functions technique) of a quantum-mechanical analysis of oscillations of δj_{A-B} around the mirage image of a bilayer island formed on the other side of symmetric PNJ in the monolayer sheet. To compare Fig. 2D shows the calculated mirage image of a spike of electrostatic potential (smooth at the scale of the lattice constant in graphene), which induces LDOS oscillations equal on the two sublattices. The difference between these two images is caused by the lack of backscattering off A-B symmetric scatterers specific to graphene (21).

Unlike the ideal left-handed metamaterial (10), focusing in the PNJ is not perfect. In symmetric junctions, it occurs only for electrons exactly at the Fermi level, and it is spread into caustics for electrons excited to higher energies. Therefore, the sharpness of electron focusing decreases with temperature. If the focused electron flow is detected by a contact of size $d \gg \lambda_F$, a pronounced signal in the focus will persist up to $T \sim \hbar v \, k_c d/a$. For example, in a ballistic structure with $a \sim 1$ μm, $d \sim 0.1$ μm, and $\rho_e = \rho_p \sim 3 \times 10^{12}$ cm^{-2}, focusing may persist up to the nitrogen temperature. The interference effects shown in Figs. 2 and 3 are washed out at a much smaller temperature scale, $T \sim \hbar v/a$.

Focusing of electrons by a sharp p-n junction in graphene can be used to turn the n-p-n junction into a Veselago lens for electrons. In such a device (Fig. 4A), the density of charge carriers in the p-region (with width w) can be controlled by the top gate. If the densities in the n- and p-regions are equal ($\rho_h = \rho_e$), charge carriers injected into graphene from the contact S shown in Fig. 4A would meet again in the focus at the distance $2w$ from the source (contact D_3 in Fig. 4A). Varying the gate voltage over the p-region changes the ratio $n^2 = \rho_h/\rho_e$. This enables one to transform the focus into a cusp displaced by about $2(|n|-1)w$ along the x axis and, thus, to shift the strong coupling from the pair of leads SD$_3$ to either SD$_1$ (for $\rho_h < \rho_e$) or SD$_5$ (for $\rho_h > \rho_e$). Fig. 4, B and C, illustrate another graphene-based device in which a prism-shaped top-gate may be used as a focusing beam splitter. For example, electrons emitted from contact B (Fig. 4B) are distributed between the contacts b and β, whereas the signal sent from contact A (Fig. 4C) is replicated into the pair of contacts a and α. Graphene has recently been brought into contact with a superconducting metal, and the Josephson proximity effect through graphene has been observed (22). Consequently, a beam splitter (Fig. 4, B and C) can be used to experiment with Einstein-Podolsky-Rosen (23) pairs of particles.

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Halwaxiids and the Early Evolution of the Lophotrochozoans

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Halkieriids and wiwaxiids are cosmopolitan sclerite-bearing metazoans from the Lower and Middle Cambrian. Although they have similar scleritomes, their phylogenetic position is contested. A new scleritomous fossil from the Burgess Shale has the prominent anterior shell of the halkieriids but also bears wiwaxiid-like sclerites. This new fossil defines the monophyletic halwaxiids and indicates that they have a key place in early lophotrochozoan history.

Burgess Shale–type faunas house numerous taxa that are phylogenetically controversial and open to widely different interpretations. One approach is to incorporate these taxa into the stem groups of major phyla (1), but this often presupposes homologies of disparate structures and typically depends on an attenuated fossil record. Alternative views regard such taxa as either belonging to extant phyla (2, 3) or representing extinct phyla (4). These differences have major evolutionary implications. For example, the assignment of taxa to either extant or extinct phyla implies that body plans arose by macroevolutionary mechanisms. This is consistent with body plans having a seemingly abrupt appearance and potentially with claims of a protracted (albeit cryptic) history (5). In contrast, hypotheses based on the construction of stem groups generally imply microevolutionary processes. The component taxa would be initiated in the latest Neoproterozoic, with body plans emerging by functional transitions that were connected to feeding, locomotion, and defense (6, 7). This view is consistent with an explosive diversification of metazoans (8, 9).

