A MIDDLE CAMBRIAN CHELICERATE FROM MOUNT STEPHEN, BRITISH COLUMBIA

by DEREK E. G. BRIGGS *and* DESMOND COLLINS

ABSTRACT. A recently discovered arthropod, *Sanctacaris uncata* gen. et sp. nov., from the *Glossopleura* Zone, Stephen Formation of Mount Stephen, British Columbia belongs in the Chelicerata. The head shield is wider than long, convex axially, and extends laterally into two flat triangular projections. It bears at least six pairs of biramous appendages. The first five are similar, increasing in size posteriorly and arranged with their inner rami in a raptorial array of inwardly facing, segmented, spinose limbs, accompanied by antenna-like, presumably sensory, outer rami. The outer ramus of the sixth appendage is also antenna-like, but the inner is short and terminates in a fringe of radiating spines. The eyes are at the front of the head shield. The trunk has eleven tergites, each with a convex axis and projecting pleurae. The corresponding somites of the first ten each bear a pair of biramous appendages with an inner segmented spinose ramus and an outer lamellate ramus, fringed with long setae, which functioned in swimming and respiration. The wide flat telson is adapted for stabilizing and steering.

Sanctacaris displays characters which are all derived for some member of the chelicerates. These include: 1, at least six pairs of appendages (the first five raptorial) on the head shield; 2, a cardiac lobe; 3, the division of the body into tagmata comparable to the prosoma and opisthosoma of merostomes; and 4, the anus at the rear of the last trunk segment. Such a combination is unique to the chelicerates. The apparent lack of chelicerae, an advanced character present in all other chelicerates, is consistent with the primitive biramous appendages on both the head and trunk. It places *Sanctacaris* in a primitive sister group of all other chelicerates.

Sanctacaris demonstrates that chelicerates, although rare, were present in Middle Cambrian seas. Moreover, even at this early stage of chelicerate evolution, *Sanctacaris* had the number and type of head appendages that are found in modified form in the eurypterids and xiphosurids, the major Palaeozoic groups that succeeded it.

C. D. WALCOTT's extraordinary discovery, the Middle Cambrian Burgess Shale of Yoho National Park in southern British Columbia, has become celebrated for perhaps the most important biota of soft-bodied organisms known from the fossil record (Whittington 1985). Walcott's material came from a single section on the west side of the ridge between Mount Wapta and Mount Field and was collected from the main quarry in the 'Phyllopod bed' and the smaller Raymond quarry some 23 m above (Whittington 1971). The Burgess Shale section occurs in the lower two-thirds of the Stephen Formation where the basinal shales abut against the steep face of the adjacent dolomite reef of the Cathedral Formation. The conditions necessary for the preservation of the soft parts of the organisms appear to have been controlled by the proximity of this reef front. Away from the reef front the exceptional preservation is less common.

The Burgess Shale was long considered to be a unique occurrence. In 1977 McIlreath demonstrated that the reef front, or Cathedral Escarpment as it is known, could be traced for about 20 km southeast of Walcott's quarry and that the contact between reef and basinal shales cropped out again on Mount Field, Mount Stephen, Mount Odaray, Park Mountain, and Curtis Peak. One of us (D.C.) speculated that more localities of soft-bodied fossils might be found in the basinal shales near these contacts, and, indeed, a few indications were later reported by Aitken and McIlreath (1981) along the line of the Escarpment. In 1981 and 1982 field-work organized by D.C. and involving D.E.G.B. and others led to the discovery of about a dozen new localities (Collins *et al.* 1983).

The most promising of the new localities (locality 9 of Collins *et al.* 1983, fig. 1) occurred in a large *in situ* block of pale grey-blue siliceous shale about 1500 m south-west of the outcrop of the Cathedral Escarpment on the north shoulder of Mount Stephen. This is about 5 km almost directly

south of the Burgess Shale quarries. The site was excavated by a Royal Ontario Museum party in the summer of 1983 when the arthropod described here was discovered (Collins 1986).

The stratigraphic level where the block occurred is characterized by the trilobite, *Glossopleura*, which is the local zone fossil for the basal part of the basinal Stephen Formation (Fritz 1971). In the Stephen Formation section about 1000 m to the north on Mount Stephen measured by Fritz (1971, fig. 6), the top of the *Glossopleura* Zone is 40 m below the level equivalent to the main Burgess Shale quarry. The block excavated was at least 40 m below the top of the *Glossopleura* Zone, so was 80 m or more stratigraphically below the level of the Burgess Shale 'Phyllopod bed'.

The faunal assemblage from the block is dominated by the arthropods, *Alalcomenaeus* and *Branchiocaris*, which are very rare in the Burgess Shale. Many other Burgess Shale animals were found (Collins *et al.* 1983) but not the most common one, *Marrella*. A number of new forms are also present (Collins 1986). It is evident, therefore, that this fauna is distinct from those in the Burgess Shale. It is also older. This is the first of a number of papers describing the animals from the *Glossopleura* faunal assemblage in the Stephen Formation.

Terminology and methods. The morphological terms used in the description are those of Størmer (1955) as far as possible. The orientation of specimens relative to bedding is given as parallel (i.e. dorsoventral) or oblique (Whittington 1971); the restoration (text-fig. 6) is based on the approach described by Briggs and Williams (1981). The explanatory diagrams which face the plates were made from tracings of large colour photographs of the specimens and *camera lucida* drawings using a Wild M7S microscope. The specimens were photographed either immersed in water or dry, with the light directed at about 30° to the horizontal. The direction of illumination was varied where necessary to illustrate different features.

A small amount of preparation was carried out using a needle inserted in a percussion hammer with an adjustable throw driven by a dental drill motor.

Repository. All material is held by the Department of Invertebrate Palaeontology of the Royal Ontario Museum, Toronto (abbreviated ROM).

Preservation. All five specimens are complete and appear to be carcasses rather than moults. A number of lines of evidence suggest that the mode of deposition at this locality on Mount Stephen (locality 9 of Collins *et al.* 1983) was essentially similar to that of the beds in the Walcott quarry (Whittington 1971, 1980), reflecting a similar geological setting. The fossils are likewise preserved in a variety of orientations to bedding, the compacted layers separated by a veneer of sediment, indicating deposition from a turbulent cloud of sediment. The intervening layers of sediment allow the specimens to be prepared in the same manner as those from the Walcott quarry. However, the sediment does not separate as readily from the layers of the specimen and the potential for 'palaeodissection' is consequently more limited. The layers show evidence of fining upward from an erosive base, in the manner of deposits from a density current. There is no evidence of scavenging or much decay and this, together with a lack of bioturbation, suggests that deposition was rapid and that bottom conditions may have been anoxic. Thus, like those excavated in the Walcott quarry, the organisms were deposited in a 'post-slide' environment inimical to life, which was very different to the 'pre-slide' living environment (Conway Morris 1979; Whittington 1980). The Cathedral Escarpment is, at most, 1500 m away from the locality, but the distance or direction of transport is unknown. Allison (1986) has shown that live or freshly killed arthropods can undergo transport over extensive distances (more than 10 km) without significant damage.

SYSTEMATIC PALAEONTOLOGY

Phylum ARTHROPODA
Subphylum CHELICERATA

Taxa of lower rank above genus. Not assigned, plesion (*sensu* Patterson and Rosen 1977), primitive sister group of all other chelicerates.

Genus SANCTACARIS gen. nov.

Derivation of name. Latin *sanctus* (saint; sacred, holy), referring to Santa in Santa Claws, the field name for the holotype of this arthropod (Collins 1986), and *caris* (crab).

Type species. Sanctacaris uncata sp. nov.

Diagnosis. Head shield with pronounced axial convexity and triangular lateral projections; bearing at least six pairs of biramous appendages, first five similar, increasing in size posteriorly and arranged with inner rami in concentric array of inwardly facing, segmented, spinose limbs; sixth inner ramus short, with radiating spines, outer rami antenna-like; eyes situated anterolaterally at front of head shield.

Trunk not subdivided into tagmata, comprised of eleven tergites, first ten each bearing a pair of similar biramous appendages, decreasing in size posteriorly; inner ramus segmented with short spines, outer ramus broad and lamellate with long setae. Anus at posterior of eleventh trunk segment, beneath telson; telson wide, flat, and paddle-shaped.

Geological horizon. Middle Cambrian, Stephen Formation, *Glossopleura* Zone, British Columbia.

Sanctacaris uncata sp. nov.

Plates 71–73; text-figs. 1–6

Derivation of species name. Latin *uncata* (bent inward, hooked, barbed), referring to claws in 'Santa Claws'.

Holotype. ROM 43502, part and incomplete counterpart, Plate 71.

Other material. ROM 43503–43506, part and counterpart.

Diagnosis. As for the genus.

Locality and stratigraphical horizon. Locality 9 of Collins *et al.* (1983, fig. 1), *c.* 7000 feet (2286 m) elevation, 1500 m south-west of the north shoulder of Mount Stephen, British Columbia; 40 + m below top of *Glossopleura* Zone, Stephen Formation.

