Paleoecology of a large Early Cambrian bioturbator

JAMES W. HAGADORN, STEPHEN A. SCHELLENBERG AND DAVID J. BOTTJER

LETHAIA

The Lower Cambrian Poleta Formation in the White-Inyo Mountains of eastern California contains well-preserved and laterally extensive exposures of the large looping and meandering trace fossil *Taphrhelminthopsis nelsoni* n.isp. Such traces are typical features on upper bed surfaces of Lower Cambrian shallow marine sandstones and occur with Ediacaran fossils at other localities. Morphologic, sedimentologic and goniogram analyses suggest that the inferred tracemaker was a large soft-bodied echinozoan- or mollusc-grade animal with a volume greater than 14 cm^3 that actively grazed or ingested sediment at the sediment–water interface. Although portions of these traces appear to reflect relatively 'complex' behavior, looping patterns are not periodic as expected for a systematic foraging strategy. *T. nelsoni* traces are patchy in distribution and commonly associated with suspect-microbial features, suggesting that tracemakers may have been targeting microbial-based or related concentrations of food resources. Such behavioral patterns are typical of shallow late Neoproterozoic–early Cambrian settings, and like suspect-microbial structures are later restricted to deep marine or stressed settings. □ *Cambrian, Poleta, Taphrhelminthopsis, trace fossils.*

James W. Hagadorn [hagadorn@caltech.edu], Division of Geological and Planetary Sciences, California Institute of Technology, Pasadena, CA 91125, USA; Stephen A. Schellenberg [schellen@usc.edu] and David J. Bottjer [dbottjer@usc.edu], Department of Earth Sciences, University of Southern California, Los Angeles, CA 90089-0740, USA; 17th February, 1999; 4th April, 2000.

Trace fossils provide important information about the Proterozoic–Phanerozoic transition by recording the temporal and paleoenvironmental evolution of early animal habits (see summaries in Crimes & Droser 1992; Bottjer & Droser 1994; Crimes & Fedonkin 1996). Among the many trace fossils characterizing this interval, *Taphrhelminthopsis nelsoni* is important because it is one of the larger meandering traces predominant in early Cambrian shallow marine siliciclastic settings, together with *Cruziana* and ichnomorphs ascribed to *Plagiogmus* and *Psammichnites* (hereafter referred to as *Plagiogmus*; after McIlroy & Heys 1997). Unlike *Cruziana* and *Plagiogmus* (Seilacher 1970, 1995, 1997; McIlroy & Heys 1997), little is known about the paleobiology and paleoecology of the organism which produced *T. nelsoni*. Furthermore, *Taphrhelminthopsis* is one of only two early Cambrian trace fossils documented to occur with Ediacaran fossils (Jensen *et al.* 1998; Hagadorn & Waggoner 2000), indicating the tracemaker occupied environments suitable for Ediacaran soft-body preservation.

The paleobiology and paleoecology of early soft-bodied, trace-producing animals, such as the producer of *T. nelsoni*, is often poorly known (but see Seilacher 1970, 1997; Jensen 1990; Yochelson & Fedonkin 1993; McIlroy & Heys 1997). This gap stems from difficulty identifying specific tracemakers with their traces (e.g. Osgood 1970) and thereby inferring the behavioral

processes preserved as sedimentary patterns. However, innovative approaches have been utilized to extract such information from the trace fossil record, and provided insight on early animal behavior, body size and ecologic strategies (Seilacher 1967a, 1970, 1974, 1977, 1995, 1997; Hofmann & Patel 1989; Hofmann 1990; Crimes 1992; Yochelson & Fedonkin 1993; McIlroy & Heys 1997). A similar approach is presented here by evaluating behavior recorded in well-preserved examples of *T. nelsoni* to provide paleobiologic, paleoethologic and paleoecologic information on large, and presumably soft-bodied, unknown early Cambrian metazoans.

