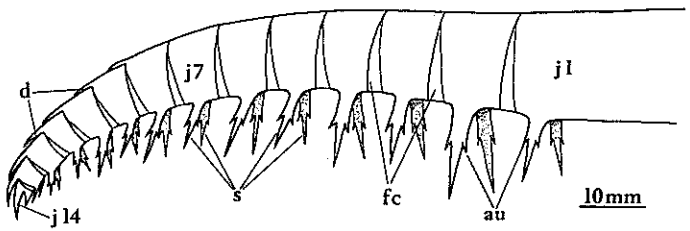
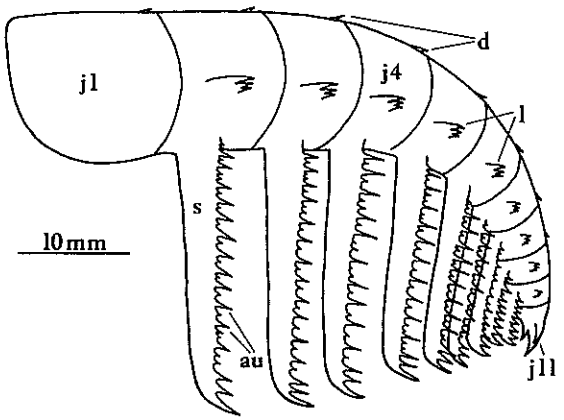
I could not have made up a better story to illustrate the power and extent of the Burgess revision than the actual chronicle of *Anomalocaris*—a tale of humor, error, struggle, frustration, and more error, culminating in an extraordinary resolution that brought together bits and pieces of three "phyla" in a single reconstructed creature, the largest and fiercest of Cambrian organisms.

The name *Anomalocaris,* or "odd shrimp," predates the discovery of the Burgess Shale, for this is one of the few soft-bodied Burgess creatures endowed with parts solid enough for preservation in ordinary faunas (the spicules of *Wiwaxia* are another example). The first *Anomalocaris* were found in 1886 at the famous *Ogygopsis* trilobite beds, exposed on the next mountain over from the Burgess Shale. In 1892, the great Canadian paleontologist J. F. Whiteaves described *Anomalocaris* in the *Canadian Record of Science* as the headless body of a shrimplike arthropod. Walcott accepted the standard view that this fossil represented the rear end of a crustacean, with the long axis as the trunk and the ventral spines as appendages (figure 3.60). Charles R. Knight followed this tradition in his famous painting of the Burgess fauna (see figure 1.1), where he constructed a composite organism by attaching *Anomalocaris* to *Tuzoia,* one of the bivalved arthropod carapaces that lacked associated soft parts and was therefore a good candidate for the cover of *Anomalocaris*'s unknown head.

But this official name-bearer of *Anomalocaris* provides only one piece of



3.60. The fragment of a segmented creature originally called *Anomalocaris* in 1886 (Briggs, 1979). For many years this fossil was considered to represent the trunk and tail of an arthropod. It has now been correctly identified as one of a pair of feeding appendages from the largest of all Cambrian animals.



3.61. Reconstruction of appendage F by Briggs (1979). Walcott originally described this structure as a feeding limb of *Sidneyia.* Briggs reinterpreted it as an appendage of a giant arthropod. Recent research shows that appendage F is actually one of a pair of feeding organs from the largest known Cambrian animal.

our story. Three other structures, all named by Walcott, play central roles in this complex tale.

1. The head of *Sidneyia,* the arthropod that Walcott named for his son Sidney and then described first among Burgess creatures (1911a), bears a pair of antennae and no other appendages. Walcott also found a large isolated arthropod feeding limb, later (1979) called "appendage F" (for feeding) by Derek Briggs (figure 3.61). *Sidneyia* was, in Walcott's judgment, the only Burgess creature large enough to carry such an appendage; its rapacious character also fitted well with Walcott's concept of *Sidneyia* as a fierce carnivore. So Walcott made the marriage without direct evidence, and joined appendage F to the head of *Sidneyia.* Bruton (1981) later determined that *Sidneyia*'s head shield does not contain enough space to accommodate such a structure.