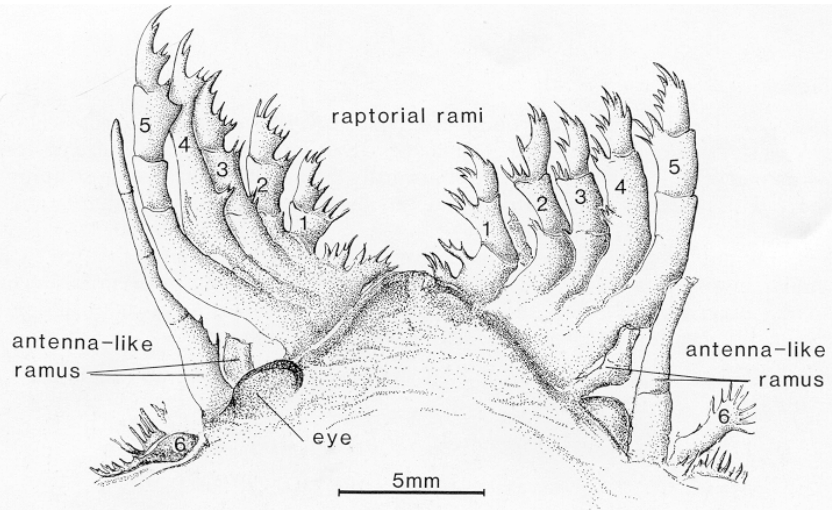*Associated fauna.* Listed in Collins *et al.* (1983, table 1).

Description
Head shield. All five specimens are preserved in parallel or oblique orientation. ROM 43506 (Pl. 73, fig. 5; text-fig. 5) most nearly approaches a lateral aspect, but the outline of the head shield is obscured. Hence the three-dimensional appearance is difficult to restore.
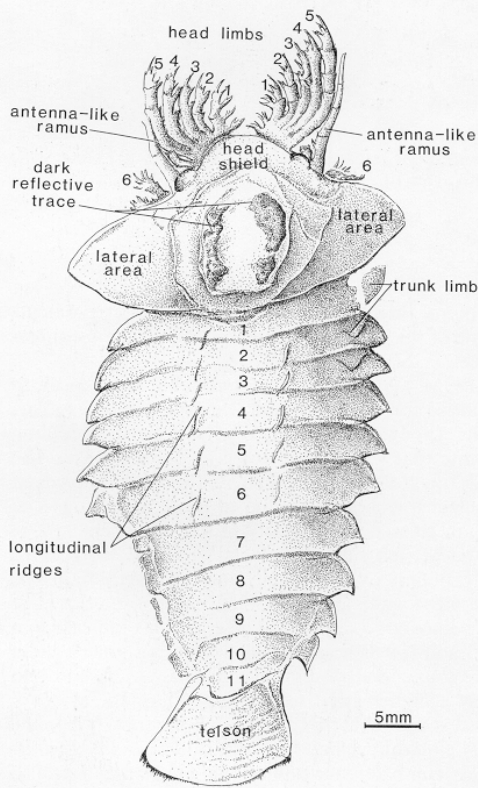
The outline of the head shield in dorsal view is shown by ROM 43505 (Pl. 73, figs. 1 and 2; text-fig. 3). Both the anterior and to a lesser degree the posterior margins are curved convexly. The lateral areas are subtriangular. A pronounced convexity of the axial area is evident in relief, though it has been largely reduced by folding during compaction. The curved compaction wrinkles indicate that the axial region was dome-shaped. The head shield of the holotype, ROM 43502 (Pl. 71, figs 2 and 3; text-fig. 1B), is similar, although the apices of the lateral areas are more acutely angled, and the head shield foreshortened, due to posterior tilting. The strongly convex projection of the front of the head shield can be seen more clearly in this specimen.

The original outline of the lateral areas is best revealed on the left side of the head of ROM 43504. This specimen affords a dorsal view, but is tilted slightly obliquely, mainly by rotation around the longitudinal axis (Pl. 72, figs. 1 and 3; text-fig. 2B). The left lateral area has a more acute apex and a less convex anterior edge than that in ROM 43505 (Pl. 73, figs. 1 and 2), and it lacks compaction wrinkles. These features indicate that the plane of the left lateral area of ROM 43504 (Pl. 72, figs. 1 and 3) was near parallel to bedding when buried. In contrast, the right lateral area of this specimen has a more rounded apex, a more convex anterior edge, and is covered in compaction wrinkles indicating that it was at a higher angle to bedding. Thus, the evidence suggests that the lateral areas were inclined ventrally in life (text-fig. 6). If they had been horizontal (i.e. in the same plane), both right and left lateral areas in ROM 43504 would have had the same outline (angled to the same extent above or below the bedding plane) and similar compaction wrinkles. This interpretation also explains why the apices of the lateral areas of ROM 43505 (Pl. 73, figs. 1 and 2; text-fig. 3), although symmetrical about the axis, are more rounded and less acute than the left lateral area of ROM 43504. In ROM 43503 (Pl. 73, figs. 3 and 4; text-fig. 4) the head shield has been tilted downwards at a high angle to the bedding.

A paired row of dark reflective traces is present on the axial area of three of the specimens. They are most distinct in ROM 43505 (Pl. 73, fig. 2; text-fig. 3) where they occur as paired black spots. Two pairs are distinct and two indistinct. In ROM 43502 (Pl. 71, fig. 3; text-fig. 1B) the traces occur as two irregular black streaks,

raptorial rami

antenna-like ramus

antenna-like ramus

eye

5mm

TEXT-FIG. 1A.

head limbs

antenna-like ramus

antenna-like ramus

dark reflective trace

head shield

lateral area

lateral area

trunk limb

longitudinal ridges

telson

5mm

TEXT-FIG. 1B.

EXPLANATION OF PLATE 71

Figs. 1–3. *Sanctacaris uncata* gen. et sp. nov., holotype, ROM 43502, dorsal view. 1, counterpart (text-fig. 1A), ×4, dry, appendages projecting beyond the head shield, illuminated from the north: 2 and 3, part (text-fig. 1B), ×1·5; 2, immersed in water, showing structures beneath the dorsal exoskeleton; 3, dry, showing relief, illuminated from the north-west.
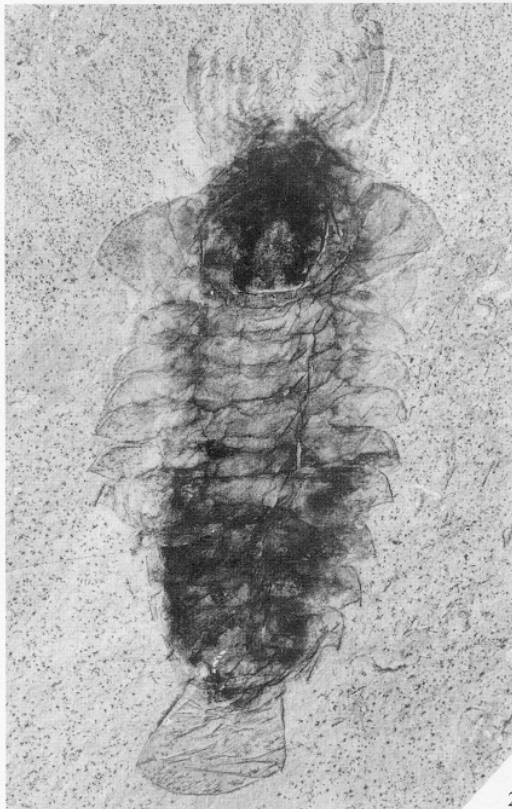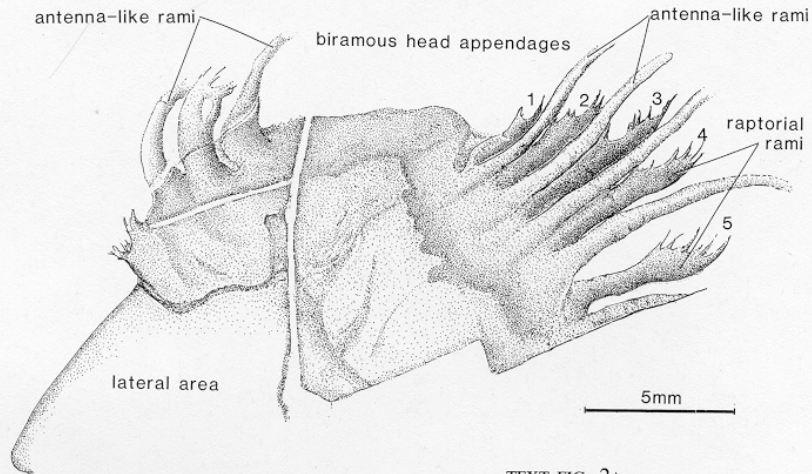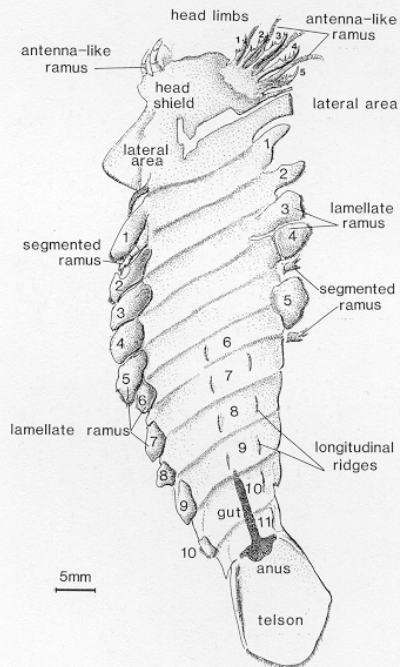
PLATE 71
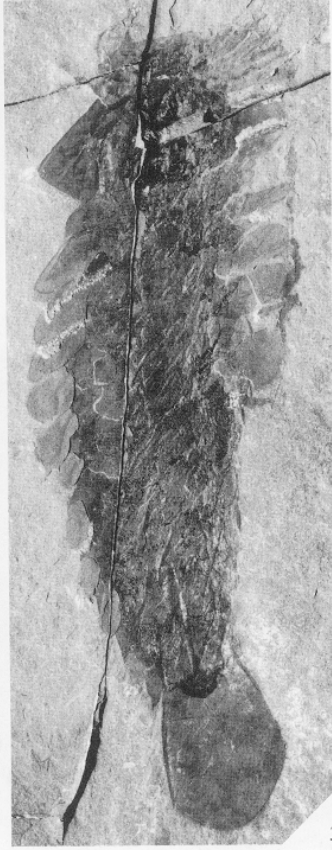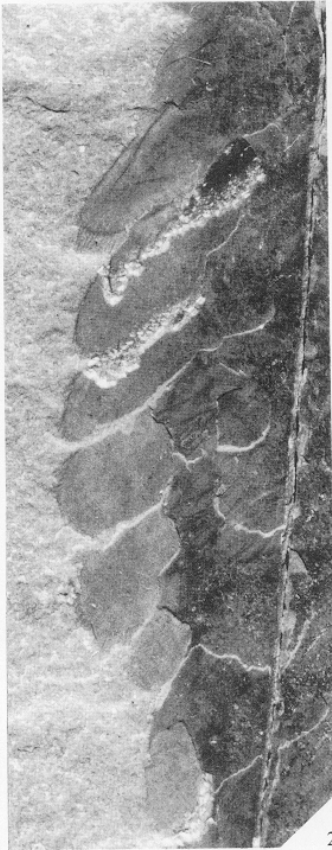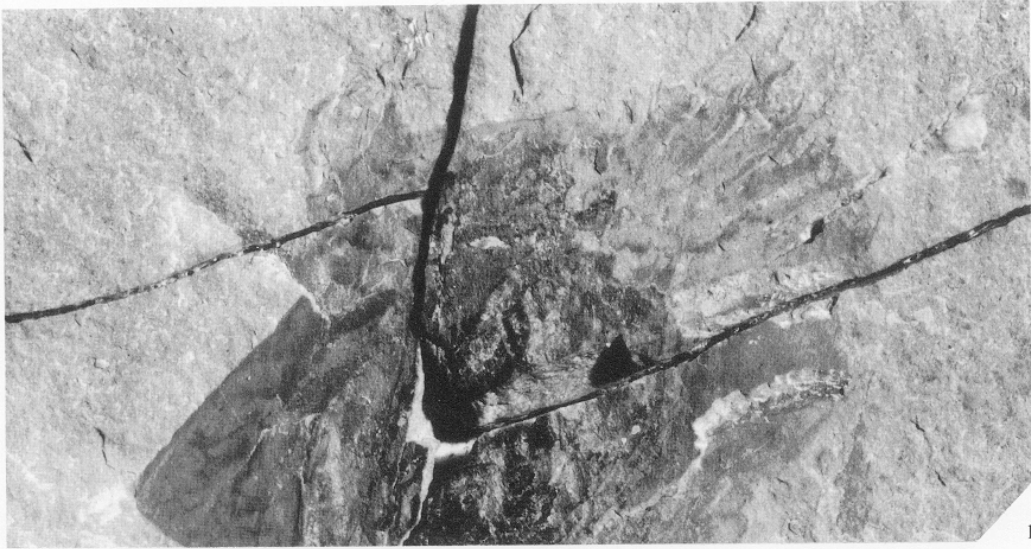

