A hypothetical reconstruction of *Hallucigenia*

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Hallucigenia is an odd genus of Early Cambrian lobopod whose history is fraught with changes. Presented in this article is three reconstructions showing the three known species of *Hallucigenia* in further detail; culminating research into single reconstructions. A wrinkled cuticula scattered with tiny papillae is suggested for all species; a pair of antennae suggested for *H. sparsa* and *H. hongmeia*; fine anterior appendages lined with hair-like setae suggested for all species as an adaptation for filter feeding. Inferences on diet and method of feeding can be made. Further anatomical connections are made between *Hallucigenia* and Onychophora.

Introduction

Hallucigenia (Morris, 1977) was an genus of Lobopodian from the Early Cambrian. *Hallucigenia* specifically has had a history of erroneous reconstructions. First described in 1911 by Charles Doolittle Walcott, *Hallucigenia sparsa* was originally assigned to the genus *Canadia (Walcott, 1911)*, under the specific name *Canadia sparsa*. Until 1977, *Canadia sparsa* was believed to be a polychaete worm. Simon Conway Morris provided a redescription of the animal in 1977, and upon realizing this animal was quite distinct from *Canadia*, he assigned to a new genus, *Hallucigenia*. Under this new genus, *H. sparsa* was reconstructed erroneously, mirrored both vertically and horizontally. It was believed to have walked on its scleritized "spines", with a single row of tentacles on its back. The decay products often preserved at the back end of *Hallucigenia* were misidentified as the organisms head. In 1991, a new reconstruction of *Hallucigenia* was presented, interpreting the animal as belonging to the phylum Onychophora (*Grube, 1853),* a small group of animals more commonly known as Velvet Worms. A new specimen prepared in 1992 by Lars Ramsköld revealed a second row of tentacles on the back of *Hallucigenia*, which was then known to actually be a pair of legs, similar to those of modern Onychophora. *H. sparsa* was inverted so that its sclerite spines were on its back, and the seven pairs of legs were on the ground, each bearing an Onychophora-like claw, giving the theory that these animals were closely related to Velvet worms even more traction. The three pairs of fine anterior appendages of *H. sparsa* interpreted as tentacles used for moving food to the circular mouth. In 2015, Martin Smith and Jean-Bernard Caron published a description of the head of *H. sparsa*, revealing two simple eyes, a circular array of pharyngeal teeth within the buccal chamber (the inside of the mouth) compared to those of tardigrades, as well as a foregut lined with teeth.

Two other species of *Hallucigenia* were described as *H. sparsa* was transformed; first *H. fortis* (Hou et al, 1995), and later, *H. hongmeia* (Steiner et al, 2015). In 2015, a new genus closely

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related to *Hallucigenia* was described under the genus *Collinsium* by Yang *et al. Collinsium ciliosum* has proven useful in reconstructing *Hallucigenia*. Presumably due to the larger size of *Collinsium* (*Collinsium* reaches lengths of up to 85 millimeters, compared to the maximum length of 30 millimeters for *Hallucigenia hongmeia*), fossils belong to this genus preserve anatomical features in higher detail. Here, the author used fossil evidence from all species of *Hallucigenia* and *Collinsium*, as well as inferences from modern Onychophora, to create a new, tentative reconstruction for all three species of *Hallucigenia*.

Hallucigenia hongmeia

Hallucigenia hongmeia (Steiner *et al*, 2012) is the largest known species of *Hallucigenia*, reaching lengths of around 30 millimeters. The true size is hard to determine, as no specimen preserved the anterior-most or posterior-most sections. The specific name honours Li Hongmei, who discovered the holotype of *H. hongmeia*. It differs from other *Hallucigenia* species in several ways; the scleritized spines running down its back are curved and relatively shorter than those of *H. sparsa*, and have a different microstructure. While the spines of *H. sparsa* are shown to have been covered in microscopic triangular "scales" (Caron *et al,* 2013*)*, the spines of *H. hongmeia* form a net-like pattern of microscopic, circular openings, believed to be remains of tiny sensory and secretory papillae. The claws of *H. hongmeia* are also seemingly adapted for climbing upon sponges and rock surfaces, based on their length and curvature. This is unlike the more hoof-like claws of *H. sparsa*, which are adapted for walking upon muddy substrate (Smith *et al,* 2014*)*.

Below, the author presents a new tentative reconstruction of *Hallucigenia hongmeia*.

