

Fig. 5. Sectioned *Taphrhelminthopsis* trace (LACMIP 12872), including an oblique view of the trace furrow and cut slab (A), a cross-section perpendicular to the furrow axis, illustrating sharp truncation of laminations by the burrow fill (B); and an x-radiographic positive print of the counterpart to (B), indicating overlap of burrow fill on undeformed laminated sediment (C). Note that ends of laminations are not deformed at intersection with burrow trough. Field of view in (A) is 7.5 cm, 7.2 cm in (B) and 5.4 cm in (C).

known locality in the 'Poleta Folds' region (Snail Canyon), approximately 25 km northeast of Big Pine, along the western margin of Deep Springs Valley in the White-Inyo Mountains (Fig. 1). The sandstone sub-unit of the middle member is dominated by laminated, thinly bedded, low-angle cross-laminated and mottled bedding. *Taphrhelminthopsis*-bearing hori-

zons are a few meters above the base of the *Bonnia-Olenellus* trilobite zone and primarily consist of thin- to thick-bedded very fine- to medium-grained quartz arenite, with minor amounts of sandy siltstone and sandy limestone.

In general, exposures consist of repeating packages of massive, blocky quartzitic beds (20–40 cm thick), overlain by thinly-bedded, more easily fragmented beds (5–10 cm thick). The thinner beds cap and grade upward into the thicker, more resistant massive beds (Fig. 1). A variety of ichnotaxa are preserved at the interface between massive blocky beds and thinly-bedded intervals, likely representing a hiatus between coarsening and thickening-upward sequences.

Within the study section, *T. nelsoni* typically occur on the top of massive 20–40 cm thick sandstones, within white, very fine- to fine-grained, well-sorted 3–4 cm thick laminated sand layers (laminae thickness = 0.1 mm to 1 mm). Laminated *T. nelsoni*-bearing layers alternate with darker gray-to-black, mottled to poorly laminated, rarely micaceous, 0.5–2 cm-thick silty sandstones and sandy siltstone. Laminated layers are underlain by mottled dark gray-to-black well-sorted, very fine-grained silty sandstones between 0.5 and 6 cm thick. Where bioturbated, internal surfaces of underlying darker silty layers are irregular in cross-sectional view. Bases of the *T. nelsoni*-bearing laminated beds are almost always planar, suggesting erosion of the upper surfaces of the darker beds, followed by rapid deposition of laminated sediments on top. No burrow escape structures are visible in cut slabs.

Paleoenvironmental and paleoecologic context

The middle member of the Poleta records a transition from foreshore to shoreface to offshore environments, probably within a locally emergent sand bar complex with minor tidal influence (Fig. 1; Moore 1976a, b). These facies interpretations are based on the presence of tidal laminations, herringbone cross laminae, low-angle cross lamination, flat-topped interference ripple marks, *Skolithos*, and mudcracks near the study area. Although polygonal desiccation cracks, evaporite crystal pseudomorphs and other subaerial exposure features were not observed, physical sedimentary structures, stratigraphic relationships, as well as autochthonous marine trace fossils and body fossils, are consistent with previous regional-scale facies interpretations suggesting a shallow, but dominantly subtidal setting adjacent to a tidal complex (Fig. 1; Moore 1976a, b). Studied sequences are interpreted to reflect oscillation between storm-related deposition of coarser-grained sediment into a region typically characterized by more quiescent, muddier subtidal