2. Walcott's second paper (1911b), on the supposed jellyfish and holothurians (sea cucumbers of the echinoderm phylum) from the Burgess Shale, does not rank among his more accurate efforts. He described five genera. *Mackenzia* is probably a sea anemone and therefore a coelenterate in the same phylum as jellyfish, but Walcott placed this genus in his other group, the holothurians. A second creature turned out to be a priapulid worm (Conway Morris, 1977d). A third, *Eldonia,* still ranks as a peculiar

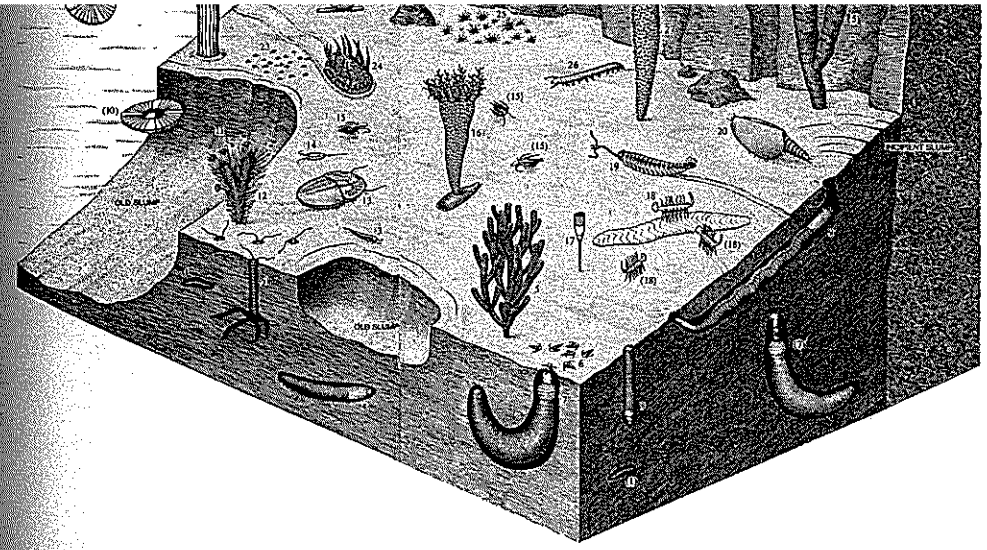
wager a reasonable sum that it will finally end up as another Burgess oddball.

Walcott named a fourth genus *Laggania,* and identified this fossil as a holothurian, on the basis of one specimen. He noted a mouth, and thought that it might be surrounded by a ring of plates. Poor preservation had effaced all the distinctive features of holothurians. Walcott admitted: "The body of the animal is so completely flattened that the tube feet are obscured, the outline of the ventral sole lost, and the concentric bands almost obliterated" (1911b, p. 52).

3. As a fifth and last genus, Walcott named the only Burgess jellyfish *Peytoia.* He described this peculiar creature as a ring of thirty-two lobes around a central opening. This series of lobes could be divided into four quadrants, with a larger lobe at each of the four corners of the squared-off ring, and seven smaller lobes between the corners in each quadrant. Walcott noted two short points on each lobe, projecting inward toward the central hole. He interpreted these structures as "points of attachment of the parts about the mouth, or possibly oral arms" (1911b, p. 56). Except for radial symmetry, Walcott found no trace of the defining characters of a jellyfish—no tentacles or concentric muscle bands. *Peytoia,* looking more like a pineapple slice than a medusa, made an awfully odd jellyfish. No true member of the group has a hole in the center. Nonetheless, Walcott's interpretation prevailed. The best-known modern reconstruction of the Burgess fauna, published in *Scientific American* several years after Whittington and colleagues began their revisions (Conway Morris and Whittington, 1979), shows *Peytoia* as a kind of Frisbee *cum* flying saucer *cum* pineapple slice, entering the scene from the west (figure 3.62).

Now who ever dreamed about a connection between the rear end of a shrimp, the feeding appendage of *Sidneyia,* a squashed sea cucumber, and a jellyfish with a hole in the center? Of course, no one did. The amalgamation of these four objects into *Anomalocaris* came as an entirely unanticipated shock. Moreover, the successful resolution did not emerge from this unimproved initial chaos. Several intermediate efforts, all basically erroneous but each supplying an important link in a developing story, preceded the successful conclusion.

Anomalocaris has been the nemesis of recent Burgess research. This creature eventually yielded its secret, but not until both Simon Conway Morris and Derek Briggs had committed their biggest mistakes in coping with its various parts. One cannot hope to do anything significant or original in science unless one accepts the inevitability of substantial error along the way. Three steps, however, did inch matters forward toward a resolution, whatever the longer lateral errors.