Numerous Cambrian groups have multi-plated skeletons (or scleritomes) (10). Typically, the scleritomes of these groups occur as disarticulated fossils, notably in the small shelly assemblages. Burgess Shale–type faunas, however, yield articulated material such as the halkieriids, which are probably related to the siphogonuchitids [known only from disassociated sclerites (10)], and wiwaxiids. However, the wider relationships of these groups, the members of which are similar to armored slugs, are uncertain. One hypothesis interprets the halkieriids as stem-group lophotrochozoans, closely linking them to the origin of annelids and brachiopods (11).

The evolutionary route to the annelids was hypothesized to be via the related wiwaxiids (12), and the peculiar halkieriid arrangement of a prominent anterior and posterior shell presaged the bivalved brachiopods (11). More recently, the micrinids and tannuolinids, known only as isolated shells, have been interpreted as key intermediates (13) between the halkieriids and brachiopods. Alternative hypotheses have assigned the halkieriids to the crown-group mollusks (3), questioned the relevance of the micrinids and tannuolinids (14), and rejected the wiwaxiids as stem-group annelids (15). One substantial contribution to this debate is the identification of *Odontogriphus* and *Wiwaxia* as stem-group mollusks (16). Despite these conflicting hypotheses, the Cambrian fossil record, in principle, will be central to unravel-

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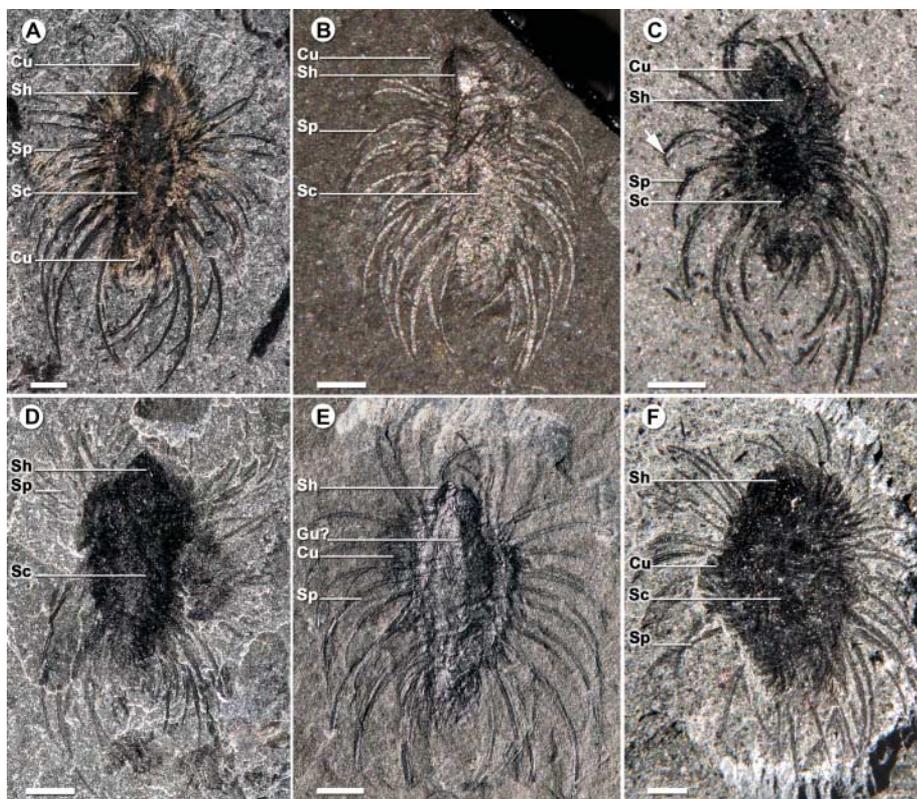
Fig. 1. *O. reburrus* from the Middle Cambrian Burgess Shale. (**A** to **D**) Dorsal view. (**A**) Holotype, ROM 57197; (**B**) ROM 57837; (**C**) ROM 57835; (**D**) ROM 57839. White arrow in (C) indicates a bended spine. (**E** to **F**) Ventral view. (**E**) ROM 57836; (**F**) ROM 57838. Only the doublure of the shell is visible in (E). Images were obtained by light microphotography on uncoated material. Scale bars, 1 mm. Cu, cultrate; Gu, gut; Sc, dorsal sclerites; Sh, shell; Sp, dorso-lateral spines.

ing many aspects of early lophotrochozoan evolution, even though substantial lacunae remain, not least those concerning the origins of the nemerteans and sipunculans.

