J. Paleont., 83(1), 2009, pp. 140–146

0022-3360/09/0083-140$03.00

WALKING TRAILS OF THE GIANT TERRESTRIAL ARTHROPOD *ARTHROPLEURA* FROM THE UPPER CARBONIFEROUS OF KENTUCKY

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INTRODUCTION

ARTHROPLEURIDS WERE terrestrial, millipede-like arthropods. The genus *Arthropleura* Jordan from the Upper Carboniferous reached an enormous size of 2 m or more in length (Hahn et al., 1986). Occurrences are rare and the chronologic and paleogeographic distribution of *Arthropleura* coincides with the tropical Euramerican floral belt of the Carboniferous (Rolfe, 1969). The Carboniferous was a time of high atmospheric O2 levels (35%) compared to the current 21%, which may have favored the development of large terrestrial arthropods of this time (Dudley, 1998; Graham et al., 1997; Berner, 2001). Body fossils of *Arthropleura* range from the Visean to Early Permian (Rolfe, 1969; Schneider and Barthel, 1997), while trackways have been reported from the Visean (Pearson, 1992) to Stephanian (Langiaux and Sotty, 1977; Castro, 1997; Fig. 1). *Arthropleura* fragments have been described from Ohio, Pennsylvania, Illinois, and Nova Scotia. Only four *Arthropleura* trackway sites have been described from North America (New Mexico, Kansas, Nova Scotia, and New Brunswick). Trackways provide information about size and locomotion that is not discernable from fragmentary body fossils.

The specimens of this study are well-preserved casts from which individual tracks and patterns may be distinguished. This is the first report of *Arthropleura* trackways from the Appalachian basin, and the first ever example in association with tetrapod tracks, which confirms that the largest land animals of the time shared the same habitat. This co-occurrence may be more than a coincidence, since the main predators for arthopleurids were probably amphibians (Tasch, 1980). The results of this study will significantly augment the available trackway database for North America and provide new information on the stratigraphic range, mode of life, habitat, and functional morphology of *Arthropleura*.

GEOLOGIC SETTING

Occurrence.—All samples were recovered in float from a roadcut along Kentucky Rt. 23 in Boyd County. The site occurs in the Burnaugh 7.5-minute quadrangle, 300 m north of the Savage Branch, a small tributary to the Big Sandy River (Coordinates: UTM 17 360004E 4245159N, WGS84/NAD83, Elevation: 196 m; Fig. 2).

