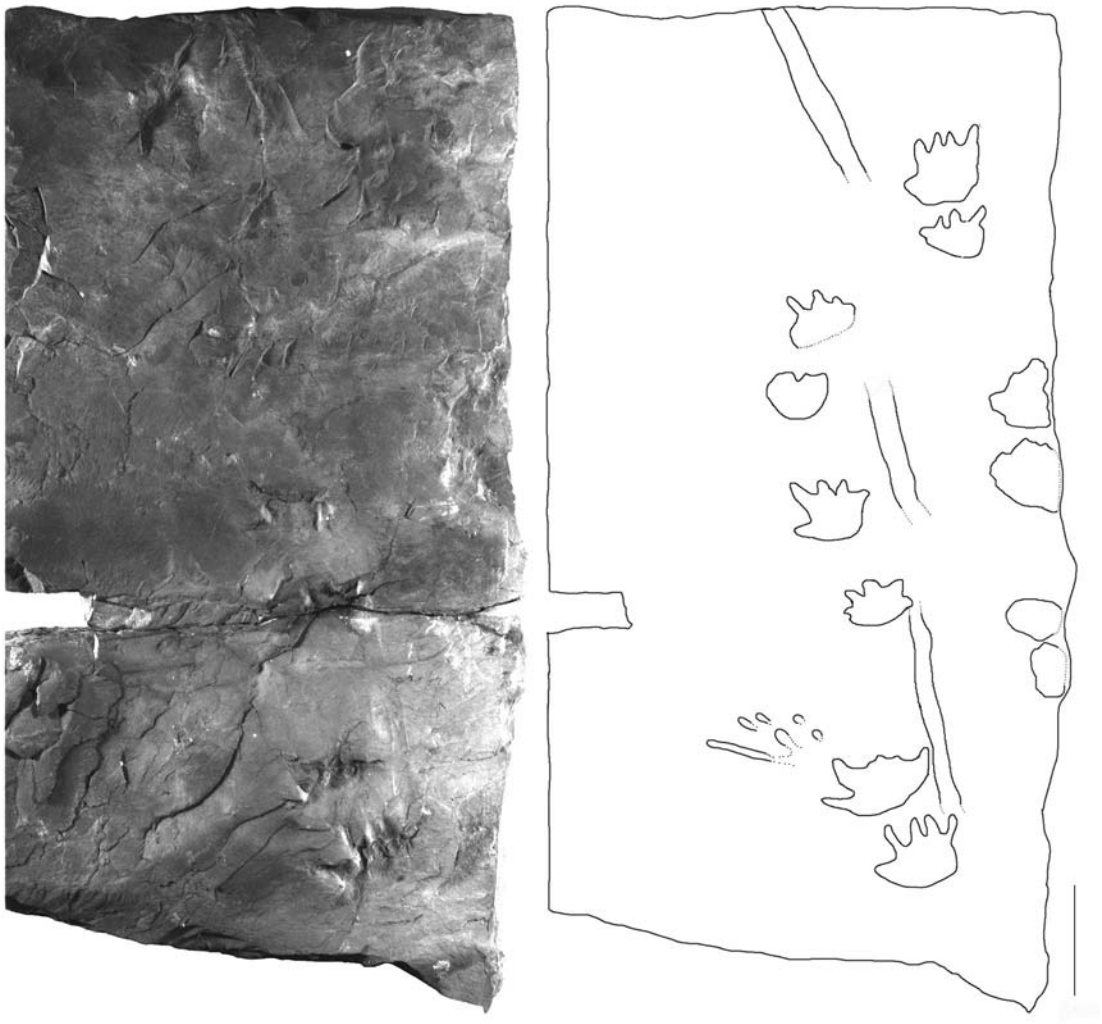

Fig. 3. *Palaeosauropus* sp. (ANSP 22652), Mauch Chunk Formation, near Tamaqua, Schuylkill County, Pennsylvania. A, slab showing the trackways. B, outline drawing of main trackway of ten footprints, as well as toe marks to the lower left. Note the putative tail drag. Scale bar is 50 mm.

