Morphology and taphonomy of an exceptional trackway from the Flathead Sandstone (Middle Cambrian) of Wyoming

Donald W. Boyd

Department of Geology and Geophysics, The University of Wyoming, Laramie, Wyoming 82071-3006, U.S.A.

email: boyd@uwyo.edu

ABSTRACT

Two sandstone slabs from the Cambrian Flathead Sandstone of Wyoming exhibit different preservational modes of an exceptionally large and unusual trackway. On the smaller slab, the trackway is a depression on the top of the bed (concave epirelief). A greater length of the trackway is preserved on the larger slab, where it is a raised feature on the bottom of the bed (convex hyporelief). The latter trace is a cast of the original trackway made on a now-missing mud layer, whereas the epirelief trace likely represents an undertrack.

The original trackway consisted of two parallel pockmarked furrows separated by a broad ridge. Individual depressions in furrows cannot be matched across the ridge and do not contain discrete scratch marks. At one place the linear succession of imprints comprising one furrow changes to a scattering of discrete pits. Although taxonomic identity of the trackway's maker is uncertain, the animal was bilaterally symmetrical and had paired appendages like an arthropod or an onychophoran.

The sole of the large slab exhibits several unilobate traces that intersect the major trackway as well as one another. Their smooth surfaces, lack of marginal ridges, and discontinuous nature suggest that they were made by burrowers or furrowers following the sand/mud interface subsequent to casting of the major trackway. Their origin remains problematic.

KEY WORDS: Cambrian, Flathead Formation, ichnology, Paleozoic, taphonomy, trace fossil, undertrack, Wyoming.

INTRODUCTION

The purpose of this contribution is to describe and interpret a Cambrian trackway of unusual size and morphology. The evidence, limited to the surfaces of two sandstone slabs salvaged from a rockfall, does not allow a confident identification of the trackmaker. It does, however, add support to the evidence from Lagerstätten (e.g., Conway-Morris, 1998) that large invertebrates were an important part of Cambrian faunas.

The slabs studied for this report were discovered by Thomas D. Anderson in a rockfall at the base of a road cut in the Flathead Sandstone in Wind River Canyon, central Wyoming (Fig. 1). The two slabs (Figs. 2 and 3), a latex peel (Fig. 4) made from the large slab, and a polished section from the small slab are housed with the Collection of Fossil Invertebrates, Department of Geology and Geophysics, University of Wyoming (specimen numbers A4088 a–d). Locality information and other pertinent data are recorded in the electronic database for that collection, which is supervised by the Department's Collections Manager.

SOURCE OF TRACKWAY-BEARING SLABS

The only possible source for the rockfall that included the slabs under discussion is the cliff of Flathead Sandstone shown in Figure 1*B*. Examination of the section yielded no evidence of traces like those in Figures 2 and 3. However, sandstone beds similar in lithology and bedding to that of the figured ones are present in the uppermost part of the cliff, and one such layer includes a colonization surface featuring diminutive burrows identical to those shown in Figure 5. These similarities suggest that the trackway slabs came from this part of the exposure, an interval 15–21 m (50–70 ft) below the contact with the overlying Gros Ventre Formation.

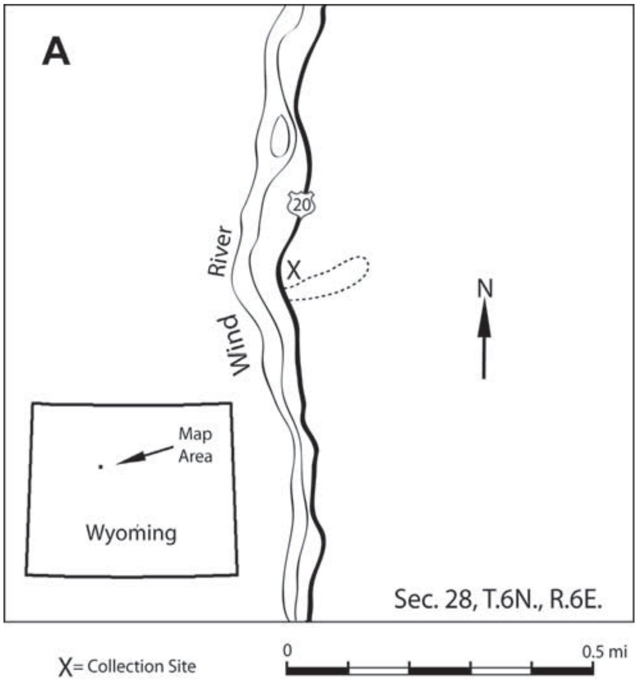

Figure 1. ***A***, Map showing location of collecting site (x) in Wind River Canyon, central Wyoming. Dashed line = private lane. Detail from U.S. Geological Survey Boysen 7.5' quadrangle. ***B (facing page)***, Cliff of Flathead Sandstone at intersection of private lane and U.S. Highway 20. Specimens were collected from rockfall originally located several meters to right of white-topped highway marker (personal communication, T. Anderson, 2008); height of marker = 2.1 m (7 ft).

The Flathead Sandstone consists mainly of cross-stratified coarse- to fine-grained quartz sandstone deposited as the Cambrian sea transgressed across an eroded terrane of Precambrian crystalline rocks (Middleton et al., 1980). Minor intercalations of red mudstone become more common upward in the formation. As interpreted by Middleton et al. (1980), depositional environments range from foreshore and upper shoreface to intertidal flats and lagoons. These authors note that, although the formation lacks datable fossils, overlying shales at several Wyoming and Montana localities contain Middle Cambrian trilobites. Considering the regional distribution of the trilobite data, A. R. Palmer (personal communication, 2009) considers the Wind River Canyon Flathead strata to be no older than early Middle Cambrian.