3.62. The best-known reconstruction of the Burgess Shale, drawn for the 1979 *Scientific American* article by Conway Morris and Whittington. Note priapulid worms in their burrows, and several Burgess oddballs—including *Dinomischus* (17), *Hallucigenia* (18), *Opabinia* (19), and *Wiwaxia* (24). In a major error, two jellyfish (10) are shown swimming in like pineapple slices from the west. This structure is actually the mouth of *Anomalocaris.* (From "The Animals of the Burgess Shale," by Simon Conway Morris and H. B. Whittington. Copyright © 1979 by Scientific American, Inc. All rights reserved.)

1. In 1978, Conway Morris applied Whittington's new techniques for distinguishing three-dimensional structure to *Laggania,* now regarded as a sponge rather than a holothurian. He took a dental microdrill to the counterpart of the unique specimen, and uncovered a pineapple slice of *Peytoia,* where Walcott had identified the indistinct mouth. Conway Morris stood on the threshold of the proper interpretation, but he guessed wrong. He considered the possibility that the "sponge" called *Laggania* was not a distinct creature, but a body attached to *Peytoia,* which would then become the centerpiece of a strange medusoid. But Conway Morris rejected this reconstruction because he regarded almost all Burgess organisms as discretely preserved, rather than disaggregated into parts. He wrote: "The vast majority of Burgess Shale fossils are preserved complete and it may reasonably be concluded that the body of *Laggania cambria* is not an

soid which is interpreted here as a sponge" (1978, p. 130). He argued that the association was simply an accident of deposition from the Burgess mudslide: "The association of the medusoid and sponge is presumably by chance. The phyllopod bed was deposited as a series of turbidites, and it is likely that after transport the two specimens settled together" (1978, p. 130).

Conway Morris guessed wrong about the reasons for a link between *Peytoia* and *Laggania,* but he had uncovered (literally) a key association, joining the first two of four pieces that would form *Anomalocaris.*

2. In 1982, Simon tried to grapple with the strangeness of *Peytoia* (Conway Morris and Robison, 1982). He called *Peytoia* "one of the most peculiar of Cambrian medusoids" (1982, p. 116), and even used the word "enigmatic" in his title. Simon did not correctly resolve this beast, but he cast doubt upon its affinity with medusoids, and thus kept the channels of questioning wide open. Writing about the central hole, Conway Morris and Robison concluded: "This feature is unknown in either living or fossil cnidarians and may indicate that *Peytoia nathorsti* is not a cnidarian. Its relationship with any other phylum would seem to be even more obscure" (1982, p. 118).

3. *Anomalocaris* itself, Whiteaves's original rear end of a shrimp, had been allocated to Derek Briggs in the original divvying up of the Burgess Shale. It was, after all, supposed to be the body of an arthropod with a bivalved carapace.

In 1979, Briggs published a provocative reconstruction of his assignment. He made two outstanding observations that contributed to the resolution of *Anomalocaris:*

First, he recognized that *Anomalocaris* was an appendage with paired spines on its inner borders, not an entire body with appendages on its ventral edges. If *Anomalocaris* was the trunk of an entire organism, then some of the more than one hundred specimens should show traces of a gut, and at least a few would be found with arthropod joints on their supposed appendages.

Second, he argued that *Anomalocaris* and appendage F (Walcott's feeding limb of *Sidneyia*) were variants of the same basic structure, and probably belonged together. This conclusion, as we shall see, was not quite correct, but Briggs's argument did properly unite two more pieces of the *Anomalocaris* puzzle.