Here we describe a new taxon [scleritomorph C in (*17*), *Orthrozanclus reburrus* (*18*), based on 11 specimens recovered from the Burgess Shale] that shares characters with both the halkieriids and wiwaxiids (Figs. 1 to 3). Like other Burgess Shale fossils (*19*), they are exceptionally preserved, although their small size and degree of having been crushed result in fine details sometimes being difficult to discern. Some specimens also have abundant diagenetic pyrite (Figs. 1A and 2, A, D, and E). Including their spinose sclerites, the specimens are 6 to 10.3 mm long. The central zone of the dorsal body is strongly convex but is flanked by flatter margins. The ventral side was evidently soft-bodied and tapered to a broad termination. The scleritome consists of three zones or sets of sclerites and at least one shell (Fig. 1). One set extends around the entire body. At the anterior end, two types of sclerites project forward: Most are blade-like and slightly recurved abaxially (Fig. 2A), but much more elongate spines are also interspersed. This anterior array of sclerites then extends posteriorly to form a lateral component of symmetrical sclerites (Fig. 1E),

whereas, at the posterior end, the array comprises abaxially recurved sclerites (Fig. 1A). The prominent second set of sclerites consists of about 16 to 20 elongate, recurved spines on either side of the body, which are inserted abaxial to the lateral sclerites (Fig. 1). Distal to the body, these sclerites may lie at slightly different levels in the sediment and overlap. This disposition suggests that, although these sclerites arose from a narrow zone, their arrangement may not have been as a single row. These sclerites taper quite strongly but individually appear to have an expanded base (Fig. 2, F and H). Externally, they may bear one or two ridges. Pyritized material indicates that they probably had an internal cavity (Fig. 2, D and E). In cases of heavy pyritization, these sclerites reveal a circular cross section, which may be the original configuration in life. A few sclerites are kinked, which is suggestive of a nonmineralized composition (Fig. 1C). The third set of sclerites covers the convex central region and, as a result of crushing, is the least well preserved (Figs. 1 and 2, F and G). These small sclerites appear to have formed a posteriorly imbricated array.

In addition to the sclerites, the anterior bears a prominent convex shell (Fig. 1). In outline, it is roughly triangular, with an anterior umbo, an arched posterior margin, and a medial ridge ex-

panding posteriorly (Fig. 2, B, C, and F). Finely spaced growth lines indicate accretionary growth (Fig. 2, C and F). The shell also bears coarser ridges (Fig. 2, A to C and F); they may represent either the internal surface of the shell or more probably metamerism, traces of which are also discernible more posteriorly. In the ventral view, the shell is largely obscured by soft tissue, but the anterior margin is fairly acute and bears a prominent doublure (Fig. 1E). A relatively prominent strand (that begins close to the margin of the anterior shell and can be traced indistinctly toward the posterior) may represent the gut.