At the Wind River Canyon exposure, thick sandstone beds in the lower part of the roadcut are characterized by north-dipping (to left in Fig. 1*B*) planar cross bedding. They are separated by thin layers of reddish-brown mudstone, a lithology that becomes more prominent in the upper part of the cliff, where sandstones are typically thinner and less conspicuously cross bedded. Common Cambrian burrows such as *Monocraterion* and *Skolithos* dominate some of the uppermost ledges, including those that step back from the cliff face. One especially prominent unit of "piperock" (crowded *Skolithos*) is 3.4 m (11 ft) thick. Considered together, the animals that produced these fossils might have lived in shallow marine to emergent depositional environments like those hypothesized by Middleton et al. (1980).

GENERAL DESCRIPTION OF SLABS

Maximum dimensions of the small slab (Fig. 2) are 45 cm (length), 34 cm (width), and 4 cm (thickness). Remnants of the underlying layer, a pale brown mudstone, adhere to the undulatory (1 cm relief) bottom surface. The upper surface is distinctively colored; approximately half the area is brown and the remainder pale green. The trackway is pale green except for a brown area on part of the medial ridge. The bed surface, excluding the trackway, exhibits minor relief (e.g., 2.5 mm) in the form of small pits and furrows. The irregularity is enhanced by scattered coarse grains protruding from the fine-grained matrix. A uniform coat (0.05 to 0.1 mm thick) consisting of chlorite and illite (XRD by N. G. Swoboda-Colberg, personal communication, 2008) is continuous over the surface, covering coarse and fine grains alike.

The slab is predominantly fine-grained quartz sandstone, but a thin (5 mm) zone beneath the surface coat is characterized by coarse to very coarse subrounded quartz grains unevenly distributed through the fine-grained matrix (Fig. 6*A*). Some of the large grains are in contact with one another, whereas others are matrix-supported. On the slab sides (e.g., Fig. 6*B*), no erosional discontinuity separates the bimodal layer from underlying fine-grained material, which continues downward to an irregular parting surface 8 to 15 mm below the top of the slab. Below that surface, the fine-grained sandstone is prominently marked by light-brown Liesegang bands.

As shown in Figure 6, the trackway is an impression made by bending but not breaking the underlying laminae. The distinctive texture of the overall surface of the slab is also present in the troughs and central ridge of the trackway.

Maximum dimensions of the large slab are 90 cm (length), 45 cm (width), and 15 cm (thickness). As discussed below, the surface shown in Figure 3 is the underside of the slab. It is coated with a clay-like film similar in coloration to that of the small slab. The entire surface is characterized by irregular microtopography consisting of millimeter- to centimeter-scale bulges and depressions (e.g., to left of scale in Fig. 3). The resemblance to the small-scale load structures illustrated by Porada and Bouougri (2007, fig. 6(a)-4G) is striking. These authors note that load structures are found on the soles of sandstones overlying mudstone, whereas similar microtopography of microbially-induced structures occurs on upper surfaces of sandstone beds.

The slab consists of several poorly defined layers of fine-grained quartz sandstone. As shown in Figure 5, the mid-thickness interval exhibits slightly inclined lamination penetrated by numerous small-diameter burrows. The burrowed zone is traceable on three of the four sides of the slab.

TOP AND BOTTOM INTERPRETATION

Two features visible on sides of the large slab indicate that the trace fossils are on the bottom of the bed and are preserved in convex hyporelief. A colonization surface similar to that illustrated by Bromley (1996, fig. 10.16) is separated from the trace-bearing surface by approximately 10 cm of sandstone (Fig. 5). The colonizers were diminutive organisms that produced irregularly vertical burrows extending varying distances in the direction of the trace-bearing surface. A typical burrow is 1 mm in diameter, 3 cm long, open, and with a halo of brown stain on adjacent sand grains. On one side of the slab, a thin layer 2 cm below the tracked surface is missing for a distance of 14 cm. The gap is occupied by a convex-upward (in terms of Fig. 3) body of sand,