Vendian-Lower Cambrian sequences in the White-Inyo Mountains of eastern California (Fig. 1) are well known for their diverse and well-preserved trace fossil assemblages, many of which have been the focus of taxonomic and stratigraphic studies (Alpert 1973, 1974, 1975, 1976a, b, 1977; Langille 1974). Among the many well-preserved ichnotaxa in the Poleta Formation, *T. nelsoni* is notable because of its large size, exceptional preservation and occurrence on a number of accessible, laterally extensive bedding plane exposures; at several of these exposures, trace-bearing and overlying strata can be examined and sampled *in situ*. Traces are typically ~5 cm wide and several meters long, making them significantly larger and longer than other contemporaneous trails in the region.
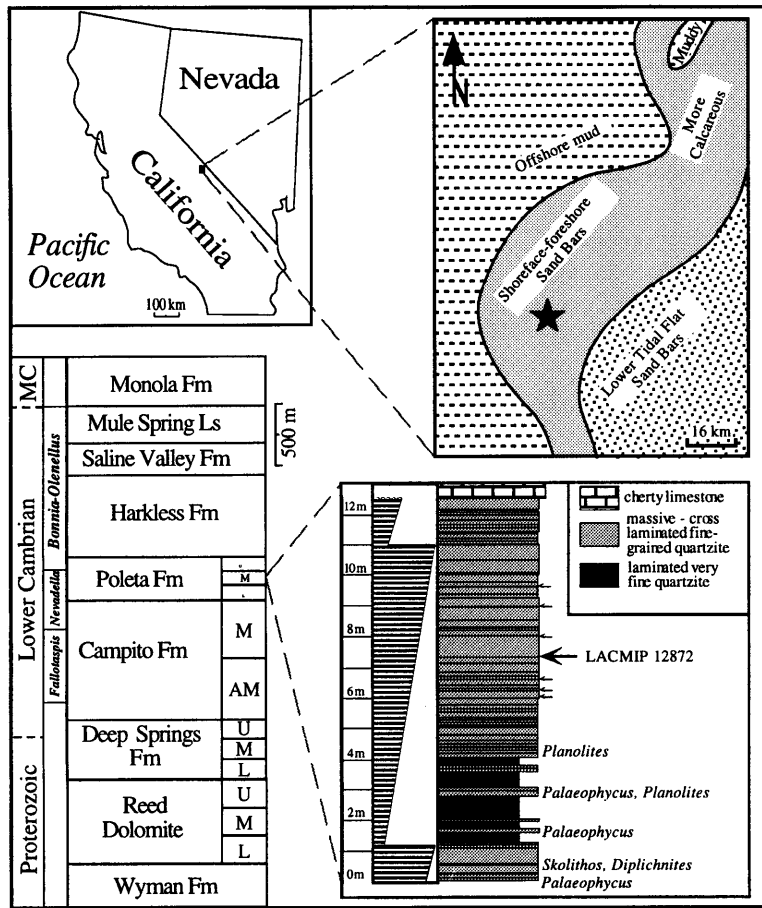
Fig. 1. Stratigraphic, geographic, and paleoenvironmental context of studied *Taphrhelminthopsis* traces. Traces occur at a variety of horizons (arrows) and are laterally extensive at one study section (lower right inset), where they extend for tens of meters. The thick arrow (4th of 7 arrows) indicates horizon illustrated in Fig. 2F (LACNHM 17188) where holotype (LACMIP 12872) was collected. Generalized paleoenvironmental context of study region in the White–Inyo Mountains is noted with a star in upper right inset diagram (modified from Moore, 1976b). Generalized regional lithostratigraphy (lower left inset) based on Nelson (1976) and Corsetti & Kaufman (1994).

Previous research

Alpert (1974) noted trails from the Poleta Folds area of the White-Inyo Mountains which cover large bedding surfaces, commonly cross themselves, form distinctive loops and lack transverse markings. These trace fossils are very common on bed tops of Cambrian strata in California, Nevada, Utah and elsewhere. Although he did not formally figure these fossils or section them in his thesis studies, Alpert (1974) ascribed these ichnofossils to *Scolicia*, and suggested the *nomen provisorium*, *S. nelsoni*. At that time, *Scolicia* were thought to be formed by shell-less gastropod-like molluscs crawling or grazing horizontally on or within the substrate (see summaries in Häntzschel 1975; Smith & Crimes 1983). *Scolicia*, however, are typically preserved in convex hyporelief on bed soles and in concave epirelief on bed surfaces (Häntzschel 1975; Uchman 1995), whereas the trace fossils from the White-Inyo Mountains (noted in Alpert (1974) and described herein) are preserved in full relief and concave epirelief on bed surfaces. Furthermore, after Alpert's original studies, Smith & Crimes (1983) suggested that use of the ichnogenus *Scolicia* be restricted to traces produced by spatangoid echinoids.

Uchman (1995) expanded the usage of *Scolicia* to include forms such as *Laminites, Subphyllochorda* and *Taphrhelminthopsis*, which sometimes reflect preservational variants of *Scolicia*. Given the Jurassic origination of irregular echinoids and lack of *Scolicia*-specific morphologic features, the White-Inyo ichnofossils are not *Scolicia*. In their gross surface morphology, these fossils are very similar to *Taphrhelminthopsis circularis*, except that they occur on bed surfaces, rather than on bed soles. Because the internal morphology and mode of formation of these fossils differ significantly from previously described ichnospecies, a new ichnospecies name is required.