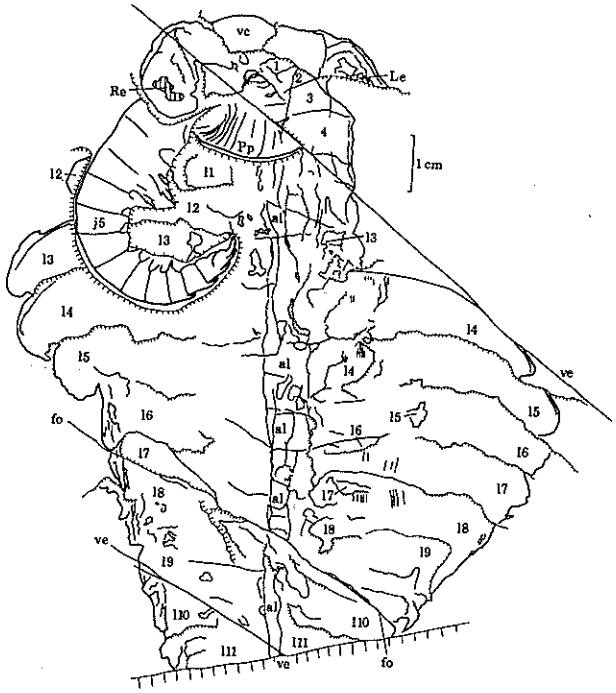
Beyond these important insights, Briggs's reconstruction was basically erroneous, though spectacular. He continued to view both *Anomalocaris* and appendage F as parts of an arthropod, conjecturing that *Anomalocaris* was a walking leg, and appendage F a feeding structure, of a single giant *"Anomalocaris,* the Largest Known Cambrian Arthropod."

But Briggs was scarcely convinced by his own reconstruction. So many mysteries remained. He puzzled over the failure to find any sign, even fragmentary, of the giant body that supposedly held these appendages. Could a structure three feet long be entirely absent from a soft-bodied fauna? Briggs conjectured that such pieces might exist as organic sheets and films, thus far ignored for their lack of distinguishable structures. He wrote: "Large, previously unidentified, relatively featureless fragments of the body cuticle of *Anomalocaris canadensis* almost certainly await discovery on the scree slopes of Mt. Stephen" (1979, p. 657). Little did Derek realize that the body of *Anomalocaris* had been known and named since Walcott's time, but masquerading as the "holothurian" *Laggania,* later interpreted as a sponge with a jellyfish on top.

The Geological Survey of Canada expedition had discovered an odd specimen in the Raymond quarry, just above Walcott's phyllopod bed. Whittington had taken this large, ill-defined, and virtually featureless fossil and placed it in a drawer—hoping, I think, to bury it by the old cliché: Out of sight, out of mind. But he kept thinking about this peculiar fossil of a creature so much larger than anything else in the Burgess Shale. "I used to open the drawer and then close it," Harry explained to me. One day in 1981, he decided to excavate the fossil in the hope that some details of structure might be resolved. He dug into one end of the creature and, to his astonishment, found a specimen of *Anomalocaris* apparently attached and in place (figure 3.63). Harry told Derek Briggs about his discovery, and Derek simply couldn't believe it. The excavated object was surely *Anomalocaris,* but, like Simon's interpretation of the jellyfish *Peytoia* on the sponge *Laggania,* perhaps this specimen of *Anomalocaris* had been accidentally entangled with a large sheet of something else as the mudslide coalesced.

Soon afterward, Whittington and Briggs were studying a suite of specimens borrowed from the Walcott collections. These slabs showed relatively featureless blobs and sheets that had never attracted much attention, including the body of *Laggania* with *Peytoia* on top. On a single momentous day—the positive counterpart (in the vernacular, not technical, sense) of another key Burgess moment, nearly a decade before, when Whittington had cut through the head and sides of *Opabinia* and found nothing underneath—they excavated and found *both Peytoia* and appendage F as organs of a larger creature.

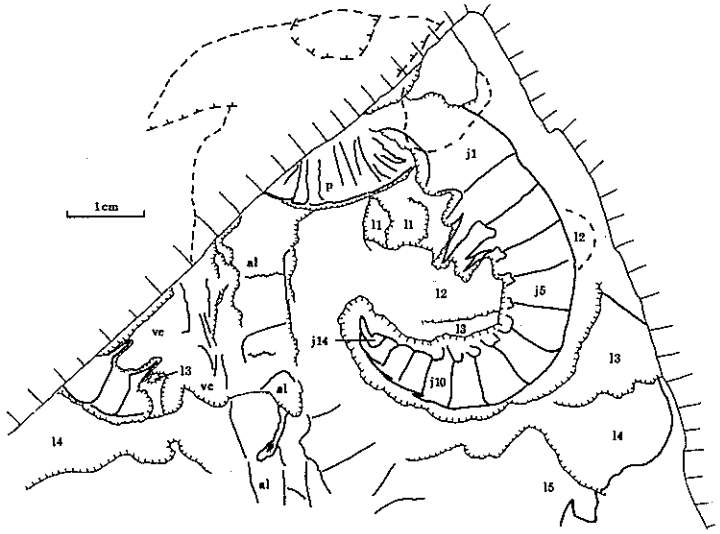
As they assimilated this greatest of all Burgess surprises, and kept finding *Peytoia* and appendage F in the same association on other slabs, Harry and