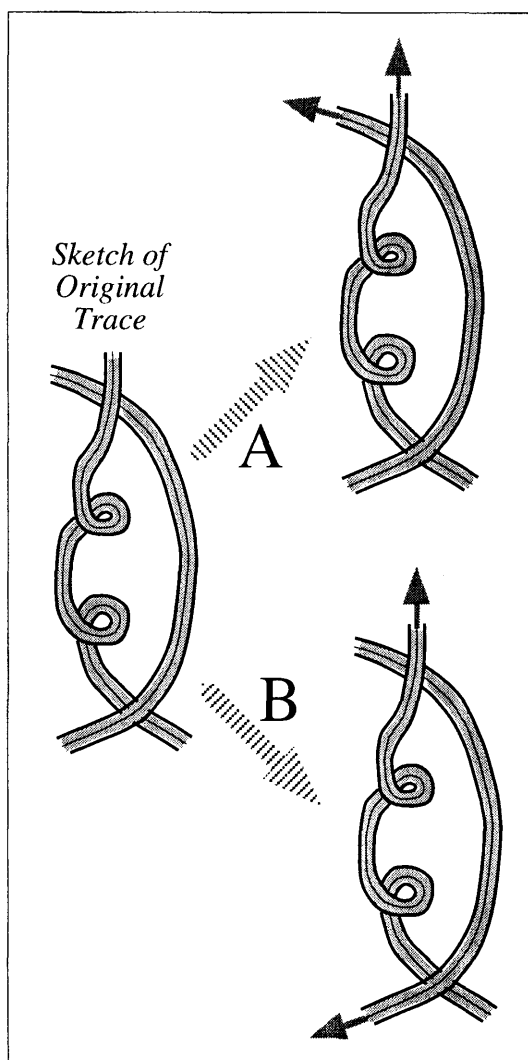


Fig. 6. Simplified schematic illustration of cross-cutting relationships of two looping traces outlined on acetate sheets from bedding plane illustrated in Fig. 2C. In the looping trace, one can determine the direction of tracemaker movement from over-under and burrow deformation. In this specimen, the looping tracemaker was moving from bottom to top of the diagram – overlapping its own trace (as in Fig. 3) the same way twice.

conditions. In this case, laminated sandy layers likely provided a freshly deposited substrate for opportunistic organisms to exploit.

Taphonomy

In the study area, *T. nelsoni* is common on many bedding planes within an 8 m-thick interval in the upper sandstone sub-unit of the middle member of the Poleta Formation. This *T. nelsoni*-rich interval was examined at 22 sites over a ~ 10 km² area, but efforts concentrated on a region where *T. nelsoni* occurs on

five bedding planes that can be traced for more than 50 m along the margins of a steep gorge (Fig. 1). Individual exposures of *T. nelsoni*-rich bedding planes within this gorge range from 1.5 to 21 m² (Fig. 2).

Considering its large size and extensive lateral distribution, why is *Taphrhelminthopsis* so well preserved at these study localities, and elsewhere in the Lower Cambrian? In addition to obvious factors of rapid burial and minimal vertical bioturbation, other taphonomic factors may be involved. In particular, *Taphrhelminthopsis* is one of two trace fossils directly associated with Lower Cambrian occurrences of Ediacaran biotas (Jensen et al. 1998) and is only present in shallow marine settings prior to the Ordovician (Crimes et al. 1992). Although some Ediacaran forms may have lived buried within or on the sediment, Gehling (1996, 1999) has demonstrated that preservation of surface-dwelling soft-bodied Ediacarans is typically restricted to environments with microbially bound sediment surfaces. At studied localities, traces are found on bedding planes with suspected tidal laminations and suspect-microbial features, such as wrinkle structures (Hagadorn & Bottjer 1997). Furthermore, the sharp trace fill and lamination contacts (described below) and lack of peristaltic trackways adjacent to the burrow fill (features which might be expected of animals moving across unconsolidated sediment) suggest that the surface of laminated sediment layers was cohesive. Because carbonate cements are absent, this primary cohesiveness is suspected to have resulted from microbial binding. Such microbial binding has been documented from adjacent, overlying and underlying strata in the vicinity (Hagadorn & Bottjer 1999), and may provide an explanation for concentrated grazing activity on particular bedding planes (discussed below).

Trace fossil analyses

Trace characteristics

Size and shape variations between specimens of the same ichnospecies may suggest different-sized individuals or trace-making variations due to behavior, such as avoidance (see overview in Bromley 1996). Single factor analysis of variance (ANOVA) suggests *T. nelsoni* burrow width (measured as the maximum width of the excavated trough; Figs 4, 5) does not vary significantly within ($p < 0.05$, $X = 31.4 \pm 0.32$ mm, $n = 73$) or between ($p < 0.01$, $n = 5$) measured traces. Similarly, burrow trough depth, measured relative to bedding surface, does not vary significantly within ($p < 0.05$, $X = 12.35 \pm 0.49$ mm, $n = 73$) or between

($p < 0.01$, $n = 5$) measured traces. Assuming the tracemaker retained a similar mass throughout its path, the consistent trace depth within and between individual traces suggests a specialized sediment ingestion strategy and/or movement across a substrate of relatively homogeneous consistency. Furthermore, consistent burrow trough width also suggests individuals of similar size were active within and between the studied bedding planes.