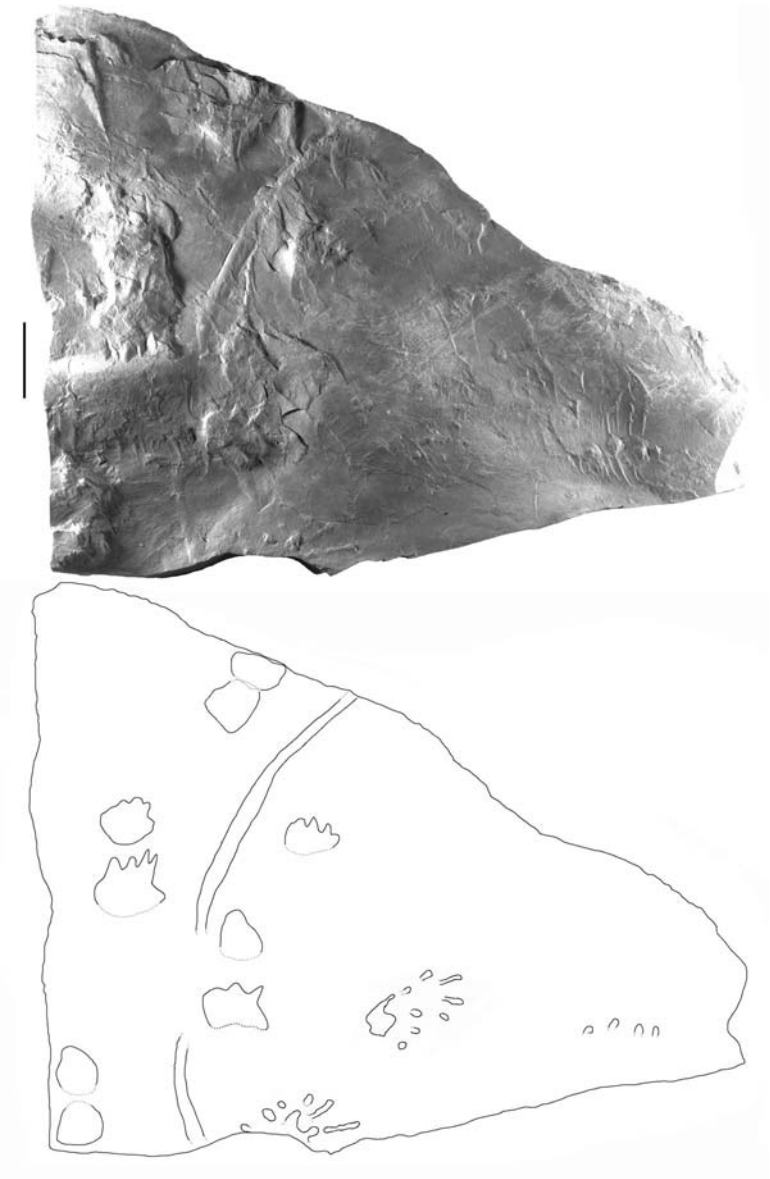

Fig. 4. *Palaeosauropus* sp. (ANSP 22653), Mauch Chunk Formation, near Tamaqua, Schuylkill County, Pennsylvania. A, slab showing the trackways. B, outline drawing showing the main trackway of nine footprints, as well as toe marks to the lower right. Note the putative tail drag. Scale bar is 50 mm.

is probably the best-known tetrapod track from Pennsylvania. The type species, *Palaeosauropus primaevus* (Lea, 1849), was recorded from the Mauch Chunk Formation in Schuylkill County, Pennsylvania, about 25 km from the site of the recent discoveries south of Tamaqua. Lea (1849) placed this form in the Jurassic ichnogenus *Sauropus*, but Hay (1902) moved it to the new ichnogenus *Palaeosauropus*. Following Lea's discovery, other footprints that are similar to *P. primaevus* were noted by Rogers (1858) and Barrell (1907) from the same area, but these were never named or figured. Lucas *et al*. (2006) report on additional material of *P. primaevus* from eastern Pennsylvania awaiting further description. Dawson (1882) described and named *Sauropus antiquior* from Parrsboro, Nova Scotia, later reassigned by Haubold (1970) to *Palaeosauropus*. Colbert and Schaeffer (1947) described *Palaeosauropus* sp. from Indiana.

The digits of the primary trackways of ANSP 22652 and 22653 are more comparable to the long, broad and distally rounded digits of *P. primaevus* and *Palaeosauropus* sp., rather than the relatively thin and curved digits of *Hylopus*. The length/width measurements of the first trackway on ANSP 22652 also conform closely to those seen in *Palaeosauropus* sp. noted by Colbert and Schaeffer (1947), especially when allowing for the fact that the distal ends of the digit impressions are not well preserved. The relative shortness of digit length in relation to sole length is therefore considered an artifact of preservation. The primary tracks on each slab also show the same wide and short pes sole, and sole length to width ratios as seen in figured specimens of *Palaeosauropus* (Colbert and Schaeffer 1947), and they also display a similar large divarication angle between digits IV-V. The secondary tracks on each slab are comparatively short and thin (cf. *H. hamesi* rather than Palaeosauropus) and therefore may have been from a different trackmaker.

