A NEW METAZOAN FROM THE CAMBRIAN BURGESS SHALE OF BRITISH COLUMBIA

by SIMON CONWAY MORRIS

ABSTRACT. *Hallucigenia sparsa* (Walcott) gen. nov. from the Burgess Shale (Middle Cambrian) is redescribed. It is characterized by an elongate trunk supported by seven pairs of long spines. The trunk also bears seven tentacles with bifid tips and a group of short posterior tentacles. A globular head lacks appendages. Despite certain similarities to the polychaetes *H. sparsa* is not an annelid. Its systematic position, as well as its mode of life, remain problematical.

C. D. WALCOTT, who discovered the Burgess Shale (Middle Cambrian) and described much of its fauna and flora, placed seven species in the genus *Canadia* Walcott, 1911 (Polychaeta: Annelida). They are *C. spinosa* (the type species), *C. setigera*, *C. sparsa*, *C. dubia*, *C. irregularis* (Walcott, 1911), *C. grandis*, and *C. simplex* (Walcott, 1931). Recent research has shown that with the exception of the type species none of these worms can be placed in *Canadia*. New genera have been proposed for them, with the exception of *C. irregularis* and *C. grandis* which are junior synonyms of *C. spinosa*. Furthermore, *C. sparsa* and *C. simplex* cannot be accommodated in the polychaetes (Conway Morris 1976*b*).

C. sparsa was very briefly described by Walcott (1911), but it was not illustrated until 1931 (Walcott, pl. 6, fig. 3). Although the illustration is poor, it clearly does not tally with Walcott's earlier account where he noted 'two strong setae on each very short parapodia [*sic*]'. Prominent pairs of 'setae' are visible along one side of the animal, but the structures along the other side are clearly different. The purpose of this communication is to illustrate the bizarre morphology of this animal which precludes any relationship with *Canadia*.

In addition to the holotype, consisting of part and counterpart, thirty other specimens have been found during three searches through the collections of Burgess Shale fossils in the National Museum of Natural History (formerly the U.S. National Museum (USNM)), Washington, D.C. One specimen has been located in the Museum of Comparative Zoology (MCZ), Harvard. Three specimens were collected by the Geological Survey of Canada (GSC) team led by Dr. J. Aitken in 1966 with the co-operation of the authorities of the Yoho National Park and the Parks Canada, Department of Indian Affairs and Northern Affairs, Ottawa (see Whittington 1971*a*).

A brief review of the excavation of the Burgess Shale and its stratigraphic position were given by Conway Morris (1976*a*). All the USNM specimens are labelled 35k, which is the locality number for the Phyllopod bed exposed in the Burgess quarry (Walcott 1912*a*). Walcott did not give any details of the vertical distribution of this species. Two of the GSC specimens are from 88·9–101·6 cm (2 ft 11 in.–3 ft 4 in.), whilst the third is from 88·9–91·4 cm (2 ft 11 in.–3 ft) above the base of the quarry. The total known range is, therefore, 12·7 cm (5 in.).

[Palaeontology, Vol. 20, Part 3, 1977, pp. 623–640, pls. 73–76.]

SYSTEMATIC PALAEONTOLOGY

Phylum UNCERTAIN

Family HALLUCIGENIIDAE fam. nov.

Diagnosis. Seven-fold repetition of the dorsal tentacles and pairs of ventral spines that arise from the trunk, which also bears a globular head.

Genus HALLUCIGENIA gen. nov.

Type and only known species. *Hallucigenia sparsa* (Walcott, 1911) gen. nov.

Derivation of name. *Hallucigenia* refers to the bizarre and dream-like appearance of the animal.

Diagnosis. Elongate (*c*. 2 cm) bilaterally symmetrical metazoan. Body consists of globular head without appendages and long narrow trunk. Trunk supported by seven pairs of ventro-lateral spines, and bears medially seven dorsal tentacles with bifid tips. Each tentacle opposed to a pair of spines, except for anteriormost tentacle. Posterior to seventh tentacle is a cluster of shorter dorsal tentacles. Posterior trunk bent upwards and forwards.

Hallucigenia sparsa (Walcott, 1911) gen. nov.

Plates 73–76; text-figs. 1, 3, 4

1911 *Canadia sparsa* Walcott, p. 119.
1912 *Canadia sparsa* Walcott, p. 190.
1931 *Canadia sparsa* Walcott, p. 5, pl. 6, fig. 3.

Diagnosis. As for the genus.

Holotype. USNM 83935 (Walcott 1931, pl. 6, fig. 3) from the Stephen Formation (Middle Cambrian), Burgess Shale Member (*Pagetia bootes* faunule of the *Bathyuriscus–Elrathina* Zone: Fritz 1971). The Phyllopod bed (2·31 m) lies within division h of the Burgess Shale (Walcott 1912*b*), and is exposed in the Burgess quarry which is 4·8 km north of Field, southern British Columbia.

Other material. USNM 188602, 193996 (two specimens), 194137, 194890 (three specimens), 194906, 196348, 198584, 198658–198662, 198663 (two specimens) 198664–198666, 198777, 199699 (counterpart is 199732), 200272, 201290, 203135, and five un-numbered specimens.

GSC 8231 (located by D. E. G. Briggs), 45332, 45333, and an un-numbered specimen.

MCZ 1084.

A note on the photography and interpretation of specimens. All the specimens have been photographed in ultra-violet light from a directional lamp using Panatomic-X film. The majority were photographed in high-angle light. The lamp was inclined to the horizontal specimen at about 60°, the specimen was then tilted through about 10° towards the lamp until maximum reflectivity, as observed down the focusing tube, was obtained. Unless stated otherwise the plate-figures were photographed in high-angle light. A few specimens (Pl. 73, fig. 2; Pl. 74, figs. 1, 3, 6; Pl. 76, fig. 4) were photographed in low-angle light. The inclination of the lamp was about 30° and the specimen was placed as near horizontal as possible. Focusing was undertaken in ordinary light.