In contrast, ANOVA of trace ridge widths (Fig. 4) reveals significant variation within and between individual traces, ranging from approximately 22 mm to 56 mm ($p \gg 0.05$, $X = 35.03 \pm 7.52$ mm, $n = 73$). Similarly, the depth of the trace furrows is highly variable, ranging from 2 mm to 14 mm ($X = 7.03 \pm 5.24$ mm, $n = 73$). The irregularity of the ridge width, height and shape suggests that fill was less consolidated than adjacent undeformed laminated sediment and that upper portions of this fill may have been deformed passively, as indicated by the erratic knobby shapes of the burrow ridges (Fig. 3A). Furthermore, upper portions of the fill are not flattened (as they would be if one or more cylindrical fecal streams were compressed by overlying bedding), nor preferentially folded over in one direction, as might be expected from burial by a unidirectional flow (Fig. 2B). Rather, burrow ridges are roughly semi-cylindrical and separated by a median furrow typically extending to or just below the level of the adjacent sediment surface (Figs 3, 4). This fill has been pushed to the side of the main burrow path and rests upon adjacent unbioturbated sediment (Fig. 5C). Collectively, these observations suggest that the trace ridges formed as the tracemaker's body passed over its backfilled trail, perhaps splitting the trail with its posterior into two ridges.

How many tracemakers were there?

Cross-cutting relationships within and between individual traces provide evidence about the number of coeval tracemakers and their morphology. Cross-cutting structures consist of a bilobate trace that partially excavates and infills an earlier trace's median furrow and trough (Figs 3, 5B). A total of 50 cross-cutting relationships were recorded among the 35 *Taphrhelminthopsis* specimens. Reversals in cross-cutting relationships were examined to test the possibility that one tracemaker was responsible for traces on a particular bedding plane. At least two of the studied traces illustrate a reversal in cross-cutting relationships between multiple intersections of two individual traces, thus providing positive evidence for at least two coeval tracemakers on studied bedding planes (Fig. 6). Although increasing density of traces

commonly obscures such details, when one considers the high density of traces on some studied bedding planes, there were likely more than two tracemakers moving across a given surface.

How big were they?

Given that the studied traces do not reflect domiciles, agricultural networks, brood chambers or other structures formed by organisms significantly smaller than their traces, the tracemaker's body size can be constrained by analyzing the volume of sediment processed by the tracemaker and the cross-cutting relationships of its looping trails. At trace intersections, underlying traces are not deformed beyond the extent of the overlying trace, indicating that the tracemaker's body was no wider than the ridge width, or that the tracemaker exerted insufficient force to deform these earlier traces (Fig. 3). Burrow trough diameter can thus be used as a proxy for maximum tracemaker diameter, and by retrodeforming the cross-sectional area of the backfilled trail into a circle, the tracemaker's maximum cross-sectional area can be estimated [π (average trough radius ≈ 1.5 cm) $^2 \approx 7$ cm 2]. Assuming a spherical shape, the tracemaker may have been as small as a golf ball (~ 14 cm 3), but was likely somewhat elongate. The smallest self-crossing *T. circularis* loop allows us to constrain tracemaker length to ~ 24 cm, and assuming a cylindrical form, the tracemaker could have been as large as a tightly rolled issue of *Lethaia* (~ 170 cm 3).

What were they doing?

The above analyses allow inferences on abundance and body size, but provide little insight into the locomotion mechanism that produced *Taphrhelminthopsis*. This problem is compounded by the smooth surfaces of the convex ridges and absence of lateral, oblique and transverse striae. In all serially sectioned trace fossils, burrow trough edges are sharp and laminations abruptly terminate at the margins of the U-shaped burrow trough. Surficial laminations are not deformed as might be expected if organisms were resting on the surface or deforming it through locomotive processes exemplified in *Climactichnites* (Yochelson & Fedonkin 1993). Observed sharp and uniform sediment excavation features seem highly specialized for mere locomotive purposes. Rather, they suggest the tracemaker was actively ingesting or removing sediment in the act of food processing or searching.

How did they move and who made these traces?

