

A soft-bodied mollusc with radula from the Middle Cambrian Burgess Shale

Jean-Bernard Caron^{*}, Amélie Scheltema^Ω, Christoffer Schander[§] & David Rudkin^{*}

^{*} Department of Natural History-Palaeobiology, Royal Ontario Museum, 100 Queen's Park, Toronto, Ontario, M5S 2C6, Canada

^Ω Woods Hole Oceanographic Institution, Woods Hole, Massachusetts 02543, USA

[§] University of Bergen, Department of Biology, P.O. box 7800, N-5020 Bergen, Norway

Summary:

Odontogriphus omalus was originally described as a problematic non-biom mineralized lophophorate organism. Here we reinterpret *Odontogriphus* based on 189 new specimens including numerous exceptionally well-preserved individuals from the Burgess Shale collections of the Royal Ontario Museum. This additional material provides compelling evidence that the feeding apparatus in *Odontogriphus* is a radula of molluscan architecture comprising two primary bipartite tooth rows attached to a radular membrane and showing replacement by posterior addition. Further characters supporting molluscan affinity include a broad foot bordered by numerous ctenidia located in a mantle groove and a stiffened cuticular dorsum. *Odontogriphus* has a radula similar to *Wiwaxia corrugata* but lacks a scleritome. We interpret these animals to be members of an early stem-group mollusc lineage that likely originated in the Neoproterozoic Ediacaran Period, providing support for the retention of a biomat-based grazing community from the late Precambrian until at least the Middle Cambrian.

Burgess Shale-type deposits in Lower and Middle Cambrian strata yield a number of “problematic” organisms that can potentially reveal key steps in the origin, relationship and evolution of phyla¹. *Odontogriphus omalus* is one of the most enigmatic fossils from the Middle Cambrian Burgess Shale². This animal, known originally from a single, incomplete and poorly preserved specimen, was described as a dorso-ventrally flattened and possibly annulated organism². A conspicuous U-shaped feeding apparatus flanked by toothlike structures was thought to be reminiscent of the lophophore of brachiopods, phoronids and ectoprocts, with a possible connection with some Cambrian conodonts². The view that *Odontogriphus* could have played a key role in chordate evolution³ has remained marginal especially following the subsequent discovery of conodont animals bearing no resemblance to *Odontogriphus*⁴. Hypothetical tentacles originally reconstructed around the toothlike structures are themselves dubious, and cannot be used to refer *Odontogriphus* to a known lophophorate group⁴. The suggestions that *Odontogriphus* could be related to the Early Cambrian problematic fossil *Vetustovermis* or to the poorly known Late Permian *Bowengriphus*⁵ are very unlikely based on the abundant and exceptionally well preserved new material presented in this study. *Odontogriphus* shares a virtually identical radula with the noncalcified scleritome-bearing animal *Wiwaxia*⁶ supporting the idea that both organisms are stem-group molluscs, contrary to views that *Wiwaxia* was a polychaete⁷ or a stem-group polychaete⁸ (but see⁹). Our study provides new insights into the origin and early evolution of the Mollusca, which together with the discovery of fossils showing probable molluscan affinities from the latest Precambrian (*Kimberella*¹⁰) and Early Cambrian strata

(*Halkieria*^{8, 11}), confirms that the origin of eutrochozoans is deeply rooted and predates the Cambrian explosion¹².

Stem-group Mollusca

Odontogriphus omalus Conway Morris, 1976

Material and Locality: Royal Ontario Museum -188 specimens from the Greater Phyllopod Bed on Fossil Ridge (including one from talus) and one talus specimen from Mount Stephen (S7), Yoho National Park, British Columbia, Canada.

Holotype: USNM 196169, (35K), National Museum of Natural History, Washington, D.C.

Horizon: Middle Cambrian Burgess Shale Formation.

Preservation: Specimens appear as black reflective films on a dark mudstone matrix and often co-occur with large sheets of the cyanobacterium *Morania* (Figs. 1a, b; 2). The radula retains some original three-dimensionality, but its original composition has not been preserved (Energy Dispersive X-ray Spectrometer (EDS) analyses show no difference between the radula and matrix). Evidence of decay is rare and most specimens are preserved parallel to bedding planes, implying that the body was flattened dorso-ventrally and that animals were buried very rapidly with limited or no transport (see¹³). *Odontogriphus* represents less than 0.5% of 50,900 individuals in the Greater Phyllopod Bed community¹⁴.