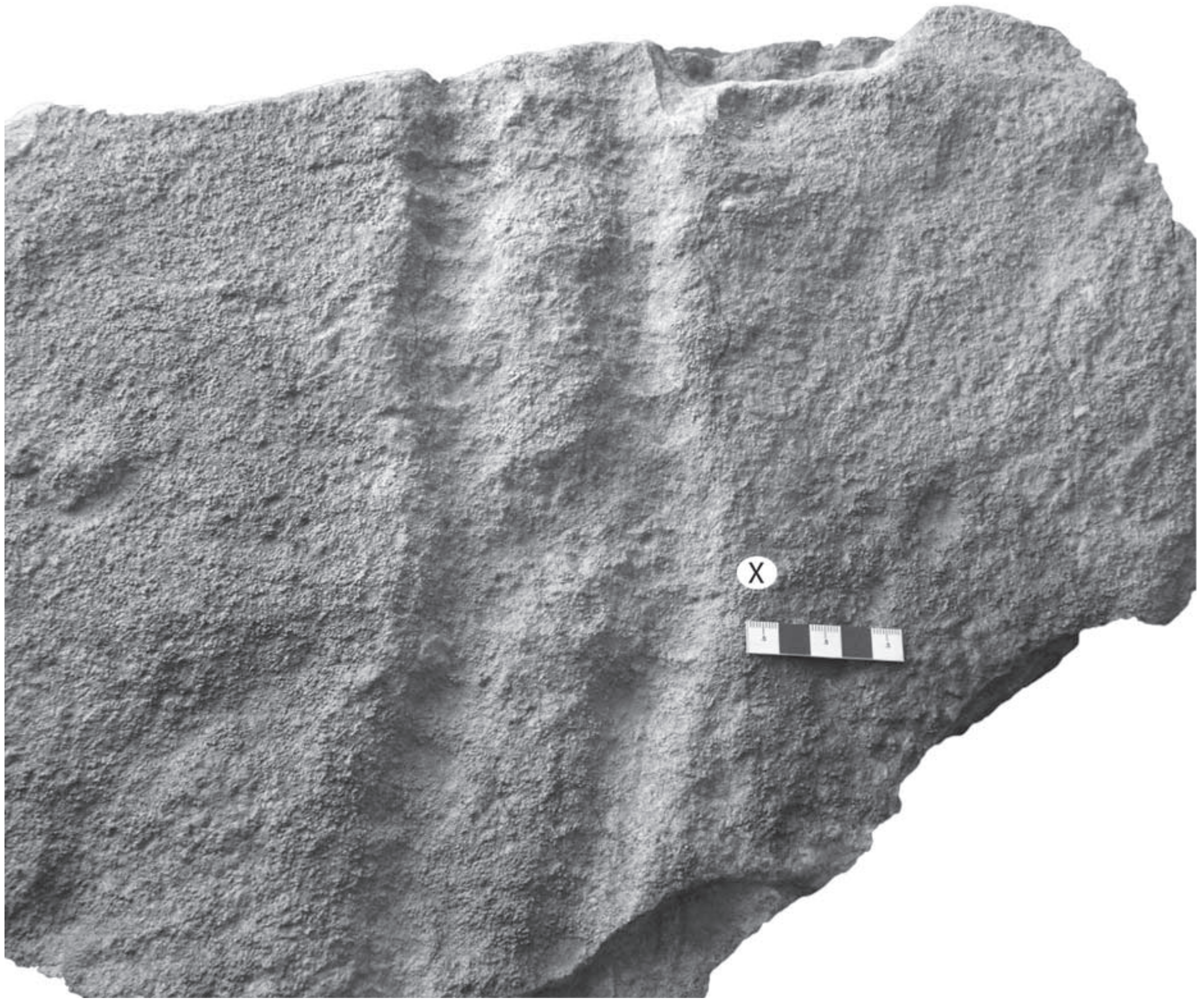

Figure 2. Small slab of Flathead Sandstone with trackway on bed top, preserved in concave epirelief. Specimen found in rubble at base of cliff (Fig. 1*B*). Symbol "x" marks equivalent locations on Figures 2, 3, and 4. Scale = 5 cm. UW A4088a.

interpreted as the product of cut-and-fill surface processes.

The sides of the small slab exhibit small cut-and-fill features interrupting lamination adjacent to the untracked surface. They indicate that the trackway-bearing surface is the bed top and that the trace is preserved in concave epirelief.

RELATIONSHIP OF SLABS

In width, curvature, and general pattern of ridges and grooves, the trackway on the small slab (Fig. 2) can be matched with an equivalent length of trackway at the right end of the large slab (Fig. 3*A*), indicating that the slabs represent partial part-counterpart preservation of the same trace. When the trace-bearing surface of the small slab is positioned over the equivalent part of the large slab, the fit is imperfect and a distance of 3 to 4 mm separates the two surfaces. Considered together with the mud veneers on both slabs, this indicates that mudstone originally separated the two sandstone beds.

These stratal relationships suggest that the trace was created on the surface of the mud layer and cast at the sole of the overlying bed of sand when it was deposited over the mud. The weight of subsequently deposited sand, or perhaps the weight of the trace-maker, was sufficient to press the mud downward and deform the surface of underlying unlithified sand.

In the above scenario the small-slab trace is a variety of compressive undertrace (Seilacher, 2007a, p. 8). Undertraces of this type are commonly formed when the tracemaker's weight is sufficient to deform bedding surfaces below the one directly contacted by the animal. In the Flathead case, neither the weight of the tracemaker nor the thickness of mud originally separating trace and undertrace is known, so the animal cannot be ruled out as the source of pressure that produced the trackway copy on the small slab. Overburden weight, however, has an argument in its favor as the source of pressure. Whereas downward-directed pressure from the animal was localized on an unconfined mud surface and occurred only during making of the trace, overburden weight had a cumulative effect and pressure affected a broad area of mud/sand interface that included the trackway cast.

SURFACE VERSUS INTRASTRATAL ORIGIN OF LARGE-SLAB TRACES

Literature on the common Cambrian trace fossil *Cruziana* exemplifies the difficulty of determining whether invertebrate trackways expressed as convex hyporeliefs represent the makers' activity at the sediment surface or beneath it. Although ichnologists generally agree that *Cruziana* is the trace of a trilobite or similar arthropod (e.g., Seilacher, 2007b), they have differed strongly concerning the site of the makers' activity. The evidence cited in this and similar debates is applicable to interpretation of the Flathead traces.

In arguing against origin of *Cruziana* as an open furrow at a mud/water interface, Seilacher (1970) and others (e.g., Goldring, 1985) have maintained that such traces would probably be smoothed or removed by currents bringing the overlying sand. Their preferred alternative envisions the tracemaker plowing through a thin layer of sand before encountering underlying mud, then producing the trace by digging at the sand/mud interface. This two-fold process was considered unnecessary by Crimes (1975), who presented reasons to believe traces on a mud surface could survive and be cast by the influx of sand.

Cross sections of *Cruziana* casts have been cited as evidence both for and against open-furrow origin. Cross-laminated internal structure (Baldwin, 1977) indicates a seafloor depression filled by physical processes, whereas backfilled and bioturbated casts with lensoid cross section imply filling of a subsurface burrow (Goldring, 1985). Intrastratal origin can also be suspected for convex hyporelief trails that begin or end by gradual loss of relief on the sole. Such terminations suggest that the maker penetrated and/or exited a mud layer at an oblique angle to an existing sand/mud interface (Goldring, 1985).

Large Cambrian trackways assigned to the ichnogenus *Climactichnites* had been interpreted as trails produced at the sediment surface (e.g., Yochelson and Fedonkin, 1993), but Getty and Hagadorn (2008; 2009) recognize two ichnospecies, one for surface trails and one for burrows. Criteria for the latter category include inclination to bedding, elliptical cross section, and lack of lateral ridges. The absence of lateral ridges is taken as evidence for intrastratal origin because an animal moving forward while encapsulated in sand could not displace it by pushing it to the sides as would an animal plowing through surface sediment.