3.63. The specimen dissected by Harry Whittington that revealed the true nature of *Anomalocaris.* In this camera lucida drawing, the mouth misidentified by Walcott as the jellyfish *Peytoia* is at top center (labeled *Pp*); the oblique line *(ve)* just above it represents a crack in the rock. The structure originally named *Anomalocaris* is the curved feeding appendage just to the left of the mouth with its middle segment labeled *j5.* Also visible is the trace of the central gut, or alimentary canal *(al).*

Derek realized that they had resolved a forest of problems into one creature. *Peytoia* was no jellyfish, but the mouth of the large beast, attached to the ventral surface near the front. Appendage F was not one member of a large sequence of repeated limbs on an arthropod; rather, two appendage F's formed a single pair of feeding organs attached, in front of the mouth, to the bottom end of the new animal.

But Whittington's specimen back in England bore *Anomalocaris,* not appendage F, in this frontal position (see figure 3.63). When he dissected this specimen more fully, he found traces of both the *Peytoia* mouth and a second *Anomalocaris,* forming a pair of feeding organs in the same posi-



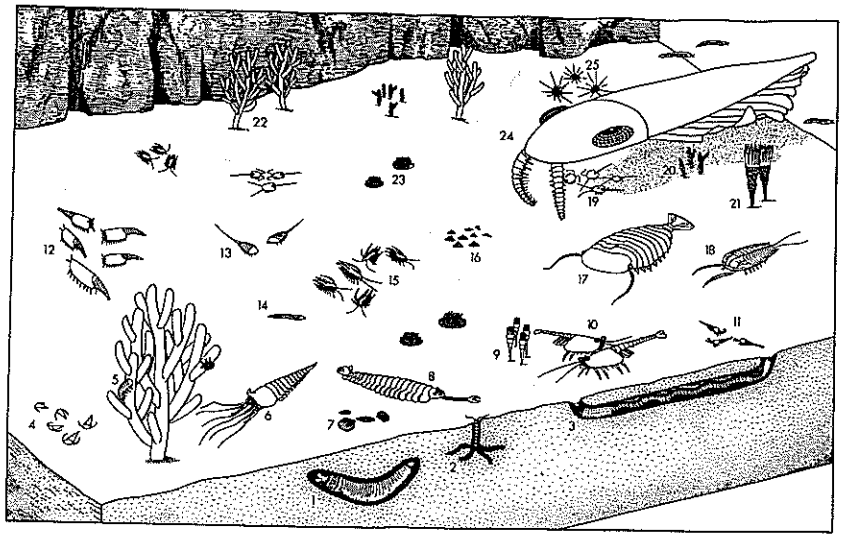
3.64. The key specimen of *Anomalocaris* further dissected to reveal parts of both feeding appendages. This is the other slab, and therefore a mirror image, of part of the specimen represented in figure 3.63. Note the mouth (labeled *p*) and the first discovered appendage *(j1–j14).* But now a trace of the second feeding appendage has been excavated at the lower left, just below the oblique line representing the crack in the rock.

tion as the appendage-F pairs on the specimens in Washington (figure 3.64).

