Skimming the surface with Burgess Shale arthropod locomotion
Nicholas J. Minter1,*, M. Gabriela Mángano1 and Jean-Bernard Caron2,3

1Department of Geological Sciences, University of Saskatchewan, 114 Science Place, Saskatoon, Saskatchewan, Canada S7N 5E2
2Department of Natural History (Ichnology section), Royal Ontario Museum, 100 Queen’s Park, Toronto, Ontario, Canada MSS 2C6
3Department of Ecology and Evolutionary Biology, University of Toronto, 25 Willcocks Street, Toronto, Ontario, Canada MSS 3B2

The first arthropod trackways are described from the Middle Cambrian Burgess Shale Formation of Canada. Trace fossils, including trackways, provide a rich source of biological and ecological information, including direct evidence of behaviour not commonly available from body fossils alone. The discovery of large arthropod trackways is unique for Burgess Shale-type deposits. Trackway dimensions and the requisite number of limbs are matched with the body plan of a tegopeltid arthropod. *Tegopeltes*, one of the rarest Burgess Shale animals, is over twice the size of all other benthic arthropods known from this locality, and only its sister taxon, *Saperion*, from the Lower Cambrian Chengjiang biota of China, approaches a similar size. Biomechanical trackway analysis demonstrates that tegopeltids were capable of rapidly skimming across the seafloor and, in conjunction with the identification of gut diverticulae in *Tegopeltes*, supports previous hypotheses on the locomotory capabilities and carnivorous mode of life of such arthropods. The trackways occur in the oldest part (Kicking Horse Shale Member) of the Burgess Shale Formation, which is also known for its scarce assemblage of soft-bodied organisms, and indicate at least intermittent oxygenated bottom waters and low sedimentation rates.

**Keywords:** Burgess Shale; Cambrian; ichnology; locomotion; trackway; palaeoecology

1. INTRODUCTION

Discovered over 100 years ago, the world-famous Burgess Shale continues to yield important new insights into the evolution and ecology of animals during the Cambrian explosion [1–5]. The exceptional preservation of soft tissues in the Burgess Shale permits functional morphological inferences on the modes of life and palaeoecology of early metazoans [6,7]. Trace fossils, including trackways and burrows, provide direct evidence for animal behaviour in the fossil record, and can add further crucial insights for unravelling the palaeoecology of their producers and placing temporal and palaeoenvironmental constraints on the origin of functional novelties. Here, we report and discuss the significance of the first arthropod trackways discovered from the Burgess Shale Formation.

Functional morphological studies of the benthic Burgess Shale arthropods *Olenoides* [8,9], *Naraonia* [10], *Sidneyia* [11], *Malaria* [12] and *Tegopeltes* [13] postulated that they employed slow, low-gearered, stable gaits with many propulsive limbs in contact with the substrate when walking, and could launch themselves off the substrate to swim or drift. Limb morphology, with spinose coxae and podomeres, also led to the suggestion that *Olenoides*, *Naraonia*, *Sidneyia* and *Malaria* were predators or scavengers [6,8–12]. The coxae are not known in *Tegopeltes*, but it is also inferred to have been a benthic predator or scavenger [6,13]. The aims of this paper are to (i) describe the first known arthropod trackways from the Burgess Shale Formation; (ii) identify their potential producers; (iii) integrate trackway and body fossil data to derive the locomotory techniques employed in producing the trackways; and (iv) test previous hypotheses on their locomotory capabilities and mode of life.

2. GEOLOGICAL SETTING

The Middle Cambrian (Series 3) Burgess Shale Formation in Yoho National Park (British Columbia, Canada) is a basinal succession of mudstone and carbonate that has yielded several fossil assemblages of soft-bodied animals [14,15]. The trackways were collected from two separate localities on Mount Stephen and Mount Field (electronic supplementary material, figure S1) within the Kicking Horse Shale Member of the Burgess Shale Formation [14,15]. The Kicking Horse Shale Member comprises thinly bedded, calcareous muddy siltstone and thin slaty limestone [14,15]. With the exception of the *Sanctacaris* locality on Mount Stephen [16], the Kicking Horse Shale Member generally contains a low diversity assemblage of soft-bodied animals [14,15]. The Kicking Horse Shale Member is the oldest unit (*Glossopterus* Zone) of the Burgess Shale Formation [14,15].