In light of the criteria described above, and in spite of some contradictory evidence described below, I conclude that the convex hyporelief traces shown in Figure 3 include representatives of both surface and subsurface activity. The major trackway maintains its relief and general morphology on a single bedding surface throughout its course as would be expected of a trail left by an animal crawling on a seafloor or tidal flat. By contrast, the several smooth-surfaced unilobate traces (Fig. 3a–c) vary in relief along their respective lengths, suggesting activity of a burrower generally following a sand/mud interface but occasionally moving above or below it. The lack of lateral ridges on the smooth traces lends support for their intrastratal origin. The maker of the major trackway produced no conspicuous marginal ridges probably because locomotion was by crawling and/or walking rather than plowing. Moreover, any grooves that would be evidence for lateral ridges were overprinted when the casts of individual footprints were partially flattened by loading of subsequent deposits.

The contrast between the sharp surface detail of the major trackway and the smooth surfaces of the other traces (Fig. 3a–c) may be due to surface versus subsurface origin. The major trackway interrupts the surrounding surface, whereas the smooth traces rise from it like wrinkles in a carpet. Relationships at trace intersections indicate that the major trackway

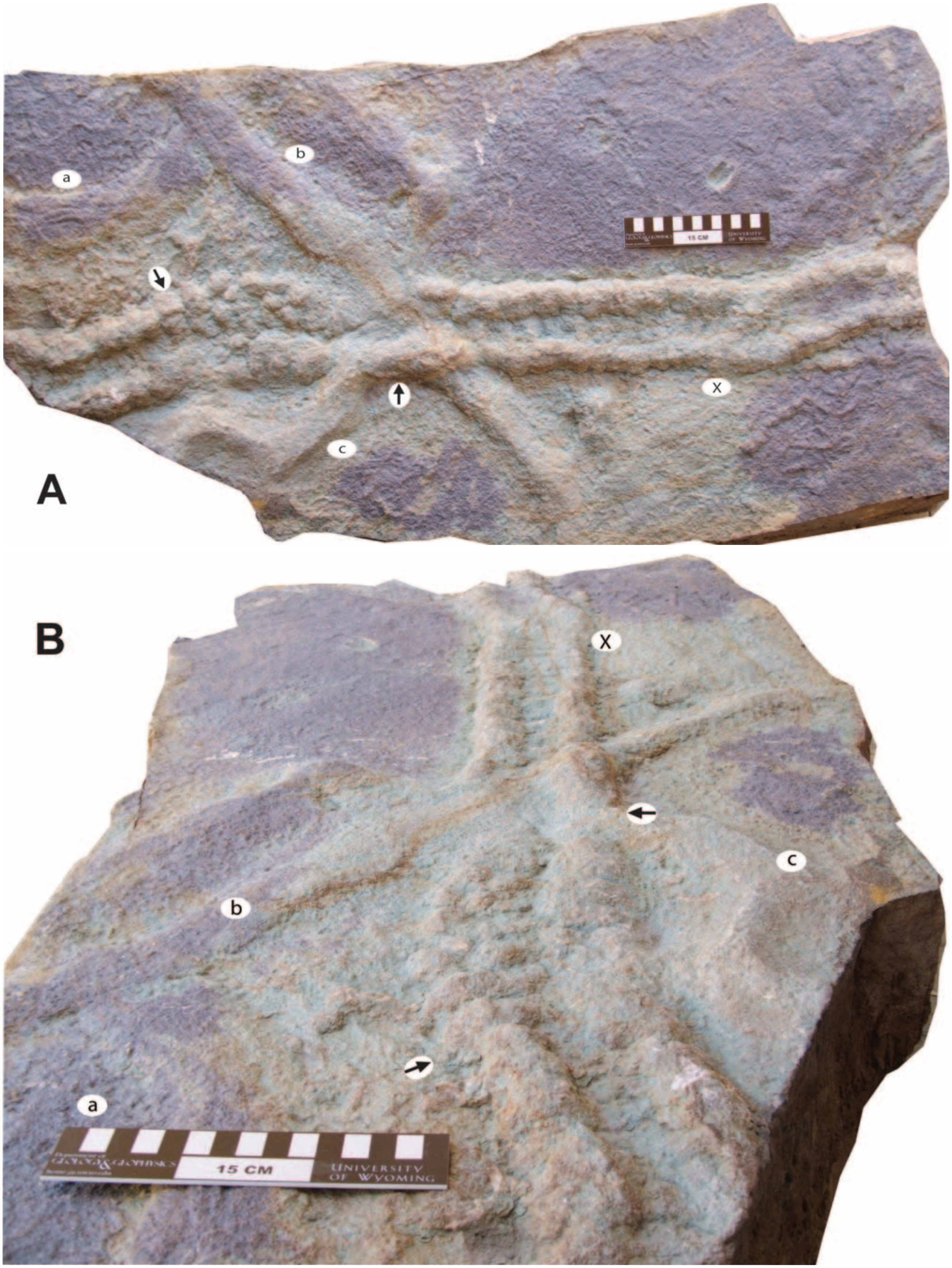
a
b
X
c
A
15 CM
UNIVERSITY OF WYOMING
B
X
c
b
a
15 CM
UNIVERSITY OF WYOMING

Figure 3, facing page. ***A*****,** Sole of large slab of Flathead Sandstone collected from same rockfall as specimen in Figure 2. Major trace (left to right in photo) interpreted as cast of trackway made on subjacent mud; smooth traces (a–c) interpreted as bedding-parallel burrows. Symbol "x" = reference point on major trackway for comparison with Figures 2, 3*B*, and 4; left arrow = change in morphology of upper border of major trackway (narrow ridge on left; multiple knobs on right); right arrow = reworked part of lower border of major trackway. Scale = 15 cm. UW A4088b. ***B*****,** Oblique view of sole of large slab; foreground features are at left in Figure 3*A*. Note transverse marks between bordering ridges of major trackway. Symbols as in Figure 3*A*.

was present before the smooth trails were made. The possibility that the smooth-surfaced forms are undertraces imprinted on the preexisting major trackway is unlikely, because the slab sides show no nested laminae above the hyporeliefs in question.