Revised diagnosis: Bilaterally symmetrical oval body, parallel-sided, compressed dorso-ventrally. Anterior and posterior semi-circular in outline and of similar size. Mouth ventral with two primary bipartite tooth rows attached to a radular membrane and showing replacement by posterior addition. Gut straight with a large stomach, narrow

intestine and a sub-terminal anus. Simple ctenidia present in a groove running laterally and posteriorly around a muscular foot. With non-biomineralized, stiffened cuticular mantle dorsum lacking sclerites.

Description (Supplementary Figure I): Specimens range from 3.3 to 125 mm in length (mean=47.5, SD=29, N=89) and from 1.5 to 43 mm in width (mean=18.5, SD=10.5, N=123). Length-width ratio identical in juveniles and adults ($L=2.74W$, $r_s=0.97$, $p<0.0001$, N=78) demonstrating isometric growth. Symmetry of the body outline is maintained in all complete specimens, even those in which internal features have been preserved asymmetrically (Fig. 1h), implying that the dorsal body coverage is relatively stiff. The radula is located at about 15% of the total body length from the anterior margin on the mid-longitudinal axis (Fig. 1a, b, g, h, j, k). It typically consists of two rows of teeth preserved at different angles (Supplementary Figure II) and is bipartite (= distichous) with paired mirror teeth connected axially (1:0:1) (Fig. 1c). There are usually 7 pointed or rounded denticles on each tooth with the longest ones positioned laterally (Fig. 1c). In 81% of radulae the posterior row is as wide as or wider than the anterior row, the widest up to 5.3 mm; radula growth is isometric with increasing body size. One or two faint, narrow posterior rows are visible in many individuals (Fig. 1d, e) implying, first, that new rows were periodically formed posteriorly, but only the anteriormost two rows were fully functional; and second, because the distance between the rows is closely similar, they were added at regular intervals. The anteriormost row was sloughed off periodically and occasionally ingested (Supplementary Figure III), the sloughed off rows were replaced by new ones from behind. Isolated radulae with two rows of paired teeth (Fig. 1c) imply that

the rows of teeth were connected by a strong decay-resistant material, a radular membrane (Fig. 1e).

A circular structure surrounding the radula is interpreted to represent the mouth and pharynx (Fig. 1f). The oesophagus is straight and narrow (Fig. 1f). It expands posteriorly into a straight stomach which is usually as wide anteriorly as the radula itself (Fig. 1b, f-h, k). The stomach narrows posteriorly towards a straight intestine (Fig. 1b, g), and the anus is sub-terminal (Fig. 1g). Broad transverse wrinkles, parallel to each other and usually straight, sometimes occur across the midsection of the body (Fig. 1a, j). These vary in number between specimens and are only present in the central region of the body, demonstrating that they are not expressions of internal or surficial segmentation. Wrinkles probably resulted from compression of a thickened central structure that we interpret to be ventral and thus likely represents a muscular sole. As a ventral sole it is limited anteriorly by the radula and thus lies posterior to the mouth. The sole is surrounded on all its sides except the front by darker and serially identical structures that we interpret to represent-ctenidia (Fig. 1a, b, g-k). Ctenidia (up to 100) are sometimes separated from the mantle by a thin layer of sediment-(Fig. 1h, i), demonstrating that they are located in a narrow recess we interpret to be a-mantle groove. A pair of circular structures interpreted as salivary glands flanks the radula (Fig. 1h, j, k). Another pair of structures, elongate and ovoid, composed of a bundle of fibrous elements, is preserved, one element on either side of the posterior part of the stomach and anterior part of the gut (Fig. 1b). Our interpretation is that they are gonads or digestive glands.

Discussion

The phylogenetic tree (Fig. 3) depicts the total-group Mollusca based on our interpretation of the morphology of *Odontogriphus omalus* (Fig. 2) and *Wiwaxia corrugata* (Fig. 4). It does not take into account many early mollusc-like forms of uncertain affinities which may represent various stem-group eutrochozoans (i.e., *Machaeridia*, *Acaenoplax*, *probivalvia*, *Hyalitha*).

