MIDDLE CAMBRIAN PRIAPULIDS
AND OTHER SOFT-BODIED FOSSILS
FROM UTAH AND SPAIN[1]

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Abstract—The fossil priapulid worms *Ottoia prolifica, Selkirkia willoughbyi* n. sp., *Selkirkia spencei,* and *Selkirkia* sp. are illustrated from the Middle Cambrian of Utah. New records of *O. prolifica* from the Spence Shale and Marjum Formation represent notable geographic and stratigraphic extensions of its previously unique occurrence in the Stephen Formation of British Columbia. *O. prolifica* has a range through much of the Middle Cambrian (?15 Ma), during which time it shows minimal morphological change. New records of *S. spencei* augment previous finds in the Spence Shale. *S. willoughbyi* n. sp. occurs in the Marjum Formation and Wheeler Formation. It differs from the type species *S. columbia* in details of tube size and degree of tapering, although the poorly known soft parts appear to be broadly similar. These occurrences extend significantly the stratigraphic range of *Selkirkia,* and are augmented by the discovery of *Selkirkia* sp. in the Wheeler Formation. A unique specimen of the possible annelid worm *Palaeoscolex, P.* cf. *P. ratcliffei,* is described from the Middle Cambrian of Spain, thereby extending the geographic range from previously known occurrences in England, Utah, and South Australia. Papillate ornamentation of various species of *Palaeoscolex* is compared, and the new class Palaeoscolecida is erected. These descriptions of soft-bodied organisms provide further information on the diversity of Cambrian life. The possibility that present information on soft-bodied and lightly skeletized biotas is biased toward deeper water, possibly conservative, forms is discussed. Brief descriptions of possible soft-bodied worms and trace fossils (burrows and questionable coprolites) from Utah are also given.

OF THE MANY BIASES that distort our perception of the fossil record, probably none is as significant as the almost total loss of the soft-bodied component of a fauna. As yet there is no clear indication of the relative change in this component through geologic time, and so it may be unwise to infer that a given percentage of soft-bodied animals is absent from a fossil fauna. Indeed, even were percentages of change known, it remains to be demonstrated whether taphonomic factors have themselves shown systematic changes through the Phanerozoic that might either favor or inhibit the chances of soft-part preservation. Trace fossils can at best hint at former levels of diversity, and rarely provide reliable estimates of a missing soft-bodied component. Accordingly, any information of actual soft-part preservation that helps to supplement our knowledge of this missing fraction of a fauna is of considerable significance.

For the Middle Cambrian, the exemplar of a soft-bodied fauna is from the Burgess Shale. It has been suggested that the unusual character of this fauna lies in its favored history of preservation rather than the original biotic assemblage (Conway Morris, 1981; Conway Morris and Robison, 1982). If this is correct then such soft-bodied faunas may provide a guide to original diversity and paleoecologic insights more reliable than those provided by normal shelly assemblages, for which a substantial fraction of the fauna failed to fossilize. Recent discoveries of exceptionally preserved Middle Cambrian fossils in the immediate vicinity of the Burgess Shale (Collins, Briggs, and Conway Morris, 1983) and in similar open-shelf lithofacies of Idaho and Utah (Willoughby and Robison, 1979; Rigby, 1980, 1983; Gunther and Gunther, 1981; Robison and Richards, 1981; Conway Morris and Robison, 1982; Briggs and Robison, 1984; Robison, 1984b, 1985) support the notion that soft-bodied organisms comprised a significant proportion of these faunas. As information on soft-bodied and lightly skeletized taxa from Middle Cambrian localities in Utah and Idaho has accumulated in the last few years, it has become apparent that the great majority of soft-bodied genera so described are known also from the Burgess Shale or nearby sites in the Stephen Formation. Thus, of the approximately 40 genera of arthropods, sponges, priapulids, annelids, medusoids, *incertae sedis,* and algae known from these localities, almost 75 percent occur in the

Burgess Shale [excluding the poorly known *Dioxycaris argenta* (see Briggs, 1976; Briggs and Robison, 1984) and assuming various questionable assignments to *Perspicaris, Emeraldella, Leanchoilia, Sidneyia* (Briggs and Robison, 1984), and *Stephenoscolex* (Conway Morris, 1979a) are correct]. Although new genera will no doubt continue to be described, the overall generic diversity of the soft-bodied component from moderately deepwater biofacies in the western Cordillera appears to be tolerably well documented.

Brief descriptions follow for the priapulids *Ottoia* and *Selkirkia* from Utah and the possible annelid *Palaeoscolex* from Spain. This information extends known geographic and stratigraphic ranges. Mention is made also of other soft-bodied material and trace fossils. Although data are scanty, it appears that some lightly skeletized genera such as *Anomalocaris* (Briggs and Mount, 1982; Briggs and Robison, 1984) and the aberrant trilobite *Naraoia* (Robison, 1984b) have lengthy stratigraphic ranges with examples known from the upper Lower Cambrian (*Bonnia-Olenellus* Zone) to upper Middle Cambrian (*Ptychagnostus punctuosus* Zone). Robison (1984b) noted that the stratigraphic range of *Naraoia* exceeds that of most other Cambrian trilobite genera. A parallel exists, however, in the trilobite *Ogygopsis,* which has a similar stratigraphic range (reviewed in Conway Morris, 1985). Recently, there has been speculation on whether certain habitats promote generic and specific longevity (e.g., Jablonski and Valentine, 1981). Although some data are contradictory, in the context of Lower Paleozoic marine communities Fortey's (1980) documentation of many long ranging Lower Ordovician genera being confined to "deep-water sites with low oxygen concentration, and probably beneath the thermocline" could be directly relevant to explaining the longevity of such Cambrian forms as *Ogygopsis, Anomalocaris,* perhaps *Naraoia,* and by implication a number of other genera. In this context the occurrence of *Ogygopsis* is of particular interest. Several workers (Nelson, 1963; Palmer and Halley, 1979) have commented on the likelihood that the sporadic appearance of this trilobite in the rock record reflects the onset of a particular set of environmental conditions, specifically paleooceanographic factors involving access to the open ocean, or bathymetric changes, or both. One such possibility is occasional and

nonperiodic incursions of deeper and presumably cooler waters into proximal regions of the open shelf. It is suggested that at least some of the soft-bodied taxa known from the Cambrian of the western Cordillera represent conservative forms inhabiting relatively deep water. It may be no coincidence that if their occurrences are linked to more poorly aerated water masses, then the proximity of anoxic conditions may be a major factor in promoting soft-part preservation. Our knowledge of Cambrian biotas with a relatively extensive soft-part component may be biased toward those deeper water faunas that, given certain oceanographic conditions, were able to migrate shoreward. Equally diverse assemblages may have flourished in shallower and more aerated water, but there the chances of extensive soft-part preservation were correspondingly reduced, making it less likely that paleontologists will be afforded the insights provided by the Burgess Shale and analogous deeper water deposits. Nevertheless, even if further evidence suggests the existence of relatively conservative deepwater Cambrian faunas, there is little reason to suppose they were biotically homogeneous. Thus, although *Ogygopsis* occurs in association with soft-part preservation, including *Anomalocaris,* in part of the Stephen Formation, elsewhere *Anomalocaris* and *Naraoia* occur independently.

LOCALITIES AND STRATIGRAPHY

The Utah material illustrated here is from three localities, two in the Marjum Formation (R. A. Robison localities 347 and 811) and one in the Spence Shale (R. A. Robison locality 781). Mention is also made of related material from two localities in the Wheeler Formation.

Locality 347 (locality 3 of Rigby, 1983), otherwise known as Sponge Gully, occurs in a dry stream bed about 700 to 800 m east of the western road between Marjum Pass and Wheeler Amphitheater, and approximately 4.7 km east-northeast of Marjum Pass [NW¼SE¼, sec. 4 (unsurveyed), T. 18 S., R. 13 W.], central House Range, Millard County. Other details of the rich fauna from this locality are available in Robison and Richards (1981), Rigby (1983), Robison (1984a), and Briggs and Robison (1984). The fossils were collected about 60 m above the base of the Marjum Formation in a grayish-blue, weathering to pale yellowish-brown, finely laminated calcareous shale.

Locality 781, also known as Gunther Quarry, occurs on the south side of Antimony Canyon, on the west side of Wellsville Mountains, about 4 km north of Brigham City (NW¼, sec. 31, T. 10 N., R. 1 W.), Box Elder County. The fossils were collected about 4 m below the top of the Spence Shale in a rather tough blue-gray shale, which is in places micaceous. In addition to the priapulids described here, the locality has yielded a diverse assemblage of trilobites, ctenocystoid and eocrinoid echinoderms, brachiopods, hyolithids, sponges, and algae. Adjacent localities in the Spence Shale are also highly fossiliferous and the overall nature of the biota was reviewed by Briggs and Robison (1984).

Descriptions of locality 811, about 200 m above the base of the Marjum Formation in the

House Range, are recorded in files of the U. S. National Museum of Natural History, Washington, D. C., and the University of Kansas Museum of Invertebrate Paleontology. In addition to the trace fossils and questionable soft-bodied worms described here, the biota includes trilobites and other arthropods, echinoderms, brachiopods, sponges, hyolithids, trace fossils, and algae (Ubaghs and Robison, 1985:2).

The material from the Wheeler Formation is from:

1. The type locality (R. A. Robison locality 115) in the Wheeler Amphitheater (SE¼, sec. 2, T. 17 S., R. 13 W.), central House Range, immediately adjacent to a small commercial quarry. The diverse biota includes numerous species of trilobite and other arthropods, brachiopods, sponges, echinoderms, hyolithids, monoplacophorans, a possible medusoid, algae, and trace fossils (Robison, 1971; Rigby, 1978; Willoughby and Robison, 1979; Robison and Richards, 1981).