Systematic paleontology

Specimens are reposited in the invertebrate paleontology collections (LACMIP) of the Los Angeles County Natural History Museum, under holotype number 12872. All specimens were collected from Los Angeles County Natural History Museum (LACNHM) locality number 17188, which is located in a deep northwest-trending ravine in the NE 1/4, SW 1/4, NE 1/4, section 25, T7S, R35E of the Deep Springs Lake, California 7.5 minute quadrangle, USA.   INYo Co.
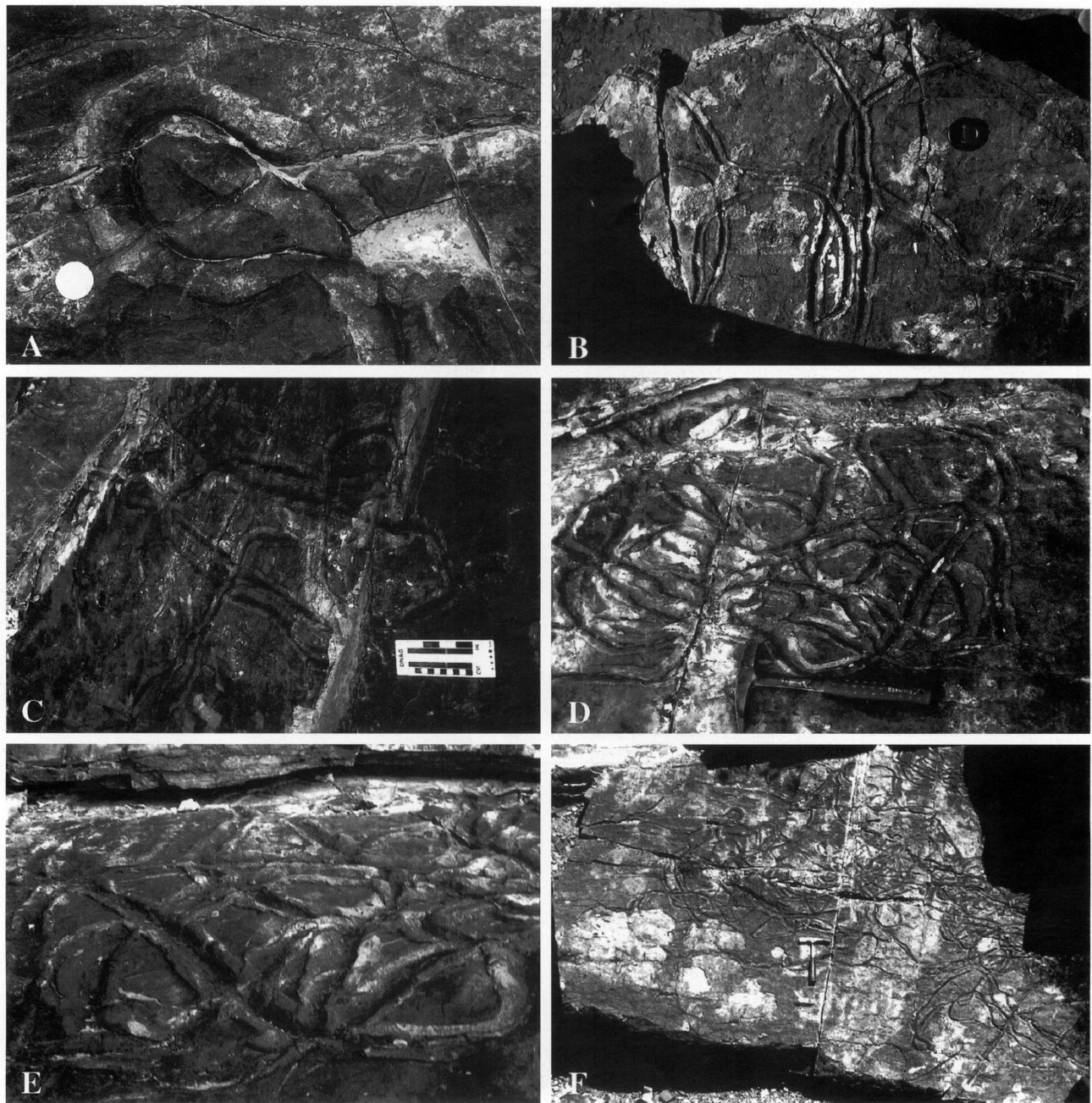
Fig. 2. Field photographs of *Taphrhelminthopsis* traces from the Poleta Folds region of the White–Inyo Mountains, eastern California. Bilobate looping and meandering patterns are clearly visible on upper bedding plane surfaces, including traces with single tight loops (A), broad arcuate loops (B), multiple self-crossings (C, E) and regions of high density and self-crossing (D, E). Note that the fill lobes are not splayed or deformed in any preferential direction and are slightly semicircular in relief. Bedding planes often exhibit centers of high trace density, or 'patchy' distributions (F). Coin in (A) is 2.4 cm in diameter, lens cap in (B) is 5 cm in diameter, lowest scale bar in scale card (C) is in cm, rock hammer (D,F) is 30 cm long, and field of view in (E) is ca. 60 cm.