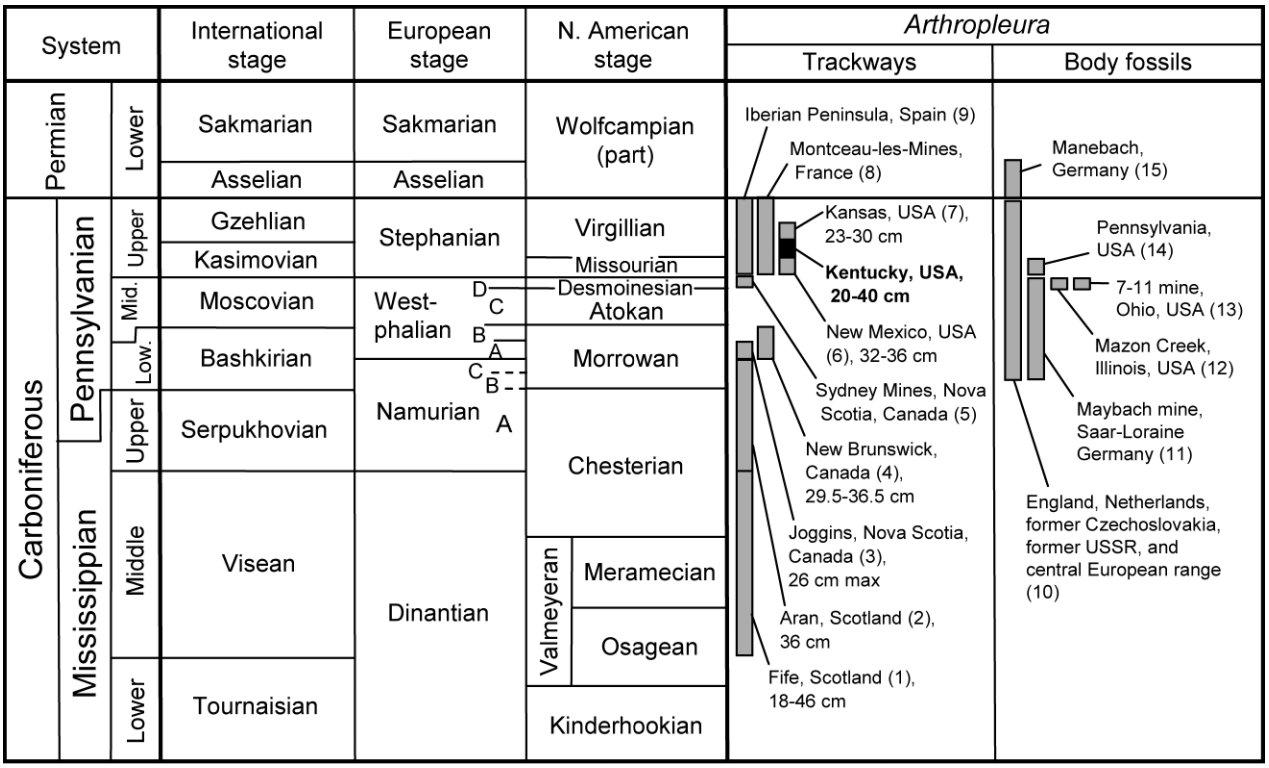

FIGURE *1*—Stratigraphic distribution and age for *Arthropleura* body and trace fossils. Numbered references in table: 1—Pearson (1992); 2—Briggs et al. (1979); 3—Ferguson (1966, 1975); 4—Briggs et al. (1984); 5—Briggs et al. (1984), Ryan (1986), McDonald and Gibling (2001); 6—Hunt et al. (2004); 7—Mangano et al. (2002) 8-Langiaux and Sotty (1977); 9—Castro (1997); 10—Rolfe and Ingham (1967); 11—Waterlot (1934, 1935), Guthoerl (1935, 1936); Rolfe (1969), Becker and Engel (1984); 12—Richardson (1959); 13—Hannibal (1997), Easterday (2001); 14—Proctor, 1998; 15—Schneider and Barthel (1997).

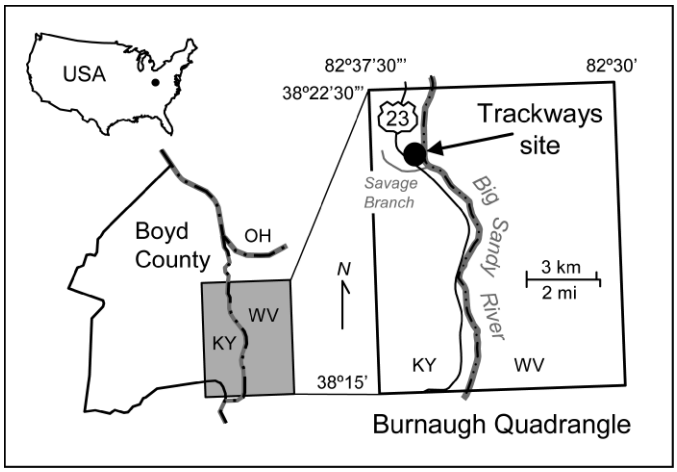

FIGURE 2—Location of trackway site in the Burnaugh 7.5-minute Quadrangle, Boyd County, Kentucky, USA.

Stratigraphic and paleogeographic framework.—The trackways were found in the lower Conemaugh Formation of Kentucky, equivalent to the Glenshaw Formation of the Conemaugh Group in neighboring West Virginia. The Glenshaw Formation consists predominantly of coastal plain fluvial sandstones and red and olive mudrocks deposited in a tropical flood-basin setting (Martino, 2004).

The trackways were derived from a 4-m thick interbedded sandstone and shale interval. The base of the trackway interval is 4.3 m below the base of the Harlem coal and 6.5 m below the base of the Ames limestone (Martino, 2004, figs. 2 and 8D), which makes them earliest Virgilian (Stephanian) in age (Joeckel, 1995, fig. 1; Heckel et al., 1998, fig. 2). The sandstones occur as 3 broad thin sheets and a small channel-fill, and contain graded bedding, parallel lamination, current ripple cross-lamination, rare mudcrack casts, and sparse root traces. The sandstones are interpreted as crevasse splay deposits which accumulated along the margin of an ephemeral lake. The Pittsburgh red shale directly underlies the trackway interval and consists of a regionally developed thick, calcic vertisol (Martino, 2004). This type of paleosol indicates a low-relief terrain with open woodlands and subhumid to semiarid climate with a pronounced dry season (Retallack, 2001). During the Stephanian, such woodlands likely consisted of pteridosperms and gymnosperms with an understory of ferns and, in disturbance-prone areas, sphenopsids (DiMichele and Hook, 1992; Greb et al., 2006).

