Function and hydrostatics in the telson of the Burgess Shale arthropod *Burgessia*

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***Burgessia bella* is a characteristic Burgess Shale arthropod (508 Ma), but the unusual preservation of its telson in both straight and bent modes leads to contradictory interpretations of its function. A reinvestigation of the fossil material, including burial attitudes, combined with a comparison with the decay sequence and mechanics of the telson in living *Limulus*, demonstrates that the telson of *Burgessia* was flexible in its relaxed state but could be stiffened in life. Evidence of fluid within the telson indicates that this manoeuvrability was achieved by changes in hydrostatic pressure and muscular control. The dual mode in the *Burgessia* telson is, to my knowledge, the first documented among fossil arthropods. It indicates that the requirement for a rigid telson, which is resolved by a thick sclerotized cuticle in most arthropods, may first have been achieved by hydrostatic means.**

Keywords: fossil preservation; animal behaviour; arthropod telson; *Burgessia*; *Limulus*

1. INTRODUCTION

Burgessia bella Walcott 1912 is an enigmatic arthropod with a relatively long telson, which is the terminal, pointy portion of the body without appendages. Walcott (1912, 1931) described *B. bella* as having a segmented telson, but it was reinterpreted as bearing an unsegmented conical caudal spine by subsequent workers (Simonetta 1970; Hughes 1975; Briggs *et al.* 1994). Hughes (1975, p. 427), in particular, observed that some specimens exhibit some degree of telson flexibility and stated that ‘since they show no definite joint structure nor any regularity in position, it is preferred to consider them as *post-mortem* fractures’. Whittington (1985, fig. 4.55) also noted the flexible telson in *Burgessia* but did not specify whether it was a biological feature or a taphonomic artefact. During re-examination of Burgess Shale specimens ($n=1734$), many well-preserved *Burgessia* were observed to exhibit various degrees of telson flexibility, such as strongly curved (figure 1*b*), and both strongly curved and sinuous (figure 1*c*), in addition to straight (figure 1*a*). The two contrasting modes of *Burgessia* telson preservation are: (i) a straight

(spine-like) telson (figure 1*a,d,f*) as reconstructed in Hughes (1975) and (ii) a bent telson (figure 1*b,c,i–k*). Four scenarios are proposed to explain these observations: (i) a straight telson is a biological feature and a non-straight telson is a taphonomic artefact, (ii) vice versa, (iii) both telson modes are biological features, and (iv) both modes are taphonomic features. Hughes’ (1975) straight telson interpretation is supported by comparison with the living analogue *Limulus* (see the electronic supplementary material); thus, a straight telson in *Burgessia* may at best be a biological feature, and two of the four scenarios ((ii) and (iv)) can be discarded. Whether or not the bent telson mode is a taphonomic artefact (scenario (i) versus scenario (iii)) can be tested by conducting actualistic taphonomic experiments on *Limulus* carcasses (figures S1 and S2 in the electronic supplementary material). Finally, observing how live *Limulus* uses its telson can help us to interpret some behavioural information about *Burgessia*.

2. MATERIAL AND METHODS

Figured fossil specimens are deposited in the Smithsonian Institution, National Museum of Natural History (NMNH), Washington, DC. Among 1734 specimens examined, a total of 281 specimens containing well-exposed telsons were measured for statistical analyses (figure 2). Lin (2006) showed that orientation of entombment can provide indications about the transport history of organisms prior to complete burial. Measured specimens are categorized into six categories based on their entombment postures (figure 2). Data with measurable axial length are compiled as box plots (figure 2*b*). Axial length is defined as the sagittal length of the body, excluding the telson. Procedures of conducting taphonomic experiments on *Limulus* follow Babcock *et al.* (2000).

3. RESULTS

Only 16 per cent (21 out of 130) of telsons are straight and parallel to the body axis (category A) in laterally/obliquely compressed specimens. Instead, *Burgessia* is most commonly preserved with a bent telson. Besides, the telson was probably movable because it can be directed away from (category B) or towards (category C) the appendages. Among all the bent telsons examined, there is no sign of fracture or detachment as seen in coeval arthropods (e.g. Lin 2006, fig. 4; Hou & Bergström 1997, fig. 41). Furthermore, telson modes and entombment postures are not size/age dependent (figure 2).