The poorly laminated to mottled silty layers that overlie traces typically fill depressions in the surface of

burrow backfill, are thinner over burrow ridges, are laterally continuous across burrow ridge crests, do not grade downward into laminated layers, and are not incorporated into burrow fill. These observations suggest that deposition of overlying silty sediment occurred after production of the *Taphrhelminthopsis* burrows, or that tracemakers were moving through a thin, poorly consolidated mud layer while mining the more consolidated underlying sands. Absence of erosive features on bed surfaces and bed soles, however, makes it unlikely that *Taphrhelminthopsis* formed as a deep subsurface trace which was later uncovered and then cast, akin to undertracks like *Cruziana* (Seilacher 1953a, b) or varying preservational styles characteristic of *Plagiogmus* (Seilacher 1995, 1997; McIlroy & Heys 1997).

Lack of prod or scratch marks, lateral markings and related features precludes suggesting that the tracemaker had a firmly mineralized skeleton, given that parts of the tracemaker's body were in contact with the substrate. Furthermore, an arthropod interpretation seems difficult to accept considering the abundance of diagnostic features typically found in other coeval arthropod traces. Furthermore, absence of annulations on burrow boundaries, meniscate backfill or overlying sediment deformation suggests the animal was not an infaunal organism that burrowed like a spatangoid echinoid. Lack of evidence for peristaltic motion and intrastratal burrowing also precludes suggesting that the tracemaker was an infaunal annelid or infaunal mollusc, like the *Plagiogmus*-maker (Seilacher 1995, 1997; McIlroy & Heys 1997). Despite similarities in surficial meandering and looping patterns, *Taphrhelminthopsis* fill is unlike trails produced by modern enteropneusts or echiuroid worms (Bourne & Heezen 1965). Exceptionally preserved Cambrian priapulid and polychaete worms thought to be mobile deposit-feeders, carnivores or scavengers (e.g. *Burgessochaeta*, *Canadia*, *Ottoia*, *Pernochoeta*, *Wiwaxia*) are possible candidates, but are significantly smaller than *Taphrhelminthopsis* traces. Furthermore, priapulids would be expected to leave evidence of peristaltic motion along burrow margins (as is seen in *Plagiogmus*), and foraging polychaete tracemakers would be expected to leave distinctive markings along the bases or walls of burrow troughs – features absent from *Taphrhelminthopsis*. Although trails of comparable size could have been made by early molluscs such as *Kimberella* (Fedonkin & Waggoner 1996), traces associated with *Kimberella* are thought to consist of radular scratch marks ('*Radulichnus*') or shallow ovate impressions on bed surfaces (Gehling 1996; Seilacher 1997). Based on these considerations, and a survey of traces produced by animals in deep marine settings (where

traces similar to 'typical' shallow Vendian–early Cambrian bedding-parallel trace fossils are commonly produced; Bourne & Heezen 1965; Seilacher 1967b; Heezen & Hollister 1971), possible *Taphrhelminthopsis* tracemakers might include echinozoan- or mollusc-grade animals with a soft body or at least a soft underside, capable of excavating a relatively steep-sided trough without preferentially prodding or scratching sediment at the base of the trough.

Modern echinozoan analogues for the tracemaker include irregular echinoids and holothurians (see Heezen & Hollister (1971) for an overview). Modern spatangoid echinoids burrow through sediment utilizing arrays of specialized mineralized spines to excavate sediment and then pass it behind the animal (Bromley & Asgaard 1975), but no burrow ornamentation is present in our studied specimens that supports excavation by this method. Thus, although the overall geometry and size of *Taphrhelminthopsis* is similar to burrows made by spatangoid echinoids, the morphologic details of *Taphrhelminthopsis* do not support interpretation of the tracemaker as an organism that behaved similar to spatangoids. However, some deep-sea holothurians produce traces similar to *Taphrhelminthopsis* in overall morphology, and one would not expect such holothurian traces to have burrow markings or meniscate backfill. Hollister et al. (1975, p. 499) report that '*Pseudostichopus*, unlike the majority of large holothurians, plows a broad U-shaped path through sediment, somewhat resembling the furrow of an irregular echinoid'. Thus it is possible that an unknown echinozoan-grade animal (which burrowed like a modern holothurian) may have been responsible for *Taphrhelminthopsis* traces. Lack of skeletonized evidence for such an echinozoan precludes such an interpretation. In light of coeval occurrences of other echinozoans (e.g. helicoplacoids – although sessile their presence indicates an earlier unskeletonized history for echinozoans), and other animals which could have employed holothurian-like locomotive styles, perhaps during the early Cambrian such forms may have been soft-bodied and thus not preserved? If so, then a soft-bodied echinozoan organism which crawled across the seafloor, ingesting sediment along its path, may be responsible for *Taphrhelminthopsis*.