2. An isolated outcrop of shale in the Drum Mountains, Millard County (R. A. Robison locality 712), about 100 m east of a stream gully in center S½NE¼, sec. 20, T. 15 S., R. 10 W. The locality is in the uppermost part of the Wheeler Formation. Details of its biota are provided below.

The Spanish specimen of *Palaeoscolex* is from the Middle Cambrian Murero Shales (Valdemiedes Beds), exposed in the classic locality of Murero (Valdemiedes Valley), close to Villafeliche about 70 km southwest of Zaragoza. Details of the Cambrian succession of the area were reviewed by Lotze and Sdzuy (1961:311).

PALEOECOLOGY AND TAPHONOMY

The priapulid worms *Ottoia* and *Selkirkia* were interpreted as members of the vagrant infauna in the Burgess Shale (Conway Morris, 1977), and it seems reasonable to suppose that the examples described here from Utah were also burrowers. Structures interpreted as burrows from the Wheeler Formation are described below, but priapulids have not been recorded at the locality (115), and the nature of the makers of these burrows is problematic. Trace fossils attributable to priapulid activity have not been recognized in localities yielding priapulid body fossils, and this supports suggestions (see below) that the

fossils are allochthonous.

On the basis of gut contents that include hyolithids and articulate brachiopods, *Ottoia* was interpreted as a predator (Conway Morris, 1977); and although such contents were not identified in *Selkirkia*, the similarity in mouth armature to *Ottoia* suggests that this tubicolous priapulid belonged to the same trophic category. Aspects of the paleoecology of the Marjum and Wheeler formations are not extensively documented, although Rogers (1984) and Robison (1985) provide some information, of which Rogers' account of locality 347 is of direct relevance to this work. Robison (1985) drew attention to "rare carnivores and scavengers" in the Wheeler Formation fauna, and the occurrences of priapulids reported here provide further records of Cambrian predators (see Conway Morris, 1985). Paleoecological comparisons with the classic Burgess Shale fauna are justified because of strong biotic similarities (Conway Morris and Robison, 1982; see also above), but different taphonomic histories render difficult any detailed comparisons of factors such as infauna : epifauna ratios, proportions of different trophic groups, composition of trophic nucleus, and dominance-diversity within various ecological groupings, for all of which there is detailed information from the Burgess Shale Phyllopod bed (Conway Morris, 1981; in preparation). Furthermore, Rogers (1984) emphasized the localized occurrences of various elements, especially sponges in the Marjum Formation, which he suggested may reflect sampling of a sponge-rich area of the seafloor by currents. Correspondingly, Robison (1985) noted a rarity of sponges in a Wheeler Formation locality (see also Rogers, 1984), which he attributed to possible benthic turbidity.

Regarding taphonomic history, the relative paucity of preserved soft parts may reflect less appropriate conditions than those prevailing in the Burgess Shale, rather than an original predominance of well-skeletized groups. Briggs and Robison (1984) suggested "episodic storm deposition on a gently sloping shelf" as a mechanism of burial, whereas Rogers (1984) presented detailed evidence from two localities, in the Marjum and Wheeler formations, indicating deposition from turbidity currents. This study adds little information on the mode of deposition, although the strong preferred orientation of *S. willoughbyi* (Fig. 4,*1*) on several slabs from the

Wheeler Formation (locality 712) accords with Rogers' observations.

Little is known of the paleoecology of *Palaeoscolex*, although Whittard (1953) indicated that it was a deposit feeder and Robison (1969) suggested the worm was infaunal. Both Whittard (1953) and Robison (1969) tentatively suggested that associated trace fossils represented the activities of *Palaeoscolex*. The absence of locomotor appendages and a presumably circular transverse section are both consistent with an infaunal mode of life. There is, moreover, a striking resemblance between the papillate ornamentation of *Palaeoscolex* and the prominent transverse bands of trunk spines alternating with narrower unarmed zones in the Middle Cambrian priapulid worm *Louisella pedunculata* (Conway Morris, 1977, pl. 22, fig. 7; pl. 23, fig. 4). *Louisella* and *Palaeoscolex* are unrelated, and the similarity in ornamentation may represent a functional convergence, although in other aspects of anatomy these two genera are not particularly comparable. It is possible that the transverse rows helped to grip the sediment during the burrow-

ing cycle. With the trunk contracted by the action of longitudinal muscles, the spines or papillae would be pressed against the sediment to act as a penetration anchor (see Conway Morris, 1977) while the anterior section probed into the sediment. The inferred position of the papillae in *Palaeoscolex* on intersegmental sections (see below) would also help to ensure their proximity to the sediment during this stage. Upon formation of the terminal anchor, the anterior transverse rows would relinquish their grip before the worm moved forward in preparation for another burrowing cycle. Whatever advantages these transverse rows may have conferred on the burrowing activities of *Louisella* and *Palaeoscolex* (and *Protoscolex*), comparable features do not appear to be common in either fossil or recent infaunal worms.

The occurrence of *Palaeoscolex* in the Murero Shales may point to an episode of rapid deposition, but the apparent scarcity of soft-bodied fossils from this Spanish locality may indicate a chance local event.

SYSTEMATIC PALEONTOLOGY

Phylum PRIAPULIDA
Class and Order uncertain
Family OTTOIIDAE Walcott, 1911
Genus OTTOIA Walcott, 1911

OTTOIA PROLIFICA Walcott, 1911

Figures 1–3

This monospecific genus was originally described by Walcott (1911), and has been reassessed by Conway Morris (1977). *O. prolifica* is the most abundant of the five priapulid species (excluding those of the problematic *Lecythioscopa* and *Scolecofurca*, the latter known only from Raymond's Quarry) in the Phyllopod bed of the Burgess Shale (Walcott Quarry), where it accounts for about 83 percent of individuals [remainder: *Selkirkia* (excluding the more abundant empty tubes) about 10 percent, *Louisella* 5 percent, *Fieldia* 1 percent, *Ancalagon* 1 percent]. Moreover, this priapulid and *Selkirkia* (see below) are the only genera to have been found at other localities within the Stephen Formation with soft-bodied fossils (Conway Morris, 1977; Col-

lins and others, 1983). Whether their predominance extended to other Middle Cambrian priapulid assemblages is not known. For *O. prolifica*, such occurrences as those described here, the first beyond the Stephen Formation, may indeed reflect the increased probability of preservation one would expect of originally large populations. For *Selkirkia*, however, such an argument is equivocal given the enhanced preservation potential of the tube. Evidence from the Phyllopod bed for a moderately long postmortem residence time of the tubes in the sediment comes from rare examples of epizoic attachment that must have occurred after the death of the priapulid. The relative scarcity of *Selkirkia* specimens having intact soft parts in contrast to vacated tubes also suggests the latter were more resistant to decay (Conway Morris, 1977).

New material.—Two specimens are described. Part and counterpart of a complete individual, KUMIP 204770 is from locality 347 in the Marjum Formation, central House Range, and was collected by T. T. Johnson. It occurs in a
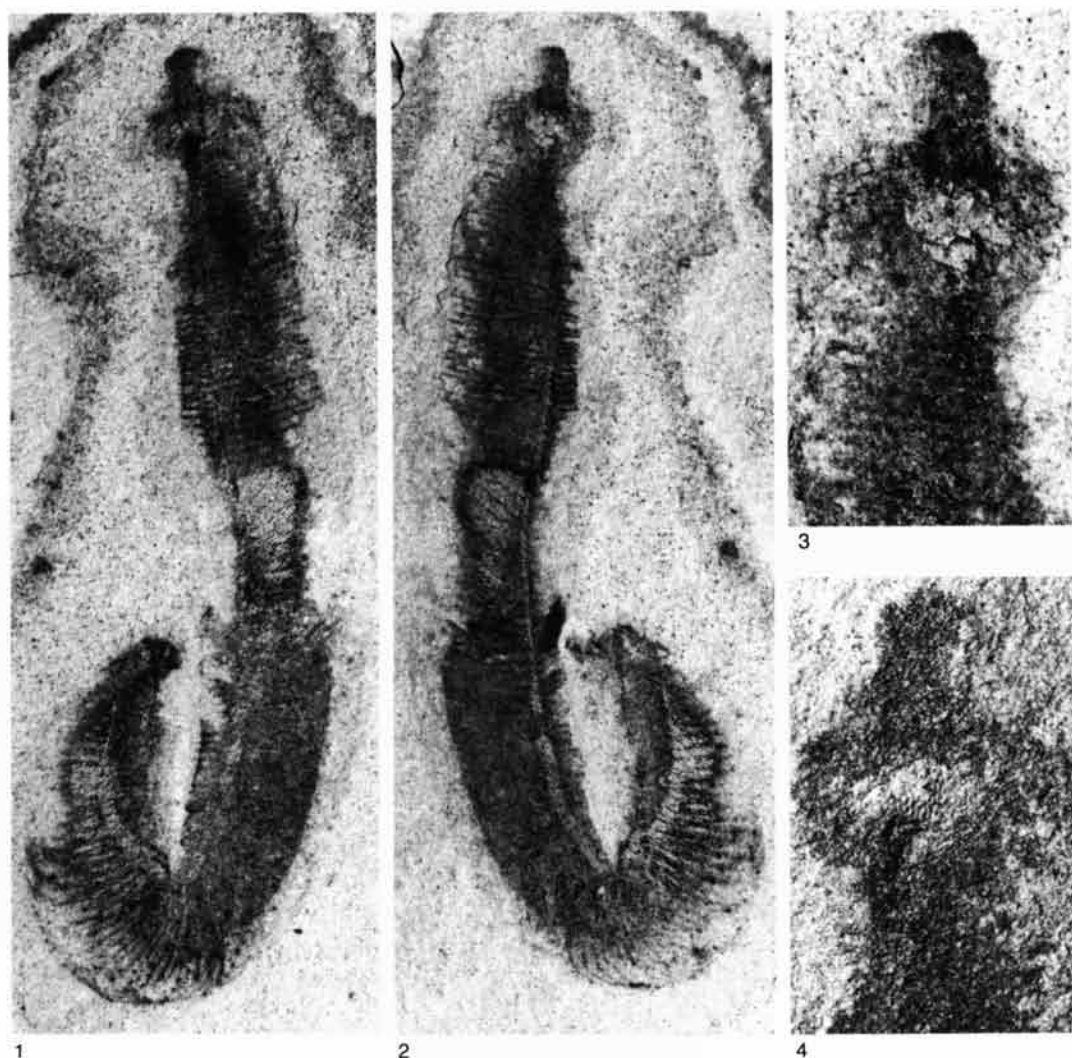
Fig. 1. *Ottoia prolifica*, KUMIP 204770; Marjum Formation, central House Range, locality 347; *1–3* photographed under alcohol, *4* photographed under high angle UV radiation.——*1*. Part, ×3.9.——*2*. Counterpart, ×3.9.——*3*. Anterior trunk and partially retracted proboscis with hooks, ×9.2.——*4*. Proboscis with possible retracted teeth, ×9.5.