Figure 1. A possible reconstruction for *H. hongmeia*. Colouration is entirely speculative. Skin is slightly translucent, likely being mere microns thick. Digestive tract can be seen below the skin.

All reconstructions presented in this paper have traits present in *Collinsium*, as phylogenetic bracketing allows us to preserve these traits in other close relatives. The cuticula, or skin, is wrinkled and scattered with many microscopic papillae, smaller in scale but similar in appearance and function to the papillae on the cuticula of living Onychophora *(*Yang *et al,* 2015*)*. These papillae are also supported in the fossil record, as the body of *Collinsium coilium* was described as having the remains of numerous small papillae covering the surface. The larger of these papillae may be reconstructed with small hair-like papillae, as seen in the fossils of *Collinsium*. The wrinkles, or annualations, are also supported in the fossil of *Collinsium*, and more significantly, the fossil of *Hallucigenia hongmeia* (Steiner *et al*, 2012).

The head region and the two fine anterior appendages on *H. hongmeia* are not preserved, but are here inferred from its closest relatives. The head is based upon that *H. sparsa*, with two simple eyes, a slightly bulbous head, and a simple jawless mouth at the front. Additionally, a pair of antennae have been added anterior to the eyes. These antennae are inferred from the small antennae preserved on the head region of *Collinsium (*Steiner *et al,* 2015*)*, and also from living Velvet Worms.

The fine anterior appendages have been given a lining of hair-like setae, which have only so far been preserved in *Collinsium (Steiner et al,* 2015*)*. These are used for filter feeding; the tentacles may have sifted through the water, catching any potential microscopic food on the small bristles, before delivering the food to the mouth. The pharyngeal teeth of *Hallucigenia (*Smith *et al,* 2015*)* could therefore be used to scrape food off of the bristles, before the food is transferred into the gut. The author has included these anterior tentacle setae on the reconstructions for each species, under the assumption that they were more likely filter feeders.

Beneath the translucent cuticula of *Hallucigenia*, a digestive tract is slightly visible. It is comprised of a long gut, with digestive glands placed regularly along its sides. This is inferred from specimens of *Hallucigenia* that preserve a gut, and a specimen of the closely related fossil onychophoran*, Megadictyon (*Liu *et al,* 2007*)*, which preserves both a gut and a series of digestive glands (Vannier *et al,* 2014).

The sclerite spines of *H. hongmeia* are almost certainly not for defence purposes (Steiner *et al*, 2015). Instead, the describing authors of *H. hongmeia* believe the circular openings contained sensory and/or secretory papillae. These papillae have been included in the reconstruction, speculatively coloured with a light blue. The cuticula is coloured green, although all no colour is known from *Hallucigenia* or its close relatives. The greenish colour and transparent cuticula could have served to help the animal blend in with sponges and algae, but this is still speculative and not to be taken as fact.

Hallucigenia sparsa

Hallucigenia sparsa (Morris, 1977) is the most common species of *Hallucigenia*, as well as the most well represented in media. It lived worldwide, with complete fossils known from the Burgess Shale and disarticulated sclerites known from around the world (Steiner *et al*, 2015). *H. sparsa* was adapted for life on muddy substrate, and its spines were almost certainly adapted for defensive purposes (Steiner *et al,* 2015). They were covered in triangular "scales", and were much taller and sharper than the spines of both *H. hongmeia* and *H. fortis (*Caron *et al,* 2013*)*.

Below, the author presents a new tentative reconstruction of *Hallucigenia sparsa*.

