Beyond the Burgess Shale: Cambrian microfossils track the rise and fall of hallucigeniid lobopodians

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Burgess Shale-type deposits are renowned for their exquisite preservation of soft-bodied organisms, representing a range of animal body plans that evolved during the Cambrian ‘explosion’. However, the rarity of these fossil deposits makes it difficult to reconstruct the broader-scale distributions of their constituent organisms. By contrast, microscopic skeletal elements represent an extensive chronicle of early animal evolution—but are difficult to interpret in the absence of corresponding whole-body fossils. Here, we provide new observations on the dorsal spines of the Cambrian lobopodian (panarthropod) worm Hallucigenia sparsa from the Burgess Shale (Cambrian Series 3, Stage 5). These exhibit a distinctive scaly microstructure and layered (cone-in-cone) construction that together identify a hitherto enigmatic suite of carbonaceous and phosphatic Cambrian microfossils—including material attributed to Mongolitubulus, Rushtonites and Rhombocorniculum—as spines of Hallucigenia-type lobopodians. Hallucigeniids are thus revealed as an important and widespread component of disparate Cambrian communities from late in the Terreneuvian (Cambrian Stage 2) through the ‘middle’ Cambrian (Series 3); their apparent decline in the latest Cambrian may be partly taphonomic. The cone-in-cone construction of hallucigeniid sclerites is shared with the sclerotized cuticular structures (jaws and claws) in modern onychophorans. More generally, our results emphasize the reciprocal importance and complementary roles of Burgess Shale-type fossils and isolated microfossils in documenting early animal evolution.

1. Introduction

Cambrian lobopodian worms are pivotal to understanding the emergence of panarthropods (Arthropoda, Tardigrada and Onychophora) [1]. Although the fossil record reveals a diversity of extinct marine lobopodians, these are largely restricted to a small number of Cambrian Burgess Shale-type deposits with exceptional whole-body preservation—in particular, the Chengjiang and Burgess Shale biotas [2]. Burgess Shale-type preservation is rare after the middle-Cambrian [3], which limits our understanding of longer-term trends in lobopodian diversity, abundance and geographical distribution. However, various early lobopodians possessed recalcitrant sclerites that have the potential to be recognized as small shelly fossils (SSFs) and/or small carbonaceous fossils (SCFs), which in general tend to be more abundant, more diverse and more widely distributed in space and time than corresponding macrofossils [4].

To date, secure identifications of lobopodian microfossils have been limited to the dorsal sclerites of Microdictyon and Onychodictyon, which occur among SSF assemblages as well as in situ on body fossils in the Chengjiang Lagerstätte [5]. Surface texture has been documented on the spines of Hallucigenia from Chengjiang [5], although details are obscured by extensive weathering. Here, we describe unweathered Hallucigenia sparsa spines from whole-bodied Burgess Shale macrofossils (Cambrian Series 3, Stage 5; British Columbia, Canada) [6,7]. Our new observations allow previously enigmatic SCFs and SSFs to be recognized as hallucigeniid spines. We discuss the implications for the taphonomy, mode of growth and broad-scale distributions of armoured marine lobopodians.


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2. Spines of *Hallucigenia sparsa* from the Burgess Shale

*Hallucigenia sparsa* bears seven pairs of slender, slightly curved dorsal spines that measure up to 12 mm in length. Each is elliptical in cross-section (based on bedding-perpendicular specimens) and tapers uniformly from its non-flaring base to its pointed apex, with an apical angle of ca 6° (figure 1a–g, j–k). The spines comprise thick carbon films (figure 1I), indicating that the original carbonaceous component was notably robust [8]. Phosphate is also present (figure 1m), although in much lower concentrations than in organophosphatic Burgess Shale shells [9], indicating that these spines were at most lightly phosphatized in life.

The spines bear a distinctive external ornamentation comprising a repeated motif of distally directed and inclined triangular scales that are raised above the smooth surface of the spines (figure 1h,i,n–p). These reach 10 μm in length, have a 30° apical angle and are most pronounced in the central region of each spine (figure 1n), disappearing towards each spine’s tip (figure 1f,g). The scales are arranged in intersecting diagonal series; towards the base, the number and density of scales increases, with individual scales becoming smaller, less regularly arranged and less prominent (figure 1o). The spines also contain a series of edge-parallel lineations that are most prominent near the spine apex (figure 1f,g).