BRIGGS and COLLINS, *Sanctacaris*

TEXT-FIG. 2A.

TEXT-FIG. 2B.

EXPLANATION OF PLATE 72

Figs. 1–5. *Sanctacaris uncata* gen. et sp. nov., ROM 43504, oblique dorsal view, part (text-fig. 2A, B). 1, × 3·5, dry, appendages projecting on both sides beyond the head shield, illuminated from the north-east. 2, × 2·5, dry, segmented ramus of left trunk appendage 1, lamellate rami of 1 to 7, illuminated from the north. 3, × 1·25, dry, illuminated from the north-east. 4, × 2·25, dry, segmented rami of right trunk appendages 4 and 5, flanking lamellate ramus of 5, illuminated from the north-west. 5, × 3, immersed in water, telson and dark stain beyond anus.

PLATE 72
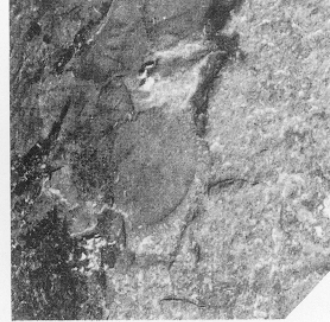
BRIGGS and COLLINS, *Sanctacaris*

and they are even more indistinct on the head shield axis of ROM 43504 (Pl. 72, figs. 1 and 3). The occurrence of streaks rather than distinct spots may be the result of greater distortion of the head shields of ROM 43502 and 43504, compared to that of ROM 43505. Similar dark traces have been interpreted as muscle attachment sites in the heads of synziphosurines (Eldredge 1974), where they are equivalent to the cardiac lobe, and in phacopine trilobites (Eldredge 1971).

Head appendages. The head appendages are best preserved on the holotype, ROM 43502 (Pl. 71, fig. 1; text-fig. 1A). Five pairs of spinose, raptorial limbs are evident curving forward from below the head shield, flanked by two pairs of antenna-like structures. The outer pair of the two is more completely preserved; the structures are elongate and slender and both right and left show large isolated proximal spines. Outside these antenna-like structures two paired projections with radiating spines at the end extend a short distance beyond the margin of the head shield. The five raptorial limbs are arranged in series, each pair increasing in length and lying below and outside that preceding it. The number of segments in the limbs increases from at least four in the first to eight or more in the fifth. The limbs are otherwise similar in structure, the terminal segment bearing three inwardly curving spines, the more proximal segments bearing projecting bundles of three or more inwardly-angled spines. A similar radiating spread of head appendages is evident in dorsal view on ROM 43505, but they are poorly preserved and details are difficult to discern (Pl. 73, fig. 1; text-fig. 3).

A different view of the head appendages is provided by ROM 43504. Those of the right side are straight and inclined anterolaterally (Pl. 72, fig. 1; text-fig. 2A). Five raptorial limbs, presumably equivalent to those in ROM 43502, are preserved. In addition, five antenna-like limbs, similar to those flanking the raptorial limbs in ROM 43502, are evident, suggesting that a raptorial limb and an antenna-like limb together make up a biramous appendage. No further limb elements can be seen on the right side of ROM 43504. The left head appendages are strongly curved and overlapping. They show the antenna-like ramus lying outside the raptorial one indicating its probable relative position in the biramous appendage (Pl. 72, fig. 1; text-fig. 2A).

Poorly preserved head appendages incline anteroventrally from the head of ROM 43506 (Pl. 73, fig. 5; text-fig. 5) in a similar orientation to those on the right side of ROM 43504.

The structure and arrangement of the first five pairs of appendages in the head are clear. They are biramous, the raptorial rami facing inwards and presumably bearing gnathobases proximally, the antenna-like rami flanking them on the outside. They appear to have been attached parallel to the mid-line: an indication of a narrow gap between the limb bases, in which the mouth was presumably situated, is present in ROM 43502, particularly in the frontal projection (Pl. 71, figs. 1 and 2).

The arrangement of the structures preserved outside the raptorial limbs in ROM 43502 is more problematic. On the counterpart (Pl. 71, fig. 1; text-fig. 1A), the outer, antenna-like ramus is seen to converge with a short projection fringed with radiating spines or setae, on both sides of the head. Together, the two structures seem to comprise a biramous sixth head appendage. If this is so, then the pair of antenna-like structures just inside the outer pair probably belong with the fifth raptorial limb, and, at least on the left side, appear to curve beneath the head shield parallel to it. Lastly, a small array of spines lies beneath the short spiny projection on both sides of the head. Unfortunately, the rest of this structure is concealed by the head shield, so it is not clear whether it is a third ramus of the sixth appendage or belongs to a seventh. However, whatever the interpretation of the structures outside the raptorial limbs, it is evident that *Sanctacaris* has at least six pairs of biramous appendages in the head.

Eyes. ROM 43505 preserves a well-defined dark rounded structure on the left side of the head shield (Pl. 73, figs. 1 and 2; text-fig. 3), just abaxial of the appendages, which is probably an eye. A narrow marginal rim recalls the eyes of *Odaraia* (Briggs 1981) and other Burgess Shale arthropods. A similar round structure with a marginal rim occurs in the same position at the front of the head shield on the right side of ROM 43502, best seen on the counterpart (Pl. 71, fig. 1; text-fig. 1A). A matching, but less distinct, structure occurs on the left side, also seen best on the counterpart. None of the other specimens preserves clear evidence of eyes, but they could be concealed in the matrix.

Trunk. The trunk consists of eleven tergites (presumably corresponding to somites) and a telson (Pl. 71, figs. 2 and 3; text-fig. 1B). The first five increase in length slightly; tergites 6 to 11 are very similar in length. The trunk widens slightly to the fourth tergite, then tapers gradually to the eleventh. The dimensions of the tergites provide no obvious basis for a subdivision of the trunk (into thorax and abdomen, or pre- and postabdomen, for example). The axial area of the trunk, like that of the head, shows a pronounced convexity which has been reduced in large measure by folding during flattening. Short longitudinal ridges, one pair per tergite, define an axis along the centre of this raised area (Pl. 71, fig. 3; text-fig. 1B; Pl. 73, fig. 4; text-fig. 4). The pleurae are

similar in width to the raised area. The anterior margin of each pleura curves posteriorly at its lateral extremity to meet the posterior margin at a high angle. A well-defined narrow ridge runs parallel to the lateral and anterior margin of each pleura delimiting a narrow, steeply sloping border (Pl. 71, fig. 3; text-fig. 1B). The trunk was evidently flexible to some degree as indicated by the curvature in ROM 43505 (Pl. 73, fig. 2; text-fig. 3).