Ichnogenus *Taphrhelminthopsis* Sacco, 1888

Type species. – *Taphrhelminthopsis auricularis* Sacco, 1888.

Taphrhelminthopsis nelsoni n.sp.
Figs 2, 3, 5.

Holotype. – LACMIP 12872, Figs 2, 3, 5.

Etymology. – From Clemens A. Nelson, the UCLA geology professor who first mapped these exposures, and who developed the biostratigraphic and lithostratigraphic framework for Proterozoic–Cambrian strata of this region.

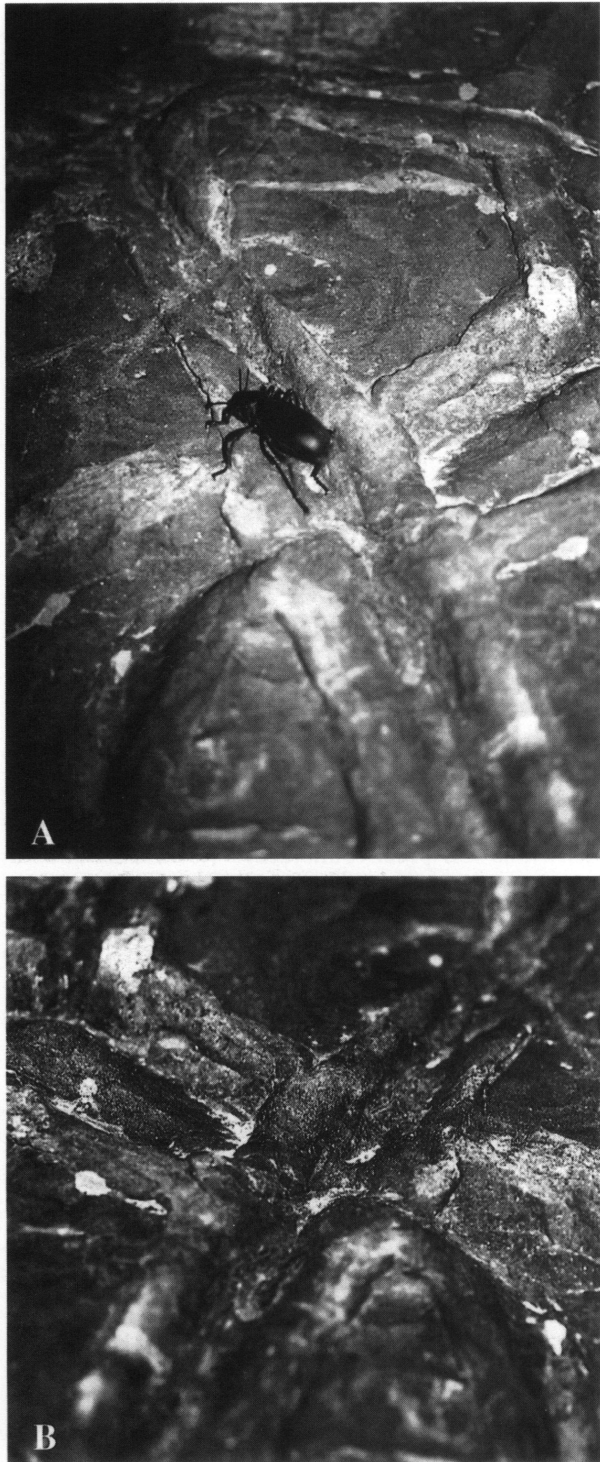*Diagnosis.* – Non-branching bilobate trail filling U-

Fig. 3. Field photographs of the detailed expression of typical *Taphrhelminthopsis* burrow crossings. In (A) and (B), note that parts of the trough and fill of the lower trace are excavated by the upper crossing trace, and the upper portions of the lower trace ridges are deformed by the more recent upper trace ridges and fill. In both cases, it is clear that the underlying trace preceded the overlying form, as the upper trace's fill ridges are draped across the underlying trace's ridges. These relationships suggest self-crossing occurred on or at the seafloor surface. Beetle in (A) is ~2.5 cm long and coin in (B) is 2.4 cm in diameter.

shaped burrow trough. Upper half of burrow fill has narrow central furrow. Ridge crests elevated above surrounding bedding plane. Always occurs on bed tops.