Camera-lucida drawings are placed beside Plate 73, figs. 1–3; Plate 74, figs. 5, 6; Plate 76, figs. 1, 2, as a guide to their interpretation.

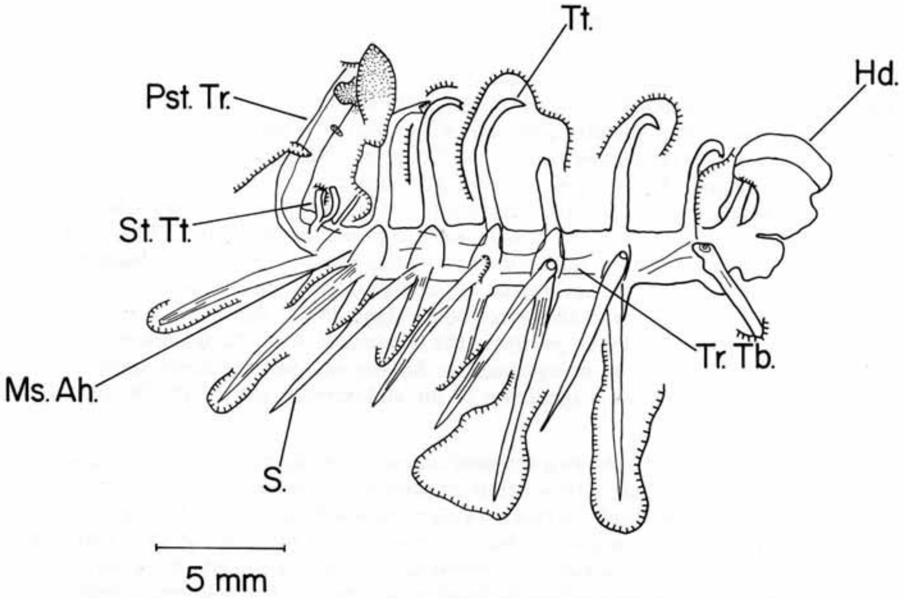
Preservation. The specimens are preserved as very thin films. The spines and tips of the tentacles are preserved as reflective films, whilst the rest of the body is usually less reflectively preserved. The composition of the film in a specimen of the priapulid *Ottoia prolifica* was determined by R. A. Chappell (National Physical Laboratory, Teddington) using Auger spectroscopy to consist of calcium aluminosilicates, although reflective areas contain additional magnesium. It is apparent that the great majority of Burgess Shale fossils are composed of this silicate film. The diagenetic processes that led to the formation of this film are, however, obscure.

With two exceptions the specimens are comparatively poorly preserved and are often associated with considerable amounts of algae (Pl. 75, figs. 3, 6), as well as other fossils such as the priapulid *O. prolifica*, the trilobitoid *Marrella splendens* and other arthropods. MCZ 1084 is exceptional in having at least eighteen specimens of *H. sparsa* associated with a specimen of an undescribed worm (Pl. 76, figs. 1, 2; text-fig. 4).

Morphology. Text-fig. 2A shows a reconstruction of the animal in life. The basic form of the animal was a long narrow trunk supported by seven pairs of ventro-lateral spines. One end of the trunk carried a swollen mass which presumably was the head. There was a single median row of dorsal tentacles, and more posteriorly there were about six short tentacles. Dorsal and ventral surfaces are identified on the assumption that the spines were embedded in the bottom sediments. The bilateral symmetry of the animal was defined by the pairs of ventro-lateral spines. The length of the animals varied between about 0·5 and 3·0 cm, the average being about 1·8 cm.

All, save one, of the specimens are preserved laterally, so that the plane of bilateral symmetry is more or less parallel to the bedding plane. No dorsally or ventrally flattened specimens have been recognized. The longitudinal axis of one GSC specimen (Pl. 76, figs. 3–5) is, however, steeply inclined to the bedding plane. Burial in a mudflow seems to be the most probable explanation for such steeply and vertically orientated specimens (Whittington 1971*a*) and, as is the case with *M. splendens*, such specimens are far outnumbered by those with the longitudinal axes parallel to the bedding plane.

The head is preserved in two specimens. Its poor definition may be due partly to an enveloping dark stain similar to that associated with *M. splendens* (Whittington 1971*a*, *b*). Whittington interpreted the dark stain as body contents that were squeezed out by the pressure of superincumbent strata. The stain has been reinterpreted as the product of body contents seeping out of the corpse during decay, because the time taken to deposit sufficient overburden would have far outweighed the time taken for a specimen to decay (Conway Morris 1976*b*). In the Burgess Shale the stain is restricted to a few species which presumably had a peculiar body composition in common. The stain often occurs around the anterior and posterior ends suggesting that the mouth and anus acted as points of egress. More extensive stains that flank the body probably represent rupturing of the body wall. The extent of the stain is, therefore, probably directly proportional to the degree of decay. A similar feature has been noted in both fossil and recent conditions. Bardack (1974) reported a light-coloured



TEXT-FIG. 1. Camera-lucida drawing of USNM 83935 (holotype), combining features of the part and counterpart. Lines with hachures indicate definite breaks in slope, the hachures being directed downslope. Stippled areas represent rock. Hd., Head; Ms. Ah., Muscle attachment area; Pst. Tr., Posterior trunk; S., Spine; St. Tt., Short tentacle; Tr. Tb., Trunk tube; Tt., Tentacle.

stain around the anus of partially decayed fish from the Pennsylvanian of Illinois. In modern subaerial conditions Schäfer (1972, fig. 17) noted that in rotting seals oily liquids are discharged from the mouth and anus, and later from the abdominal area. The head was probably globular and there were no appendages or mouth parts (Pl. 73, fig. 3; Pl. 74, figs. 1, 6; text-figs. 1, 3). Apart from the trunk tube (see below) entering the head (Pl. 74, figs. 5, 6) and an indistinct area of greater reflectivity in USNM 83935 (Pl. 73, fig. 3), no internal detail is discernible.