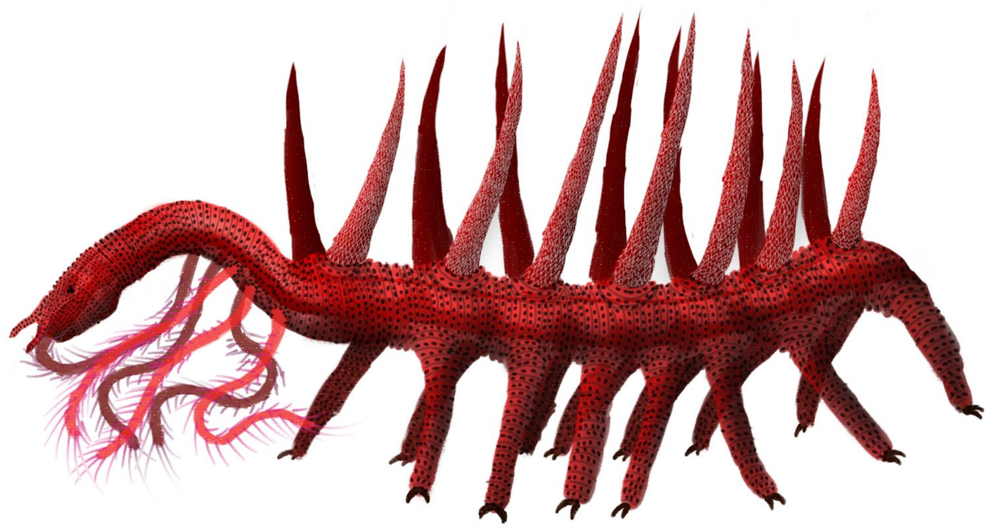

Figure 2. A tentative new reconstruction of *Hallucigenia sparsa*. Colouration is entirely speculative. Skin is slightly translucent, likely being mere microns thick. Digestive tract can be seen below the skin.

For this new reconstruction of *H. sparsa*, many of the features shared in *Collinsium* and *H. hongmeia* are present, or in a slightly altered form. The cuticula and the scattered papillae upon it are more densely packed and thicker, as *H. sparsa* appears to have been more defensively adapted than *H. hongmeia*. *H. sparsa* differs also in the number of limb pairs it possesses. It has 7 pairs of walking appendages, and 3 pairs of fine anterior appendages (Ramsköld, 1992), which have been lined with fine setae for filter feeding.

The papillae are not preserved in any *Hallucigenia*, nor the setae; however, both of these features are possible if not likely for the animal. In 2015, Smith & J-B Caron uncovered the eyes and pharyngeal teeth of *Hallucigenia sparsa* on some of the best preserved specimens from the Burgess Shale (Smith et al, 2015). If the setae were present on the fine anterior appendages, they could be used to catch falling or drifting detritus, plankton, or other sources of nutrients on the

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setae, and then put the fine appendage into the buccal chamber. The pharyngeal teeth at the back of the buccal chamber could then scrape the food off of the setae as the fine appendage exited the mouth, at which point the food would be transported to the gut with the assistance of a row of aciculae.

This feeding behaviour is only hypothetical, and is not intended to be taken as fact.

In 2002, Desmond Collins presented an Abstract at the Paleontological Association (Palass) 46th annual meeting, where Collins suggested there may be two distinct forms of *Hallucigenia sparsa*, indicating the presence of sexual dimorphism. According to the abstract, the larger of the two had a more robust and rigid trunk (the body region), a more globular head (something considered odd, as *Hallucigenia* was previously reconstructed with a very globular head, but this idea was abandoned). The second form was smaller, thinner, and more flexible; the head was supported by a long and thin neck; the head seemed to preserve a pair of eyes, “two fanglike projections”, and “two short horns”.

This research has yet to be formally published, but the author believes that the “two short horns” or the “two fanglike projections” may be Antennae. This has been incorporated into the reconstruction tentatively. In modern *Onychophora*, the female of the species is typically larger. As such, the *H. sparsa* depicted in Figure 2 may represent a male of the species, according to the traits described by Desmond Collins. A possible reconstruction of a female Hallucigenia head has been included below, with relatively smaller antennae on a globular head.

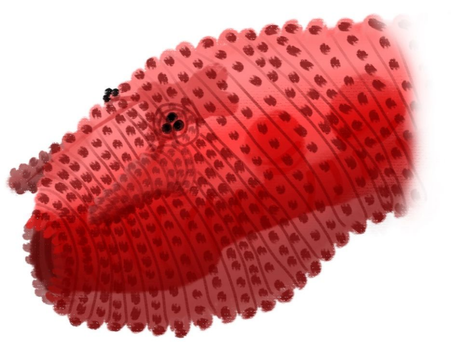

Figure 3. A possible reconstruction of the head of the larger Hallucigenia morph, which may represent a female of the species. Colour available online.

The idea that one of these mystery projections of the head region may be antennae is not only supported by the presence of antennae in Collinsium, but also by the brains of *Hallucigenia's*

relatives. A fossil preserving the brain of an Anomalocarid was described in 2014 (Cong *et al*, 2014), and found to be very similar to extant onychophorans, Velvet Worms. The brains of both animals are roughly "x" shaped. In the Anomalocarid, named *Lyrarapax unguispinus (*Cong *et al,* 2014*)*, two nerves led from the anterior portion of the brain directly into the great appendages. In Velvet Worms, two nerves led from the anterior portion of the brain into the antennae. The great appendages of Anomalcarids are not comparable to the antennae of either insects or crustaceans, but are very similar to the antennae of modern Velvet Worms.
This has given more evidence to the close relation between Onychophora and Radiodonta (which Anomalocarids are a part of). *Hallucigenia* is closely related to both (Smith *et al*, 2015), so it seems reasonable to believe that the brain of *Hallucigenia* was shaped similarly. The two nerves at the anterior portion of the brain could therefore lead into a pair of antennae, which are known in *Collinsium*.

