

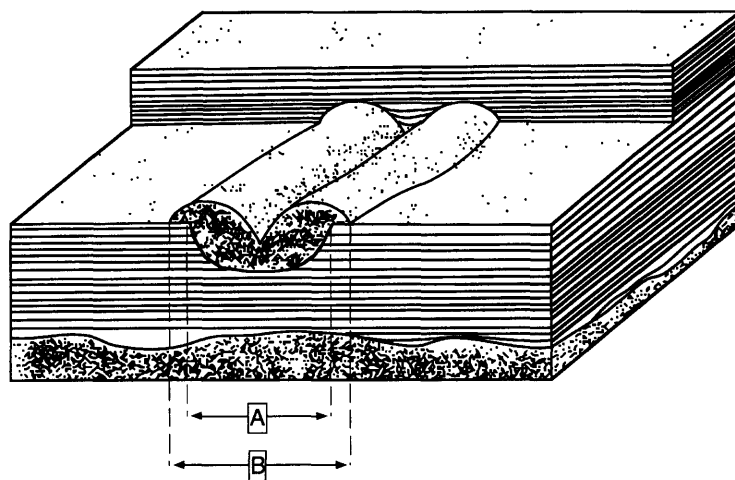
Fig. 3. Field photographs of the detailed expression of typical *Taphrhelminthopsis* burrow crossings. In (A) and (B), note that parts of the trough and fill of the lower trace are excavated by the upper crossing trace, and the upper portions of the lower trace ridges are deformed by the more recent 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 repositied 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 intrastratally.

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-