bluish-gray shale with dark laminae, and is associated with agnostoid trilobites and organic (possibly algal) debris. Part only, lacking anterior end owing to mechanical fracture, KUMIP 144857 is from locality 781 in the Spence Shale, Antimony Canyon north of Brigham City, and was collected by Lloyd Gunther. It is on a slightly weathered shale surface in association with abundant algae.

Description.—Neither specimen rivals in preservational quality those from the Phyllopod bed of the Burgess Shale (Conway Morris, 1977), but the preserved morphology gives no reason to suppose that they are not conspecific with *O. prolifica.*

KUMIP 204770 (Figs. 1, 2), with an unfolded length of about 43 mm, is a small individual as compared with an average of about 80 mm for samples from the Burgess Shale (Conway Morris, 1977). The quality of preservation is relatively indifferent and may reflect the effects of limited microbial decay. Some diffuse and

poorly defined areas on the edge of the specimen may represent cuticular remnants, with the better defined central region largely representing body-wall musculature that became detached during the early stages of decomposition (compare Conway Morris, 1977).

The proboscis is partially everted, equivalent to proboscis position 3 (Conway Morris, 1977, text-fig. 12). The proboscis armature is not particularly clear. The proboscis hooks are

Fig. 2. *Ottoia prolifica*, KUMIP 204770, explanatory drawing of part (compare Fig. 1,*1*).

poorly preserved (Fig. 1,*3*), although there is evidence suggesting that they vary from anteriorly slender with narrow bases to posteriorly shorter and recurved with wider bases, as observed in Burgess Shale specimens. Possible remains of the proboscis spines have also been identified. The teeth (or spinules) are not evident, unless faint traces within the inverted proboscis represent these structures (Fig. 1,*4*).

Within the trunk, annulations are especially clear in the anterior region (spacing about 19 per 5 mm) and to a lesser extent toward the posterior (Fig. 1,*1*,*2*). A similar arrangement of annuli has been observed in a number of Burgess Shale specimens (Conway Morris, 1977, pl. 12, fig. 6; pl. 13, fig. 4; pl. 14, fig. 1) and may be correlated with more powerful circular muscles whose contractions raised fluid pressure within the body cavity in order to evert the anterior proboscis and posterior bursa. A posterior hook appears to be preserved (Fig. 1,*1*,*2*), and presumably represents one of the row that encircled much of the posterior end. Little is known of the internal structure (Conway Morris, 1977). There are two prominent longitudinal strands in the anterior (Figs. 1,*1*,*2*; 2). Although the more median and broader strand could be interpreted as the alimentary canal, it is the narrower strand near the margin that may be traced into the posterior trunk. Accordingly, the median strand may represent retractor muscles that in life helped to withdraw the everted proboscis.

KUMIP 144857 (Fig. 3) is incomplete, lacking the proboscis and anteriormost trunk. The preserved portion as measured along the curvature of the trunk is 68 mm, with the original length probably in the order of 80 mm and thus comparable to an average-sized specimen from the Burgess Shale. The posteriormost part appears to be everted as a bursa (compare Conway Morris, 1977, text-fig. 14; pl. 3, fig. 4; pl. 8, fig. 5; pl. 14, figs. 1, 2). Faint annulations are preserved, and internally the alimentary tract may be traced in the posterior region with evidence of looping (compare Conway Morris, 1977, pl. 10, fig. 1; pl. 12, fig. 6; pl. 14, fig. 1).

The surface on which this specimen occurs is densely strewn with algal filaments, apparently *Marpolia* (Fig. 3,*1*). Some of this alga is preserved in a black material that may represent carbonaceous remnants. In the Phyllopod bed of the Burgess Shale, *Marpolia* (*M. spissa* Walcott, 1920) is relatively abundant, but rarely (less
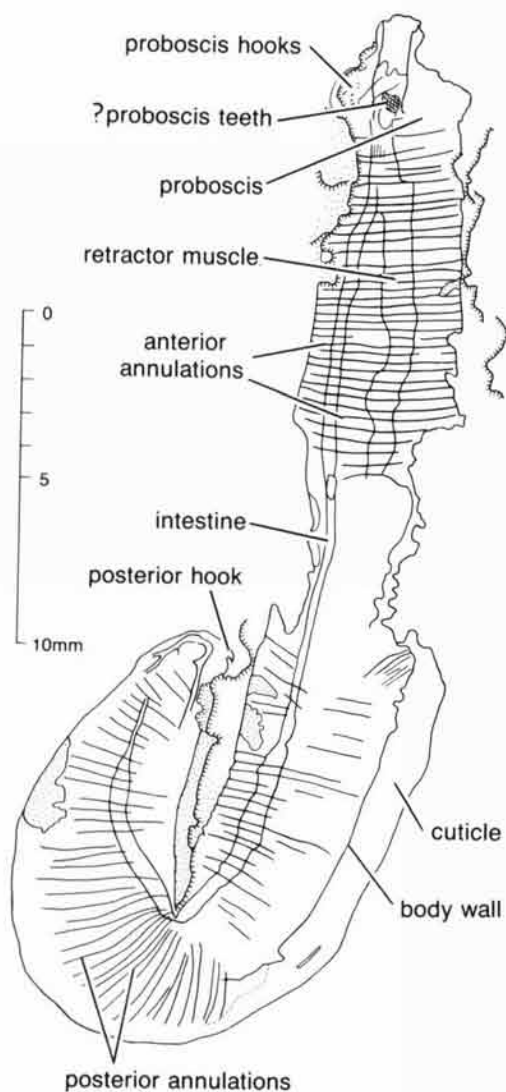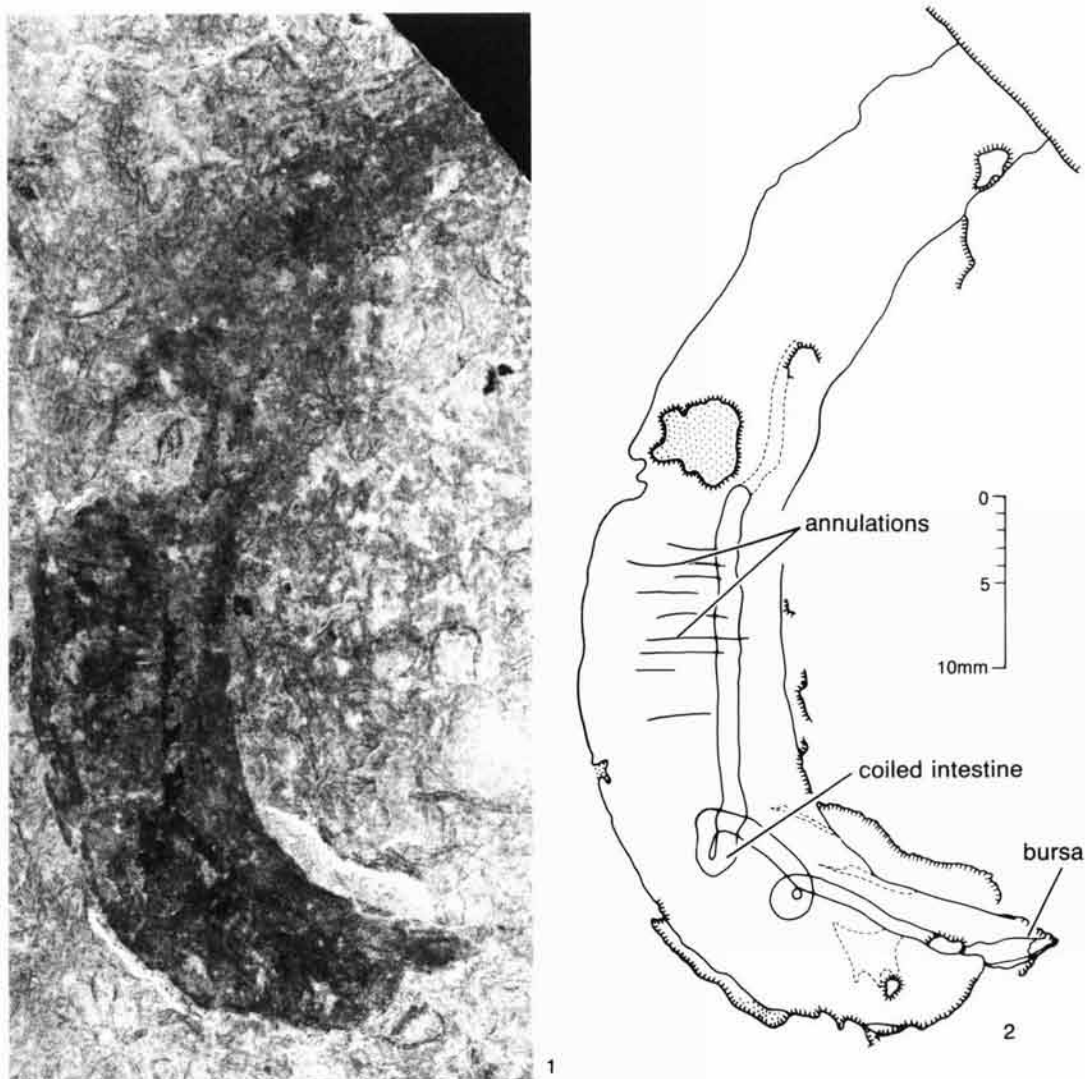
Fig. 3. *Ottoia prolifica*, KUMIP 144857; Spence Shale, Antimony Canyon, locality 781,——*1*. Part, photographed under alcohol, ×2.3.——*2*. Explanatory drawing.