Evidence of the alimentary canal is limited. A dark linear trace, slightly concave in section, is preserved along the axis of the posterior somites in ROM 43504. The relief trace terminates in the posterior margin of the last trunk somite, presumably at the anus, but the dark trace expands in the anterior part of the telson (Pl. 72, figs. 3 and 5; text-fig. 2B), probably representing seepage of organic material from the anus. Similar dark stains occur at the posterior of other arthropods from the Burgess Shale. A relief trace in the eleventh somite of ROM 43506 also extends just into the telson (Pl. 73, fig. 5; text-fig. 5). Thus the anus lies at the posterior margin of the eleventh segment, presumably beneath the insertion of the telson. The dark reflective material in the axial area of the head shield of ROM 43506 may be the remains of the contents of the stomach (Pl. 73, fig. 5; text-fig. 5). A similar dark trace occurs in the head shield and first trunk segment in ROM 43503 (Pl. 73, fig. 3; text-fig. 4).

Trunk appendages. Traces of the trunk appendages are evident on all the specimens, but only ROM 43504 (Pl. 72, figs. 2-4; text-fig. 2B) preserves much detail of their morphology. Each segment, with the probable exception of the last, bears a pair. The most obvious preserved structure of these appendages is a flat lamellate ramus. Its outer anterior border is gently convex, the rest of the margin more strongly so and fringed with long setae. These setae are also evident in ROM 43503 (Pl. 73, fig. 3; text-fig. 4) as lineations on the overlapping lamellate rami of the ventrally exposed posterior segments. The flat lamellate rami in ROM 43504 form a graded series, with the largest at the front (Pl. 72, figs. 2 and 3; text-fig. 2B). Their arrangement beneath the front trunk segments can be seen in ROM 43502 (Pl. 71, fig. 2; text-fig. 1B). In this specimen, the lamellate ramus of the first right trunk segment appears to be much larger than the succeeding ones, but this disparity in size is not evident in the other specimens. A second ramus, spinose and segmented, is evident in association with some of the lamellae in ROM 43504 (Pl. 72, figs. 2 and 4) and ROM 43503 (Pl. 73, fig. 4), although the outline in the latter is very faint. Attempts to reveal details of this ramus by removing parts of the overlying lamellae have been moderately successful. The segmented ramus between left lamellae 1 and 2 of ROM 43504 reveals the most detail (Pl. 72, fig. 2). The articulations between the three or four distal podomeres are evident, and the limb bears elongate spines on the posterior preserved margin.

The lamellae are preserved extending beyond the margin of the pleurae in ROM 43504, and overlapping anteriorly (Pl. 72, figs. 2 and 3; text-fig. 2B). In ROM 43506 (Pl. 73, fig. 5; text-fig. 5) they overlap posteriorly. This contrast is a function of the configuration of the limbs and the attitude of the specimens to bedding. A similar difference in overlap occurs in the outer rami of the trunk limbs of the Burgess Shale crustacean, *Canadaspis perfecta*, for example. In specimens in parallel or parallel-oblique aspect they are preserved overlapping anteriorly; in lateral aspect they overlap posteriorly (compare Briggs 1978, figs. 83 and 116 with figs. 111 and 115).

The outlines of both left and right lamellae in the first five trunk limbs of ROM 43504 (Pl. 72, figs. 2 and 3; text-fig. 2B) form a graded series. The first is tilted at a relatively high angle to the bedding and is folded and foreshortened (particularly evident on the right side). The following lamellae are oriented progressively more nearly parallel to bedding and consequently their apparent size increases as foreshortening decreases. However, this variation cannot be explained simply as the result of curvature of the trunk, with successive lamellae maintaining the same attitude to the rest of the body (the trunk would have to curve dorsally to account for the variation in this way). Instead, the attitude of the appendages may reflect successive positions in the backward swing of the limb (cf. Briggs 1978, p. 463). Beyond appendage 5 only the left limbs are exposed and the degree to which they extend beyond the pleurae is much reduced (Pl. 72, fig. 3; text-fig. 2B). Their outline appears to progressively narrow and this may represent foreshortening (perhaps as they are swung forward in a recovery stroke). The trunk appendages of ROM 43506 (Pl. 73, fig. 5; text-fig. 5) may also reflect different positions during a metachronal swimming wave. The first pair are swung backward as if in a propulsive stroke; the more posterior limbs are swung forward as in a recovery stroke.

The segmented rami that are evident in ROM 43504 (Pl. 72, figs. 2 and 4) appear to belong with the lamellate outer ramus lying immediately in front of them. This is suggested by the relative levels and preserved overlap of the appendages. If the segmented ramus belonged with the lamella behind it, this would imply that the lamellae lay posterior and adaxial of the segmented rami and were interleaved between them, which seems unlikely on functional considerations. In life the segmented ramus would have been adaxial to the lamellate ramus.

TEXT-FIG. 3.
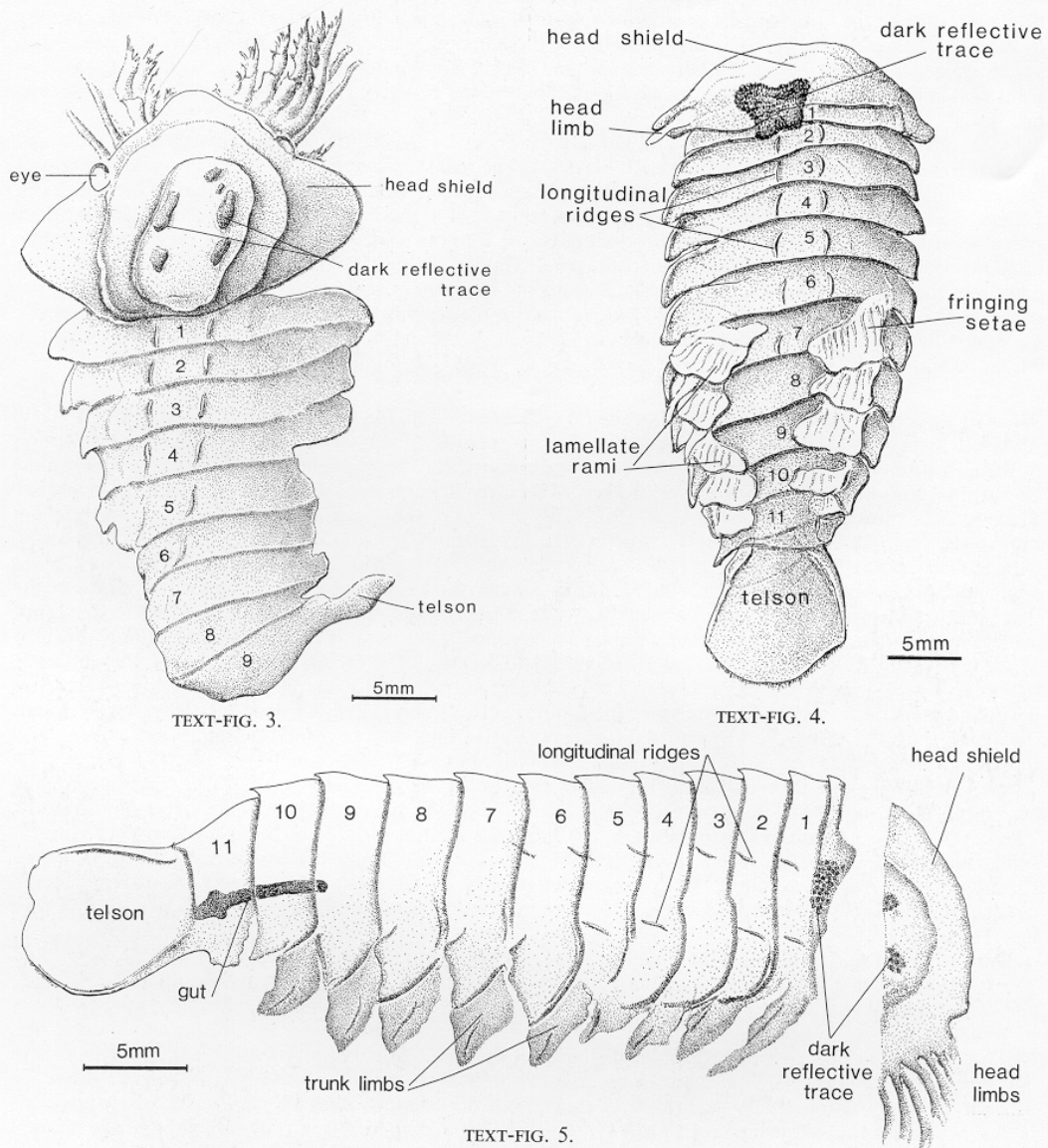
TEXT-FIG. 4.

TEXT-FIG. 5.

