Phylogeny of *Hallucigenia*

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Abstract

Hallucigenia is an extinct genus from the lower-middle Cambrian. A small worm-like organism with dorsal spines, *Hallucigenia* is rare in fossil history, and its identity and morphology have often been confounded. Since its original discovery in the Burgess Shale by Walcott, *Hallucigenia* has since become an iconic fossil. Its greater systematics and place in the phylogenetic tree is controversial and not completely understood. New evidence and the discovery of additional species of *Hallucigenia* have contributed much to the understanding of this genus and its broader relations in classification and evolutionary history.

Introduction

Hallucigenia is a genus that encompasses three known species that lived during the Cambrian period—*Hallucigenia sparsa*, *Hallucigenia fortis*, and *Hallucigenia hongmeia* (Ma et al., 2012). *Hallucigenia*'s taxonomy in figure 1.

Kingdom	Animalia
Phylum	Onychophora (Lobopodia)
Class	Xenusia
Order	Scleronychophora
Genus	*Hallucigenia*

Figure 1. Taxonomy of *Hallucigenia* species.

Collectively, all *Hallucigenia* specimens are rare, with a portion of specimens incomplete. The understanding of *Hallucigenia* and its life mode has been confounded since the

original discovery of *H. sparsa*, but subsequent species discoveries has shed light on some of its mysteries (Conway Morris, 1998). Even more information concerning *Hallucigenia* is currently being unearthed—its classification into the phylum Onychophora and wider relations to other invertebrate groups like Arthropoda and the poorly understood Lobopodian group (Campbell et al., 2011). *Hallucigenia*, an iconic fossil of the Burgess Shale, demonstrates the well-known diversity of the Cambrian period, its morphology providing increasing numbers of clues to its connection into the greater systematic system.

Morphology

Hallucigenia was a marine organism with a worm-like body ranging from 5-30mm long (Gould, 1989). The trunk holds seven pairs of long dorsal spines and eight pairs of slender leg-like lobes that usually terminate in a pair of claws. The pairs of spines are rigid with inflexible basal plates and are shifted forward so that they do not correspond to the posterior pair of legs. A pair of tentacle-like appendages have been noted in two species of *Hallucigenia*. These tentacles appear in the neck region and are much more slender than the other leg appendages, lacking claws. Due to incomplete specimens in all fossils of *H. hongmeia*, it is currently challenging to tell if this third species also bore the pair of tentacles (Liu and Dunlop, 2013). *Hallucigenia*'s head varies slightly in shape based on species, but has an anterior mouth and a straight gut that ends in a posterior anus (Gould, 1989).

Possible Life Mode of *Hallucigenia*

Hallucigenia was a marine onychophoran that was most likely benthic, vagrant, and epifaunal. Some new studies about the morphology of *Hallucigenia*'s claws suggest that they appear less adapted for walking in muddy substrate than to a climbing mode of life, perhaps even on other benthic organisms (Steiner et al., 2012). *Hallucigenia* was carnivorous, most likely a scavenger. Depicted in figure two, *Hallucigenia* has often been found in association with the demo-sponge *Vauxia,* and various other organic debris.