The exceptional preservation of animals within the younger (*Bathyuriscus* Zone) Phyllopod Bed in the Walcott Quarry Shale Member [14,15] has been attributed to...
rapid burial by mud-rich slurry flows [17]. This indicates
that the animals were transported, although recent tapho-
nomic analysis suggests transport and decay were
negligible, and most benthic animals were probably buried
within their habitats [18]. Geochemical analysis of Burgess
Shale-type deposits indicates exaerobic conditions, with the
anoxic–oxic boundary occurring at the sediment–water
interface, rather than anoxic bottom water [19]. Trace fos-
sils are preserved in situ and therefore represent reliable
indicators of local environmental conditions. Simple bur-
rows and trails within the Burgess Shale Formation [14,18,20]
and other Burgess Shale-type deposits of the USA [21] demon-
strate at least intermittent oxygenation and in situ colonization of the sediment. Diminutive trace fossil assemblages are also found in association with carapaces of soft-bodied animals in the Stephen Formation of Canada [22,23] and Chengjiang [24] and Kaili biotas of
China [25,26]. Such occurrences in Burgess Shale-type
deposits have been attributed to increased benthic oxygen
levels following soft-tissue stabilization under anoxic condi-
tions [21]. High rates of sedimentation have also been
invoked to explain the near absence of burrows in parts of
the Burgess Shale Formation [17], although the emplace-
ment of simple trails only requires short colonization
windows [27]. The diminutive nature and shallow
penetration depth of the trace fossils in the Stephen For-
mation are indicative of oxygen-deficient conditions, and
suggest that oxygen rather then sedimentation rate is the
primary control on their occurrence in Burgess Shale-type
deposits [23].

3. TRACKWAY DESCRIPTION
The five known trackway specimens are reposited at
the Royal Ontario Museum, Toronto, Canada (ROM).
The longest trackway (ROM 61454) is preserved for
over 3 m (figure 1a,b; electronic supplementary material,
figures S2–S5). The trackway comprises overlapping
series of up to 25 tracks. It is slightly dimorphic in form. The tracks on one side are elliptical to curvilinear in shape and orientated obliquely to the midline of the trackway, while those on the other are more elongate and orientated perpendicularly to the midline. The sets of tracks are also all offset and orientated obliquely relative to the long-axis of the trackway and the direction of travel. The external width is 100–120 mm. Tracks are 2–27 mm long and spaced 7–28 mm apart. The stride is 200–230 mm.

ROM 61455 preserves a trackway making a gradual turn (figure 1c). The external width is 120–135 mm. The trackway splays on the outside of the turn, making the series more apparent. Highly overlapping series of up to 25 tracks are observed and the stride is 90–95 mm on the outside of the turn, decreasing to 60–85 mm on straighter sections. Tracks are circular to comma-shaped, 2–15 mm long and spaced 5–21 mm apart. Intermittent paired medial imprints are present. ROM 61456 preserves a trackway making a tight U-turn (figure 1d). The series splay strongly on the outside of the turn, although a high degree of overprinting obscures the precise number of tracks per series. Short spurts of tracks are present on the inside of the turn. Tracks range from elliptical to curvilinear in shape and at least 20 are present within each series. The external width is approximately 70 mm, and tracks are 5–18 mm long and spaced 8–22 mm apart.

Several smaller trackways with differing orientations are preserved in ROM 61457 (electronic supplementary material, figure S6) with external widths of 58–70 mm and overlapping series of up to 22 elliptical to curvilinear tracks. Tracks are 3–10 mm long and spaced 7–22 mm apart. The stride is 145–150 mm. ROM 61458 is a small slab that preserves a partial trackway similar to those of ROM 61457. All trackways can be ascribed to the ichnogenus *Diplichnites* (electronic supplementary material). *Helminthoidichnites*-like trails are also associated with the trackways (electronic supplementary material, figure S7).

4. PRODUCER IDENTIFICATION

Trace fossil morphology is influenced by the anatomy of the producer, its behaviour and the substrate conditions. Compared with other types of trace fossils, trackways are more strongly influenced by, and therefore more reflective of, the anatomy of the producer [28]. Fortey & Seilacher [29] established a set of criteria for assigning a particular trace fossil taxon to a specific producer: (i) close association in the field; (ii) concurrent stratigraphic range; (iii) minimal choice of available candidates; (iv) consistent size range; and (v) consistent biogeographic range. These ideas can be built upon to create criteria for assigning individual trackways or assemblages of trackways to producers with varying levels of confidence and corresponding approximate biotaxonomic rank. In increasing order, these assignment levels are: (i) general correlation of trackway features with the body plan of an animal group (class or higher equivalent taxonomic rank at the stem or crown-group levels); (ii) correlation of features with coeval body fossils (class–order); (iii) correlation of features with coeval body fossils from the same palaeobiogeographic region and environment (order–family); (iv) correlation of features with body fossils from the same formation (order–genus); and (v) producer at the end or in close association with the trackway (species).