SYSTEMATIC ICHNOLOGY

Descriptive terminology for *Diplichnites cuithensis* is adopted from Trewin (1994) and Braddy (2001).

Ichnogenus DIPLICHNITES Dawson, 1873
Ichnospecies DIPLICHNITES CUITHENSIS Briggs, Rolfe and Brannan, 1979
Figures 3, 4, 6, 7

Description.—Trackway consisting of two parallel rows of tracks preserved as convex hyporeliefs in fine to very fine, micaceous sandstone that is interbedded with silty shale. Morphology of the tracks falls into three groups: large simple ridges, clusters of small ridges, and evenly spaced small ridges. The width of the track rows increases where the trackway curves (PC-6) compared to straight trackways (PC-5, PC-7). In general, each ridge has a tapered internal morphology. The orientation of simple and composite ridges is typically inclined obliquely to the trackway midline.

In PC-5, the trackway is straight over a distance of 90 cm (based on field photo). The external width is 30.5 to 31.5 cm and internal width is 10 to 12 cm. The width of the track rows is 9.5 to 10.5 cm. Large simple ridges are 3.3 to 4 cm long and spaced at regular intervals of 3.5 to 4.5 cm, and are inclined at 70 to 85 degrees to trackway midline. Clusters containing 5 to 6 imprint casts form elongate ridges 9–11 cm long which are obliquely inclined at an angle of 50 to 70 degrees to the trackway midline. The individual ridges within these clusters are 1.5 to 3 cm in length. The clusters are spaced from 3.5 to 5 cm based on innermost ridge measured parallel to the trackway midline. A gutter cast occurs as prominent ridge along the lower side of the trackway margin (C. Maples, personal commun., 2007). The recurrence of a distinctive pair of footfalls indicates a repeat distance of 20 cm (Figs. 4 and 7).