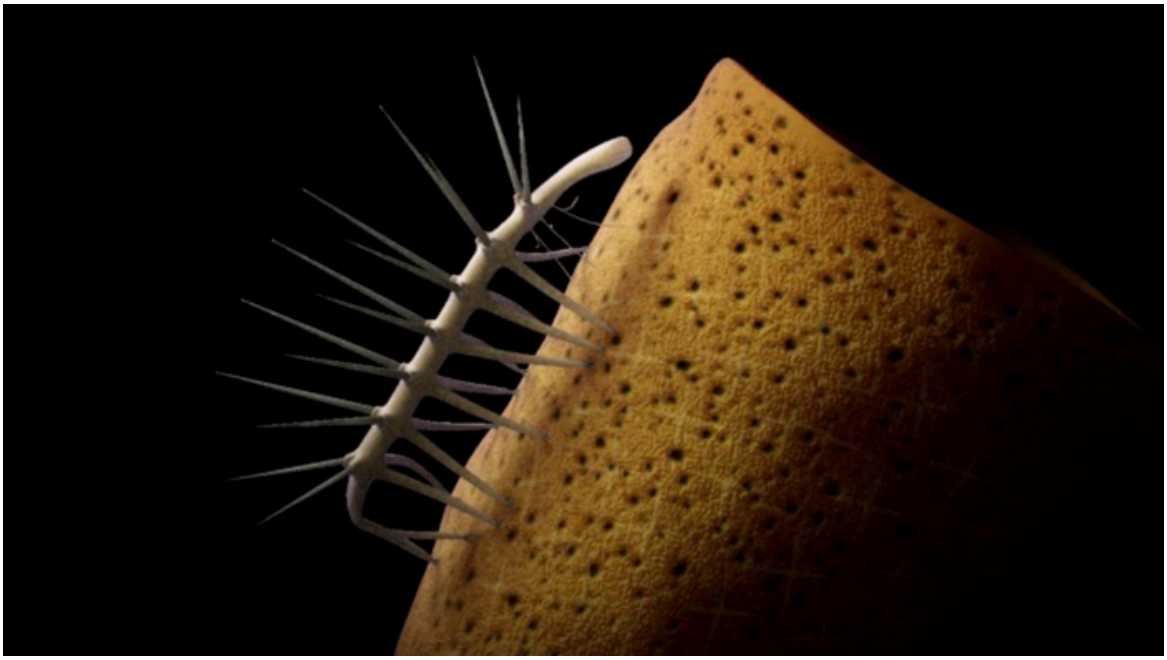

Figure 2. *Hallucigenia sparsa* model on unidentified demosponge (http://www.rom.on.ca/sites/default/files/imce/pb.png)

In one instance, 18 hallucigeniids were found by a large organic mass, in another, one specimen was found on top of an undescribed worm (Conway Morris, 1998). These co-occurrences have contributed to the belief that *Hallucigenia* was a scavenger of dead animal remains, and perhaps additionally fed on sponges, using its spines for protection and its clawed legs to hang on (Steiner et al., 2012).

Hallucigenia likely lived in the photic zone of the ocean; its eating habits and the discovery of preserved eyes on some specimens are an indication of this. Since *Hallucigenia* has a dietary association with sponges, considering the life mode of demosponges like *Vauxia* can indicate at what depth *Hallucigenia* also may have lived. In the case of *H. fortis*, two to three visual units have been shown to compose the eyes of *Hallucigenia*, indicating at least basic light detection (Ma et al., 2012). Not much else is known about *Hallucigenia*'s paleoecology; overall *Hallucigenia* is a rare genus in the fossil record.

Species of *Hallucigenia*

There have been three species of *Hallucigenia* identified so far, *H. sparsa*, *H. fortis*, and *H. hongmeia*. The span of discovery from the first species of *Hallucigenia* (though at the time it was classified as *Canadia sparsa*) to the second was 84 years, with the third species discovered 17 years later (Liu and Dunlop, 2013). All specimens were found in the Burgess Shale, or faunas that have been related to the Burgess Shale in terms of their quality of preservation (Steiner et al., 2012). Though the three species are undoubtedly related, they do possess differentiating qualities.

H. sparsa

Hallucigenia sparsa was the original species discovered, and thus serves as the index fossil for the group. *H. sparsa* was discovered in the Burgess Shale by Charles Walcott, the original excavator of the Burgess Shale. While Walcott made impressive contributions to paleontology in the Burgess Shale, he incorrectly classified *Hallucigenia*. In 1911 Walcott named what is now *Hallucigenia*, *Canadia sparsa,* and classified it as a polychaete annelid

(Conway Morris, 1998). Later, studying the specimens, Conway Morris noted that this classification was incorrect, and created a new genus, renaming the creature *Hallucigenia sparsa* in 1977; *Hallucigenia*—"wandering of the mind"—for its bizarre-like appearance and retained *sparsa*—"rare, scattered" –for the rarity of the specimens in the original study, though the phylum Annelida was incorrectly kept (Conway Morris, 1998).