Description. – Traces consist of meandering, looping, cross-cutting, passively filled ridge and trough structures preserved on upper bedding surfaces (Figs 2, 3, 5). Troughs have strongly convex sides and are preserved in concave epirelief; trace fill is preserved in full relief. The center of the upper trace surfaces consists of a broad, deep v-shaped trough. Burrow fill overlaps adjacent laminated sediment surfaces in two convex lateral ridges (Fig. 3). Troughs are typically 3 cm wide and ~1 cm deep; burrow fill ranges from ~2 cm to 5 cm in width. Ridge crests are always elevated above the surrounding bedding plane, with the base of the median furrow slightly below the bedding surface. Other than the absence of sediment laminations, burrow fill is lithologically similar to burrow troughs and adjacent undisturbed sediments, and does not appear to be lined. Removal of burrow fill and sectioning of traces (including furrow-parallel, furrow-perpendicular and bedding-parallel transects) reveals no parallel laminations, meniscate fill, perpendicular striae, trough scratches, trough prodmarks or other features typical of other large furrowed Vendian–Cambrian traces such as *Plagiogmus* or *Cruziana* (Seilacher 1970, 1995, 1997; Häntzschel 1975; McIlroy & Heys 1997). Where counterpart soles could be extracted, traces are preserved in convex and concave hyporelief. Ten specimens collected and reposited together with LACMIP 12872; others preserved on bedding plane exposures at LACNHM loc. No. 17188.

Discussion. – *T. nelsoni* can be compared to several bilobate surface trails, including *Bolonia lata, Archaeonassa fossulata, Olivellites plummeri* and *Taphrhelminthopsis circularis*. *T. nelsoni* is unlike *B. lata*, which is much smaller, has a wider and ornamented furrow and does not exhibit looping (Meunier 1886), or *Archaeonassa fossulata*, which consists of two convex parallel levees commonly characterized by transverse or oblique ornamentation (Fenton & Fenton 1937b; Buckman 1994). *T. nelsoni* is also unlike *Olivellites plummeri*, which is much smaller, only occurs on bed soles and is characterized by transversely ornamented bilobate trails (Fenton and Fenton 1937a). *T. nelsoni*'s looping pattern exhibits strong similarity to *T. circularis* (Crimes *et al.* 1977) and its surface morphology is similar to *T. circularis* figured in Jensen *et al.* (1998). The major internal difference between *T. circularis* and *T. nelsoni* is that *T. circularis* either occurs on bed bases resulting from scouring of an intrastratal spatangoid echinoid burrow (see synonymy in Uchman 1995) or on bed surfaces from

Fig. 4. Simplified reconstruction of the typical mode of *Taphrhelminthopsis* preservation. Burrows cross-cut underlying laminations (Fig. 5) and are overlain by thinly bedded to mottled layers (bed thicknesses and laminations not to scale). Maximum burrow trough width (A) and maximum burrow ridge width (B) were measured to distinguish between relatively uniform trough excavation processes (a possible proxy for the diameter of the tracemaker body) and the more variable widths of the fill ridges, which were presumably deformed passively by the tracemaker's posterior.
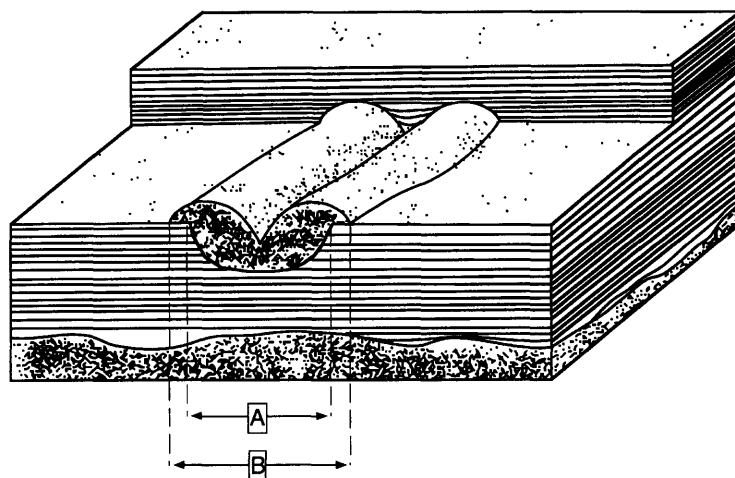
upward arching of sediment from an intrastratal burrow (see discussion of *Plagiogmus* below and also McIlroy & Heys 1997).