If the tracemaker was a mollusc-like animal, glide-crawling is the most probable means of trace production and locomotion. This type of motion is best illustrated in the hollow, muscular foot of gastropods, in which directed waves of rhythmic, alternating contractions on the sole of the gastropod foot are produced (Schäfer 1972). Waves are propagated in the direction of motion such that the contraction's termination lifts the sole's anterior

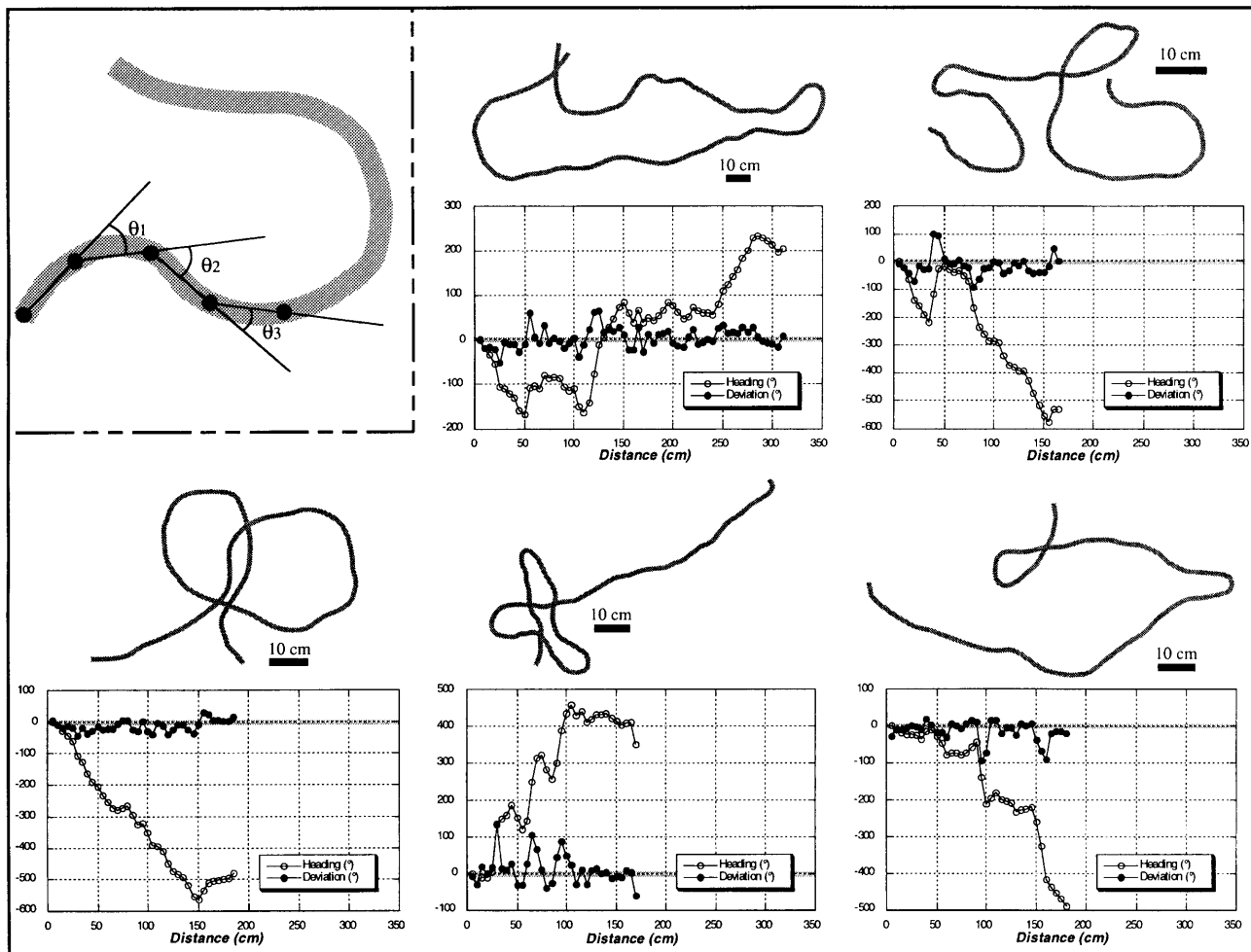


Fig. 7. Goniogram methodology and data. Heading was measured using a Brunton compass, and relative deviation (inset) was noted at every 5-cm sampling interval. Goniogram plots of the heading (open circles) and deviation (closed circles) are plotted below sketches of trace outlines for 5 of the 35 studied traces.