Digital number is a critical determining feature of tetrapod ichnotaxa and *Palaeosauropus* is always indicated (e.g. Colbert and Schaeffer 1947; Haubold 1971) as having five digits on the pes and four on the manus. This is apparently the case in *P. primaevus* (Lea 1849, 1855), and yet the manus print in the type specimen (ANSP 9752) consists only of impressions of the digits, with no palm print. Study of the original specimen shows that the four anteriorly directed digits (digits II-V) were imprinted at the front of the manus, while the small medial digit I is not seen. Colbert and Schaeffer (1947) noted uncertainty about the number of manus digits in *H. hardingi*, whether four or five, and our specimens show that the first digit is very small. The same uncertainty is evident concerning some materials of *Palaeosauropus*, and we suggest that revision of the ichnotaxon may reveal that, when complete, like *Hylopus*, *Palaeosauropus* should also have five manus digits. Other undescribed specimens of *Palaeosauropus* with five-digit manus are known from Nova Scotia (Lucas, S. G. pers. comm., March 2005), although Lucas *et al*. (2006) note that their material of *Palaeosauropus* from the Mauch Chunk Formation shows a tetradactyl manus.

DISCUSSION

Identity of trackmakers

Both *Hylopus* and *Palaeosauropus* have been identified as the products of edopsoid temnospondyls (Matthew 1904; Haubold 1970, 1971; Cotton *et al*. 1995). This is unlikely for *Hylopus*, and possibly for *Palaeosauropus* if it had a pentadactyl manus, because most temnospondyls had four digits on the manus. A number of other Mississippian tetrapods had five digits - for example, colosteids, crassigyrinids, whatcheeriids, and most tetrapods on the anthracosaur/ reptiliomorph branch of the cladogram (Ruta *et al*. 2003). Indeed, Sundberg *et al*. (1990) identified the maker of *Hylopus* as an anthracosaur like *Proterogyrinus scheeli* (Holmes 1984), a species that is known from body fossils in the Mauch Chunk Formation of West Virginia.

The occurrence of the new *Hylopus* and *Palaeosauropus* material in the Mauch Chunk Formation is consistent with the known distribution of these ichnogenera in eastern North America and their age range through the Mississippian. These records are also consistent with the Mississippian Tetrapod Province of Milner (1993) that covered much of North America from Utah and Iowa in the west, to Nova Scotia and West Virginia (and now Pennsylvania) in the east, and some of Scotland.

Size and posture

Measurements of pace or stride length can give a rough estimate of the size of the track-maker, assuming the stride length is equivalent to the shoulder to hip length (glenoacetabular length, GAL). Total body length is then about twice the GAL. The problems are in determining which pairs of pes and manus prints make a stride, and then whether the animal walked with primary or secondary overstep. In primary overstep, usually seen in shorter animals, the pes is placed onto the manus print immediately following removal of the manus from the substrate. In secondary overstep, seen in longer animals, there may be several steps between overlap. First, assuming primary overstep, the GAL of *Hylopus* (ANSP 22651) is 90 mm (Figure 1), giving a total body length of 180 mm. If the animal were exceptionally long, and therefore displayed secondary overlap, then the GAL would be 180 mm, and the animal itself around 360 mm long. Sundberg *et al*. (1990) believed that *H. hardingi* exhibited secondary overstep, and so, if ANSP 22651 were a similar trackmaker, its GAL would have been nearer to 360

mm than 180 mm long. Estimates for the GAL of *Proterogyrinus* are at least twice this distance (Holmes 1984), so it may be that the maker of ANSP 22651 was simply a smaller animal. In *Palaeosauropus* (ANSP 22562, 22563), variation in the manus-pes distance also suggests secondary overstepping. The GAL of the trackways would then be ca. 400 mm, giving an approximate total body length of 800 mm. This estimated body length is the same as that estimated by Colbert and Schaeffer (1947) for the trackmaker of *Palaeosauropus* sp. from Indiana.