Odontogriphus and perhaps the Ediacaran form *Kimberella*¹⁰ possess distinctive characters that place them in the molluscs prior to the acquisition of a calcified dorsum. That is, they or their closest ancestor arose in the latest Neoproterozoic (certain for *Kimberella*) following the node designating separation of the Annelida and Mollusca stems (Fig. 3 – stem 1). The Mollusca ancestor is thought to have been a creeping and nonsegmented bilateral animal¹⁵ whereas the Annelida probably descended from a segmented parapodia-bearing form¹⁶, possibly a sister group of the molluscan ancestor¹⁵. Mesodermal segmentation (metamerism) involving the coelom gave rise to the stem annelid (Fig. 3 – 2). Noncoelomic iteration of organ systems, or seriation¹⁵, led to the ancestral Mollusca (Fig. 3 – 3); this condition is present in *Odontogriphus* as iterated ctenidia and radula teeth.

The characters held in common by *Odontogriphus* and *Kimberella*, the latter without preserved internal anatomy, are a dorso-ventrally flattened ovoid shape; large size; a cuticular dorsal exoskeleton shown by the integrity of the dorsum relative to soft anatomy (cf. Fig 1h with fig. 1h in *Kimberella*¹⁰); a noncuticularized ventral sole; and iterated structures (Fig. 3 – 3). These are evolutionary novelties which arose since the estimated time of the last common ancestor of bilaterians^{17, 18}. If the interpretation of *Kimberella* as an early mollusc-like organism with radula is correct¹⁹ these characteristics

combined with the soft and internal anatomy of *Odontogriphus* define the plesiomorphic molluscan morphologies: pre-eminently and unique to Mollusca, an anterior radula with periodically sloughed off and replaced rows of teeth on a radular membrane²⁰ (certain for *Odontogriphus*). The acquisition of a ventral mantle groove with replicated ctenidia represents a younger evolutionary innovation (Fig. 3 – 4).

Wiwaxia corrugata with its dorsum covered by noncalcified sclerites co-occurs with *Odontogriphus* in the Burgess Shale and has a nearly identical radula (Fig. 4) with a tooth morphology similar to plesiomorphic Neomeniomorpha²⁰. Its affinities with the polychaetes and annelids have been refuted based on absence of externally expressed mesodermal segmentation, prostomial appendages and parapodia⁹. On the basis of its radula, ovoid shape, lack of segmentation, and zonation of different sclerite types similar to that in *Halkieria*^{8, 11}, it is considered here to belong to the clade Mollusca (Fig. 3 – 5).

Initial acquisition of a calcified exoskeleton and subsequent rapid radiation of shelly forms in the early Cambrian²¹ marks the turning point for molluscan diversity. The process began with nucleation of sclerites within the epidermis which then pushed through the overlying cuticle (Fig. 3 – 6), a process retained by Polyplacophora and Aplacophora (Neomeniomorpha and Chaetodermomorpha²²), and may have been the same for *Halkieria*. Shells in the Polyplacophora and possibly *Halkieria* have been thought to be the result of merging of sclerites²³. However, it is more likely that the acquisition of shell fields provided the functional ability to deposit calcareous shell (developmentally separate from sclerite formation in the Polyplacophora^{22, 24}). The polytomy of *Halkieria* (and other halkieriids), Neomeniomorpha, and Polyplacophora (Fig. 3 – 7, 8, 9) includes on the polyplacophoran stem the extinct *Matthevia*²⁵ and the

Multiplacophora²⁶. *Halkieria*, originally described as probably a molluscan-grade organism, in part due to the presence of a putative radula¹¹ (but see⁸), has been interpreted most recently as a sister taxon to the Polyplacophora²⁷. However affinities of *Halkiera* still remain highly contentious. Neomeniomorpha have several morphologies homologous to those in Polyplacophora²⁸. Some of these are plesiomorphies of the Mollusca (Fig. 3 – 3), but others cannot be accommodated on the tree as plesiomorphies, including eight shell fields, embryologically vestigial in a neomeniomorph²⁹, manner of sclerite deposition²² and unique epidermal gland cells^{30, 31}. The molecular evidence for the relationship among the Polyplacophora and the two taxa of Aplacophora is still ambiguous.