just above and forward over the substrate. In some modern gastropods, two discrete and slightly out-of-phase contraction waves, separated by a longitudinal membrane of connective tissue, produce a ditaxical type of direct wave motion; other types include monotaxical and tetrataxical motion (e.g. Ankel 1936; Schäfer 1972). In the rare case of extreme substrate plasticity, ditaxically glide-crawling gastropods (i.e. *Nucella lapillus*) can leave a divided trace with relatively smooth sides (Ankel 1936). This modern prosobranch gastropod trace is smaller, but analogous to studied *Taphrhelminthopsis*. Together with appearance of prosobranchs and *Taphrhelminthopsis* in the Tommotian (Runnegar 1981; Crimes 1987), and evidence for the relatively cohesive nature of studied laminated substrates, these observations might collectively implicate a relatively large early mollusc as a potential trace-producer.

Based on these observations, the studied *T. nelsoni*-maker is hypothesized to have been either a soft-bodied echinozoan or a mollusc. Both of these suspected tracemakers are known from modern deep marine settings, and have been documented in modern settings making similar backfilled bilobate traces on seafloor surfaces.

Were they systematically foraging?

A conspicuous feature of the studied trace fossils is their looping and meandering nature. Such looping and meandering might represent a systematic locomotive pattern, perhaps associated with efforts to actively mine the sediment or search for food resources. Hofmann & Patel (1989) and Hofmann (1990) developed a goniogram technique which allows quantitative description of trace fossil mor-

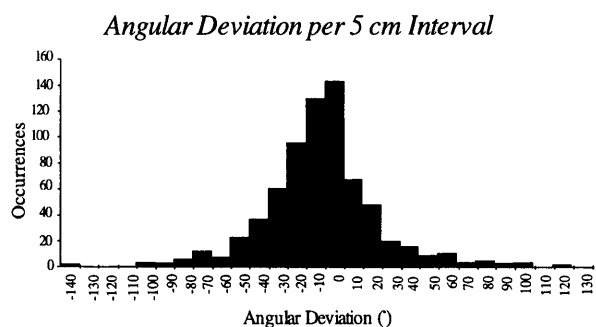


Fig. 8. Distribution of deviation measurements for all studied traces. Distribution is not heavily skewed, as would be expected with organisms that exhibit preferred turning direction (right- vs. left-handedness). Note that the negative offset of this distribution may not be significant because direction of tracemaker movement could not be determined in all studied traces.

phology and evaluation of hypothesized 'systematic' burrowing patterns. Goniograms are plots of local trace orientation versus the distance along the trace path and illustrate: (1) the distance of any one point on the studied trace from the origin of the trace data; (2) the local heading with respect to the origin heading; (3) relative and absolute maximum and minimum values of headings; and (4) mode of looping and spiraling (Hofmann 1990). Goniograms also provide a straightforward presentation of rate of change between headings, by plotting the angular deviation between sequential heading pairs, which is analogous to the first derivative of a line. Trace heading data can easily be measured in the field using a compass and ruler, providing a simple means for collecting large amounts of quantitative trace fossil information in poorly accessible or difficult-to-sample locales. In this study, goniogram analysis is used to determine if studied traces exhibited periodic looping or meandering patterns and provide an initial datum for analyzing *Taphrhelminthopsis*'s role within suspected larger-scale patterns in the evolution of burrowing behavior.

Goniogram methodology. – In the field, individual *T. nelsoni* traces were outlined on acetate sheets at a 1:1 scale to provide an oriented record of the relative position of each trace. Only well-preserved and relatively long traces were outlined for goniogram analysis. At the largest contiguous bedding plane exposure, *T. nelsoni* was not homogeneously distributed over the bedding plane, but instead exhibited a distinct center of high trace density. Within this region, it was difficult to identify discrete, continuous traces. Thus, traces used in goniogram analysis represent a non-random distribution of available

traces, as sampling was biased toward more distal, discretely preserved trace populations.