The majority of Cambrian trackways are broadly attributed to trilobites [30,31] on the basis of a correlation between trackway features and the general trilobite body plan (assignment level i), or more specific groups [32] on the basis of correlation with coeval body fossils from the same palaeobiogeographic region and environment (assignment level iii). Trackways from the shallow marine Bright Angel Shale of Arizona have been correlated with a producer similar to the coeval (but deeper-water) Burgess Shale arthropod *Habelia* [33] (assignment level ii). A second trace fossil from the same formation was identified as a trackway, potentially related to a lobopodian animal resembling *Ayshaia* [34], although this particular trace fossil may instead be an unusual expression of a serially and alternating branched burrow system [34,35].

The Burgess Shale trackways described herein are unique in their large size and occurrence in Cambrian Burgess Shale-type deposits. The trackways are of different sizes (58–135 mm wide) and probably come from different stratigraphic levels within the Kicking Horse Shale Member, and were thus produced by different individuals. However, they all share the same characteristics of relative dimensions and numbers of tracks, and were therefore all made by the same type of animal. Comparison of key trackway characters (including size and number of tracks) with potential producers from the Burgess Shale is facilitated by the exceptional preservation of soft tissues in census and time-averaged communities [18]. This provides the potential opportunity to correlate the trackways with body fossils from the same formation (assignment level iv).

The producers of the Burgess Shale trackways were large (up to 300 mm long and 135 mm wide) and possessed at least 25 pairs of walking limbs. Among known Burgess Shale and other Lower–Middle Cambrian arthropods with walking limbs (electronic supplementary material, table S1), only *Tegopelte* [13] (figure 2) fits these criteria, reaching 280 mm in length, 140 mm in width and possessing 33 pairs of walking limbs. The posteriormost limbs are reduced and are unlikely to have been used in locomotion [13]. Fragmentary remains of *Sidneyia* from the Middle Cambrian of Utah are estimated to approach the appropriate size [36], although *Sidneyia* only has nine pairs of walking limbs [11]. All other known Burgess Shale arthropods with walking limbs are too small to have made all but the smallest trackways, but still possess insufficient numbers of appendages (electronic supplementary material, table S1). *Saperion*, from the Lower Cambrian Chengjiang fauna of China, reaches 151 mm in length and possesses approximately 25 pairs of walking limbs [37].

*Tegopelte* is the largest benthic arthropod from the Burgess Shale (figure 2; electronic supplementary material, figure S8) and is at least twice the size of any other known benthic Burgess Shale bilaterian. It is also one of the rarest, with the only two known specimens occurring from the Walcott Quarry Shale Member [13]. *Tegopelte* was originally described as a ‘soft-bodied trilobite’ with a thin unmineralized divided exoskeleton [13]. Subsequent analysis has determined that the divisions are folds, arising from compaction during preservation, in an undivided dorsal shield [37]. *Tegopelte* is often regarded as belonging to the lamellipedia [38], a group that includes trilobites; however, the position of this group is largely unconstrained [39]. Phylogenetic analysis has resolved a sister relationship
of *Tegopelte* with *Saperion* and position in the Order Helmetiida/Conciliterga [40,41]. Body fossils of *Tegopelte* are not known from the Kicking Horse Shale Member, but the trackways can be attributed to *Tegopelte* (or, at the very least, a tegopeltid) on the basis of correlation with body fossils from the same formation (assignment level iv).

5. LOCOMOTION

Animal locomotion can be defined by three parameters: the gait ratio \(p : r\), which is the proportion of the step cycle that a limb spends in the forward, recovery, protraction period \(p\) to that spent in the backward, propulsive, retraction period \(r\); the successive phase difference \(\text{succ}\), which is the proportion of the step cycle that a limb moves before the limb in front; and the opposite phase difference \(\text{opp}\), which is the proportion of the step cycle that a limb on one side of the body moves after the paired limb on the opposing side of the body [42,43]. These parameters can be derived from trackways and a reconstruction of the producer (electronic supplementary material), and have been used to reconstruct the locomotion of numerous extinct animals [44–46].