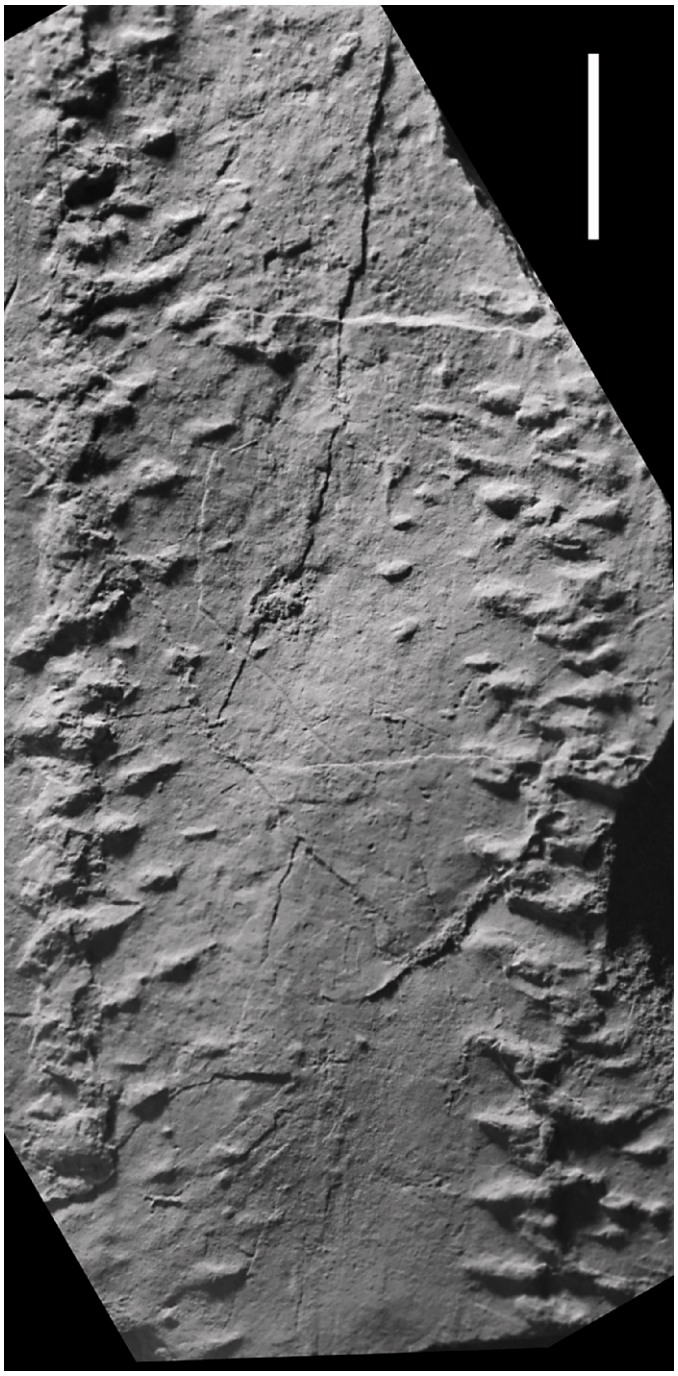

FIGURE 3—*Diplichnites cuithensis*, specimen PC-5. Trackway preserved as convex hyporelief. Note footfall clusters in right series toward top, and gutter cast along left side of trackway. Scale bar is 10 cm. Low angle illumination is from top.

In PC-6, the external width of the trackway ranges from 30 to 42 cm and preserved length is 47 cm, with a slight curvature at one end. The track row width ranges from 7 to 21 cm with the row on the outside of the meander

FIGURE 4—*Diplichnites cuithensis*, specimen PC-6, convex hyporelief. Note cast of tetrapod manus (*Limnopus glenshawensis*) below 10 cm bar scale in upper left of photo. Crescentic shaped footfalls in middle of photo indicate changing direction of *Arthropleura* toward ''left.'' Fracture in lower left separates two horizons with same tracks indicating that most of footfalls are preserved as shallow undertracks. Low angle illumination from upper left.

having the greatest width. Most ridges are tapered internally in morphology and have a length of 1.4–3.5 cm, but crescentic ridges also occur in the left track row. A cast of a tetrapod manus also occurs on this specimen (Figs. 4, 5.1).

In PC-7, the trackway is smaller and simpler in morphology with an external width of 20 cm, an internal width of 12 to 13 cm, and a track row width of 4 cm. Ridges 1 to 2.5 cm long are oriented perpendicular to trackway midline.

Material.—10016-PC-5, 10017-PC-6, 10018-PC-7 stored at Marshall University, Department of Geology, Museum Collection.

ICHNOGENUS LIMNOPUS Marsh, 1894
LIMNOPUS GLENSHAWENSIS Martino, 1991
Figure 5.1, 5.2

Description.—Tetradactyl manus, digits short (10 to 15 mm long, about 10 mm wide) with rounded terminations preserved as convex hyporelief and semirelief. Manus width: 75–80 mm, length: 53?–57 mm. Digit terminations often deeper and subspherical with diameter of about 10 mm. Digit I is furthest medial (''thumb''); digit IV is furthest lateral (''little finger'').

Material.—10017-PC-6 and 10019-PC-8 stored at Marshall University, Department of Geology, Museum Collection.

INTERPRETATION AND DISCUSSION

Trace makers.—*Arthropleura* is the likely trace maker for *Diplichnites cuithensis* in PC-5, PC-6, and PC-7. *Arthropleura* is known to have made tracks of similar scale (e.g., Briggs et al., 1979). *Arthropleura* fragments have been found in Ohio and Pennsylvania in Desmoinesian and Missourian strata (McComas and Mapes, 1988; Hannibal, 1997). Although Hibbertopteroid eurypterids may have grown as large, they produced trackways which had two track rows of appendage prints elongated parallel to the trackway midline and a sub-central groove produced by dragging the posterior part of the body (Whyte, 2005).

Trackways of *Eryops* (*Limnopus glenshawensis*) have been described from lower Conemaugh strata in West Virginia about 25 km from the Savage Branch locality. PC-6 and PC-8 both represent left manus footfalls as seen from the bottom of the trackway and are about 25% smaller in width than the average previously reported from West Virginia (Martino, 1991, figs. 7–9, table 7).