Plagiogmus and preservational variants thereof have previously been compared with *T. nelsoni* (e.g. Seilacher 1995, 1997; McIlroy & Heys 1997). Like *T. nelsoni*, *Plagiogmus* is a common fossil in Vendian-early Cambrian siliciclastic marine settings, and later in the Phanerozoic is only known from deeper marine settings (Häntzschel 1975; Crimes 1987). Although both traces are large and show bedding-parallel looping, *Plagiogmus* differs from *T. nelsoni* because it is an intrastratal backfilled trace characterized by transverse ridges and a lack of level self-crossing. *Plagiogmus*-makers burrowed beneath the seafloor, remaining in contact with the surface through the use of a snorkel or siphon, which punctured the overlying sediment layers (Seilacher 1995, 1997; McIlroy & Heys 1997). As the animal moved, its body displaced overlying sediments, arching them upward into a semicircular profile, which was then bisected by the snorkel – thus creating a bilobed trail in overlying layers which is superficially similar to *T. nelsoni*, and which has been identified under a wide variety of ichnogeneric names in the literature, including the original description of *T. circularis* (Crimes *et al.* 1977). In contrast, *T. nelsoni* is formed by active excavation of sediment by an organism moving on the seafloor (see Paleoecology section below). Furthermore, bilobate trails overlying *Plagiogmus* burrows do not cross one another at the same level, indicating the tracemaker may 'sense' the previous burrow and vertically shift its burrowing path, thus stacking burrows without eradication or excavation (McIlroy & Heys 1997). In contrast, studied *T. nelsoni* burrows *do* cross at the same level, and excavate and deform previously existing burrow ridges with new burrow ridges. In addition, thinning of beds which drape *T. nelsoni* coupled with evidence of backfill overlying bed surfaces suggest *T. nelsoni* was produced at the sediment surface, rather than instrastratally.

Bed surfaces characterized by bilobate trails are quite common in Phanerozoic marine strata, yet are rarely sectioned, making the taxonomic assignment of such trails less precise. In future work, a distinction should be made between (1) bilobate traces which reflect deformation of sediments into parallel furrows (which typically occur on bed surfaces, akin to sinusoidally furrowed bilobate trails which overly *Plagiogmus*; Seilacher 1995, 1997; McIlroy & Heys 1997; Zhu 1997), (2) bilobate traces which reflect erosion or casting of epichnial burrows (which can be preserved on bed surfaces or bed soles and are commonly called *Scolicia*; Häntzschel 1975; Smith & Crimes 1983; Uchman 1995), and (3) bilobate traces which reflect trails formed after excavation of sediment (and are typically preserved on bed surfaces, such as *T. nelsoni* described herein; Fig. 5). In this study, sectioning of studied *T. nelsoni* clearly demonstrates that the *T. nelsoni*-maker was actively excavating sediment, and thus allows discrimination between the aforementioned three modes of bilobate trace fossil genesis.