The smooth, narrow trunk extended horizontally posterior to the head. The plane of splitting appears to have cut across the steeply inclined specimen GSC 45332 so

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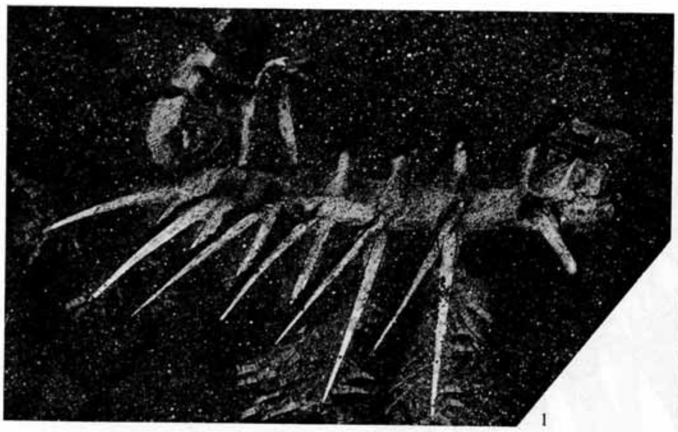
EXPLANATION OF PLATE 73

Figs. 1–5. *Hallucigenia sparsa* (Walcott) gen. nov. USNM 83935 (holotype). 1, part, light from south-west, ×3·7. 2, part, low-angle light from north-east, ×3·7. 3, counterpart, light from north-west, ×5·2. 4, part, enlargement of posterior trunk with short tentacles, light from south-west, ×6. 5, counterpart, enlargement of tentacle with bifid tip, light from east, ×16.

PLATE 73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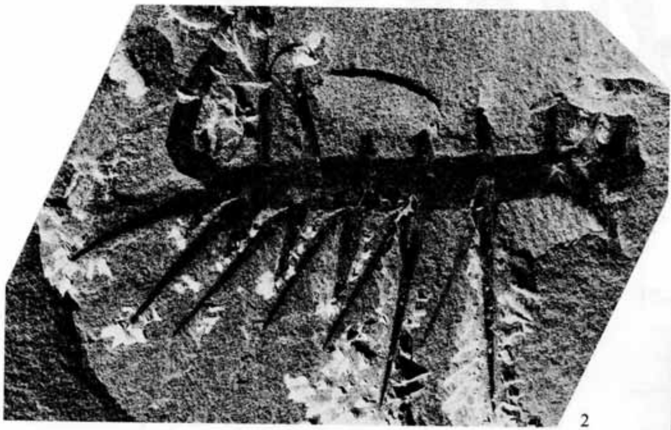
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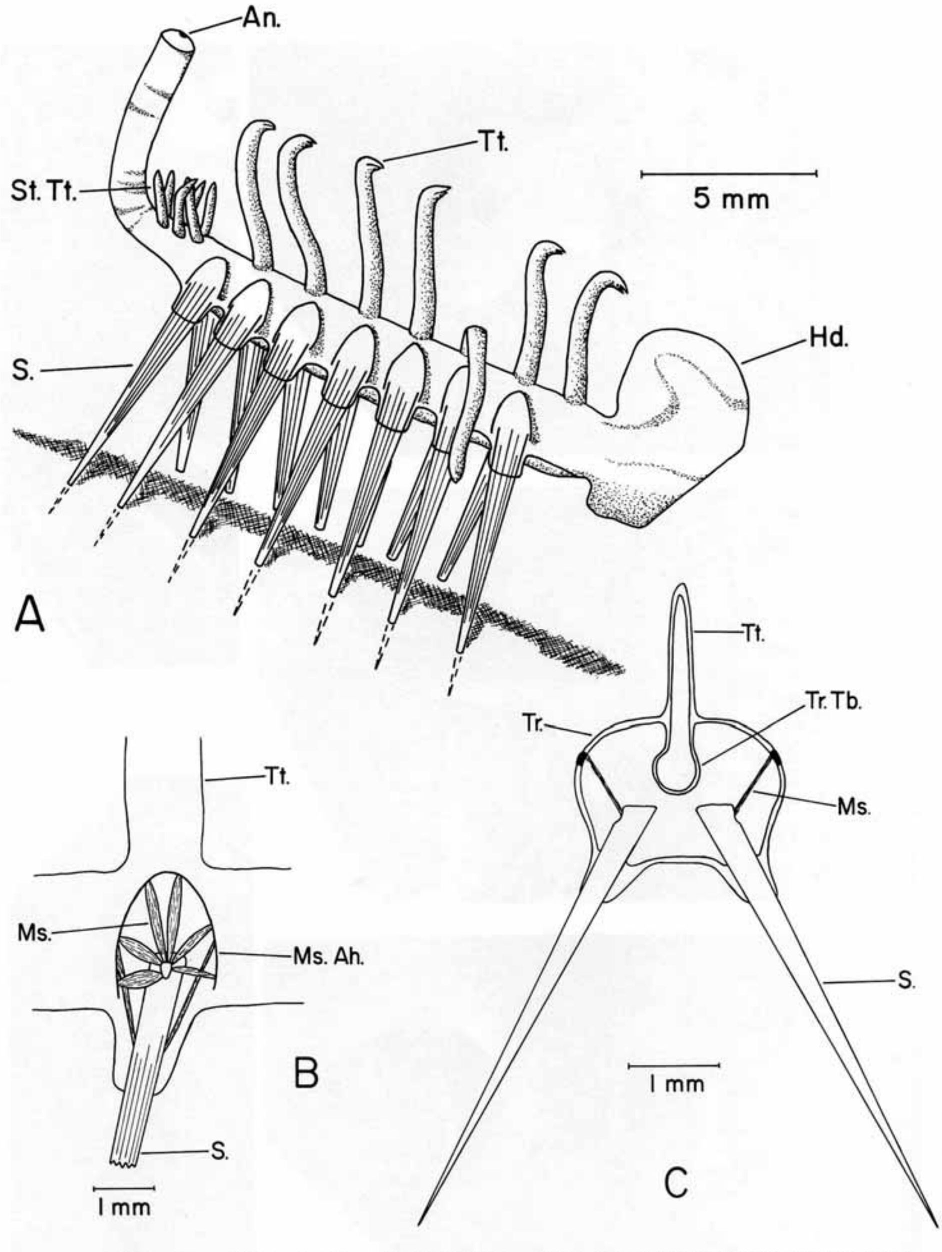