The evidence from *Odontogriphus*, *Wiwaxia*, *Halkieria*, and *Kimberella* indicates that early molluscs were not small. Diversity of body form increased with the loss of sclerites and the advent of a true periostracum secreted from a groove in the mantle lobe as found in all extant Mollusca except the Aplacophora and Polyplacophora²² (Fig. 3 – 10). This diversification was concomitant with the appearance of crown-group (except Scaphopoda) and other stem-group molluscs by the end of the Cambrian³².

The Cambrian substrate revolution and ecological implications

Body (*Kimberella*) and trace (*Radulichnus*) fossil evidence from Ediacaran shallow marine sediments demonstrates the establishment of a bilaterian microphagous mat-grazing guild by at least 555 Ma ago^{19, 33}. The subsequent transition from Neoproterozoic biomat-dominated seafloors to Phanerozoic-style seafloor conditions, characterized by increasingly fluidized substrates, was driven by a shift to more intensive and vertically oriented bioturbation across the Precambrian-Cambrian boundary³⁴ (see

also the “Cambrian substrate revolution”³⁵, Fig. 3). The redistribution of extensive microbial mats and biofilms (along with metazoan grazers) from the open shallow marine to stressed nearshore and shelf-edge to deep-sea settings³⁵ was not abrupt, but took place over a protracted interval in the Cambrian during which relict mat-based communities persisted in at least some marine environments³⁶, including the Burgess Shale³⁴. This persistence is evident from the intimate association of *Odontogriphus* and *Wiwaxia* with dense, sheet-like aggregates of the fossil cyanobacterium *Morania*³⁷, which often cover extensive bedding surfaces¹⁴ (Figs. 1a, 2). *Morania* probably provided a food source and stable substrate for an array of Middle Cambrian benthic grazers adapted to Neoproterozoic-style substrates³⁸.

Odontogriphus joins a handful of Cambrian fossils that probably represent surviving Neoproterozoic lineages^{e.g.,39-41}. Explanations for the disappearance of other soft-bodied elements of the Ediacaran biota (“vendobionts”) vary from a mass extinction following global environmental changes, to changes in taphonomic conditions, to the emergence of predators⁴². The widespread appearance of biomineralized organisms near the beginning of the Cambrian is believed to be in large part the consequence of rapidly expanding predatory selection pressure^{e.g.,43}. However, the presence of a diverse soft-bodied biota in Cambrian *Lagerstätten*, including representatives of relict lineages, demonstrates that other survival strategies were in play. *Odontogriphus* would have been a prime target for predators, but it is possible that its featureless dorsum (Fig. 2) afforded a cryptic lifestyle on the substrate. In the case of the *Kimberella-Odontogriphus* lineage, reduction of suitable habitat could have been at least as important as direct predation pressure in explaining the apparent demise of the group after the Middle Cambrian.

Methods

Digital photography utilized polarizing filters at the camera and light-source to increase contrast of internal organs and other anatomical features. Backscattered Electron images (BSE) were taken of radulae with a SEMCO Nanolab 7 at the Royal Ontario Museum with an acceleration voltage of 30KV (15KV for EDS analyses)(see Ref⁴⁴ for a successful application of this technique). Specimens were wrapped in aluminium foil to limit charging in a manner described previously by Allison⁴⁵.

Acknowledgments

We thank one anonymous referee and, S. Bengtson, G. Budd, S. Conway Morris, S. Dornbos, W. Hagadorn, T. Høisaeter, and B. Runnegar for reviewing different drafts of this paper. N. Butterfield, University of Cambridge, suggested using the BSE technique and provided unpublished pictures of *Wiwaxia*. Our research was in part supported by a Post-Doctoral Natural Sciences and Engineering Research Council of Canada grant (to JBC-2005) and by a Swedish Research Council grant (to CS). Permission to collect Burgess Shale specimens was given by Parks Canada to D. Collins. We are thankful to M. Back and J. Waddington from the Royal Ontario Museum for technical help. This is Royal Ontario Museum Burgess Shale Research Project #6.