than 1 percent of specimens) is it in immediate association with *O. prolifica*. While *Marpolia* has been noted in association with several other taxa in the Phyllopod bed (for example, *Burgessia, Canadaspis, Marrella, Waptia,* agnostoid and eodiscacean trilobites, *Anomalocaris,* articulate and inarticulate brachiopods, *Canadia, Eldonia,* various sponges, hyolithids, *Isoxys, Mackenzia,* ostracodes, *"Ottoia" tenuis, Pollingeria, Scenella, Selkirkia, Tubulella*), such association also is very rare and may reflect some degree of ecologic separation.

Discussion.—Although these new examples of *O. prolifica* add nothing material to its known anatomy, they are important in extending the stratigraphic and geographic ranges of this priapulid, previously known only from the Stephen Formation (*Ptychagnostus praecurrens* Zone). The occurrence near the top of the Spence Shale (locality 781) extends its range downward to the underlying *Peronopsis bonnerensis* Zone, whereas an upward extension is shown by its presence in the Marjum Formation (locality 347) within the *Ptychagnostus punctuosus* Zone (see Robison,

1984a). *O. prolifica* is thus known to range through a substantial portion of the Middle Cambrian. The preservational quality of the material is sufficient to show that this priapulid had minimal morphological change over a substantial period, perhaps in the order of 15 Ma (see Harland and others, 1982). Whatever the merits of the debate on the recognition of morphological stasis in the fossil record (see Schopf, 1982; Levinton, 1983), it is worth recording an apparent example of such stasis in soft-bodied material instead of the usual hard parts.

The occurrence of this priapulid also extends its geographic range from southern British Columbia to northern (Wellsville Mountains) and west-central (House Range) Utah, a distance today of approximately 1,300 km.

Family SELKIRKIIDAE Conway Morris, 1977

Genus SELKIRKIA Walcott, 1911

The tubicolous priapulid *Selkirkia* (as *S. columbia*) was originally described from the Stephen Formation (Burgess Shale, *Ogygopsis* Shale) on the basis of both empty tubes and a smaller proportion with associated soft parts (Conway Morris, 1977). Unoccupied tubes attributed to this genus *(S. spencei)* have been recorded from the Spence Shale of Idaho and northern Utah (Resser, 1939; Conway Morris, 1977). Here, further examples of *S. spencei* are illustrated from this latter horizon, an extension of its range as *Selkirkia* sp. to the stratigraphically higher Wheeler Formation is recorded, and *S. willoughbyi* n. sp. from the Marjum Formation and Wheeler Formation is described from material that includes soft-part preservation.

SELKIRKIA WILLOUGHBYI, n. sp.

Figures 4–6

Etymology.—After R. H. Willoughby who made an initial study of some of this material.

Holotype.—Tube with associated soft parts, part and counterpart, KUMIP 204788 (Figs. 4,2,3; 5,1) from the Marjum Formation, locality 347 in the central House Range. It was collected by G. F. Rockers. The specimen is preserved in dark-gray shale associated with organic debris and fragmentary trilobites.

Paratypes.—Other new material (see Figs. 4,1,4–9; 5,2,3) consists of 17 specimens,

KUMIP 144846, 144847–144849 (each part and counterpart), 144850, 144854, 144855, 144858–144861, 144867, 144869, 144870–144873, from the Wheeler Formation, locality 712 in the Drum Mountains, which were collected by Robison. The specimens are preserved in medium-gray, thinly bedded shale that weathers a buff color. The associated fauna on the slabs is restricted to possible worms and a poorly preserved agnostoid trilobite. This locality has also yielded *Selkirkia* sp. (see below), the trilobites *Asaphiscus wheeleri*, *Brachyaspidion sulcatum* and *Olenoides nevadensis*, and the alga *Margaretia* sp.

Description.—Small tubes with smooth external surface; average length about 16 mm. Tubes taper posteriorly, degree of tapering variable; posterior end open. Soft parts poorly preserved; distally tapering spinose proboscis protruding from anterior opening of tube, but apparently capable of retraction; alimentary canal extending length of tube, presumably with terminal anus.

Discussion.—This new species of *Selkirkia* is known from 18 specimens. Of these, six specimens (33 percent) have unequivocal soft parts in association with the tubes. This proportion compares with approximately 20 percent of specimens of *S. columbia* in the Burgess Shale with soft parts. Although the small sample makes the conclusion tentative, the smaller proportion of empty tubes of *S. willoughbyi* may indicate that the tubes had a lower resistance to decay and hence a shorter residence time within the sediment as compared with those of *S. columbia*.