In life, this animal was evidently benthic (Fig. 3), and it is assumed to have moved on a muscular foot. Feeding habits are conjectural, but the convex central region of the organism may have housed a voluminous sediment-filled gut. The scleritome, especially the elongate spines, was presumably protective and/or sensory in function. The shape of the spines suggests that they extended outward and then upward. Given their relative position in the scleritome, the spines are less likely to have provided any snowshoe-like support on the surface of flocculent sediment. The function of the anterior shell is conjectural, but, as hypothesized in the halkieriids (*11*), it could have provided a platform for the attachment of muscles associated with a feeding apparatus. *Orthrozanclus* combines features of both wiwaxiids and halkieriids. The smaller size and partial crushing in *Orthrozanclus* make precise comparisons with the wiwaxiid scleritome (*20*) somewhat tentative, but both were evidently unmineralized, and the overall arrangement is similar. There are convincing equivalents to both the cultrate (lateral) sclerites (including those that extend around the anterior) and the larger spines in *Wiwaxia*. The dorsal sets of spines are equivalent as well, but, in *Orthrozanclus*, the sclerites are smaller and do not seem to have any obvious segmental pattern. The most substantial difference appears to be the absence of siculate (ventro-lateral) sclerites in *Orthrozanclus*. The halkieriid scleritome is also comparable, in particular with marked similarities between the cultrate sclerites. The sclerites of halkieriids are, however, mineralized. Nevertheless, unlike *Wiwaxia* (*21*), both *Orthrozanclus* and the halkieriids have prominent shells. The shells of the halkieriids are best known in articulated material in which they consist of a prominent anterior and posterior shell, the former being notably more convex (*11*). Although *Orthrozanclus* seems to lack a posterior shell, its anterior shell is similar in shape to that of the halkieriids. In contrast, the direction of growth, as inferred from the location of the umbonal region, is reversed, presumably to allow the arched posterior margin to match the convex dorsal region. The shell of *Orthrozanclus* is also similar to a number of isolated small shelly fossils, notably *Ocruranus* (as well as *Eohalobia*) from the

Lower Cambrian of China (*10*, *22*) that are also likely to be halkieriid (*22*, *23*).

Orthrozanclus may also shed light on the Burgess Shale taxon *Oikozetetes* (*24*). This taxon was described on the basis of two shell morphs (A and B), which were suggested to derive from a halkieriid-like animal. The shell of morph B is similar to that of *Orthrozanclus*, apart from lacking the medial ridge (*25*).

The sclerites of halkieriids and wiwaxiids are similar in terms of mode of construction and external ornamentation (*26*), and members of both groups have a tripartite scleritome (*11*). Wiwaxiids, however, have unmineralized sclerites (*12*, *20*) and lack shells (*21*). In combining key features of halkieriids and wiwaxiids, *Orthrozanclus* provides evidence for the monophyletic halwaxiids (*18*). The importance of this group to the understanding of the early evolution of lophotrochozoans depends, however, on a number of critical assumptions, especially concerning the origin of mollusks. The discovery that seriality in monoplacophorans and polyplacophorans, long thought to be amongst the most primitive of mollusks, may be highly derived could undermine long-held assumptions about the nature of the ancestral mollusk (*27*). Indeed, this question may be most readily answered on the basis of fossil material. In this context, the best candidate appears to be the *Kimberella-Odontogriphus* clade (*16*), but, although the dorsal zone presumably had the potential to biomineralize, it remains difficult to establish convincing homologies between any molluskan shell or spicule array and the halwaxiid shell or sclerite field, respectively. It is also clear that shoehorning the halkieriids into the crown-group mollusks (*3*) fails on account of inappropriate comparisons of sclerite structure and unconvincing homologies with younger multiplacophorans (*28*).