Though Conway Morris was correct to rename *Hallucigenia*, his reconstruction of the animal was quite incorrect. Until the Chengjiang fauna in China of the lower Cambrian was discovered in 1991, *Hallucigenia sparsa* had essentially been constructed both upside-down and with its posterior and anterior switched. Its spines were thought to be its legs, and its legs a singular row of tentacle-like feeding apparatuses (Gould, 1989). The discovery of the Chengjiang fauna included armored lobopodians, animals whose similar use of spines for defense led to the realization that *Hallucigenia* was in fact upside-down. Lars Ramskold later found traces of a second row of limbs on one of the best specimens of *Hallucigenia.* This officially confirmed the flip and the switching of the anterior and posterior orientation of the animal, its correct orientation shown in figure 3 below (Ramskold, 1992).

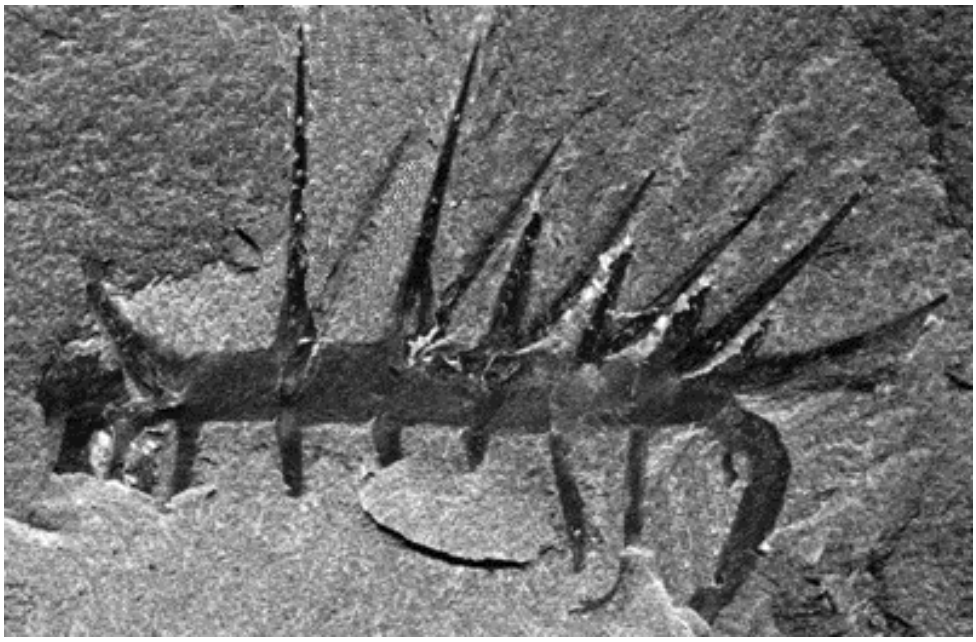

Figure 3. Burgess Shale fossil of *Hallucigenia sparsa* in its correct orientation, posterior on the left, anterior on the right (http://burgess-shale.rom.on.ca/en/fossil-gallery/view-species.php?id=60).

In addition to its colorful history, *Hallucigenia sparsa* has had additional contributions to its morphology. *H. sparsa*'s preserved spines are comprised of thick carbon films, indicating a notably robust original carbonaceous component (Caron et al., 2013). Variations of the curve of the spine and its shape are often indications of the different *Hallucigenia* species. *H. sparsa* spines are generally longer and more slender than other species' counterparts, their range depending on the size of the specimen. Their spines, otherwise known as sclerites, can range from 2.6mm-9.3mm (Caron et al., 2013). Size and shape of *Hallucigenia's* head also shows variation among species, *H. sparsa* having a slender, small head. Additionally, the presence of eyes has also been noted in *H. sparsa* (Ma et al., 2012).

H. fortis

The second species of *Hallucigenia* was found by Chen in 1991 in the Chengjiang fauna. The species was described from an incomplete specimen as *Hallucigenia fortis* in 1995 by Hou and Bergstrom. Following this Ramskold and Chen added new data from 15 specimens and noted errors of interpretation in 1998. Overall there are 23 specimens of *H. fortis* (Liu and Dunlop, 2013). There are some variations from *H. sparsa* in this species, including a sub-rounded head which varies in appearance based on preservation. The head of one specimen may be smooth while the head of another is rough and sclerotized, a process that occurs when a substance is hardened by conversion into sclerotin (Liu and Dunlop, 2013). No claws have been observed on its limbs, though this could be due to preservation. The trunk bears seven pairs of dorso-lateral plates and spines, with the first and last plate pairs and spines being slightly smaller and shorter than the other pairs. Additionally the dorsal spines do not all point in the same direction: four pairs point forwards while three posterior pairs point backwards (Liu and Dunlop, 2013).