Although it is mostly obscured by the cuticula, a brain and neural pathway to the end of the trunk is included in Figure 2. Once again, the author wishes to clarify that this is not confirmed by fossil evidence, and is still tentative.

This reconstruction has been given a red colouration, as to try out new possible ideas. Animals that live in deep sea environments, or other aquatic regions with scarcely any light, trend towards adapting a red hue. Because red light diffuses in water faster than blue light and green light, a red colouration makes these animals very difficult to detect visually, as the red colour does not reflect off of their bodies (Johnsen *et al*, 2005). If *H. sparsa* lived in a darker habitats, perhaps near a brine seep, this red colouration could help it avoid predation. However, this is entirely speculative.

Additionally featured in the *H. sparsa* reconstruction (Fig. 2) is the microstructure of the sclerites; triangular "scales" densely packed along the length of the spine.

Hallucigenia fortis

Hallucigenia fortis (Hou & Bergström, 1995) is a lesser known and more mysterious species of *Hallucigenia*. However, this species has provided knowledge on the ocular structure of *Hallucigenia*. It is known from Early Cambrian deposits in China. (Ma *et al*, 2012)

Its scleritized spines were oriented similarly to *H. hongmeia*, with the larger of the sclerites curving outwards the more anteriorly/posteriorly they are positioned on the trunk. The microstructure of this species is undescribed or unknown, though due to its closer phylogenetic position to *H. sparsa*, the author believes that the sclerites of *H. fortis* have similar form to those of *H. sparsa* (small triangular "scales").The claw on each walking appendage of *H. fortis* is similar in shape to *H. sparsa*, indicating a benthic lifestyle and adaptations for life on muddy substrate.

Below, the author presents a new tentative reconstruction of *Hallucigenia fortis*.

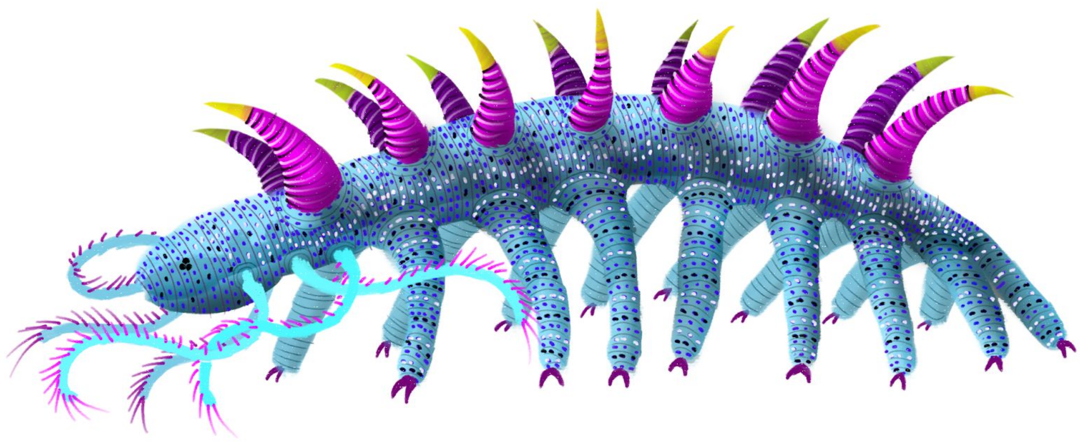

Figure 4: A possible new reconstruction of Hallucigenia fortis. Colour is entirely speculative.

H. fortis can tell us more about the possible behaviours of *Hallucigenia*, being preserved well enough in at least one case to preserve traces of the ocular systems. One fossil was described from *H. fortis* that is believed to have preserved three pigment cups in the eyes; three lenses on each eye (Ma *et al,* 2012). A study conducted on the vision of modern Onychophora has revealed the visual capabilities of Velvet Worms. Using only one lense per eye, Onychophora are able to distinguish light from dark (being particularly fond of darkness, while trying to avoid bright light), an adaptation useful for protecting the organism from drying out in the sun. And while they cannot detect colour, they are able to distinguish shapes several centimeters from their eyes (Kirwan *et al*, 2018).