Taphonomy.—The tracks are preserved along bedding planes where mud was overlain by sand. Falling water level may have exposed cohesive lake bed muds, making them firm but still soft enough to preserve impressions; they were subsequently baked hard enough to resist erosion and were infilled by sand during the next flooding event. In PC-6, two separate horizons separated by 4 mm of sandstone preserve tracks from the same track row (Fig. 4). This indicates that many imprint casts from *Arthropleura* are preserved as shallow undertracks, which also seems likely for the manus track based on its low relief. The occurrence of tracks from *Eryops* and *Arthropleura* from the same facies and as undertracks on the same bedding plane indicates they both frequented the lake margin habitat at, or very close to, the same time.

Trace maker morphology.—Although several species of *Arthropleura* lived during the Stephanian (*A. armata*, *A. fayoli*), only *Arthropleura armata* has been reconstructed (Rolfe, 1969; Briggs and Almond, 1994). The body was trilobed with nearly uniform width except for anterior and posterior tapering (Rolfe, 1969; Hahn et al., 1986). Rolfe (1969) showed 28 tergites with one pair of legs per tergite, but subsequently Briggs and Almond (1994) concluded that at least some trunk tergites had 2 pairs of walking legs. Rolfe's (1969) *A. armata* was 50 cm wide with legs ranging from 10 to 15 cm in length, and with shorter legs at the anterior and posterior margins. Maximum leg length was 30% of maximum body width. It had a length of 1.73 m and width of 50 cm,

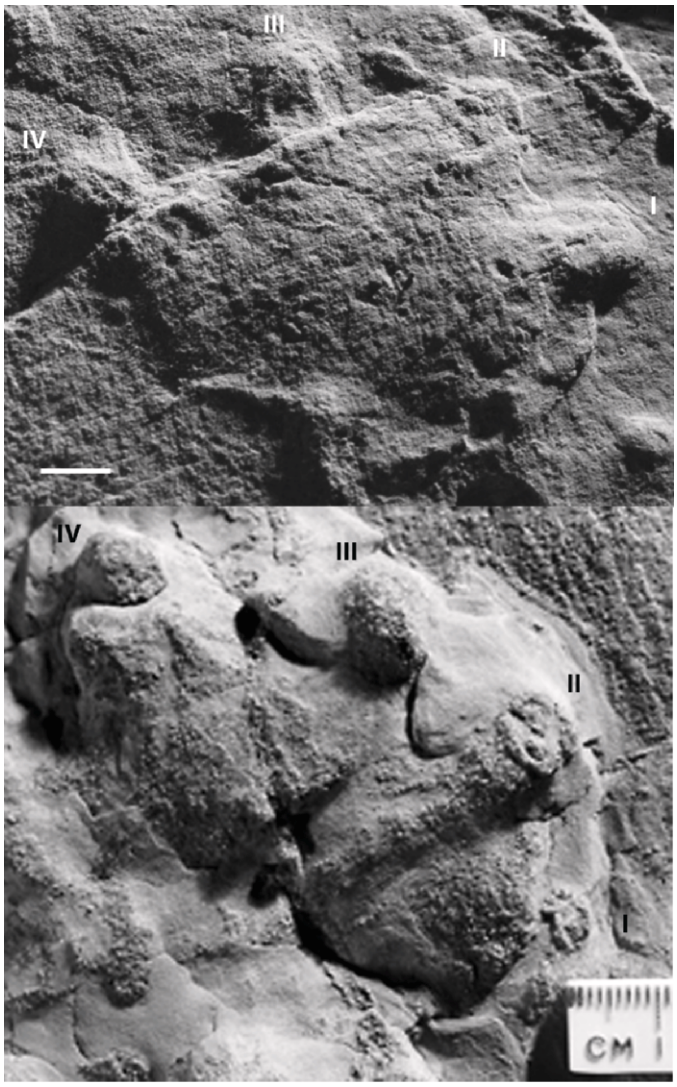

FIGURE 5—Casts of tetradactyl manus from Eryopoid amphibian; digits numbered I–IV (Martino, 1991). Scale = 1 cm. Samples PC-6 above (5.1), and PC-8 below (5.2). Low angle illumination from top.