The tubes range in length from about 10.4 to 23.2 mm, with a mean of 16.2 mm. A size frequency histogram (Fig. 6) indicates a more or less symmetrical distribution about the mean, with an absence of certain size fractions presumably due to small sample size. Lack of annulations on the outer wall of the tube, structures that are present in *S. columbia* and *S. spencei* (Conway Morris, 1977), is possibly preservational rather than an original feature. In *S. columbia* the variable degree of tapering of the tube was explained as the result of its having an oval cross section, different configurations ("narrow aspect" and "broad aspect") arising according to the angle of burial of individual specimens to the plane of bedding (see Conway Morris, 1977:37–38). In average-length specimens of *S. willoughbyi*, the ratio between anterior and posterior widths of the most "narrow
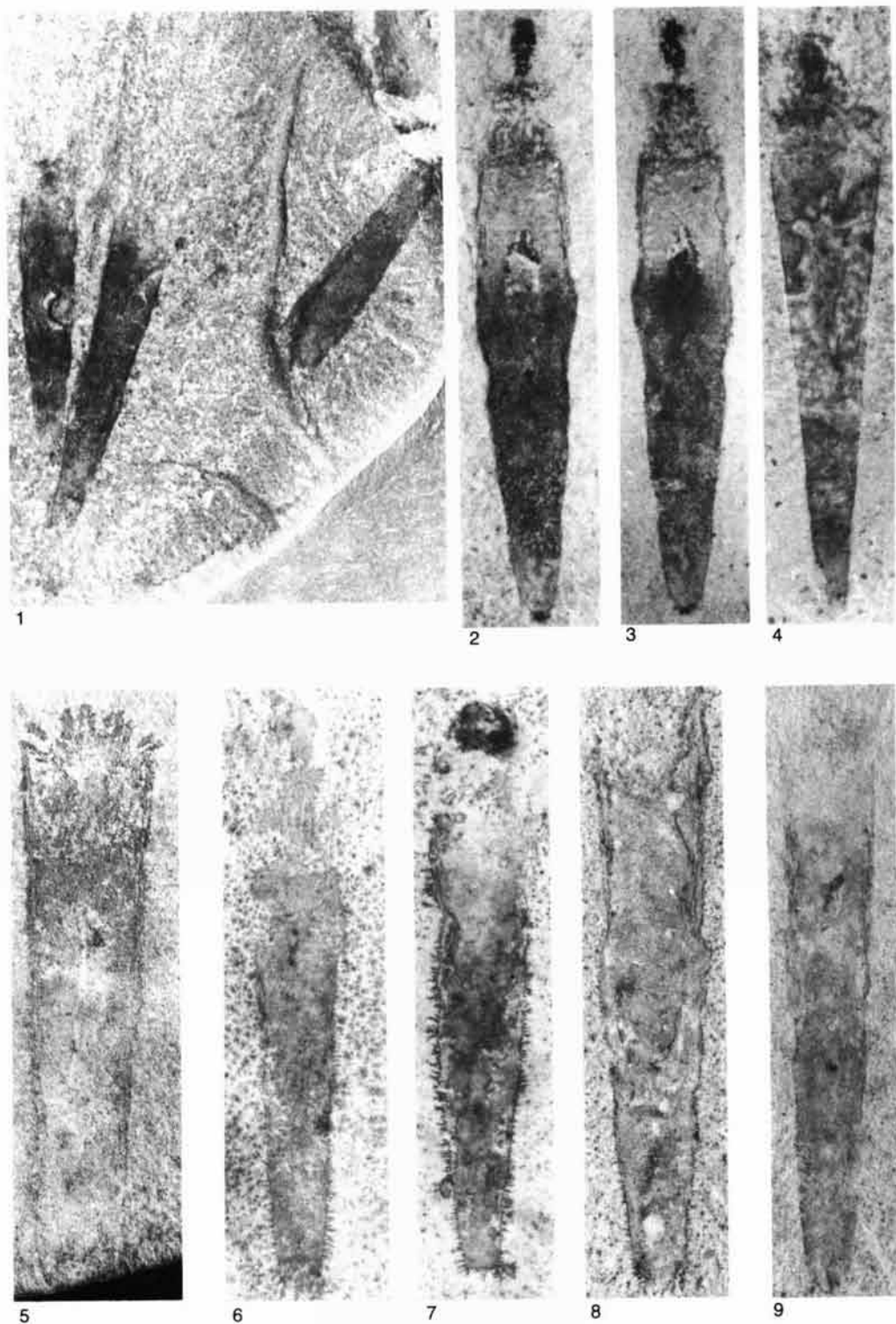
Fig. 4. *Selkirkia willoughbyi* n. sp.; *1, 4-9* from Wheeler Formation, Drum Mountains, locality 712, *2,3* from Marjum Formation, central House Range, locality 347; *1,8,9* photographed dry, *2-4,6,7* photographed under alcohol, *5*
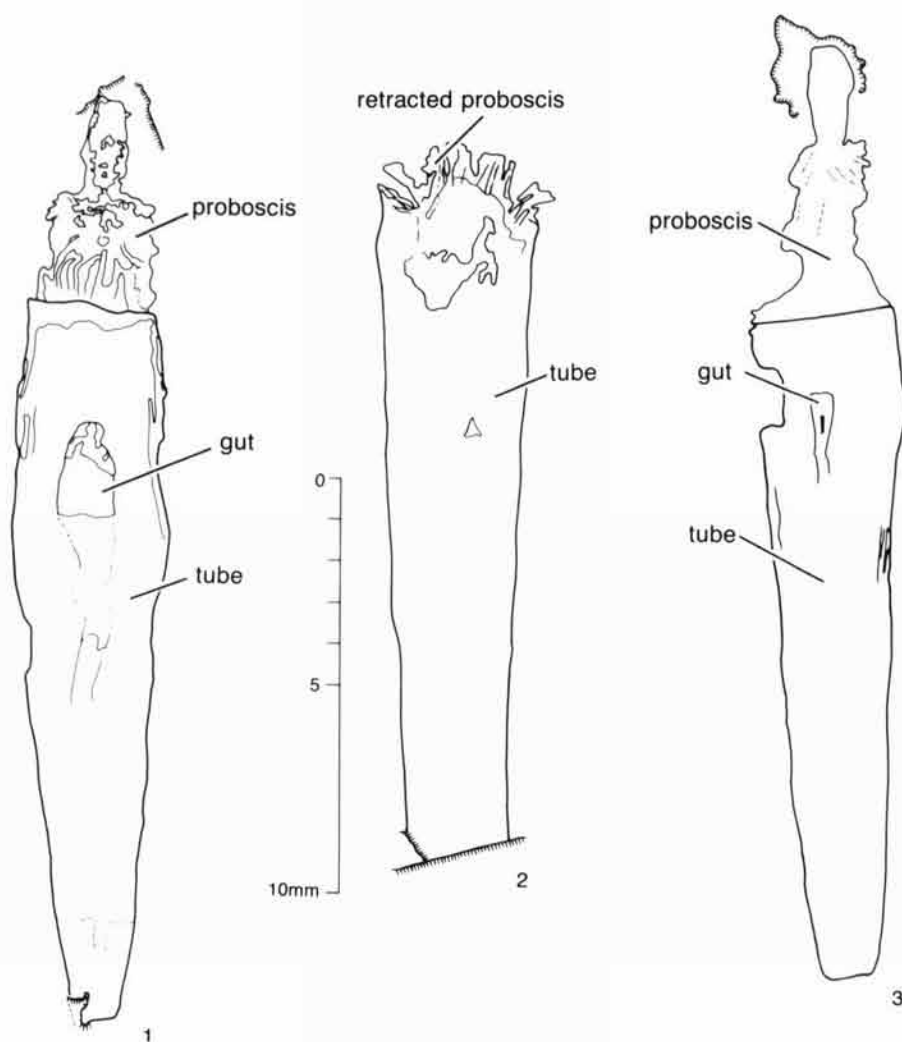
Fig. 5. *Selkirkia willoughbyi* n. sp., explanatory drawings.——*1.* Holotype, part, KUMIP 204778 (compare Fig. 4,*2*).——*2.* KUMIP 144867 (compare Fig. 4,*5*).——*3.* KUMIP 144871 (compare Fig. 4,*6*).

aspect" specimen (KUMIP 144849) is about 1 : 2.1, while the corresponding ratio of the most "broad aspect" specimen is 1 : 3.4 (KUMIP 144870). In comparison, values for *S. columbia* are approximately 1 : 1.7 and 1 : 1.9, respectively, indicating that the tube of *S. willoughbyi* was considerably more compressed in life.

The soft parts are poorly known and do not rival in preservational quality those of *S. columbia* from the Phyllopod bed in the Burgess Shale, but appear to be broadly similar (Figs. 4,*1–6*; 5). An anterior unit that projects from the tube presumably represents the proboscis. The relatively narrow distal part may represent the

photographed under high angle UV radiation.——*1.* Group of subparallel specimens, left and right individuals with poorly preserved soft parts, central individual tube only, KUMIP 144847–144849, ×2.3.——*2,3.* Holotype, part and counterpart, respectively, tube with soft parts, KUMIP 204778, ×4.1.——*4.* Tube with poorly preserved soft parts, KUMIP 144873, ×4.3.——*5.* Tube with partially retracted proboscis, KUMIP 144867, ×5.1.——*6.* Tube with poorly preserved soft parts, KUMIP 144871, ×3.7.——*7.* Tube with questionable soft parts, KUMIP 144872, ×3.5.——*8.* Vacated tube, KUMIP 144855, ×4.1.——*9.* Vacated tube, KUMIP 144854, ×3.7.
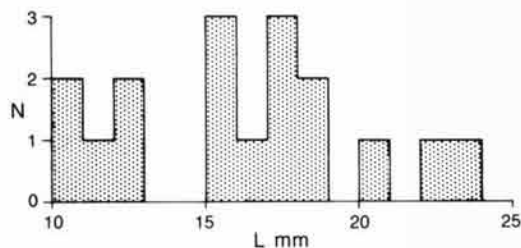
Fig. 6. Size-frequency histogram of tube length (in mm; excluding soft parts) in 17 specimens of *Selkirkia willoughbyi* n. sp. (mean 16.2 mm, SD 3.85).

section that bore the teeth and succeeding terminal cone (division A; see Conway Morris, 1977, pl. 15, fig. 9; pl. 16, figs. 1, 7; pl. 17, fig. 8). The posterior proboscis has a diameter slightly less than the tube and bears structures that appear to represent proboscis hooks, although unlike *S. columbia* there is no clear distinction into divisions B and C (Conway Morris, 1977). Examples of *S. columbia* with the proboscis partially withdrawn into the tube were documented by Conway Morris (1977, pl. 18, fig. 1), and KUMIP 144867 (Figs. 4,5; 5,2) appears to show a comparable condition. Little is known of the soft-part anatomy within the tube, but remains of the intestine can be traced for much of the length of the tube and suggest that the anus was terminal.

Although indifferent preservation of the soft parts hinders comparisons with the type species, the specimens placed in *S. willoughbyi* are regarded as distinct on the basis of tube morphology, in particular the smaller size and the more pronounced tapering that is reflected in differences in the cross section.

The occurrence of *S. willoughbyi* in the uppermost Wheeler Formation and overlying Marjum Formation marks a somewhat higher stratigraphic position (*Ptychagnostus atavus* to *P. punctuosus* zones) than *S. columbia* from the Burgess Shale (*Ptychagnostus praecurrens* Zone). Discovery of the soft parts in specimens of the yet older *S. spencei* would permit some comment on the phylogenetic relationships of the known species of *Selkirkia*.

SELKIRKIA SPENCEI Resser, 1939

Figure 7,3,4

Unlike *S. columbia* from the Burgess Shale, in which approximately 20 percent of the sample has associated soft parts, the specimens of *S. spencei* consist of vacated tubes which presumably had an enhanced preservation potential because of a relatively high resistance to decay and a prolonged residence time in the sediment. Accordingly, the assignment to *Selkirkia* is dependent on overall similarities to the tube of the type species *S. columbia*. As noted by Conway Morris (1977) such a procedure is probably warranted with specific distinction based largely on the degree of tapering of the tube, which in *S. spencei* is so slight that the sides of the tube are subparallel.

New material.—KUMIP 144845 and 144858 are from the Spence Shale, locality 781 in Antimony Canyon north of Brigham City, collected by Lloyd and Val Gunther. They occur in a gray, micaceous, silty shale.

Description.—KUMIP 144858 (Fig. 7,4) is incomplete, owing to rock breakage, but the available length (73 mm; maximum width 11.5 mm) suggests that it exceeded in length the largest known examples of *S. columbia* from the Burgess Shale (about 75 mm; Conway Morris, 1977). KUMIP 144845 (Fig. 7,3) is smaller (29 mm long; maximum width 8 mm), but appears to be broken transversely. Whether this breakage is due to decay processes or other causes (for example, predation) is not clear. In both specimens there is evidence in the form of irregularities along the tube margins to suggest that the wall was originally flexible. As in other specimens of *S. spencei* (Conway Morris, 1977) evidence of annulations comparable to those of *S. columbia* is generally wanting, but very faint traces are present in 144845.

SELKIRKIA sp.