The spines comprise a series of nested internal structures with a consistent outline (figure 1e–i). In the smallest whole-body specimens (presumably representing juveniles), a single internal cone is present within the spines, which are typically less than 2 mm long (figure 1k,l). The number of cones increases in larger (presumably adult) specimens, with at least four cones within a 6.3 mm-long spine (figure 1c). The distance from the apex of the spine to the tip of the most distal internal cone represents 4–10% of the total spine length; in the largest specimens, the tip of the most proximal cone is located at the mid-length of the spine.

3. ‘Small carbonaceous’ hallucigeniid spines

In light of these new data, a suite of widespread but previously enigmatic SCFs can be clearly identified as isolated hallucigeniid spines. These specimens are comparable in size with the smallest Burgess Shale spines (ca 1 mm) and exhibit an identical ornamentation of inclined scales that becomes more diffuse towards both base and tip, with local irregularities. As in the Burgess Shale, some specimens exhibit a cone-in-cone construction in their apical portion and bear fine-scale longitudinal lineations (figure 2a,b,g,h). Beyond this, variations in outline suggest that the SCFs represent a diversity of hallucigeniids. Slender specimens from the Kaili Formation (Cambrian Series 2 and 3, Northwest Territories, Canada; figure 2a–e,g,h and fig. 3.5–3.7 [10]) are indistinguishable from the spines of *H. sparsa* from the Burgess Shale (see also fig. 5 of [11]). By contrast, SCF specimens from the Kaiji Formation (Series 3, Guizhou Province, China; fig. 7a–e [12]) are more variable in shape and include robust and sometimes strongly curved forms resembling the spines of *Hallucigenia forris* from the Chengjiang Lagerstätte (Series 2, Yunnan Province, China [13]). A third distinct form is represented by a specimen from the Forteau Formation (Series 2, Newfoundland, Canada; figure 2i–k), which has a notably broad profile and is further distinguished by having ornamenting scales with finely fringed tips (figure 2k). This form resembles certain isolated spines attributed to *Hallucigenia hongmeia* (fig. 7f of [5]).

4. ‘Small shelly’ hallucigeniid spines

A *Hallucigenia*-like surface ornament also characterizes various isolated spines that occur as phosphatic, three-dimensionally preserved SSFs. The best studied of these is *Mongolitubulus*, a demonstrably polyphyletic form-taxon that includes components of bradoriid and trilobite carapaces [14,15] and has speculatively been linked to lobopodians [16]. Most specimens assigned to *Mongolitubulus* are readily distinguished from hallucigeniid spines, including the type material of the type species, *Mongolitubulus squamifer*; this has rhomboidal rather than triangular scales that form an uninterrupted spiral from the spine base to tip. The spines of other *Mongolitubulus* species have wide flaring bases and lack internal lineations, in clear contrast to *Hallucigenia*. However, a subset of specimens ascribed to *M. squamifer* do exhibit non-flaring bases, locally interrupted ornamentation and internal longitudinal lineations [17–20]; we re-interpret these as hallucigeniid spines (see the electronic supplementary material, table S1). In summary, hallucigeniid spines can be recognized on the basis of their shape (gently curving, without a flared base), ornament (a locally perturbed diagonal arrangement of rounded triangular scales, diminishing near the tip and base) and structure (a cone-in-cone construction and an internal layer with longitudinal lineations). This diagnostic suite also characterizes the type material of a second SSF taxon, *Rushtonites* [21]. *Rushtonites*, which has previously been linked to both the Mount Cap SCFs [10] and to particular forms of *Mongolitubulus* [17], can thus be reinterpreted as a hallucigeniid lobopodian.