Pace angulation (PA) may indicate the posture of the trackmaker (Peabody 1959). Animals with a sprawling gait generally have a PA of less than 100°, as is seen in *Hylopus* (ANSP 22651), though Peabody (1959) noted that some amphibians were capable of producing a much larger angle. The tail drag on ANSP 22651 perhaps confirms this posture. Although less well preserved, a similar sprawling posture is indicated also for the *Palaeosauropus* specimens, the continuous tail drag supporting this.

Behavior and environment.

The *Hylopus* tracks (ANSP 22651) were made by an animal walking across damp sand, but they show little more. The *Palaeosauropus* tracks, however, are more informative. Both ANSP 22652 and ANSP 22653 contain walking ('terrestrial') and swimming/resting ('aquatic') traces on the same slab. The walking traces are deeper and more defined footprints, while shallow toe scrapes and digit-tip marks with no tail drags indicate swimming or paddling (toe-propping) while afloat. Such toe marks and digit impressions have been seen elsewhere. Brand (1979, 1996) found that, when in water, newts tend to balance on their toes rather than emplacing their footsole on the substrate and Sundberg *et al*. (1990) interpreted *Hylopus hamesi*, based on partial prints and toe scrapes, as swimming traces.

CONCLUSIONS

ANSP 22651, 22652 and 22653 were made by basal tetrapods. ANSP 22651 is identified as *Hylopus* sp. and may have been created by a basal anthracosaur. If this identification is correct, ANSP 22651 represents the second known example of *Hylopus* in Pennsylvania, and only the third area in eastern North America where this taxon has been found. The primary trackways of ANSP 22652 and 22653 are here considered to be *Palaeosauropus* and were possibly produced by a temnospondyl or anthracosaur, however poor preservation and a limited number of measurable footprints make this attribution somewhat tenuous. The swimming traces of ANSP 22652 and 22653 are here interpreted as cf. *H. hamisi*.

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LITERATURE CITED

Barrell, J. 1907. Origin and significance of the Mauch Chunk shale. Bulletin of the Geological Society of America 18: 449-476.

Brand, L. 1979. Field and laboratory studies on the Coconino Sandstone (Permian) vertebrate footprints and their palaeoecological implications. Palaeogeography, Palaeoclimatology, Palaeoecology 28: 25-38.

Brand, L. 1996. Variations in salamander trackways resulting from substrate differences. Journal of Paleontology 70: 1004-1010.

Busanus, J. W. and Hoare, R. D. 1991. Bivalves (Mollusca) from the Mauch Chunk Group (Mississippian, Chesterian) of northern West Virginia and southwestern Pennsylvania. Journal of Paleontology 65: 465-480.

Colbert, E. H. and Schaeffer, B. 1947. Some Mississippian footprints from Indiana. American Journal of Science 245: 614-623.

Cotton, W. D., Hunt, A. P. and Cotton, J. E. 1995. Paleozoic vertebrate tracksites in eastern North America. New Mexico Museum of Natural History and Science Bulletin 6: 189-211.

Dawson, J. W. 1863. The air-breathers of the Coal Period in Nova Scotia. Canadian Naturalist and Geologist 8: 1-8.

Dawson, J. W. 1882. On the results of recent explorations of erect trees containing animal remains in the Coal Formation of Nova Scotia. Proceedings of the Royal Society, London 173: 621-659.

Edmunds, W. 1996. Correlation chart showing suggested revisions of uppermost Devonian through Permian stratigraphy, Pennsylvania. Pennsylvania Geological Survey, Open File Report 96-49: 1-9.

Edmunds, W., Berg, T., Sevon, W., Piotrowski, R., Heyman, L. and Rickard, L. 1979. The Mississippian and Pennsylvanian (Carboniferous) systems in the United States. U.S. Geological Survey, Professional Paper 1110: B1-B33.

Fillmore, D. L., Simpson, E. L. and Lucas, S.G. 2006. An investigation of the *Paleosauropus primaevus* type locality: An ichnofossil assemblage from the Mississippian Mauch Chunk Formation, Schuylkill County, Pennsylvania. Geological Society of America Abstracts with Programs 38(7): 436.

Gradstein, F. M., Ogg, J. G. and Smith, A. G. 2004. A Geologic Time Scale 2004. Cambridge University Press, Cambridge.

Griesmer, J. 1980. A petrographic study of the Mauch Chunk-

Pottsville transition zone in Northeastern Pennsylvania. Unpublished MS thesis, Lehigh University, Bethlehem, PA.