Further discussion of the phylogenetic position of the halwaxiids, and hence their role in early mollusk evolution, depends crucially on the assumed polarity of the three component taxa (Fig. 4). Taking *Odontogriphus* as a stem-group mollusk would suggest that the acquisition of a shell in *Orthrozanclus* and the biomineralization of sclerites in halkieriids were later events. This scheme, however, makes it difficult to accommodate the stratigraphically older siphogonuchitids, which have a simpler scleritome (*10*, *29*) and a shell composed of fused sclerites (*23*). An alternative phylogeny is to take *Kimberella* and *Odontogriphus* as stem-group lophotrochozoans, with the halwaxiids forming a distinct clade with a polarity opposite to the first scheme. Accordingly, we hypothesize that mollusks had already diverged before the evolution of the halwaxiids. This
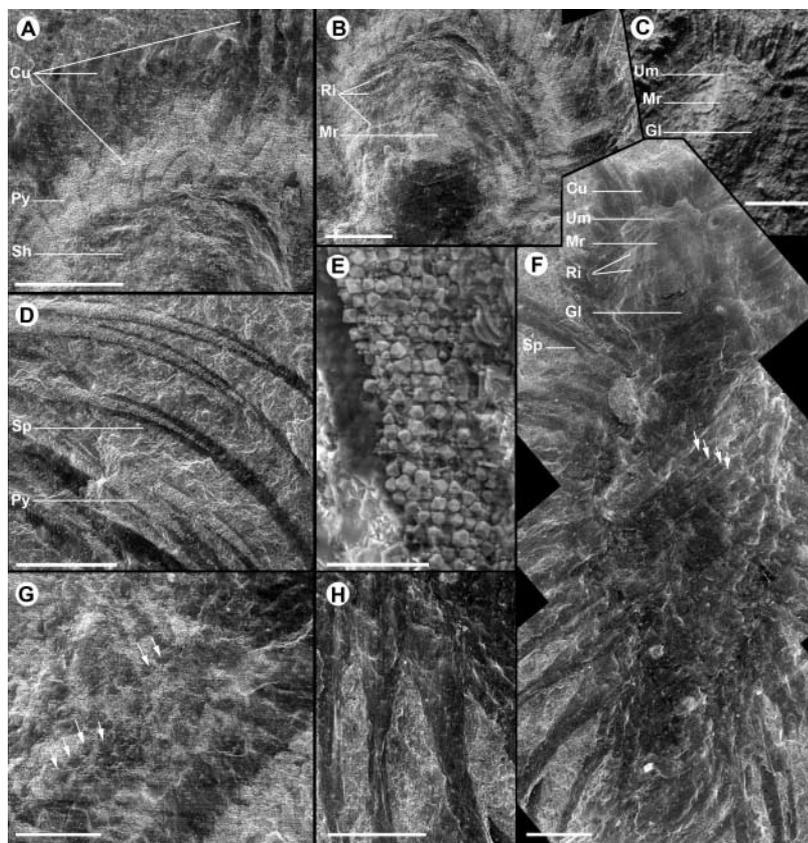
Fig. 2. *O. reburrus* from the Middle Cambrian Burgess Shale. (**A**) Close-up view of the anterior cultrates. (**B** and **C**) Close-up views of the shell. (**D**) Pyritized spines. (**E**) Close-up view of (D) showing octahedra. (**F**) Entire individual. A composite of three images is shown. (**G**) Detail of the dorsal sclerites. White arrows in (F) and (G) point to dorsal sclerites. (**H**) Close-up view of the posterior spines from (F). In (A), (B), and [(D) to (H)], images were obtained by environmental scanning electron microscopy on uncoated material. In (C), image was obtained by light microphotography; specimen was coated with ammonium chloride. Scale bars, 0.5 mm except (E), 0.05 mm. Gl, growth lines; Mr, medial ridge; Py, pyrite; Ri, ridge; Um, umbo.
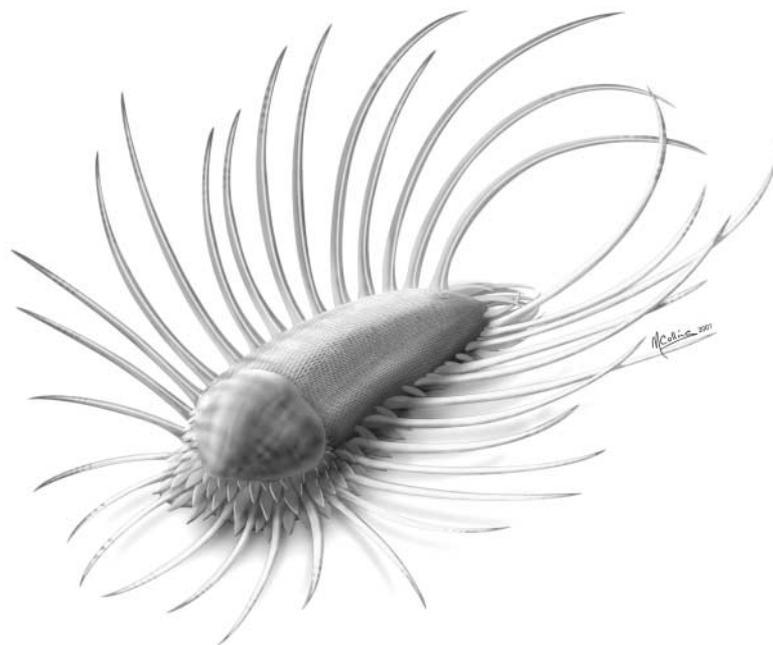
Fig. 3. Reconstruction of *O. reburrus* by M. Collins. The precise arrangement of the anteriormost region remains somewhat conjectural.