The maker of the long trace crossing the sole from upper left to lower right (Fig. 3*A*b) appears to have encountered the major trackway after the latter had already been cast by overlying sand. This is suggested by the difference between the two borders of the major trackway where crossed by the smooth trace. As shown in Figure 3*A,* the upper border is smoothed out at the intersection, whereas the lower border is not. Apparently the maker of the smooth trace was moving intrastratally at the same level as the cast where the erasure occurred but was moving above it where crossing the lower border. It should be noted that the lower border exhibits independent alteration where intersected by another tracemaker. The animal constructing that trail (Fig. 3*A*c) abruptly changed course twice outside the major trackway, although direction of movement is uncertain. In any case, as viewed in Figure 3*A*, the smooth trail intersects the lower margin of the major trackway and appears to merge with it for a distance of approximately 10 cm to the right of the intersection. In this interval the knobby topography typical of the trackway borders is absent. Perhaps the tracemaker of Figure 3*A*c plowed and deepened the preexisting border. If so, the distal end of the reworked interval presumably marks the point of exit or entry (depending on direction of movement) of the burrower across the sand/mud interface.

An intrastratal origin for the smooth traces (Fig. 3a–c) seems reasonable given the evidence cited above and the resemblance to the lower half of long, narrow, bedding-plane-parallel burrows of the ichnogenus *Psammichnites* (e.g., Seilacher, 2007a, p. 81) and *Olivellites* (e.g., Yochelson and Schindel, 1978). These traces, however, exhibit an elliptical outline in cross section as would be expected of a burrow. Examination of the sides of the large slab at places where the smooth traces are truncated shows no evidence of disturbed sediment or backfill lamination in sand subjacent to each sole convexity. Perhaps the sand is too uniform to have recorded such detail, but the lack of lensoid cross sections leaves the intrastratal interpretation of the smooth traces in doubt.

UNIQUE ASPECTS OF MAJOR TRACKWAY

The prominent trackway shown in Figure 3 is of special interest because of its dimensions and unusual morphology. Considering the size of typi-

Figure 4. Latex peel made from natural cast of major trackway (convex hyporelief) shown in Figure 3. Peel replicates pits and furrows (concave epirelief} of original trackway. Symbol "x" = reference point for comparison with Figures 2 and 3; arrow = point equivalent to that of left arrow in Figure 3. Scale = 10 cm. UW A4088c.

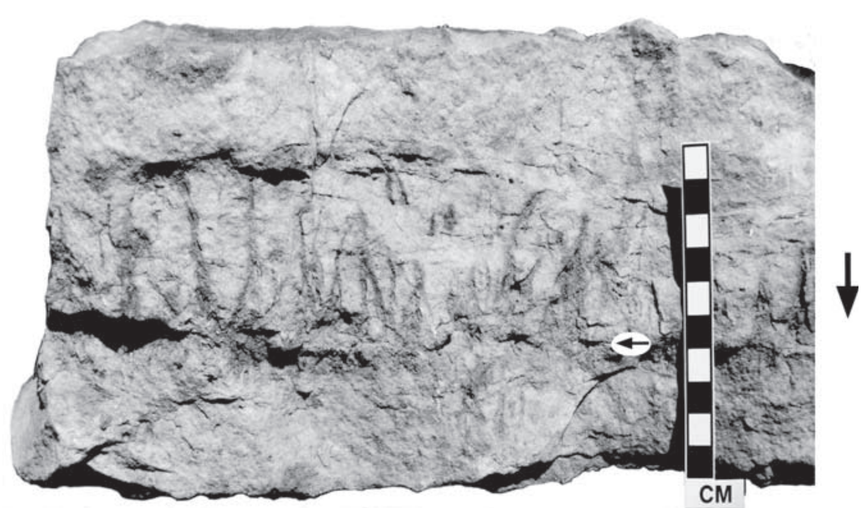

Figure 5. Burrowed layer exposed on side of large slab (Fig. 3). Burrows of diverse lengths extend from colonization surface (horizontal arrow) toward trackway-bearing surface (upper edge of photo). Vertical arrow indicates stratigraphic top. Scale = 10 cm.

cal Cambrian invertebrates, the maker of the trackway in question was a large animal for its time. The 9 cm width of the Flathead trackway exceeds that of all but a few described Cambrian trace fossils. The largest traces are *Climactichnites* and *Protichnites*, well known from numerous Cambrian exposures in eastern and central North America (Getty and Hagadorn, 2008). The maker of *Climactichnites* is thought to have been a primitive mollusk or mollusk-like animal with muscular foot (Getty and Hagadorn, 2008, 2009), whereas *Protichnites* is commonly interpreted as an arthropod trackway (e.g., Seilacher, 2007a). Specimens of *Climactichnites* vary from 1 to 32 cm in width (Hagadorn and Seilacher, 2009) and widths of 13 to 18 cm are common (Yochelson and Fedonkin, 1993). *Protichnites* varies in width from 1.5 to 23 cm with typical specimens in the 4 to 8 cm range (Hagadorn and Seilacher, 2009). Other wide Cambrian trails such as *Cruziana* and *Plagiogmus* were made by animals of less width than the Flathead trackmaker. Large Cambrian specimens of *Cruziana*, trails attributed to trilobites or similar arthropods (Seilacher, 2007b), typically have maximum widths of 5 to 6 cm (e.g., Crimes, 1970; Seilacher, 1970). *Plagiogmus*, a bedding-parallel burrow represented in the Flathead Sandstone, includes specimens as much as 3 cm wide (Cloud and Bever, 1973).