Figure 7,1,2

New material.—SM X7800 (part and incomplete counterpart) and KUMIP 144844 are both from the Wheeler Formation, locality 712 in the

Fig. 7. *Selkirkia* sp. *(1,2)* from the Wheeler Formation, Drum Mountains, locality 712, and *Selkirkia spencei (3,4)* from the Spence Shale, Antimony Canyon, locality 781; *1,2* photographed dry, *3,4* photographed under low angle UV radiation. ——*1.* Tube, KUMIP 144844, ×2.9.——*2.* Tube, incomplete posteriorly, SM X7800, ×2.1.——*3.* Incomplete tube, KUMIP 144845, ×2.5.—— *4.* Tube, incomplete anteriorly, KUMIP 144858, ×2.4.

1   2   4

3

Fig. 7. (For explanation see facing page.)

Drum Mountains. They are preserved on weathered slabs of yellowish-brown shale in association with algal and trilobite fragments. Details of the associated biota are given above.

Description.—SM X7800 (Fig. 7,2) is about 40 mm in length, with a maximum width of 10 mm. Faint traces of annulations are visible in various areas. Measurement of their spacing is difficult, but there appear to be about 10 per mm, which is considerably less than values for *S. columbia.* No soft parts are evident, and the tube appears to have been filled with sediment that has now compacted to a thin layer of shale. There is evidence to suggest that this infill included some trilobite fragments, although elsewhere along the tube superposition has clearly arisen with trilobite debris that was outside the tube. The other specimen (Fig. 7,1) is a complete tube, lacking soft parts, with a length of about 64 mm and a maximum anterior width of 12 mm, tapering posteriorly to 8.5 mm.

Discussion.—These specimens appear to be somewhat more similar to *S. spencei* than to *S. columbia,* and the availability of larger sample size may confirm placement in the former species. Like *S. willoughbyi,* these specimens materially extend the upward stratigraphic range so that *Selkirkia* is now known from a substantial portion of the Middle Cambrian, ranging from the *Peronopsis bonnerensis* Zone (Spence Shale) through the *Ptychagnostus praecurrens* Zone (Burgess Shale) and the *Ptychagnostus atavus* Zone (uppermost Wheeler Formation) to the *Ptychagnostus punctuosus* Zone (Marjum Formation) (see Robison, 1984a). The geographic distribution of *Selkirkia* is comparable to that of *O. prolifica,* with a possible occurrence in the Lower Cambrian of Pennsylvania requiring confirmation (Resser and Howell, 1938; Conway Morris, 1977).

?Phylum ANNELIDA

Class PALAEOSCOLECIDA, new

Diagnosis.—Vermiform metazoans with a papillate epidermis, papillae typically arranged in transverse rows that may be duplicated, the annular arrangement of the papillae probably reflecting metameric segmentation. Jaws may be present, and the alimentary canal is more or less straight with a terminal anus. Geologic range is from Lower Cambrian to Upper Silurian; geographic distribution is cosmopolitan.

Discussion.—*Palaeoscolex* and the closely related *Protoscolex* (see Conway Morris, Pickerill, and Harland, 1982) represent a highly characteristic and relatively diverse (about 9 species) group of Lower Paleozoic worms that together range from the upper Lower Cambrian to the Upper Silurian (reviewed in Conway Morris, 1977; see also Glaessner, 1979). The most conspicuous feature is the papillate surface, with typically double rows of papillae; the possibly papillate worm *Deuteronectanebos papillorum* from the Carboniferous Bear Gulch Limestone (Schram, 1979) appears to be unrelated. Specific differences are based on spacing and number of the papillae and papillate rows, number of segments, and overall dimensions. Much less is known about the internal anatomy. Whittard (1953) described anterior jaws in the type species *P. piscatorum* from the Lower Ordovician of Shropshire, England, while a gut trace has been noted in both this species and *P. ratcliffei* (Robison, 1969). Whittard (1953) proposed that pits associated with the papillae marked the housing of chaetae; if this inference is correct, it would strongly support an annelidan affinity. The oligochaetoid aspect of palaeoscolecidans has elicited comment on their possible role as a stem group of the annelids (Conway Morris, 1977; Runnegar, 1982). Nevertheless, until the presence of chaetae is established, a place within the Annelida cannot be regarded as unequivocal. The presence of jaws is not likely to be a firm indicator of an annelidan relationship, and other fossil worms with scolecodont jaws are known (Schram, 1979) that may not be annelids.

Whittard (1953) erected the family Palaeoscolecidae, while Conway Morris (1977) noted that this might not represent a high enough taxonomic category to encompass adequately this distinctive group. Accordingly the new class Palaeoscolecida is proposed herein. The principal justification for this step lies in the recognition of a shared body plan among the species of *Palaeoscolex* and *Protoscolex* that is distinct from those used to identify other high-level metazoan taxa. The most striking feature of this body plan is the papillate bands that encircle the body. If the presence of chaetae ultimately is confirmed, then this would provide strong support for regarding the Palaeoscolecida as a new and extinct class of the Annelida. However, at present a realistic alternative is that this class belongs to a separate phylum, albeit related to other metameric coelomates.
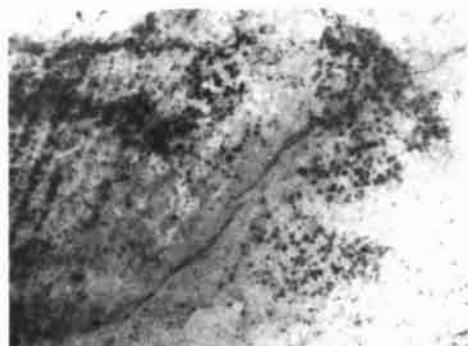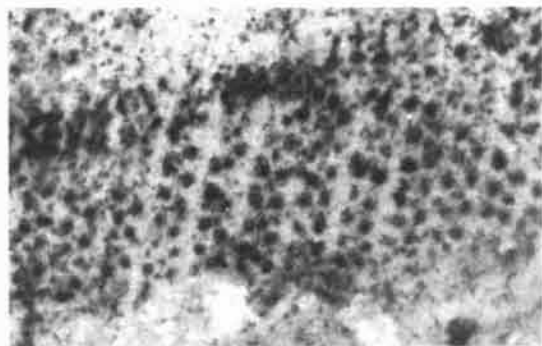
Fig. 8. *Palaeoscolex* cf. *P. ratcliffei*, SM X7802; Murero Shale (Valdemiedes Beds), northeast Spain; *1* photographed dry, *2–4* photographed under alcohol.——*1, 2*. Entire specimen, ×2.8.——*3*. Anterior trunk and questionable head, ×7.6.——*4*. Papillate bands on left posterior, ×14.1.

Family PALAEOSCOLECIDAE Whittard, 1953

Genus PALAEOSCOLEX Whittard, 1953

PALAEOSCOLEX cf. P. RATCLIFFEI
Robison, 1969

Figure 8

New material.—Apparently more or less entire soft-bodied worm, part only, SM X7802, from the Murero Shale (Valdemiedes Beds) in northeast Spain, donated by J. C. Gutierrez.

Description.—The only available specimen (Fig. 8) is from the Middle Cambrian of northeastern Spain. The worm is preserved in fine-grained calcareous silt as a flattened compression, possibly of carbonaceous composition. It is folded upon itself, toward what is interpreted as the posterior end. By the time decay processes had either ceased or been interrupted, the worm may have consisted largely of a bag of cuticle with most of the internal organs destroyed. In such a condition folding would be probably facilitated, and it may be significant that other specimens of *Palaeoscolex* show comparable features (Whittard, 1953, pl. 4, figs. 1–3; Robison, 1969, pl. 138, fig. 1).

The unfolded length of the specimen is about 81 mm. The body tapers only slightly from a maximum width of about 7 mm. Morphological details at either end are obscure. At what is taken to be the anterior end there is a suggestion of a lateral expansion and possibly a broad median cleft (Fig. 8,*3*). Whether this represents a head is most uncertain, as no similar feature has been commented upon in other material of *Palaeoscolex* (Whittard, 1953; Robison, 1969; Glaessner, 1979). Nevertheless, the papillate bands that occupy the remainder of the body do not appear to extend onto this anteriormost region, although irregularly scattered brown spots may represent some original ornamentation. No jaw apparatus is apparent (compare Whittard, 1953).

Almost the entire external surface is occupied by transverse rows of papillae alternating with unarmed bands (Fig. 8,*1,2*). Their oblique trend is not believed to be original and in life they were presumably transverse. Toward the anterior the exact arrangement of the papillae is obscure, possibly because of superposition of both sides of the body. The majority of papillae are preserved in positive relief, and

they extend across the entire body. More posteriorly, however, the lateral regions are separated by a broad median division across which only faint traces of the bands occur. The reason for this smoothness is uncertain, but if it reflects a broad alimentary tract then it is considerably wider than the gut in other species of *Palaeoscolex* (Whittard, 1953; Robison, 1969). In this part of the body the papillae are preserved in positive relief on the left, and as negative impressions (pits) on the right, whereas on the recurved length of the body the sides of negative and positive relief are transposed. This fact suggests that folding of the body also involved twisting through about 180°, a feature consistent with the behavior of largely cuticular remains (Conway Morris, 1977, pl. 12, fig. 8) unless the animal was strongly compressed in life. The transverse shift across the body from positive to negative relief preservation of the papillae is best explained by a jump in the plane of splitting from one side of the animal to the other.