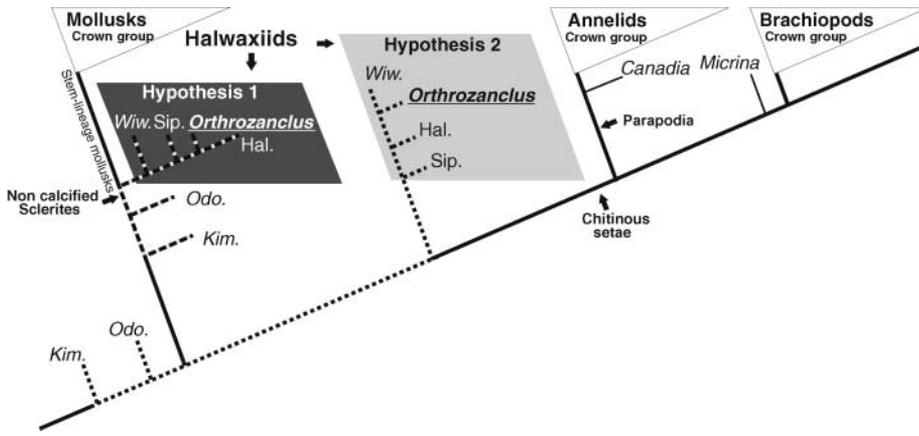
Fig. 4. An outline of lophotrochozoan phylogeny showing the two most plausible positions of the halwaxiid *O. reburrus*, depending on the assumed polarity of sclerite acquisition and bio-mineralization in the associated taxa *Kimberella* (*Kim*.), halkieriids (Hal.), *Odontogriphus* (*Odo*.), siphogonuchitids (Sip.), and *Wiwaxia* (*Wiw*.). Dashed lines indicate alternative interpretations of the phylogeny (see the SOM). The first hypothesis (hypothesis 1) accepts *Odontogriphus* (and probably *Kimberella*) as stem-group mollusks (*16*), with the halwaxiids as a sister group of mollusks. In this latter clade, chitinous sclerites are first acquired (in *Wiwaxia*), followed by their biomineralization in the siphogonuchitids. Members of this latter group, however, are stratigraphically older and appear to have a simpler scleritome (*10*). Halkieriids would then reacquire a more complex scleritome [similar to that of *Wiwaxia* (*11*)] and shells. In the sister group represented by *Orthrozanclus*, the sclerites demineralize, and the posterior shell is probably lost (or highly reduced). The second hypothesis (hypothesis 2) treats the halwaxiids as monophyletic, with the further implication that *Odontogriphus* (and probably *Kimberella*) are stem-group lophotrochozoans. In hypothesis 2, the earliest halwaxiids are the siphogonuchitids with a mineralized scleritome of two types of sclerite (*10*) and with a shell composed of fused sclerites (*23*). Shells are then acquired, along with a third type of sclerite, in the halkieriids. Demineralization of sclerites occurs in *Orthrozanclus*, and (finally) complete shell loss occurs in *Wiwaxia*. A cladistic analysis gives some support for hypothesis 1, but the best tree is not robust (see the SOM).