Morphological details of the Flathead trackway under discussion differ significantly from those of the large Cambrian trails noted above. As interpreted from the latex peel (Fig. 4), the trace of the Flathead animal consists of two narrow furrows separated by a ridge broader than either furrow. Furrow surfaces exhibit many minor ridges and concavities, suggesting that each furrow is the cumulative result of repeated and overlapping penetration of the substrate by one or more lateral appendages as the animal moved forward. In places along the trackway furrows, a succession of minor ridges produces a faint transverse pattern, but it is nothing like the array of sharply defined transverse ridges that characterize many *Climactichnites* (e.g., Yochelson and Fedonkin, 1993) and the basal surface of *Plagiogmus* (e.g., McIlroy and Heys, 1997). *Cruziana* is bilaterally symmetrical, but the original furrows are broad and the intervening ridge very narrow (e.g., Crimes, 1970). Furthermore, its surfaces commonly exhibit a distinctive pattern of scratch marks produced by the pointed appendages involved in excavation (Seilacher, 2007a).

POSSIBLE ORIGINATORS OF MAJOR TRACKWAY AND ASSOCIATED TRACES

The major trackway's pair of indented furrows (Fig. 4) indicates that the maker was a bilaterally symmetrical animal with paired appendages. The most logical candidate tracemaker is an arthropod-grade animal and many Cambrian traces have been attributed to members of that group. The ichnogenera *Protichnites* and *Diplichnites* resemble the Flathead major trackway in consisting of two parallel series of appendage imprints. The footprints in *Protichnites* are irregularly spaced and the two rows are commonly separated by a median drag trace (Seilacher, 2007a, p. 30 and pl. 10). Footprints in *Diplichnites* are elongate and oblique to the trackway midline, which lacks a drag trace (Seilacher, 2007a, pl. 8). In these ichnogenera the individual footprints are either small pits or narrow grooves made by pointed appendages. The major trackway

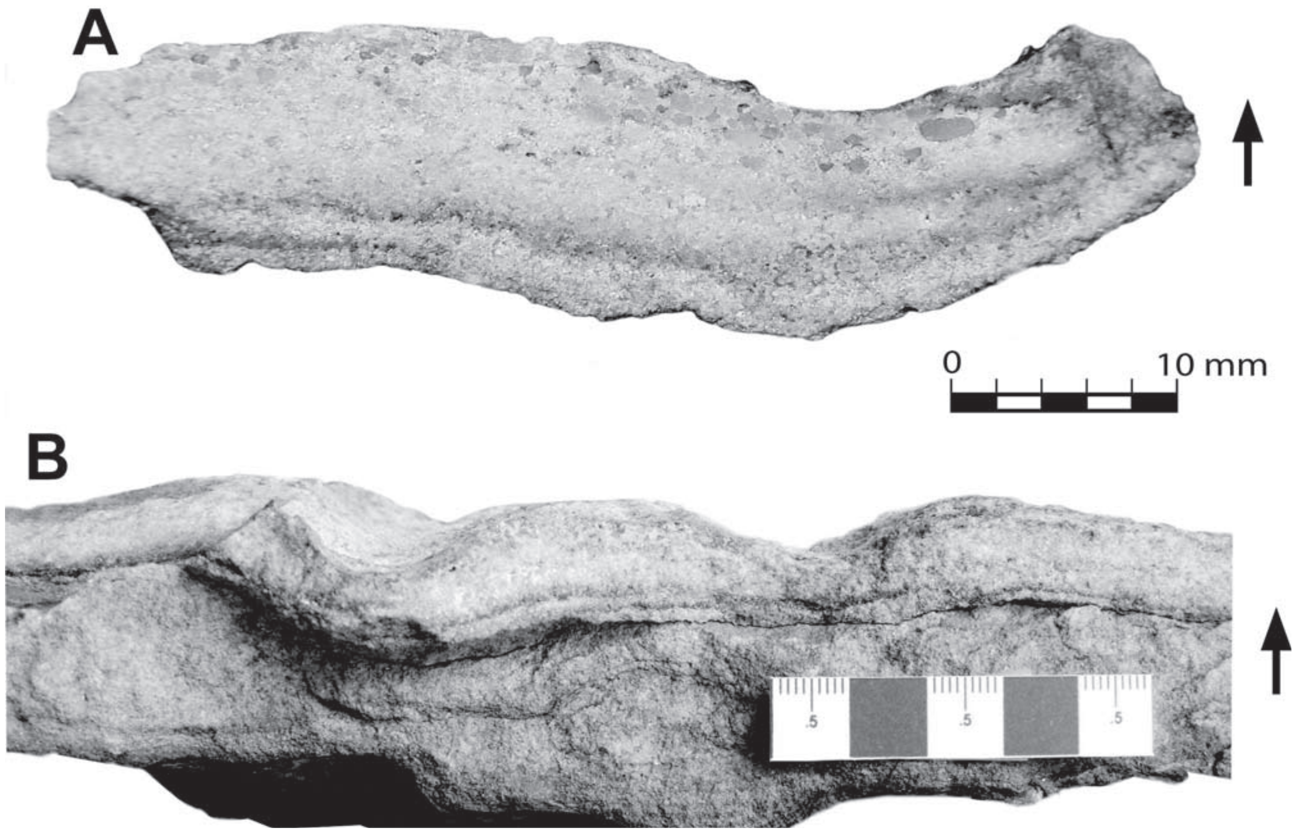

Figure 6. ***A,*** Polished section of piece cut from overhanging edge of small slab (left side of Fig. 6*B*; upper edge of Fig. 2) showing downwarped laminae beneath left furrow of trackway. Note scattered coarse grains in upper lamina and its continuity across specimen. Arrow indicates stratigraphic top. Scale = 10 mm. UW A4088d. ***B***, Side view of small slab (Fig. 2, upper edge) showing cross section of trackway. Note depressed lamination beneath furrows (left and right indentations of upper margin). Arrow indicates stratigraphic top. Scale = 5 cm.

lacks such features, but their absence does not prove that the tracemaker lacked pointed appendages. Legs of that type would leave sharply defined pits and grooves only on a stiff substrate, and that may not have been a characteristic of the surface traversed by the Flathead animal.