Geologic context

In eastern California, the Lower Cambrian Poleta Formation is divided into three stratigraphically distinct members (McKee & Moiola 1962; Stewart 1970). The studied horizons occur in the upper sandstone sub-unit of the middle member at a well-
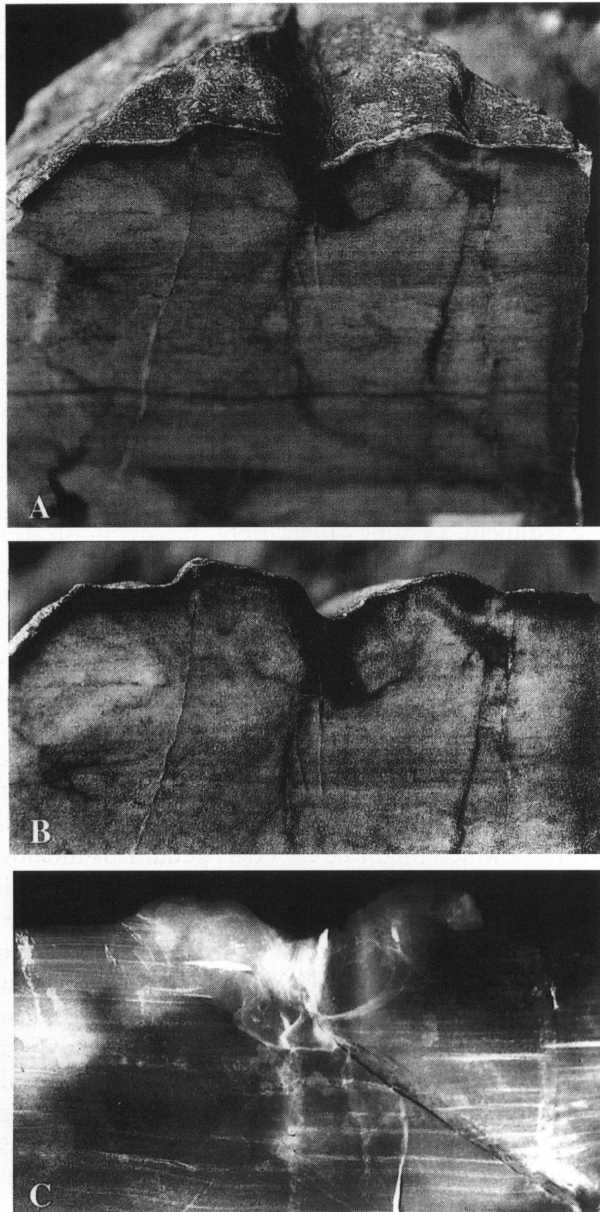
Fig. 5. Sectioned *Taphrhelminthopsis* trace (LACMIP 12872), including an oblique view of the trace furrow and cut slab (A), a cross-section perpendicular to the furrow axis, illustrating sharp truncation of laminations by the burrow fill (B); and an x-radiographic positive print of the counterpart to (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 dessication 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
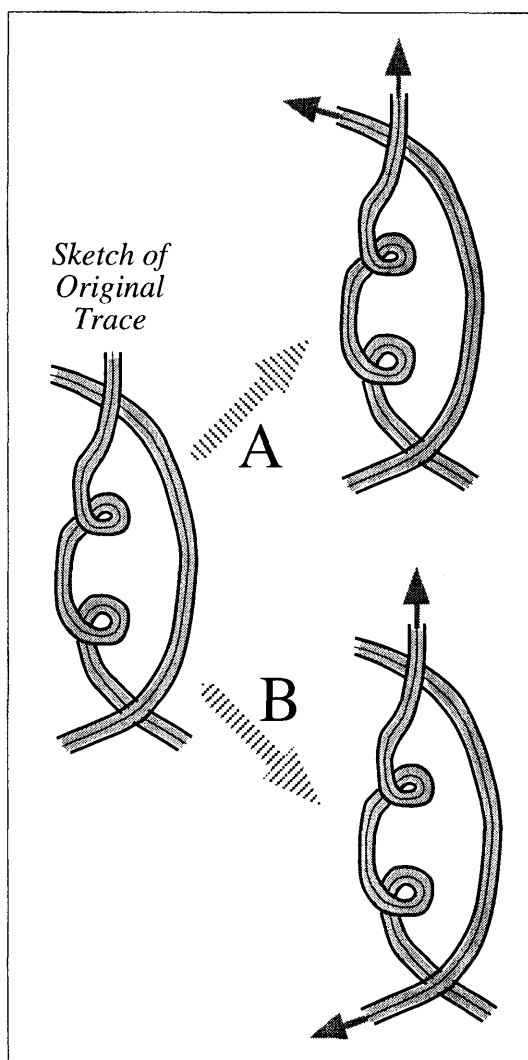
Fig. 6. Simplified schematic illustration of cross-cutting relation-ships of two looping traces outlined on acetate sheets from bedding plane illustrated in Fig. 2C. In the looping trace, one can determine the direction of tracemaker movement from over-under and burrow deformation. In this specimen, 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 opportu-nistic 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 pre-served 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 indivi-duals 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 ($p >> 0.05$, $X = 35.03 \pm 7.52$ 