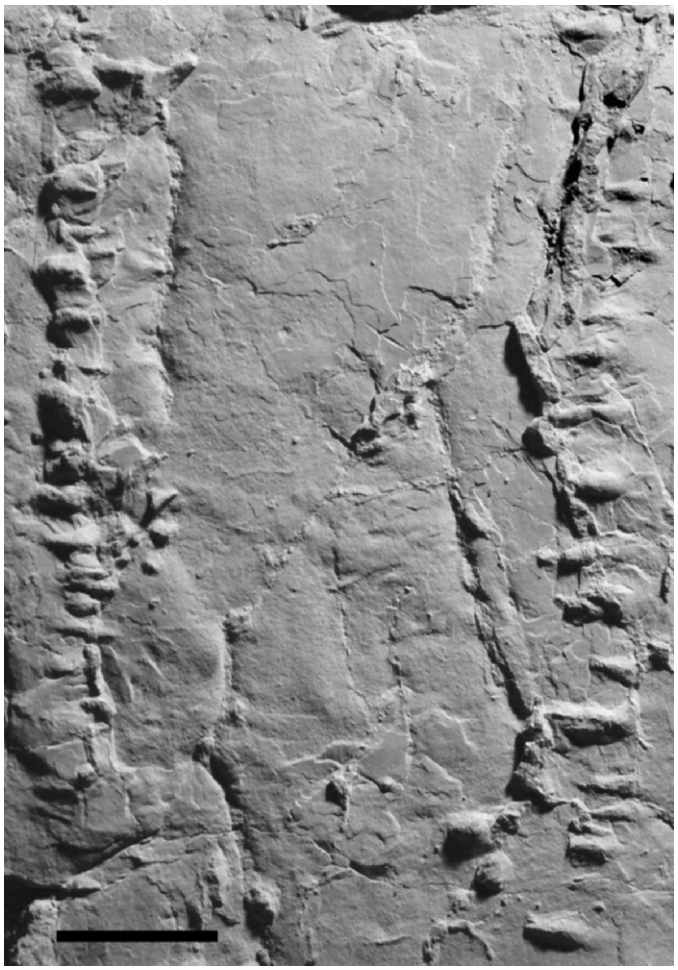

FIGURE 6—*Diplichnites cuithensis*, specimen PC-7. Bar scale = 5 cm, low angle illumination from top.

giving it a length/width ratio of 3.46. Rolfe and Ingham (1967) reported a length of 85 cm and width of 24.5 cm based on the largest most complete body fossil known, which yields a length/width ratio of 3.47.

The trackways in PC-5 and PC-6 are similar in width and may have been made by the same individual. Using the range of length/width ratios discussed above, trace maker(s) for PC-5 and PC-6 was 106 cm in length. The maximum leg length would have been 9.3 cm; this compares well with an estimate of 8 to 9 cm based on previous analysis of a Namurian trackway from Scotland (Briggs et al., 1979). Specimen PC-7, only 20 cm wide, would have been made by an *Arthropleura* approximately 69 cm long.

The number of walking legs can be determined from the number of footfalls that occur between successive imprints of the same appendage which occur at 20 cm intervals in PC-5 (Fig. 7). Trampling and dragging the carapace greatly reduced the number of distinct footfalls preserved along the left side of PC-5; along the upper right side, at least 25 footfalls occur within a 20 cm interval, indicating that this *Arthropleura* had a minimum of 25 pairs of walking legs. It is likely that if there were 2 pairs of walking legs per tergite, that at least some of the ridges represent coincident footfalls that are not individually distinguishable. Otherwise the trace maker would have had only 12–13 segments, and an *Arthropleura* that was 30 cm wide and 106 cm long would most likely have had more than 12–13 segments, based on what is known from body fossils (Rolfe, 1979).

Gait.—In millipedes, locomotion is accomplished by a propulsive backstroke, while recovery occurs during the forward stroke. The stride length can be determined by using footfalls from the shorter appendages, which are located closer to the trackway midline than the majority and less likely to be blurred by subsequent trampling. In specimen PC-5, two closely spaced footfalls of shorter appendages occur four times at a uniform interval of 20 cm (Fig. 7).

Wilson (2003) surveyed available *Arthropleura* trackways from North America and Europe and found two distinct groups of strides, which she compared to trackways made by the living (much smaller) penicillate millipede *Polyxenus*. At slow speeds, *Polyxenus* footfalls plot in a continuous series. At faster speeds, which produced a longer stride, footfalls were grouped into crescentic clusters. Specimen PC-5 shows discrete clustering of 5 to 6 footfalls at regular spacing, suggesting a faster speed than recorded in PC-6 and PC-7.