1. Budd, G. E. The Cambrian fossil record and the origin of the phyla. *Integr. Comp. Biol.* **43**, 157-165 (2003).
2. Conway Morris, S. A new Cambrian lophophorate from the Burgess Shale of British Columbia. *Palaeontology* **19**, 199-222 (1976).
3. Dzik, J. *Yunnanozoon* and the ancestry of chordates. *Acta Palaeont. Pol.* **40**, 341-360 (1995).
4. Briggs, D. E. G. & Conway Morris, S. Problematica from the Middle Cambrian Burgess Shale of British Columbia. In *Problematic Fossil Taxa* (eds. Hoffman, A. & Nitecki, M. H.) 167-183 (Oxford Univ. Press & Clarendon Press, New York, 1986).
5. Ritchie, A. & Edgecombe, G. D. An Odontogriphid from the Upper Permian of Australia. *Palaeontology* **44**, 861-874 (2001).

6. Conway Morris, S. The Middle Cambrian Metazoan *Wiwaxia corrugata* (Matthew) from the Burgess Shale and *Ogygopsis* Shale, British Columbia, Canada. *Phil. Trans. R. Soc. Lond. B* **307**, 507-582 (1985).
7. Butterfield, N. J. A reassessment of the enigmatic Burgess Shale fossil *Wiwaxia corrugata* (Matthew) and its relationship to the polychaete *Canadia spinosa* Walcott. *Paleobiology* **16**, 287-303 (1990).
8. Conway Morris, S. & Peel, J. S. Articulated halkieriids from the Lower Cambrian of North Greenland and their role in early protostome evolution. *Phil. Trans. R. Soc. Lond. B* **347**, 305-358 (1995).
9. Eibye-Jacobsen, D. A reevaluation of *Wiwaxia* and the polychaetes of the Burgess Shale. *Lethaia* **37**, 317-335 (2004).
10. Fedonkin, M. A. & Waggoner, B. M. The Late Precambrian fossil *Kimberella* is a mollusc-like bilaterian organism. *Nature* **388**, 868-871 (1997).
11. Conway Morris, S. & Peel, J. S. Articulated halkieriids from the Lower Cambrian of north Greenland. *Nature* **345**, 802-805 (1990).
12. Erwin, D. H. & Davidson, E. H. The last common bilaterian ancestor. *Development* **129**, 3021-3032 (2002).
13. Caron, J. B. & Jackson, D. A. Taphonomy of the Greater Phyllopod Bed Community, Burgess Shale. *Palaios* (In press).
14. Caron, J. B. Ph.D. thesis. Graduate Department of Zoology (Univ. of Toronto, Toronto, 2005).
15. Valentine, J. W. *On the origin of Phyla* (The University of Chicago Press, Chicago and London, 2004).
16. Balavoine, G. & Adoutte, A. The Segmented Urbilateria: A Testable Scenario. *Integr. Comp. Biol.* **43**, 137-147 (2003).
17. Peterson, K. J. *et al.* Estimating metazoan divergence times with a molecular clock. *PNAS* **101**, 6536-6541 (2004).
18. Douzery, E. J. P., Snell, E. A., Bapteste, E., Delsuc, F. & Philippe, H. The timing of eukaryotic evolution: Does a relaxed molecular clock reconcile proteins and fossils? *PNAS* **101**, 15386-15391 (2004).
19. Seilacher, A. Biomat-related lifestyles in the Precambrian. *Palaios* **14**, 86-93 (1999).
20. Scheltema, A. H., Kerth, K. & Kuzirian, A. M. Original molluscan radula: Comparisons among Aplacophora, Polyplacophora, Gastropoda, and the Cambrian fossil *Wiwaxia corrugata*. *J. of Morph.* **257**, 219-244 (2003).
21. Runnegar, B. in *Origin and evolutionary radiation of the Mollusca* (ed. Taylor, J. D.) 77-87 (Oxford University Press, 1996).
22. Haas, W. Early evolution of the Mollusca: the fossil record. In *Origin and Evolutionary Radiation of the Mollusca* (ed. Taylor, J. D.) 77-87 (Oxford Univ. Press, 1996).
23. Bengtson, S. The cap-shaped Cambrian fossil *Maikhanella* and the relationship between coeloscleritophorans and molluscs. *Lethaia* **25**, 401-420 (1992).
24. Henry, J. Q., Okusu, A. & Martindale, M. Q. The cell lineage of the polyplacophoran, *Chaetopleura apiculata*: variation in the spiralian program and implications for molluscan evolution. *Dev. Bio.* **272**, 145-160 (2004).