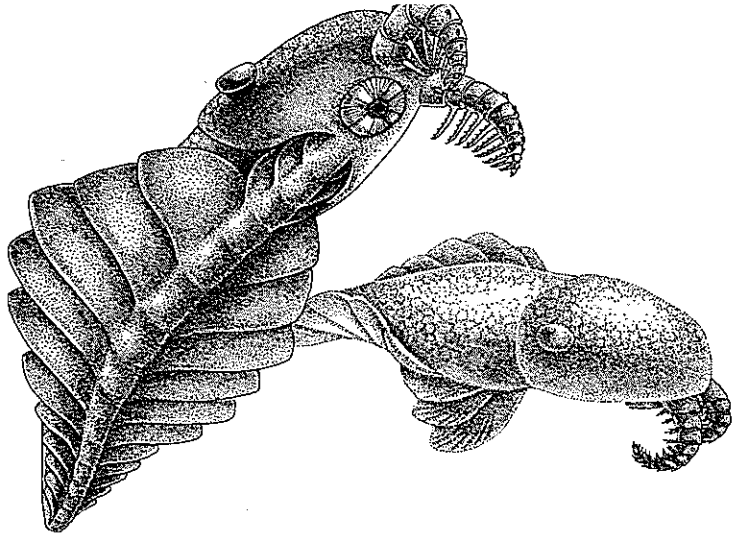
All the pieces had finally come together. From four anomalies—a crustacean without a head, a feeding appendage that didn't fit, a jellyfish with a hole in the middle, and a squashed sheet that had bounced from one phylum to another—Whittington and Briggs had reconstructed two separate species of the single genus *Anomalocaris. Laggania* was a squashed and distorted part of the body; *Peytoia,* the mouth surrounded by a circlet of toothed plates, not a series of lobes with hooks; *Anomalocaris* the pair of feeding organs in one species *(Anomalocaris canadensis);* appendage F a feeding organ in the second species (*Anomalocaris nathorsti,* borrowing the old trivial name of *Peytoia*). The uncompromising rules of nomenclature, honoring oldest first, required that the entire genus be called *Anomalocaris,* to recognize Whiteaves's original publication of 1892. But what a happy and appropriate imposition in this case—an "odd shrimp" indeed!

inches in length when extended, the entire animal must have dwarfed nearly everything else in the Burgess Shale. Whittington and Briggs estimated the biggest specimens as nearly two feet in length, by far the largest of all Cambrian animals! A recent reconstruction of the whole fauna (Conway Morris and Whittington, 1985), basically an update of the 1979 *Scientific American* version, has replaced the pineapple-slice *Peytoia* that used to angle in from the west (see figure 3.62) with a large and menacing *Anomalocaris,* purposefully advancing from the east (figure 3.65).

Whittington and Briggs published their monograph on *Anomalocaris* in 1985, a fitting triumph to cap what may be the most distinguished and important series of monographs in twentieth-century paleontology. The long oval head of *Anomalocaris* bears, on the side and rear portion of its dorsal surface, a large pair of eyes on short stalks (figure 3.66). On the ventral surface, the pair of feeding appendages attaches near the front,



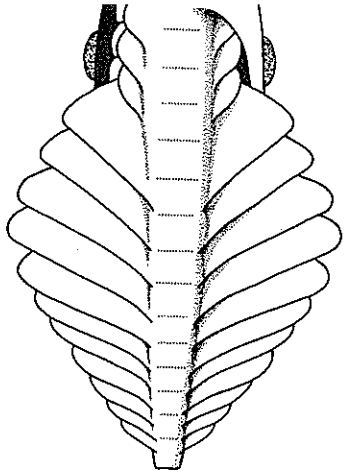
3.65. A recent reconstruction of the Burgess Shale fauna (Conway Morris and Whittington, 1985), showing the new interpretation of *Anomalocaris* (24), and the great size of this creature compared to the others. Note the weird wonders *Opabinia* (8), *Dinomischus* (9), and *Wiwaxia* (23); and the arthropods *Aysheaia* (5), *Leanchoilia* (6), *Yohoia* (11), *Canadaspis* (12), *Marrella* (15), and *Burgessia* (19).



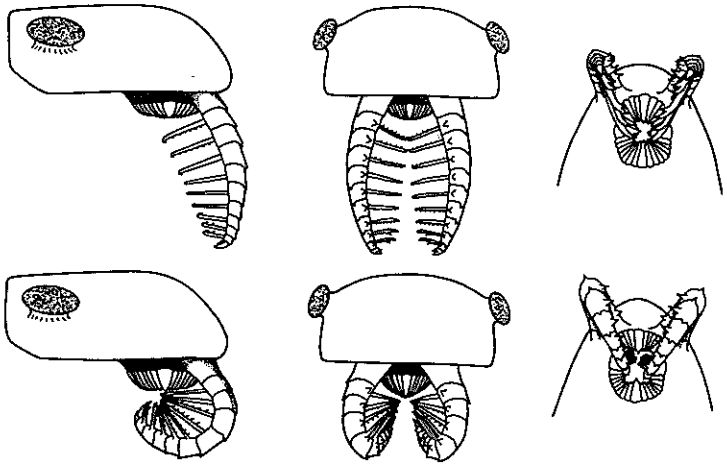
3.66. The two known species of *Anomalocaris:* top, *Anomalocaris nathorsti* as seen from below, showing the circular mouth, misidentified by Walcott as a jellyfish, and the pair of feeding appendages; bottom, *Anomalocaris canadensis* as seen from the side, in swimming position. Drawn by Marianne Collins.