A further spinose SSF with probable lobopodian affinities is *Rhombocorniculum* [22]. Like the spines of *Hallucigenia*, *Rhombocorniculum* exhibits a non-flaring base, a central longitudinal cavity and a perturbed cancellate ornament [23]. Its distinctive microstructure of longitudinal, edge-parallel or slightly inclined canals has been interpreted as indicating accreционary growth, either internally (in the manner of protoconodonts) [23] or by microvilli (as in annelids) [24]. However, the internal structure and related surface lineations in *Rhombocorniculum* compare favourably with the equivalently fine-scale longitudinal lineations observed in *Hallucigenia* spines from the Burgess Shale and as SCFs (figures 1f,g and 2h), and some specimens additionally exhibit external basal constrictions (e.g. [21], plate 10.1; [24]), which conceivably correspond to the nested cone structure of *H. sparsa* and related SCFs. Assemblages of *Rhombocorniculum* often include both right- and left-handed variants, and include forms that vary considerably in their aspect ratio, degree of flattening and curvature [21]. All these features are compatible with a reconstruction as a lobopodian scleritome similar to that of *H. hongmeia* [5], in which the paired dorsal spines vary in size, outline and curvature along the length of the body. As such, it is possible that the surface features of *H. hongmeia* are equivalent to the similarly distributed scales on *H. sparsa* spines, although extensive weathering undermines a detailed comparison (see the electronic supplementary material).

Together, *Rushtonites* and *Mongolitubulus* (*partim*) allow hallucigeniids to be recognized globally among SSF assemblages from Cambrian Stages 3–4, expanding the known...
Figure 1. Hallucigenia sparsa from the Burgess Shale: (a,b) Smithsonian Institution, National Museum of Natural History (NMNH) 83935 (holotype), articulated specimen, showing seven pairs of spines, partially decayed towards the rear, presumed head to the right. (a) composite image of part and counterpart; (b) enlargement of the basal part of the spines; (c,d) Royal Ontario Museum (ROM) 61513, complete specimen showing seven pairs of spines and backscatter image of boxed area (d); (e–i) ROM 57776, backscatter images (overview and close-ups of boxed areas) of spine showing four internal cones and lineations; (g) ROM 61513, backscatter image showing lineations and a distal cone; (j–o) ROM 62269, backscatter images of several spines, showing elemental distribution of carbon (l) and phosphorous (m) and details of ornamentation near spines’ mid-length (n) and base (o) (arrows indicate local disturbances in the rhomboid pattern); (p) ROM 61513, backscatter image showing details of ornamentation showing scales in positive relief (top left) and negative relief below the carbon film. Ba, basal region of spines; C, cone; Li, lineations. Scale bars: (a–d) 1000 \( \mu \text{m} \); (e–i) 100 \( \mu \text{m} \); (f–i) 50 \( \mu \text{m} \); (n–p) 10 \( \mu \text{m} \). (Online version in colour.)
Figure 2. Hallucigeniid spines preserved as small carbonaceous fossils. (a–h) Isolated spines from the Mount Cap Formation (Little Bear biota), northwestern Canada: (a–b) Geological Survey of Canada (GSC) 136957, showing longitudinal striations within spine; (c–f) GSC 136958, showing that the spine does not flare at its base, where the ornament thins; (g,h) GSC 136959, cone-in-cone structure and lineations within spine, surface ornament diminishing towards apex; (i–k) GSC 136960, potential new hallucigeniid morph from the Forteau Formation, Newfoundland, showing diffuse ornament and straight sides near base. C, cone; Li, lineations. Scale bars: (a,c,g–i) 100 μm; (b,d–f,j,k) 25 μm. (Online version in colour.)
palaeogeographic range of the group to include England [21], Antarctica [19], Greenland [17], Australia [18], Mongolia [25] and Kazakhstan [16,26], and complementing the macroscopic and SCF records from northwestern Canada and south China (see the electronic supplementary material, table S1). With the addition of *Rhombocorniculum*, the first appearance of hallucigeniid spines can be extended to the latest Terreneuvian (Stage 2), and the geographical range further extended into Siberia, North America, Baltic, and the Mediterranean [24,27,28].

5. Construction and growth of hallucigeniid spines

Hallucigeniid spines lack an obvious modern analogue. However, the preservation of specimens in three different taphonomic modes offers new insights into their construction and growth. Several lines of evidence suggest an originally biomineralized, phosphatic component. The spines preserved as SSFs are often robustly mineralized, and fulfill a number of criteria that have been used to distinguish biophosphatic SSFs from those that have been diagenetically phosphatized; notably, they occur in a broad range of lithologies and typically exhibit well-preserved internal microstructures. By contrast, the Burgess Shale specimens of *H. sparsa* contain only weak traces of phosphate, and the SCFs were at most lightly mineralized: they lack a phosphatic component (although this may have been removed during diagenesis and/or laboratory processing) and, as with the Burgess Shale macrofossils, are flattened with no evidence of brittle deformation. These observations are consistent with a proposed link to *Rhombocorniculum*, whose seemingly high organic content [23] perhaps allowed some original pliability [29]. Overall, hallucigeniid spines seem to have had a rigid yet flexible construction, with a degree of phosphatic mineralization that may have varied between taxa. A similar organophosphatic composition potentially explains the range of expression of *Microdictyon*-type sclerites [5].