Three specimens of *H. fortis* have been found with preserved eyes, one depicted below in figure 4. The rounded eyes are situated in the anterior half of the head and are composed of two or possibly three visual units. Superficially, the triangularly arranged visual units in *H. fortis* resemble the frontal ocelli of insects and the nauplius eyes of crustaceans (Ma et al., 2012). It has been argued that the eyes of *H. fortis* contribute to direct fossil evidence in support of the hypothesis that arthropod compound eyes originated from a basic compound eye possessed by a worm-like ancestor (Ma et al., 2012).

Figure 4. *Hallucigenia fortis* specimen, with sub-rounded head and indication of an eye (Ma et al., 2012 Figure 3, A).

H. hongmeia

Hallucigenia hongmeia was recently discovered in the Guanshan Biota of China in 2012. All specimens of *hongmeia* are incomplete, with the head region and anterior-most appendages missing, as shown in figure five. *H. hongmeia* claws, however, are well preserved (Lui and Dunlop, 2013). Nevertheless, even with incomplete specimens it is apparent that this species differs from the others. Compared to *H. fortis*, the dorsal spines show anterior-posterior differentiation. The anterior and posterior hold large spinose sclerites while the sclerites in-between are considerably smaller and cone shaped (Lui and Dunlop, 2013). *H. hongmeia*'s spines range between 0.48 mm and 5.1mm (Steiner et al., 2012).

Figure 5. Incomplete fossil of *Hallucigenia hongmeia*, with the head and posterior almost completely obscured (Steiner et al., 2012 Figure 6, C).

The trunk sclerites in *Hallucigenia* have been presumed to serve as a protective function, however an alternative theory has also been suggested. While large, closely arranged, sharp spines on *H. sparsa* may have served as protection, this seems perhaps less likely for the other species of *Hallucigenia*, especially *H. hongmeia* with its small, cone shaped sclerites (Steiner et al., 2012). An interpretive diagram of *H. hongemia* is shown below in figure six, which notes the size differentiation between sclerites and depicts the well-preserved claws. The head and anterior most appendages are purely hypothetical.

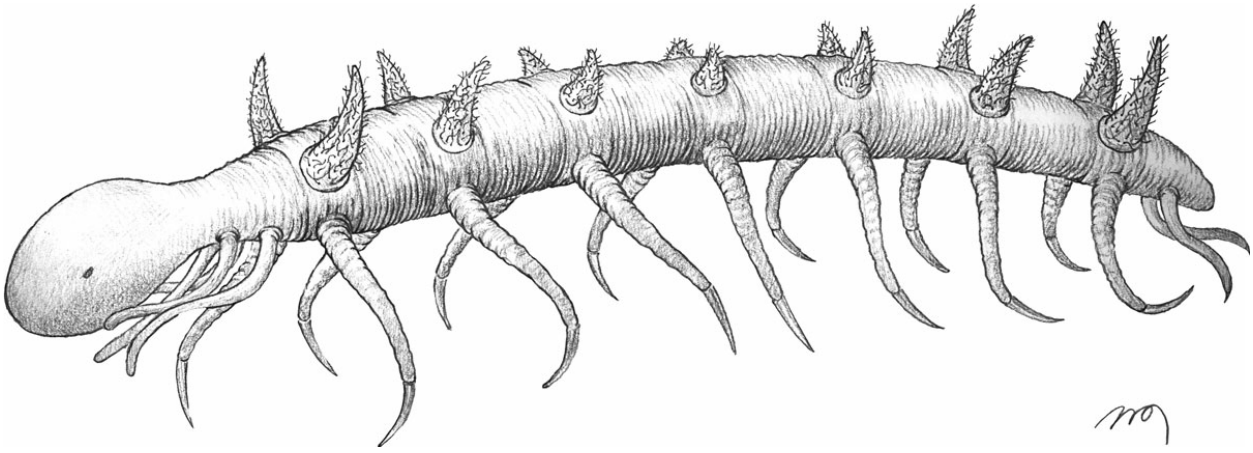

Figure 6. Interpretive depiction of *Hallucigenia hongmeia* (Steiner et al., 2012 Figure 11).