TEXT-FIG. 2. Anatomy of *Hallucigenia sparsa* (Walcott) gen. nov. A, reconstruction of appearance in antero-lateral view. B, hypothetical arrangement of muscles running from the proximal end of the spine to the horseshoe-shaped attachment area on the trunk. C, hypothetical transverse section of the trunk and a tentacle. An., Anus; Ms., Muscle; Tr., Trunk. See text-fig. 1 for other abbreviations.

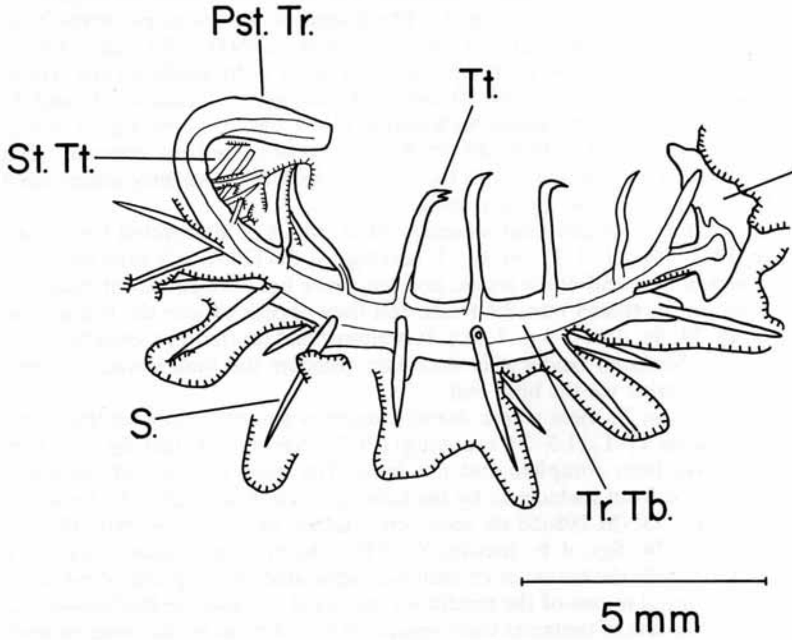
producing a transverse section of the trunk (Pl. 76, figs. 3, 4). The cross-section of the trunk was more or less circular. In this specimen the trunk is traversed by a dorso-ventral strand that may represent the remains of the trunk tube or some vertical septum (Pl. 76, fig. 3). The trunk carried seven median tentacles (T_1–T_7) and, more posteriorly, six short tentacles on its dorsal surface. Seven pairs of ventro-lateral spines (S_I–S_{VII}) projected into the sediment. Each tentacle was opposite a pair of spines, except for the anteriormost one (T_1) which was unopposed. Thus, the most posterior pair of spines (S_{VII}) was also unopposed (Pl. 73, figs. 1, 2, 4; Pl. 74, figs. 5, 6; text-figs. 1, 3).

The spacing of the tentacles is more or less constant, with the exception of T_1 which is separated from T_2 by a lesser distance. The tentacles decreased slightly in length anteriorly (Pl. 73, fig. 3; text-fig. 1). The length of the tentacles varies from 2·7 mm (USNM 198658, total length 1·6 cm) to 5·5 mm (USNM 83935, total length 3·0 cm). Typically the tentacles are preserved running at right angles to the trunk, with the distal part bent forwards (Pl. 73, figs. 1–3; text-fig. 1). Tentacles T_6 and T_7 of USNM 198658 are, however, flexed backwards (Pl. 74, figs. 5, 6; text-fig. 3), whilst the tentacle bases of USNM 198659 (Pl. 75, fig. 8) appear to be bent ventrally. The tips of the tentacles were bifurcate, with the superior fork being slightly longer than the other (Pl. 73, fig. 5; Pl. 74, fig. 6; text-fig. 3).

The trunk contains a longitudinal reflective band, which is interpreted here as an internal tube (Pl. 73, figs. 1, 3; Pl. 74, fig. 5; text-figs. 1, 3). This trunk tube ran from the head to the posterior end of the trunk, and may have been the gut. Continuations of the tentacles can be traced into the trunk and they appear to join the trunk tube (Pl. 73, fig. 3; Pl. 74, fig. 2; text-figs. 1, 2C). It is almost certain that the tentacles were hollow, but as is discussed below it is uncertain whether the lumen was in direct contact with the exterior via the bifid end.

Posterior to tentacle T_7 there was a dorsal cluster of smooth tentacles that were shorter than tentacles T_1–T_7 (1·5–2·0 mm long) (Pl. 73, figs. 1, 2, 4; text-fig. 1). Their tips appear to have been complete and not bifid. The most anterior of the short tentacles is separated from tentacle T_7 by the same spacing as separates the tentacles from each other. In USNM 198658 six short tentacles are preserved on two different bedding planes (Pl. 74, figs. 4–6; text-fig. 3). This observation suggests that they formed three pairs, with the tentacles of each pair separated by the plane of bilateral symmetry. Upon burial in one of the mudflows that went to form the Phyllopod bed (Piper 1972), the two sets of tentacles were separated by sediment in the same manner as the appendages of *M. splendens* (Whittington, 1971*a*, *b*). In USNM 83935 the posteriormost of the three short tentacles preserved can be traced entering the trunk and apparently joining the trunk tube (Pl. 73, fig. 4; text-fig. 1). It is probable that this feature was common to all the short tentacles. Posterior to the short tentacles the trunk decreased in diameter by about a half (Pl. 73, fig. 2) This narrower length was smooth and lacked appendages. Characteristically it was bent upwards and then forwards, so that it overlay the posterior tentacles T_{6-7}. (Pl. 73, figs. 1, 2; Pl. 74, figs. 5, 6; text-figs. 1, 3). The swollen end of USNM 198584 (Pl. 75, fig. 1) may be original, but it could owe its appearance to decay reducing the rest of the posterior trunk to a thin strand.