Haubold, H. 1970. Versuch einer Revision der Amphibien-Fährten des Karbon und Perm. Zur Paläontologie und Biostratigraphie des Paläozoikums and Mesozoikums Europas. Freiberger Forschungshefte, Reihe C 262: 83-127.

Haubold, H. 1971. Ichnia Amphibiorum et Reptiliorum fossilium. Handbuch der Paläoherpetologie 18: 1-124.

Hay, O. 1902. Bibiography and catalogue of fossil vertebrata of North America. U. S. Geological Survey Bulletin 179: 1-868.

Hoque, M. U. 1968. Sedimentologic and paleocurrent study of Mauch Chunk sandstones (Mississippian), south-central and western Pennsylvania. American Association of Petroleum Geologists Bulletin 52: 246-263.

Holmes, R. 1984. The Carboniferous amphibian *Proterogyrinus scheeli* Romer, and the early evolution of tetrapods. Philosophical Transactions of the Royal Society of London, Series B 306: 431-524.

Jennings, J. R. 1985. Fossil plants from the Mauch Chunk Formation of Pennsylvania: Morphology of *Adianites antiquus*. Journal of Paleontology 59: 1146-1157.

Lea, I. 1849. On the reptilian footmarks found in the gorge of Sharp Mountain near Pottsville, Pa. Proceedings of the American Philosophical Society 5: 91-94.

Lea, I. 1855. Fossil foot-marks in the red sandstone of Pottsville, Pa. T. K. and P. G. Collins, Philadelphia, 16 pp.

Leonardi, G. 1987. Discussion of the terms and methods. Pp. 43-51. In Leonardi, G. (ed.), Glossary and manual of tetrapod footprint paleoichnology. Departmento Nacional da Producao Mineral, Brasilia.

Leidy, J. 1879. Fossil foot tracks of the anthracite coal measures. Proceedings of the Academy of Natural Sciences of Philadelphia 331: 164-165.

Lucas, S.G., Fillmore, D. L. and Simpson, E. 2006. Tetrapod footprint assemblage of Mississippian Much Chunk Formation, Schuylkill County, Pennsylvania. Geological Society of America (Northeastern Section) Abstracts with Programs 38(2): 64.

Lyell, C. 1843. On the evidence of fossil footprints of a quadruped allied to the *Cheirotherium*, in the coal strata of Pennsylvania. American Journal of Science 148: 81-84.

Matthew, G. 1904. Note on the genus *Hylopus* of Dawson. Bulletin of the Natural History Society of New Brunswick 5: 247-252.

Milner, A. 1993. Biogeography of Palaeozoic tetrapods. Pp. 324-353 in Long, J. (ed.). Palaeozoic vertebrate biostratigraphy and biogeography. Belhaven, London.

Opdyke, N. D. and Divenere, V. J. 2004. The magnetic polarity stratigraphy of the Mauch Chunk Formation, Pennsylvania. Proceedings of the National Academy of Sciences 101: 13423-13427.

Peabody, F. 1959. Trackways of living and fossil salamanders. University of California Publications, Bulletin of the Department of Zoology 63: 1-72.

Rogers, H. 1858. The Geology of Pennsylvania. J. B. Lippincott, Philadelphia.

Ruta, M., Coates, M. I. and Quicke, D. L. J. 2003. Early tetrapod relationships revisited. Biological Reviews 78: 251-345.

Sarjeant, W. A. S. and Mossman, D. 1978. Vertebrate footprints from the Carboniferous sediments of Nova Scotia: A historical review and description of newly discovered forms. Palaeogeography, Palaeoclimatology, Palaeoecology 23: 279-306.

Sundberg, F. A., Bennington, J. B., Wizevich, M. C. and Bambach, R. K. 1990. Upper Carboniferous (Namurian) amphibian trackways from the Bluefield Formation, West Virginia, USA. Ichnos 1: 111-124.

Ward, P., Labandeira, C., Laurin, M. and Berner, R. A. 2006. Confirmation of Romer's Gap as a low oxygen interval constraining the timing of initial arthropod and vertebrate terrestrialization. Proceedings of the National Academy of Sciences, USA 103: 16818-16822.

Wood, G. H., Jr., Trexler, J. P. and Kehn, T. M. 1969. Geology of the west-central part of the Southern Anthracite Field and adjoining areas, Pennsylvania. U.S. Geological Survey Professional Paper 602: 1-150.