With three lenses in each eye, although at a smaller size, the vision of *Hallucigenia* would likely have similar capabilities, and may have been used to tell day from night, or to detect shadows above it (which may communicate the presence of predators). These three lenses have been incorporated into the *H. sparsa* reconstruction in *Figure 3*. As with all reconstructions present, H. fortis is given a cuticula of tiny papillae and annulation. No antennae are know from *H. fortis*, and the fossil material appears complete enough to rule our antennae on this species; though sexual dimorphism could allow for the further addition of antennae.

As no detail on the sclerite microstructure has been described, the author has instead chosen to reconstruct the sclerites spines of *H. fortis* with low detail, and a simple pattern. *H.*

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fortis has 8 pairs of walking appendages, and 3 pairs of fine anterior appendages. It reaches lengths of up to 24 millimeters (Steiner *et al*, 2015).

The reconstruction is this time coloured blue, with yellow-tipped pink spines. These colours are purely speculative, and are only meant to be experimental and visually appealing (as to compliment the colours given to the other two reconstructions; red, blue, and green together).

Discussion and Conclusions

Hallucigenia and its close relatives have long been thought of as Cambrian oddballs. With the reconstructions and evidence presented in this article, it is more evident that these animals are understandable, and not out of place in the context of life on earth. While they are admittedly "odd", the reconstructions shown here may not look totally out of place in a modern ocean. Each reconstruction is inspired by modern Onychophora, and grounded in fossil evidence and reasonable inference and speculation.

One needs to keep this in mind: these reconstructions are all tentative and subject to change; the history of *Hallucigenia* research seems to indicate that at some point in the future, the appearance is likely to change or be given more definition, perhaps with different and unpredicted features.

Some features present in these reconstructions may have implications for the possible behaviour of *Hallucigenia*. The presence of hair-like setae on tentacles near the mouth seen in a close relative, combined with the description of the buccal chamber of *Hallucigenia*, could imply a filter feeding behaviour in which the teeth scrape food off of small setae. Meanwhile, the presence of an eye roughly equal in resolution to a modern Velvet Worm indicates it may have been able to make out shapes within a close distance (a few centimetres at most), while also being able to detect organisms above it (assisted by the dorsally oriented location of the eyes).

The reconstructions shown here are intended to give more detail and context to the appearance of *Hallucigenia*. This work is admittedly not near as transformative as the research done by Martin Smith and Jean-Bernard Caron in 2015, or the work of those before them. The detail given to the reconstructions here however, could help to understand the ecology and life of *Hallucigenia*, further strengthening its relations to Onychophora.

Once again, on a final note, these findings are tentative, and often speculative. Each reconstruction should be taken with a grain of salt; not doing so would be a disservice to the research in this report and before it.

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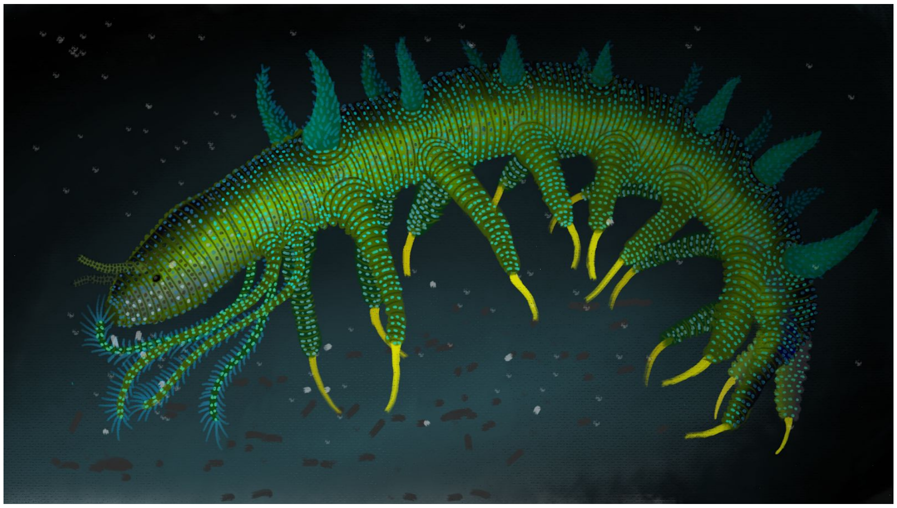

Figure 5. A reconstruction of Hallucigenia hongmeia shown in a deep sea environment, filter feeding.

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