EXPLANATION OF PLATE 73

Figs. 1–5. *Sanctacaris uncata* gen. et sp. nov. 1 and 2, ROM 43505, dorsal view (text-fig. 3); 1, counterpart,
×3·2, dry, head shield, appendages projecting beyond it, and eye, illuminated from the south-west; 2, part,
×2, dry, showing reflective spots on head shield, and body flexure, illuminated from the east. 3 and 4, ROM
43503, ventral view of dorsal exoskeleton, counterpart (text-fig. 4), ×2; 3, immersed in water, showing setae
fringing lamellate ramus of trunk limbs which are adhering to dorsal exoskeleton; 4, dry, showing relief,
illuminated from the north-west. 5, ROM 43506, oblique view of right side, part (text-fig. 5), ×2·6, immersed
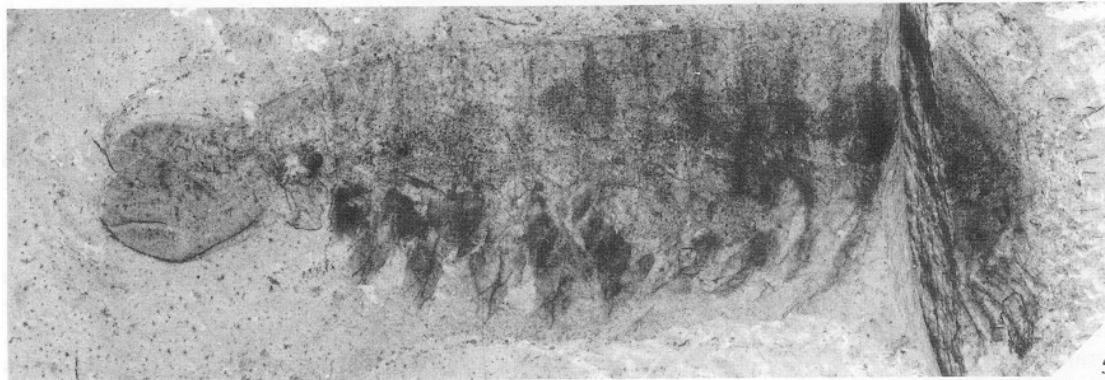in water.

PLATE 73
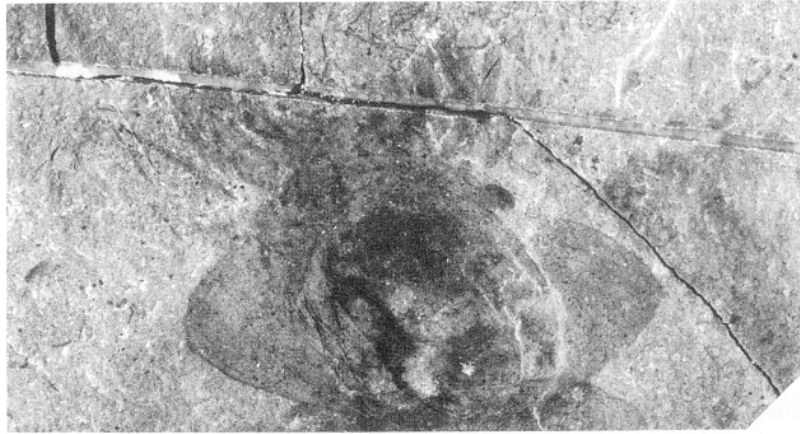
BRIGGS and COLLINS, *Sanctacaris*

Telson. The telson widens posteriorly, the lateral margins roughly straight and paralleled by a ridge demarcating a narrow sloping border, as on the pleurae (Pl. 71, fig. 3; text-fig. 1B; Pl. 73, fig. 4; text-fig. 4). The posterior margin is convex posteriorly and fringed by very short spines or setae. The lateral aspect is unknown, but the telson was presumably dorsoventrally flat in life, i.e. paddle-like.

Size. Size is difficult to assess accurately due to the effects of compaction at different orientations to the bedding (the length of ROM 43502 (Pl. 71, figs. 2 and 3), for example, is clearly reduced by foreshortening). ROM 43504 (Pl. 72, fig. 3) is probably the largest individual and is about 93 mm long (measured along the curved axis from the anterior border of the head shield to the posterior of the telson). ROM 43506 (Pl. 73, fig. 5) is probably the smallest with a length of 46 mm.

DISCUSSION

Generic assignment

The two genera to which *Sanctacaris* shows closest similarity are *Alalcomenaeus* Simonetta, 1970 and *Actaeus* Simonetta, 1970. The sole definitely assigned species of *Alalcomenaeus*, *A. cambricus*, occurs at the same locality as *S. uncata* (locality 9 of Collins *et al.* 1983) and therefore the possibility that the two are conspecific requires particular consideration. *A. cambricus* is rare in the Burgess Shale (Whittington 1981) but a large collection from locality 9 is presently under study. This shows that it has eleven trunk tergites following the head shield (Briggs and Robison 1984, p. 156) not ten as reconstructed by Simonetta (1970) or twelve as reconstructed by Whittington (1981), and a flat paddle-like telson ('terminal plate' of Whittington 1981), all characters shared with *S. uncata*. Hou (1987) tentatively referred a new arthropod from the Lower Cambrian of Chengjiang, eastern Yunnan, which appears to have twelve trunk tergites, to *Alalcomenaeus* (as *A.? illecebrosus*). *Actaeus armatus*, which is based on a single poorly preserved specimen from the Burgess Shale (Whittington 1981), is similar in many ways to *Alalcomenaeus cambricus*.

Sanctacaris differs from *Alalcomenaeus* and *Actaeus* in a number of important respects. It has at least six pairs of head appendages, of which the first five are raptorial and similar to each other. *Alalcomenaeus* and *Actaeus*, in contrast, have only four pairs of head appendages. The first of both is very distinctive, with a broad base and elongate distal extension that may be twofold; the remainder of the head appendages are essentially similar to those of the trunk, whereas those in *Sanctacaris* differ greatly from the trunk appendages.

The outline of the head shield is poorly displayed in the specimens of *Alalcomenaeus* and *Actaeus* known from the Walcott quarry (Whittington 1981), but they preserve no evidence of the subtriangular lateral projections characteristic of *Sanctacaris*. This is borne out by dorsoventrally compacted specimens of *Alalcomenaeus* from locality 9 on Mount Stephen (Collins *et al.* 1983) which show the head shield to have a trapezoidal outline. The telson of *Sanctacaris* is relatively larger than that in *Alalcomenaeus*. The outline of the telson in *Actaeus* is unknown.

Leanchoilia superlata is similar to *S. uncata* in possessing a head shield, followed by eleven trunk tergites and a spinose telson. The head of *Leanchoilia*, however, bears a pair of great appendages followed by two pairs of biramous limbs similar to those of the trunk (Bruton and Whittington 1983). This contrasts with the head of *S. uncata* which bears a series of at least six pairs of appendages that are very different from those of the trunk.

The differences between *S. uncata* and previously described taxa are thus clearly sufficient to warrant the erection of a new genus and species.

Functional morphology

The formidable array of inwardly facing raptorial limbs at the front leaves no doubt that *Sanctacaris* was a predator. The arrangement of the raptorial limbs in a graded series with the smallest on the inside and succeeding larger ones around and below, indicates that they functioned as a unit, grasping prey below and to the front (i.e. *Sanctacaris* probably fed on bottom dwellers). It seems likely that the raptorial limbs were equipped with gnathobases that aided in comminuting food and

pushing it into the mouth. It is possible that they were also ambulatory, like the walking legs on the prosoma of eurypterids. The antenna-like outer ramus on each head appendage was probably sensory; a sensory function was attributed to a similar ramus in the head appendages of *Burgessia* (Hughes 1975). The short, spine-fringed ramus on the sixth appendage (Pl. 71, fig. 1; text-fig. 1A) probably had a sensory function, too, although it may also have been used in grooming.

The large flap-like rami of the trunk appendages and the paddle-shaped telson both indicate that *Sanctacaris* was an active swimmer. The broad rami would have provided propulsion, moving in metachronal rhythm, whereas the telson would have provided lift and steering in the vertical plane. Steering in the horizontal plane would have been achieved mainly by differential movement of the lamellate trunk limbs on either side of the body. The long fringing setae would have increased the effective area of the rami in the propulsive stroke, and been folded back during the recovery stroke. Presumably, movement of the broad rami through the water also helped in respiration. It is unlikely that *Sanctacaris* used its telson for forward propulsion. This kind of swimming is unusual in arthropods (see Lochhead 1961, for example) and *Sanctacaris* would have been inhibited in up and down flexing of the trunk by the large tergites and the overlap between them. Furthermore, *Sanctacaris* lacks the narrow trunk near the tail that is characteristic of animals using caudal fin propulsion (Webb 1975, 1984; Plotnick and Baumiller (1988) apply similar arguments to the function of the telson of pterygotid eurypterids). Conceivably, *Sanctacaris* could have moved rapidly backwards to escape from predators by flexing its trunk and tail as some crustaceans such as shrimps do today. ROM 43505 shows evidence of ventral flexure (Pl. 73, fig. 2; text-fig. 3). The segmented ramus on the inside of the trunk appendages may have been ambulatory; if so, its distal spines would have provided better footing on the bottom, and may also sometimes have helped in capturing prey.

In addition to steering, the broad telson would have helped to stabilize *Sanctacaris*. As Lochhead (1961) pointed out for crustaceans 'the most usual method of controlling rotations around the transverse axis is by the action of a flattened structure at the end of the abdomen'. The two large triangular lateral areas on the head would also have provided stability.

AFFINITIES AND CLASSIFICATION

The discovery of *Sanctacaris* adds a further major type to the arthropods with preserved appendages known from the Middle Cambrian of British Columbia. Most of these, however, cannot be classified in any of the four major groups. Indeed, of the twenty genera with well-preserved appendages described from the Burgess Shale, none is assigned to the chelicerates or uniramians, three are assigned to the trilobites, one to the crustaceans, and sixteen are 'not placed in any phylum or class of Arthropoda' (Whittington 1985, p. 138).