scheme is more congruent with respect to the siphogonuchitids. It also suggests that bio-mineralization was achieved independently in the earliest mollusks and halwaxiids, with the latter group later demineralizing its sclerites and subsequently losing the shells. A cladistic analysis (with the use of Phylo-genetic Analysis Using Parsimony software) gives some support for hypothesis 1 over hypothesis 2 (Fig. 4), but the bootstrap values are generally very low and the most parsimo-nious tree is far from robust [see the Sup-porting Online Material (SOM)]. In addition, when discussing the origin of major body plans, it is likely that the genetic and mor-phological gaps in the Cambrian were much smaller than the present disparity of phyla would suggest.

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18. Systematic section is as follows: Superphylum Lophotrochozoa. Stem-group Halwaxida, defined as cataphract metazoans with three principal zones of sclerites and usually at least one shell. Component genera include *Australohalkieria*, *Drepanochites*, *Eohalobia*, *Halkieria*, *Lomasulcochates*, *Ninella*, *Ocruranus*, *Oikozetetes*, *Orthrozanclus*, *Sinosachites*, *Siphogonuchites* (*Lopochites* and *Maikhanella* may be junior synonyms), *Thambetolepis*, and *Wiwaxia*. This list is likely to be incomplete and possibly also includes synonyms, not in the least because most taxa are only known from disarticulated material. Family Orthrozanclidae Conway Morris and Caron fam. nov. Component genus is *Orthrozanclus* and possibly *Oikozetetes*. Genus *Orthrozanclus* Conway Morris and Caron gen. nov. *Orthrozanclus reburrus* sp. nov. Etymology: Generic name is compound, based on sickle-like (Greek *zanclon*) sclerites and oblique reference to ancestral nature (Greek *orthros*, or "dawn"); specific name refers to hairy (Latin *reburrus*) appearance. Holotype: Royal Ontario Museum (ROM) 57197. Other material: ROM 57833 to 57840, National Museum of Natural History (USNM) 213695 and 213696. Stratigraphy and locality: Burgess Shale Formation, Walcott Quarry Member, Middle Cambrian. All specimens are from the Greater Phyllopod Bed, Fossil Ridge, near Mount Field, British Columbia, Canada (*17*). Diagnosis: Cataphract metazoan, scleritome of individual sclerites, and at least one shell. Sclerites form at least three zones: small dorsal sclerites, prominent dorso-lateral spines, and lateral (cultrate), including elongate, anterior spines. Anterior shell convex, anterior umbo, arched posterior margin, ventrally anterior doublure.
19. Sclerites show similar preservation to co-occurring wiwaxiids, which are known to be unmineralized and probably were originally chitinous (*12*). The shell shows prominent relief and clear growth lines and was almost certainly composed of calcium carbonate, although it is now demineralized.
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21. In one disarticulated specimen of *Wiwaxia* [figures 46 and 47, A to D, in (*11*)], there is a shell-like structure, but this is unlike those in either *Orthrozanclus* or *Oikozetetes* and appears to be an occurrence known only in this case. It may be a fortuitous association.
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25. The holotype of *Oikozetetes seilacherii* was based on morph A (*24*), so synonymy with *Orthrozanclus* is not appropriate. Although earlier tentatively placed in the Halkieriidae (*24*), these two genera are almost certainly closely related (*18*). The relationships, however, between these two taxa are difficult to resolve on present evidence, in particular because *Orthrozanclus* only shows one definite shell. Morph B could be another species of *Orthrozanclus* or, alternatively, *Oikozetetes* may be correctly identified. In contrast to the interpretation of (*24*) and consistent with the evidence presented here, it is more likely that morph A represented the posterior shell (and so is possibly equivalent to the tentatively identified and much smaller posterior shell in *Orthrozanclus*), and, correspondingly, morph B would be equivalent to the anterior shell.
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30. We thank V. Brown for technical support in Cambridge; D. Evans, C. Schander, A. Scheltema, and D. Zanatta for assistance and comments on the cladistic analysis; M. Collins for drafting the reconstruction; and three anonymous referees for constructive criticism. This work is supported by the Royal Society, Cowper-Reed Fund, St. John's College, Parks Canada, and the Royal Ontario Museum. Collections were made under the direction of D. Collins. This is Royal Ontario Museum Burgess Shale Research Project #10.