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 ~ 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. circularlis* 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, Pernochaeta, 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
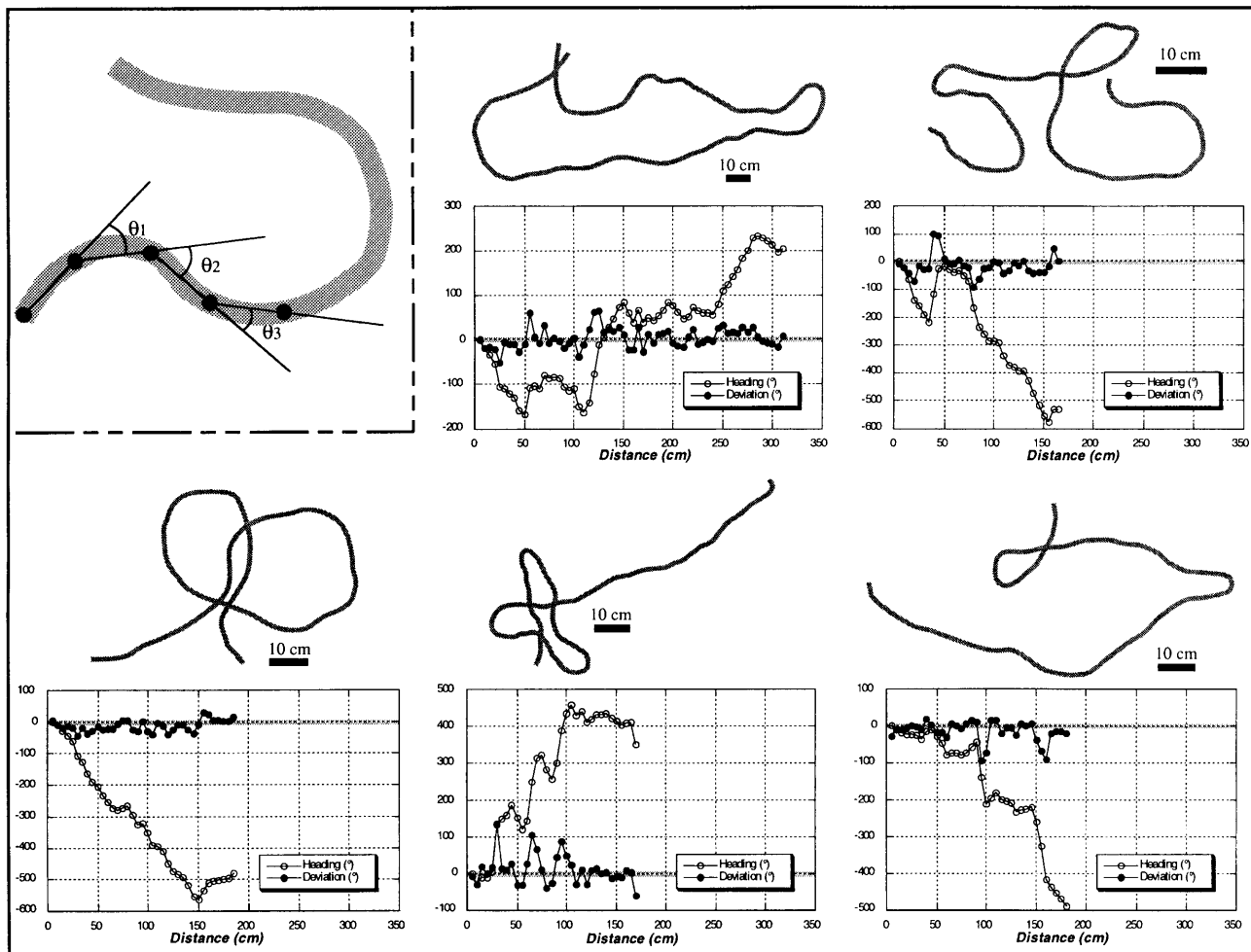
Fig. 7. Goniogram methodology and data. Heading was measured using a Brunton compass, and relative deviation (inset) was noted at every 5-cm sampling interval. Goniogram plots of the heading (open circles) and deviation (closed circles) are plotted below sketches of trace outlines for 5 of the 35 studied 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 loco-motive 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-
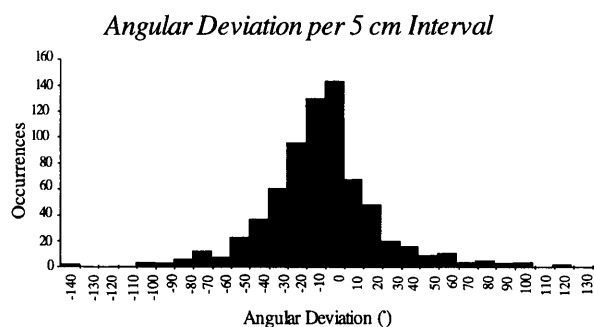
Angular Deviation per 5 cm Interval

Y-axis: Occurrences (0 to 160 by 20). X-axis: Angular Deviation (°) from -140 to 130.

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 $\sim 180°$ 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 $-2° \pm 30°$ 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 *Helminthoida*, 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 m^2, 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%, $X ≈ 60\%$). 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 ingesters 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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