The pattern of gait (i.e., ratio of duration of forward stroke to that of backstroke) in PC-5 can be estimated from the stride (20 cm), appendage length (9.3 cm), and assumed angle of appendage swing (Briggs et al., 1979). The angle of appendage swing will be proportional to the speed at which the animal is moving, and ranged through an angle up to 60° in *Arthropleura* (Briggs et al.,

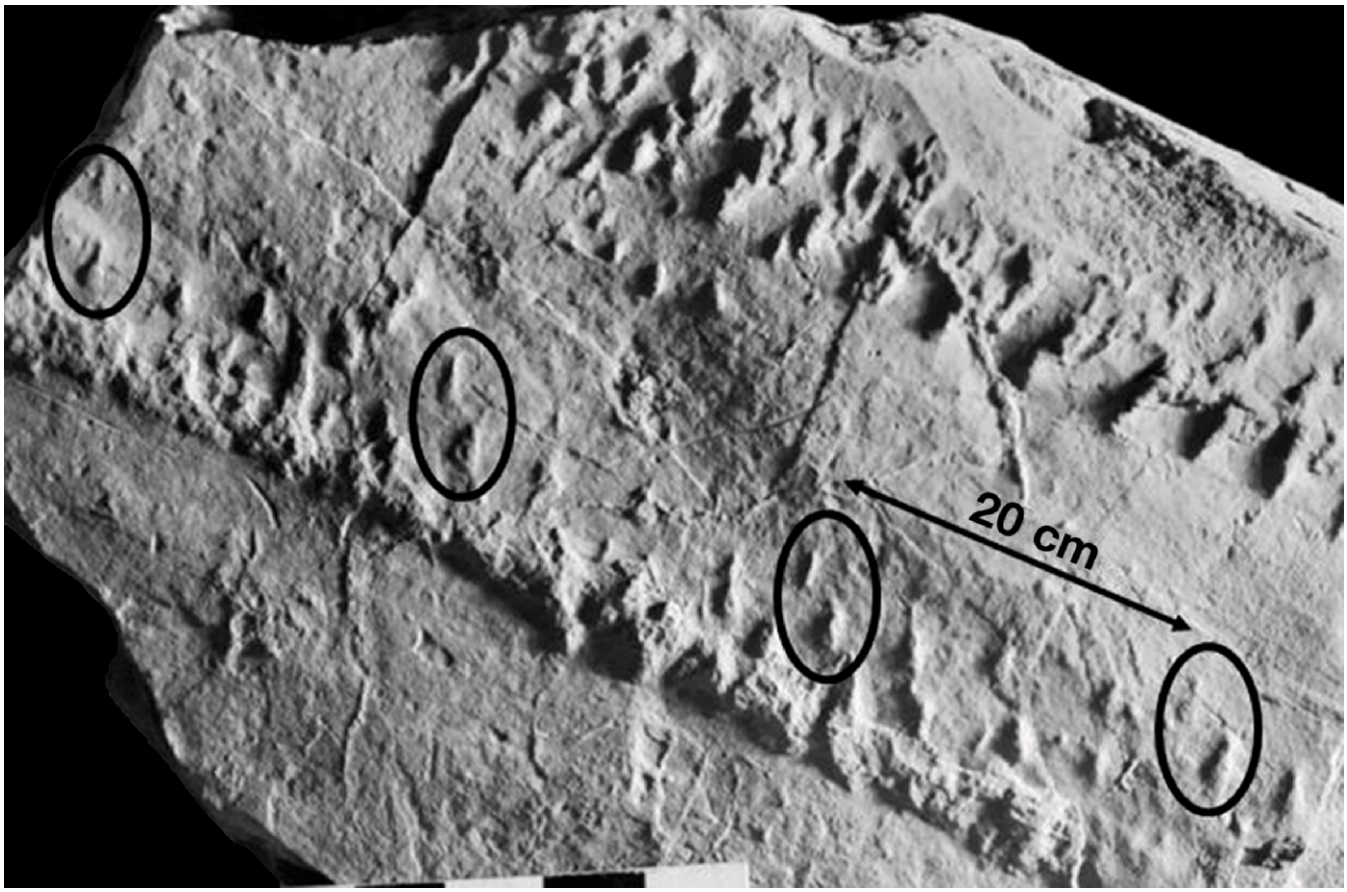

FIGURE 7—Stride length of 20 cm interpreted from specimen PC-5 using footfalls from a pair of shorter appendages (circled) which are located closer to the trackway midline. Low angle illumination from right.