Unlike the footprints of *Protichnites* and *Diplichnites*, indentations in the long furrows of the Flathead trackway (interpreted from both natural cast and latex peel) are broad, irregular hollows that overlap one another in linear succession. At one place (Fig. 3*A*, left arrow; Fig. 4, arrow) the succession in the upper furrow is replaced (left to right) first by a pair of imprints, then by a cluster of them. The shape of individual imprints in this area suggests that the appendages creating the furrows were blunt rather than pointed although, as noted above, substrate character rather than appendage shape could have been the major factor controlling imprint shape. More importantly, the different pattern of imprints shown by upper and lower parts of the trackway in this area indicates that the two rows of appendages were not coordinated in movement. This independence is confirmed by the lack of recognizable pairs of imprints across the medial ridge throughout the length of the trackway.

The lobed ridges of the Flathead trackway cast (Fig. 3) resemble those of aglaspidid traces from Upper Cambrian strata in Wisconsin (Hesselbo, 1988). Although bilaterally symmetrical, these hypichnial casts are rusophyciform in that they are "resting" traces rather than trackways. As with the Flathead cast, each bounding ridge is formed by a series of lobes. However, the dimensions of the lobes in the Wisconsin casts vary systematically along the ridge and they match across the inter-ridge area well enough to allow determination of the number of pairs of appendages. A key feature for assigning the

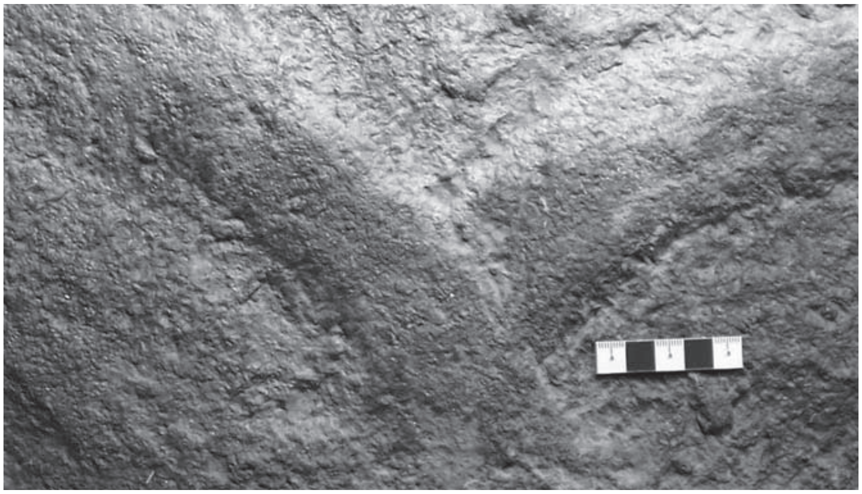

Figure 7. Close-up view of intersection of two smooth traces (a and b in upper left of Fig. 3*A*). Scale = 5 cm.

Wisconsin traces to the enigmatic arthropod taxon Aglaspida is the impression of a tail spine. The Flathead trackway lacks such evidence.

Another atypical arthropod group, the Onychophora, deserves mention while discussing possible makers of the Flathead trackway. Reconstructions of *Aysheaia*, an onychophoran body fossil from the Burgess Shale Lagerstätte (Conway Morris, 1998), show a caterpillar-like body with pairs of short stubby legs (lobopods). If they operated as interpreted by Conway Morris (1998, p. 91), the process might produce furrow topography that would, after casting, resemble the slightly imbricate lobes that form the ridges on the Flathead cast. However, the very small size of Cambrian onychophoran fossils is a strong argument against a member of that group being the maker of the Flathead trackway.

In summary, several aspects of the Flathead trackway resemble morphological features of Cambrian traces and body fossils attributed to atypical arthropod taxa. It seems likely that the Flathead trackmaker was an animal of arthropod grade, but the two slabs under study lack sufficient evidence for a more definitive statement. Furthermore, it should be remembered that the original morphology of the trackway probably suffered some distortion as the natural cast underwent loading and pre-lithification compaction.

As discussed in a previous section of this report, the smooth mounds (Fig. 3a–c) are interpreted as burrows made by animals moving generally parallel to the sand/mud interface. *Psammichnites* is a well-known Cambrian trace exemplifying such behavior (Seilacher, 2007a). Like the Flathead elongate mounds, *Psammichnites* has a small width/length ratio, lacks marginal ridges, and has a meandering pattern including crossovers. Unlike the Flathead traces, some *Psammichnites* trails have a bottom surface marked by *Plagiogmus*-like transverse ridges (Seilacher, 2007a, p. 80; McIlroy and Heys, 1997, p. 169). *Didymaulichnus*, another smooth trail found in convex relief on soles of Cambrian sandstones, differs from the unilobate Flathead specimens in possessing a medial furrow (Häntzschel, 1975, p. W61).

The smooth bottom surface of the Flathead traces (Fig. 7) resembles that of the bedding-parallel burrow *Olivellites plummeri* in Pennsylvanian sandstones of Texas (Yochelson and Schindel, 1978). The Texas specimens exhibit a meandering pattern, including sharp turns and intersections where the maker cut through its own trace, or in other cases, passed over a previously formed part. Seilacher (2007a, p. 82) assigned this ichnospecies to *Psammichnites* and interpreted the maker to have been a slug-like animal. If so, it probably had a ventral surface comparable to the molluscan foot. Muscular contraction in such an organ should have left distinctive marks on the trace, but no such evidence is present on the smooth sole marks under discussion.

CONCLUSIONS

1. Two sandstone slabs from the Middle Cambrian Flathead Sandstone of central Wyoming contain a trackway of unusual size and morphology. The sole of one slab bears a cast of the trackway. whereas a partial undertrack is present on the top surface of the other slab.

2. The trace was made on the surface of a now-missing mud layer and cast by subsequently deposited sand. The undertrack formed when pressure, probably

from weight of overburden, pressed the mud downward and deformed the surface of underlying unlithified sand.

3. As interpreted from the cast and a latex peel made from it, the trackway consists of two parallel furrows separated by a broad ridge; furrows lack scratch marks and bear overlapping appendage imprints.