There were seven pairs of ventro-lateral spines. The spacing between the pairs was fairly constant, although S_I was separated from S_{II} by a greater distance. The total of seven pairs is invariable, even in the smallest known specimen (5 mm long). Each spine was straight and tapered to a fine point (Pl. 73, figs. 1, 2; Pl. 74, figs. 5, 6; Pl. 75, figs. 1–8; text-figs. 1, 3). They varied in length from 0·8 mm (GSC 45333, total length 5·0 mm) to 10·0 mm (USNM 83935, total length 3·0 cm), and the average was about 4·0 mm. In similar-sized specimens each spine has about the same proximal diameter (0·7 mm) whether preserved laterally (Pl. 73, figs. 1, 2; text-fig. 1), or vertically (Pl. 76, figs. 3, 4). This suggests that they had a circular cross-section. Well-preserved spines have about ten longitudinal lines each, which probably represent original ribbing (Pl. 73, fig. 4; Pl. 74, fig. 3). The blunt square ends of the spines were



TEXT-FIG. 3. Camera-lucida drawing of USNM 198658. See text-fig. 1 for explanatory notes and abbreviations.

EXPLANATION OF PLATE 74

Figs. 1–6. *Hallucigenia sparsa* (Walcott) gen. nov. USNM 83935 (holotype), figs. 1–3; USNM 198658, figs. 4–6. 1, counterpart, enlargement of anterior trunk and head, low-angle light from south-east, ×7·1. 2, counterpart, enlargement of tentacle entering trunk and joining trunk tube, light from north, ×11. 3, part, trunk with horseshoe-shaped muscle attachment areas, low-angle light from north-west, ×5·3. 4, enlargement of posterior trunk with short tentacles, light from north, ×16. 5, complete specimen, light from north-east, ×7·6. 6, complete specimen, low-angle light from north, ×7·6.

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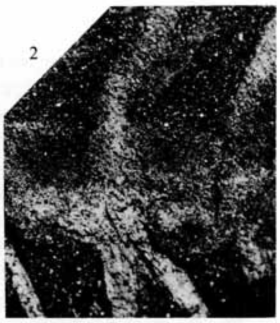

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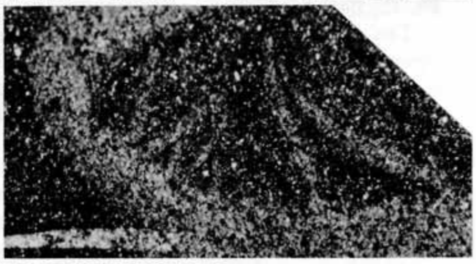

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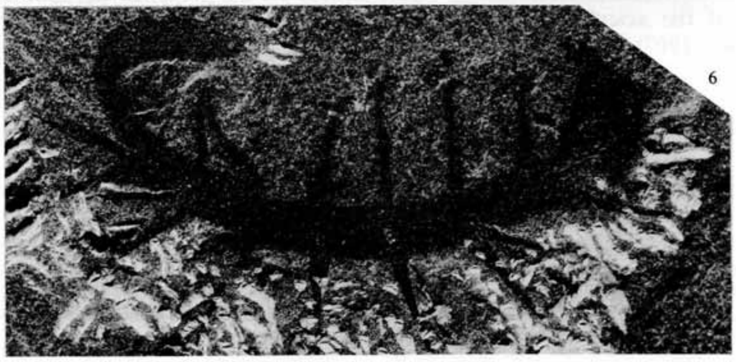

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inserted within the trunk. Furthermore, the trunk itself extended as a sheath along a short distance of each spine (Pl. 73, fig. 2; Pl. 76, figs. 3, 4; text-fig. 1). The spines of each pair did not articulate against each other, and they were probably separated by the trunk tube (Pl. 76, fig. 3; text-fig. 2C). They formed an interspinal angle of about 70°. In laterally preserved specimens the angle between the spines of each pair can vary; in USNM 198665 from 0° (S_{VI}, S_{VII}) to 20° (S_{I}) (Pl. 75, fig. 3). This suggests that the spines could move independently. The orientation of the specimen may, however, also determine the angle of separation, especially in cases where the angle increases by a regular amount along the length of the animal. This may be due to the specimen lying at a progressively steeper angle to the bedding plane along its length (e.g. Pl. 75, figs. 5, 7).