Each papillate band (0.28 to 0.36 mm wide) is separated by an unarmed narrower zone (0.08 to 0.14 mm). There are approximately 24 papillate bands per cm, so that in the specimen their total was about 190. Each papillate band (Fig. 8,*4*) bears two rows of papillae separated by a median zone that is conspicuously darker than the interpapillate band and appears to bear occasional isolated papillae. However, the finer ornamentation of minute pits and median ridges that occupied the intrapapillate zone of *P. piscatorum* (Whittard, 1953) is not evident here, although its absence may be preservational. The papillae are preserved as minute (about 80 μm diameter) hemispherical structures composed of some dark material (compare Robison, 1969). Each transverse band contains about 35 papillae, so that the original ring of papillae probably totaled about 70.

Discussion.—For the purposes of comparison discussion is restricted to similarities between the Spanish specimen and the three species (*piscatorum, ratcliffei, antiquus*) currently assigned to *Palaeoscolex*. The ornamentation of the Spanish specimen most closely resembles the arrangement in *P. ratcliffei*. Whether a morphological pattern similar to the intrapapillate zone of *P. piscatorum* was present originally in *P. ratcliffei* (Robison, 1969) or the Spanish specimen, but has not been preserved, is unre-

Table 1. *Comparative data on* Palaeoscolex.

(Length-width ratio approximate, for worms presumably could contract and elongate considerably. See text.)

	Maximum length: width	Segments per cm	Papillae per ring	Diameter large papillae, μm
P. antiquus	12 : 1	6–20	60	ca. 90–150
P. piscatorum	33 : 1	80–100	60–80	25
P. ratcliffei	25 : 1	30–40	50–80	40–65
Spanish specimen SM X7802	11 : 1	24	70	80–100

solved. It is clear, however, that the ornamentation of *P. antiquus* is rather different (see below). Other data (Table 1) in general support the notion that the Spanish specimen is most similar to *P. ratcliffei* (see also Robison, 1969, table 1). The decision of whether or not it is conspecific, however, is best postponed until additional specimens are available and the extent of intraspecific variation is better understood.

Comparisons between the ornamentation patterns of *P. piscatorum, P. ratcliffei,* and the specimen described here appear straightforward, with the absence of small papillae in zone 2 (Fig. 9) in the latter possibly due to preservational factors. Establishing homologies, however, between the aforementioned species and *P. antiquus* is less easy. The ornamentation of *P. antiquus* consists of single rows of large papillae,

flanked by narrow unornamented zones and bands of much smaller papillae (pustules) (Glaessner, 1979; SCM personal observations on type material). If it is assumed that each of the divisions is equivalent in all species of *Palaeoscolex* then there are a variety of repeat patterns that could correspond by themselves or in multiplicands to segmental units (Fig. 9). However, there seems to be no simple way to homologize the repeat patterns of *P. piscatorum* and *P. ratcliffei* with that of *P. antiquus* without making various effectively *ad hoc* transformations. However, if it is assumed that unornamented bands (zone 3) are in fact absent in *P. antiquus* then the ornamentation pattern in the remaining species could be generated by duplicating zone 1 (large papillae) and interpolating an unornamented band (zone 3). Assuming the various bands were budded from a pygidial
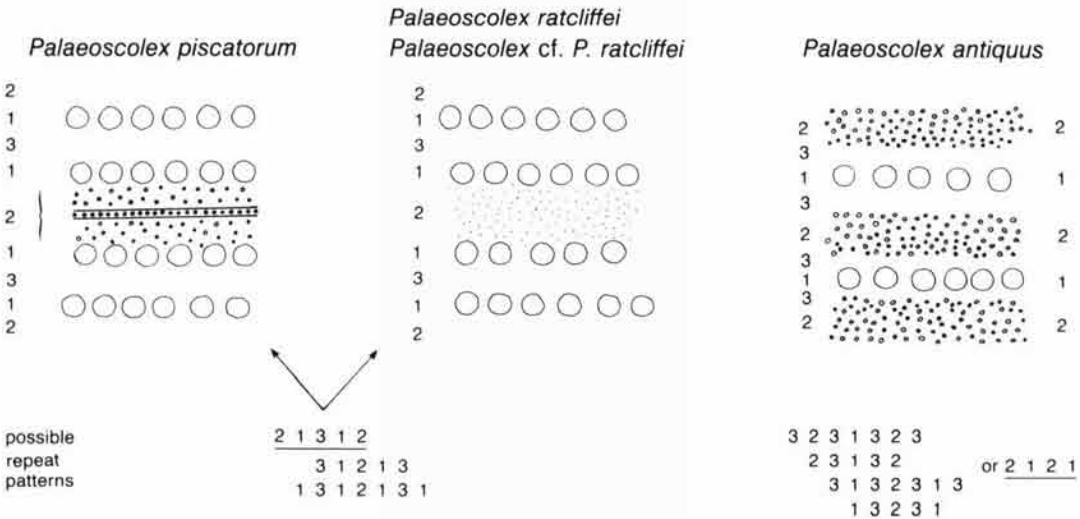

Fig. 9. Ornamentation patterns of papillae on three species of *Palaeoscolex,* and the different repeat patterns that could define metameric segmentation. The underlined repeat patterns are the preferred options.
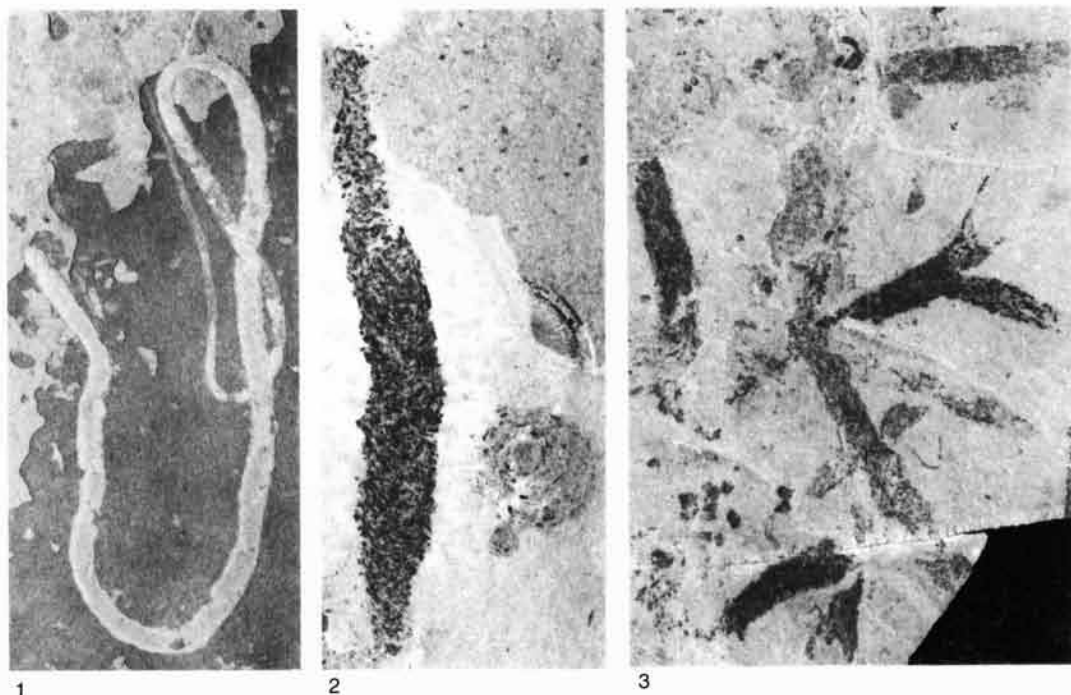
Fig. 10. Trace fossils from the Marjum Formation, House Range localities 347 *(1)* and 811 *(2),* and Wheeler Formation, House Range locality 115 *(3); 1* photographed under high angle UV radiation, *2,3* photographed under alcohol.——*1.* Elongate questionable burrow with some evidence of backfill, KUMIP 204775, ×1.8.—— *2.* Coprolite and possible fecal ball (right), KUMIP 204771, ×1.7.——*3.* Burrows with pellets, KUMIP 204772, ×1.6.

zone, then a small alteration in the sequence of budding presumably involving a genetic change could generate a new pattern.

It is not known whether the papillate bands reflect an underlying metameric segmentation, although this is inferred by both Whittard (1953) and Robison (1969). Whittard (1953) regarded each metamere as being composed of paired papillate and interpapillate bands, whereas Robison (1969) identified the segment boundaries as lying between each papillate band. Glaessner (1979) suggested that in *P. antiquus* the ridge formed on the inner half of the papillate band in curved specimens and "appears to be doubled in places and to mark the boundaries between segments." If these boundaries are correctly identified and the interpolation sequence to produce the observed pattern in *P. ratcliffei* and *P. piscatorum* is accepted, this would imply that the segment boundaries probably lay within the unornamented bands (zone 3) as Robison (1969) sug-

gested. Whatever homologies exist between the ornamentation patterns, the differences between *P. antiquus* and other species must cast doubt on whether the former species should be placed in the genus *Palaeoscolex.* Accepting that a transition in ornamentation occurred, the older stratigraphic position of *P. antiquus* suggests that its ornamentation pattern was primitive, with the derived pattern seen in *P. ratcliffei* and *P. piscatorum* arising near the Lower-Middle Cambrian boundary and persisting to at least the Lower Ordovician.