The Burgess Shale trackways reveal that their producers were capable of performing fast, high-gear gaits and also able to ‘skim’ across the substrate with few limbs in contact with the substrate at any one point in time. Trackway analysis (electronic supplementary material) yields gait ratios of 9.3 : 0.7 and 9.4 : 0.6, indicating that limbs only spent 7 and 6 per cent of the step cycle in the propulsive backstroke phase for ROM 61454 (figure 1a,b and electronic supplementary material, figures S3–S5) and ROM 61457 (electronic supplementary material, figure S6), respectively. Successive limbs on one side of the body would have moved in advance of the limb in front by 88 per cent of the step cycle. The trackways have opposite symmetry and so paired limbs on either side of the body moved synchronously. These parameters indicate that only one to two pairs of limbs were in contact with the substrate at any one point in time that metachronal waves of eight limbs appeared to travel backwards along the body with short gaps between the placement of proceeding limbs (figure 3; electronic supplementary material, figures S9a and S10, and animation S1). ROM 61455 demonstrates a slower but still high-gear gait. Analysis of the straighter section yields a gait ratio of 7.6 : 2.4, where limbs spent 24 per cent of the step cycle in the propulsive backstroke phase and successive limbs moved in advance of the limb in front by 69 per cent of the step cycle. The trackway has opposite symmetry and so paired limbs on either side of the body moved synchronously. These parameters indicate that six pairs of limbs were in contact with the substrate at any one point in time, and metachronal waves of three limbs appear to have travelled backwards along the body with short gaps between the placement of proceeding limbs (electronic supplementary material, figure S9b).

ROM 61456 indicates the producer was capable of performing tight turns (figure 1d); however, unlike trilobites, *Tegopelte* has an unarticulated dorsal shield rather than an articulated dorsal exoskeleton. Detailed examination of *Tegopelte* and the trackway demonstrates how the execution of a tight turn can be ameliorated with an arthropod with an unarticulated dorsal exoskeleton. In *Tegopelte*, the compression of gill filaments on the surface of the cuticle suggests that its dorsal shield was thin and would have had some flexibility. In the trackway, the track series on the outside of the turn are splayed, but...
only with a low degree of curvature, and short spurts of tracks are present on the inside of the turn (figure 1d). Such a tight turn could therefore be achieved by a tegopeltid through a combination of limited lateral flexure and side-stepping.

The reconstructed method of trackway production shows that the anterior tracks of each series are produced by the posterior limbs (figures 3 and 4). In ROM 61454, the anterior tracks of each series are situated more medially to the midline of the trackway (figure 1a,b, electronic supplementary material, figures S3–S5), which is consistent with the method of production and the posteriormost limbs being shorter in Tegopelt. The en-echelon arrangement of tracks in this trackway and ROM 61457 results from the body of the producer being offset obliquely relative to the long axis of the trackway and direction of travel. This is caused by the animal being partly buoyed up while producing the trackway and could be related to a current or the producer being less able to control the yaw of its body while employing a high-geared gait ratio. There are no tool marks or scours preserved with the trackways to indicate the action of a current. These may not be observed if the trackways are undertracks [47]; however, undertracks are unlikely to be produced by an animal that was buoyed up. Also, in ROM 61457, several trackways have differing orientations (electronic supplementary material, figure S6), but were all produced by high-geared gaits, and this is inconsistent with the producers all being subject to a unidirectional current. The alternative is that the producers were less able to control the yaw of their body at these higher-geared gaits, owing to fewer limbs being in contact with the substrate at any one point in time, compared with more normal trackways produced by lower-geared walking gaits (figure 1c).

6. DISCUSSION

The discovery of trackways in the Burgess Shale permits direct insights into animal behaviour and environmental conditions during the Cambrian. The trackways can be attributed to the Burgess Shale arthropod Tegopelt, or at least a tegopeltid (figure 4). No other types of trackways have been found so far in the Burgess Shale Formation. On the basis of functional morphology, Tegopelt was hypothesized as employing a walking gait that was slow and low-geared \( (p : r = 3.75 : 6.25, \ suc = 0.125) \), with many propulsive limbs in contact with the substrate at any one point in time, but could also perform higher-geared gaits to launch from the substrate and drift or swim [13]. The trackways provide direct evidence to largely support this hypothesis, showing that such animals could indeed employ fast, high-geared gaits akin to ‘skimming’ across the substrate. The trackways also demonstrate that they were capable of a slower and lower-geared walking gait that is similar to those calculated for subaquously walking myriapods [45]. This walking gait is higher-geared than that