25. Runnegar, B., Pojeta, J., Jr., Taylor, M. E. & Collins, D. New species of the Cambrian and Ordovician chitons *Matthevia* and *Chelodes* from Wisconsin and Queensland; evidence for the early history of polyplacophoran mollusks. *J. Paleontol.* **53**, 1374-1394 (1979).
26. Vendrasco, M. J., Wood, T. E. & Runnegar, B. N. Articulated Paleozoic fossil with 17 plates greatly expands disparity of early chitons. *Nature* **429**, 288-291 (2004).
27. Vinther, J. & Nielsen, C. The Early Cambrian *Halkieria* is a mollusc. *Zool. Scr.* **34**, 81-89 (2005).
28. Scheltema, A. H. Aplacophora as progenetic aculiferans and the coelomate origin of mollusks as the sister taxon of Sipuncula. *Biol. Bull. (Woods Hole)* **184**, 57-78 (1993).
29. Scheltema, A. H. & Ivanov, D. L. An aplacophoran postlarva with iterated dorsal groups of spicules and skeletal similarities to Paleozoic fossils. *Invertebr. Biol.* **21**, 1-10 (2002).
30. Scheltema, A. H., Tscherkassky, M. & Kuzirian, A. M. Aplacophora. In *Microscopic Anatomy of Invertebrates* (eds. Harrison, F. W. & Kohn, A. J.) 13-54 (Wiley-Liss, New York, 1994).
31. Fischer, F. P. Die Mantelpapillen und Stacheln von *Acanthochiton fascicularis* L. (Mollusca, Polyplacophora). *Zoomorphologie* **94**, 121-131 (1980).
32. Budd, G. E. & Jensen, S. A critical reappraisal of the fossil record of the bilaterian phyla. *Biol. Rev.* **75**, 253-295 (2000).
33. Seilacher, A., Buatois, L. A. & Mángano, L. G. Trace fossils in the Ediacaran-Cambrian transition: Behavioral diversification, ecological turnover and environmental shift. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* **227**, 323-356 (2005).
34. Seilacher, A. & Pflüger, F. From biomats to benthic agriculture : a biohistoric revolution. In *Biostabilization of Sediments* (eds. Krumbein, W. E., Peterson, D. M. & Stal, L. J.) 97-105 (Bibliotheks und Informationssystem der Carl von Ossietzky Universität Oldenburg, Oldenburg, Germany, 1994).
35. Bottjer, D. J., Hagadorn, J. W. & Dornbos, S. Q. The Cambrian substrate revolution. *GSA Today* **10**, 1-7 (2000).
36. Dornbos, S., Bottjer, D. & Chen, J.-Y. Evidence for seafloor microbial mats and associated metazoan lifestyles in Lower Cambrian phosphorites of Southwest China. *Lethaia* **37**, 127 - 137 (2004).
37. Satterthwait, D. F. Ph.D. thesis. Graduate Department of Biology (Univ. of California, Los Angeles, 1976).
38. Dornbos, S. Q., Bottjer, D. J. & Chen, J.-Y. Paleoecology of benthic metazoans in the Early Cambrian Maotianshan Shale biota and the Middle Cambrian Burgess Shale biota: evidence for the Cambrian substrate revolution. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* **220**, 47-67 (2005).
39. Conway Morris, S. Ediacaran-like fossils in Cambrian Burgess Shale-type faunas of North America. *Palaentology* **36**, 593-635 (1993).
40. Hagadorn, J. W., Fedo, C. M. & Waggoner, B. M. Early Cambrian Ediacaran-type fossils from California. *J. Paleontol.* **74**, 731-740 (2000).

41. Jensen, S., Gehling, J. G. & Droser, M. L. Ediacara-type fossils in Cambrian sediments. *Nature* **393**, 567-569 (1998).
42. Narbonne, G. M. The Ediacara biota: Neoproterozoic origin of animals and their ecosystems. *Annu. Rev. Earth Pl. Sc.* **33**, 421-442 (2005).
43. Bengtson, S. Origins and early evolution of predation. In *the Fossil Record of Predation* (eds. Kowalewski, M. & Kelley, P. H.) 289–317. (The Paleontological Society, 2002).
44. Orr, P. J., Kearns, S. L. & Briggs, D. E. G. Backscattered electron imaging of fossils exceptionally-preserved as organic compressions. *Palaios* **17**, 110-117 (2002).
45. Allison, P. A. Phosphatized soft-bodied squids from the Jurassic Oxford Clay. *Lethaia* **21**, 403-410 (1988).