The proximal end of each spine was surrounded by a horseshoe-shaped line that opened ventrally (Pl. 73, figs. 1, 2; Pl. 74, fig. 3; text-fig. 1). This line may represent a strengthened part of the body wall which acted as the insertion point for muscles that ran to the proximal end of the spine. The proximal end of the spine is sometimes raised with respect to the rest of the spine and the muscles were probably inserted at this point. The muscles may have been in the form of a fan that radiated from the spine, but they were more probably grouped into several discrete bundles (text-fig. 2B). Additional muscles may have run from the horseshoe-shaped line to more distal parts of the embedded spine, while other muscles could have been inserted within the area defined by the horseshoe-shaped line. Contraction of the different muscle bundles would have moved the spine. A parallel exists with the acicular muscles of polychaetes. Aciculae are stout spines that support and move the parapodia, particularly during the power stroke of walking (Mettam 1967). They project to, or just beyond, the distal end of the parapodia and also into the body cavity. Typically there is one aciculum in each ramus of a parapodium, although multiples are known. In *Hermodice carunculata*, however, the aciculae are replaced functionally by the setal sacs (Marsden, 1966). Protractor and generally weaker retractor muscles inserted on the base of the aciculum, and neurosetal sac of *H. carunculata*, radiate outwards and are attached to the trunk and parapodial walls. Information on acicular muscles and their points of insertion is available in Clark and Clark (1960), Clark (1964), Marsden (1966), Manton (1967), Mettam (1967, 1971), and Lawry (1971). In *Nereis diversicolor* the insertion line on the posterior parapodial wall of most of the acicular protractors of the neuropodium forms an incomplete arc (Mettam 1967), and thus is not dissimilar to the horseshoe-shaped insertion line of

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EXPLANATION OF PLATE 75

Figs. 1–8. *Hallucigenia sparsa* (Walcott) gen. nov. All partially decayed specimens. Note algae associated with specimens in figs. 2–4, 6, 7. 1, USNM 198584, light from south, ×12. 2, USNM 198662, light from south, ×3·6. 3, USNM 198665, light from north-west, ×5·8. 4, USNM 198660, light from north, ×3·6. 5, USNM 198664, light from south-east, ×4·6. 6, USNM 198663, light from north, ×2·4. 7, USNM 198661, light from south-west, ×3·2. 8, USNM 198659, light from south, ×4·2.

PLATE 75

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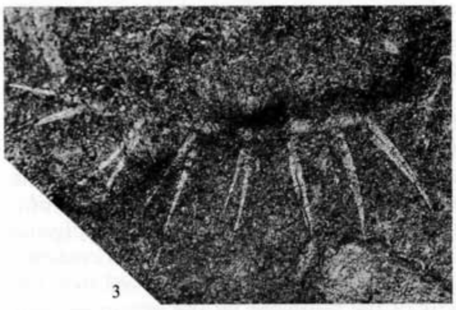

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CONWAY MORRIS, Cambrian metazoan

Hallucigenia sparsa. In *N. diversicolor*, however, the arc is not raised on the wall of the parapodium, nor is it complete as in *H. sparsa*. The polychaete parapodium possesses other muscles that are also used in its movement (Mettam 1967, 1971). No analogous muscles have been identified in *H. sparsa*.

DISCUSSION

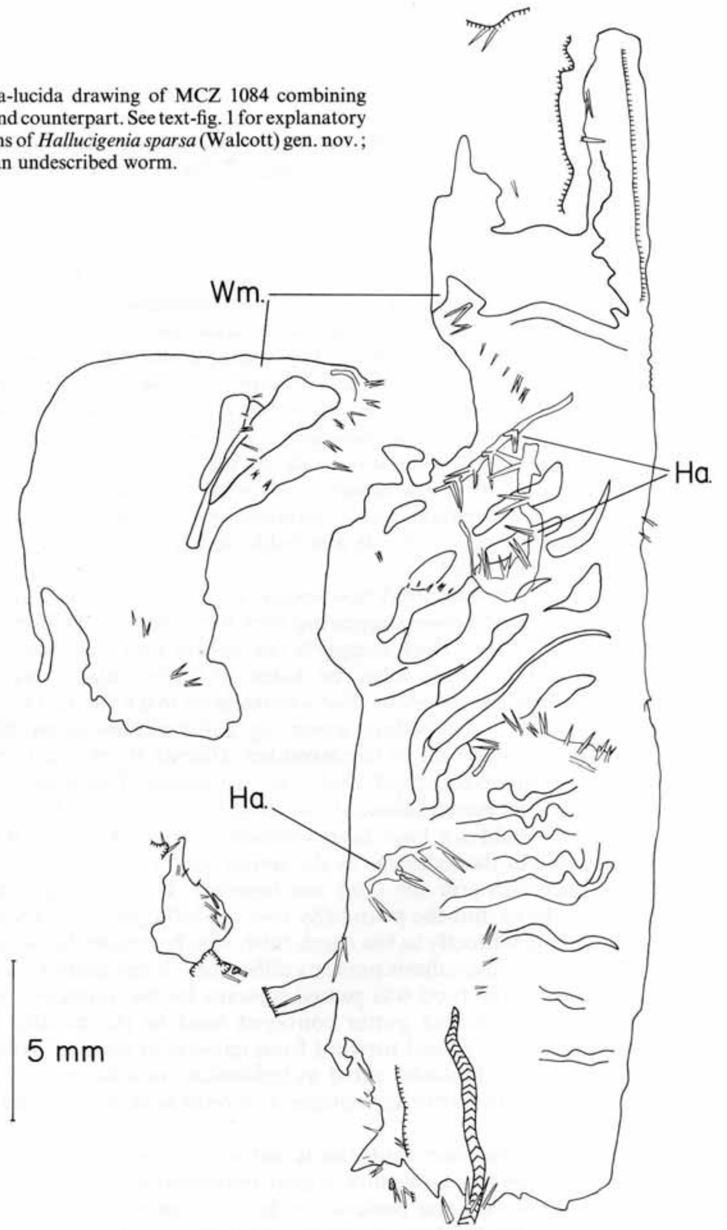
Mode of life. As no animal like *H. sparsa* is known today its mode of life is rather problematical. It must have been epifaunal, as it is impossible to imagine it either swimming or burrowing. The spines appear to be suitable for supporting the animal on a muddy bottom (text-fig. 2A). The large interspinal angle of each pair would have given a high degree of stability. The varying position of the independent spines with respect to each other, and the postulated existence of muscles indicates that the spines could move and were not rigidly fixed. The movement of the spines may have been similar to the locomotory cycle of walking polychaetes, and the notopodial 'poling' movements with which tubicolous polychaetes such as *Sabella* progresses along the tube (Clark 1964, fig. 74). In addition, the section of the trunk that extended around the proximal spine may have been extended by coelomic fluid during the power stroke, as occurs in the neuropodia of *Hermodice carunculata* (Marsden, 1966). If this was the case it is probable that like the polychaetes the trunk of *Hallucigenia sparsa* was subdivided by transverse septa to maintain turgor pressure. No evidence of septa has, however, been preserved. Thus the creature could have moved over the mud, with the spines presumably lifted clear of the sediment by the action of their muscles during the recovery stroke. Some specimens are curved so that the tentacles lie on the concave side (Pl. 74, figs. 5, 6; text-fig. 3). This configuration, which may have arisen by contraction of longitudinal muscles in the dorsal trunk, could have helped to lift the spines clear. Marsden (1966) noted that *Hermodice carunculata* often raises its anterior end, apparently to test the environment. It is possible that *Hallucigenia sparsa* had the same behavioural pattern. Locomotion would, however, have been far more effective if the pointed tips of the spines could have pushed against a resistant substrate. This is because the ends would have tended otherwise to be pushed into the sediment during the power stroke, without giving effective leverage. For this reason one may speculate that *H. sparsa* could have lived on a hard bottom. The Phyllopod bed was deposited immediately adjacent to a carbonate bank (Fritz 1971), and it is possible that *H. sparsa* lived on the bank itself. However, unless the mudflows that went to form the Phyllopod bed swept over the basal apron of the bank, it is difficult to see how the specimens could be swept away. *H. sparsa* probably did not progress rapidly over rocks or mud, and much of its time may have been spent stationary. The movement of *H. sparsa* may not, however, have been as awkward as it intuitively appears. Mettam (1971), for example, reported that during locomotion *Aphrodite* (Polychaeta) can support its entire body on about six neuropodial bundles of setae at any one time. In addition, some echinoids can support the test above the sediment on long spines. In the recent echinoid *Plesiodiadema indicum* the adoral spines have terminal thickenings to prevent sinking (Mortensen 1940). Specimens of *Pseudodiadema* sp. from the Ringstead Waxy Clay (Upper Oxfordian) of Dorset have, however, long thin spines without terminal thickenings, which suggests a relatively firm clay surface (Dr. M. Brookfield pers. comm.). It might be postulated that the sediments of the pre-slide environment of the Burgess Shale showed a similar resistance to penetration, perhaps due to early hardening.