Oriented continuous traces were measured at 5-cm intervals and reduced to relative headings and deviation between sequential headings. Changes in direction to the right of the previous path vector were given positive degree values, those to the left were given negative degree values (Fig. 7). Although cross-cutting relationships can occasionally be used to infer direction of movement (Fig. 6), lack of striae precludes determination of a unique locomotive direction or defining an arbitrary, but consistent, data collection direction between traces. Thus, the 'starting' point for quantifying each trace was arbitrarily chosen based on outcrop accessibility. The 5-cm interval was selected so that the smallest observed trace loop was represented by at least four data points. Relative heading and angular deviation between sequential heading pairs were used to construct goniograms for individual *T. nelsoni* traces.

Goniogram results. – Thirty-five distinct traces were measured for goniogram analyses, with a total length of 36.15 m. The average length was 1.03 ± 0.68 m with a maximum individual trace length of 3.15 m and a minimum individual trace length of 0.25 m. Although looping was present in 37% of the traces and isolated meanders are common (defined here as $\sim 180^\circ$ turns), examination of all heading-based goniograms revealed neither consistent nor strong periodicity at any scale above the 5-cm interval. Qualitative examination also failed to show any periodicity below this interval. Examples of representative goniograms are presented in Fig. 8. Based on goniogram analyses, *Taphrhelminthopsis* specimens were not deemed sufficiently complex or long to warrant further statistical analyses, such as auto-correlation, cross-correlation or spectral analysis.

Trace data were also plotted using deviation-based goniograms as an additional test for periodicity. The mean of all angular deviation datums ($n = 688$) was $-2^\circ \pm 30^\circ$ per 5-cm interval with a median of -3° and mode of 5° . Deviation data were binned at 10° intervals from 140° to 0° (right deviations) and 0 to -140° (left deviations). The resultant frequency distribution exhibited a roughly normal distribution (Fig. 9). Like the heading-based goniograms, these 'first derivative' goniograms also lack strong or consistent periodicity.

Lastly, to evaluate the possibility that tracemakers may have exhibited preferential turning directions or 'handedness', consistent angular deviation of loops was examined in the field. Because such observations were restricted to traces where burrowing direction could be determined (as indicated above), only one

measured trace appeared to exhibit consistent angular deviation in one direction. Thus, unlike marks of predation on trilobites (Babcock 1993), we cannot determine if the *Taphrhelminthopsis*-producer exhibited a preferred direction of looping, and thus cannot evaluate if 'right- and left-handedness' may have been involved in development of intricate tracemaking capabilities or presumed neurological complexity.

Goniogram implications. – Temporal shifts in the development of intricate foraging patterns are of interest because they demonstrate how metazoans increased their behavioral complexity and/or developed neurological return-response mechanisms concomitant with, or perhaps in the wake of, the Cambrian explosion, as well as shifts in bioturbation occurring across the Proterozoic–Phanerozoic transition. Previous experimental and analytical studies have examined the distribution of such tracemaking behaviors in order to test hypotheses about development of early animal behavior. For example, Seilacher (1967a, 1974, 1977) hypothesized that the complexity of looping and meandering traces increased through time, reflecting an increased behavioral complexity. Documentation of 'complex' Vendian and early Paleozoic traces, such as Tommotian *Helminthoidea*, restricted such shifts to the Vendian–Cambrian transition, and further suggested existence of distinct onshore–offshore colonization patterns among many meandering, spiraled and networked trace fossil genera (see summary in Crimes 1992). However, documentation of looping and broadly meandering traces in Vendian flysches of Spain (Vidal *et al.* 1994) suggests such complexity and deep-sea colonization hypotheses may need refinement, since presence of these 'complex' behaviors in the early Vendian clearly contradicts existing deep-sea colonization hypotheses (e.g. Crimes *et al.* 1992). Together with experimental simulations of systematic foraging behavior (Raup & Seilacher 1969; Hammer 1998) goniogram analyses may quantitatively test hypotheses suggesting progressive colonization of deep-sea environments by organisms capable of producing 'complex' tracemaking behaviors.