As ecdysozoans, hallucigeniids presumably moulted their cuticle in order to grow. Some specimens of *Microdictyon* and *Onychodictyon* show evidence of moulting, with a larger sclerite preserved attached to the base of a smaller sclerite [3,30–32]. In *Hallucigenia*, the apparent ontogenetic increase in the number of cones within a spine seems to suggest growth by the retention of molts, in the manner of some arthropod structures (for example, conchostracan and eridostracine carapaces [33,34]). However, this hypothesis is contradicted by the restriction of scales to the outer surface and their non-uniform arrangement, and by the absence of external discontinuities or multiple, superimposed exterior walls. Although moulting may seem difficult to reconcile with the cone-in-cone construction of hallucigeniid spines, the sclerotized claws and jaws of modern onychophorans bear a comparable accretion-like pattern [35], despite being moulted with the unhardened cuticle [36]. Notwithstanding the morphogenetic mechanism that produces this pattern, which has yet to be determined, a cone-in-cone construction of sclerotized cuticular structures provides a link, and a potential synapomorphy, between hallucigeniids and onychophorans.

6. Distribution in space and time

Together, SSFs and SCFs extend the known range of hallucigeniid lobopodians beyond 'macropscopic' Burgess Shale-type deposits to include intracraticor as well as deeper-water settings, in regions of carbonate as well as siliciclastic deposition, and reveal a previously unrecognized global distribution of the group (see electronic supplementary material, figure S1). Combined with the record of reticulate *Microdictyon/Onychodictyon*-type sclerites [5], it is clear that armoured lobopodians were substantially more widespread and ecologically important in early to middle Cambrian communities than their whole-body record alone would suggest. Subsequently, they appear to have declined: a conspicuous decrease in diversity and range in the middle to late Cambrian is now seen across three different taphonomic modes that, to an important extent, complement one another [4]. But how much of this decline can be explained by changing taphonomic windows, and how much represents authentic biological signal?

Burgess Shale-type preservation requires a particular combination of ocean and sediment chemistry, and Burgess Shale-type deposits decline in step with the increase in bioturbation seen towards the end of the Cambrian [3,37]. SCFs, by contrast, require a fundamentally less demanding set of preservational conditions than their macroscopic carbonate counterparts [4]. But until late Cambrian and younger assemblages are better documented, the apparent decline of hallucigeniid SCFs could be attributed to a sampling artefact. 'Exceptional' SSF preservation also occurs in a limited timeframe, diminishing in importance after an early Cambrian (Stages 2–3) peak [38]. Nevertheless, the original phosphatic component of many lobopodian sclerites would increase their preservation potential outside this window of 'exceptional' phosphatization, subject to the extent of biomineralization. Microfossils with a similar original composition offer a useful taphonomic comparison. Notably, the organophosphatic proto- and paraconodonts are thought to have been lightly mineralized in life [39], include forms of similar size and shape to hallucigeniid spines, and occur as both SSFs and SCFs [12]. Despite these similarities in taphonomic potential, they exhibit a much wider overall range than hallucigeniids, from the very early Cambrian (Fortunian) to the early Ordovician [40]. Therefore, the absence of hallucigeniids (and microdictyonids) after Cambrian Stage 5 may indicate a genuine decline in biological importance. When armoured lobopodians went extinct is a different question; a possible example has been figured from the early Ordovician Fezouata biota (fig. 1c of [41]).

Whatever the fate of the armoured lobopodians, their first appearance in the fossil record in early Stage 3 or the latest Terreneuvian (i.e. Cambrian Stage 2— to include *Rhombocorniculum*) does not coincide with the opening of a taphonomic window, but with a polyphyletic explosion in defence and biomineralization [40]; it is likely to approximate their first evolutionary appearance. Their dramatic subsequent radiation, even if short-lived, saw them become important members of Cambrian marine communities.

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