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

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Summary:

Odontogriphus omalus was originally described as a problematic non-biomineralized

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 phyla[1]. *Odontogriphus omalus* is one of the most enigmatic fossils from the Middle Cambrian Burgess Shale[2]. This animal, known originally from a single, incomplete and poorly preserved specimen, was described as a dorso-ventrally flattened and possibly annulated organism[2]. 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 conodonts[2]. The view that *Odontogriphus* could have played a key role in chordate evolution[3] 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 *Odontogriphu*s to a known lophophorate group[4]. 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 polychaete[7] or a stem-group polychaete[8] (but see[9]). 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 explosion[12].

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 (see[13]). *Odontogriphus* represents less than 0.5% of 50,900 individuals in the Greater Phyllopod Bed community[14].

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, Hyolitha).

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 animal[15] whereas the Annelida probably descended from a segmented parapodia-bearing form[16], possibly a sister group of the molluscan ancestor[15]. Mesodermal segmentation (metamerism) involving the coelom gave rise to the stem annelid (Fig. 3 – 2). Noncoelomic iteration of organ systems, or seriation[15], 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 correct[19] 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 membrane[20] (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 Neomeniomorpha[20]. Its affinities with the polychaetes and annelids have been refuted based on absence of externally expressed mesodermal segmentation, prostomial appendages and parapodia[9]. 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 Cambrian[21] 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 Chaetodermomorpha[22]), 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 sclerites[23]. 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

Multiplacophora[26]. *Halkieria*, originally described as probably a molluscan-grade organism, in part due to the presence of a putative radula[11] (but see[8]), has been interpreted most recently as a sister taxon to the Polyplacophora[27]. However affinities of *Halkiera* still remain highly contentious. Neomeniomorpha have several morphologies homologous to those in Polyplacophora[28]. 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 neomeniomorph[29], manner of sclerite deposition[22] 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 Polyplacophora[22] (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 Cambrian[32].

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 boundary[34] (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 settings[35] 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 environments[36], including the Burgess Shale[34]. 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 surfaces[14] (Figs. 1a, 2). *Morania* probably provided a food source and

stable substrate for an array of Middle Cambrian benthic grazers adapted to

Neoproterozoic-style substrates[38].

     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 predators[42]. 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 Ref[44] for a successful application of this technique). Specimens were wrapped in aluminium foil to limit charging in a manner described previously by Allison[45].

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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 revolution[35]. 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**; 250µm in **b** and **d**. ra=radula,

r1, r2, r3=tooth rows, sc=sclerite.