In this study, goniogram analysis was used to determine if studied traces exhibited periodic looping or meandering patterns, and to collect quantitative data about a typical large early Cambrian bioturbating organism. Looping and meanders are present in many of the studied traces, but show no evidence of stereotypical behavior. Although looping patterns appear to be quite rounded and loop sizes are similar – suggesting a relatively organized neurological control over looping behavior – such looping can also occur as a natural result of quasi-random meandering

search patterns (Hofmann & Patel 1989; Hammer 1998). These data represent a first step toward analyzing *Taphrhelminthopsis*'s role within suspected larger-scale patterns in the evolution of burrowing behavior, and our interpretations require testing at other sites.

Patchiness

Based on examination of the same stratigraphic interval at 22 different sites, larger trace-covered bedding surfaces at most of the study localities exhibit highly patchy distributions of trace density (Fig. 1D, F). Across-sampled bedding plane exposures of approximately 950 m², approximately 25% of outcrop surfaces are covered by a monotaxic assemblage of *T. nelsoni* traces. Without taking into account 'behavioral' implications of regions characterized by overlapping traces, bioturbation intensity on individual surfaces (as estimated by relative trace density using Bedding-plane Bioturbation Indices, hereafter BBI) is either very rare (BBI of 1–2, reflecting areal bioturbation of <10%; Miller & Smail 1997) or extensive (BBI of 4–5, reflecting areal bioturbation of ≈45–75%, $X \approx 60\%$). Similarly, at various localities, the five most distinguishable bedding planes within the *Taphrhelminthopsis*-rich interval exhibited BBI of either 2 or 4–5. Together, these semiquantitative observations suggest two distinct modes of bioturbation: vigorous bioturbation of localized areas and sparse bioturbation of intermediary regions.

Discussion

Morphologic and sedimentologic features suggest the tracemaker was extracting sediment in a very precise and uniform manner consistent with active sediment ingestion or sediment manipulation. Despite relatively uniform burrow excavation and looping in the studied traces, no systematic organization of such strategies was identified. However, tracemaking organisms appear to have concentrated their efforts in specific bedding plane regions. Does this extreme heterogeneity in trace distribution reflect stochastic behavior over a relatively stable sedimentary surface, or directed behavioral activities over a heterogeneously distributed food regime? We favor the latter, in which centers of trace density reflect active concentration of sediment-ingestion activities. On adjacent studied surfaces, wrinkle-structures occur – features which can be formed by microbial sediment binding (Hagadorn & Bottjer 1997). In addition, analyses of burrow:sediment relationships suggest that the tracemaker bur-

rowed through relatively cohesive and laminated sediment – features which are typical of subtidal Vendian–lower Cambrian paleoenvironments where microbial mats may dominate. In modern ‘stressed’ settings, and in dysaerobic realms of the deep-sea where microbial mats such as *Beggiatoa* flourish, semi-infaunal and epifaunal echinozoans (e.g. spatangoid echinoids, holothurians) and gastropods are well-documented ingestors and bulldozers of microbially bound sediment, and often leave bilobate traces similar to *Taphrhelminthopsis* (e.g. Heezen & Hollister 1971; Grant 1991). Furthermore, such sediment grazers have return-response mechanisms whereby they turn, loop, or circle back towards concentrated regions of food resources, leaving highly bioturbated patches similar to the apparent loci of *Taphrhelminthopsis* density. Seilacher & Pflüger (1994) have hypothesized that many such Vendian–Cambrian meandering tracemakers strip-mined sediment from mat-rich layers – and such activities have recently been documented on and within suspect-microbially bound Vendian–early Cambrian sediment (Hagadorn & Bottjer 1999). We hypothesize that the *T. nelsoni* maker employed similar ecologic strategies as it moved across the surface of the early Cambrian Poleta sediments.

Conclusions

Analysis of well-preserved, laterally extensive exposures of the looping trace fossil *T. nelsoni* provides evidence for relatively large soft-bodied epifaunal or semi-infaunal echinozoan or mollusc-like animals that fed by actively ingesting relatively cohesive sediment. Although tracemakers appear to have incorporated looping into their search strategy, no systematic patterns were detected. Together with further quantitative analyses of patchiness, these data may aid in determining whether such patterns reflect tracemaker efforts to increase food intake per distance traveled and/or a neurological return response to patchily distributed food resources. When combined with other analyses of key trace fossils characteristic of the Vendian–Cambrian transition, such analyses provide a starting point for development of a larger-scale quantitative database on early animal burrowing behavior – a database which may help refine our understanding of larger-scale shifts in niche colonization, tiering and escalation of ecologic interactions through the late Neoproterozoic–Paleozoic transition.

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