---

**Figure 3.** Locomotion and trackway production of a tegopeltid animal, based on ROM 61454 using a gait ratio of 9.3 : 0.7 and successive phase difference \( \text{suc} \) of 0.88. (a) Manton gait diagram. Horizontal axis represents progression through time. The phase relationships of the anterior 10 limbs on one side of the body are depicted. Each complete step cycle of a limb is represented by a couplet of a thick downward sloping line, corresponding to the relative duration of the propulsive, backward, retraction phase \( (r) \) when the limb is in contact with the substrate; and a thin upward sloping line corresponding to the relative duration of the recovery, forward, protraction phase \( (p) \) when the limb is lifted above the substrate. The successive phase difference is the proportion of the step cycle that a limb \( n + 1 \) moves in advance of the limb \( n \) in front. Vertical time lines \( (t_0 - t_0) \) capture snapshots of the positions of the limbs that are depicted in (b). (b) Time-lapse trackway production. ‘Gait still’ snapshots represent the positions of the limbs and development of the trackway between the placement of limbs \( n \) and \( n + 1 \) in the proceeding step cycle. Light-coloured limbs indicate those in contact with the substrate. The en-echelon arrangement of the series of tracks has been exaggerated to show the individual tracks.
previously proposed for *Tegopelte*, although it falls within the hypothesized locomotory end-members [13].

On the basis of functional morphology, *Tegopelte* is considered to have been much like the large *Sidneyia* and smaller *Olenoides*, *Naraoia* and *Molaria* in being a benthic predator or scavenger [6]. The trackway evidence supports the hypothesis of a predatory or scavenging mode of life, demonstrating that they could employ fast, high-geared gaits and were also capable of performing tight turns. Fast, high-geared gaits could potentially be associated with predator avoidance, although the producers of these trackways would have been twice the size of any other benthic Burgess Shale arthropod and over half the estimated size of the largest *Anomalocaris* [48]. In addition, our re-examination of *Tegopelte* identified the presence of gut diverticulae (figure 2b,c). This provides strong evidence of a predatory or scavenging mode of life [49,50]. The presence of eyes in *Tegopelte* [13] was considered to be uncertain [40], but they are confirmed herein and are probably ventral in position (figure 2d and electronic supplementary material, figure S8a).

The presence of trackways, along with interface trails, in the Kicking Horse Shale Member of the Burgess Shale Formation also permits inferences on environmental conditions. Burrows have been observed in other members of the Burgess Shale Formation and indicate at least intermittent oxygenation of the sediment [20], while the diminutive and shallow nature of burrows and trails in the adjacent Stephen Formation suggests that oxygen was a major control on their occurrence [23]. The trackways described herein are the first to be discovered from the Burgess Shale Formation and they are unique for Burgess Shale-type deposits in their large size. They provide evidence of arthropods living within the environment, extending the stratigraphic range of tegopelids, and indicate that the bottom waters must have been sufficiently oxygenated, at least intermittently, to sustain large benthic animals during deposition of the oldest member of the Burgess Shale Formation. The preservation of such trackways would also have required that the substrate was dewatered and stiff owing to breaks in, or slow rates of, sedimentation. Contrary to younger Burgess Shale localities [14], the fossil-bearing layers of the Kicking Horse Shale Member do not lie directly at the base of the Cathedral Escarpment, and are of low diversity and abundance. This might suggest that the Kicking Horse Shale Member represented an environment generally unfavourable for a rich community to thrive. The presence of large trackways also suggests that the general scarcity of soft-tissue preservation may be taphonomic, with a greater prevalence of oxygen and/or low sedimentation rates throughout deposition of the Kicking Horse Shale Member.

The Burgess Shale biota provides key insights into the evolution and ecology of body plans during the Cambrian explosion. The discovery of arthropod trackways from the Kicking Horse Shale Member highlights their application as indicators of environmental conditions. The results also provide insights into the locomotory capabilities of extinct animals that can be used to test functional morphological hypotheses on modes of life. Integrated trace and body fossil evidence provides an innovative and dynamic picture of arthropods such as *Tegopelte* as active carnivores. Early marine communities were therefore occupied not just by large nektonic predators such as *Anomalocaris*, but also by large benthic predators, emphasizing the importance of such lifestyles in shaping early complex marine communities and evolution during the Cambrian explosion.

We thank Parks Canada for collecting permits (to ROM—Desmond Collins and J.-B.C.), and Doug Erwin, Mark Florence and John Pojeta (Smithsonian Institution) for access to the *Tegopelte* specimens and technical assistance. N.J.M.’s research is supported through a Government of Canada Post-doctoral Research Fellowship under the Canadian Commonwealth Scholarship Programme. M.G.M.’s research is supported by Natural Sciences and Engineering Research Council (NSERC) Discovery Grant 311727 and University of Saskatchewan StartUp fund 411435. J.-B.C.’s research is supported by NSERC Discovery Grant 341944 and ROM research and fieldwork grants. Marianne Collins produced figures 3b and 4, and electronic supplementary material, figure S10 and animation S1. This is Royal Ontario Museum Burgess Shale project number 34. The manuscript benefitted from...
the comments of Greg Edgecombe as the Associate Editor, and two anonymous reviewers.

REFERENCES