Classification

The classification of *Hallucigenia* has a long history that is still currently evolving. After being originally classified as a polychaete annelid by both Walcott and Morris, *Hallucigenia* finally emerged from this incorrect group with its classification as an onychophoran by Ramskold and Hou (Gould, 1992). Though it is generally accepted that *Hallucigenia* belongs to this phylum, often *Hallucigenia* will be additionally referred to as a lobopodian. Due to the discrepancy in terms used and ever emerging data on *Hallucigenia's* phylogeny, *Hallucigenia's* official classification can become quite confounded.

Lobopodian

Often *Hallucigenia* is referred to and classified as a lobopodian. Interestingly, the origin of this term (lobopod) was not used in taxonomy but to describe a specific type of limb (Steiner et al., 2012). However, Lobopodia has since become a widely accepted unofficial group. While it is well constrained at the phylum level, its detailed systematic position is poorly understood. A number of new taxa have been described in the last decade, showing that Lobopodia is not a monophyletic group as previously thought. Generally it appears that lobopodian organisms fall into two major groups: one related closely to Arthropoda and one more closely related to Onychophora, in which *Hallucigenia* falls (Steiner et al., 2012).

It has been suggested that lobopodians may be onychophoran ancestors to some degree. Cambrian lobopods are closely associated with the origin and early evolution of Panarthropoda, a

taxon that combines phyla Arthropoda, Tardigrada, and Onychophora (Ma et al., 2012). However, there is some molecular data that suggests that Tardigrada does not belong in Panarthropoda, but instead is a sister group to Lobopodia, with a sister group also existing between Onychophora and Arthropoda (Campbell et al., 2011). Other recent publications that studied the claws of *Hallucigenia* in relation to other lobopods suggest that Hallicgeniid lobopodians may be a stem group of onychophorans, with further evidence proving the wider pararthropod relationship, which is depicted below in figure seven (Smith and Ortega-Hernadez, 2014). Though the taxonomy term lobopodian has become widely accepted in the paleontological world, it is important to recognize that it is still not an official group, but rather is in a fluid state and requires further revision.