Compared to their modern counterparts, most Burgess Shale arthropods can be seen from their morphology to be at the primitive end of the spectrum: a high proportion have 'short' heads with few appendages (seven have three or fewer); in many the posterior head appendages are the same as those of the trunk; about half have undifferentiated biramous trunk limbs. These Middle Cambrian arthropods fall into three categories. First, some are not sufficiently advanced morphologically to be included in any of the major groups; *Marrella*, for example, is primitive enough to have given rise to any of them. Secondly, others like *Yohoia* and *Branchiocaris* have a body plan or specialized appendages which exclude them from the trilobites and major living groups—indeed they are arguably sufficiently advanced to represent separate taxa of equivalent rank. Thirdly, a small number can be assigned to the living groups, although some of the features which characterize their Recent descendants have yet to evolve. *Canadaspis*, for example, can be assigned to the crustaceans, even though it retains some primitive features: the inner rami have a very large number of podomeres (up to fourteen) and the posterior head appendages are little differentiated from those of the trunk (Briggs 1978, 1983). *Sanctacaris* likewise, although it can be assigned to a living group, the chelicerates, retains some strikingly primitive features. Thus the Middle Cambrian arthropods comprise a much wider morphological spectrum than the three distinct major groups of arthropods living today.
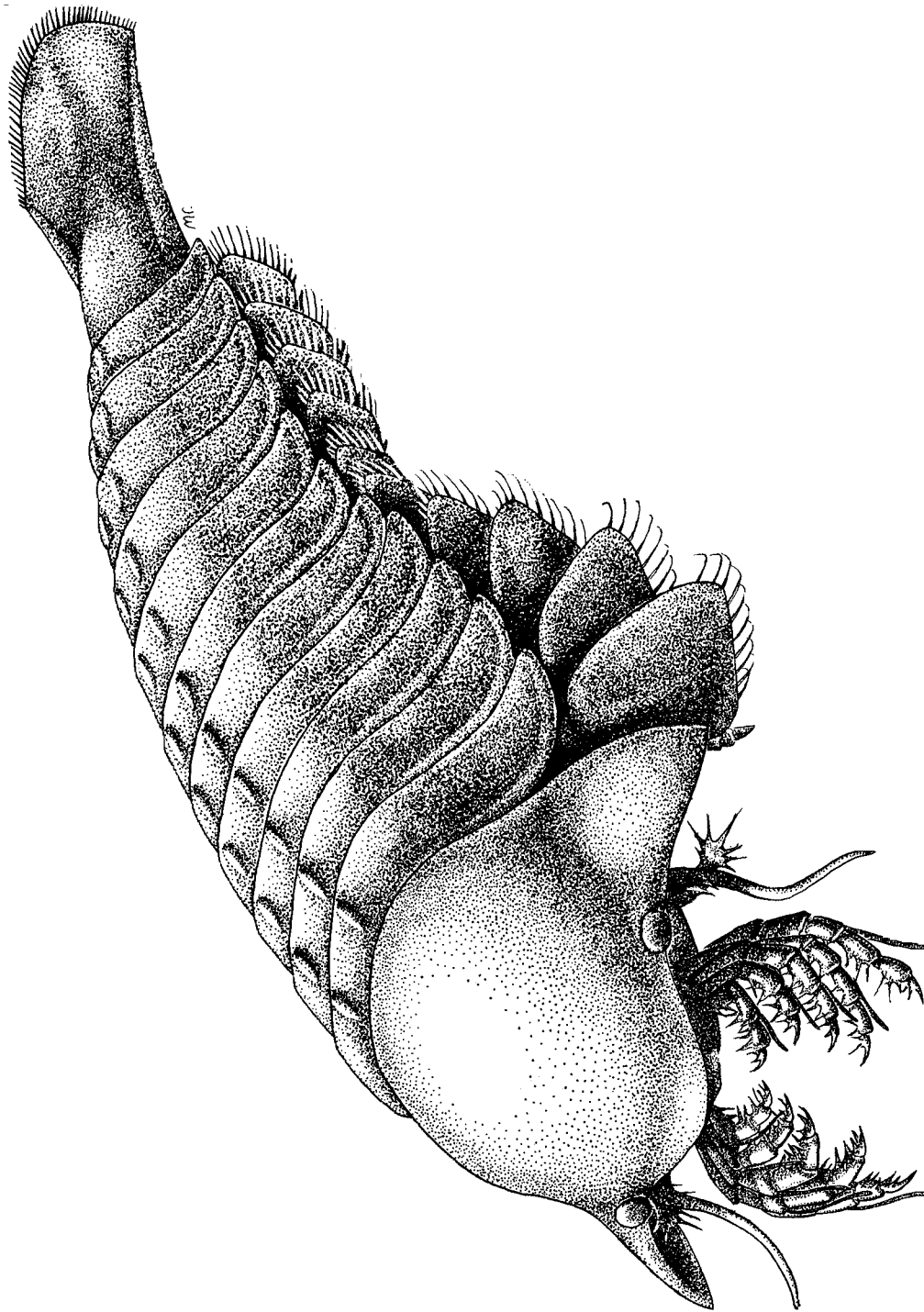
TEXT-FIG. 6. Restoration of *Sanctacaris uncata* seeking prey, with its raptorial head limbs and its lamellate trunk limbs moving in a metachronal wave.

The following characters indicate that *Sanctacaris* has a chelicerate affinity:

1. At least six pairs of head appendages. This is more than any other arthropod group apart from the chelicerates and *Emeraldella*. The majority of chelicerates have six pairs of prosomal (head) appendages: a chelicera and five others. An additional appendage pair is present at the posterior of the prosoma in the Devonian synziphosurine *Weinbergina* (Stürmer and Bergström 1981), and this appendage may be represented by the chilaria in *Limulus* and the metastoma in eurypterids. The first five pairs of head appendages of *Sanctacaris* form a graded but otherwise undifferentiated series and so could be equivalent to five pairs of prosomal appendages behind the chelicerae in later chelicerates.

2. The nature of the head appendages. Functionally the first five head appendages were raptorial and also possibly ambulatory. They increase in size toward the posterior and each podomere of the raptorial rami bears distal spines. These features are characteristic of the prosomal appendages of eurypterids (Plotnick 1983).

3. The presence of a cardiac lobe. This is represented by the dark reflective areas in the head shield. Eldredge (1974) pointed out that a cardiac lobe is common to the merostomes (occurring in eurypterids, xiphosurids, chasmataspids) although it also occurs in Aglaspida. The lobe 'need not be defined by sharply emplaced cardiac furrows, but instead may be distinguished by . . . simply color' (Eldredge 1974, p. 36).

4. The nature of the tagmosis. There is a clear morphological and functional separation of the body into a head region specialized for catching prey, and a trunk with lamellate rami that presumably served for swimming and respiration. Such a division is characteristic of the merostomes, although it also occurs in other arthropods including the crustaceans (e.g. the Remipedia).

5. The position of the anus. The anus lies at the posterior margin of the last trunk segment, ventrally below the insertion of the telson. This position is characteristic of the merostomes.

6. The nature of the telson. The telson is undivided and lacks associated appendages. This morphology is characteristic of the merostomes, although comparable arrangements occur in other arthropods.

Sanctacaris differs from chelicerates in two important respects. First, its limbs are biramous. A biramous limb, however, has long been considered primitive for the chelicerates, not least on the basis of the abdominal limbs of *Limulus* which are interpreted as comprising a short telopodite and an expanded outer lobe bearing the gill lamellae (e.g. Størmer 1944, p. 69; Tiegs and Manton 1958, p. 500). The outer rami in the prosoma (head) and inner rami in the opisthosoma (trunk) have been lost in later chelicerates, apart from *Limulus*, which may be specialized (Schram 1978, p. 86). An equivalent loss in *Sanctacaris* would result in tagmata with limbs specialized in a manner similar to those in merostomes. Secondly, and more importantly, *Sanctacaris* preserves no evidence of chelicerae, the chelate anteriormost limbs characteristic of the chelicerates. The primitive morphology of chelicerae is unknown. They are not preserved in early eurypterids or xiphosurids. Studies of the embryology of the living limulid *Tachypleus* indicate that the chelicera originates from a post-cephalic lobe separate from the other limbs and is differentiated at a very early larval stage (Anderson 1973). It is therefore unlikely, but not impossible, that the anteriormost preserved raptorial limb in *Sanctacaris* is equivalent to the chelicara.

In summary, the morphological characters present in *Sanctacaris*—number and nature of head appendages, cardiac lobe, body tagmosis, position of the anus, nature of the telson—are all derived for some member of the chelicerates and demonstrate the affinity of *Sanctacaris* to this major group. Chelicerae are apparently absent, but this is perhaps not surprising considering the primitive biramous nature of the appendages on both the head and trunk. Equally they may simply not be preserved. The chelicerae of *Megalograptus ohioensis*, the earliest well-preserved eurypterid, are revealed in detail on only two specimens although 'several hundred specimens, a few of which are essentially complete, have been found' (Caster and Kjellesvig-Waering 1964, p. 301). Similarly, the posterior head appendages of *Canadaspis perfecta* from the Burgess Shale are only clearly evident in two or three of over 4000 specimens (Briggs 1978).

Is *Sanctacaris* a chelicerate? This is not the first time a question of this kind has been raised. Smith (1984*a*), for example, noted similar difficulties in incorporating the features of Palaeozoic echinoids into a diagnosis of the Class Echinoidea. Diagnosing the Class is easy when only the living representatives are considered. However, when the fossils are included, the Class Echinoidea 'can only be recognized on the basis of a unique combination of features which individually can be found in other echinoderm groups' (Smith 1984*a*, p. 158). Thus the absence of some characters diagnostic of the Recent members of a higher taxon need not preclude more ancient representatives, provided that these fossil forms display a combination of characters unique to that group. In this solution, *Sanctacaris* is a chelicerate because its combination of characters occurs only in the chelicerates and in no other group.