Results from *Limulus* decay experiments indicate that the telson is the most resistant body part to microbial decay, although decay timing is individual specific (see the electronic supplementary material). Flexible *Limulus* telsons with various degrees of sinuosity resulting from decay represent good proxies for the late stages of *Limulus* decay in the absence of predation and scavenging activities. Sinuous folds and wrinkles on the telson (figure S2*c* in the electronic supplementary material) are due to collapse of decayed cuticles. However, the decay history of *Limulus* indicates that the telson becomes slimy and flexible only after detachment of the appendages. *Burgessia* does not follow the decay sequence of *Limulus*, because, in *Burgessia*, straight and bent telson modes both occur with appendages still attached to the carcasses (figure 1*a–d, f–k*). *Burgessia* and other nekton–benthic arthropods have been interpreted as being transported (a relatively short distance)

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Figure 1. (a–d, f–k) Representative specimens of *B. bella* preserved in different orientations and telson modes from the Burgess Shale biota (Cambrian) and (e) a comparison with modern *Limulus polyphemus*. (a) NMNH 155626, oblique, straight telson. (b) NMNH 83947h, dorsal, strongly bent telson. (c) NMNH 83947a, oblique, sinuous telson. (d) NMNH 83947j, lateral, straight but tilted telson. (e) *L. polyphemus*, lateral, bending its telson away from the body axis ($\theta \approx 35^\circ$) during overturn recovery. (f) NMNH 155680, oblique, straight telson with a significant tilting ($\theta \approx 60^\circ$). (g) Enlarged view in (f) showing a fluid-bearing vessel in a *Burgessia* telson; boundaries of cuticle walls marked by paired arrows; v, fluid-bearing vessels (preserved as a silvery film; see the electronic supplementary material for additional examples in *Marrella splendens*). (h) NMNH 114240, overturned, straight but tilted telson. (i) NMNH 57680, overturned, curved and tilted telson. (j) NMNH 114243 part, overturned, mostly straight but tilted telson. (k) NMNH 83947g, overturned, curved and tilted telson. Scale bars, (a–d, f, h–k) 5 mm, (e) 15 cm and (g) 3 mm.

and buried alive via muddy turbidity currents (Caron & Jackson 2006). Except for two specimens (NMNH 155665 and 204711; Hughes 1975) that show clear evidence of decay, there is no correlation between degree of decay and flexibility of the telson.

If a bent telson was a taphonomic feature formed after burial, it could be regarded as a sign of rigor mortis. However, rigor mortis cannot be the cause of observed telson postures because rigor mortis is due to the contraction of muscles and tissues between bones or vertebrae, and the *Burgessia* telson lacks joints. Rigor mortis cannot produce the multiple, sinuous folds on some *Burgessia* telsons (figure 1c), neither could these specimens be the result of a long period of decay, as indicated by the presence of intact appendages and gut contents.

Likewise, tectonic distortion is not the main cause for telson flexibility in *Burgessia*. Several specimens in category E show a flexible telson bending notably away from the axis (figure 1b). These specimens are not distorted tectonically because the digestive systems and dorsal shields are still bilaterally symmetrical. Most of the distortion of flattened specimens is derived from early burial processes. In addition, Briggs & Williams (1981) showed that

three-dimensional objects can be flattened into a two-dimensional surface with distortion or folding, but it is difficult to create noticeable curvature by flattening. Based on the evidence presented above, there are no other plausible taphonomic hypotheses to explain a bent telson in *Burgessia*. Thus, scenario (i) (the taphonomic origin of a bent telson) can be rejected in favour of scenario (iii)—that both straight and bent telson modes are biological features for *Burgessia*.

4. DISCUSSION

Some other Burgess Shale arthropods, including *Habelia*, *Sarotrocercus* and *Emeraldella*, have been reconstructed with a gently curved telson in the living position (Whittington 1981; Bruton & Whittington 1983). Although flexible cuticle has been suggested as evidence of a freshly moulted individual in *Marrella*, it is rare (one in 25 000+ specimens; García-Bellido & Collins 2004). *Burgessia* specimens with a bent telson (figure 1b,c) are far too common to be considered as freshly moulted individuals. Besides, they are not moults because of the soft-part preservation.