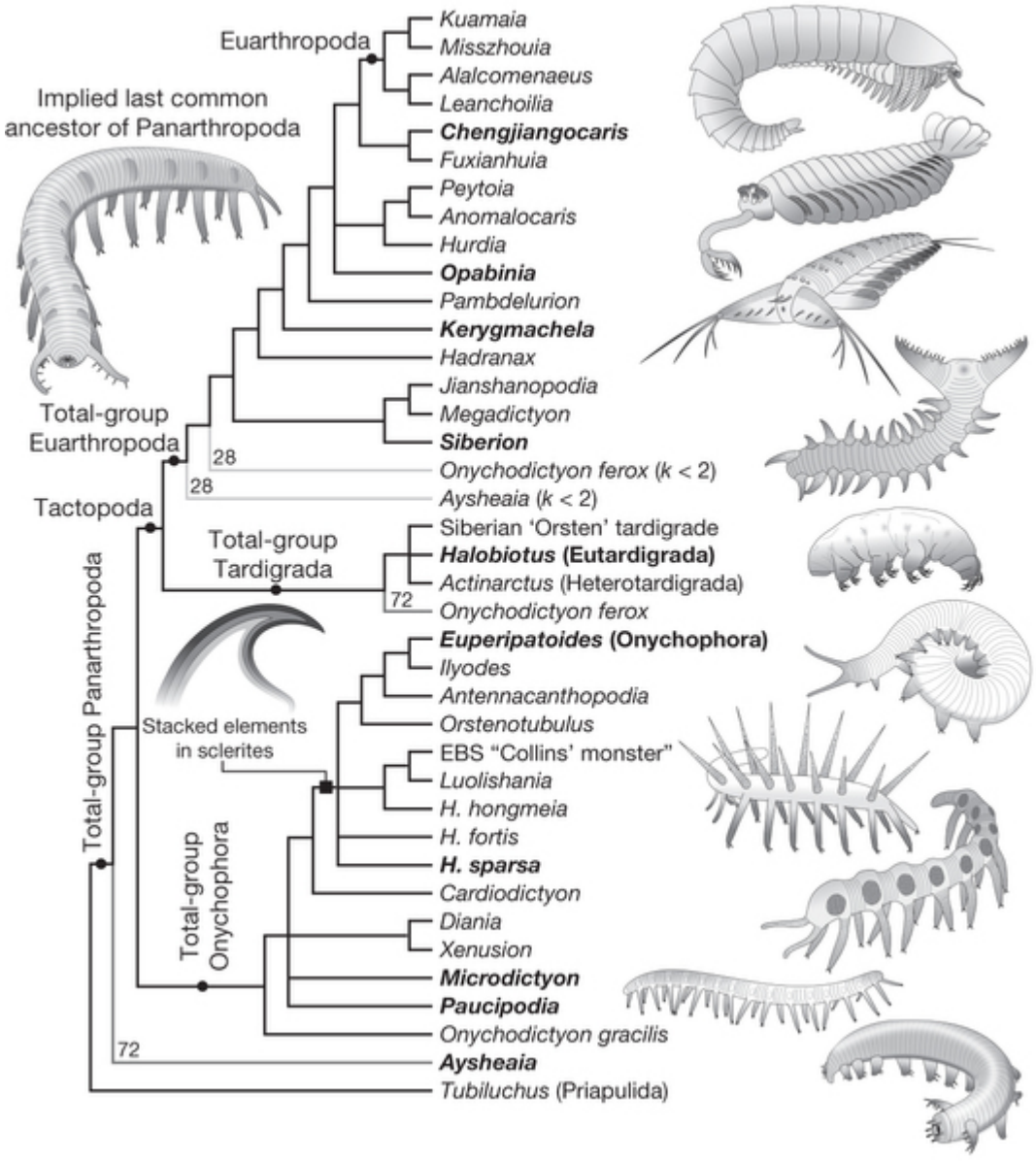

Figure 6. Proposed panarthropod phylogeny, showing the shared morphology of studied sclerites in determining likely systematic connections. *Hallucigenia* is shown in connection to Onychophora and larger group Panarthropoda (Smith, Ortega-Hernadez, 2014 Figure 2).

Onychophora

Onychophora, meaning "claw bearer," can be regarded as *Hallucigenia's* official phylum (Smith and Ortega-Hernandez, 2014). Today, the modern onychophora group is rather small, but there is reason to believe that it was a much richer phylum in the past. Modern onychophorans

are most commonly known as velvet worms and are terrestrial organisms. The group's move from the sea to land is suspected to have occurred during the Paleozoic (Taylor and Lewis, 2005). Onychophorans have traditionally been viewed as the missing link between annelids and arthropods, however, molecular studies suggest that they may not be closely related to annelids but have simply experienced convergent evolution on annelid shapes (Taylor and Lewis, 2005). Additional information related to the group Lobopodia as discussed above places Onychophora in a sister relationship with Arthropoda.

Hallucigenia's exact position in the phylogenetic has not quite been decided, and continues to evolve with further discoveries and studies concerning not only the genus, but *Hallucigenia's* broader classifications as well. Both unofficial phylum Lobopodia and phylum Onychophora play an important role in this ever evolving classification, as well as the classification of other so-called lobopodian animals.

Conclusion

Hallucigenia is a fascinating genus of organisms who can still be regarded as relatively mysterious. Since its discovery in 1911, *Hallucigenia* has gone through many morphological and systematic classifications. New methods of study, including the ability to examine eye and sclerite components along with the discovery of new specimens have added much to our understanding. *Hallucigenia's* classification and place in the phylogenetic tree still remains a mystery, though much has been unearthed and continues to be discovered. New finds and studies of other animals considered lobopodians can offer significant information in relation to *Hallcuigenia*. Additionally, molecular studies can provide evidence for evolutionary

relationships between phyla and organisms within them. Theories of *Hallucigenia's* evolutionary implications and morphology have come a long way since Walcott's findings in the Burgess Shale, and continue to evolve. Since its discovery, much information about *Hallucigenia* has been uncovered, increasing our understanding exponentially. Even so, there is still much more left to realize about this mysterious Cambrian organism.

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