1979). An individual with a 9.3 cm leg length would be propelled forward 9.3 cm during the backstroke and 10.7 cm during the forestroke. These values indicate a gait pattern of 10.7/9.3 or 55.5 to 46.5 and imply that 46.5% of the walking appendages were in contact with the ground. When less than half the appendages are in contact with the ground, this suggests a higher geared gait, and relatively rapid locomotion. For *Arthropleura*, such a gait would be more likely when moving across open firm ground (Briggs et al., 1979), like that of the exposed splay deposits inferred for the study location. Manton (1954) found that a freely running *Polydesmus angustus* has 41% of appendages in contact with the ground (high gear). The same individual used a slower, more powerful gait with 78% of appendages in contact (lower gear, ''4-wheel drive'') when moving under resistance.

The prominent gutter cast in PC-5 suggests that the carapace may have been dragged through the sediment as *Arthropleura* walked transverse to a minor slope (C. Maples, personal commun., 2007) that would be common on splays and lake margins.

In PC-6, an increase in the track row width occurs from top to bottom in Figure 4, which corresponds to increased curvature of the track caused by a change in direction of locomotion. This phenomenon was previously reported by Briggs et al. (1984) in a Westphalian trackway from Canada. Footfalls in the left track row produced crescent-shaped ridges that and taper toward the trackway midline. The forward direction would be toward the top of the picture. As *Arthropleura* turned left, maximum track row width (width 21 cm) was achieved. As it turned, it dragged its clawed foot back toward its body and upward.

Paleoecology.—*Arthropleura* was an herbivore or possibly an omnivore (Rolfe, 1969). A juvenile specimen of *A. armata* had a gut packed with lycopod fragments (Rolfe and Ingham, 1967). *Arthropleura* ranged through habitats including forested floors of peat swamps (Rolfe, 1969) to river floodplain environments with an open mesophilic vegetation (Lucas et al., 2005). Manton (1953, 1954) compared the habits of *Arthropleura* to those of modern flat-backed millipedes such as *Polydesmida*, which are well-adapted to pushing their way beneath layers of damp leaf litter. *Arthropleura* likely sought out aquatic environments for support when molting (Hahn et al., 1986) and would have been especially vulnerable to predators at this time.

The superfamily *Eryopoidea* was the dominant temnospondyl amphibian group in the Late Pennsylvanian (Carroll, 1988). *Eryops* lived in and around rivers and lakes as modern alligators do today and probably fed mainly on fish, supplemented by terrestrial animals (Colbert, 1980). The presence of an opportunistic *Eryops* may have induced an *Arthropleura* to ''run'' across open areas between the forest and the water (Fig. 8). Other possible predators included another temnospondyl, *Cochleosaurus*, which grew to lengths of 1.6 m (Milner, 1980), as well as anthracosaurs (e.g., *Pholiderpeton*) up to 4 m long (Smithson, 1985; Clack, 2002), and large rhizodont fish, which grew to lengths in excess of 7 m.

The disappearance of *Arthropleura* coincides with that of the Euramerican floral belt, suggesting its extinction resulted from loss of habitat (Rolfe, 1969), although increasing size of potential predators including reptiles and amphibians during the Late Pennsylvanian-Early Permian may also have contributed to their demise.

ACKNOWLEDGMENTS

Reviewers D. E. G. Briggs and C. Maples provided many helpful comments from which this paper benefited. J. Calder initially identified PC-5 as the

FIGURE *8*—Reconstruction of an *Eryops* stalking an *Arthropleura* along the dessicating margins of a Late Pennsylvanian ephemeral lake.

trackway of *Arthropleura* from a field photo in 1990. J. Hannibal provided encouragement and reprints. J. E. Martino recovered specimen PC-8. Thanks are due to A. Johnson for enhancement of photos. Various phases of this project have been supported by grants to Martino from the West Virginia Geological Survey, Marshall University Graduate School, and the Petroleum Research Fund administered by the American Chemical Society (grant 34516-B8).

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Accepted 5 September 2008