4. Although the taxonomic identity of the tracemaker is uncertain, it may have been an animal of arthropod grade with body and appendages resembling those of the Onychophora.

5. Other large trace fossils associated with the trackway are smooth unilobate ridges on the slab sole bearing the trackway cast. The makers may have been animals of mollusk grade burrowing along a sand/mud interface subsequent to origin of the trackway cast.

6. The Flathead trackway adds to the evidence that large invertebrates were a significant part of Cambrian faunas. The trackway's enigmatic aspects suggest that much is yet to be learned about their bodies, behavior, and taxonomic relationships. The search for evidence pertinent to the walking and crawling members of the fauna will more likely be successful where bedding surfaces are broadly exposed rather than where ledge-forming outcrops focus observation on cross sections of beds.

ACKNOWLEDGMENTS

The two slabs that are the subjects of this paper were discovered by Thomas Anderson on the property of John Hursh. Mr. Hursh kindly donated the specimens to the Department of Geology and Geophysics at The University of Wyoming. The major effort expended by Mr. Anderson in getting the slabs to Laramie is much appreciated. Early in the investigation I received helpful advice from Drs. J. W. Hagadorn, S. P. Hesselbo, and A. R. Palmer. At various stages in the research numerous colleagues in my Department offered useful suggestions. Those who helped in specific ways are Drs. M. C. Clementz (carbon isotopes), S. M. Swapp (thin sections), and N. G. Swoboda-Colberg (x-ray analysis). Brent Breithaupt generously supplied liquid latex for the peel. Critical assistance with specimen photography was provided by Joshua Slattery and David DeMar. Slattery took most of the photos and Ashley Sandness produced the map. The final figures reflect the computer expertise of Brendon Orr. The quality of the submitted manuscript was greatly improved by the work of reviewers Steven Dornbos and J. W. Hagadorn, and editor J. A. Lillegraven. Hagadorn's thorough critique was especially helpful for calling attention to problems in the original manuscript and for offering suggestions to correct them.

REFERENCES CITED

Baldwin, C. T., 1977, Internal structures of trilobite trace fossils indicative of an open surface furrow origin: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 21, p. 273–284.

Bromley, R. G., 1996, Trace fossil biology, taphonomy and applications: London, Chapman and Hall, 361 p.

Cloud, P., and Bever, J. E., 1973, Trace fossils from the Flathead Sandstone, Fremont County, Wyoming, compared with Early Cambrian forms from California and Australia: Journal of Paleontology, v. 47, p. 883–885.

Conway Morris, S., 1998, The crucible of creation: Oxford, Oxford University Press, 242 p.

Crimes, T. P., 1970, Trilobite tracks and other trace fossils from the Upper Cambrian of North Wales: Geological Journal, v. 7, p. 47–68.

____1975, The production and preservation of trilobite resting and furrowing traces: Lethaia, v. 8, p. 35–48.

Getty, P. R., and Hagadorn, J. W., 2008, Reinterpretation of *Climactichnites* Logan 1860 to include subsurface burrows, and erection of *Musculopodus* for resting traces of the trailmaker: Journal of Paleontology, v. 82, p. 1161–1172.

____ 2009, Palaeobiology of the *Climactichnites* tracemaker: Palaeontology, v. 52, p. 753–778.

Goldring, R., 1985, The formation of the trace fossil *Cruziana*: Geological Magazine, v. 122, p. 65–72.

Hagadorn, J. W., and Seilacher, A., 2009, Hermit arthropods 500 million years ago?: Geology, v. 37, p. 295–298.

Häntzschel, W., 1975, Trace fossils and problematica, *in* Teichert, C., ed., Treatise on invertebrate paleontology, Part W, Miscellanea, Supplement 1: Boulder, Colorado, Geological Society of America (and University of Kansas Press), 269 p.

Hesselbo, S. P., 1988, Trace fossils of Cambrian aglaspidid arthropods: Lethaia, v. 21, p. 139–146.

McIlroy, D., and Heys, G. R., 1997, Palaeobiological significance of *Plagiogmus arcuatus* from the lower Cambrian of central Australia: Alcheringa, v. 21, p. 161–178.

Middleton, L. T., Steidtmann, J. R., and DeBour, D. A., 1980, Stratigraphy and depositional setting of some Middle and Upper Cambrian rocks, Wyoming, *in* Hollis, S., ed., Stratigraphy of Wyoming: Wyoming Geological

Association, 31st Annual Field Conference Guidebook, p. 21–35.

Porada, H., and Bouougri, E., 2007, “Wrinkle structures” — a critical review, *in* Schieber, J., Bose, P. K., Eriksson, P. G., and four others, eds., Atlas of microbial mat features preserved within the siliciclastic rock record: Amsterdam, Elsevier, p. 135–144.

Seilacher, A., 1970, *Cruziana* stratigraphy of “non-fossiliferous” Paleozoic sandstones, *in* Crimes, T. P., and Harper, J. C., eds., Trace fossils: Liverpool, Seel House Press, p. 447–476.

_____ 2007a, Trace fossil analysis: Berlin, Springer, 226 p.

_____ 2007b, Principles of ichnostratigraphy, *in* Bromley, R. G., Buatois, L. R., Mangano, G., and two others, eds., Sediment-organism interactions: A multifaceted ichnology: Tulsa, Oklahoma. Society of Economic Paleontologists and Mineralogists Special Publication 88, p. 53–56.

Yochelson, E. L., and Fedonkin, M. A., 1993, Paleobiology of *Climactichnites*, an enigmatic Late Cambrian fossil: Smithsonian Contributions to Paleobiology 74, 74 p.

Yochelson, W. L., and Schindel, D. E., 1978, A reexamination of the Pennsylvanian trace fossil *Olivellites*: Journal of Research, U.S. Geological Survey, v. 6, p. 789–796.

Manuscript Submitted August 26, 2009

Revised Manuscript Submitted December 17, 2009

Manuscript Accepted December 26, 2009