Authors' contributions: All four authors made significant contributions to this article.

Competing Interests statement: The authors declare that they have no competing financial interests.

Correspondence: Correspondence and requests for materials should be addressed to J.B.C. (jcaron@rom.on.ca).

Figure labels;

Figure 1. *Odontogriphus omalus* from the Middle Cambrian Burgess Shale. All specimens are preserved dorso-ventrally, anterior to the top. **a**, ROM57712, complete specimen showing the sole (crescentic wrinkles) lying on the surface of the cyanobacterium *Morania*. **b**, ROM57725, nearly complete specimen showing putative paired gonads or digestive glands and the cyanobacterium *Morania*. **c**, ROM57713, backscattered image of an isolated two-rowed radula. **d**, ROM57716, three-rowed radula. **e**, ROM57717, four-rowed radula with putative traces of the radular membrane. **f**, ROM57714 view of the mouth area and anterior end of the stomach. **g**, ROM57721, complete specimen showing the intestine and gut content. **h-i**, ROM57720 complete specimen; **h**, overall view; **i**, detail of ctenidia from **h**. **j**, ROM57723, complete specimen showing the sole (wrinkles). **k**, ROM57724 complete specimen with paired salivary glands and ctenidia. Scale bars: 2cm in **a**; 1cm in **g**, **h**, **k**; 5mm in **b**, **f**, **i**, **j**; 1mm in **c-e**.

an=anus, cr=crack, ct=ctenidia, ctg=ctenidia groove, dg?=digestive glands? gc=gut content, go?=gonads?, in=intestine, ma=mantle, mo=*Morania*, oe=esophagus, ph=pharynx and mouth area, ra=radula, r1, r2, r3, r4=tooth rows, sg=salivary glands, so=sole, st=stomach.

Figure 2. Reconstruction of a colony of *Odontogriphus omalus* grazing on the cyanobacterium *Morania* (illustration by Marianne Collins © 2006).

Figure 3. Evolutionary tree of the molluscs in the context of the Neoproterozoic-Cambrian substrate revolution³⁵. 1. Protostome bilaterian; serial replication; triploblastic. 2. Segmentation by coelomic metameres. 3. Large size; with iteration but not coelomic segmentation; ovoid; dorsoventrally flattened; stiffened cuticular dorsum; flat, noncuticularized ventral sole; radula of iterated, paired teeth and radular membrane (certain for *Odontogriphus*); feeding on biomat? 4. Groove (mantle cavity) between dorsum and ventrum with serial ctenidia; paired salivary glands; straight digestive tract; nervous system ladderlike?; coelom posterior, restricted to reproductive and excretory organs? 5. Noncalcified scleritome, sclerites arranged in 3 mirror image longitudinal zones. 6. Calcification of epidermally nucleated sclerites that pass through cuticle; calcified shell from serial shell fields; no periostracum from periostracal groove of mantle lobe. 7. Two shell fields. 8. Tubiform; reduced foot; sclerites in 1-3 longitudinal rows beside foot groove; progenetic loss of gills and shells; embryological evidence of vestigial shell-fields. 9. Eight or more shell fields; sclerites not in longitudinal zones. 10.

Loss of sclerites and serial shell fields; true periostracum secreted from mantle lobe; shells paired or single; reduction of gills; further variety of body plans.

Figure 4. *Wiwaxia corrugata* from the Middle Cambrian Burgess Shale. All specimens are preserved ventrally, anterior to the top. **a, b**, ROM57707, pictures courtesy N. Butterfield, University of Cambridge. **a**, complete specimen and location of the radula. **b**, backscattered image of the radula. **c, d**, ROM57726. **c**, complete specimen and location of the radula. **d**, detail of the radula highlighted with ammonium chloride sublimate. Note the presence of 3 rows of teeth. Scale bars: 5mm in **a** and **c**; 250 μ m in **b** and **d**. ra=radula, r1, r2, r3=tooth rows, sc=sclerite.