TRACE FOSSILS AND POSSIBLE SOFT-BODIED REMAINS

Figures 10–11

The importance of trace fossils in paleontology and geology is now well understood (Frey and Seilacher, 1980), and many studies have emphasized their use as indicators of activities of soft-bodied animals that have themselves
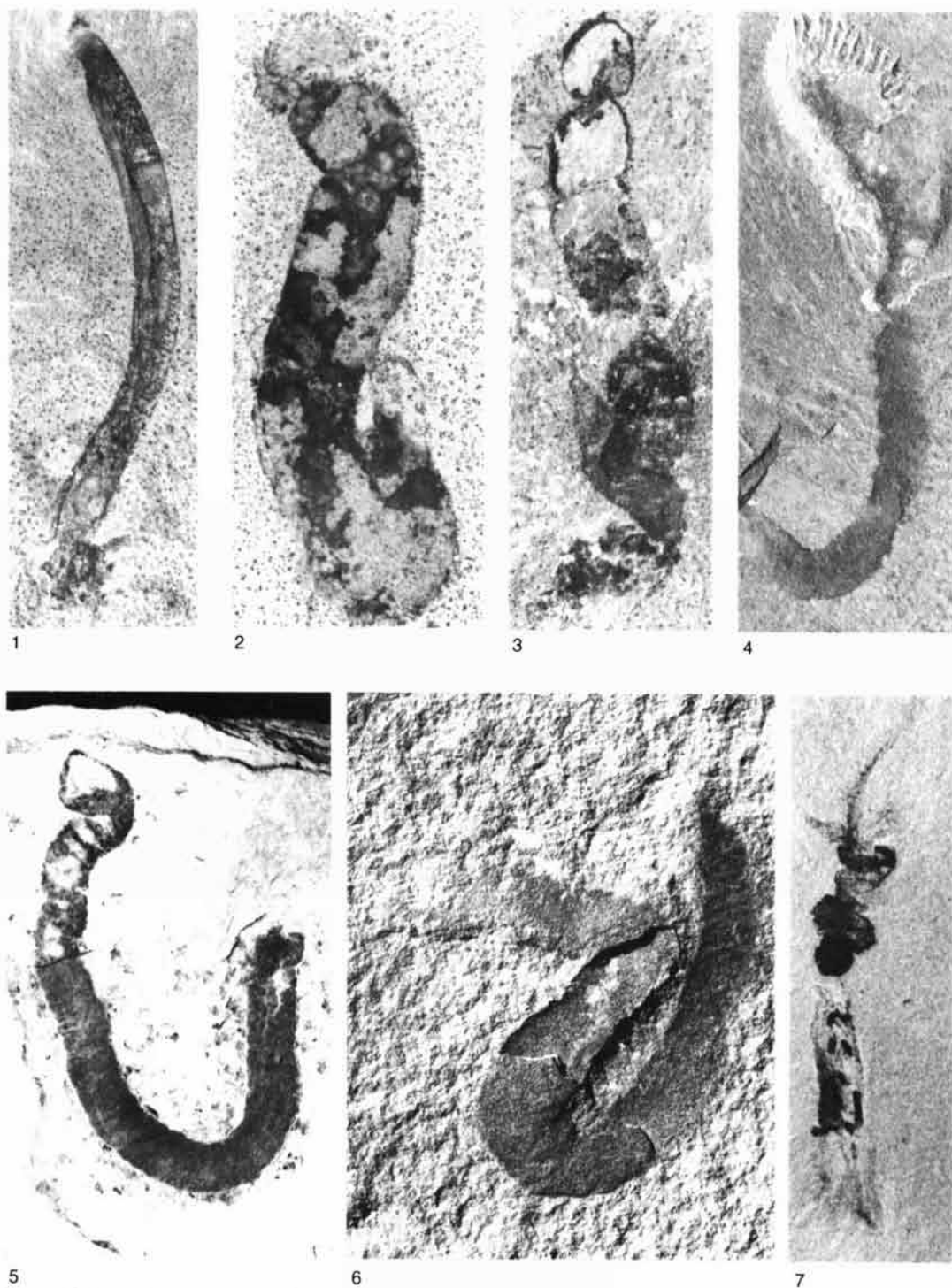
Fig. 11. Indeterminate fossil worms from the Wheeler Formation, Drum Mountains locality 712 (1-4), and Marjum Formation, House Range localities 347 (5) and 811 (6,7); 1,3,6 photographed dry, 2,5,7 photographed under alcohol, 4 photographed under high-angle UV radiation.——1. KUMIP 144852, ×2.8.——2. KUMIP 144875, ×3.5.——3. KUMIP 144863, ×3.8.——4. KUMIP 144853, counterpart, ×3.4.——5. KUMIP 204773, ×4.4.——6. KUMIP 204774, ×4.1.——7. KUMIP 204776, ×1.5.

failed to survive as body fossils. The occurrence of trace fossils in stratigraphic units with soft-part preservation is of special significance because of the possibility of linking trace and maker; however, at none of the localities (347, 712, 781) with preservation of priapulids with soft parts have trace fossils been found that might help confirm their proposed burrowing habits (Conway Morris, 1977). Absence of such traces is consistent with catastrophic burial, as for the Burgess Shale where transport of the fauna has destroyed tracks and burrows.

Brief descriptions of some trace fossils from horizons in which soft-part preservation is also known are given, together with mention of equivocal material that may represent either trace fossils or indeterminate soft-part preservation.

KUMIP 204771, part and counterpart (Fig. 10,*2*) is from locality 811 in the Marjum Formation. An elongate fossil (54 mm long), tapering toward either end from a maximum width of 7 mm, it is crowded with small black structures set in a dark gray groundmass. These structures are of variable size and may represent either pellets or particulate fragments; the latter appears more likely as they tend to have irregular rather than rounded shapes. In places the fragments are arranged in an arcuate fashion that may have arisen during packing. Two alternatives are that the fossil represents either a pellet-filled burrow or a coprolite. While they appear to be uncommon, pellet-filled or lined burrows have been recorded from Lower and Middle Cambrian rocks (Robison, 1969; Nations and Beus, 1974). In the case of the abundant examples from the Spence Shale, Robison (1969) compared them with the Ordovician ichnogenus *Tomaculum*. He suggested these Middle Cambrian examples may have been produced by *Palaeoscolex*, echoing a comparable suggestion by Whittard (1953). The shape of this specimen, however, appears more consistent with a coprolitic origin than a burrow, in which case the particulate structures more likely represent comminuted debris rather than discrete pellets.

Immediately adjacent to this trace is a more or less circular fossil (diameter 11 mm) which has a spiral internal structure defined by scattered elongate flecks of probable carbonaceous matter set in a slightly darker groundmass (Fig. 10,*2*). A small bulbous extension on one side recalls the structures produced in Carboniferous coprolites by escaping gas generated during decay (Zangerl and Richardson, 1963) and it may have had a similar origin. While this fossil could represent a burrow it seems more likely to be a coprolitic fecal ball.

If these trace fossils are accepted as coprolites it is intriguing to speculate upon their origin. The biota of locality 811 contains no obvious candidate in either likely feeding habits or size that appears capable of producing these coprolites. One possible exception is the arthropod *Tuzoia guntheri*, the carapace of which may reach 125 mm in length (Robison and Richards, 1981), or less likely the trilobite *Hemirhodon amplipyge*. Nothing, however, is known of the appendages of *Tuzoia*, and it seems plausible that this assemblage housed a large predator whose rarity and light skeletization minimized its chances of preservation. Other records of Cambrian coprolites (e.g., Matthew, 1891; Durham, 1971; Conway Morris, 1979b) may provide important insights into the activities of early predators (Conway Morris, 1985).

KUMIP 204772 (Fig. 10,*3*) and SM X7801 are more convincing examples of burrow systems lined by more or less oval, possibly carbonaceous pellets. They are also known from locality 115 in the Wheeler Formation where they occur in some abundance, with individual bedding planes strewn with specimens. The burrows are between about 2 and 3 mm wide, and rarely exceed 30 mm in length. There are rare branches, which usually have a slightly narrower diameter than the main stem. The ends of the burrows tend to be rather indeterminate, but rare patches of more poorly grouped pellets suggest these traces had little coherence once abandoned. Within the burrows the pellets form in places very dense accumulations, and more locally show a crude orientation into stringers parallel to the burrow axis. In contrast to the contents of the supposed coprolite, the pellets are rounded and somewhat smaller (about 0.35 to 0.55 mm long, 0.17 to 0.25 mm wide).

These pelleted burrows differ from previously described Cambrian material (Robison, 1969; Nations and Beus, 1974) in being somewhat smaller, showing branching, and containing correspondingly smaller pellets.

Elongate vermiform structures (Figs. 10,*1*;

11) from localities 347 and 811 (Marjum Formation), and 712 (Wheeler Formation) may represent either trace fossils or extensively decayed soft-bodied organisms. Several variants have been recognized, but all lack diagnostic features that would permit confident assignment even to a metazoan phylum. One type (KUMIP 144853, part and counterpart; 144862; 204773, parts only; 204774, part and counterpart) is known from localities 347, 712, and 811 (Fig. 11,*4–6*). It consists of recurved vermiform structures with slight relief that typically show arcuate structures that could be consistent with sediment being packed into either a gut or burrow. Regarding the former alternative some of the specimens resemble examples of the priapulid *Fieldia lanceolata* from

the Burgess Shale in which the alimentary canal is typically sediment filled (Conway Morris, 1977, see especially pl. 28, fig. 4). Another variant is a featureless vermiform structure (KUMIP 144851, 144856) that in some examples possesses prominent transverse constrictions (KUMIP 144863, 144875, 150602; Fig. 11,*2,3*); all specimens are from locality 712. Various other fossils include a relatively slender worm (KUMIP 144852, part only) from locality 712 (Fig. 11,*1*), an extremely elongate (length 13.5 cm) structure (KUMIP 204775, part and counterpart) from locality 347 that may represent a trace fossil (Fig. 10,*1*), and other very poorly preserved material (KUMIP 204776, part only) from locality 811 (Fig. 11,*7*).

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