One possible function for bearing a straight telson is accelerated recovery from an overturned posture. In order to explore some possible explanations for the

Figure 2. Distribution of *Burgessia* telson preservation based on entombment postures. (a) Frequency diagram of *Burgessia* specimens with exposed telson in the NMNH collection ($n=281$). (b) Box plots of *Burgessia* specimens with measurable axial length ($n=243$). Categories of entombment postures: A, laterally/obliquely compressed carapace with a straight telson; B, laterally/obliquely compressed carapace with a telson bending upwards (away from trunk appendages); C, laterally/obliquely compressed carapace with a telson bending downwards (towards trunk appendages); D, dorsoventrally compressed carapace with a straight telson; E, dorsoventrally compressed carapace with a bent or curved telson; F, dorsoventrally compressed carapace with a sinuous telson.

behavioural differences between the straight and bent modes of *Burgessia* telsons, righting experiments on *Limulus* were conducted (figure 1e). When a *Limulus* is overturned, it arches its dorsal sclerites and quickly rolls to the side, bending the telson and moving the gills at the same time to right itself. One specimen (figure 1d) of *Burgessia* is preserved in a comparable posture. Specimens in the category B (figure 1f) are often preserved with a telson bending more than 40° from the body axis.

Based on comparative anatomy of other well-preserved arthropods in the Burgess Shale deposit, there is evidence to support the proposition that *Burgessia* could use its telson to aid in overturn recovery. In some well-preserved specimens of *Marrella* (figure S3 in the electronic supplementary material), there are highly reflective bands traversing the lateral and median spines, and such features were interpreted as fluid-filled canals (Whittington 1971) or part of the nervous system (García-Bellido & Collins 2006). A similar feature is present in the telson of at least four *Burgessia* specimens (figure 1f,g). This feature

is preserved as a silvery film, and similar preservation can also be found in some *Burgessia* diverticulae (figure 1b), which are composed mainly of graphite (see Butterfield *et al.* 2007). Thus, it is not an external feature. Based on this line of evidence, the *Burgessia* telson probably became straight by stiffening when the animal injected body fluid (i.e. haemolymph) into the caudal spine by changing the hydrostatic pressure. Although there is no exact analogue existing among extant arthropods, haemolymph control is critical for sudden stiffening (in milliseconds) of spider legs during jumping (Parry & Brown 1959). In addition, *Burgessia* probably could manoeuvre its telson via muscular control in the same way as *Limulus* (figure 1e). However, conclusive evidence to support this interpretation is required.

As indicated by both the preserved material and mechanics of motion, lateral flexibility (curved or sinuous) is the relaxed state. Both the dorsoventral flexibility and stiffening require active control of the telson; thus, they are considered as active states. Sudden stiffening could be achieved by changing hydrostatic pressure, and the dorsal-ventral motion was probably under muscular control. Second, some *Burgessia* specimens are interpreted here as preserving signs of escape response/overturn recovery based on modern analogues (figure 1e). Observations consistent with such interpretation include: (i) a straight/stiff telson (figure 1f,j) or a strongly curved telson bent notably dorsal-ward (figure 1h,i,k), (ii) appendages fully extended in laterally compressed specimens (figure 1j,k), (iii) a carapace angled from the body axis, suggesting intense body motion (figure 1h-k), and (iv) dorsoposteriorly projecting antennae, indicating an upside-down posture (figure 1i). Finally, the telson flexibility suggests that the composition of the *Burgessia* exoskeleton is different from that of *Limulus*. The closest analogues are basal panarthropods (i.e. onychophorans/lobopodians; Brusca & Brusca 1990), which also have a flexible cuticle and can change their morphology by hydrostatic, haemocoelic-based forces. Thus, *Burgessia* cuticle is probably so thin that hydrostatic pressure is the only way to stiffen its telson. By contrast, this function was superseded by thickening and stiffening of the telson cuticle among extant marine arthropods.

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