with the circlet of the mouth behind and in the mid-line (figure 3.67). The plates of the circlet could substantially constrict the area of the mouth but not fully come together (in any orientation that Whittington or Briggs could reconstruct), so the mouth probably remained permanently open, at least partially. Whittington and Briggs conjecture that the mouth may have worked like a nutcracker, with *Anomalocaris* using its appendages to bring prey to the opening (figure 3.68), and then crushing its food by constriction. The inner borders of the plates in the *Peytoia* circlet all bear teeth. In one specimen, Whittington and Briggs found three additional rows of teeth, stacked one above the other parallel to the circlet of mouth plates. The teeth in these rows may have been attached to the circlet, but they probably extended from the walls of the gullet—thus providing *Anomalocaris* with a formidable array of weapons both in the mouth itself and in the front end of the gut (figure 3.69).

Behind the mouth at the ventral surface, the head carries three pairs of strongly overlapping lobes (see figure 3.67). The trunk behind the head is divided into eleven lobes, each triangular in basic shape, with the apex

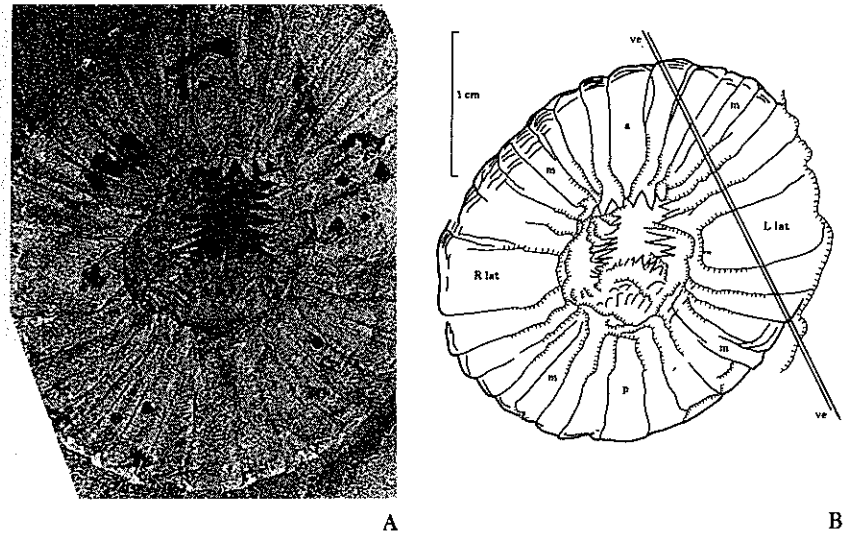


3.67. *Anomalocaris* as seen from below, showing how the feeding appendages could bring food to the mouth (Whittington and Briggs, 1985). Just behind the mouth at the left, part of the ventral surface of the animal has been omitted, to show the gills lying above the three posterior segments of the head.



A B C

3.68. The probable mode of feeding of *Anomalocaris.* (A) The head of *Anomalocaris nathorsti* seen from the side, with the feeding appendage extended (top) and coiled up to bring food to the mouth (bottom). (B) The same operation viewed from the front. (C) As seen from below, the feeding appendage coiled to bring food to the mouth, in *Anomalocaris nathorsti* (top) and in *Anomalocaris canadensis* (bottom).



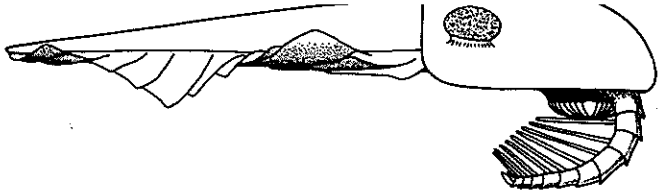
A B

3.69. The mouth of *Anomalocaris,* mistaken by Walcott for the jellyfish *Peytoia.* Several rows of teeth can be seen extending down from the central space; these tooth rows may be projecting from the gullet of the animal. (A) A photograph of the specimen. (B) A camera lucida drawing of the same specimen.

pointed back in the mid-line. The lobes are widest at the middle of the trunk, evenly tapering both in front and behind. These lobes, like the three at the rear of the head, strongly overlap. The termination of the trunk is short and blunt, without any projecting spine or lobe. A multilayered structure of stacked lamellae, presumably a gill, attaches to the top surface of each lobe.