MCZ 1084 has at least eighteen specimens of *H. sparsa* associated with a new undescribed worm (Pl. 76, figs. 1, 2; text-fig. 4). This association cannot be by chance because practically all the specimens lie on the worm and not beyond it. The variation in size and lack of coherent arrangement demonstrates that the specimens did not form a colony. It is proposed that they were attracted from the surrounding area and congregated to feed on the corpse. The spines could have been embedded in the decaying flesh. *H. sparsa* was, therefore, probably a scavenger. In modern deep-sea communities similar occurrences have been observed where various crustacea, ophiuroids, and later fish come together to scavenge bait lowered from ships (Isaacs and Schwartzlose 1975). The slow-walking polychaete *Hermodice carunculata*, to which comparison with *Hallucigenia sparsa* was made above, 'is a scavenger or else feeds on sessile alcyonarians and zooantharians . . . and does not prey on active animals' (Marsden 1966, p. 275). It is possible that *H. sparsa* included sessile creatures such as sponges in its diet.

The tentacles with their bifid tips appear to have been suited for grasping food. Evidence is presented below suggesting that the bifid tips were more cuticularized and resistant to decay, which supports the notion that they were used for biting. Food may have been taken from the water, or if the tentacles were bent ventrally from either prey or the sediment. For a tentacle to reach the surface of the sediment or corpse on which it was feeding, assuming that it was not extensible, two-thirds of the ventral spine would have to be embedded. Despite the pointed spines, the animal could not have sunk to this depth under its own weight. This is because the sea-water would have almost counterbalanced the weight of the animal by buoyancy, and the residual weight would not have been sufficient to allow the animal to embed itself. Thus penetration of the sediment by the spines would have required active muscular effort. It is uncertain how the food was ingested. The food may have been passed forward to the head, but the possibility that the bifid tip of each tentacle contained an opening that led directly to the trunk tube, which presumably was the gut, cannot be dismissed. Either hypothesis presents difficulties. If the mouth was at the anterior, it is uncertain how the food was passed forward by the tentacles. One possibility is that a longitudinal ciliated gutter conveyed food to the mouth. It seems highly unlikely that food was passed forward from tentacle to tentacle. Alternatively, if the bifid openings of the tentacles acted as individual mouths, only the comparatively short length of gut posterior to tentacle T_7 would have been available for effective digestion.

The function of the short tentacles is unknown. Their posterior location renders their use as food-sorters or sensory organs improbable. It has been suggested to the author that the anterior and posterior ends of the animal should be reversed. Thus, it is conceivable that the short tentacles sorted food, and the curved posterior trunk bent down to take the food. Definitive evidence is lacking. The author prefers to regard the tentacles as bending forwards, and the swollen anterior end as the head rather than the simple posterior trunk.

TEXT-FIG. 4. Camera-lucida drawing of MCZ 1084 combining features of the part and counterpart. See text-fig. 1 for explanatory notes. Ha., Specimens of *Hallucigenia sparsa* (Walcott) gen. nov.; Wm., Specimen of an undescribed worm.