Should *Sanctacaris* be included in the subphylum Chelicerata? Here we are dealing with a question of taxonomic practice rather than biological relationship. Fortunately there are precedents, including one involving Burgess Shale echinoderms. Because it had 'well-developed uniserial erect arms (perhaps bearing tube feet)', Sprinkle (1973, p. 178) could 'see no alternative but to regard *Echmatocrinus* as a true crinoid' even though it lacks regular plating of the calyx and a columnal-bearing stem, important characters present in all other Palaeozoic crinoids. Likewise, *Sanctacaris* can be assigned to the Chelicerata because of its basic chelicerate morphology, such as the six pairs of appendages (five raptorial) on the head, even though it apparently lacks chelicerae. The alternative would be to erect a new taxon (e.g. the Protochelicerata) to include chelicerate-like arthropods without chelicerae. This would not change our understanding of the biological relationships of *Sanctacaris* or of the chelicerates. Moreover, it would create taxonomic problems in the future if further material of *Sanctacaris* revealed chelicerae. Including *Sanctacaris* within the Chelicerata, on the other hand, emphasizes its biological affinity. The diagnosis of the Chelicerata should therefore be broadened to include biramous appendages and the possibility of a lack of chelicerae.

Smith (1984*b*, text-fig. 15) incorporated *Echmatocrinus* into the classification of the Crinoidea as a plesion with generic rank (in the sense of Patterson and Rosen 1977), a primitive sister group of all other crinoids. The biramous appendages (and lack of chelicerae, if real) define the position of *Sanctacaris* as a primitive sister group of all other chelicerates and we likewise designate it a plesion.

EVOLUTIONARY SIGNIFICANCE

None of the previously described arthropods from the Stephen Formation preserves characters that indicate as close a chelicerate affinity as *Sanctacaris* (Briggs and Whittington 1981; Briggs 1983, 1985). Bruton (1981) pointed out the striking similarity between the morphology of the trunk limbs of *Sidneyia* and those of the living limulid *Tachypleus*. Further resemblance between *Sidneyia* and the chelicerates is slight, however; it has a single pair of antennae and no other appendages in the head.

Emeraldella has six pairs of head appendages. The first, however, is an antenna, and the others are very similar to the trunk appendages, which differ only in the possession of an additional lobe (Bruton and Whittington 1983). The only Burgess Shale arthropod showing the same degree of differentation between head and trunk appendages as *Sanctacaris* is *Yohoia* (Whittington 1974), but it has only four pairs of head appendages, the first of which is highly specialized.

The aglaspids were long considered to be chelicerates (Raasch 1939; Størmer 1955) based on the interpretation of one appendage-bearing specimen from the late Cambrian of Wisconsin. This specimen, assigned by Raasch to *Aglaspis spinifer*, was restudied by Briggs *et al.* (1979) who demonstrated that it had only four or perhaps five pairs of appendages on the head, of which the first could not be shown to be chelate, and the rest were walking legs like those on the front of the trunk. Thus, *Aglaspis* cannot be recognized as a chelicerate.

Wahlman and Caster, in a 1978 abstract, reported a new Upper Cambrian chelicerate with preserved appendages from the Hickory Sandstone of central Texas and suggested that it warranted a subclass 'on a par with the Xiphosura and Eurypterida', as did the chasmataspids from the

Lower Ordovician of Tennessee (Caster and Brooks 1956). Further discussion of the affinities of the Hickory Sandstone arthropod awaits the publication of a full description.

Fragments of possible limbs occur in association with *Kodymirus* from the Middle Cambrian of Bohemia, assigned by Chlupáč and Havlíček (1965) to the merostomes, but the morphology of the appendages is unknown. The remaining Cambrian fossils described as chelicerates do not preserve evidence of the appendages (Bergström 1968, 1975) and their affinities are therefore uncertain. *Sanctacaris* is thus the only Cambrian chelicerate recognized at present.

The earliest known chelicerates with chelicerae are the eurypterids, which appear in the Ordovician. *Sanctacaris* shares a number of characters with 'the primitive eurypterid' (Plotnick 1983). These include subdued carapace relief with a cardiac lobe, similarity and increase in size of the prosomal appendages toward the posterior, distal spines on the podomeres of these appendages, and a trilobed opisthosoma. A paddle-shaped telson also occurs in some eurypterids, but is probably derived from a primitive styliform morphology (Plotnick 1983, p. 206). In general morphology and life habit (both were swimming benthic predators), therefore, *Sanctacaris* makes a fine progenitor to the eurypterids. Indeed the raptorial head limbs in *Sanctacaris* are similar to the generalized eurypterid appendage of the *Hughmilleria* type which Størmer (1974, text-figs. 1-10) used to derive the different limbs of the eurypterid prosoma, including the swimming paddle (appendage VI). The opisthosoma of eurypterids, on the other hand, is much more derived than that of *Sanctacaris*. Twelve somites are divided into a pre-abdomen and a post-abdomen, and the abdominal appendages are modified to form chambers that enclose gills on the ventral body wall. Such appendages, although very different, could have been derived from the generalized *Sanctacaris* trunk appendages once the swimming function was taken up by the eurypterid prosoma. There is no evidence that *Sanctacaris* had the metastoma or genital appendages which are characteristic of eurypterids, but the posterior appendages of the head may be their forerunners.

The characters that *Sanctacaris* shares with the eurypterids are for the most part primitive for the xiphosurids as well (see Eldredge 1974, for a discussion of xiphosurid relationships). However, *Sanctacaris* appears to be separated from the xiphosurids to a greater extent than from the eurypterids. Thus the head of *Sanctacaris* is much smaller than the trunk, whereas the two are of nearly equal length in xiphosurids. *Sanctacaris* shows no sign of any differentiation of the trunk into pre- and post-abdominal sections and the first trunk somite is not reduced. *Sanctacaris* lacks a defined interopthalmic area with ridges and furrows.

Sanctacaris demonstrates that chelicerates had evolved by the Middle Cambrian. Moreover, its combination of primitive and diagnostic morphological characters places it near the origin of the Chelicerata. On one hand, the presence of biramous appendages throughout and the lack of differentiation in the trunk limbs indicate its position at the primitive end of the arthropod spectrum, along with most of the Burgess Shale arthropods; on the other, the degree of 'cephalization', with at least six pairs of appendages in the head, and the similarity of the five raptorial limbs to prosomal appendages in 'the primitive eurypterid', indicate that it is none the less a chelicerate. This assessment of *Sanctacaris* is paralleled by that of *Canadaspis*, which occurs at the same locality (Collins *et al.* 1983, table 1) and which is an early member of the other major living aquatic arthropod group, the Crustacea (Briggs 1983). *Canadaspis* also has primitive morphological characters (large number of podomeres in the head appendages; similar posterior head and anterior trunk appendages) but the presence of two pairs of antennae, a mandible and a maxilla, for example, indicates that it is a crustacean (Briggs 1978). Is it likely that chelicerae had developed by the early stage of chelicerate evolution represented by *Sanctacaris*? Indications are equivocal. On one hand, the primitive biramous nature of the head appendages suggests that chelicerae may not have yet evolved; on the other, in view of the presence of highly modified head appendages in some Burgess Shale arthropods (*Yohoia*, *Branchiocaris*, and *Leanchoilia*, for example) it is reasonable to presume that chelicerae could have evolved by this time. However, whether or not chelicerae had evolved by the Middle Cambrian, it is evident that *Sanctacaris* is a chelicerate.

From the five specimens known in the *Glossopleura* Zone and none in the Burgess Shale, it is evident that chelicerates are rare in the Middle Cambrian rocks of British Columbia. This rarity is

probably a true reflection of their scarcity in Middle Cambrian seas, at least in the off-shore, relatively deep water environments, because the tens of thousands of diverse exceptionally preserved fossils in the Burgess Shale and *Glossopleura* Zone should provide a relatively complete sample of the communities they represent. Why were chelicerates so rare then? Two reasons come to mind. First, Middle Cambrian arthropods are very diverse morphologically and most do not fall into well-defined groups (Briggs and Whittington 1981; Briggs 1983). Thus, except for the trilobites, no arthropod group has many different representatives. However, even by this minimal standard, chelicerates are rare. Secondly then, the rarity of chelicerates may reflect their predatory way of life. Even the most numerous predator in the Burgess Shale, *Sidneyia*, has only 177 individuals compared to 15 092 *Marrella*, 4179 *Canadaspis*, and 2158 *Burgessia* (Conway Morris 1986), although the numerical comparison is misleading because an adult *Sidneyia* is several times larger than *Canadaspis*, and many times larger than *Marrella* and *Burgessia*.

Why have the chelicerates been so successful while most of their Middle Cambrian arthropod contemporaries have died out? Chance probably played a role, particularly during mass extinctions, by sparing the chelicerates and eliminating the other arthropods. Alternatively chelicerates may have some unique morphological characters that contributed to their success. The most obvious are the large number and morphological flexibility of the head appendages, shown by the raptorial limbs in *Sanctacaris* and the grasping, walking, balancing, and swimming prosomal appendages of the eurypterids and xiphosurids. However, whether or not these were significant factors in the success of the chelicerates, the basic pattern evident in *Sanctacaris* has persisted to the present while those in most of the other Cambrian arthropods have long since disappeared.