Since *Anomalocaris* has no body appendages, it presumably did not walk or crawl along the substrate. Whittington and Briggs reconstruct *Anomalocaris* as a capable swimmer, though no speed demon, propelled by wavelike motions of the body lobes in coordinated sequences (figure 3.70). The overlapping lateral lobes would therefore work much like the single lateral fin flap of some fishes. An *Anomalocaris* in motion may have resembled a modern manta ray, undulating through the water by generating waves within the broad and continuous fin.

Again, as with *Wiwaxia* and *Opabinia,* one can make reasonable conjectures about the biological operation of *Anomalocaris*—a creature can, after all, only eat and move in so many ways. But what could such an odd



3.70. Reconstruction of *Anomalocaris* as seen from the side, in the act of swimming (Whittington and Briggs, 1985).

animal be in genealogical terms? The feeding appendages had been read as arthropod parts for a century—and their segmented character does recall the great phylum of joint-footed creatures. But repetition and segmentation, shown by the sequence of lobes as well as the feeding appendages, are not restricted to arthropods—think of annelids, vertebrates, and even the molluscan "living fossil," *Neopilina.* Nothing else about *Anomalocaris* suggests a linkage with arthropods. The body bears no jointed appendages, and the mouth, with its perpetual gape and circlet of plates, is unique, utterly unlike anything in the phylum Arthropoda. Even the pair of feeding appendages, though segmented, strays far from any arthropod prototype as soon as we attempt any comparison in detail. Whittington and Briggs concluded that *Anomalocaris* "was a metameric animal, and had one pair of jointed appendages and a unique circlet of jaw plates. We do not consider it an arthropod, but the representative of a hitherto unknown phylum" (1985, p. 571).

Coda

The Burgess work will continue, for many genera remain ripe for restudy (the bulk of the arthropods have been monographed, but only about half of the known weird wonders). However, Harry, Derek, and Simon are moving on, for various reasons. The Lord gives us so little time for a career—forty years if we start early as graduate students and remain in good health, fifty if fortune smiles. The Devil takes so much away—primarily in administrative burdens that fall upon all but the most resistant and singularly purposeful of SOBs. (The earthly rewards of scholarship are can't spend an entire career on one project, no matter how important or exciting. Harry, in his seventies, has returned to his first love, and is spearheading a revision of the trilobite volume for the *Treatise on Invertebrate Paleontology.* Simon's burgeoning career includes a Burgess Shale project or two, but his main interests have moved backward in time to the Cambrian explosion itself. Derek's expanding concerns center on weird wonders and soft-bodied faunas of post-Burgess times.

Others will finish this generation's run at the Burgess Shale. And then the next generation will arrive with new ideas and new techniques. But science is cumulative, despite all its backings and forthings, ups and downs. The work of Briggs, Conway Morris, and Whittington will be honored for its elegance and for the power of its transforming ideas as long as we maintain that most precious of human continuities—an unbroken skein of intellectual genealogy.

No organism or interpretation can have the last word in such a drama, but we must respect the closure of a man's work. The epilogue to this play belongs to Harry Whittington, who in his typically succinct and direct words, wrote to me about his Burgess monographs: "Perhaps these necessarily dry papers conveyed a little of the excitement of discovery—it certainly was an intriguing investigation which had its moments of great joy when a new and unexpected structure was revealed by preparation" (March 1, 1988). "It has been the most exciting and intriguing project that I have been associated with" (April 22, 1987).

Summary Statement on the Bestiary of the Burgess Shale

Disparity Followed by Decimation: A General Statement

If the soft-bodied components had never been found, the Burgess Shale would be an entirely unremarkable Middle Cambrian fauna of about thirty-three genera. It contains a rich assemblage of sponges (Rigby, 1986) and algae, seven species of brachiopods, nineteen species of ordinary trilobites with hard parts, four of echinoderms, and a mollusk and coelenterate