EXPLANATION OF PLATE 76

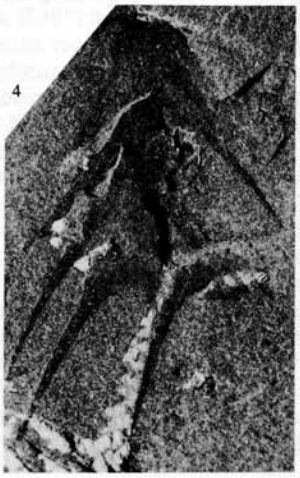
Figs. 1–5. *Hallucigenia sparsa* (Walcott) gen. nov. MCZ 1084, figs. 1–2; GSC 45332, figs. 3–5. 1, part, specimens of *H. sparsa* distributed over an undescribed worm, light from north-east, ×3. 2, counterpart of fig. 1, light from north-west, ×3. 3, part, specimen steeply orientated with respect to the bedding plane, light from west, ×6·4. 4, part, low-angle light from east, ×6·4. 5, counterpart of figs. 3–4, light from east, ×6·4.

1

2

3

4



5

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There is no evidence that the specimens of *H. sparsa* are detached fragments of a colonial organism. The vast majority of Burgess Shale fossils are complete, and a special explanation must be invoked for species such as the arthropod *Anomalocaris gigantea* Walcott, 1912*a* which is only found as isolated appendages (D. E. G. Briggs pers. comm.).

Preservation and decay. The poor preservation of the majority of specimens is attributed to decay, which was stopped by the onset of fossilization. The spines, however, are always well preserved and show no signs of deterioration. This suggests that they were made of a tough resistant material, but their exact composition is unknown. The trunk is usually poorly preserved (Pl. 75, figs. 3–5, 7, 8), and sometimes almost completely absent (Pl. 75, figs. 1, 2, 6). The head and tentacles are well preserved only in two specimens (Pl. 73, figs. 1–5; Pl. 74, figs. 1, 2, 4–6; text-figs. 1, 3), although in some specimens the basal stumps of some of the tentacles are present (Pl. 75, fig. 7). The bifid end of each tentacle is, moreover, preserved as a more reflective film than the remainder of the tentacle (Pl. 73, figs. 3, 5). The bifid ends appear to be more resistant to decay so that they apparently persist after the disappearance of the rest of the tentacle (Pl. 75, figs. 2, 4). The body wall of the head and tentacles was probably thinner than that of the trunk. It is concluded that the decreasing order of resistance to decay was: spines, trunk, tentacles, and head.

Systematic position. *H. sparsa* cannot readily be compared to any living or fossil animal. As noted above, Walcott's (1911) placement of this worm in the genus *Canadia* (Polychaeta) cannot be upheld. There are virtually no similarities between the type species, *C. spinosa* Walcott, and this animal. The new genus *Hallucigenia* has, therefore, been proposed. Walcott (1911) assigned the species to the polychaetes on the supposition that the spines were enormous setae which arose from tiny parapodia. Although parallels with the polychaetes have been drawn above with the spine muscles and method of locomotion, the author believes that a direct relationship is unjustified. The polychaete aciculae do not project as far beyond the trunk as the spines of *H. sparsa*. Furthermore, Manton (1967) noted that in polychaetes that walk upon their neuropodia the aciculae are never enlarged to act as stilts. The proposed similarity between the polychaete acicular muscles and those inserted on to the spines results from a common attempt to obtain a universal-joint system, and is without phylogenetic significance. The horseshoe-shaped insertion lines of *H. sparsa* have no direct counterpart in the polychaetes. Thickened acicular setae replace some or all the normal setae in some polychaetes. To the author's knowledge, however, the acicular setae are never reduced to one per parapodium, nor are they as large. Moreover, if the ventro-lateral spines were to be interpreted as arising from the neuropodia, there is no trace of the corresponding notopodia. There is no evidence to suggest that the pairs of spines exposed in laterally preserved specimens belong only to one side of the animal, with another pair hidden beneath the body. In these specimens the spines of each pair are often separated by a layer of rock, that in USNM 83935 and USNM 198658 was removed with a dental micro-drill to expose the lower spines (Pl. 73, figs. 1, 2; Pl. 74, figs. 5, 6; text-figs. 1, 3). This indicates that each spine of a pair belongs to one side of the animal. Vertically orientated specimens confirm this observation (Pl. 76, figs. 3–5). In the great majority of polychaetes, the number of setiferous segments increases with age, whereas *H. sparsa* has seven pairs of spines regardless of size.

Similarly the tentacles cannot be compared with the cirri of polychaetes. The Heterospionidae and Cirratulidae have numerous dorsal cirri, and the Cossuridae has a single dorsal tentacle. None of these polychaetes, however, has seven cirri arranged in a single median row, succeeded by three pairs of shorter cirri. These three polychaete families are, moreover, typical of their class and show no especially aberrant features. The cirri of polychaetes do not have bifid tips, and although the gills of the oligochaete *Alma nilotica* are sometimes bifid (Gresson 1927), they are in no other way at all comparable. Unlike the tentacles of *H. sparsa*, the cirri never project into the body cavity and join a central tube, but arise instead from the surface. The tentacles of *H. sparsa* were almost certainly hollow. Although the polychaete cirratophore contains a coelomic space (Lawry 1971), the cirrus itself is solid with a central mass of nervous tissue (Lawry 1967; Boilly-Marer 1972*a*, *b*).

It may be concluded that *H. sparsa* cannot be placed in the polychaetes. Its affinities remain uncertain. The seven-fold repetition, presumably some sort of segmentation, of the tentacles and spines is unusual. The total number of 'segments' is difficult to evaluate. There are at least seven, but the unopposed tentacle T_1 and spine S_{VII}, and the cluster of short tentacles suggest that there may be another three 'segments'. There are very tentative grounds for suggesting a comparison with the Echinodermata. If the tentacles were joined to the trunk tube, they would not be dissimilar to the canal and podia of the water vascular system of the Echinodermata. The tentacles and trunk tube might have formed a hydrostatic system with food-collecting movements of the tentacles being powered by fluid pressure. This interpretation assumes that the bifid tips did not house mouths, and raises the question of the location of the gut. This suggestion must, therefore, remain speculative.

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S. CONWAY MORRIS
Department of Geology
Sedgwick Museum
Cambridge

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