REFERENCES:

AITKEN, J. D. and McILREATH, I. A. 1981. Depositional environments of the Cathedral Escarpment, near Field, British Columbia. *In* AITKEN, J. D. and TAYLOR, M. E. (eds.). *The Cambrian System in the southern Canadian Rocky Mountains, Alberta and British Columbia, Second Int. Symp. Cambrian System, Guidebook for Field Trip 2*, 35–44. US geol. Surv., Denver, Colorado.

ALLISON, P. A. 1986. Soft-bodied animals in the fossil record: the role of decay in fragmentation during transport. *Geology*, **14**, 979–981.

ANDERSON, D. T. 1973. *Embryology and phylogeny in annelids and arthropods*, 495 pp. Pergamon, Oxford.

BERGSTRÖM, J. 1968. *Eolimulus*, a Lower Cambrian xiphosurid from Sweden. *Geol. For. Stockh. Forh.* **90**, 489–503.

—— 1975. Functional morphology and evolution of xiphosurids. *Fossils and Strata*, **4**, 291–305.

BRIGGS, D. E. G. 1978. The morphology, mode of life, and affinities of *Canadaspis perfecta* (Crustacea: Phyllocarida), Middle Cambrian, Burgess Shale, British Columbia. *Phil. Trans. R. Soc.* **B281**, 439–487.

—— 1981. The arthropod *Odaraia alata* Walcott, Middle Cambrian, Burgess Shale, British Columbia. Ibid. **B291**, 541–584.

—— 1983. Affinities and early evolution of the Crustacea: the evidence of the Cambrian fossils. *In* SCHRAM, F. R. (ed.). *Crustacean Phylogeny. Crust. Issues*, **1**, 1–22. A. A. Balkema, Rotterdam.

—— 1985. Les premiers arthropodes. *La Recherche*, **16**, 340–349.

—— BRUTON, D. L. and WHITTINGTON, H. B. 1979. Appendages of the arthropod *Aglaspis spinifer* (Upper Cambrian, Wisconsin) and their significance. *Palaeontology*, **22**, 167–180.

—— and ROBISON, R. A. 1984. Exceptionally preserved nontrilobite arthropods and *Anomalocaris* from the Middle Cambrian of Utah. *Kansas Univ. Contribs. Paleont.* **111**, 23 pp.

—— and WHITTINGTON, H. B. 1981. Relationships of arthropods from the Burgess Shale and other Cambrian sequences. *Proc. 2nd International Symposium on the Cambrian System. US geol. Surv. Open-file rept.* **81-743**, 38–41.

—— and WILLIAMS, S. H. 1981. The restoration of flattened fossils. *Lethaia* **14**, 157–164.

BRUTON, D. L. 1981. The arthropod *Sidneyia inexpectans*, Middle Cambrian, Burgess Shale, British Columbia. *Phil. Trans. R. Soc.* **B295**, 619–656.

—— and WHITTINGTON, H. B. 1983. *Emeraldella* and *Leanchoilia*, two arthropods from the Burgess Shale, Middle Cambrian, British Columbia. *Ibid.* **B300**, 553–585.

CASTER, K. E. and BROOKS, H. K. 1956. New fossils from the Canadian-Chazyan (Ordovician) hiatus in Tennessee. *Bull. Am. Paleont.* **36**, 157–199.

—— and KJELLESVIG-WAERING, E. N. 1964. Upper Ordovician eurypterids of Ohio. *Palaeontogr. am.*, **32**, 301–358.

CHLUPÁČ, I. and HAVLÍČEK, V. 1965. *Kodymirus* n. g., a new aglaspid merostome of the Cambrian of Bohemia. *Sborn. Geol. Ved. Praha*, **6**, 7–20.

COLLINS, D. 1986. Paradise revisited. *Rotunda*, **19**, 30–39.

—— BRIGGS, D. and CONWAY MORRIS, S. 1983. New Burgess Shale fossil sites reveal middle Cambrian faunal complex. *Science, NY*, **222**, 163–167.

CONWAY MORRIS, S. 1979. Middle Cambrian polychaetes from the Burgess Shale of British Columbia. *Phil. Trans. R. Soc.* **B285**, 227–274.

—— 1986. The community structure of the Middle Cambrian Phyllopod Bed (Burgess Shale). *Palaeontology*, **29**, 423–467.

ELDREDGE, N. 1971. Patterns of cephalic musculature in the Phacopina (Trilobita) and their phylogenetic significance. *J. Paleont.* **45**, 52–67.

—— 1974. Revision of the Suborder Synziphosurina (Chelicerata, Merostomata), with remarks on merostome phylogeny. *Am. Mus. Novit.* **2543**, 1–41.

FRITZ, W. H. 1971. Geological setting of the Burgess Shale. In *Proceedings of the North American Paleontological Convention, Chicago, 1969*, part I, 1155–1170. Allen Press, Lawrence, Kansas.

HOU, XIAN-GUANG, 1987. Two new arthropods from Lower Cambrian, Chengjiang, eastern Yunnan. *Acta Palaeont. Sinica*, **26**, 236–256.

HUGHES, C. P. 1975. Redescription of *Burgessia bella* from the Middle Cambrian Burgess Shale, British Columbia. *Fossils and Strata*, **4**, 415–435.

LOCHHEAD, J. H. 1961. Locomotion. *In* WATERMAN, T. H. (ed.). *The physiology of Crustacea*, vol. 2, 313–364. Academic Press, New York.

McILREATH, I. A. 1977. Accumulation of a Middle Cambrian, deep-water limestone debris apron adjacent to a vertical, submarine carbonate escarpment, southern Rocky Mountains, Canada. *Spec. Publs Soc. econ. Paleont. Miner. Tulsa*, **25**, 113–124.

PATTERSON, C. and ROSEN, D. E. 1977. Review of ichthyodectiform and other Mesozoic teleost fishes and the theory and practice of classifying fossils. *Bull. Am. Mus. nat. Hist.* **158**, 81–172.

PLOTNICK, R. E. 1983. *Patterns in the evolution of eurypterids.* Ph.D. thesis (unpublished), University of Chicago.

—— and BAUMILLER, T. 1988. The pterygotid telson as a biological rudder. *Lethaia*, **21**, 13–27.

RAASCH, G. O. 1939. Cambrian Merostomata. *Sp. Pap. geol. Soc. Am.* **19**, ix + 146 pp.

SCHRAM, F. R. 1978. Arthropods: a convergent phenomenon. *Fieldiana, Geol.* **39**, 61–108.

SIMONETTA, A. M. 1970. Studies on non trilobite arthropods of the Burgess Shale (Middle Cambrian). *Palaeontogr. ital.* **66** (NS 36), 35–45.

SMITH, A. B. 1984a. *Echinoid Palaeobiology*, 190 pp. Allen (George) & Unwin, London.

—— 1984b. Classification of the Echinodermata. *Palaeontology*, **27**, 431–459.

SPRINKLE, J. 1973. Morphology and evolution of blastozoan echinoderms. *Spec. Pub. Mus. Comp. Zool.* 284 pp.

STØRMER, L. 1944. On the relationships and phylogeny of fossil and Recent Arachnomorpha. *Skr. norske Vidensk-Akad., Mat.-naturv. Kl.* **5**, 1–158.

STØRMER, L. 1955. Merostomata. *In* MOORE, R. C. (ed.). *Treatise on Invertebrate Paleontology. Part P. Arthropoda 2*, P4-P41. Geological Society of America and University of Kansas Press, Boulder, Colorado and Lawrence, Kansas.

—— 1974. Arthropods from the Lower Devonian (Lower Emsian) of Alken an der Mosel, Germany. Part 4: Eurypterida, Drepanopteridae, and other groups. *Senck. leth.* **54**, 359-451.

STÜRMER, W. and BERGSTRÖM, J. 1981. *Weinbergina*, a xiphosuran arthropod from the Devonian Hunsrück Slate. *Paläont. Z.* **55**, 237-255.

TIEGS, O. W. and MANTON, S. M. 1958. The evolution of the Arthropoda. *Bio. Rev.* **33**, 255-337.

WAHLMAN, G. P. and CASTER, K. E. 1978 Bearing of new Texas Upper Cambrian arthropods on merostome classification. *Geol. Soc. Am. North-central section at Ann Arbor, Michigan. Abstracts with Programs*, **10** (6), 286.

WEBB, P. W. 1975. Hydrodynamics and energetics of fish propulsion. *Bull. Fish. Res. Bd Can.* **190**, 159 pp.

—— 1984. Form and function in fish swimming. *Sci. Am.* **251**, 58-68.

WHITTINGTON, H. B. 1971. The Burgess Shale: History of research and preservation of fossils. In *Proceedings of the North American Paleontological Convention, Chicago*, 1969, part I, 1170-1201. Allen Press, Lawrence, Kansas.

—— 1974. *Yohoia* Walcott and *Plenocaris* n. gen., arthropods from the Burgess Shale, Middle Cambrian, British Columbia. *Geol. Surv. Can. Bull.* **231**, 63 pp.

—— 1980. The significance of the fauna of the Burgess Shale, British Columbia. *Proc. geol. Ass.* **91**, 127-148.

—— 1981. Rare arthropods from the Burgess Shale, Middle Cambrian, British Columbia. *Phil. Trans. R. Soc.* **B292**, 329-357.

—— 1985. *The Burgess Shale*. xiv + 151 pp. Yale University Press, New Haven and London.

DEREK E. G. BRIGGS

Department of Geology
University of Bristol
Wills Memorial Building
Queen's Road
Bristol BS8 1RJ

DESMOND COLLINS

Department of Invertebrate Palaeontology
Royal Ontario Museum
Toronto
Ontario M5S 2C6